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

Andrey Stepanyuk
Bogomoletz Institute of Physiology, Kiev, Ukraine, standrey@biph.kiev.ua

The grid cells (GCs) of the medial entorhinal cortex (MEC) and place cells (PCs) of the hippocampus are key elements of the brain network for the metric representation of space. Currently, any of the existing theoretical models can explain all aspects of GC-specific spatially selective patterns of activity. It is also not clear how these patterns are formed during the network development. On the other hand, it was previously shown that the network that can learn to extract high principal components from the activity of the place cells could provide the basis for GC-like activity patterns development. Supporting this hypothesis is the finding that PC activity remains spatially stable after the disruption of the GC firing patterns and that grid patterns almost disappear when hippocampal cells are deactivated. Development of the early PCs before GCs formation also supports the role of PCs as the spatial information providers to GCs.

Here we have developed a new theoretical model of grid fields formation based on synaptic plasticity in synapses connecting PCs in hippocampus and neurons in entorhinal cortex.

Learning of hexagonally symmetric fields in the model is 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 which restrict synaptic weights.

In contrast to previously described models, this network could learn GC patterns after a very short experience of navigation in a novel environment.

In conclusion 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 familiar environments.

I. INTRODUCTION

Existing models of the grid fields self-organization in the entorhinal cortex (EC) could be divided into two types [1–6]. Models of the first type imply the emergence of a network controlled by the signals about the animal’s speed and direction of movement in order to provide integration of movements along the path [1]. Models of this type have a number of disadvantages. First, 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. Second, integration process in these models is assumed to be continuous and gradually accumulating integration errors should constantly be adjusted by some additional mechanism [7].

Another type of the grid fields self-organization models suggests that the feedforward network is formed from hippocampal place cells (PCs) or MEC/parasubicular stripe cells and grid cells (GCs) [3–6]. In several models of this type, formation of grid fields in a given environment is associated with formation of synaptic connections selectively to GCs from those PCs whose firing fields are located in a nodes of hexagonal lattice [3, 4]. However, such models (with feedforward connections from hippocampal PCs to GCs in entorhinal cortex) fail to explain the fact that animal’s navigation is actually possible in darkness using probably just velocity and head direction signals [7–9]. They also do not explain the fact that in a novel environment relative phases of grid fields in the pairs of grid cells do not change while place fields are completely rebuilt and their relative phases in place cell pairs before and after remapping are not correlated [7–9]. Modular organization of grid cells and the fact that formation of new grid fields in a novel environment usually do not require prolonged sensory experience in this environment are the other issues that require explanation within the framework of these models [7–9].

Models of the second group rely on specific plasticity rules and differ by their characteristics. For example, the model of Korpf and Treves [3, 4] assumes that a mechanism of GCs firing rate adaptation besides Hebbian plasticity rules in PC-GC synapses is important for grid fields development. The model of Castro and Aguiar [6] assumes the existence of a specific complex rule linking plasticity rate and direction with a frequency of presynaptic activity in PC-GC synapses. At the same time, it is well known that the patterns with hexagonal symmetry are one of the most ubiquitous types of patterns that emerge as a result of symmetry breaking bifurcations in many physical systems [10], in particular in the models of self-organization based on Hebbian plasticity in neural networks [11, 12] described by the neural fields equations. Thus it is interesting to explore other possible mechanisms of grid fields development with a more general types of plasticity rules.

The goal of this work is to describe a wide class of models in which the grid fields are formed as a result of plasticity of PC-GC synapses or synapses from sensory neurons to GC and to demonstrate a number of possible grid fields formation scenarios in these models.
The main difference of the model proposed in this paper from the previously proposed models is that it uses only simplest rules of synaptic plasticity, similar to those supported by experimental data, and does not require assumptions about the firing rate adaptation. Learning of grid fields in proposed model could be very fast and does not require a large exploratory experience in a novel environment. In addition, the proposed model is compatible with CAN models of GCs network and could serve as a basis for path integration error correction and self-organization of attractor control in them.

