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Rapid response of head direction cells to reorienting visual cues: a computational model

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Abstract

In this model of the head direction cells in the limbic areas of the rat brain, the intrinsic dynamics of the system is determined by a continuous attractor network of spiking neurons. Synaptic excitation is mediated by NMDA and AMPA formal receptors, while inhibition depends on GABA receptors. We focus on the temporal aspects of state transitions of the system following reorientation of visual cues. The model reproduces the short latencies (80 ms) observed in recordings of the anterodorsal thalamic nucleus. The model makes an experimentally testable prediction concerning the state update dynamics as a function of the magnitude of the reorientation angle.

Keywords: Head direction cells; Continuous attractor networks; Spiking neurons

1. Introduction

Head direction (HD) cells constitute a likely neural basis for the spatial orientation capabilities of rats. The response of these limbic neurons is tuned to the animal's allocentric heading in the azimuthal plane. A HD cell i discharges selectively only when the head of the animal is oriented in one specific 'preferred' direction θ_i, regardless of the animal's ongoing behavior and position [11]. The preferred directions of all HD cells, $\Theta = \{\theta_i \,|\, \forall i\}$, are evenly distributed over 360°, such that the HD system could work as an allocentric neural compass. When the head of the animal remains oriented in a given direction θ, the subpopulation of HD cells with preferred directions $\theta_i \simeq \theta$

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remains active for an indefinite period of time (demonstrating persistence of the neural coding). During head turns, the active subpopulation of HD cells provides an ongoing neural trace of the orientation of the animal $\theta(t)$, according to the head angular velocity signal $\omega(t)$.

HD cells have been observed in a network spanning a variety of structures centered on the brain's limbic system, including postsubiculum (PSC), anterodorsal thalamic nucleus (ADN), and lateral mammillary nucleus (LMN) [11]. Inertial self-motion signals (e.g., vestibular) are likely to converge onto the HD system via subcortical projections from the dorsal tegmental nucleus (DTN) [2]. DTN receives vestibular inputs from the medial vestibular nuclei and conveys this information to LMN and ADN. Visual inputs are likely to enter the HD system via the PSC and the retrosplenial cortex (which also contains HD cells [11]). The PSC receives afferents from the visual areas 17 and 18, whereas the retrosplenial cortex receives inputs from higher associative areas such as the posterior parietal cortex [11].

Although the HD cell system has properties resembling those of a compass, the allocentric coding of HD cells is independent of geomagnetic fields. Rather, the preferred directions are anchored to visual fixes in the environment: in a neutral setting, rotating a dominant visual cue by an angle $\Delta\theta$, induces a shift in all preferred directions such that $\Theta' = \{\theta_i + \Delta\theta \,|\, \forall i\}$ [11]. Recent electrophysiological studies by Zugaro et al. [13] have focused on the temporal aspects of the preferred direction updates in ADN following the reorientation of a visual cue. The experimental setup consisted of a black high-walled cylinder with a large white card attached to the inner wall and serving as dominant visual cue. ADN cells were first recorded in light conditions. Then, in the darkness, the cue card was rotated by 90°. Finally, the light was switched back on and the time necessary to the HD system to update its directional representation (i.e., to shift the preferred directions of the HD cells) was measured. The quantitative results showed rather short update latencies of approximately 80 ± 10 ms.

The interrelation between allothetic (e.g., visual) and idiothetic (e.g., vestibular) cues for determining the dynamics of the HD cell system is a relevant issue for both experimental and computational neuroscience (e.g., [1,9]). This paper proposes a continuous attractor network that models the ensemble activity of HD cells as a gaussian-shaped profile encoding the current head direction. The model is based upon spiking neurons, which allow us to study the dynamics of the fast update transient (≈ 80 ms) exhibited by rat HD cells. Earlier models (e.g., [12]) predicted update latencies of about 200–250 ms for the HD representation to be reoriented by a visual cue. These models employed analog (firing rate) computational units, which are intrinsically limited for quantitatively describing the temporal properties of real neural populations.

2. Methods

2.1. Global model architecture

Fig. 1(a) shows the global architecture of the model inspired by the HD circuit of rats [11]. It includes four neural networks modeling PSC, ADN, LMN, and DTN.

