

RESEARCH NOTE

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The effects of disorientation on visual landmark control of head direction cell orientation

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Abstract Head direction (HD) and place cells were recorded in rats that had previously exhibited significant acquisition deficits on a radial arm maze task following disorientation treatment. In this study we determined whether this behavioral impairment was associated with a lack of landmark stimulus control over the preferred orientations of HD and place cells. Neurons were recorded as animals retrieved food pellets in a cylindrical apparatus containing a single cue card. Some of these HD cells were also recorded while animals explored an eight-arm radial maze in a similar cue-controlled environment. The stimulus control of the landmarks in each environment was assessed by rotating the landmark and examining the subsequent preferred orientations of HD and place cells. Animals underwent disorientation treatment before and after each recording session. Despite this disorientation, rotation of the cue card in the cylindrical apparatus resulted in a corresponding shift in the preferred orientations of HD and place cells in 13 of 15 and 7 of 7 recording sessions, respectively. On the radial arm maze, rotation of the landmark cue was associated with a corresponding shift in the HD cell's preferred orientation in 7 of 9 sessions. These results suggest that a visual landmark's stimulus control may *not* require a learned association between that landmark and an animal's stable experience in an environment. Furthermore, instability in the HD cell system is unlikely to account for the impaired performance of the disoriented animals in the radial arm maze. Rather, these impairments may be due to the animal's inability to utilize stable representations of the environment provided by HD and place cells.

Key words Head direction cells · Navigation · Landmarks · Place cells · Spatial · Orientation

Introduction

Previous studies have shown that the place fields of hippocampal place cells and the preferred firing direction of head direction (HD) cells can be controlled by salient visual cues in an environment (O'Keefe and Conway 1978; O'Keefe and Speakman 1987; Muller and Kubie 1987; Taube et al. 1990b; Goodridge and Taube 1995; Taube 1995). Interestingly, however, individual visual cues do not appear necessary for the directional firing of HD cells, as the cells appear to be able to maintain a preferred orientation following the removal of salient visual cues (Taube et al. 1990b; Goodridge and Taube 1995), in darkness for a short time following illuminated exposure to an environment (Mizumori et al. 1993), following blindfolding (Goodridge Dudchenko; Worboys and Taube 1995; in preparation), or when the animal enters an unfamiliar environment (Taube and Burton 1995). Thus, a number of recent studies have suggested that place and HD cells may also be influenced by vestibular, proprioceptive, or motor efference copy cues, in addition to visual cues (McNaughton et al. 1991; Knierim et al. 1995; Sharp et al. 1995; Stackman and Taube (in press); Taube and Burton 1995; Wiener et al. 1995; Blair and Sharp 1996; Taube et al. 1996).

What is the relationship between these internal sources of information and external landmarks with respect to the orientation of spatial cells? McNaughton and colleagues (1995, 1996) (Knierim et al. 1995) have hypothesized that landmarks come to control the orientation of HD and place cells through their association with stable internal sources of orientation. Thus, a stable perceptual experience with a landmark is necessary for it to serve as a means of correcting the "accumulating error" which is inherent in any internal, self-generated system for maintaining orientation. One implication of this view is that, if an animal is consistently disoriented before being

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placed in an environment, it would be unable to form a stable association between landmarks in the environment and its own internal "sense" of orientation. Animals may thus have a predisposition towards perceiving the landmarks in an environment as unreliable indicators of their location and directional heading.

Knierim et al. (1995) have recently provided data which support this view. They recorded HD and place cells from freely-moving animals in a cylindrical apparatus containing a single salient landmark (a white cue card) and separated from other room cues by a surrounding black curtain. Two groups of animals were monitored: one group was repeatedly disoriented before placement in the environment, while a second group was brought into the testing room without disorientation and with full view of the environment outside the curtained enclosure. The authors reported that the animals which were disoriented exhibited a significantly greater number of instances in which the orientation of the HD or place cell shifted by $> 45^\circ$ ("transitions") relative to the cell's previous orientation with respect to the cue card. Thus, the stimulus control exerted by the cue card over HD and place cell spatial orientation was significantly diminished for the disoriented group relative to the non-disoriented group.