II. THEORY

1. Description of the model

In this work we develop a hypothesis that grid cells recognize sets of sensory signals, associated with the location of an animal in certain places in the room, with the help of clusters of synapses from hippocampal place cells to grid cell or from neurons of different sensory systems to grid cell. Clusters are composed of synapses with correlated presynaptic activity and form as a result of Hebbian associative plasticity. In addition, under the action of both associative synaptic plasticity and homeostatic plasticity which limits the weights of the individual synapses or groups of synapses, separation of clusters occur in such a way that different clusters will encode maximally different sets of local sensor signals.

As a possible mathematical model of such a system we consider a network of neurons with linear activation rule

\[ y_t = w^T_t x_t \]  

were \( x_t \) is a vector of firing rates of presynaptic neurons at time moment \( t \), \( w_t \) vector of PC-GC synaptic weights and \( y_t \) - firing rate of postsynaptic neuron.

We will consider several types of synaptic plasticity rules which will lead to different scenarios of grid fields self-organization. Let start from the general form of equation describing synaptic weights change as a function of rates of presynaptic and postsynaptic action potentials:

\[ \dot{w}_{it} = \eta(x_{it}, y_t) + \zeta(y_t, w_t) w_{it} + P(w_{it}, x_{it}) \]  

where \( \zeta \) and \( P \) terms describe global and local homeostatic plasticity and \( \eta \) term describes associative plasticity corresponding to LTP and LTD. For simplicity we will approximate homeostatic plasticity terms by polynomials: \( \zeta(y_t) = -\sigma y_t^2 \) or \( \zeta(w_t) = -\sigma \sum_k w_{ikt}^2 \) and \( P(w_{it}, x_{it}) = A(x_{it}) w_{it} + B(x_{it}) w_{it}^2 \) were \( A(0) = 0, B(0) = 0 \). Here we assume that local homeostatic plasticity rate is relatively low, so that third and higher order terms of its Taylor series expansion could be neglected.

From experiments it is known that transition from LTD at low postsynaptic AP rates to LTP at high rates could occur. To describe this phenomenon, polynomial approximation of \( \eta(x_{it}, y_t) \) should contain terms up to at least third order:

\[ \eta(x_{it}, y_t) = -\eta_- x_{it} y_t + \eta_+ x_{it} y_t^2 + \eta_{2+} x_{it}^2 y_t \]  

where coefficients \( \eta_- \), \( \eta_+ \) and \( \eta_{2+} \) are positive. Without last term this equation is similar to the BCM rule [13][14]. Similar plasticity rule was obtained by averaging the plastic changes that occur in response to a Poisson stream of pre- and postsynaptic spikes in detailed phenomenological models of STDP [15][17]. Other possible interpretations of Eq.(3) is that its first and second terms are equivalent to linear and quadratic terms of the Taylor series expansion of anti-Hebbian plasticity rate dependence on postsynaptic activity. This could occur, for example, if neuron has nonlinear activation function \( S(y) \)

\[ f_t = S(y_t) = S(w^T_t x_t) \]  

\[ \eta(x_{it}, y_t) = -\eta_0 x_{it} f_t = -\eta_- x_{it} y_t + \eta_+ x_{it} y_t^2 + o(y_t^3) \]  

Here \( f_t \) is output firing rate and \( y_t \) is the average change in postsynaptic membrane potential evoked by synaptic activity.

Last term in Eq.(3) could be a result of nonlinearity of LTD rate dependence on presynaptic activity. As we will see later, relatively small nonlinearity of this dependence could be sufficient for grid fields formation. There are experimental results which support assumption that this term indeed could be required for precise description of STDP at least at low rates of postsynaptic activity. For example, it was shown that spike time dependent LTD could be observed in absence of postsynaptic spiking [18][19]. Probably, in this case at low postsynaptic activity levels
the rate of synaptic changes could approximately linearly depend on \( y_t \) and nonlinearly on \( x_t \). Other motivation for introducing terms with differences in dependence of LTP component of plasticity on presynaptic activity with respect to LTD is experimental results suggesting that LTP and LTD could be supported by different postsynaptic receptors \[19\]. But as we will see later the existence of LTP component is not required for development of grid fields.

