The anatomical and computational basis of the rat head-direction cell signal

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As a rat navigates through space, neurons called head-direction (HD) cells provide a signal of the rat's momentary directional heading. Although partly guided by landmarks, the cells also show a remarkable ability to track directional heading based on angular head movement. Theoretical models suggest that the HD cells are linked together to form an attractor network, and that cells which signal angular velocity update the directional setting of the attractor. Recently, cell types similar to those required theoretically have been discovered in the lateral mammillary and dorsal tegmental nuclei. Lesion and anatomical data suggest these nuclei might constitute the postulated attractor-path integration mechanism, and that they provide the HD cell signal to cortical areas where it has been observed.

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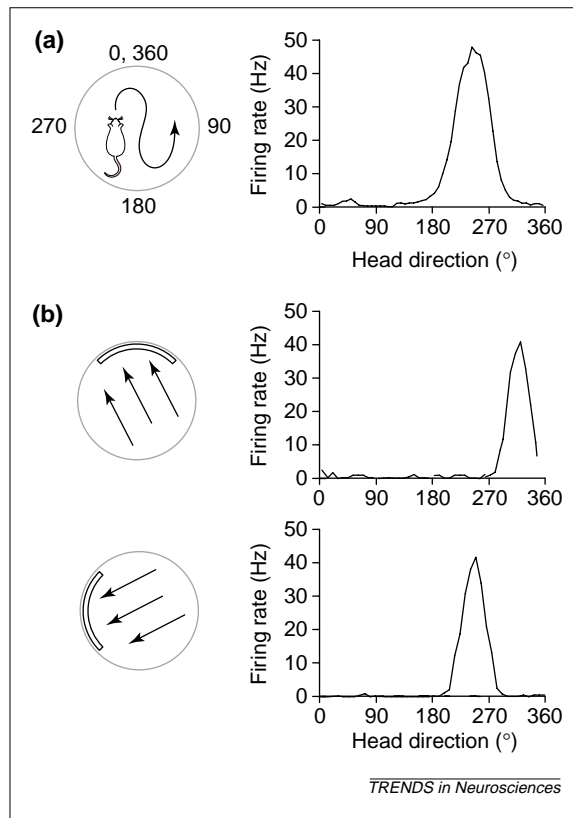
When a rat navigates through an environment, a set of cells, known as head-direction (HD) cells, provides a constant signal of the rat's momentary directional heading[1,2]. Each cell fires whenever the rat faces one particular direction, regardless of where the rat is within the environment or what it is doing. Different cells have different preferred directions, so that, for each possible directional heading, there is a unique set of HD cells that will be active.

The HD cells are typically recorded from during sessions in which a rat forages for tiny food pellets that are continually dropped to random locations on the chamber floor. When the average firing rate of one of these cells is plotted as a function of directional heading, the resulting tuning function consists of a single Gaussian peak that covers one portion of the directional range (Fig. 1a).

These HD cells were initially discovered in the postsubicular region of the hippocampal formation[1,2], and, as described below, have since been discovered in several additional, anatomically connected regions.

HD cell signals

HD cells are not sensitive to the geomagnetic field

One possibility for how these direction-specific firing patterns are generated could be that the cells are somehow sensitive to the local geomagnetic field, so that they can detect heading, in earth-centered coordinates, directly. Numerous observations, however, have suggested that this is not the case[3–6]. For example, Taube *et al.*[3] recorded from HD cells in the postsubiculum as rats foraged in a cylindrical enclosure equipped with a single, white card located on one portion of the wall (Fig. 1b). When the card was left in the same, standard location over repeated sessions, each HD cell maintained the same preferred direction over days. However, when the position of the card was moved to a new location on the wall, the preferred direction of the HD cells also shifted, so that each cell maintained the same preferred direction relative to the card. Thus, the cells did not maintain a constant relationship to the local magnetic field, but, rather, to an experimenter-placed cue.

HD cells are influenced by visual landmarks

Because the HD cells will shift their preferred direction so that they maintain a constant relationship to the cue card provides the possibility that the cells might simply be driven primarily by visual (or other sensory) cues. For example, it could be that the cell shown in Fig. 1b fires whenever there is a large, white stimulus in the right portion of the rat's visual field.