If the HD/place cell systems and an animal's spatial behavior with respect to a given landmark are correlated, the results of Knierim et al. (1995) imply that a given landmark should be unable to exert reliable stimulus control over the spatial behavior of an animal when an animal is consistently disoriented before being exposed to the landmark. Recent evidence from our laboratory suggests that there is a general correlation between the response of HD cells and an animal's spatial behavior. Specifically, we have shown that on a reference memory radial arm maze task in non-disoriented animals, the same landmark cue that exerted control over the animals' spatial behavior typically exerted control over the orientation of recorded HD cells (Dudchenko and Taube 1997).

We tested the hypothesis that disoriented animals should have difficulty learning to follow a stable landmark cue by training animals in a reference memory radial arm maze task, where a specific maze arm – relative to a large white cue curtain – was consistently reinforced (Dudchenko et al. 1997). We found that none of the eight animals which were placed in an opaque container and disoriented before every trial (via gentle spinning back-and-forth by the experimenter) exhibited any sign of task acquisition over 45 days of training. In contrast, the majority (7/8) of animals that were brought into the training room in a clear container and were *not* disoriented acquired the task within the same time period. Interestingly, in a third group of animals that were not explicitly disoriented but simply placed in an opaque container before each trial, the majority (6/8) did not acquire the task readily. We hypothesized that the mere lack of access to the visual cues in the testing room (for the "opaque" group) may itself contribute to an animal's impaired sense of orientation. However, further testing on a Morris water maze revealed no differences between groups in task acquisition. Thus, the effects of disorientation may

not be attributed solely to the rotation of the animal and do not appear to generalize across spatial tasks. However, at least for the radial arm maze task, disorientation (or placement in an opaque container) did indeed appear to interfere with the animal's ability to form an association between a salient visual cue and a given goal location. This surprising lack of acquisition following disorientation has also been reported with rats on a plus-maze (Martin et al. 1997) and is consistent with spatial deficits following disorientation reported in rats (Cheng 1986; Margules and Gallistel 1988) and small children (Hermer and Spelke 1994).