2. Analysis of weakly nonlinear version of the model

To analyze potential mechanism of grid fields formation in single neuron model with Hebbian and anti-Hebbian synaptic plasticity described by Eqs. (2)-(3) it is convenient to consider a variant of this model which is weakly nonlinear with respect to synaptic weights. Namely, we will assume that in Eqs. (2)-(3) all the terms that are nonlinear with respect to synaptic weights. Namely, we will assume that in Eqs. (2)-(3) all the terms that are nonlinear with respect to \( w_t \) are small, except for those which are equal for all synapses \((\sigma(y_t, w_t)w_t)\). If learning rate is slow with respect to the exploration speed, learning equations Eqs. (2)-(3) could be integrated over \( t \):

\[
\dot{w}_i = -\eta_1 R_{1i} w + \eta_2 R_{2i} w + \eta_2^T Q_i w + \sigma(w) w_i + P(w_i)
\]

We assume that all place fields are spherically symmetric within some distance from their centers and are approximately equal:

\[
F_i(r) \approx f(||r - r_i||)
\]

For gaussian place fields \( F_i(r) \approx F \exp\left(-\frac{1}{2\sigma^2}||r - r_i||^2\right) \), cross-correlation \( R_1 \) has simple analytical expression:

\[
R_{1ij} \approx 2\pi \frac{\sigma^2}{4} F^2 \exp\left(-\frac{1}{4\sigma^2}||r_i - r_j||^2\right)
\]

Analogously for \( R_2 \) and \( Q \):

\[
R_{2ij} \approx \int F_i(r)^2 F_j(r) dr^D = 2\pi \frac{\sigma^2}{6} F^3 \exp\left(-\frac{1}{3\sigma^2}||r_i - r_j||^2\right)
\]

\[
Q_{ijk} \approx \int F_i(r) F_j(r) F_k(r) dr^D = (R_{1ij} R_{1jk} R_{1ij})^{\frac{3}{2}}
\]

It is known that development of periodic patterns with different symmetries can be observed in systems described by equations similar to Eq. (6) as a result of symmetry breaking bifurcations. The symmetry of periodic pattern which begins to grow in this and more general systems just after bifurcation can be predicted using neural fields approximation and methods of weakly nonlinear analysis \[20,22\]. The stability of stationary periodic patterns can be investigated using methods of symmetry breaking bifurcations analysis for neural fields equations \[10,11\]. Here we only briefly discuss mechanism of formation of spatially periodic sensory fields with hexagonal symmetry in the system Eq. (6).

We assume for simplicity that domain for place fields spatial locations is a twisted torus. In other words, each place field \( F(r) \) have periodic structure

\[
F(r) = F(r + n_1 v_1 L + n_2 v_2 L)
\]

where \( n_1, n_2 \in \mathbb{Z}, v_1 = (1, 0) \) and \( v_2 = \left(\frac{1}{2}, \frac{\sqrt{3}}{2}\right) \) are basis vectors of hexagonal lattice of the size \( L \). In this case, first three terms in equation Eq. (6) are convolutions. As follows from convolution theorem, the equation for the spatial
Fourier decomposition of weights distribution $w$ as a function of place fields positions $r$ has simple form:

$$w_r = \sum_{k \in \Lambda} \alpha_k e^{ikr} \quad (13)$$

$$\dot{\alpha}_k = -\eta - \hat{R}_1|[k] \alpha_k + \eta_+ R_2|[k] \alpha_k + \eta_2 + \sum_{k'} Q_1|[k],[k'] \alpha_{k'}^* \alpha_{k-k'}$$

$$-\sigma \sum_{k'} |\alpha_{k'}|^2 \alpha_k + P_1(\alpha, k) \quad (14)$$

$$P_1(\alpha, k) = \varepsilon_1 \alpha_k + \varepsilon_2 \sum_{k'} \alpha_{k'} \alpha_{k-k'}$$

where wavevector $k$ is defined on the hexagonal lattice $\Lambda$ which is dual to the lattice $\Lambda$, and $Q_1|[k],[k']|k-k'| = F_q exp \left(-\frac{\sigma_2^2}{2} |k|^2 - \frac{\sigma_2^2}{2} |k'|^2 - \frac{\sigma_2^2}{2} |k+k'|^2 \right)$ for place fields described by equation Eq.$(16)$.

