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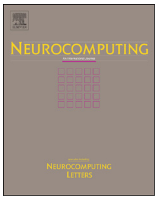

The sensori-motor model of the hippocampal place cells

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ABSTRACT

Hippocampal place cells are important in spatial navigation as their place specific firing provides a spatial map of the environment. Empirically, the place cell firing pattern seems to be determined by both the sensory and the motor inputs. However, the current models of the place cells assign either the sensory or the motor integration as the reason for their firing. In this paper, we propose an explanation for place cell firing based on integration of both sensory (vision, auditory, olfactory etc.) and motor inputs (through grid cells which process head direction cell and vestibular inputs). The inspiration for this model is the difference in visual information processing in animals with and without binocular vision, and empirical observations from the hippocampal formation in animals.

1. Introduction

Spatial navigation is quintessential to the survival of any animal species, as it aids the animal in its quest for food, shelter, mate etc. The requirements for spatial navigation [1] are a map of the environment and knowledge of direction of movement of the animal. The hippocampal formation [2] of the brain is thought to perform this function in biology. The hippocampal formation consists of the hippocampus, the subiculum and the medial entorhinal cortex among other regions. The hippocampus contains the place cells, the subiculum the head direction cells and the medial entorhinal cortex the grid cells primarily. Each place cell fires when the animal is located at a particular place in the environment. As such, ensembles of place cells are thought to maintain a map of the environment. The head direction cells provide information on heading direction by increasing their firing rate when the animal's head points to a particular direction. Each grid cell fires whenever the animal is positioned at corners of a regular hexagon in the environment. Thus, their firing pattern provides a matrix spanning the environment like the grid on a map. Therefore, with their place specific firing patterns, the cells of the hippocampal formation aid in spatial navigation in animals. Several computational neuroscience models have been postulated to describe the place specific firing of the hippocampal place cells. All these models assign either the sensory (processed by the boundary vector cells) or the motor inputs (processed by the grid cells) as the cause of this firing. However, the available empirical and phylogenetic evidence suggests that a combination of the two inputs might be a more plausible answer. This is what the sensori-motor model presented in this paper attempts to look at.

2. Background

Behavioral evidence for role of the hippocampal formation in spatial navigation comes from experiments on rats. The mean latency on radial maze tasks [3] fails to reduce with training in rats with hippocampal lesions as compared to those without these lesions. And its role in formation of new episodic memories is evident from the case of the patient Henry G Molaison [4] who lost his ability to form new episodic memories after surgical removal of his temporal lobe. Thus, it is reasonably certain that the hippocampal formation is involved in spatial navigation and memory encoding. However, the mechanism of doing so can be better understood by looking at the anatomy of the hippocampal formation, empirical studies on its cells and the phylogenetic evidence summarized in the following sections.

2.1. The hippocampal formation

The hippocampal formation [5] is a C shaped structure located on the medial aspect of the cerebral hemispheres in the brain. It consists of the subiculum, the medial and the lateral entorhinal cortices and the hippocampus proper, among other areas.

The subiculum contains the head direction cells [6,7] which fire whenever the animal is moving in the cells' preferred firing direction or within 45° thereof. The head direction cells act as a system, i.e., the relative orientation of each cell to the rest remains the same. The baseline position for the system is determined w.r.t. an orienting sensory cue in the environment. The representation of the environment by the head direction cells is allocentric (and not egocentric as is true of sensory modalities like vision).

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The medial entorhinal cortex contains the grid cells [8] which fire when the animal is located at the corners of an equilateral triangle in space. The firing pattern of every grid cell repeats over the entire surface as the animal moves around. The neighboring grid cells show similar spacing, field size and orientation but differ in their vertex locations. The spatial frequency of the grid firing pattern increases along the dorso-ventral axis of the medial entorhinal cortex-from 30–45 cm in the most dorsal to about 1 to several meters in the most ventral region. Increasing the size of the environment leads to increase in the number of activity nodes of the grid cells along the direction of expansion of the environment. Thus, the grid cells provide a matrix which spans the environment.

The hippocampal place cells fire when the animal is present at particular locations in the environment [9–11]. Their firing field sizes scale along the dorso-ventral axis like the spatial firing frequencies of the grid cells. Moreover, as the size of the environment increases, their field size also increases. Same place cell can fire at different locations (remapping) in different environments [12]. It has also been observed that the firing time (as evidenced by phase precession relative to theta) for both the grid and the place cells located at similar dorso-ventral location is the same [13] and that both undergo remapping [12].

