Interactions Between Idiothetic Cues and External Landmarks in the Control of Place Cells and Head Direction Cells

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INTRODUCTION

Animals use many types of cues to navigate efficiently and to build robust cognitive representations of their environment. These cues can be divided broadly into two classes: external landmarks and idiothetic (self-motion) cues. An animal’s navigational strategy is based on a complex interaction between these two classes of information. Many studies have shown that rodents use visual landmarks to guide them to goal locations (Collett et al. 1986; O’Keefe and Conway 1980; Suzuki et al. 1980). They also can find their way back to a starting location in the complete absence of landmarks by using self-motion cues to update a representation of the distance and bearing to that starting location—an ability known as path integration or dead reckoning (Etienne 1992; Gallistel 1990; Mittelstaedt and Mittelstaedt 1980). The self-motion information can derive both from internal sources (e.g., vestibular cues or proprioceptive cues) and from external sources (e.g., optic flow cues). It appears that, at least under certain experimental conditions, rodents initially rely on path integration mechanisms to navigate, even when spatial information from stable landmarks is available. Only after many trials do the rodents begin to use these landmarks to guide navigation (Alyan and Jander 1994; Weisend et al. 1995).

The hippocampus appears to play a key role in navigation and spatial learning (O’Keefe and Nadel 1978). Hippocampal lesions consistently produce major deficits in spatial learning tasks, while sparing many other types of learning (Jarrard 1993). Nevertheless, hippocampal activity probably contributes to other forms of learning as well, possibly by providing an indexing function based on a spatial coordinate code (McNaughton et al. 1996; Nadel et al. 1985; Teyler and Discenna 1986). The most striking behavioral correlate of hippocampal principal cells in the CA1, CA3, and dentate gyrus regions is the spatial location of the animal; these cells have been named place cells (Jung and McNaughton 1993; Muller et al. 1987; O’Keefe 1976; O’Keefe and Dostrovsky 1971; Wilson and McNaughton 1993). Cells in the entorhinal cortex and in the subicular complex also show varying degrees of spatially selective firing (Barnes et al. 1990; Quirk et al. 1992; Sharp and Green 1994; Taube 1995b).

Another group of cells identified with navigation and spatial orientation are head direction cells, which were discovered originally in the postsubiculum (Taube et al. 1990a,b, 1996). These cells fire when the rat’s head is pointed in a particular direction, regardless of the animal’s location in the environment or the position of the body relative to the head. They are sensitive to head direction in the yaw axis only (horizontal plane); head direction in the pitch and roll axes are irrelevant to these cells. Head direction cells may serve as an “internal compass” underlying an innate sense of direction. Head direction cells have been reported subsequently in other brain regions: the anterior thalamus (Taube 1995a), the lateral dorsal thalamus (Mizumori and Williams 1993), the retrosplenial cortex (Chen et al. 1994a,b), the striatum (Wiener 1993), and the lateral mammillary nuclei (Leonhard et al. 1996).

The firing properties of place cells and head direction cells are controlled by an interaction between landmarks and idiothetic cues, just as an animal’s spatial behavior is controlled by such an interaction. Both types of cells can be controlled by visual landmarks, in that rotation of the landmarks while the animal is absent from the environment...
can, under most circumstances, cause an equal rotation of the firing location/direction of the place cells or head direction cells (Bostock et al. 1991; Muller and Kubie 1987; O'Keefe and Conway 1978; O'Keefe and Speakman 1987; Taube et al. 1990b). Also, radical changes in the landmarks can result in an apparently complete orthogonalization of place field distribution (Bostock et al. 1991; O'Keefe and Conway 1978). Neither type of cell, however, requires visual input to fire appropriately; they can both maintain their location/direction tuning for many minutes in total darkness, provided that the rat had established its bearings before the light was turned off (Chen et al. 1994a; Markus et al. 1994; McNaughton et al. 1989a; Mizumori and Williams 1993; Quirk et al. 1990; Taube et al. 1990b). In contrast, vestibular input does appear to be necessary for these cells to maintain their selective firing properties (Stackman and Taube 1996, 1997). Both types of cells also are influenced by the ‘‘motor set’’ of the animal in that they will shut off or reduce firing dramatically if the rat is restrained tightly, even if the rat is placed in the proper firing location/direction of the cell under study (Foster et al. 1989; Knierim et al. 1995; Taube 1995a).

Numerous studies have attempted to tease apart the relative influences of visual landmarks and idiothetic cues in controlling place cells and head direction cells (see Knierim et al. 1996 for a review); however, the results have been inconsistent. Some studies suggest that visual landmark cues predominate over idiothetic cues (Goodridge and Taube 1995; Mizumori and Williams 1993), whereas other studies suggest the opposite (Chen et al. 1994a; Wiener 1993; Wiener et al. 1995). Still other studies show mixed results, depending on the exact conditions of the experimental test (Blair and Sharp 1996; McNaughton et al. 1995; Sharp et al. 1995). A number of computational models have addressed the interactions between idiothetic cues and visual landmark cues in controlling place cells and head direction cells (Blair 1996; McNaughton et al. 1991, 1996; Redish et al. 1996; Samsonovich and McNaughton 1997; Skaggs et al. 1995; Zhang 1996). These models incorporate one- and two-dimensional attractor network architecture for head direction cells and place cells, respectively, to stabilize the network activity at the representation of the current heading and location of the animal. As the animal moves through the environment, the attractors are updated by a combination of idiothetic and visual landmark cues, although the precise nature of this interaction varies among the models.

The present study investigated the dynamic interaction between idiothetic input and visual landmarks over the firing of head direction cells and place cells. The multiple experiments are divided into three sets. In the first set of experiments (apparatus rotation experiments), hippocampal place cells or anterior thalamic nuclei (ATN) head direction cells were recorded as rats foraged for food in a high-walled apparatus. In the middle of the session, the apparatus and rat were rotated abruptly, thereby introducing an explicit conflict in directional information from idiothetic and visual landmark cues. Vestibular and other idiothetic sources informed the rat that it had been rotated and was facing a new direction; however, the single salient landmark, which was rotated by the same amount as the rat, informed the rat that it was facing the same direction as before.

In the second set of experiments (light/dark experiments), the tuning curves of head direction cells were measured under normal conditions, and then the lights were turned off. The head direction cell system was allowed to build up error as the rat explored or was rotated passively in the dark. After the head direction cell tuning curve had drifted relative to the external environment, the lights were turned back on to see if the visual landmarks could correct the error and reset the system to its original alignment relative to the landmarks, as reported by Mizumori and Williams (1993) in a study of head direction cells in the lateral dorsal thalamus (LDT).

In the third set of experiments (place field drift experiment), observations were made on the firing properties of multiple, simultaneously recorded place cells of a single rat, which, as part of a separate investigation, had a local lesion of the dentate gyrus in the hemisphere contralateral to the recording site. The observations from this animal are included here because they shed light on the relative influence of intrinsic network dynamics versus external sensory input on the firing of place cells under conditions where visual landmarks exerted no control over the cells.

Some of the results from these experiments have been reported previously in preliminary form (Knierim et al. 1994, 1997; McNaughton et al. 1995).

METHODS

Subjects

Three groups of rats were used in these experiments. Group 1 consisted of 12 specific-pathogen–free male Fischer-344 rats obtained from Taconic Farms at ~4 mo of age; they were ~8 mo of age by the time recording commenced. Group 2 consisted of eight male, Fischer-344, retired breeder rats obtained from Charles River Laboratories at 9 mo of age. Group 3 consisted of a single male, Fischer-344, retired breeder rat obtained from Charles River Laboratories at 9 mo of age. All animals were put on a controlled feeding schedule to maintain their weights at 80–90% of their ad libitum weights. The rats had free access to water. During the experiments they were handled and weighed daily. The rats were housed individually and maintained on a 12:12 h reversed light-dark cycle (lights off 10 AM to 10 PM). Most recording was done during the dark portion of the cycle. Animal care, surgical procedures, and euthanasia were carried out according to National Institutes of Health (NIH) guidelines.

Training

GROUP 1. The rats originally were shipped to NASA Ames Research Center in Moffett Field, CA, for purposes of another experiment there. Although the activities there were not relevant to the present study, they are described briefly so that the reader is informed of the prior history of these animals. The rats received ~40 days of training (30–45 min/day) to shuttle back and forth for 45-mg food pellets at each end of a 91 ´ 13 cm alley. Four to 6 days after surgical implant of recording electrodes and medial forebrain bundle (MFB) stimulation electrodes (see further), they resumed daily training on the alleys, initially for food reward and then for MFB stimulation reward (30–150 µA current, 300-µs pulses at 100 Hz for 0.5 s). After 7 days, the rats were trained to perform two more tasks for MFB stimulation: to run clockwise around a rectangular track (15 ´ 25 cm) that could be tilted up to a 45° angle along its long axis and to run clockwise a small plus
maze (20 cm per arm). Training sessions occurred each day for ~30 min for 14 days.

After the cessation of activities at NASA-Ames, the rats were shipped to the University of Arizona for the present experiments. The rats were then divided into three groups. Group 1 underwent 15 min of training in a 76-cm-diameter, 51-cm-high cylinder with a single white cue card covering 90% of the east wall.

### Group 2

Rats received 2–3 wk of daily training sessions (15 min/session) to forage for chocolate sprinkles dropped intermittently from an automated pellet dispenser mounted on the ceiling. The training and recording sessions were performed in the same room. Seven rats were trained to run in the same gray-walled cylinder described above, with a single white cue card or a white card with diagonal black stripes along the east wall. Another 10 rats were trained in a square, brown cardboard box (68-cm high, 68-cm side) with a white card with assorted black spots along the east wall. Brown paper covering the floor of each environment was replaced between training sessions to minimize olfactory cues on the floor.