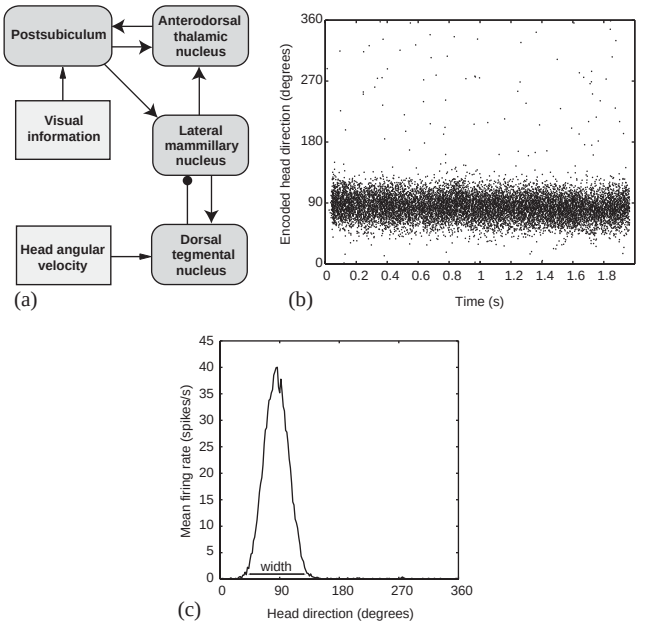

Fig. 1. (a) The model of the HD circuit (adapted from [11]). Arrows and circles indicate excitatory (NMDA and AMPA) and inhibitory (GABA) synapses, respectively. An attractor–integrator network is formed by the interaction between LMN and DTN. (b) Rastergram of the activity of the HD cells in ADN over time (each dot represents one spike). (c) Mean firing rate of ADN cells computed by averaging over $\Delta t = 2$ s.

The dynamics of the entire system is primarily determined by idiothetic signals (e.g., vestibular) that enter the circuit via DTN and are integrated over time through the DTN–LMN interaction. This permits head rotations to be tracked based on the head angular velocity signal ω. Visual stimuli are signaled in the PSC and allow the system to reorient the directional representation following changes in the visual scene. Extrinsic background noise arrives at all formal neurons simulating external spontaneous activity. This noise is defined by a Poisson distribution. In the model, PSC, ADN, and LMN networks consist of a population of $N_E = 1000$ excitatory directional units with evenly distributed preferred directions. The intermodule connectivity (see Fig. 1(a) for reciprocal projections) is such that, for instance, a HD unit $j \in$ PSC with preferred direction θ_j projects to a cell $i \in$ LMN with preferred direction θ_i according to

$$w_{ij} = W^- + (W^+ - W^-) \exp\left(- \frac{(\theta_i - \theta_j)^2}{2\sigma^2} \right), \quad (1)$$

where w_{ij} is the connection weight, W^- and W^+ are, respectively, the minimum and maximum weight, and σ is the width of the gaussian.

In the model, a continuous attractor–integrator network is formed based on the interconnections between LMN and DTN [3]. The HD cells within LMN are connected by recurrent excitatory collaterals such that neurons encoding similar states (i.e., having

similar preferred directions) are strongly coupled. The weight of the collateral projection between cells i, $j \in$ LMN is defined according to Eq. (1). Global inhibition, necessary to implement the center-surround attractor scheme, is provided by a population of interneurons $\xi \in$ DTN. The intrinsic dynamics of the LMN–DTN attractor network make the system settle down to stable (self-sustained) attractor states, in which subpopulations of HD cells with similar preferred directions are active while the others remain silent [3,12].

To integrate non-zero angular velocities (i.e., to shift the stable state over the continuous attractor state space according to ω), two other subpopulations of interneurons $\xi_{cw}, \xi_{ccw} \in$ DTN are considered [3]. The neuronal responses of the ξ_{cw}, ξ_{ccw} cells are correlated with both head direction $\theta(t)$ and angular velocity $\omega(t)$. An interneuron $j \in \xi_{cw}$ with preferred direction θ_j receives excitatory afferents from all HD cells $i \in$ LMN. The weights of these connections are defined by Eq. (1) (i.e., gaussian-distributed matching projections). The interneuron $j \in \xi_{cw}$ sends inhibitory efferents to all HD cells $i \in$ LMN by means of a gaussian weight distribution centered at $\theta_i = \theta_j - \delta$, with $\delta = 50°$, (i.e., gaussian-distributed leftward offset projections). Similarly, each ξ_{ccw} interneuron receives gaussian-distributed matching inputs from LMN and sends gaussian-distributed rightward offset inhibition to LMN. The activity of ξ_{cw} and ξ_{ccw} formal neurons is linearly modulated by the amplitude of the angular velocity $|\omega|$ for $\omega > 0$ and $\omega < 0$, respectively. Therefore, during clockwise head turns for instance, ξ_{cw} cells inhibit the left side of the LMN hill of activity encoding the current direction θ (i.e., introduce an asymmetry within the recurrent coupling between HD cells [3,12]) and yield a clockwise shift $\Delta\theta$ proportional to $|\omega|$. At any time t, the direction representation $\theta(t)$ encoded by the LMN ensemble activity is transmitted to the other subnetworks of the system, via the LMN–ADN–PSC excitatory pathway (Fig. 1(a)).

