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Spatial orientation in navigating agents: Modeling head-direction cells

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Abstract

A model that is consistent with several neurophysiological properties of biological head-direction cells is presented. The dynamics of the system is primarily controlled by idiothetic signals which determine the direction selectivity property. By means of LTP correlation learning, allothetic cues are incorporated to stabilize the direction representation over time. The interaction between allothetic and idiothetic signals to control head-direction cells is studied. Experimental results obtained by validating the model on a mobile Khepera robot are given. The neural system enables the robot to track its allocentric heading effectively. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Head-direction cells; Place cells; Hippocampus; Path integration

1. Introduction

Spatial orientation is a crucial issue for both biological and artificial systems involved in spatial navigation. Ethological data suggest the existence of an internal directional sense supporting animal navigation [7,12]. In particular, animals seem to rely on an internally maintained directional reference when homing by *path integration*, a route-based mechanism which implies the continuous estimation of the rotational and translational components of motion [8]. Neurophysiological findings on rodents show the existence of *head-direction cells*, neurons whose activity is tuned to the animal's allocentric heading in the azimuthal plane [10]. A directional cell *i* fires

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maximally only when the animal's orientation θ is equal to the cell's preferred direction θ_i, regardless of the animal's ongoing behavior and spatial location. Direction-sensitive neurons have been recorded from the following brain regions: postsubiculum (PSC) [10,12], anterodorsal thalamic nuclei (ADN) [11,2], laterodorsal thalamic nucleus (LDN) [9], lateral mammillary nuclei (LMN) [6], parietal and cingulate cortices [3], and dorsal striatum [15].

In particular, ADN, LMN, and PSC may be considered as fundamental structures with respect to the direction selectivity property. ADN and LMN seem primarily related to idiothetic signals (e.g., vestibular inputs), whereas PSC seems more involved in incorporating allothetic information (e.g., visual stimuli) coming from cortical afferents (e.g., via the posterior parietal cortex) [16]. Although the actual mechanism underlying head-direction cells is still unclear, a general consensus is now emerging which identifies inertial self-motion information as primary input. Thus, directional cells would mainly rely on the integration of head's angular velocity over time. Nevertheless, since self-motion information is vulnerable to cumulative drift, animals might use external cues in order to maintain the direction code consistent over time [7].

2. A computational model for head-direction cells

We put forth a neural model in which idiothetic and allothetic signals are combined to establish a stable direction representation. The dynamics of the system is primarily controlled by inertial signals which determine direction selectivity. On the other hand, allothetic information may occasionally modify the system's dynamics to calibrate head-direction cells. Fig. 1(a) shows the model architecture. The directional circuit includes three coupled head-direction populations, namely ADN, LMN, and PSC. To validate the model experimentally, we have implemented it on a real robotic platform.

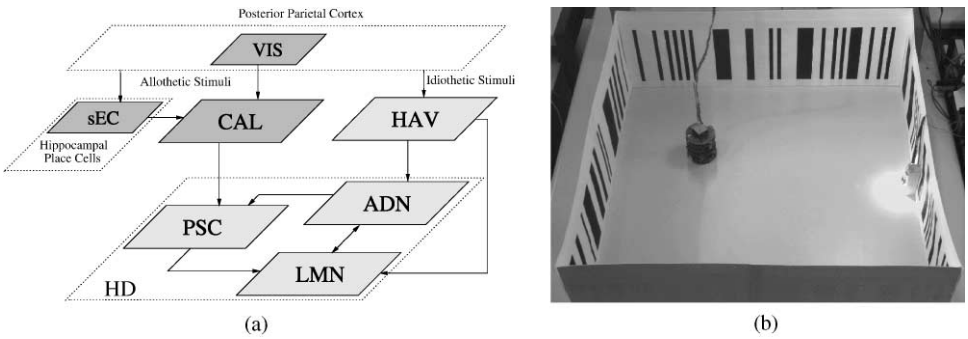

Fig. 1. (a) Model architecture. Light gray regions determine the idiothetic-based dynamics of the system. Dark gray structures are used for allothetic-based calibration. (b) The experimental arena with the Khepera robot inside. A light source is used to calibrate the system. Black and white stripes provide the visual input for hippocampal place cells [1].

The experimental setup consists of a square arena where the robot can freely move and sense the real world (Fig. 1(b)). The system's dynamics is such that the interaction between ADN, LMN, and PSC populations enables the robot to estimate its current allocentric heading $\theta(t)$.

2.1. Idiothetic-based dynamics

To continuously assess angular displacements, we consider a population of head angular velocity cells (HAV) that are correlated to the sign and magnitude of the angular velocity ω. Neurons encoding rotational velocity have been observed in the parietal, somatosensory, and visual cortices [7,2].