### Surgery

Surgeries for these rats were performed according to NIH guidelines using techniques described in detail elsewhere (Gothard et al. 1996). Briefly, rats were anesthetized with pentobarbital sodium (Nembutal, 40 mg/kg ip), supplemented with methoxyflurane (Metofane) inhalation as necessary. Intramuscular penicillin (30,000 units of Bicillin in each hindlimb) was administered as a prophylactic antibiotic. For group 1, a recording device (called a “hyperdrive”) that allowed the independent manipulation of 14 recording probes was implanted over the right hemisphere of each rat (3.8 mm P, 2.0 mm L from bregma). Each recording probe was a tetrode—an electrode made of four lengths of fine nichrome wire (13-μm diameter; H. P. Reid, Neptune, NJ) twisted together (McNaughton et al. 1983b; Reecce and O’Keefe 1989; Wilson and McNaughton 1993). In addition, each rat was implanted bilaterally with a bipolar stimulating electrode in each hemisphere aimed at the MFB (0.25 mm A, 1.9 mm L from bregma, 8.5 mm V from brain surface at an angle of 19.5° posteriorly in the sagittal plane).

The stimulating electrode was made of two lengths of 0.003-in-diameter, Teflon-insulated, stainless steel wire (Medwire, Mount Vernon, NY) twisted together with ~1 mm spacing between the two electrode tips. For group 2, a smaller number of tetrodes were implanted, using a microdrive assembly described in detail in McNaughton et al. (1989b). Two tetrodes separated by ~300 μm were implanted in each hemisphere in a position to encounter the ATN and/or dorsal hippocampus. The rat in group 3 underwent a single injection of 1 μl of colchicine (4 mg/ml) in the dorsal dentate gyrus of the right hemisphere; histological analysis revealed that this caused a loss of granule cells in most of the dorsal dentate gyrus of that hemisphere with no detectable damage to the contralateral hemisphere. Six tetrodes were implanted in the contralateral, control hippocampus. After surgery, rats from all groups recovered from anesthesia in an incubator, and they were administered 26 mg of acetaminophen (Children’s Tylenol) orally for analgesia. They also received 2.7 mg/ml acetaminophen in their drinking water for 1–3 days after surgery.

### Recording electronics

After 2–7 days postsurgical recovery, the electrodes were advanced over the course of a few days. Neuronal signals were passed through a custom-built headstage of low-noise, unity gain, complementary metal oxide semiconductor (CMOS) operational amplifier (group 1) or field-effect transistors (FETs) (groups 2 and 3) that could be attached to the hyperdrive. Also mounted on the front of the headstage was an array of infrared light-emitting diodes (LEDs), and attached to the back was an arm with a single LED on the end (16 cm from the front LEDs) to track the animal’s position and head direction during the recording trials. The LED signals were sampled at 20 Hz (SA-2 Dragon Tracker, Boulder, CO) and stored on disk, at a pixel resolution of ~1.5 cm. Electrical signals were amplified between 2,500 and 10,000 times and filtered between 600 Hz and 6 kHz, before being digitized at 32 kHz and stored in a 25 MHz IBM 80486-based workstation. (See Gothard et al. 1996 for a description of the multunit recording system.) Activity also was monitored through an audio monitor (Grass Instruments).

### Apparatus rotation experiments

### PLACE CELL RECORDINGS.

Group 1 rats were used for these experiments. Before each recording session, the tetrodes were monitored for isolated units while the rat sat quietly in a 24-cm-diameter holding dish in the experiment room (a 3.5-mm-diameter, black room), which was adjacent to the equipment room that housed the data-acquisition computer system and the recording electronics. Lighting was provided by a 64-cm-circle of 100 small, white Christmas tree lights centered 160 cm over the apparatus floor. The room was surrounded by black curtains. Under these conditions, there were no salient visual directional cues available to the rat other than the cue card along the east wall of the apparatus. In most cases, a sufficient number of cells (3) was present to perform the experiment without further tetrode adjustment. In cases where the tetrodes did not adjust, immediately before the experiment, recording was delayed by a minimum of 30 min to ensure recording stability during the course of the session; cells that drifted away during the recording session were excluded from the analysis.

After recording for a 10-min baseline period while the rat was in the holding dish, one experimenter entered the experiment room, closed the door and black curtain behind, and placed the rat in the cylinder, which was mounted on a turntable. Neuronal activity and rat position data were recorded while the rat foraged for sprinkles. After ~10 min, when the rat was in a location near the center of the apparatus, the experimenter rotated the cylinder and floor manually clockwise, either 45° or 180°, at a rate of ~90–180°/s. The onset of the rotation was abrupt, but the rotation itself was smooth. Neuronal and position data were recorded for ~10 more min, and then the experimenter began to rotate the cylinder and floor slowly and steadily counterclockwise (~0.5°/s), so as to provide minimal vestibular stimulation to the rat, until the cue card returned to its original position. Data were recorded for another 10 min, and then the rat was removed from the cylinder, returned to its holding platform nearby, and a second baseline period was recorded for ~10 min. Comparison of the baseline periods before and after the experiment aided in the determination of recording quality and unit isolation stability throughout the session. Each rat underwent four recording sessions (1 session per day) during a period of 7 days, receiving alternately a small (~45°) rotation of the apparatus or a large (~180°) rotation. The sessions were counterbalanced such that half of the rats received the small rotation first and the other half received the large rotation first. Session 1 was in all
cases the animal’s second experience in the cylinder and its first rotation experience. Before each recording session, the brown paper covering the floor of the cylinder was replaced with a fresh sheet, thus eliminating any local cues on the floor between sessions. In the off-days between Sessions 1 and 2, each rat received one supplementary training session in the brown box in the training room.

HEAD DIRECTION CELL RECORDINGS. Group 2 rats were used for these experiments. The recording electronics differed slightly from those used for group 1 rats, and the details are described in Knierim et al. (1995). Head direction cells were sought by advancing the tetrodes in increments of 20 μm and then rotating the rat passively on a pedestal in the equipment room, listening for a cell tuned for head direction. Once a head direction cell had been isolated and judged stable for ≥30 min, the preferred firing direction of the cell in the equipment room was noted. The rat then was carried openly into the adjacent experiment room and placed into the recording apparatus. One experimenter usually stayed in the experiment room with the rat to perform apparatus manipulations. The second experimenter in the equipment room monitored the directionality of the head direction cell by listening to the cell’s activity on the audio monitor and watching the rat’s activity on a video monitor. When this experimenter judged that the cell’s firing pattern was stable, he signaled the other experimenter to perform the apparatus rotation.

The rotations were identical to the place cell recording sessions above, except that 1) for all rats except 3803, only 2–3 min of data were recorded before and after the apparatus rotations (as opposed to 10 min for place cell recordings); 2) the large rotations were 180° in 13 sessions, 150° in 2 sessions, and 135° in 1 session; and 3) only four rats experienced the 45° rotation, always after all of the large rotations had been performed. The rats ran either in their familiar training apparatus (the gray cylinder or the brown box described above) or in a new apparatus that they had not experienced previously. The new apparatus could be either the gray cylinder or brown box or one of the following: a gray square box (51-cm high, 69 cm/side) or a triangular enclosure made of three curved pieces of green poster board (50-cm high, 78 cm/side); each apparatus had a single salient cue card, with different patterns of markings, covering one wall. At the end of the session, the rat was removed from the apparatus and returned to the equipment room, where the preferred firing direction of the head direction cell was again noted as the rat was rotated passively on a pedestal.

Eight rats underwent this procedure multiple times, usually separated by 1–9 days (Table 1). Each of these rats experienced the rotation in both its familiar apparatus (used for training) and in a novel apparatus. In between recording days, five of the rats were given additional training sessions in the familiar apparatus, with no rotations.

Preferred firing directions of head direction cells were assessed in the equipment room by rotating the rat passively on a pedestal and listening to the firing of the cell on an audio monitor. The rat then was moved into the experiment room and placed onto the open platform, where the cell was either allowed to move freely or a stopped, intermittent light source was used to provide a visual cue. The rat was rotated continuously in one direction (clockwise or counter-clockwise) during both light and dark phases. Under irregular bidirectional rotation, the rat was rotated in a more random fashion, in which clockwise and counterclockwise turns of different amounts (∼45–180°) were interleaved irregularly.

Light/dark experiments

ACTIVE FORAGING TASK. Three rats from group 2 were used in these experiments, after all recordings from the apparatus rotation experiments were complete. The rats performed the same random foraging task, but in this experiment they foraged on an open platform (76-cm diam) in the middle of a cue-rich room. No measures were taken to minimize olfactory cues on the platform. The environment was a 3.5 × 3.5 m experiment room with black and white curtains running just inside its perimeter. In addition to the curtains, a number of objects were placed in the room as visual cues: a chair, a cue card with an abstract pattern, and a coat rack with a white laboratory coat, at varying distances from the center of the room. Illumination was provided by four ambient light ceiling lights at the same distance and orientation from each wall of the room. All training sessions and recording sessions took place in the same room.

Place field drift experiment

The single rat constituting group 3 was used in this experiment, in which four to five sessions were recorded per day for 7 days as the rat foraged for chocolate pellets in a high-walled apparatus, either its familiar training environment (a gray cylinder with a white cue card on the east wall) or a new environment (a cylinder with the cue card rotated north; a cylinder with a black or black/white striped cue card on the east or north wall; or a square environment with a white cue card on the east or north wall). The between- and-within-session stability of the place fields relative to the visual cues was assessed within each 12- to 16-min recording session, to look for rotations of the place fields similar to that reported previously for head direction cells (Knierim et al. 1995). All data reported here are from CA3 of the control hemisphere of this rat.
### Table 1. Order of manipulations for apparatus rotation experiment with head direction cells

<table>
<thead>
<tr>
<th>Rat</th>
<th>Session Number*</th>
<th>Apparatus</th>
<th>Familiar or Novel</th>
<th>Apparatus Rotation, °</th>
<th>Deviation From Visual Landmark Control</th>
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<td>180</td>
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<td>Familiar</td>
<td>180</td>
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</tr>
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<td>-10</td>
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<td>Brown box</td>
<td>Familiar</td>
<td>45</td>
<td>-10</td>
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* Days intervening are in parentheses.

### Data analysis

**OFF-LINE UNIT ISOLATION.** The tetrode (McNaughton et al. 1983b; Recce and O’Keefe 1989; Wilson and McNaughton 1993) allows the isolation of single units based primarily on the relative amplitudes of signals recorded simultaneously at four slightly different locations. Additional waveform characteristics, such as spike width, also are used. Waveform characteristics were plotted as a scatter plot of one of the electrodes versus another. Individual units formed clusters of points on such scatter plots, and the boundaries of these plots were defined with the use of a custom interactive program running on a Sun Sparcstation. The spike times of individual units then were combined with the position and direction information provided by the tracker to generate firing rate maps.