However, numerous observations have shown that the system is not that simple (see, for example, Refs 3,6–9). These cells show a remarkable ability to somehow track directional heading, even in the absence of reliable orienting landmarks. For example, postsubicular HD cells can continue to show directional properties even when visual landmarks are removed entirely[3], or when the animal travels from a familiar environment into a novel environment[7].

Another example of this tracking ability is derived from a study that utilized a vertically striped, cylindrical chamber[9] (Fig. 2). The stripes created a visually symmetrical environment, so that, although there were salient visual cues, no one cue could serve as an orienting landmark. Thus, if the cells were simply sensory driven it might be expected that the fourfold symmetry of this environment would result in each HD cell having four directional peaks. However, this was not the case. During any one session, each cell had only one directional peak, just as in a more standard, single cue card environment. Moreover, the preferred direction during any one session was determined by the position at which the rat was first placed down into the cylinder. Thus, the cell activity was not controlled by the stripes (because this would have resulted in a fourfold symmetry in the directional tuning curves), and also was not controlled by some

Fig. 1. Recording chamber and directional tuning curves for typical head direction (HD) cells under standard, and cue manipulation conditions. (a) Overhead view of the 76 cm diameter, high-walled cylindrical chamber typically used during HD cell recordings (left panel). Rats perform a pellet-chasing task throughout the 20–60 min sessions, during which they constantly forage throughout the chamber, repeatedly facing every different direction. The rat's directional heading is constantly monitored, and numeric values are assigned to each possible direction, as indicated. After a session, the cell's directional tuning curve is constructed by calculating the cell's average firing rate as a function of directional heading. The right panel shows the tuning curve for a typical HD cell, which fires as an approximately Gaussian function of head direction. The directional heading at which the peak of the Gaussian function is located is referred to as the cell's preferred firing direction (this is 245° for the cell shown here). (b) Example of a HD cell that shows control of preferred firing direction by a salient landmark, as originally demonstrated by Taube *et al.*[3] The upper, left panel shows an overhead view of the gray cylindrical apparatus which was equipped with a single white cue card located on the inner wall, as indicated. The arrows within the cylinder indicate the directional heading at which the HD cell fired when the card was in this standard position. The directional tuning curve for this session is shown to the right. The lower, left panel shows the position of the cue card during a probe session, as in Ref. 3. As shown, the cell's preferred firing direction rotated along with the angular displacement of the card.

extraneous cue (such as an odor), since the recording environment was exactly the same throughout the series of probe sessions in which the animal's entry location was varied. Rather, the system somehow 'initialized' the directional setting in a way which was fixed, relative to the start position (i.e. the cells acted as though the start position was always near the 'east' card, heading 'north'), and then determined all other directions relative to this initial setting.

HD cells appear to use a process known as path integration
Data, such as that described above, suggest that the cells use information about the rat's own head

movements (such as might be provided by vestibular or motor command signals) to track directional heading. According to this idea, the HD cell activity pattern is constantly updated by integration of the animal's angular head movement. For example, if the rat starts out facing 'north', and then makes a 90° counterclockwise turn, then this angular motion, alone, will somehow cause the 'north ' cells to turn off, and the 'west' cells to turn on. This will be true even if the view when facing 'north' is identical to that when facing 'west'.

Further support for this idea is provided by the observation that lesions of the vestibular system cause a loss of the directional signal in thalamic HD cells[10].

Neural network models explaining the directional firing properties

HD cells are linked together to form an attractor network
Interestingly, almost all the models developed to explain the HD cells are similar in their basic features[11–16]. Most begin with the idea that the HD cells are somehow linked together, via a set of excitatory and inhibitory connections, to form an attractor network. One example of such a network is provided in Fig. 3a. In this network, cells that are meant to represent adjacent directions are located next to one another. The excitatory HD cells provide excitatory input to other nearby HD cells, and also provide inhibitory input to distant HD cells, via the inhibitory cell layer. In the absence of external influences, the population activity pattern will settle into an attractor state in which one HD cell will fire maximally, and neighboring HD cells will show
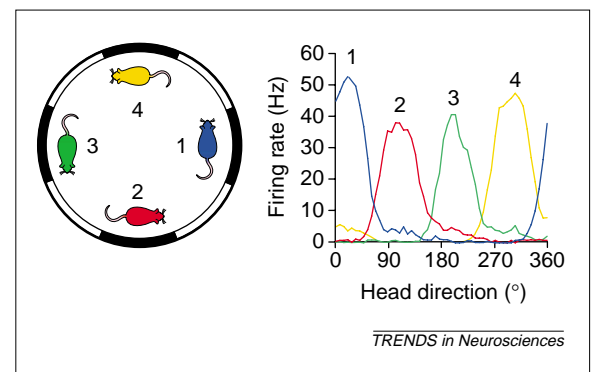

