

2008 Special Issue

# Impact of temporal coding of presynaptic entorhinal cortex grid cells on the formation of hippocampal place fields<sup>☆</sup>

Colin Molter<sup>\*</sup>, Yoko Yamaguchi

*Laboratory for Dynamics of Emergent Intelligence, RIKEN BSI, 2-1 Hirosawa, Wako Saitama 351-0198, Japan*

Received 8 August 2007; received in revised form 30 November 2007; accepted 14 December 2007

## Abstract

Many behavioural experiments have pointed out the important role played by the hippocampus in spatial navigation. This role was enlightened by the discovery of hippocampal cells in rodents firing only at very specific locations in an environment, the so-called 'place field'. Recently, it has been observed that one synapse upstream of the hippocampus, entorhinal cells fire when the rat is located at any of the vertices of grid fields covering the environment. Furthermore, it was reported that both hippocampal and entorhinal cells have firing activity modulated by the theta local field potential in term of theta phase precession. In a previous report, the authors suggested that the temporal code driven by theta phase precession should play an important role in the building of hippocampal place cells from entorhinal grid cells. Here, with the help of a simpler computational model, we further investigate the implications of our hypothesis. We demonstrate that the nonlinear nature of the shape of the phase precession predicts that place field location are slightly backward shifted according to the direction of the rat.

© 2007 Elsevier Ltd. All rights reserved.

*Keywords:* Theta phase precession; Place cell; Grid cell; Dentate gyrus; Entorhinal cortex; Temporal code

## 1. Introduction

One important role of the hippocampus is to facilitate spatial memory in the form of navigation, with damage resulting in impaired ability to navigate in familiar areas (Maguire et al., 2000; OKeefe & Nadel, 1978). In rodents, it was observed that hippocampal principal cells had firing activity only when the rodent was running at specific locations in a given environment; the "place fields" (OKeefe & Dostrovsky, 1971). Furthermore, during exploratory behavior, the rhythmic theta oscillation (4–12 Hz) is the dominant network activity pattern in the hippocampus, and the firing activity of the "place cells" is modulated by this theta local field potential in term of theta phase precession (OKeefe & Recce, 1993): When the rat is entering a place field, firing activity occurs at late theta phase, then, the spiking activity shifts progressively to earlier phases of the theta rhythm as the rat passes over the place field (Fig. 2).

To have a better understanding of how spatial navigation works, it is important to understand why the firing activity of hippocampal place cells correlates with the behavioural space. Cortical inputs are conveyed to the hippocampus mainly through the entorhinal cortex layer II/III (EC) which contains two distinct regions, the medial entorhinal cortex (MEC) and the lateral entorhinal cortex (LEC) (Witter & Amaral, 2004). According to evidence that MEC neurons displayed modest spatial selectivity (Barnes, McNaughton, Mizumori, Leonard, & Lin, 1990; Quirk, Muller, Kubie, & Ranck, 1992), some researchers proposed that the hippocampal place field representation was directly received from the entorhinal layer. In a different view, other researchers proposed that the place field representation could result from an intra-hippocampal loop (Jensen & Lisman, 1996; Tsodyks, Skaggs, Sejnowski, & McNaughton, 1996). Recently, this story received a new direction with the discovery that MEC cells were not characterized by a usual place field property: they fire according to a triangular grid pattern (Fyhn, Molden, Witter, Moser, & Moser, 2004; Hafting, Fyhn, Molden, Moser, & Moser, 2005). As a rat moves through an environment, the MEC neuron fires in multiple spots, which are located at the vertices of an imaginary grid made of equilateral triangles that

<sup>☆</sup> An abbreviated version of some portions of this article appeared in Molter and Yamaguchi (2007) as part of the IJCNN 2007 Conference Proceedings, published under IEE copyright.

<sup>\*</sup> Corresponding author. Tel.: +81 (0) 48 462 1111x7426 (office); fax: +81 (0) 48 467 6938 (office).

E-mail address: [cmolter@brain.riken.jp](mailto:cmolter@brain.riken.jp) (C. Molter).