**PLACE CELL FIRING RATE MAPS.** Firing rate maps were constructed by dividing the behavioral apparatus into 2.4-cm square bins. The firing rate for each bin was calculated with an “adaptive binning” formula, which optimizes the tradeoff between sampling error and spatial resolution (see Skaggs et al. 1996). The results were plotted as a color-coded or a gray-scale rate map. Separate rate maps were constructed for time periods before and after experimental manipulations (e.g., cylinder rotation). The specificity of spatial tuning for each cell was calculated as the amount of information about the rat’s position conveyed by the firing of a single spike from the cell (Skaggs et al. 1993). It was defined as

\[ I = \sum_{j} p_j \frac{\lambda_j}{\lambda} \log_2 \left( \frac{\lambda_j}{\lambda} \right) \]

where, if the cylinder is divided into square bins, \( I \) is the information in bits per spike, \( p_j \) is the probability of the rat occupying bin \( j \), \( \lambda_j \) is the mean firing rate for bin \( j \), and \( \lambda \) is the mean firing rate for the whole cylinder. The information score is a good measure of whether a cell has a statistically significant spatial firing bias, and it correlates well with the experimenter’s subjective judgments of the quality of a place field.

**ROTATIONAL CORRELATION ANALYSIS.** To determine whether place fields were maintained relative to the cue card after the apparatus rotations, a mean rotation score was calculated for all the cells that fired \( \geq 100 \) spikes in both the pre- and postrotation periods and that had statistically significant information scores \((P < 0.01)\) in both periods. First, the firing rate maps of each cell for the period before rotation were correlated, pixel by pixel, with the firing rate maps for the period after rotation. The maps then were rotated with respect to each other in 5° steps, and the correlation was measured for each step. The angle of highest correlation was taken as the amount of rotation for that cell. Because there were usually multiple cells recorded each day, the amount of rotation of the ensemble of cells was calculated as a weighted mean of all complex-spike cells meeting inclusion criteria (see RESULTS). To ensure that cells with weak place fields, unreliable firing, or place fields in the center of the cylinder did not produce spurious contributions to the mean rotation score, the weight assigned to each cell was based on a number of variables, including the information score (see previous text), the distance of its field from the apparatus center, and the magnitude of its maximum spatial correlation for the pre- and postrotation periods (see Knierim et al. 1995 for the formula and a discussion of its rationale).

**HEAD DIRECTION CELL TUNING CURVES.** Directional tuning curves for head direction cells were constructed by dividing the number of times a cell fired when the rat faced a particular direction (in bins of 10°) by the amount of time the rat faced that direction.
The results were plotted in polar coordinates. Separate tuning curves were constructed for different epochs of each experiment (e.g., before and after rotation), and also at finer temporal scales (ranging from 5 s to 1 min), to reveal the time course of any change in the tuning of the cell.

**Rotation Analysis of Head Direction Cells.** The polar tuning curves of the head direction cells were smoothed by recomputing each firing rate bin as the average of itself and its immediately adjacent bins. The bin with the maximum firing rate was then taken as the preferred direction for that cell. The effects of cylinder rotation or extinguishing the lights were evaluated by calculating the angular distance between the preferred firing directions in the pre- and postmanipulation periods. In situations where multiple head direction cells were recorded simultaneously, an average angular distance was computed from the individual cell results.

**Descriptive Statistics.** Circular statistics (Batschelet 1981) were used to describe the overall population results of the cylinder manipulations. The mean population vector for all recording sessions of all rats was calculated. The angle of this vector represents the mean angle by which the place cells and head direction cells rotated relative to the visual landmark, and the length of the vector is inversely related to the variance around this mean angle. Comparison between 45 and 180° rotations were made by testing the null hypothesis that there was no difference in visual landmark control between the two manipulations. Each rat’s weighted mean rotation score was subtracted from the expected value of rotation assuming visual landmark control (i.e., 45 and 180°), and a Wilcoxon-Mann–Whitney rank-sum test was performed on the absolute values (the “angular distance”) of these numbers (Batschelet 1981).

**Histology**

For groups 2 and 3, small electrolytic lesions were made at the end of all the experiments at the tips of the electrodes by passing current (10 μA for 10 s) through one channel of each tetrode to facilitate identification of the recording sites. The animals then were killed with an overdose of Nembutal and perfused transcardially with a 3.7% solution of formal saline. The brain was placed in a 30% solution of sucrose in formal saline for ≈48 h, after which the tissue was sliced in 40 μm coronal sections, mounted, and stained with cresyl violet.

**Results**

**Apparatus Rotation Experiments**

**Place Cell Recording Sites.** An average of 7.7 well-isolated complex-spine cells were analyzed for each recording session (range 1–24). This number does not include the many cells that were dropped from the analysis because of low firing rates (<100 spikes) in all sessions or because they had an information score with a $P$ value $>$0.01 during each of the pre- and postrotation periods. Often, the same cells were recorded over multiple sessions; because the analyses were based on the averaged properties of populations of neurons during each recording session, no attempt was made to determine which cells were recorded repeatedly. Some recording sessions were dropped because of recording instability or other technical problems. Thus the results are based on a total of 22 sessions for the fast and slow 45° rotations and 18 sessions for the fast and slow 180° rotations.

On the basis of the stereotaxic coordinates of the recording drive, the depth of the electrodes from brain surface ($\sim 2.0$ mm), and the recorded EEG signals at the tetrodes, the recording sites were presumed to be in CA1.

**Head Direction Cell Recording Sites.** One head direction cell was recorded in 19 sessions, two cells in 6 sessions, and three cells in 1 session. In many cases, the same cell was recorded in multiple sessions. In all cases of multiunit recording, the cells behaved identically. Not all recording sites were confirmed with absolute certainty for a number of reasons. For example, for each recording session, the tetrode was moved into the thalamus to record a head direction cell and then retracted 300–500 μm after the recording session; this resulted in multiple penetrations of the thalamus over many weeks, making it impossible to ascertain exactly where the recordings took place every session. All the recording sites that were identified positively were in the ATN, and other indicators of electrode passage all suggested that the remaining sites were in the ATN. The only other thalamic area in which head direction cells have been reported is the dorsal-caudal LGN (Mizumori and Williams 1993), and the electrode placements in the current study were well anterior to that location.

**Place Cell Responses to Apparatus Rotations.** Figure 1 shows examples of the responses of place cells to the 45° and 180° rotations. In Fig. 1A, the apparatus was rotated 45°, and the two representative cells are shown to rotate their place fields correspondingly after both fast and slow rotations. In such cases, the cells are said to be bound to the visual cue card, as previous work suggests that the cue card is the salient landmark that controls the cells rather than olfactory or other landmarks in the cylinder (Muller and Kubie 1987; Taube et al. 1990b). Place fields were strongly bound to the visual cue card in all 22 of the fast 45° rotations. The effects of the 180° fast rotations were more variable. Figure 1B shows one example of the 10 sessions in which the place fields rotated 180° to follow the cue card. In eight other cases (Fig. 1C), after the fast 180° rotation, the hippocampus “remapped” the environment (Bostock et al. 1991; Knierim et al. 1995; Markus et al. 1995; Sharpe et al. 1995), in that place cells changed their firing properties in arbitrary ways. During the slow rotation, the cue card had strong control over the new place fields. No studies were performed to see if the remapped fields showed stability over recording sessions. The characteristics of this remapping are described in more detail below.
Sometimes the cell rotated the same amount, sometimes it did not rotate at all, and sometimes it rotated about halfway. Examples of each are shown in Fig. 2, B–D. In contrast, when the apparatus and rat were rotated very slowly and continuously, presumably below vestibular threshold, the cells always were bound to the cue card, suggesting that there were no other external cues outside the cylinder used by the rat for spatial orientation.

COMPARISON OF PLACE CELLS AND HEAD DIRECTION CELLS. Figure 3 summarizes the results of each rotation for all rats. Because the results of individual rats were not always the same for repetitions of a given rotation type (see Table 1 for head direction cells), multiple sessions for each rat were included in this analysis. For each session, the mean rotation score for the recorded cells was subtracted from the magnitude of cylinder rotation (45° or 135–180°), thus producing a number that represents the angular deviation from the expected rotation of the fields if they were to follow the cue card. A deviation of 0°, which indicated total cue card control, was plotted at the 12:00 position on the graphs. For both place cells (Fig. 3A) and head direction cells (Fig. 3B), after the fast 45° rotations, almost all points clustered around this position. The fast 180° rotations, however, resulted in dispersed distributions. For both types of cells, the data from some sessions clustered around the 12:00 position, but for many other sessions they were distributed around the circle. For head direction cells, the distribution was bimodal, as a second set of points clustered near the 6:00 position, indicating predominantly idiothetic control in these sessions. For place cells, the distribution contained a combination of a single mode plus an apparently random component (see further). The difference in cue card control between the fast 45° and fast 180° rotations is statistically significant (place cells: Wilcoxon-Mann-Whitney U = 49.5, P < .0001; head direction cells: Wilcoxon-Mann-Whitney U = 39; P < .05). There was no difference between the slow 45° and slow 180° rotations, however. In both of these rotations, the cells always were controlled strongly by the cue card.

