

Research report

# Head direction cell activity and behavior in a navigation task requiring a cognitive mapping strategy

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## Abstract

Head direction (HD) cells fire in relation to an animal's directional heading. To examine how these cells may be involved in spatial behavior, HD cells were recorded while animals performed a navigation task requiring the use of a cognitive mapping strategy. Results showed no relationship between performance on the task and the directional stability of the HD cell activity. The HD cell signal, therefore, appears to not always be used by the animal to guide its behavior during all navigation tasks.

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Head direction (HD) cells in the anterior dorsal nucleus of the thalamus (ADN) and postsubiculum (PoS) of the rat exhibit firing activity related to the head direction of the animal [1,2]. It is thought that these HD cells provide the neural correlate of the animal's perceived HD and that the animal uses this information to orient itself within an internal spatial representation of the environment, or "cognitive map" [3–5], when performing spatial tasks. In theory, cognitive maps can be formed on the basis of external (allothetic) or internal (ideothetic) information [4]. Although much work has been done to characterize the firing properties of HD cells [6], few studies have examined the relationship between HD cell activity and behavior, and the studies that have addressed this issue have reported different results ([7–9]; see [10] for a comprehensive review of this issue). The present study examined whether the information provided by the HD system was utilized by the animal in guiding behavior when performing a navigational task requiring the use of a cognitive mapping strategy. To achieve this aim, the firing properties of ADN and PoS HD cells were examined in a spatial task based on the classic "Sunburst" maze study by Tolman et al. [11]. The results of the study by Tolman et al. [11], in which rats were able to utilize a novel route to a goal, were seen as crucial evidence in support of the notion that animals could form a cognitive representation of space and therefore solve a spatial problem in novel ways unavailable to

the animal through stimulus-response learning (where only the sequence of responses to get to the goal is learned).

Four female Long-Evans rats were trained to forage for randomly distributed food pellets in a grey cylindrical chamber ( $\approx 76$  cm diameter) while an overhead camera tracked their movement. Animals were also trained to retrieve a water reward at the end of a goal arm on a maze configuration (e.g. Fig. 1A, left) until they were able to complete five consecutive successful trials, each in less than 30 s. As motivation for the task, animals were water restricted, but allowed free access to water for at least 10 min per day following testing. The maze consisted of flat tracks elevated  $\approx 43$  cm above the floor, enclosed within a featureless black circular curtain. The environment contained no intentional allothetic cues to prevent animals from using a beacon strategy to solve the task. Training trials began with a 2-min period where animals were confined to the start box. The experimenter then opened the start box door to allow the animal free access to the maze. Upon reaching the goal, the animal was returned to the start box and a lid placed over it for a 5 min delay before the start of the next trial. Five to ten trials were run each day. Once animals had reached criterion on the maze they were anesthetized with Nembutal and implanted with movable microelectrodes containing 10 25- $\mu$ m formvar-coated nichrome electrodes positioned in the ADN ( $n = 3$ ) or PoS ( $n = 1$ ).

Following surgery, animals were screened for HD cells while they foraged in the cylinder. If no HD cells were found then the electrodes were advanced  $\approx 50$   $\mu$ m and the

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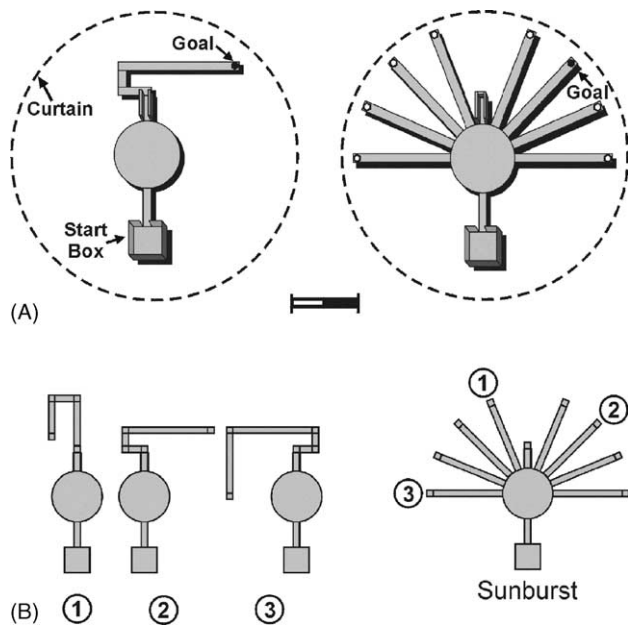