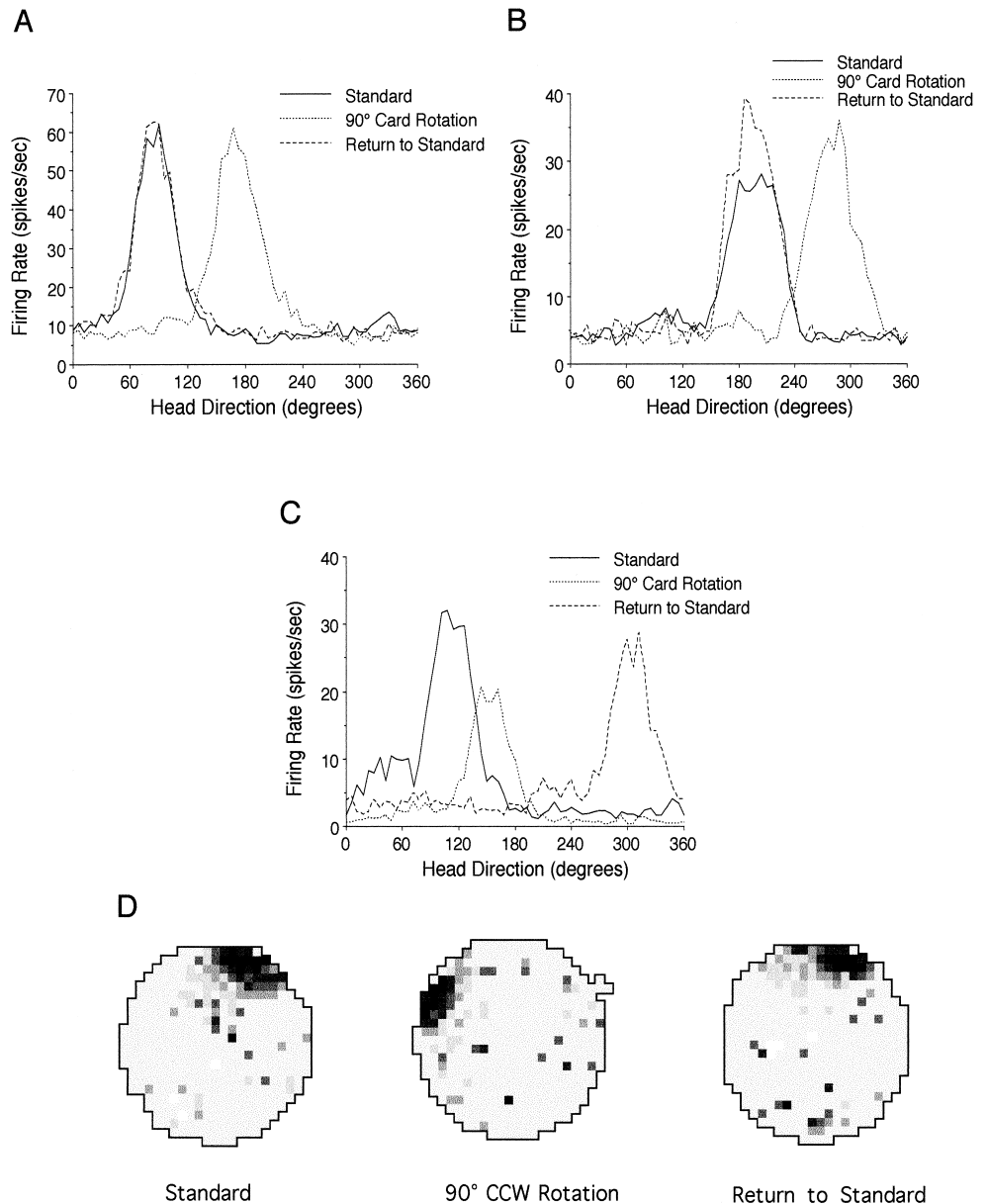
In the current study, we determined whether HD or place cells in the *same radial arm maze-impaired* animals would respond less reliably to a rotation of a salient visual landmark. Cells from these animals were monitored in a gray cylindrical "screening" apparatus and in the radial arm maze environment used in the previous behavioral training.

Materials and methods

Four animals that exhibited no signs of task acquisition during the 45 days of training on the radial arm maze (three animals were from the disorientation condition; one animal was from the opaque non-disoriented condition) were implanted with moveable 10-wire, nichrome electrodes in either the anterior thalamic nucleus ($n = 3$ animals; A-P: -1.4 ; M-L: $+1.3$; D-V: -3.6 from dura) or the CA1 hippocampus ($n = 1$ animal; A-P: -3.8 ; M-L: $+2.7$; D-V: -1.8). Animals were monitored for spatial cells in a gray cylindrical apparatus containing a white cue card attached to the wall and occupying approximately 100° of arc. During each session, animals retrieved food pellets scattered randomly on the floor. Prior to and following each screening session, animals were placed in an opaque cardboard box and rotated gently back-and-forth as the experimenter walked around the room, in an attempt to produce disorientation. These disorientation procedures are comparable to ones used by Knierim et al. (1995), who likewise placed their animals in an opaque Styrofoam box and then rotated the box gently while walking up and down a hallway.