ADN cells play a major role in determining the system's dynamics: They induce the synchronized-shifting behavior enabling directional cells to track rotations. Biological ADN cells have the key property of predicting future headings by shifting their preferred direction as a function of ω and of a time delay constant τ. In particular, they tend to anticipate future headings during head turning, whereas they encode current headings when the head is not turning [2]. In the model, cells in ADN exhibit the same property. According to experimental findings, we assume that each ADN cell has a characteristic τ: For each preferred direction θ_i we take $n = 5$ ADN cells a_j, each of which has a specific time-delay constant τ_j, with $\tau_1 = 20$ ms, $\tau_2 = 40$ ms, $\tau_3 = 60$ ms, $\tau_4 = 80$ ms, $\tau_5 = 100$ ms. Fig. 2(a) shows the polar tuning curve of a cell $a_j \in$ ADN during counterclockwise rotation and when the robot is not turning.

LMN cells are correlated to the current heading $\theta(t)$ as well as to the angular velocity $\omega(t)$. Each LMN cell receives afferents from ADN cells and modulates its firing rate according to HAV cell activity. In particular, LMN and ADN cells interact

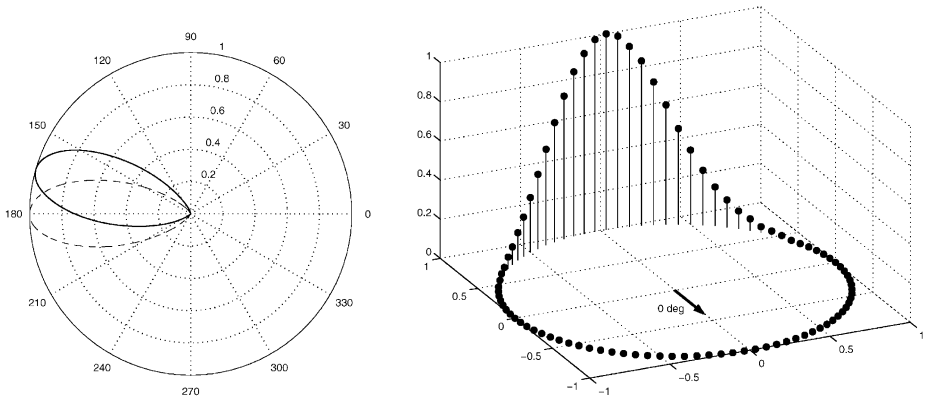

Fig. 2. Results: (a) Polar tuning curve of a cell $a_j \in$ ADN with $\tau_j = 40$ ms. When the robot is not turning, the cell's preferred direction is 180° (dashed line). During counterclockwise turning with $|\omega| = 400°/s$, cell a_j shifts its preferred direction of about 16° (solid line). (b) A sample of PSC population activity. The height of each circle is proportional to the mean firing activity of each PSC cell. The ensemble activity codes for approximately 180°.

with each other to integrate angular motion over time: LMN provides ADN with the current heading $\theta(t)$, whereas ADN informs LMN about future headings $\theta(t')$. Due to the several ADN time delays τ_j associated to each preferred heading θ_i, every cell $i \in$ LMN is actually informed about arrival at θ_i by a sequential activation on its ADN inputs. We apply a safety mechanism which consists of enabling a LMN cell i to fire if and only if all its n ADN afferents have been sequentially activated [2].

2.2. Interpreting the directional output

PSC cells form the output of our directional system. They receive afferents from ADN cells which drive them based on the same safety mechanism used for LMN neurons. The PSC population activity is used, at each time t, to estimate the robot's orientation $\theta(t)$ (Fig. 2(b)). We apply population vector decoding [4,14] to interpret the PSC ensemble activity. Thus, the robot's heading $\bar{\theta}(t)$, as estimated by the PSC population activity, is given by

$$\bar{\theta}(t) = \arctan\left(\sum_p \sin(\theta_p) r_p(t) \Big/ \sum_p \cos(\theta_p) r_p(t)\right), \tag{1}$$

where θ_p is the preferred direction of cell p, and $r_p(t)$ its spike frequency.