Fig. 1. (A) An example of a maze configuration used during training trials (left) which was replaced by the “Sunburst” maze configuration (right) during testing. Note that the location of the goal is in the same spatial location in the room in both maze configurations. Scale bar = 24 inches. (B) Each training maze used had a different correct shortcut arm, as shown on the right by the numbered arms of the Sunburst configuration.

animals were screened again the following day. Animals were given three training trials on the maze at least once a week post-surgery to assure their performance was maintained, even if no HD cells were identified during cell screening. If an HD cell was found, animals ran three identical training trials along the elevated maze route to locate

a water reward in a fixed location while unit activity was simultaneously recorded. These three training trials were followed by a “Sunburst” trial in which the normal route to the reward was blocked and eight novel routes introduced, one route being a direct path (shortcut) to the reward’s previous location (Fig. 1A, right). A water cup was positioned at the end of each arm but only the shortcut route’s cup contained a water reward. Animals that can utilize an accurate cognitive map of the environment should be able to use the novel shortcut route to reach the reward. Once a Sunburst trial was completed (animals were allowed to choose arms freely until they chose correctly or 16 min elapsed, whichever came first), the animal began training on a new maze configuration (Fig. 1B) with a different arm as the “correct” shortcut. Data from the three training trials were combined and compared to data from the Sunburst trial to determine the amount of shift in the cell’s preferred firing direction. The preferred firing direction of the cell was determined by using a triangulation method [2] as the short maze trial lengths often produced noisy firing rate  $\times$  HD functions where the apparent peak was unreliable.

Tolman et al. [11] found that approximately 36% (19 out of 53) of animals utilized the novel shortcut to reach the goal on their first exposure to the Sunburst trial, compared to 25% (1 out of 4) of animals in the present study (see Table 1 for a summary of behavioral results). Unfortunately, the low number of animals in the present study makes it difficult to determine if this difference is meaningful. Direct comparison is also made difficult because procedures of Tolman et al. [11] were modified in the present study by reducing the number of novel maze arms available from 18 to 8 to increase the angular difference between arms, and by removing the light (the only cue used by Tolman et al. [11]) from above

Table 1  
Summary of results for sunburst maze trials

Animal	Cell number	Maze configuration	Goal arm	First arm choice	Number of errors	PFD shift: Maze only ( $^{\circ}$ )	PFD shift: Full trial ( $^{\circ}$ )
GM11	15 <sup>a</sup>	C	1	8	4	-0.93	-5.45
	16 <sup>a</sup>	C	1	8	4	-6.02	12.51
	17	A	4	8	4	-6.79	5.81
GM13	1	B	7	4	7	4.18	-11.05
	2	A	4	3	6	-8.39	-10.32
	3	B	7	6	1	14.89	-3.71
	5	A	4	8	3	-9.04	2.59
	7 <sup>a</sup>	B	7	6	<sup>b</sup>	12.98	11.36
	8 <sup>a</sup>	B	7	6	<sup>b</sup>	-6.87	1.46
	9	A	4	2	2	0.98	1.66
	11	B	7	4	25	21.14	5.24
12	A	4	6	8	3.03	-6.04	
GM14	1	C	1	1	0	4.36	9.22
GM15	8	A	4	1	<sup>b</sup>	-3.29	3.44
	9	B	7	1	<sup>b</sup>	US	3.31
	11	A	4	1	2	-5.04	-8.75

PFD shift, shift in HD cell’s preferred firing direction from Training to Sunburst trials; US, cell firing undersampled due to the preferred firing direction of the cell.