Let initially consider evolution of $\alpha_k$ starting from small positive initial synaptic values. If $\varepsilon_1$ is positive, then there is some $k$ for which $-\eta - \hat{R}_1|[k] \alpha_k + \eta_+ R_2|[k] \alpha_k + \varepsilon_1 \alpha_k$ is positive as well. Since for small $\alpha_k$ influence of all high order terms in equation (16) can be neglected, then the most rapidly growing wave amplitudes are those located on the circle $|k| = k_c$, where $k_c$ is amplitude of wavevector for which expression $-\eta - \hat{R}_1|[k] + \eta_+ R_2|[k]$ is maximal. As result of exponential growth of wave amplitudes to the end of this 'linear' phase only wave amplitudes with $|k| = k_c$ will be significantly different from zero, but amplitudes of all these waves grow with approximately equal speed. In other words, the ratios of amplitudes of waves with $|k| = k_c$ do not change with time if $\eta_2 = 0$ and $\varepsilon_2 = 0$.

The influence of second order terms gradually increase with growth of $\alpha_k$, but if $\eta_2$ and $\varepsilon_2$ are small, then most of waves power will still be concentrated within narrow ring $|\hat{R}_0|[k] - \hat{R}_{0,k_c}| < \varepsilon_1$.

The action of second order terms on the waves growth generally results in gradual increase of differences in speed of growth of different wave groups, so that only small-sized group of waves will dominate at the end. Indeed, let consider a group of waves with wavevectors lying on the circle $|k| = k_c$. To a first order of approximation, the contribution of all $|k| \neq k_c$ to the second order terms of the equation Eq.$(16)$ can be neglected.

For each wavevector $k$ lying on the circle $|k| = k_c$, there is only one triple of wavevectors $k$, $k'$, $k-k'$ with $|k| = |k'| = |k-k'| = k_c$. As result the equation Eq.$(14)$ could be simplified:

$$\dot{\alpha}_k = \left(\hat{R}_0|[k] - \sigma \sum_{k'} |\alpha_{k'}|^2 \right) \alpha_k + 2Q_2|[k],[k+k] |k-k| \alpha_k \alpha_k - Q_2|[k],[k']|k-k' = \varepsilon_2 + \eta_2 + Q_1|[k],[k']|k-k' \quad (17)$$

where $k+$ and $k-$ are wavevectors obtained by rotation of wavevector $k$ by an angle $\frac{\pi}{3}$ and $-\frac{\pi}{3}$ respectively. Since synaptic weights are real valued, amplitudes of wave with wavevector $k$ is equal to the complex conjugate of the amplitude of wave with opposite wavevector: $\alpha_{-k} = \alpha_{k}$. Using this relation and equation Eq.$(16)$ we can observe that differences between amplitudes of waves with wavevectors rotated by the angle $\frac{\pi}{3}$ with respect to each other will decrease with time:

$$\dot{\alpha}_k - \dot{\alpha}_{k+} = -2Q_2|[k],[k]|k|\alpha_k - (\hat{\alpha}_k - \hat{\alpha}_{k+}) \quad (18)$$

As a result, in a steady-state all nonzero wave amplitudes should be equal. But only the configuration with three nonzero waves whose wavevectors compose equilateral triangle is stable.