2.3. Incorporating allothetic signals

The system uses external cues to maintain a stable representation, that is, to occasionally correct the error affecting the angular-velocity integrator. We let the robot estimate its egocentric bearing α relative to a light source L, and use it to calibrate its directional sense (Fig. 1(b)). However, since L is not infinitely distant, it does not provide an absolute directional reference (e.g., as the sun does for desert ants [13]). Thus, α is not invariant with respect to spatial location. Therefore, we need to combine the bearing α with some place coding information. We consider a calibrating system (Fig. 1(a)) made of: (i) Visual cells (VIS) estimating $\alpha(t)$. (ii) Place cells encoding spatial locations $\vec{p}(t)$. We take cells in the superficial entorhinal cortex (sEC) of our hippocampal model [1], which rely on vision only (Fig. 3(a)). (iii) Calibration cells (CAL), driven by VIS and sEC cells, firing as a function of $\alpha(t)$ and $\vec{p}(t)$. CAL cells project directly onto PSC. Thus, calibration is first achieved by correcting PSC directional cells. Then, PSC propagates the calibration signal to LMN, which in turn starts driving ADN based on the recalibrated signal.

Synaptic projections between PSC, VIS, sEC, and CAL cells are established by means of LTP correlational learning during exploration. Hebbian learning enables the system to correlate allothetic and idiothetic representations based on the agent's experience. CAL cells function as a long-term memory device: They allow the agent to store "snapshots" of PSC cell activity and to use the combined signal $(\alpha(t), \vec{p}(t))$ to recall this activity for achieving calibration. We have experimentally proved the benefit of allothetic-based calibration. Fig. 3(b) shows that the mean tracking error

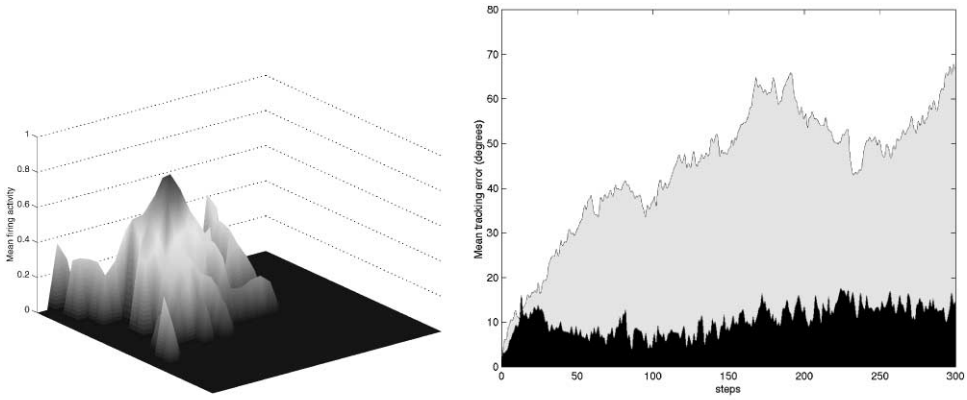

Fig. 3. Results: (a) An example of receptive field of a place cell in the superficial entorhinal cortex (sEC) of our hippocampal model [1]. Each sEC place field identifies a localized region, which enables the robot to self-localize within the environment. (b) Uncalibrated (gray curve) vs. calibrated (black curve) mean tracking error.

$\bar{e}(t) = 1/N \sum_{i=1}^{N} |\theta^i(t) - \bar{\theta}^i(t)|$ of the uncalibrated system rises continuously, whereas the calibrated error remains bounded over time.

2.4. Interrelation between allothetic and idiothetic cues

When the agent first enters an unfamiliar environment, it initializes its directional sense relative to an arbitrary absolute direction Φ. During exploration, it learns to correlate external cues (e.g., the light L) to its internal directional code. On subsequent visits, then, it can use the external reference to polarize its directional sense as soon as it enters the arena. This enables the system to maintain coherent representations across separate sessions. Nevertheless, experimental findings suggest that only visual cues that are perceived as stable by the animal do actually influence its spatial behavior [5]. The Hebb rule we employ to correlate extrinsic and intrinsic cues captures this property. Fig. 4(a) shows the strength of the correlation between external and internal representations as a function of the stability of landmark L.

To further study the interrelation between external and internal signals, we run two series of experiments to reproduce the results obtained by Knierim et al. with rodents [5]. In the first series, the robot is not disoriented at the beginning of each training trial. Thus, the robot's inertial frame of reference remains consistent across different training trials. Alternatively, in the second training series the robot is disoriented before each session (i.e., its directional system is disrupted before each trial). Then, with respect to the robot's inertial system, L is not a stable cue across sessions. After training, we run probe trials in which we record head-direction cells from both the robot that underwent disorientation before training and the one that did not. At the beginning of each recording trial the robot is disoriented and placed at the arena