The Wilcoxon-Mann-Whitney U test allows the rejection of the null hypothesis that the strength of cue card control is independent of the magnitude of the cylinder rotation. One could make the argument, however, that this rank-order test is inappropriate because the range of expected cell rotations is larger for the 180° rotations than for the 45° rotations. That is, for the 180° rotations, one might expect that values will range from 0° (total cue card control) to 180° (total idiothetic cue control), whereas for the 45° rotations, one might expect that values will range from 0° (total cue card control) to only 45° (total idiothetic cue control). Thus a statistically significant result based on a rank-order test might lead to an invalid conclusion about the relative strength of visual landmark versus idiothetic control for the two rotation types. To address this, the data were classified before the rotation but developed a field after the rotation. Cell 3 initially had a field but lost it after the rotation. This pattern of results is consistent with a “complex remapping” of the environment as defined by Bostock et al. (1991). The cue card had strong control over the remapped fields during the slow rotation. In this session, the weighted mean rotation score was 87° after the fast rotation and 189° after the slow rotation. The maximum firing rate for cell 1 was 20 spikes/s; for cell 2 was 16 spikes/s; and for cell 3 was 7 spikes/s.
were classified as ‘‘predominantly idiothetic’’ \((n = 0)\). Similarly, for the 180° rotations, all scores falling within the range \(0 \pm 90°\) were classified as predominantly cue card \((n = 12)\), whereas all scores falling in the range \(180 \pm 90°\) were classified as predominantly idiothetic \((n = 6)\). A \(\chi^2\) analysis on this contingency table revealed that these values were significantly different from chance \((\chi^2 = 8.63, P < 0.005)\), thus supporting the argument that the type of rotation had a significant effect on the relative strength of visual landmark versus idiothetic control. Similarly, for the head direction cell recordings (Fig. 3B), the data were classified into predominantly cue card (for 45° rotations \(n = 9\); for 180° rotations \(n = 8\)) and predominantly idiothetic (for 45° rotations \(n = 1\); for 180° rotations \(n = 8\)) categories, and a \(\chi^2\) test showed that the distribution of this contingency table was unlikely to arise from chance \((\chi^2 = 4.35, P < 0.05)\).

HIPOCCAMPAL REMAPPING. In each session in which the cue card lost control over the place cells, there was a radical rearrangement of the place fields relative to each other. This remapping was analyzed by calculating an ensemble spatial correlation score for each recording session. Because many of the cells either gained or lost their place fields as a consequence of the remapping, this analysis included those cells that fired few spikes in only one of the pre- or postrotation periods but still excluded those cells that fired rarely or nonspecifically in both periods. For each cell, its postrotation rate map was rotated by the mean rotation score for the data set (i.e., the rotation values in Fig. 3A), and this rotated map was correlated with the map of the prerotation period. The ensemble spatial correlation score was defined as the mean correlation of all cells of the data set. This score was plotted as a function of the mean rotation score (Fig. 4), resulting in two distinct clusters of points. In all 10 sessions in which the cue card controlled the cells, the ensemble spatial correlation scores were higher than in the eight sessions where the cue card ‘‘lost control’’ (i.e., hippocampal remapping). A Mann-Whitney \(U\) test showed that this difference was highly significant \((P < 0.002)\). Thus the hippocampal map was much more highly correlated before and after apparatus rotation in the sessions where the cue card controlled the cells than in the sessions where it did not.

As mentioned above, another indication of hippocampal remapping is that many cells with place fields in the cylinder before the rotation lost the fields after the rotation, whereas other cells that were silent before the rotation developed place fields after the rotation. The proportions of cells that had fields only before, only after, or both before and after the cylinder rotations are plotted in Fig. 5. The operational definition of a complex-spike cell with a place field was that its information score had a \(P\) value <0.01 and the cell fired \(\geq 100\) spikes in the 10-min recording segment. The 180° rotation sessions are divided into seven cue card control sessions and seven sessions where the cue card lost control. In the latter group, 50% of the cells had fields only before or only after the rotation compared with 27% in the cue card control sessions \((35/70 vs. 11/41; z = 2.37, P < 0.05)\). In all other rotation types, the large majority of cells had fields both before and after rotation; the small proportion of cells with fields only before or only after was due in large part

FIG. 2. Examples of head direction cell responses to apparatus rotation. A: visual landmark control after a 45° rotation of the cylinder. The head direction cell fired east during the first 2.5 min of the session (left). After the cylinder was rotated abruptly 45° clockwise, the cell changed its firing direction to southeast, following the cue card (center). After a slow 45° counterclockwise rotation of the cylinder back to its starting orientation, the cell returned to its initial direction (right). Axes: 70 spikes/s. B: visual landmark control after a 180° rotation of the cylinder. The bilobed tuning curve indicates that there were probably 2 cells that could not be isolated from each other. The cells fired north and southeast during the first 2.5 min (left). After the fast 180° clockwise rotation of the apparatus, the cells both rotated their tuning curves to follow the cue card (center). After the slow 180° clockwise rotation, the cells returned to their original firing directions (right). Axes: 40 spikes/s. C: idiothetic control after a 180° rotation. This cell fired southwest during the initial 4 min of the recording session (left). After the fast 180° rotation clockwise, the cell continued to fire southwest, demonstrating a complete lack of control by the cue card (center). After the slow 180° rotation clockwise, the cell rotated its tuning curve 180° and now fired opposite to its original direction (right), demonstrating that there were no other external cues that controlled the firing of the cell. Axes: 25 spikes/s. D: intermediate control after a 150° rotation. Although this cell was poorly isolated and was contaminated by background firing, there is still a clear peak of firing when the animal faced southeast during the first minute of the session (left). After the fast 150° rotation clockwise, the cell rotated its tuning curve 90°, adopting a ‘‘compromise’’ between the idiothetic cues and visual landmark (center). This compromise might be the result of purely idiothetic input with some error, perhaps arising from the motion of the rat’s head as the apparatus was rotated simultaneously. After a slow rotation of 180° clockwise, the cell’s tuning curve rotated with the visual cue (right). Axes: 25 spikes/s.

according to whether the cue card or the idiothetic cues predominated. For the place cell recordings (Fig. 3A), for the 45° rotations, all mean rotation scores falling in the range \(0 \pm 22.5°\) were classified as ‘‘predominantly cue card’’ \((n = 22)\), whereas all scores falling in the range \(45 \pm 22.5°\)
to criterion effects rather than real remapping (e.g., a cell that fired just <100 spikes before rotation and just >100 spikes after rotation).

An interesting question of great theoretical importance is whether the remapping was complete or partial; that is, did all place cells change their firing fields or did only a subset of them change while the remainder maintained their prerotation fields? Unfortunately, the present data do not resolve this question unambiguously. Although some data sets suggest strongly that the remapping can be partial, in that some cells of whether the hippocampus remapped the cylinder or not. Thus the transient rate decrease seen in Fig. 6

Interestingly, this effect was not seen in the cells that had fields only after the rotation (Fig. 6D); these cells fired at a constant rate throughout the whole 10-min postrotation period. There were no obvious behavioral differences between the remap (Fig. 6, B–D) and no-remap (Fig. 6A) sessions. For example, the rats’ average running speed did not change immediately after the rotation in either type of session. Rather the rats typically continued to forage for food within seconds after the cylinder rotation, regardless of whether the hippocampus remapped the cylinder or not. Thus the transient rate decrease seen in Fig. 6B cannot be attributed to the known influence of running speed on place cell firing (McNaughton et al. 1983a).

DELAYED CUE CARD CONTROL OVER HEAD DIRECTION CELLS.

In all five sessions in which head direction cells followed the 180° rotation, the cue card control was delayed: right after the apparatus rotation, the cells initially maintained their direction relative to the external environment, but then they rotated 180° during the course of seconds to minutes. Figure 7 shows an example of delayed cue card control. After 3 min in which the cell fired west, the apparatus was rotated 180° abruptly. By the 5th minute, the cell fired east. Minute 4 is broken down into 15-s intervals, where it is shown that the head direction cell initially maintained its west direction right after the rotation but then rotated during the course of 1 min until it fired east. Other examples are shown in Fig. 8. In Fig. 8A, the cell was tuned to the north for the first 2 min, at which time the apparatus was rotated 180°. During minutes 3–4, the cell’s preferred firing direction rotated, until by minute 5 it fired south. During minutes 6–9, the apparatus was rotated slowly clockwise, and the

FIG. 3. Angular deviation of the hippocampal map (A) and head direction cells (B) from the visual landmark after rotations of the cylinder. For each recording session, the mean rotation score for that session was subtracted from the amount of cylinder rotation (45° or 135–180°) to produce an angular deviation score. An angular deviation of 0°, plotted here at the 12:00 position, indicated absolute visual landmark control over the cells. The fast 45°, slow 45°, and slow 180° rotations all had strong visual landmark control over the cells. For place cells, the mean angles were 0, 1, and 356, respectively, and the mean vector lengths were 0.994, 0.990, and 0.986, respectively. For head direction cells, the mean angles were 4, 356, and 0°, respectively, and the mean vector lengths were 0.941, 0.974, and 0.981, respectively. Rayleigh tests showed they were significantly clustered around 0° (P < 0.001). The results of the fast 180° rotation were quite different. For place cells, the distribution was dispersed, with a cluster of points at the 0° (12:00) locations and a number of other points scattered around the circle. The mean angle was 34°, and the length of the mean vector was 0.409 (P < 0.05). For head direction cells, the distribution was bimodal, clustering around the 0° (12:00) and the 180° (6:00) locations. The mean angle was 102°, and the length of the mean vector was 0.13. A Rayleigh test was not significant.
cell’s firing was strongly locked to the rotating apparatus. Figure 8B is a particularly interesting example. This cell fired southwest for 2 min, at which time the apparatus was rotated 180°. The cell initially displayed a reduction in firing rate, but after 1 min, its firing returned strongly to the southwest. During the slow, clockwise rotation of the cylinder (minutes 6–11), however, the cell’s tuning curve rotated counterclockwise in minutes 7–8. Notice that the cell’s preferred direction during minute 8 was now identical to its original direction relative to the cue card. From this time on, the cell was locked to the cue card, and its tuning curve rotated clockwise with the rotation of the apparatus (minutes 9–11). At the end of the session, both the cue card and cell’s firing direction were at the same position/direction as at the start of the session. Thus after the fast apparatus rotation, the cue card initially lost all control over the cell, and then the cell began to drift in a direction opposite to the slow rotation of the apparatus. When the tuning curve was realigned to the cue card, the card regained control over the cell for the remainder of the slow rotation.

**Light/dark experiments**

Head direction cells and place cells initially can maintain their bearings in complete darkness, but they may eventually begin to drift, presumably as the rat’s path integration mechanisms accumulate error. In this set of experiments, the tuning curves of head direction cells were measured under normal conditions in a cue-rich room, and then the lights were turned off. After the system had drifted out of calibration by varying amounts, the lights were turned back on to see if the visual landmarks could correct the error and reset the system to its original bearing relative to the cues as reported by Mizumori and Williams (1993) in a study of head direction cells from the lateral dorsal thalamus. For the present experiment, the cell was considered to be reset to its original bearing if the tuning curves before and after the dark periods differed by no more than 30°.