<sup>a</sup> Cells recorded simultaneously.

<sup>b</sup> Goal not reached after 16 min.

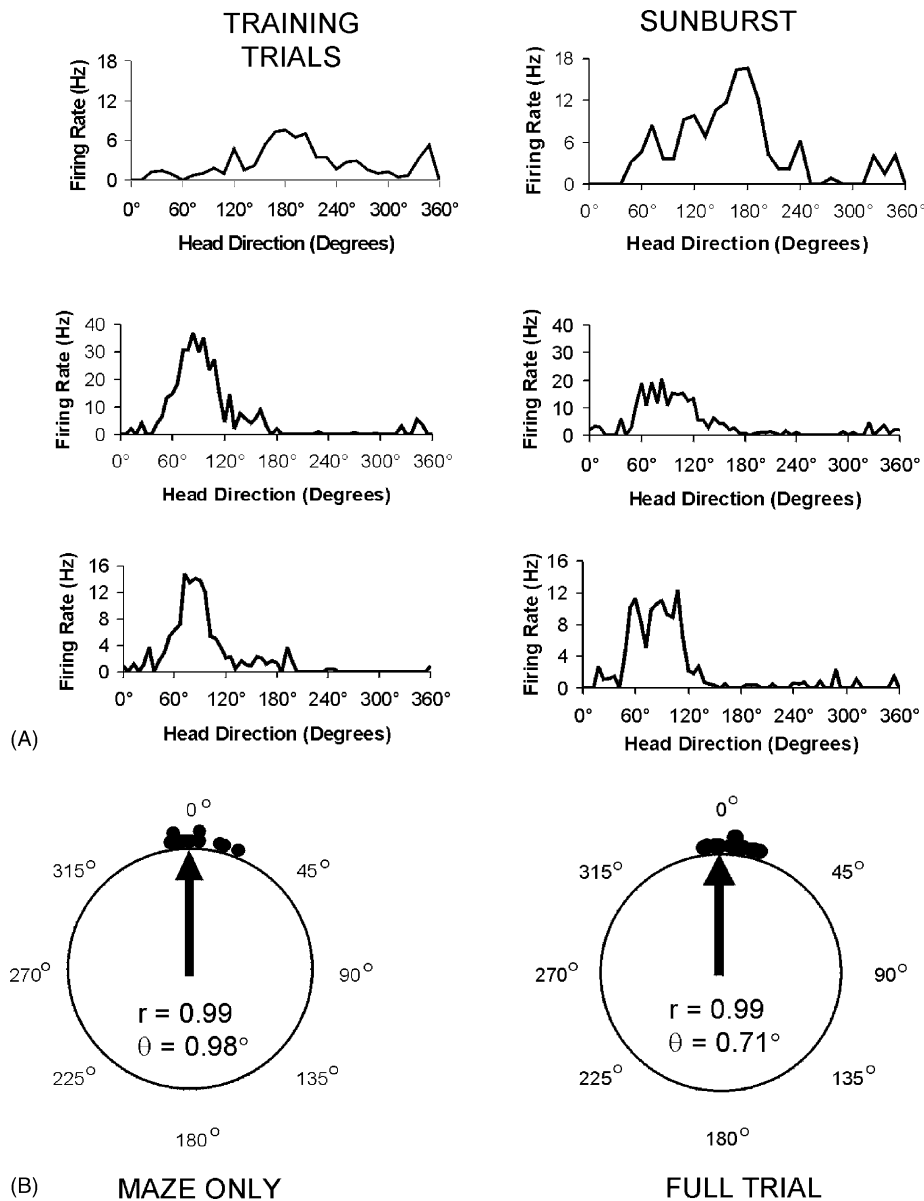


Fig. 2. (A) The preferred firing direction of ADN HD cells was unaltered from the training trials to the Sunburst trial, and was independent of the number of errors made by the rat before choosing the correct shortcut arm. The top pair of traces are from a cell where the rat selected the correct arm on the first Sunburst trial (note that the preferred firing direction of this cell is less clear due to the low firing rate and short sampling times for this cell). The middle traces are from a cell where the rat made seven errors before selecting the correct arm on the Sunburst trial. This HD cell stability was consistent for the duration the animal was on the maze. Similar results were obtained for PoS HD cells. The bottom traces are from a cell where the rat made two errors before selecting the correct arm. (B) Distributions of shifts in the preferred firing direction of HD cells from training trials to the Sunburst trial for data from the Full trial ( $n = 16$ ; left) and Maze only ( $n = 15$ ; right). The shift for each given cell is shown as a filled circle on the outside of the unit circle with degrees marked. The graphs show that the average amount of shift was negligible ( $< 1^\circ$ ) for both Full trial and Maze only data with very little angular deviation ( $r$ , mean vector length;  $\theta$ , mean phase angle).

the goal location which may have acted as a beacon in the original study. It is, however, interesting to note the existence of a number of studies which subsequently failed to replicate the results of Tolman et al. [11], either directly [12] or with some variation [13,14], and more recent challenges to the notion that animals have cognitive maps at all [15–18].

Results from the unit recording data showed that throughout the Sunburst trial, the preferred direction of both ADN and PoS HD cells remained stable relative to the training