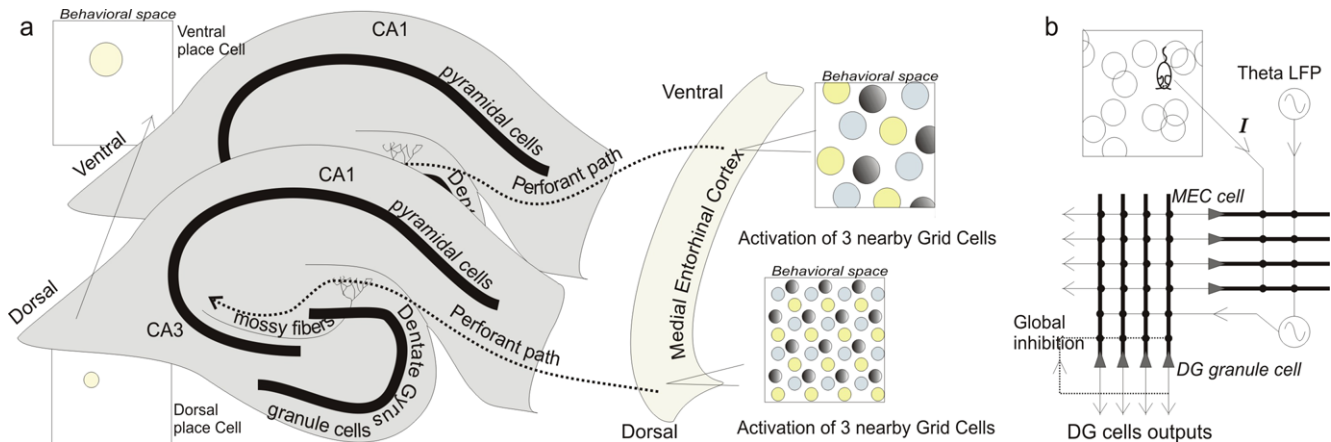


Fig. 1. (a) Schematic anatomical representation of the Hippocampal formation, including the topography of the projections of interest in this paper, i.e. the perforant pathway from the MEC layer 2. Examples of cell firing activity location, while the rat is running in the environment, are plotted. The MEC shows the presence of grid fields, while place fields show up in the Hippocampal formation. Grids at the ventral location have a larger spacing between the vertices than more dorsal grid cells. Similarly, in the Hippocampal formation, dorsal place cells have higher place resolution than ventral place cells. (b) The model: neurons having a grid field property analogous to MEC grid cells are massively connected to the main entrance point of the Hippocampal formation, i.e. the Dentate Gyrus. The firing activity of MEC grid cells is driven by the sensory input  $\mathcal{I}$  and shaped by the theta LFP with theta phase precession.

covers the entire floor of the environment (Fig. 1). Anatomically nearby neurons display grids at a similar resolution with different orientations and spatial phase shift. The scale and the field size of the grid varies only when the electrode is moved along the dorsoventral axis: small scale grids (high spatial resolution) are observed for dorsocaudal MEC cells, while more ventral MEC cells have larger scale grids (the distance between field peaks varying by at least a factor of 2).

This raises the question of how the spatially repeating responses of MEC grid cells are mapped to hippocampal place fields; and more specifically to the place fields of the dentate gyrus (DG) which constitutes the gate of the hippocampus. As suggested by Hafting et al. (2005), the interaction between multiple grids, with different scales and/or orientations, should enable to encode space without repetition. Following this idea, different models have been proposed, sharing the same concept that the conjunctive activity of multiple grids should produce unique positional encoding over a large space (Fuhs & Touretzky, 2006; McNaughton, Battaglia, Jensen, Moser, & Moser, 2006; Rolls, Stringer, & Elliot, 2006; Solstad, Moser, & Einevoll, 2006). However, these models failed to reproduce correctly the appearance of place fields. A common criticism that could be addressed with these models is that they did not elaborate on the precise temporal spiking activity found in both layers: Theta phase precession characterizes the firing activity of both MEC layer II grid cells (Hafting, Fyhn, Moser, & Moser, 2006) and, one synapse downstream, of dentate gyrus place cells (Yamaguchi, Aota, McNaughton, & Lipa, 2002).

In a previous report (Molter & Yamaguchi, 2007), the authors proposed that entorhinal theta phase precession should play an important role in the organization of hippocampal place cells from entorhinal grid cells. To illustrate this hypothesis, computational simulations were performed, using an oscillatory model originally proposed in Yamaguchi (2003). Here, after summarizing these previous results, we developed a new original computational model which encompasses in a simplistic and graphical way the essential role played by

theta phase precession in space computation. We further used this model to test how the shape of the distribution between the phase of the firing activity and the distance travelled in the field should impact on the place field formation. In agreement with neurophysiological observations made in linear environments (Mehta, Barnes, & McNaughton, 1997), we predict that the nonlinear shape of the phase distribution should lead to direction dependent place fields; the field shifting backward according to the rat's direction.

## 2. Preliminaries

A simple view of the hippocampus is considered here: only the medial Entorhinal Cortex layer II (MEC) and the DG are accounted for (Fig. 1(b)). The MEC feeds massively the DG granule cells through the perforant pathway while feedback inhibition (mediated by inhibitory interneurons) maintains a sparse DG activation.

Two computational models are tested. The first layer of both models comprises the sensory input  $\mathcal{I}$ , which fires the corresponding MEC grid cells when the rat enters the corresponding vertices of their associated grids (Fyhn et al., 2004; Hafting et al., 2005). In a given environment, a grid cell  $i$  has firing activity at multiple locations (indexed by the natural numbers  $n$  and  $m$ ) whose centres  $(cx_i^{nm}, cy_i^{nm})$  are given by the following equations:

$$cx_i^{nm} = \alpha_i + n a_i \cos \varphi_i + m a_i \cos(\varphi_i + \pi/3) \quad (1)$$

$$cy_i^{nm} = \beta_i + n a_i \sin \varphi_i + m a_i \sin(\varphi_i + \pi/3) \quad (2)$$

where  $\alpha_i$  and  $\beta_i$  give the spatial phase shift relative to an arbitrarily chosen reference point,  $\varphi_i$  gives the orientation relative to an arbitrary direction and  $a_i$ , the distance between nearby vertices, determines the scale of the grid. A further parameter,  $\sigma_i$ , specifies the radius of the grid fields (see below).

Download English Version:

<https://daneshyari.com/en/article/404672>

Download Persian Version:

<https://daneshyari.com/article/404672>

[Daneshyari.com](https://daneshyari.com)