To show this, let consider evolution of ratios of wave amplitudes $\mu_k = \frac{\alpha_k}{\alpha_{k1}}$, where $\alpha_{k1}$ is an amplitude of the wave which has maximal amplitude at $t \to \infty$:

$$\dot{\mu}_k = \alpha_{k1} \left(-2Q_2|[k]k_c,k_c,k_c \mu_{k1} + \mu_{k1} - \mu_k + 2Q_2|[k]k_c,k_c \mu_{k} \mu_{k} \right) \quad (19)$$

As follows from Eq.$(18)$, at $t \to \infty$ this expression approaches

$$\dot{\mu}_k = 2Q_2|[k]k_c,k_c \alpha_{k1} \mu_k \left(\mu_k - 1\right) \quad (20)$$

This equation shows that if at some moment of time $|\mu_k|$ becomes less than 1, for example due to some small perturbation, then if $k$ do not belong to the group of wavevectors obtained by rotations of $k1$ by angles $\frac{\pi}{3} n$, $n \in \mathbb{Z}$ then $|\mu_k|$ will be negative until $\alpha_k$ has reached zero.
We can conclude that for sufficiently small $\eta_{2+}$ and $\varepsilon_2$ the solution of Eq. (14) which start from small positive weights, will approach a pattern, which is close to the hexagonally symmetric sum of three plane waves:

$$w_r = Re \{ \alpha (e^{irk} + e^{-irk} + e^{irk+}) \}.$$  

The same proposition is true for any other starting synaptic weights distribution. It follows from the fact that Lyapunov function exists for equation Eq. (6):

$$E = -\eta - \frac{1}{2} w^T R_1 w + \frac{1}{2} \eta_+ w^T R_2 w + \frac{1}{3} \eta_{2+} \int (w_i^T x_r)^3 dr^D - \frac{1}{4} \sigma (w^T w)^2 + \sum_i \int P(w_i) dw_i$$  \hspace{1cm} (21)

As result all solutions of Eq. (6) should converge to a steady-state solution. Using first-order perturbation approximation with respect to $\eta_{2+}$ and $\varepsilon_2$ it could be shown that steady-state solution of Eq. (14) can be approximated by steady-state solution of Eq. (16) and that hexagonally symmetric sum of plane waves gives the only stable solution of Eq. (16) and Eq. (14) for sufficiently small $\eta_{2+}$ and $\varepsilon_2$.

### III. RESULTS

To confirm previous analysis we have conducted a series of computational experiments. First, we have found that formation of hexagonally symmetric fields can be observed for a broad ranges of coefficients of the second order terms $\eta_{2+}$ and $\varepsilon_2$ in Eq. (6). Typical results of computational experiments are shown in Fig. 1. Linear neuron with 961 synapses was modeled. Each synapse received spatially modulated input from a PC with Gaussian-shaped firing field centered on a vertex of 31x31 hexagonal lattice embedded in diamond-shaped environment. It can be seen that during formation of grid fields (Fig. 1A, upper panel) wave amplitudes (Fig. 1A, middle panel) rapidly concentrate on a narrow ring which corresponds to the critical wavelength and then selection of single group of six waves with equal amplitudes whose wavevectors compose hexagon occurs. Corresponding autocorrelation functions of grid fields are shown in Fig. 1A (lower panel). Dependence of gridness score on simulation time step is shown in Fig. 1B. Correlation of autocorrelation function with its rotation transform as a function of rotation angle. Gridness score was estimated as a ratio of minimum value of this correlation calculated for rotation angles $0^0, 60^0, 120^0$, to its maximum at angles $30^0, 90^0, 150^0$.

Model parameters (see Eq. (14)) used for simulations shown in Fig. 1 were the following $\sigma = 1$, $\varepsilon_2 = 50$, $\eta_{2+} = 0$, $\varepsilon_1 = 0$, $\eta_+ = 1$, $\eta_- = 1$ and $\sigma_r = 0.08L$. With these parameters maximal contribution of second order with respect
FIG. 2: Formation of grid fields in the models obtained from the basic model of neuron with associative plasticity by different modifications of local homeostatic plasticity terms (Eq. 13).

Top panel - Grid fields formed after 10000 time steps of simulation. Middle panel - corresponding synaptic weights as a function of spatial location of presynaptic PCs fields. Lower panel - Fourier transforms of synaptic weights spatial distributions shown on middle panel.