Fig. 2. Head direction (HD) cells show angular path integration. The left panel provides an illustration of the symmetrical chamber used to test the path integration abilities of the HD cells[9]. This high-walled, 76 cm diameter cylinder was equipped with eight, alternating, vertical black and white stripes, all of identical width. This created a visually ambiguous environment, so that, although there were salient visual cues, there was no one cue which could be used as a directional landmark. For example, when the rat was in the center of the cylinder facing north, it saw a black stripe straight ahead, with white stripes on either side. This was exactly the same view as seen when the rat faced east, or south, or west. During standard sessions, the rat was always placed next to the 'east', black stripe, facing 'north' to initiate the session (start position 1). For this cell, this always resulted in a preferred direction of ~30° (peak 1; right panel). During a series of probe sessions, the rat's start position was systematically varied, as indicated in the left panel. The directional tuning curve which resulted from each start position is plotted in the right panel. As can be seen, each 90° shift of the rat's entry position resulted in a corresponding 90° shift in the peak of the directional tuning curve.
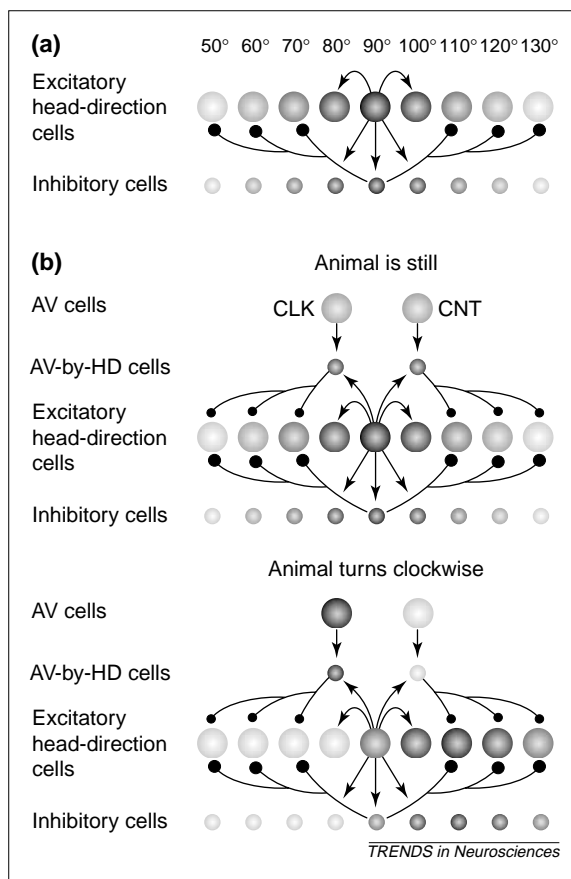
Fig. 3. Postulated mechanism to explain head-direction (HD) cell firing properties. (a) Excitatory and inhibitory cells are reciprocally connected to form an attractor network which ensures that only cells which are meant to represent similar directions are able to fire simultaneously (see text). (b) Angular velocity-related inputs are able to shift the activity packet when the animal turns its head (see text). Excitatory connections aer indicated by arrows, inhibitory connnections are indicated by lines ending in circles. Abbreviations: AV, angular velocity; HD, head direction; CLK, clockwise; CNT, counterclockwise. Firing rate is indicated by darkness of shading.

progressively lower activity levels, as a function of distance from this maximal peak. This attractor network accomplishes the basic feature of the HD cell system, in that cells which represent similar directions can fire at the same time, whereas cells that are meant to represent different directions cannot be simultaneously active. Thus, for example, the system can never indicate that the animal is facing both 'north' and 'south' at the same time.

Angular velocity input to the attractor network
To accomplish path integration, the system must first receive input about the animal's momentary angular head velocity. This is provided by the angular velocity (AV) cells shown in Fig. 3b. These cells are tonically active when the head is still, but increase their firing rate during one kind of turn (clockwise versus counterclockwise) and decrease their firing rate during the opposite kind of turn.