Upon identification of an HD or place cell, stimulus control of the cue card in the cylindrical apparatus was assessed by recording 8-min sessions with: (1) the white cue card in the standard position (0°), (2) the cue card in a 90° counter-clockwise (CCW) rotated position, and (3) the cue card returned clockwise (CW) to its standard position (0°) (for additional recording details see Taube 1990a). Before and after each individual session, the animal was placed in the opaque container and disoriented (as described above), and the floor paper beneath the cylinder was replaced. For HD cells whose waveforms were judged by the experimenter to be well isolated from background electrical noise, additional recording sessions were subsequently conducted with the animal on the eight-arm radial maze. The configuration of the maze and the white cue curtain within the curtained enclosure were essentially identical to the situation in which the animals had previously been trained, and the animals were disoriented immediately before and after each maze session. However, for sessions recorded on the radial arm maze, all maze arms were baited with three 20-mg Noyes food pellets, and the animals were permitted to explore the entire apparatus for 8 min. Following a recording session with the white curtain in a standard position (0°), the animal was removed from the maze and disoriented by the experimenter. The white curtain was then rotated 90° CCW, the maze rotated 90° CW, and the maze arms rebaited if necessary. The animal was returned to the center of the maze and a second 8-min recording session was conducted. In between each recording session, the animal was removed from the maze and underwent disorientation treatment.

Fig. 1A–D Ninety-degree rotations of the cue card in the cylinder. **A, B** Rotation of the cue card led to a corresponding shift of the head direction (HD) cell's preferred firing direction. **C** One of the two instances in which the cue card did not exhibit complete control over the cell's preferred firing orientation. **D** Place cell firing rate is shown by successively darker shades of gray such that the lightest gray represents no firing, and successive shades represent maximum firing rate boundaries of 0.57, 1.4, 3.14, 6.67, and 14.47 spikes/s. Rotation of the cue card resulted in a shift in the place cell's firing field. This result was also observed in five additional rotation sessions with this cell



Results

A total of eight HD cells and two place cells were identified in the implanted animals. In the majority of cue card rotation sessions in the cylinder (13/15 sessions; Table 1) the HD cell's preferred firing direction shifted a similar amount and remained in alignment with the cue card. Figure 1 provides examples of cells recorded in each of the four animals in the cylindrical apparatus. In the first two plots (A, B), rotation of the cue card was associated with a corresponding shift in the HD cell's preferred firing direction. Return of the cue card to the standard position was likewise associated with return of the HD cell's orientation to its initial preferred direction. Figure 1C shows one of the two sessions (both of which were from the same cell; see Animal 2/Cell 1 in Table 1) where a complete shift was not observed following rotation of the cue

card. In this cell, 90° CW rotation of the cue card resulted in a 48° shift of the HD cell's preferred firing direction (under-rotation), and a marked mismatch between the cell's preferred firing direction and the cue card position when the card was subsequently returned to its standard position. Despite this transition, the mean absolute difference between the expected shift (90°) and the observed shift (using only the first standard → 90° rotation session for each HD cell; $n = 8$) was $9.75^\circ + 5.55^\circ$, a value which does not differ from results previously reported for the same manipulation [$13.26^\circ \pm 2.45^\circ$; $t(25) = -0.678$; $P = 0.504$; Taube 1995].

Figure 1D shows representative results for a cue card rotation session conducted for a hippocampal place cell. CCW rotation of the cue card by 90° resulted in a corresponding shift of the cell's place field. Cue card rotation manipulations were conducted on six different days for