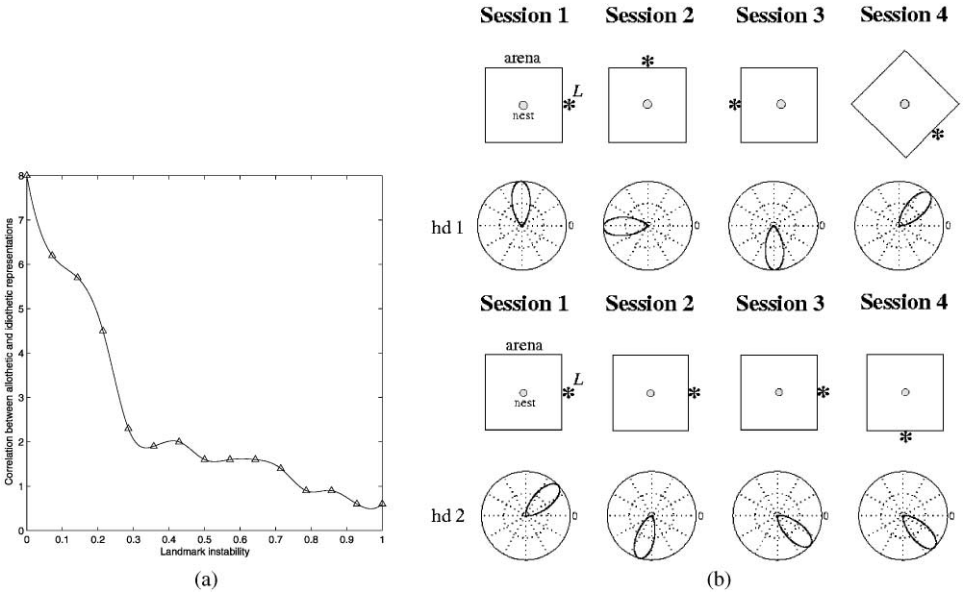

Fig. 4. Results: (a) Correlation between idiothetic and allothetic representations as a function of the instability of L. (b) The influence of L upon two cells hd_1 and hd_2 during probe trials. Cell hd_1 is recorded from the robot trained under nondisorientation conditions, whereas hd_2 from the disoriented one. L controls hd_1 but does not influence hd_2.

center (nest). Thus, the robot attempts to re-align its directional sense by using L as a polarizing cue. Fig. 4(b) shows two head-direction cells hd_1 and hd_2 recorded during 4 probe tests. Cell hd_1 is from the robot trained under non disorientation conditions. Cell hd_2 is from the robot that underwent disorientation during training. Results are consistent with neurophysiological data reported by Knierim et al. [5]: Cell hd_1 is controlled by the external cue L, whereas cell hd_2 is not.

3. Conclusions

The above model relies on anatomical as well as neurophysiological data in order to capture the functional properties of head-direction cells. Predictions of the model will be tested in the future. We have stressed the importance of integrating extrinsic and intrinsic signals to establish a coherent directional code over time. We have done experiments to investigate the interrelation between these two types of cues, and found results similar to those reported by neurophysiologists.

References

[1] A. Arleo, W. Gerstner, Biol. Cybernet. 83 (2000) 287–299.
[2] H.T. Blair, P.E. Sharp, J. Neurosci. 15 (9) (1995) 6260–6270.

[3] L.L. Chen, L. Lin, E.J. Green, C.A. Barnes, B.L. McNaughton, Exp. Brain Res. 101 (1994) 8–23.
[4] A.P. Georgopoulos, A. Schwartz, R.E. Kettner, Science 233 (1986) 1416–1419.
[5] J.J. Knierim, H.S. Kudrimoti, B.L. McNaughton, J. Neurosci. 15 (1995) 1648–1659.
[6] C.L. Leonhard, R.W. Stackman, J.S. Taube, Soc. Neurosci. Abstr. 22 (1996) 1873.
[7] B.L. McNaughton, L.L. Chen, E.J. Markus, J. Cognitive Neurosci. 3 (1991) 190.
[8] H. Mittelstaedt, M.L. Mittelstaedt, in: F. Papi, H.G. Wallraff (Eds.), Avian navigation, Springer, Berlin Heidelberg, 1982.
[9] S.J.Y. Mizumori, K.E. Ward, A.M. Lavoie, Brain Res. 570 (1992) 188–197.
[10] J.B.Jr. Ranck, Soc. Neurosci. Abstr. 10 (1984) 599.
[11] J.S. Taube, Soc. Neurosci. Abstr. 18 (1992) 708.
[12] J.S. Taube, R.I. Muller, J.B.Jr. Ranck, J. Neurosci. 10 (1990) 420–435.
[13] R. Wehner, Neujahrsblatt der Naturforschenden Gesellschaft Zürich 184 (1982) 1–132.
[14] M.A. Wilson, B.L. McNaughton, Science 261 (1993) 1055–1058.
[15] M.P. Witter, Hippocampus 3 (1993) 33–44.
[16] K. Zhang, J. Neurosci. 16 (6) (1996) 2112–2126.

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