trials and was not related to the accuracy/inaccuracy of the behavioral choice(s) made by the animal. This result was true when data from the Full trial (i.e. including the 2 min of data when the animal was confined to the start box at the beginning of the trial) were analyzed, and when only data while the animal was on the Sunburst maze were included (i.e. excluding the start box data). For example, when one animal was exposed to the Sunburst maze for the first time and correctly selected the novel shortcut to the rewarded arm,

the preferred firing direction of the ADN HD cell did not shift compared to the training trials while the animal was on the maze (Fig. 2A, top). Similarly, another animal that made seven errors before selecting the correct arm also showed stable ADN HD cell activity on the maze, both compared to the training trials and to the Sunburst trial (Fig. 2A, middle). All PoS HD cells recorded behaved similarly (e.g. Fig. 2A, bottom). Overall, the preferred firing direction of HD cells on the Sunburst maze was shifted, on average, by less than  $1^\circ$  from that seen during the training trials, while animals averaged  $5.5 \pm 1.9$  S.E.M. errors (range: 0–25) per Sunburst trial (Full trial (Fig. 2B, left),  $n = 16$  (ADN = 13, PoS = 3), mean phase angle  $\theta = 0.71^\circ$ , range =  $348.95$ – $12.51^\circ$ , mean vector length  $r = 0.99$ ; Maze only (Fig. 2B, right),  $n = 15$  (ADN = 13, PoS = 2),  $\theta = 0.98^\circ$ , range =  $350.96$ – $21.14^\circ$ ,  $r = 0.99$ ). Results of a *V*-test [19] showed that the amount of shift was not distributed evenly about the circle, but had a mean of  $0^\circ$  (Full trial,  $V = 15.87$ ,  $P < 0.01$ ; Maze only,  $V = 14.82$ ,  $P < 0.01$ ). Further, the shift in the preferred firing direction of HD cells from the cylinder to the training trials was much more variable (Full trial,  $\theta = 356.20^\circ$ , range =  $255.66$ – $68.51^\circ$ ,  $r = 0.73$ ; Maze only,  $\theta = 352.39^\circ$ , range =  $255.30$ – $61.15^\circ$ ,  $r = 0.67$ ) and significantly different from the training trials to the Sunburst maze (Watson–Williams test [19]: Full trial,  $F = -28.40$ ,  $P < 0.01$ ; Maze only,  $F = -26.81$ ,  $P < 0.01$ ). This result is to be expected given the animal is changing environments from the cylinder to the training trials [20], but not from the training trials to the Sunburst, and suggests the animals perceived the Sunburst as the same environment as they experienced on the training trials.