**ACTIVE FORAGING ON OPEN PLATFORM.** The original intent was to allow the cell to drift spontaneously in the dark. ATN head direction cells, however, could maintain their external tuning directions for long periods of time in complete darkness (Fig. 9). Thus the cells often were induced to drift relative to the external cues by rotating the platform slowly while the rat foraged in the dark. Each rat experienced a variable number of light/dark/light cycles each day. Data from two rats were recorded on >1 day, and it is not known whether the head direction cells recorded on different days were the same or not. For these analyses, all manipulations performed on three rats over multiple days were pooled together. These results

**FIG. 4.** Hippocampal ensemble spatial correlation as a function of the mean rotation score for each recording session. The rate map for each place cell after the apparatus rotation was oriented to the mean rotation score for that session, and this map then was correlated with the rate map of the prerotation period. For each session, the spatial correlation score was calculated as the mean of all individual cells recorded. The sessions separated into 2 distinct clusters. One cluster (top left) represents sessions when the visual landmark controlled the place fields after the 180° rotations. In these sessions, the place fields all rotated ~180°, resulting in a high spatial correlation score and a low deviation from visual landmark control. The other cluster (bottom right) represents sessions where the visual landmark lost control over the place cells. In these sessions, the hippocampus re-mapped the environment, resulting in a low spatial correlation score and a wide distribution of the deviation from visual landmark control scores (which is expected in cases of remapping).
Fig. 6. Mean firing rate versus time for 180° cylinder rotation experiments. The firing rate of each cell for every 5-s interval in the recording session was averaged over all cells in the groups specified in A–D. Data are plotted for 5 min before the apparatus rotation and 10 min after the rotation. Linear regression lines were calculated for the postrotation periods (minutes 0–10) to test the significance of postrotation changes in firing rates. Because the same cells often were recorded for multiple sessions, only the 1st 180°-nonremap and the 1st 180°-remap sessions were included for each rat. A: no remap sessions. Mean firing rate of 41 cells recorded in 7 sessions when the place fields followed the visual cue card. The cylinder rotation had no effect on the mean firing rate, which remained steady throughout the postrotation period ($R^2 = 0.0002, \text{n.s.}$). B: mean firing rate of 35 cells in 7 sessions when the hippocampus remapped the cylinder after the rotation; these cells had place fields both before and after the rotation. The mean firing rate decreased by \~50% immediately after the rotation and steadily increased to the prerotation level during the next 5 min ($R^2 = 0.145, P < .0001$). C: mean firing rate of 18 cells in 7 sessions when the hippocampus remapped the cylinder after the rotation; these cells had place fields only before the rotation. D: mean firing rate of 17 cells in 7 sessions when the hippocampus remapped the cylinder after the rotation; these cells had place fields only after the rotation. Interestingly, the cells did not show the same increase in firing rate as in B. Rather, the mean firing rate was steady throughout the postrotation period ($R^2 = 0.0009, \text{n.s.}$), and it was of the same magnitude as the mean firing rate of other cells before the rotation ($\sim 1–1.5$ spikes/s).

reflect the firing of a few cells. Because previous investigations suggest that all head direction cells in a given area react similarly to these types of manipulations (i.e., if 1 cell rotates its tuning curve by a certain amount, the others will rotate by the same amount), it is presumed that the firing of one cell is representative of all cells in that area.

FIG. 7. Delayed visual landmark control of head direction (HD) cell after fast 180° rotation. During the 1st 3 min, the cell fired west. After the fast rotation, the cell fired east during the last 3 min. When minute 4 is broken down into 15-s intervals, one sees that the visual landmark control was not immediate. The cell initially maintained its western firing preference right after the apparatus rotation, then slowly drifted over the course of 1 min until it was realigned with the cue card. This type of delayed visual landmark control was characteristic of all examples of visual landmark control over HD cells after the fast, large rotations. This result implies strongly that the idiothetic input is the primary drive that updates the head direction cell system, with a secondary, correcting influence of visual landmarks. Axes: 45 spikes/s (top), 57 spikes/s (bottom).
FIG. 8. Further examples of delayed landmark control. In each example, the tuning curves of the head direction cells are plotted in 1-min intervals. After the 180° fast rotation of the cylinder and rat, the cells initially maintained their preferred firing directions relative to the laboratory framework. Over time, however, the tuning curves rotated until they were realigned with the visual cue card.

A: axes: 23 spikes/s.
B: axes: 40 spikes/s.

The distal visual landmarks generally did not reset the head direction cells after they had drifted in darkness. In 37/51 tests, when the lights were turned back on, the cells either maintained their new tuning direction or rotated even slightly further to a different direction; an example is shown in Fig. 10A. In 13 of the 14 remaining cases, in which the cells reverted back to their original preferred direction after drifting in the dark, the amount of drift was small (~45°). An example is shown in Fig. 10B; by the last 14 s of the dark period, the peak of the tuning curve had drifted ~45° (this drift also was verified by the experimenter in the equipment room listening to the cell “on-line”). When the lights were turned back on, the cell reverted to its original orientation. A small drift did not guarantee that the cell would revert back to its original direction, however, for in 12 of the 37 cases where the cells maintained new directions when the lights were turned on, the amount of drift was 45° (Fig. 10C). On only one occasion did a cell reset back to its original direction after drifting >45°.

PASSIVE ROTATION. It is possible that the visual landmarks lacked strong control in the active foraging task because local cues on the platform reinforced the rats’ perception that its path integration was intact and that the distal visual landmarks were unstable. Moreover, the weight placed by the system on idiothetic cues may be stronger when the rat is actively moving as there are more potential sources of idiothetic information available (i.e., proprioceptive feedback, motor efference copy, attentional cues, etc.). To address this question, the same rats sat on a narrow pedestal in the middle of the cue-rich room and were rotated passively to measure the tuning curves of head direction cells. The type of rotation (constant unidirectional vs. irregular bidirectional) had a strong influence on the ability of cells to maintain directional tuning in the dark, but it had little effect on the strength of the visual-landmark control over the cells once the light was turned back on. The responses of the cells to the offset or onset of the lights were subjectively described based both on the experimenter’s judgment while listening to the cell’s firing during the experiment and on subsequent evaluation of the tuning curves, as one of these five response types: 1) the cell maintained a stable firing direction relative to the visual landmarks; 2) the cell adopted a new, stable firing direction; 3) the cell maintained a sharp tuning curve, but the preferred direction of this curve drifted dynamically with respect to the landmarks; 4) the directional tuning became weak as the cell maintained a preferred direction but also fired nonspecifically at other directions; or 5) the cell’s firing became erratic with apparently random bursts that had no clear or stable relationship to head direction.

CELL BEHAVIOR IN DARK. In the initial light-on period, the head direction cells maintained their firing direction during constant unidirectional rotation; however, as soon as the lights were extinguished, the cell’s preferred direction began to drift, immediately and swiftly (8 sessions) or the cell became very erratic, firing with no directional specificity (2 sessions) in 10 of 10 tests in three rats (Fig. 11).

One possible reason for the immediate drift in the dark was that the vestibular apparatus had adapted to the constant...
unidirectional rotation by the time the lights were turned off. It is possible that the cells would maintain their tuning in the dark if the rats were given vestibular input that varied in intensity and direction, as occurs during natural movement. To test this, the rats were rotated irregularly, mixing clockwise and counterclockwise rotations and varying the angular extent of each rotation from ~45° to ~180°. Under these conditions, the head direction cells maintained their tuning in the dark for much longer periods of time than under the constant rotation conditions (Fig. 12). In 11 of 15 tests on three rats, the head direction cell maintained its tuning within 90° for 10 s up to 3 min before drifting >90°. During the long periods of stability, though, the cell’s preferred firing direction would usually show variability ±45°, drifting back and forth by small amounts, before finally drifting 90° away from the original preferred direction. Thus it appears that under constant, unidirectional passive rotation, the head direction cells may not receive accurate angular velocity signals from the vestibular apparatus, and they consequently accumulate error quickly. This error can be attenuated, however, if the rotations are made short and discontinuous, balancing clockwise and counterclockwise rotations, such as occurs during natural movement.

**VISUAL LANDMARK CONTROL.** When the preferred firing direction of head direction cells drifted >45° during passive rotation of the animal in the dark, the cells generally failed to reset to their originally preferred directions when the lights were turned back on. The lack of visual landmark control was related to the type of rotation (constant unidirectional versus irregular bidirectional) experienced by the animal, although under neither condition did the visual landmarks show strong control over the cells. Under irregular bidirectional rotation, the cells’ preferred firing direction returned to the originally preferred direction in 5 of 16 cases when the lights were turned on; in the other 11 cases, the cells maintained the new direction to which they had drifted immediately before the lights were turned back on. Under constant unidirectional rotation, the cell’s preferred firing direction returned to the original preferred direction in 4 of 10 cases; in 4 other cases, the cell’s firing returned to the originally preferred direction, but the cell’s tuning was weak or eventually became erratic; and in 2 cases, the cells’ firing was totally erratic in the light (as in Fig. 11B, right).

The differences in visual landmark control between the irregular bidirectional and constant unidirectional rotation seem to be related to the behavior of the cells during the dark period. During irregular bidirectional rotation in the dark, the cells typically (11/16 cases) maintained their preferred tuning for a number of rotations (sometimes for >1 min) before drifting to a new direction; in these cases, the cells always maintained the new direction when the lights were turned on. On the five occasions when the cells’ firing became erratic in the dark, however, the cells returned to the original firing direction when the lights were turned on. During constant unidirectional rotation, the cells would become erratic in the dark or begin to drift immediately and swiftly; when the lights were turned on, the cells either reset to the original direction or, more commonly, reset only weakly or erratically. It appears that in darkness, during passive rotation, the ATN head direction cells can either maintain a sharp directional tuning that rotates with respect to the external world, or the cells can become erratic and virtually nondirectional. In the former case, when the lights are turned on, the visual landmarks have little control over the cells in that usually the cells will maintain their new firing direction. In the latter case, however, the cells gener-
SUMMARY OF LIGHT/DARK EXPERIMENTS. Figure 13 shows a summary of all dark-drift experiments, combining both the active foraging task and the passive rotations. In about half of the trials in which the drift of the preferred firing direction in the dark was $\pm 45^\circ$, the cells returned to their initially preferred directions when the lights were turned back on. When the drift was larger, however, the cells rarely reset. Overall, this analysis complements the results of the apparatus rotation experiments in that the visual landmarks could correct for small drifts of the place cells and head direction cells ($45^\circ$) but had a much weaker ability to correct for large drifts ($50^\circ - 180^\circ$).