This AV input must then be connected to the attractor network so that it causes the locus of activity in the HD cell layers to shift in a way that

accurately tracks directional changes. In the example shown in Fig. 3b, this is accomplished by a set of inhibitory cells that receive input from both excitatory HD cells and from the AV cells. Two types of such AV-by-HD cells are shown. One type receives input from excitatory HD cells to the right and excitatory input from AV cells that fire at high rates during clockwise head movement; these cells, in turn, project onto excitatory HD cells that are located to the left. The other type receives input from excitatory HD cells to the left, and from AV cells that prefer counterclockwise motion. These cells project onto excitatory HD cells located to the right. When the rat does not move, the two types of AV-by-HD cell are equally active, and so the activity packet in the HD cell layer remains stable. When the rat begins to turn clockwise, inhibitory AV-by-HD cells to the left of the activity packet increase their firing rate, while inhibitory cells on the right side decrease their firing rate. This causes the activity packet to shift to the right, thus correctly indicating the new directional heading (i.e. that which resulted from the clockwise turn). During counterclockwise turns the opposite is true.

HD cell system can be 'set' by familiar environmental landmarks
Finally, as shown above, in a familiar, unambiguous environment the HD cell firing direction can be set by the position of environmental landmarks[3]. Consequently, it is postulated that the HD cells also receive environmental sensory inputs (not shown in Fig. 3), and that sensory cell-to-HD cell connections become strengthened[5,8], in a Hebb-like manner, as a result of experience. Thus, these landmarks develop the ability to 'set' the position of the activity packet, so that in a familiar, unambiguous environment each HD cell will have the same preferred direction each time the rat visits.

Neural network models make similar sets of predictions
Several models follow this general form[11–16]; these models differ in the details of their connectivity. However, all the neural network models predict that the brain regions that contain the attractor-path integration mechanism must contain: (1) a layer of excitatory HD cells connected to a layer of inhibitory cells; (2) cells that signal angular head velocity and (3) cells that fire as a joint function of angular velocity and head direction.

HD cells are located in a set of interconnected brain regions
HD cells were initially discovered in the postsubicular cortex of the hippocampal formation[1,2]. Subsequently, they have been discovered in several additional, closely-related brain regions, including the retrosplenial cortex[17,18], the anterior thalamic nucleus (ATN) (Refs 19,20), the lateral dorsal thalamic nucleus (LDN) (Ref. 21), the lateral mammillary nucleus (LMN)
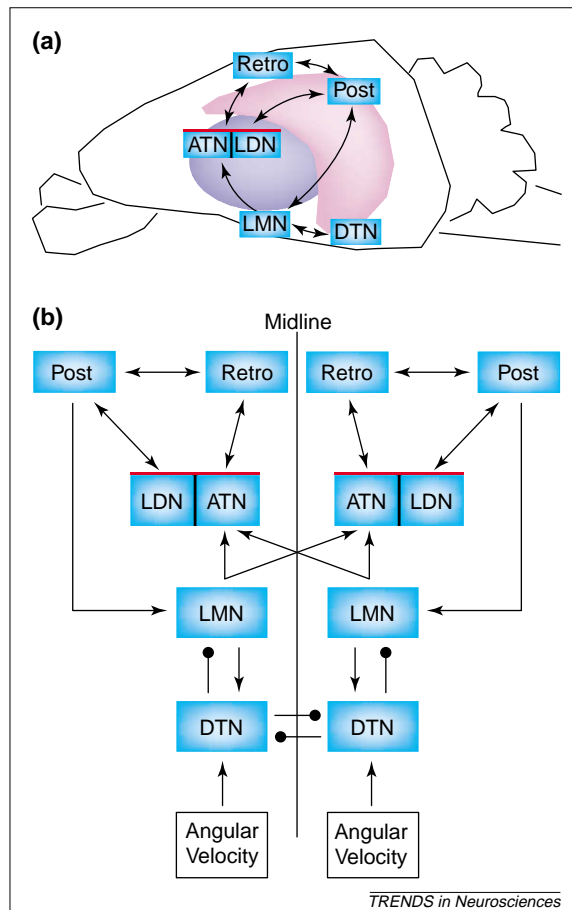
Fig. 4. Anatomy of the head-direction (HD) cell system. (a) Diagram showing the locations and major connections of brain regions known to contain HD cells. The hippocampal formation (pink), thalamus (purple) and HD cell circuit (blue) are shown. (b) Representation of these same areas, with an indication of the excitatory (arrows) versus inhibitory (lines ending in circles) nature of the major inputs and outputs of each region. Blue boxes indicate areas that contain HD cells. The red bar above the boxes containing ATN and LDN indicates that the structures show similar cortical connections. Abbreviations: ATN, anterior thalamic nucleus; DTN, dorsal tegmental nucleus of gudden; LDN, lateral dorsal thalamic nucleus; LMN, lateral mammillary nucleus; Post; postsubiculum; Retro; retrosplenial cortex.