2.2. Neuron and synapse model

The formal description of neurons and synapses of the model is taken from Brunel and Wang [4]. Both HD cells and interneurons are leaky integrate-and-fire neurons. Synaptic excitation is mediated by NMDA and AMPA formal receptors, whereas synaptic inhibition is mediated by GABA receptors. The rationale behind using two different excitatory receptors is the following: AMPA synapses are rapidly activated and generate fast evoked responses of postsynaptic neurons. However, their short time decay ($\tau_{decay} = 2$ ms) does not permit an appropriate stabilization of the network activity. On the other hand, the larger time course of the NMDA receptors ($\tau_{decay} = 100$ ms) is suitable for the stability issue.

2.3. Population vector coding

A population vector scheme [8] is employed to reconstruct the ongoing animal's heading $\theta(t)$ from the gaussian-shaped ensemble activity profile of formal

HD cells

$$\theta(t) = \arctan\left(\frac{\sum_i^{N_E} \sin(\theta_i)\delta(t-t_i)}{\sum_i^{N_E} \cos(\theta_i)\delta(t-t_i)}\right), \quad (2)$$

where the function $\delta(t-t_i)$ is equal to 1 if the neuron i fired at time t, 0 otherwise.

3. Results

This paper focuses on the effect of static visual stimulation upon the intrinsic dynamics of the HD system. An external excitatory input $\vec{v}$ is applied to the pool of HD cells in the PSC, which propagates this information to the LMN–DTN attractor network (eventually yielding a change of the attractor state) as well as to ADN. We take $\vec{v}$ as a gaussian signal with fixed width $\sigma_v = 15°$, variable amplitude $A_v \in [0,1]$ (corresponding to the intensity of the visual stimulation), and variable mean $\mu_v = \theta_v$ (corresponding to the absolute direction of the polarizing cue).

3.1. Emergence and stability of an attractor state

The rastergram of Fig. 1(b) shows the spike activity of the N_E ADN cells over time. A polarizing stimulus $\vec{v}$ centered at $\theta_v = 90°$ and of normalized amplitude $A_v = 0.2$ is applied during the first 50 ms. This establishes a stable attractor state corresponding to an ensemble activity profile in which the subpopulation of ADN neurons having preferred directions close to θ_v discharges tonically, whereas the others exhibit a very low baseline frequency. Since an attractor state would eventually emerge from random noise, a stimulus of weak intensity A_v is sufficient to polarize the system around θ_v. The barycenter of the ensemble firing pattern, computed by applying Eq. (2) and averaging over $\Delta t = 2$ s, is about $\bar{\theta} = 85°$. After stimulus removal ($50 \leqslant t \leqslant 2000$ ms) the self-sustained attractor state persists over time providing a stable directional coding (the head angular velocity ω is zero). This corresponds to the situation in which the head of the animal is immobile and oriented in a given direction θ_v and all electrophysiologically recorded HD cells with $\theta_i \simeq \theta_v$ continue to discharge tonically. Fig. 1(c) shows the mean firing rate of formal ADN cells as a function of the head direction θ. The mean peak firing rate is about 40 spikes/s and the width of the hill of activity is about 100°. These values are consistent with the mean peak firing rate and the mean width of the tuning curves of HD cells in the rat ADN [11].