Further insight into the properties of visual landmark control is gained by analyzing the small ($45^\circ$) drifts from the light/dark experiments. When the animal first entered the experiment room from the equipment room, the initial bearing of the head direction cell in the experiment room was the same ($\pm 45^\circ$) as its bearing in the equipment room in 30 of 42 cases. When the head direction cell drifted away from the session’s initial direction ($\text{direction } A$) by $\pm 45^\circ$ in the dark, the cell returned to $\text{direction } A$ in 10 of 13 cases. This was true regardless of whether this was the first light/dark/light sequence of the session or whether it was a later sequence. When the cells drifted $\pm 45^\circ$ from a different direction ($\text{direction } B$), however, the cells reset to $\text{direction } B$ in only 4 of 17 cases when the lights were turned back on; this difference was highly significant ($\chi^2 = 8.44, P < 0.005$). In the other 13 cases, the cells either adopted the new direction to which the cell had drifted immediately before the lights were turned back on ($\text{direction } C$), or they adopted an arbitrary new direction. Thus there appears to have been a single bearing ($\text{direction } A$) at which the visual cues had control over the head direction cells and reset small drifts from that bearing.

CUE CONTROL IN THE EQUIPMENT ROOM. Although the cells often behaved erratically in the experiment room and changed direction frequently, they were much more consistent in the equipment room before and after the experiments. Thus regardless of the preferred direction of the cell in the experiment room after the various manipulations were performed, the cell returned to its initial bearing in the equipment room 42 of 49 times. Thus in this highly familiar and sensory-rich environment, where the rat had not experienced any experimental manipulations, the visual and other external landmarks had strong control over the head direction cells and could reset strongly the tuning curves back to their original directions.

Place field drift experiment

The tuning curves of head direction cells sometimes rotate spontaneously within a recording session (Knierim et al. 1995). When this occurs, the cell typically starts firing at a direction different from its normal preferred direction relative to the visual landmarks, and then it rotates to the preferred direction. Place cells also can rotate their place fields spontaneously within a recording session, but it is more difficult to analyze these rotations because of the lower firing rates of place cells and the sometimes inadequate sampling
by the rat of an environment during the time course (seconds to minutes) of field rotation. These problems can be alleviated by the simultaneous recording of many place cells. In one rat (which had previously undergone a restricted lesion of the dorsal dentate gyrus of the opposite hemisphere with colchicine for purposes of another experiment), place cells were recorded from five of six tetrodes located in CA3 of the control hemisphere contralateral to the lesion. (See DISCUSSION for comments on the potential effects of the lesion on the interpretation of these results.)

Similar to the effects on head direction cells reported in a previous experiment (Knierim et al. 1995), the hippocampal place field map rotated as a whole by $\pm 45^\circ$ in 12 of 28 recording sessions in this rat. Because multiple sessions were recorded each day, in most days a single orientation of the place cell map relative to the cue card was identified as the most common; this was called the ‘correct’ bearing for that day. In at least seven of these sessions, the map started out at a wrong bearing relative to the cue card and rotated to the correct bearing. In some sessions, the usual white card was replaced by a black card. When the black card was in the standard (east) position (2 sessions), the place cells behaved normally and were bound to the black card; however, when the black card was rotated to the north between sessions (2 sessions), it had absolutely no influence over the cells’ firing, and the place fields drifted as if the rat were running in the dark with no external cues to keep the system calibrated. Figure 14A shows the spatial firing patterns of 8 of the 16 complex-spike cells recorded in one of the two sessions. Most cells fired in what appeared to be ring-shaped fields centered on the apparatus center and at varying distances from the center. When the session is broken down into 3-min intervals, one sees that the cells actually had normal place fields but that the fields rotated counterclockwise 1.5–2 full revolutions throughout the session (Fig. 14B). Figure 14C plots, for each spike fired by each cell, the polar angle of the rat’s current position in the cylinder as a function of time elapsed in the session. The hippocampal map rotated smoothly and continuously throughout the course of the session, with each place field maintaining a stable relationship to the other place fields.

DISCUSSION

Apparatus rotation experiments

The results of these experiments begin to quantify the interaction between visual landmarks and idiothetic cues in controlling head direction cells and the hippocampal ensemble map. When the rats and the apparatus were abruptly rotated $45^\circ$, thus producing a small mismatch between the directional information provided by external visual landmarks and that provided by vestibular and other idiothetic cues, the visual landmarks predominated, as the hippocampal map and the head direction cells rotated $45^\circ$ to follow the rotation of the cylinder. When the rotation was large, however, the behavior was less predictable. In some cases, the hippocampal map and the head direction cells rotated by $180^\circ$, indicating strong visual landmark control. In other cases, the head direction cells failed to follow the landmark, and the hippocampus remapped the environment. In these sessions, the mismatch between the visual landmark and the vestibular information provided during the rotation was presumably too large for the landmark to correct the error. The cells were controlled completely by the landmark during the subsequent slow, continuous rotation ($180^\circ$ during the course of 5–8 min). Mittels taedt and Mittelstaedt (1980) reported that gerbils performing...
FIG. 14. Coherent rotation of the hippocampal map in a circular environment. A: 1st column shows the firing rate maps of 8 place cells recorded from CA3 while the rat foraged in a gray cylinder with a black cue card in the north position. The rate maps indicate that these cells had little spatial selectivity over the course of the entire recording session. The other 8 cells recorded fired <100 spikes in the session and were excluded from the analysis. B: breaking the session into consecutive 3-min intervals, however, revealed that each cell had a normal, spatially selective place field that rotated counterclockwise during the course of the recording session. Examination of each place cell showed that the whole hippocampal map rotated in synchrony. C: for each spike fired by each cell, the polar angle of the rat’s current position in the cylinder (with the center of the cylinder as the origin) was plotted as a function of time in the session. All of the cells rotated smoothly and continuously during the course of the session, completing almost 2 full rotations (720°).

A homing task on a rotatable platform did not compensate for smooth angular accelerations of 0.24°/s². Although the exact rate of acceleration was not measured or controlled in the present study, on average the rate of slow rotation was ~0.5°/s. Attempts were made to make the rotation as smooth and continuous as possible to give minimal vestibular stimulation to the rat. It is presumed then that the majority of the slow rotation was below the vestibular threshold of the rat. Even if the rat experienced some vestibular stimulation from the slow rotation, the cells were nevertheless still controlled by the cue card. Thus it is unlikely that the animals were using some external sensory cue in the laboratory (e.g., a localized auditory cue) to orient their spatial maps when the cue card lost control after fast rotations; if this were so, one would predict that this putative cue also would control the cells during the slow rotation. Instead, it is more likely that the vestibular input updated the firing properties of these cells. The similarity of the results in these first two experiments present study, on average the rate of slow rotation was ~0.5°/s. Attempts were made to make the rotation as smooth and continuous as possible to give minimal vestibular stimulation to the rat. It is presumed then that the majority of the slow rotation was below the vestibular threshold of the rat. Even if the rat experienced some vestibular stimulation from the slow rotation, the cells were nevertheless still controlled by the cue card. Thus it is unlikely that the animals were using some external sensory cue in the laboratory (e.g., a localized auditory cue) to orient their spatial maps when the cue card lost control after fast rotations; if this were so, one would predict that this putative cue also would control the cells during the slow rotation. Instead, it is more likely that the vestibular input updated the firing properties of these cells. The similarity of the results in these first two experiments (Fig. 3) suggests that hippocampal remapping may occur as a result of the cue card losing control over the head direction cells, although remapping is not a necessary consequence of this lost control (Bostock et al. 1991; Knierim et al. 1995; McNaughton et al. 1995). To answer definitively the question of whether the loss of visual landmark control over head direction cells causes hippocampal remapping, or vice-versa, requires the simultaneous recording of many place fields and a population analysis of the temporal order of the hippocampal remapping and head direction cell rotation.
INTERACTIONS BETWEEN IDIOTHETIC CUES AND LANDMARKS

DELAYED VISUAL LANDMARK CONTROL. The delayed visual landmark control demonstrated in Figs. 7 and 8 suggests strongly that idiothetic cues are the primary sources of information that update head direction cells, with a secondary, corrective influence of static, external sensory cues, such as visual landmarks. In these cases, the cells were controlled entirely by the idiothetic input immediately after the apparatus rotation. It was only after many seconds to minutes that the tuning curves of the cells began to drift until they realigned with the cue card. These data, together with the findings that vestibular apparatus lesions abolish head direction cell tuning (Stackman and Taube 1997), whereas head direction cells maintain tuning in complete darkness (Fig. 9) (see also Taube et al. 1990b), support strongly the primacy of idiothetic information in controlling head direction cells and, by virtue of their tight coupling, place cells.

It is unlikely that the slow drift of the head direction cells in this experiment reflects the dynamics of an active correction mechanism by the visual landmarks for the time course seems much too long. Instead the drift probably reflects the accumulation of error in the path integration system as the rat forages. Under normal conditions, when the head direction cells are in their stable, learned alignment with the cue card, the cue card can keep the system calibrated by continually correcting errors from the idiothetic cues. After the apparatus rotation, however, when the head direction cells initially are misaligned with the cue card, the cue card has no corrective influence over the head direction cells. Thus the system can begin to drift as idiothetic error accumulates. If there is a bias for the error to accumulate in one direction, then the head direction cells will rotate their tuning curves in that direction until they realign with the cue card. At this time, the cue card regains control over the cells (e.g., Fig. 8B).