Correlations performed using the absolute amount of HD cell shift showed no relationship between the amount of shift in the HD cell's preferred firing direction and the number of errors made (Full trial,  $r = -0.027$ ; Maze only,  $r = -0.244$ , with one outlier removed), or amount of HD cell shift and the difference between the animal's first arm choice and the correct arm (i.e. the magnitude of error) (Full trial,  $r = 0.009$ ; Maze only,  $r = -0.238$ ). Additional probe training trials that were conducted on some cells by rotating the maze  $180^\circ$  relative to the room showed that the firing of the HD cells was related to the orientation of the maze and not the room, suggesting that the animals were orienting using the maze itself as a cue. If animals were indeed using the maze as a cue to orient by, and given the central platform of the maze and the start box, in particular, remained constant from the training trials to the Sunburst trials, it is therefore not surprising that the HD cell activity also remained unaltered from training to Sunburst trials. It should be pointed out, however, that just because the maze orientation appears to provide the animal with a stable orienting cue (as reflected by HD cell activity), this fact does not necessarily mean that animals were using this maze orientation information to guide their arm choice behavior. Although the animals may have lacked sufficient experience with the novel "Sunburst" component of the task to perform well, one animal that ex-

perienced the sunburst maze nine times consistently showed HD cell activity unrelated to the animal's behavioral choice across all nine sunburst trials. One possible explanation for the animals' arm choice behavior was that they were using the goal location on the previous trial to guide their arm choice behavior on the current trial (proactive interference). If so, then the angular difference between the first arm chosen on the current trial and the goal arm chosen on the previous trial should be zero. Examination of the sequence of arm choices made, however, showed no evidence of proactive interference with a random distribution in the absolute deviation from the first arm chosen on the current trial to the goal arm location on the previous trial (Rayleigh test [19],  $z = 2.51$ ). Although some variation in peak firing rates could often be observed from the training trials to the Sunburst trial (Full trial, mean firing rate change =  $-0.96 \pm 2.18$  S.E.M. spikes/s, range =  $-23.65$  to  $+15.25$  spikes/s; Maze only, mean firing rate change =  $2.58 \pm 2.24$  S.E.M. spikes/s, range =  $-12.31$  to  $+23.79$  spikes/s) these variations were likely due to short sampling times and were not consistent across cells (e.g. Fig. 2A, the top pair of traces show an increase while the middle traces show a decrease) nor related to the animal's performance on the Sunburst trial (Full trial,  $r = -0.127$ ; Maze only,  $r = -0.274$ ). The possibility remains that only animals that were able to access a cognitive map were able to solve the task efficiently, and that only one animal (GM14; see Table 1) in the present study was able to perform the task well. Unfortunately, since only one cell was recorded from this animal we cannot ascertain what would have happened on subsequent trials and cannot rule out the possibility that this result was just a chance occurrence.

The results clearly show that HD cell activity, at least in the PoS and ADN, remained robust throughout all phases of the task, independently of whether the animal performed well or poorly. This finding stands in contrast to the results reported by Mizumori and Williams [9] who suggested that HD cells in the LDN developed a more robust directional signal as an animal learned the task. Dudchenko and Taube [8] also did not find any changes in the HD cell signal in either ADN or PoS during acquisition in a reference memory task on a radial arm maze. In totality, these data are consistent with those of Golob et al. [7] who recently showed little correlation between the direction of HD cell activity and the direction of the behavioral response in two spatial navigation tasks. It appears that the animal may know its orientation upon entry into the environment, but this information may not necessarily be used to guide the animal's behavior in order to successfully reach a goal.

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