A. Imposing upper and lower bounds on the synaptic weights enable grid fields formation in the models with large second order terms. Parameters of model (Eq. 2) were: \( \sigma = 1, \varepsilon_2 = 2500, \eta_2+ = 0, \varepsilon_1 = 0, \eta_1 = 1, \eta_- = 1, \sigma_r = 0.13L \). In addition, synaptic weights were limited from above by setting \( \dot{w}_i = 0 \) for \( w_i > w_{\text{max}} \). \( w_{\text{max}} = 0.005 \). B. Imposing only lower bound on synaptic weights enable grid fields formation in models without other homeostatic plasticity terms. Parameters of the model (Eq. 2) were the same as in A except for: \( \varepsilon_2 = 0 \) and \( w_{\text{max}} = 0.005 \). C. Models with upper limit of synaptic weights learn inverted grid fields. Parameters of the model were the same as in A except for: \( \varepsilon_2 = 0, \sigma = 0 \), \( w_{\text{min}} = -0.001 \), \( w_{\text{max}} = 0.005 \).

Restrictions on the maximal value of second order terms can be weakened by introducing additional plasticity rules to restrict maximal or minimal weights of individual synapses. For example, if the following parameter values are set: \( \sigma = 1, \varepsilon_2 = 2500, \eta_2+ = 0, \varepsilon_1 = 0, \eta_1 = 1, \eta_- = 1, \sigma_r = 0.13L \) in equation Eq. (14) and synaptic weights are additionally limited from above by setting \( \dot{w}_i = 0 \) for \( w_i > w_{\text{max}} \). \( w_{\text{max}} = 0.005 \), then maximal ratio of second order term of Eq. (14) to the first order terms at the end of learning is approximately equal to 1. The resulting grid fields are shown in Fig. 2A. It is interesting to note that introducing limits on maximal or minimal weights into Eq. (14) without second order terms \( (\varepsilon_2 = 0, \eta_2+ = 0) \) is sufficient to obtain the model which could learn grid-like fields. Examples of grid fields obtained for such models are shown in Fig. 2B-D. In the models with both upper and lower bounds imposed on synaptic weights clusters of synapses are formed in which size of grid fields and size of clusters can be regulated independently. Parameters of the model were the same as in A except for: \( \varepsilon_2 = 0, \sigma = 0 \), \( w_{\text{min}} = -0.001 \), \( w_{\text{max}} = 0.005 \).
FIG. 3: Formation of grid fields in the models with different ratios of potentiation and depression components of associative synaptic plasticity.

Ratio of depression and potentiation components was regulated by changing parameter $\eta_-$ from $\eta_- = 0.6\eta_+$ (blue lines in Fig. 3A,B and Fig. 3C) to $\eta_- = 2\eta_+$ (green lines in Fig. 3A,B and Fig. 3D).

A. Dependencies of PC-GC synapse plasticity rate on the animal’s distance from the center of corresponding place fields at a fixed postsynaptic firing rate. It can be seen that in the case of small $\eta_-$ the maximal value of negative plasticity rate (which could be considered as those resulting from LTD) is less than 7% of maximal positive plasticity rate. In the case of high $\eta_-$ all plastic changes could be considered as those resulting from LTD. B. Corresponding dependencies of wave amplitude change rates on the length of its wavevectors. C-D. Grid fields (top panel), synaptic weights as a functions of spatial position of the centers of place fields (middle panel) and wave amplitudes as a function of wavevectors (lower panel).

It is possible to modify model in such a way that formation of grid fields became possible due to interaction of LTD and BCM-like LTP terms without additional homeostatic plasticity restrictions on individual synaptic weights. This can be achieved, for example, if dependence of LTD rate on presynaptic activity is sublinear. Example of learning in such model is shown in Fig. 4. Learning equation was:

$$\dot{w}_i = -\eta_- R_0 w_i + \eta_2 + w^T Q_i w - \sigma \sum_k w_k^2 w_i + \varepsilon_1$$  \hspace{1cm} (22)$$

with parameters: $\sigma = 100$, $\eta_2 = 5000$, $\varepsilon_1 = 5$, $\eta_- = 100$, $\sigma_r = 0.13L$. First term in equation was obtained by integration over time of expression describing nonlinear LTD:

$$\sum_t \eta_- y_t \sqrt{x_{it}} \approx -\eta_- R_0 w$$  \hspace{1cm} (23)$$
FIG. 4: Learning of grid fields in the model with sublinear LTD and BCM-like LTP terms without additional homeostatic plasticity restrictions on individual synaptic weights. Panels are the same as in Fig. 1.