Interestingly, there was no evidence of a delay in visual landmark control over place fields in this experiment. Although it is possible that this negative result was an artifact of inadequate location sampling by the rat in the minute immediately after the rotation, this is an unlikely explanation. In some rats, many place cells were recorded simultaneously, and thus at least some of the fields should have shown evidence of a delayed visual landmark control. It is possible, therefore, that place fields can reorient to the visual landmarks rapidly and independently of the dynamics of the head direction cells. Such decoupling has never been observed in a variety of other experiments, however, and one would need to record simultaneously from many place cells and a head direction cell in the same rat to test this possibility. Another possible explanation for the difference in reorientation latency lies in the details of the recording procedures; in the place cell recordings, the rat explored the cylinder for 10 min before the apparatus was rotated, whereas in the head direction cell recordings, the rat usually explored for only 2–3 min before apparatus rotation. Perhaps each time the rat enters an environment—even a familiar environment—there is an initial period in which the influence of the visual landmarks in that environment goes through a period of reinforcement (cf. Mehta et al. 1997; Wilson and McNaughton 1993). A large rotation performed before this reinforcement is complete may result in a delayed control by these landmarks in those situations when the landmarks control the cells, as the head direction cell system has to accumulate error to bring it within the range of visual landmark control. If enough time has elapsed before the rotation, though, perhaps the landmarks are able to assert strong control over the cells, resulting in immediate error-correction in those cases where they do control the cells.

BEHAVIORAL CONSIDERATIONS. It is conceivable that certain behavioral variables play a role in whether visual landmarks or idiothetic cues predominate in the control of place cells and head direction cells. For example, the specific navigational demands of a given behavioral task may tilt the balance in favor of one type of cue over another. Similarly, attentional variables associated with different tasks also may play a role. In pellet-chasing tasks such as the cylinder rotation experiments of the present study, different rats adopt different foraging strategies. Some rats move around the cylinder floor apparently at random; others adopt stereotyped trajectories that cover most or all of the apparatus floor in a fairly regular order; whereas other rats tend to orient to the sound of the pellets dropping and move toward them. It is thus conceivable that the visual cue card might have had stronger control in those sessions where the rat was using one type of strategy, whereas the idiothetic cues might have predominated in sessions where the rat used a different strategy. The present study was not designed to address this type of question, unfortunately, and the measurements taken were inadequate to perform a rigorous test of these hypotheses. The role of these behavioral variables is an interesting and important question that requires further study.

Light/dark experiments

The nearly complete lack of visual landmark control after most drifts of head direction cells in the light/dark experiments was surprising. The original hypothesis was that the landmarks would have stronger control in this experiment than in the apparatus rotation experiment because the visual environment was much richer and the rat had no reason to regard the landmarks as unstable in this experiment. Whereas the apparatus rotation might have made the rat perceive the cylinder as an unstable environment. These results resembled those of Chen et al. (1994a), however, in that the visual landmarks had little control over the cells and could only correct for small errors. It is possible that the rats had come to perceive the whole experiment room as visually unstable, as they had experienced it in many different visual configurations during the course of many weeks. Attempts to enhance the rats’ perception of the stability of the cues in the room, by training the rat in the room daily for a week before starting the experimental manipulations, apparently had no effect, as there was no difference in the strength of visual landmark control in these familiar environments compared with environments in which a novel configuration of visual cues was placed in the rooms (data not shown). A possible explanation of these results is that the synaptic plasticity, which presumably binds landmark information to the head direction system, has a large short-term component that normally stabilizes the system during the first few minutes of exploration. During darkness, this component might decay, which, in the absence of a strong long-term component, would prevent the system from resetting correctly when the
lights are turned back on. This possibility could be tested by varying the duration of the dark phase in such experiments.

The length of time in which the HD cells sometimes could maintain their tuning preferences in complete darkness (Fig. 9) was also surprising. It is doubtful that rats can use purely idiothetic information to keep their heading for so long under these conditions; instead, it is likely that in complete darkness, the rat became more attuned to local intramaze cues that kept it oriented, as has been observed in behavioral studies (Lavenex and Schenk 1995) and in studies of place fields in blindfolded rats (Hill and Best 1981).

It is an interesting observation that sometimes the head direction cells became erratic or even silent during the constant unidirectional rotation in the dark and that this erratic firing was sometimes preserved when the lights were turned back on (Fig. 11). This may be an indication that when the rat becomes hopelessly disoriented, the firing of head direction cells breaks down (or vice versa). An anecdotal observation, made when recording from a head direction cell while a rat explored an object in a completely novel environment with many external visual landmarks, supports this. During the exploration, the platform on which the rat was exploring was rotated slowly and constantly. The head direction cell initially maintained a sharply defined tuning curve, but its preferred direction drifted continuously as the rat’s attention was focused apparently on the object it was exploring rather than on the distal cues. Eventually, however, the cell ceased firing altogether. Although it has been shown that under conditions of tight restraint, head direction cells and place cells can become silent (Foster et al. 1989; Knierim et al. 1995; Taube et al. 1995a), these results demonstrate that head direction cells can become erratic or even silent under conditions where a normal animal was free to move. Unfortunately, multiple head direction cells were not recorded under these circumstances to ascertain whether all cells became erratic during these instances.

**Place field drift experiment**

The results of the place field drift experiment add further support to data reported in Knierim et al. (1995) that hippocampal place fields can be dissociated from external sensory landmarks but that their relationships remain tightly coupled to each other and to the head direction cell system. If place cells were bound independently to different landmarks in the environment, one would expect that, when the cells become decoupled from the only salient landmark, they should each react in different ways. Instead, the system maintains its internal spatial relationships as the spatial map drifts with respect to the external world. Thus place cell selectivity is most likely affected primarily by the firing of other place cells and by information about head direction and linear motion, and only secondarily by the influence of external landmarks, the role of which is to keep the internally coherent spatial map oriented properly.

A comment is in order about the possible contribution to this effect from the local lesion of the dorsal dentate gyrus in the contralateral hemisphere of this animal. Although the possibility cannot be ruled out that this lesion was a significant factor in the complete lack of control by the black cue card when it was rotated to the north position, the conclusion about the tight coupling of place fields to each other still holds true. It is unlikely that any lesion could produce artifactualy the kind of network architecture or dynamics that would lead to the coherent rotation of the hippocampal map seen in this experiment, although it is quite conceivable that the strength of this coherence may have been affected by the lesion. Thus regardless of whether it was the lesion or some other factor that caused the cells to decouple from the cue card, the data demonstrate an underlying neuronal circuitry that allowed the place fields to remain tightly coupled to each other even as they showed absolutely no coupling to any distal or local external landmark.

**Relevance to previous cue-conflict studies**

Although it was recognized early on by O’Keefe (1976) that self-motion information might influence the firing properties of place cells, until recently most investigators have concentrated on the influence of external landmarks, primarily visual landmarks, in controlling place cells and head direction cells. In addition to the intuitive appeal that one’s sense of location and direction is governed by the landmarks that are visible at a given location, single-unit recordings demonstrated that the tuning profiles of both place cells and head direction cells could be controlled by the salient visual cues in that rotation of these cues caused an equal rotation of the tuning profiles (Bostock et al. 1991; Muller and Kubie 1987; O’Keefe and Conway 1978; Taube et al. 1990b). Much of the data, however, do not fit into a strict “local view” interpretation of these cells. For example, both types of cells continue to fire selectively in the dark, provided that the rat had its bearings before the lights were extinguished (Chen et al. 1994a; Hill and Best 1981; Markus et al. 1994; McNaughton et al. 1989a; Mizumori and Williams 1993; Quirk et al. 1990; Taube et al. 1990b). In addition, under certain circumstances, the cells failed to be controlled by visual landmarks (Chen et al. 1994a; Jung and McNaughton 1993; Knierim et al. 1995) or were controlled only partially (Taube et al. 1990b).

A number of more recent studies have addressed the issue of the influence of self-motion cues on the firing of place cells and head direction cells. Like the present study, these studies have given the rat explicitly conflicting directional information from idiothetic cues and visual landmarks and have tested which type of cues control the cells. The results from these studies have been inconsistent, however. Chen et al. (1994a) rotated the salient visual cues in a room while the rat was sitting passively in the room but with the lights out. When the lights were turned back on, the rat experienced a conflict situation: the visual landmarks were in a new orientation, but the rat had experienced no corresponding self-motion information. Most posterior cortical head direction cells in this experiment did not rotate their firing preferences to follow the rotated cues but instead remained bound to the rat’s inertial reference framework or changed their firing preferences in unpredictable ways. This result stands in contrast with that of Mizumori and Williams (1993), who reported that when LDN head direction cells drifted in the dark as the rat ran an eight-arm maze task, the cells reverted back to their originally preferred directions when the lights were turned back on, even when the amount of drift was
90°. The reasons for this difference are not known. It is possible that LDN cells differ from ATN cells in their sensitivity to visual landmarks. In addition, differences in the experimental task (8-arm maze vs. passive sitting) also may account for the discrepant results. At this time, there is no way of distinguishing among these (and other) possibilities, and further experiments are required to address these interesting questions.

Similar to the apparatus rotation experiments in the present study, a number of investigators have performed variations on the theme of rotating the rat and/or the visual cues in a high-walled enclosure. Wiener and colleagues (Wiener 1993; Wiener et al. 1995) rotated the rat and the enclosure in darkness but kept the salient visual landmark in the same position relative to external world coordinates. Under these conditions, both hippocampal place cells and striatal directional cells tended to follow the rotation of the apparatus and ignore the salient visual landmark. In contrast, studies by Taube and colleagues (Goodridge and Taube 1995; Taube et al. 1990b) found a predominant influence of visual landmarks over head direction cells when they were put in conflict with idiothetic cues. Sharp and colleagues (Blair and Sharp 1996; Sharp et al. 1995) performed experiments in which they independently rotated either the floor of the apparatus (with the rat) or the walls or both together. Unlike the present experiments, the rotations performed by Sharp et al. took place in a cylinder that was visually symmetric (alternating black and white stripes). They found that when both visual landmark and vestibular information about rotation were consistent with each other, the behavior of place cells (Sharp et al. 1995) and ATN head direction cells (Blair and Sharp 1996) were also consistent and controlled reliably by these cues; however, when the cues were in conflict, the behavior of the cells was variable. Sometimes they followed the visual landmarks, sometimes they followed the vestibular cues, and sometimes the place cells changed their spatial firing patterns altogether. In contrast to the present study, where such remapping could occur after the first cylinder rotation, the remapping reported by Sharp et al. (1995) occurred only after the rat had experienced many cylinder manipulations over many days. This difference may be due to the lack of a polarizing visual landmark in their experiments or to the amount of experience the rats had in the recording chambers before the rotations. In the present study, because the training and recording environments were different, the rats had only one 15-min training session in the cylinder in the recording room before the onset of recordings. The rats in the Sharp et al. studies, however, had many training experiences in the recording chamber. It is conceivable, then, that as in the case reported by McNaughton et al. (1995), the hippocampal representation of the cylinder in the Sharp et al. studies was somehow more robust than that of the present study, and therefore it took more rotation experiences to cause the hippocampus to switch from its stable representation of the cylinder to a new representation.