(Refs 22,23) , the dorsal tegmental nucleus (DTN) of Gudden[24] and the striatum[25,26].

Figure 4 depicts these areas and their interconnections. (The striatum has been omitted from this Fig. for clarity.) These limbic structures are connected via a loop, which is similar to that identified by Papez[27] and thought, at that time, to be involved with processing emotional information. In this loop, information travels from the postsubiculum down to the LMN (Refs 28,29), then up to the ATN (Refs 30,31), and back to the cortex[32–34]. Note, the LMN is also reciprocally connected to the DTN (Refs 35–37), which is thought to contain GABAergic cells[28,38]. This nucleus also contains HD cells, and it might also receive angular velocity signals, as a result of its inputs from the medial vestibular nucleus and nucleus prepositus hypoglossis[39], as well as inputs from the habenula[37,39], which, in turn, receives input from the striatal system[40,41].

LMN and DTN might constitute the attractor-path integration network

The fact that HD cells exist in so many different brain regions raises the question of whether the postulated attractor-path integration functions are distributed across all (or many) of these areas, or whether, by contrast, the crucial network is located in just a subset of these regions. As noted elsewhere[42], recent data have suggested that the LMN and DTN might constitute crucial components of the HD cell system.

Role of LMN for HD signals

Bilateral lesions of the LMN abolish the HD signal in the ATN (Refs 22,43). In addition, lesions of the ATN, in turn, abolish HD signals in the postsubiculum[44]. This suggests that LMN HD signals might be crucial for HD signals in 'downstream' areas. By contrast, lesions of the postsubiculum leave the HD signal in the ATN largely intact[44].

Route for updating the directional signal

Additional evidence that the LMN and DTN might be the source of generation of the HD signal is derived from careful examination of the timing of the HD signals. In particular, ATN HD cells are actually slightly anticipatory, predicting future head direction approximately 20 ms in the future[20,45]. This predictive ability is compatible with the path integration model presented above, because it is possible that the AV signals could cause the activity packet in the HD cell layer to continually jump to the next directional setting slightly in advance of when the animal's head actually arrives at that directional heading. Interestingly, postsubicular cells do not show this anticipatory property; instead, they are best correlated with the animal's instantaneous head direction[20,45]. Finally, HD cells in the LMN are even more anticipatory than the ATN HD cells. They have been estimated to anticipate future directional heading by as much as 40–95 ms (Refs 22,23). Thus, the pathway from the LMN to ATN to postsubiculum shows a progression from more to less anticipatory. One possible interpretation of these data is that the LMN is at or near the source of generation of the signal (the path integration network), and the HD signal is then transmitted from LMN to ATN and postsubiculum, with a slight transmission delay at each step.