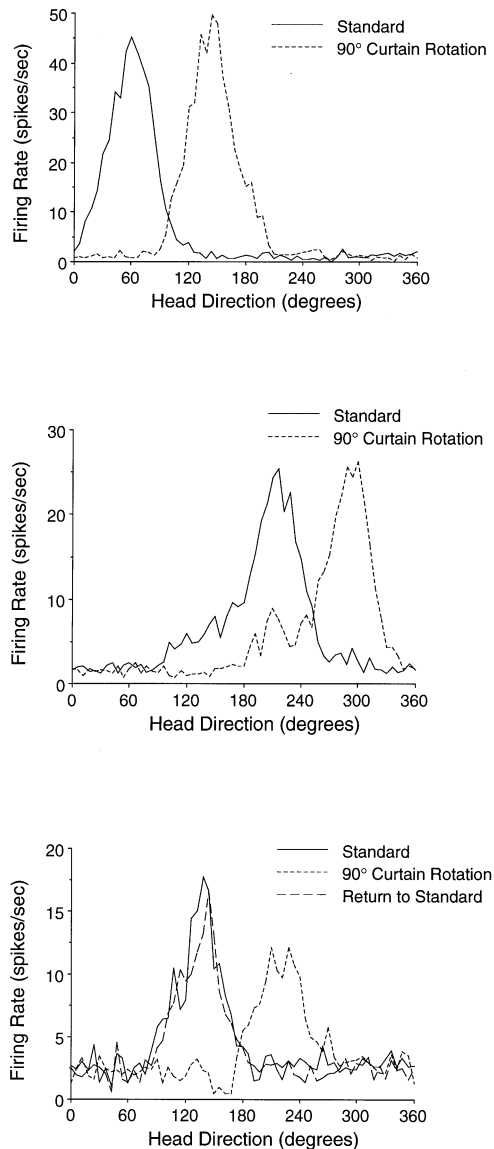


Fig. 2 Ninety-degree rotation of the cue curtain in the radial arm maze environment. Rotation of the cue curtain in the maze environment resulted in a corresponding shift in the preferred firing direction of the HD cells shown in each of the three examples

this particular cell, and once for a second place cell. In every case (7/7 rotation sessions) the place field shifted to maintain its original position with respect to the cue card.

Similar to our earlier results with this apparatus in non-disoriented animals (Dudchenko and Taube 1997), 90° rotations of the white curtain on the radial maze resulted in a corresponding shift in the HD cell's preferred firing direction in the majority of instances (7/9). Figure 2 illustrates the results of a rotation of the white curtain on the radial arm maze. The preferred firing directions of the three HD cells shown in this figure (each from a different animal) appeared to shift reliably with the 90° CCW rotation of the cue curtain. In addition, the cell's preferred firing direction shifted back to its initial orientation when

Table 1 Shift in head direction cell preferred firing direction following either a 90° rotation of the cue card in the cylinder or the cue curtain on the radial arm maze. Table values refer to the shift (in 6° increments) that optimizes the correlation between the session's firing rate versus head direction functions. Stability refers to the difference in a cell's preferred direction between two standard sessions on two consecutive days. Each row represents a different recording session. Animal 3/cell 4a was assumed to be the same cell as animal 3/cell 4, because the two cells had very similar preferred firing directions

Animal	Cell	Cylinder		Radial maze	
		0°–90°	90°–0°	0°–90°	Stability (°)
1	1	84	–84	84	
1	2	90	–90	84 ^a	
1	2	96	–90	84	–6
1	2	90	–84		6
1	2	90	–90	84	–12
2	1	42	–42	72	
2	1	42	150	48	0
3	1	84	–84		
3	2	84	–90		
3	3	84	–90		
3	4	96	–84		
	5	90	–84	66	
3	4a	84	–90	84 ^a	
3	4a	78	–78		
3	4a	90	–96	84	

^a In animal 1/cell 2 and animal 3/cell 4a, clockwise rotations of the white curtain were also conducted on the radial maze. In both sessions the cells' preferred firing directions also shifted with rotation of the white curtain. In animal 1/cell 2, the curtain rotation resulted in a shift of –78°; in animal 3/cell 4a the resulting shift was –90°.

the white curtain was similarly returned to its initial position (Figure 2, bottom plot). Furthermore, even on the two occasions in which the cell's preferred firing direction did not shift completely with the white curtain, the shifts were positive and in the correct direction (48° and 66°; see Table 1). These results suggest that, despite the disorientation treatment the animals underwent, the white curtain exerted substantial stimulus control over the preferred firing directions of the HD cells recorded on the radial arm maze. We also recorded the place cell shown in Fig. 1D on the radial arm maze, but because this cell did not exhibit a well-defined place field on the maze, we were unable to assess the extent of the cue curtain's control over the cell's preferred firing location.