3.2. Brief update latencies following reorienting visual stimuli

Fig. 2(a) shows the response of the system to a reoriented visual landmark stimulus. At time $t_1 = 500$ ms, an external stimulus $\vec{v}_1$ is applied to the system (e.g., moving from dark to light conditions) with a 90° offset, i.e. $\mu_{v_1} = \theta_v + 90°$. This triggers a 90° update of all preferred directions, which reorients the HD system according to the directional reference frame anchored to $\vec{v}_1$. As a consequence, the attractor

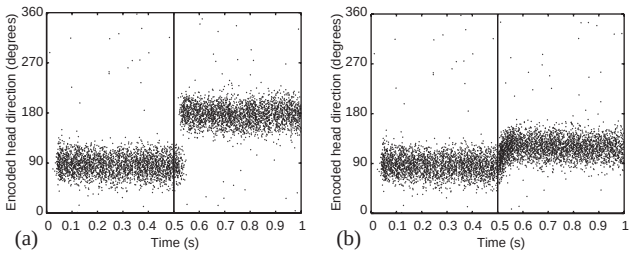

Fig. 2. (a) Raster plot showing the response of the HD system to a 90° reorienting visual stimulus applied at time $t_1 = 500$ ms. All preferred directions are updated and the attractor network settles to a new stable state abruptly (jump). (b) Response of the HD system to a 40° reorienting stimulus applied at time $t_1 = 500$ ms. The HD cells shift their preferred directions towards the new attractor state progressively.

network settles to a new stable state rapidly. The intensity of the applied stimulus is $A_{v_1} = 1$.

Let Δt_* be the time necessary for the attractor dynamics to update its state. To estimate Δt_* quantitatively we apply the same technique employed by Zugaro et al. [13] to measure the update response of HD cells in ADN. For the model, the resulting update latency is $\Delta t_* = 40 \pm 10$ ms. This is consistent with the update latency observed experimentally (80 ± 10 ms) given that the model does not take into account the transmission delay necessary for the visual signals to reach HD cells in ADN. We are not aware of any experimental data reporting this retino-thalamic transmission time, however, Galambos et al. [7] showed that about 20–30 ms are already necessary for the visual stimulation of the retina to evoke field potentials in the primary visual cortex.

3.3. State transition dynamics: abrupt jump or progressive shift?

Whether rat HD cells respond to visual reorientation by changing their preferred directions abruptly or in a gradual progressive manner, is an open question [11,13]. The 'abrupt versus progressive update' issue is also relevant for the theoretical study of state transition dynamics in associative memories [6] and in cortical working-memory models [5].

Fig. 2(a) suggests that an abrupt jump occurs when a 90° reorienting visual cue polarizes the HD system. But it is not clear whether this can be generalized to other magnitudes of shifts. For a fixed width of the gaussian-shaped activity profile, how does the magnitude of the reorienting offset $\Delta\theta$ influence the state transition dynamics of the system? We run a series of simulations in which the same external stimulus $\vec{v}_1$ ($A_{v_1} = 1$) is applied to the HD system at time $t_1 = 500$ ms. Across trials, the reorienting offset $\Delta\theta = \mu_{v_1} - \theta_v$ (with $\theta_v = 90°$) is varied within $[0°, 180°]$ by steps of 1°. Fig. 2(b) shows an example of the state transition for $\Delta\theta = 40°$. The HD cells respond to the reorienting event by progressively shifting their preferred directions towards the new attractor state. To discriminate between state transitions of the type shown in Fig. 2(a) (jump) and those of the type in Fig. 2(b) (shift), we take the instantaneous standard

deviation $\sigma(t)$

$$\sigma(t) = \left(\frac{\sum_i^{N_E} [|\theta_i - \theta(t)|\delta(t - t_i)]^2}{\sum_i^{N_E} \delta(t - t_i)} \right)^{1/2}, \quad (3)$$

of the ensemble HD cell activity around the center of mass $\theta(t)$ (Eq. (2)). We sample all $\sigma(t)$ values within the interval $t_1 \leqslant t \leqslant t_1 + 200$ ms and take the mean deviation $\bar{h}$ relative to the baseline. Let $\Delta\theta_*$ be the critical offset above which the reorienting visual cue triggers a jump rather than a progressive shift. The function $\bar{h}(\Delta\theta)$ is approximately constant for $0 \leqslant \Delta\theta \leqslant \Delta\theta_*$ and quasi-linear after. Our results show that $\Delta\theta_*$ (computed by applying the least-squares error method) is equal to $60 \pm 5°$.

4. Discussion

In contrast to earlier works that use rate code formal neurons to model HD cells, this paper describes a spiking neuron model and focuses on the temporal aspects of the state transition dynamics following reorienting visual stimulation. First, the model reproduces the very short update latencies observed experimentally [13]. Second, the model predicts that the state transition dynamics of the HD system is a function of the magnitude of the angle $\Delta\theta$ of the visual reorientation and suggests that a progressive shift of the preferred directions of HD cells would occur for $\Delta\theta \leqslant 60°$, whereas an abrupt jump would take place for larger offsets [10].

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