Like the results of Chen et al. (1994a), the visual landmarks in the present study had little control over place cells and head direction cells when the directional information from these cues was in conflict with idiothetic cues. It appears that the strength of visual landmark control depends on the degree of mismatch between the two classes of information. Thus in the apparatus rotation experiments, head direction cells and place cells followed the rotation of the cue card if the rotation was small (45°); if the rotation was large (135°–180°), however, the cells followed the cue card in a minority of cases. Similar results have been reported by Rotenberg and Muller (1997), who recorded place cells before and after moving the cue card alone (but not the cylinder or the rat) in the presence of the rat and found that place fields rotated with the cue card after 45° rotations of the card but did not follow 180° rotations (see also Sharp et al. 1995). Similarly, in the light/dark experiments, when the tuning curves of head direction cells drifted in the dark, the cells usually did not revert back to their originally preferred directions unless the amount of drift was small.

Thus the literature on the relative strengths of idiothetic cues and visual landmarks on the firing of place cells and head direction cells yields no consistent picture. Some studies find a predominant role of landmarks, others of idiothetic cues. Indeed, a case illustrated by Chen et al. (1994a) suggests that cognitive factors such as expectation that a cue rotation will be carried out may be capable of reorienting the head direction system. Possible explanations for the different results may include strain or sex differences in experimental subjects; different experimental tasks; differences in the properties of head direction cells recorded from different brain areas; or experience-dependent changes in the relative strength of visual landmark control over these cells. It is this latter possibility that is addressed below.

Theoretical considerations

McNaughton and colleagues have developed a model of place cell and head direction cell firing (McNaughton et al. 1991, 1995, 1996; Samsonovich and McNaughton 1997; Skaggs et al. 1995) that proposes that the tuning of these cells primarily reflects the integration of self-motion cues, with a learned influence of visual landmarks developed during exploration of a new environment (see also Blair 1996; Redish and Touretzky 1997; Redish et al. 1996; Touretzky and Redish 1996; Zhang 1996).

In the case of HD cells, the model proposes that the connections among these cells have a ring-like topology, with strong local excitatory interactions among cells with similar preferred directions and weak connections otherwise. When the rat is motionless and facing any arbitrary direction, a group of HD cells will be tonically active as a result of attractor dynamics specified by the local excitatory connections. As the rat’s head rotates, neurons receiving vestibular input detect this head motion and, through one intermediate computational stage, project excitation asymmetrically to the HD cell ring, thus causing a shift in the focus of activity on the ring. According to this scheme, as long as there is no error, the focus of activity on the ring reflects relative head direction. The inevitable error in such a system, however, causes the observed slow drift under some circumstances. It was suggested that learned associations between the activities of cells in the HD ring and visual landmarks could eliminate this drift. In a completely novel environment, these associations are presumably not present, and the system is controlled entirely by idiothetic information. If there is a consistent mapping between the visual input and the head
direction cells, the associations gradually will strengthen until eventually, in a well-explored environment, the visual landmarks can override the idiothetic cues when the system drifts out of calibration.

One prediction of this model is that if there is no consistent mapping between the visual landmarks in an environment and the HD cells, then the landmarks would have less than normal control over place cells and head direction cells. This prediction was confirmed in an experiment in which rats were disoriented intentionally before each entry into an environment to disrupt their internal direction sense. Under these conditions, the visual landmark exerted much weaker control over simultaneously recorded place cells and head direction cells than in rats that had not been disoriented (Knierrim et al. 1995; but see Dudchenko et al. 1997). Importantly, place cells and head direction cells always were coupled strongly to each other: wherever place cells rotated their place fields away from the visual landmark, head direction cells rotated their tuning curves by the same amount.

The essence of the model is that once strong associations between external landmarks and HD cells have been formed, the attractor dynamics inherent in the local connections will cause the system to behave in an all-or-none fashion when confronted by a mismatch. As pointed out by Zhang (1996), the dynamics of the correction process will depend strongly on the degree of mismatch relative to the width of the tuning function of the HD cells. For small mismatches, the correction will be smooth and continuous (i.e., the tuning curves will appear to rotate) because the external input overlaps the internal input (from the other HD cells). For large mismatches, in which the external and internal input distributions do not overlap, the tuning curves will either jump, if the external connections are sufficiently strong, or not move at all if they are relatively weak. In the case of weak but nonzero external associations, a delayed mismatch correction will occur when, as a result of spontaneous drift, the internal and external input distributions begin to overlap. At this point, the system will “lock-on” to the external inputs.

Implicit in the model is the idea that the control of head direction cells by visual landmarks is a dynamic process, the strength and time course of which can be changed profoundly by experience. Thus one can imagine an arbitrary number of possible “energy landscapes” (Hopfield 1982), resulting from different experimental conditions and training procedures. The disorientation protocol of Knierrim et al. (1995) might result in an energy landscape with multiple local energy wells of different depths, each corresponding to a different learned relationship of the head direction system and the visual landmarks. Experimental manipulations, such as the rotations performed in this experiment, may also rapidly change the landscape as the system experiences new configurations of the visual landmarks relative to the head direction cells. Similarly, the strength of visual landmark control may depend strongly on the type of visual cues available in the environment. Etienne and colleagues (1990, 1995a,b) have shown in behavioral experiments that the strength of visual landmark control over a hamster’s homing behavior depends strongly on the type of visual cues available and that this dependence is not straightforward. Effective visual cues might generate a landscape with a deep energy well, whereas less effective stimuli, under identical behavioral conditions, might generate a more shallow energy well. Thus it is possible that the lack of visual landmark control demonstrated in the present study may be due to the use of inadequate visual landmarks.

Why do place fields sometimes rearrange radically when the induced mismatch is large? According to the model proposed by Samsonovich and McNaughton (1997), the synaptic matrix of the hippocampus contains a set of continuous attractors that are two-dimensional analogues of the ring model proposed for the HD system. A “chart” was defined as a two-dimensional configuration of place cells in which nearest neighbors (on the chart, not anatomically) have a statistically higher probability of being strongly connected than nonneighbors. It was shown by numerical simulation that it is possible to encode many such charts in the same synaptic matrix. The local connectivity on a chart then specifies the relative relationships among place fields in the environment, and a radical rearrangement of place fields (remapping) is thought of as reflecting a state transition from one dynamic configuration to another (i.e., a chart transition). In this model, a focus of activity (an “activity packet”) moves around on a chart in a manner that is isomorphic to the rat’s motion in the environment. This isomorphism is a consequence of incoming information on the state of the HD system and on the animal’s state of motion, and it is accomplished by a two-dimensional analogue of the intermediate layer in the HD system, which has asymmetric connections into the place cell layer and causes the activity to spread in a direction corresponding to the current head direction. The same associative process as in the HD system model was postulated to permit information about familiar landmarks to correct for drift error. A single-chart variation of this scheme was proposed independently by Zhang (1996). According to the Samsonovich and McNaughton (1997) model, if the visual landmarks in a familiar environment have developed strong control over the HD system, then rotations of the apparatus would cause both the HD system and the place cell system to rotate their firing preferences correspondingly. If the landmarks have weak control over the HD system, however, the subsequent failure of the HD system to follow the external cues after the rotation of the recording apparatus could have two possible outcomes. If the visual landmarks have weak control over the place cells as well, the place field map should simply remain constant and aligned with the inertial reference frame as has been reported previously (McNaughton et al. 1995). If the landmarks have strong control over the place cells, however, the landmark and head direction signals would be in constant conflict. With each step, the idiothetic signals would push the activity packet in one direction, whereas the familiar external inputs would push it in the other. This destabilization of the activity packet would lower the barrier to a spontaneous chart transition. The conflict would be resolved by the transition.

Redish and Touretzky (1997) propose a somewhat different architecture for the updating of place representations by idiothetic information. Their model uses the same idea of a two-dimensional chart that is updated by HD and self-motion signals according to the foregoing scheme, but the chart is an input to the hippocampus and not part of the hippocampus itself. The map rearrangement is postulated to be a consequence of an orthogonalization operation performed in the dentate gyrus (Marr 1971; McNaughton and Morris 1987; Treves and Rolls 1992). According to this view, inversion of the relationship...
between the visual cues and the chart coordinates would lead naturally to radical changes in the map without having to invoke any prior learning. Of course this model would appear to have difficulties explaining the previously reported failure to observe map rearrangements in cases where the HD system failed to reorient to the visual cues after environmental rotations (McNaughton et al. 1995) or disorientation of the rat (Jung and McNaughton 1993; Knierim et al. 1995). The Samsonovich and McNaughton (1997) model predicts that the probability of remapping is an experience-dependent, complex function of differential visual landmark control over place cells and head direction cells; the Redish and Touretzky (1997) model does not predict such experience dependence, and so such an outcome might provide a means of distinguishing between the two possibilities.

Concluding remarks

An enormous amount of experimental data on the firing properties of neurons in the hippocampus and related structures has been reported in recent years. These data demonstrate the complexity of the interaction between the idiothetic cues and external landmark inputs into the system. Concomitant with this explosion of experimental data has been the development of increasingly sophisticated models of the neuronal architecture that might underlie hippocampal function and spatial navigation. Many predictions of these models are now directly testable with the use of parallel recording techniques that allow the simultaneous recording of dozens of isolated single units. This combination of theoretical modeling with sophisticated experimental design and technologies holds promise for the eventual elucidation of the mechanisms by which the hippocampus creates a representation of the environment and how animals use this representation to navigate efficiently.

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