Discussion

Our results show that disorientation procedures do not affect the stimulus control of visual landmarks over the preferred spatial orientations of HD or place cells. The observation that the HD cell's preferred direction followed the white curtain on the radial arm maze provides some insight into the nature of the acquisition deficit we previously observed on this same apparatus. Specifically, if the white curtain's control over HD and place cell orientation was similarly present when the animal was

learning the radial maze task, then disorientation may have interfered with the animal's ability to utilize, rather than the ability to perceive, the spatial relationship between itself and the landmark. This notion implies that the behavioral effects of disorientation are independent of the processes involved with the landmark's control over HD/place cell activity. Because the disorientation impairment in the behavioral task was specific for the appetitive radial arm maze and was not observed in two different water maze tasks (Dudchenko et al. 1997), disorientation may not generally preclude the animal from forming stable spatial relationships with landmarks, but instead may produce general stress or motivational effects that interfere with performance on certain types of spatial tasks.

The overall number of "transitions" (instances where the cell's discharge displayed a new spatial relationship to the salient cue following cue rotation) observed in the current findings is less than the number reported by Knierim et al. (1995). Indeed, no transitions were observed in three of four animals tested in the current study. One potential difference between these findings and those of Knierim et al. may be the previous behavioral training that the current animals received in the radial arm and Morris water mazes. Although in our previous experiment none of the currently recorded animals acquired the radial arm maze task, all animals, regardless of training condition (two animals continued in the disorientation condition in the water maze while two animals were placed in a clear container and not disoriented), exhibited normal acquisition when subsequently trained on a similarly cued Morris water maze task. Thus, it may be argued that training on the water maze may contribute to the stimulus control exerted by the cue curtain on the radial maze during recording. Although this possibility cannot be excluded, we have recently observed impaired acquisition on the radial arm maze in disoriented animals that had previously acquired a radial arm maze version of the water maze task (Dudchenko et al. 1997) – a finding which suggests that prior experience on a water maze does not abolish the effects of disorientation on a radial arm maze task. In addition, the finding of Knierim et al. (1995) that the stimulus control of a cue card improved for only one of four disoriented rats subsequently trained under "non-disorientation" conditions suggests that subsequent stable exposure to an environment may not necessarily be sufficient to overcome the effects of disorientation treatment. Finally, any carry-over effects of water maze task experience would not be expected to determine the stimulus control exerted by a cue card in the cylindrical apparatus because this environment was novel for all animals. As an alternative, then, subtle differences in the salience of the landmark or background room cues may have affected the extent to which transitions were observed in the current recordings. Specifically, if background room cues are somewhat less salient in an environment, the probability that a disoriented animal relies on a given landmark cue for orientation may increase. In addition, differences in the

strain and sex of the subjects (female Long-Evans rats vs male Fischer-344 rats) may have an unexpected influence on the probability of observing a transition. For example, the better visual acuity of pigmented rats compared with albino rats (for review see Munn 1950) may influence the degree to which each strain utilizes visual landmark cues. Taken together, our unexpected results warrant a more explicit examination of the conditions under which disorientation does, or does not, produce transitions in cells' preferred spatial orientations.

Finally, our results in the cylinder and the radial maze suggest that the stimulus control of landmark cues over HD and place cell orientation is robust even in the face of disorientation treatment. If consistently observed, this result may suggest that the view of the relationship between landmark cues and internal sources of information proposed by McNaughton and colleagues (1996) may require some modification. Specifically, the stimulus control of a spatial landmark may not be entirely attributed to its association with particular internally maintained expectations of spatial orientation. Rather, landmark control over HD and place cells may exist in the absence of consistent pairing with self-generated orientation information.

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