In short, the head direction cells provide information about the direction in which the animal is moving, the grid cells provide a matrix (like grid on a map) spanning the entire environment and the place cells maintain a map of locations of significance in the environment. This information is constantly learned, unlearned and updated based on fresh inputs from the environment. Thus, the hippocampal formation of the brain functions as a self-learning internal GPS with memory and plasticity.

2.2. Connectivity of the hippocampal formation

The hippocampal formation (HF) [14] receives highly processed sensory inputs from wide areas of the associational cortices and from the subcortical structures. Afferents arrive at the entorhinal cortex (ERC) and efferents leave from the cornu ammonis (CA) which is a part of the hippocampus along with the dentate gyrus (DG). Many closed loops are formed within the HF and with outside structures. Within the HF, there is a loop from ERC → the hippocampus and the subiculum → ERC.

Dorsal areas of the medial ERC are connected to the dorsal and the ventral to the ventral areas of the hippocampus [15,16].

2.2.1. Afferents to the HF

- The lateral entorhinal cortex (LEC) and the pre-subiculum receive inputs from the olfactory bulb and various cortical areas – including seats of convergence of multimodal sensory information like the infra-limbic, insular, cingulate and temporal polar cortices which receive their inputs from the primary visual, auditory and somesthetic areas. Within the ERC, the ventral portion receives more exteroceptive sensory information and the dorsal portion receives information from the limbic related subcortical centers, reflecting the internal status of the organism.
- The medial entorhinal cortex (MEC) receives inputs from the medial septal-diagonal band complex (theta oscillations) and from the thalamus (head direction information from the vestibular complex in the inner ear (the semicircular canals respond to rotations, the otolithic organs sense linear accelerations))

Thus, the LEC and the subiculum get a variety of processed sensory inputs from outside and within the body which they also share with the rest of the hippocampal formation. And the MEC grid cells can integrate head direction and motion information and perform temporal coding w.r.t. theta oscillations.

2.2.2. Efferents from the HF

- From the CA, the efferents project to the lateral septal nuclei → the HF through the medial septal-diagonal band complex. These could influence theta reciprocally and provide temporal information to the HF.
- Efferents from the subiculum project to the ventral pallidum and are involved in planning and control of voluntary movements and to the mammillary body, the anterior thalamic nucleus, the bed nucleus of the stria terminalis and the cell free capsular zone surrounding the ventromedial hypothalamic nucleus could influence the secretions of the anterior pituitary – the master gland.

Thus, the HF can influence both internal organs through the pituitary and external motion through control on planning and muscle movements. In [14], the authors used channel rhodopsin to track the connectivity patterns of the place cells. They found that the place cells receive inputs from the grid cells (60%), the border cells (15%) and the head direction cells (25%).

2.3. Further empirical observations

With the possibility of single cell recordings from neurons, scientists like John O'Keefe used the technique to record the firing patterns of the hippocampal pyramidal cells as the animal moved around in a defined enclosure (in lab) freely foraging for food particles. Each hippocampal place cell [9–11,17,18], was seen to fire repeatedly whenever the animal visited a particular place in the enclosure. And ensembles of place cells with their place specific firing patterns together seemed to form a spatial map of the environment. These environment specific firing patterns of ensembles of place cells (and grid cells) were observed to be more well defined over repeated trials in the same environment [19–21] – indicating a role for learning [22]. But the place cell firing patterns changed with changes in the environment – called remapping [23]. Remapping could be partial or complete. Partial remapping means change in firing rate of individual place cells while complete remapping means change in firing pattern of ensembles of place cells. Partial remapping has been observed with changes in color, shape or size of the enclosure while complete remapping is seen with shifting the animal from one enclosure to another [11,17,24–29]. Some silent cells [30] have also been observed in the hippocampus which could possibly be helping the 'active' cells in space encoding.

Another important observation [26,31] is that the place cells fire at the entrance to an enclosure which indicates that an entrance could be used by the animal as a phase (w.r.t. theta) resetting point. Also resetting is observed to occur at the turning points [32] with later space representations being anchored to the preceding turning points. Boundaries [18,29,33,34], also seem to influence place cell firing such that in a rectangular enclosure, the place cell firing field along the boundaries is linear while in a circular enclosure, it is elliptical. The place cell firing has also been observed to depend on the head direction of the animal [26,29,35,36] without any tendency for the fields to be located where the animal spends more time – this could link the place cell firing to context. Reward has been seen to shift the place fields towards itself [37], and increase the overall firing rate [38] of the CA3 cells. The activity was further enhanced during learning and reactivated coherent elements of the paths associated with the reward location. This could be a mechanism to bind rewarding outcomes to the experiences that precede them.

In [17], the results indicate that as the firing rate of one of the place cells increased, there was a reduction in firing rates of its neighbors which maintained a constant overall low mean rate.