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RESEARCH ARTICLE

Self-organization of grid fields under supervision of place cells in a neuron model with associative plasticity

Andrey Stepanyuk

Bogomoletz Institute of Physiology, Kiev, Ukraine

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Abstract
The grid cells (GCs) of the medial entorhinal cortex (MEC) and place cells (PCs) of the hippocampus are assumed to be the key elements of the brain network for the metric representation of space. Existing theoretical models of GC network rely on specific hypotheses about the network connectivity patterns. How these patterns could be formed during the network development is not fully understood. It was previously suggested, within the feedforward network models, that activity of PCs could provide the basis for development of GC-like activity patterns. Supporting this hypothesis is the finding that PC activity remains spatially stable after disruption of the GC firing patterns and that the grid fields almost disappear when hippocampal cells are deactivated. Here a new theoretical model of this type is proposed, allowing for grid fields formation due to synaptic plasticity in synapses connecting PCs in hippocampus with neurons in MEC. Learning of the hexagonally symmetric fields in this model occurs due to complex action of several simple biologically motivated synaptic plasticity rules. These rules include associative synaptic plasticity rules similar to BCM rule, and homeostatic plasticity rules that constrain synaptic weights. In contrast to previously described models, a short-term navigational experience in a novel environment is sufficient for the network to learn GC activity patterns. We suggest that learning on the basis of simple and biologically plausible associative synaptic plasticity rules could contribute to the formation of grid fields in early development and to maintenance of normal GCs activity patterns in the familiar environments.

E-mail address: standrey@biph.kiev.ua

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Introduction

The grid cells (GCs) in the medial entorhinal cortex (MEC) of mammals are the neurons whose firing activity during animal navigation is concentrated near the centers of hexagonally symmetric grid covering the environment (Hafting, Fyhn, Molden, Moser, & Moser, 2005; Fyhn, Hafting, Treves, Moser, & Moser, 2007; Moser, Kropff, & Moser, 2008; Moser, Rowland, & Moser, 2015; Stensola et al., 2012). The network of GCs is considered to be a component of the brain system for metric representation of space and navigation (Hartley, Lever, Burgess, & O'Keefe, 2014; Moser et al., 2008; Moser et al., 2015). Patterns of activity, connectivity and development of GC networks have been extensively investigated, and a number of theoretical models of GC network was developed during last decade (see Moser, Moser, & Roudi, 2014; Zilli, 2012 for review and Bush & Burgess, 2014; Castro & Aguiar, 2014; Hasselmo & Shay, 2014; Pilly & Grossberg, 2013; Widloski & Fiete, 2014 for recent models). These models differ significantly in the way they represent current position of the animal. For example, models based on continuous attractor networks (CAN) (Conklin & Eliasmith, 2005; Fuhs & Touretzky, 2006; McNaughton, Battaglia, Jensen, Moser, & Moser, 2006; O'Keefe & Burgess, 2005), interference of slow oscillations (Blair, Welday, & Zhang, 2007; Burgess, Barry, & O'Keefe, 2007; Gaussier et al., 2007; Giocomo, Zilli, Fransen, & Hasselmo, 2007) and feedforward networks (Castro & Aguiar, 2014; Kropff & Treves, 2008; Pilly & Grossberg, 2013) exist. Depending on the nature of input signals these models could be divided into path-integrating models and models that utilize location-specific combinations of input signals. Currently, none of the existing GC network models could be considered as sufficiently complete and supported by the experimental data.

Most of the GC network models could be assigned to the path-integrating type. They imply the emergence of a network, controlled by the signals about animal's speed and direction of movement, in order to provide integration of movements along the path (Moser et al., 2014; Zilli, 2012). Models of this type have a number of restrictions. For example, path integrating models use only a small part of sensory input signals from those which are received by EC and could be the source of navigational information. Other set of problems arise because path integration process in these models is assumed to be continuous, and gradually accumulating integration errors should constantly be adjusted by some additional mechanism (Cheung, Ball, Milford, Wyeth, & Wiles, 2012; Hardcastle, Ganguli, & Giocomo, 2015).

Most of the existing models of path-integrating type rely on relatively complex predefined patterns of network connectivity and do not address the problem of these patterns development. For example, many path-integrating models, which use CAN for animal position representation (Conklin & Eliasmith, 2005; Fuhs & Touretzky, 2006; McNaughton et al., 2006; O'Keefe & Burgess, 2005), are based on hypotheses that (1) two-dimensional neuronal network with toroidal topology of synaptic connections exists in the entorhinal cortex, (2) strength and symmetry of these connections are high enough for a stable localized bump or a periodic set of bumps of activity to exist in the network, and (3) additional groups of neurons exist with activity, modulated by speed and direction of animal movement, and with asymmetric connectivity within attractor network layer. As a result, the bump of activity in 2D layer of neurons could move in a coordinated manner with animal movement. Several possible scenarios of development of path integrating CAN were proposed (Hahnloser, 2003; McNaughton et al., 2006; Stringer, Rolls, Trappenberg, & de Araujo, 2002; Widloski & Fiete, 2014). The problem of development of most of connectivity patterns, assumed by hypotheses (1)—(3), was directly addressed in a recent model of Widloski and Fiete (2014). In their work, formation of path-integrating 2D network of GCs under control of both location-specific and velocity-modulated input signals was demonstrated. This network was obtained as a result of self-organization process driven by spike-time dependent plasticity (STDP) in the lateral synaptic connections in the network of excitatory and inhibitory neurons.

Another type of the GC models suggests that the feedforward network connecting neurons with spatially modulated patterns of activity, such as hippocampal place cells (PCs) or MEC/parasubicular stripe cells, to GCs is formed due to associative synaptic plasticity. (Castro & Aguiar, 2014; Kropff & Treves, 2008; Pilly & Grossberg, 2013; Si, Kropff, & Treves, 2012). In several models of this type, formation of grid fields in a given environment is associated with formation of synaptic connections to GCs selectively from those PCs whose firing fields are located in a nodes of hexagonal lattice (Castro & Aguiar, 2014; Kropff & Treves, 2008). This connectivity pattern is supported by the finding that PC activity remains spatially stable after the disruption of GC firing patterns (Bush, Barry, & Burgess, 2014; Hales et al., 2014; Koenig, Linder, Leutgeb, & Leutgeb, 2011) and that grid patterns almost disappear when hippocampal cells are deactivated (Bonnevie et al., 2013). Development of the early PCs before GCs formation also supports the role of PCs as spatial information providers to GCs (Langston et al., 2010; Wills, Cacucci, Burgess, & O'Keefe, 2010).

The limitation of models based on PC—GC feedforward network self-organization (Castro & Aguiar, 2014; Kropff & Treves, 2008) is that they do not explain explicitly how normal pattern of GC activity could persist during animal's navigation in darkness (Hafting et al., 2005). Other GC network property which seems to be difficult to explain within PC—GC feedforward network hypothesis is the fact that in a novel environment relative phases of grid fields in the pairs of GCs do not change, while place fields rebuilt completely and their relative phases in PC pairs before and after remapping are not correlated (Fyhn et al., 2007). As it was described in the work of Kropff and Treves (Kropff & Treves, 2008), alignment of grid fields orientations in the network and correlated remapping of grid fields in different environments could be, in principle, achieved if GCs activity before grid fields formation is modulated by head direction cells and if the strength of horizontal excitatory synaptic connections, which form between pairs of GCs in 2D layer of GCs, is modulated by the degree of similarity of their preferred head directions and by their relative distance in 2D layer. In the work of Si et al. (2012) it was shown that