Cell types in the LMN and DTN

Further support for this idea is provided by the fact that, in addition to HD cells, the DTN also contains cells which show a strong, linear correlate with angular head velocity[24,46] (Fig. 5a), similar to that postulated for the AV cells in Fig. 3b. In addition, many of these AV cells in the DTN also show a subtle, graded influence of directional heading[24] (Fig. 5a). Thus, these cells could possibly constitute AV-by-HD cells, similar to those postulated in Fig. 3b.
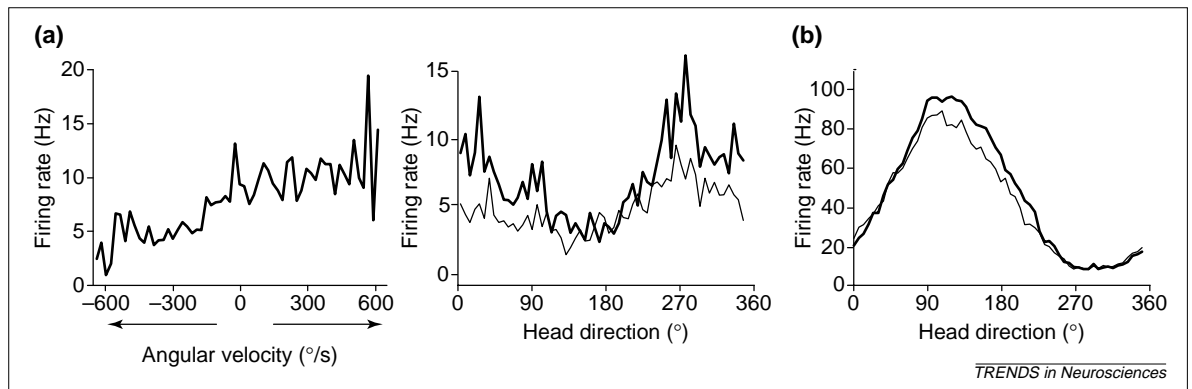
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Fig. 5. The lateral mammillary nucleus (LMN) and dorsal tegmental nucleus of gudden (DTN) contain each of the cell types postulated in the model shown in Fig. 3. (a) An example of a typical angular velocity (AV) by head-direction (HD) cell recorded from the DTN. The left panel shows average firing rate over the session as a function of angular head velocity. Counterclockwise turns are shown on the left half of the abscissa using negative numbers, with higher speeds of counterclockwise turning corresponding to larger negative numbers. Clockwise turns are plotted on the right half of the abscissa, with higher numbers corresponding to faster clockwise turning speed. Zero corresponds to no head turn. This cell showed a strong, positive, linear correlation with angular velocity, firing at higher rates during clockwise turns, and lower rates during counterclockwise turns. This type of strong, linear correlation is shown by the majority of DTN cells. The directional firing properties of this cell are shown in the right panel of (a). The influence of angular velocity on the directional properties was examined by dividing the directional tuning curve into one constructed only from samples taken when the rat was turning clockwise (thick line) and one constructed only from samples when the rat happened to turn counterclockwise (thin line). It can be seen that both tuning curves showed a similar graded influence of directional heading which was superimposed on the overall higher rates during clockwise turns. (b) A HD cell recorded from the DTN, with the tuning curve for clockwise versus counterclockwise turns shown as in (a). Note this cell showed slightly higher rates throughout much of the directional range during clockwise turns. Three of the six DTN HD cells recorded to date show this type of influence of angular velocity[24]. Note also that the tuning curve for this cell was more broad than that for HD cells in other regions, and this was typical of the DTN HD cells.

In addition, some of the HD cells, in both the LMN (Ref. 23) and the DTN (Ref. 24), have also been shown to be influenced by angular head velocity (Fig. 5b), and so, these cells are also possible candidates for the postulated AV-by-HD cells.

Investigation of cell activity in the LMN and DTN is still preliminary, and so it is premature to speculate on exactly how the cells in these two nuclei might be linked together to form an attractor-path integration network. However, these data support the idea that the LMN–DTN complex might contain a network that is functionally similar to that in Fig. 3.

Concluding remarks

The HD cell system provides a remarkably salient, robust, and tractable neural signal. Because of this, it has been possible to make quite rapid progress in the characterization of the basic behavioral features of these cells, in addition to obtaining clues about where and how the signal might be generated. Although recent evidence suggests that the signal might be generated in the LMN–DTN complex, further work is necessary to substantiate this claim.

If these two nuclei do, in fact, constitute the attractor-path integration module for the HD system, then detailed examination of how the DTN–LMN cells work could also have important implications for other neural systems. In fact, recent theoretical work suggests that attractor networks, such as that postulated in Fig. 3a, might constitute a fundamental building block for a wide variety of neural computations. For example, the attractor network constitutes a mechanism for short-term memory. For example, if a rat is facing 'north' and remains in that position for some period of time, the 'north' cells continue to fire throughout the period of immobility. Somehow the cells retain the memory for that heading. This mnemonic function is accomplished, theoretically, by the attractor network in Fig. 3a. Interestingly, a circuit remarkably similar to this has been postulated as the basis for working memory in prefrontal cortex[47]. In addition, attractor networks of this kind have been postulated to play a role in orientation tuning in the visual cortex[48], neural network multiplication of separate inputs[49], stimulus selection[50], gain modulation[50], spatiotemporal pattern generation[50], and motor cortex control of movement trajectories[51]. Thus, insight into the attractor network of the HD cell system might have far reaching implications.

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