where

\[ R_{0ij} = \int F_i(r) F_j(r) r^D = F_0 \exp \left( -\frac{1}{6\sigma_r^2} \|r_i - r_j\|^2 \right) \]  

(24)

It should be noted that learning of grid fields in this model was possible only for narrow range of parameters. For example, the range of parameter \( \varepsilon_1 \) values where formation of grid fields was observed was between 3 and 5.

To confirm results obtained for simplified model described by Eq. (6) in more realistic conditions we have modeled grid fields formation as a result of offline learning after environment exploration. In these simulations we assume that after exploration of diamond-shaped environment by an animal, episodic memory corresponding to the visited places could be spontaneously reactivated in such a way that relative activities of place cells during reactivation are similar to those at time of navigation.

We observe that for sufficiently long path of movement the process of spatially modulated fields formation was qualitatively similar to those described above for simplified model. For these simulations we directly solve equation obtained by simplification of Eqs. (1)-(3):

\[ \dot{w}_{it} = -\eta - x_{it} y_{it} + \eta_2 + x_{it} y_{it}^2 + \eta_+ x_{it} y_{it} - \sigma \sum_k w_{kt}^2 w_{it} + B w_{it}^2 H(x_{it} - \Theta) \]  

(25)

where \( H \) is Heaviside function. The set of parameter values which were used for simulations was \( \sigma = 1, B = 100, \eta_2 = 0, \eta_+ = 1, \eta_- = 3, \Theta = 0 \). Place fields was modeled with Gaussian functions \( F_i(r) \approx F_0 \exp \left( -\frac{1}{2\sigma_r^2} \|r - r_i\|^2 \right) \) with \( F = 20 \). Place field size \( \sigma_r \) was varied from 0.1L to 0.3L, where \( L \) is size of diamond-shaped environment. Centers of place fields were initially selected at vertexes of 31x31 hexagonal lattice which was embedded in environment. Then all place field centers were perturbed by addition of random vector selected from Gaussian distribution with \( \sigma = 0.5\Delta L \) (\( \Delta L \)- size of the lattice cell).

Typical result of simulations is shown in Fig. 5. The total length of traveling path in a diamond-shaped environment of size \( L \) was \( S = 175L \). It can be seen that similarly to the case of model described by Eq. (6), formation of grid fields occurred in two stages: initially, a ring of waves with critical wavelength was grown, then selection of six waves whose wavectors composed a hexagon took place. The difference with respect to simplified model is that not all waves out of hexagon of waves with maximal amplitudes dissappear completely at the end of learning and that the amplitudes of waves composing the hexagon are not equal. As result, the gridness score of observed fields vary in a broad range and highly depends on grid size and path length.

Higher quality of grid patterns was achieved when input signals in each location in environment were normalized by means of division of each input signal by the sum of square roots of this signal over whole trajectory. This
FIG. 5: Simulation of grid fields offline learning in the basic model of EC neuron resulting from memory reactivation after animal’s exploration of environment. Random path of the length $S = 172L$ in a diamond-shaped labirinth of size $L$ was simulated. Then patterns of PCs activity observed during navigation were reactivated in random order during the period of offline learning. Panels are the same as in Fig. [1].

operation could be interpreted as the result of modulation of synaptic plasticity rate by a specific novelty signal, so that in frequently visited places rate of plasticity will be lower than in relatively new places.

The dependence of gridness score on the traveling path is shown in Fig. 6A. Here, first three statistical boxes correspond to the results of simulation of online learning for $N=14$ different paths for three different path lengths (61L, 86L and 172L). Examples of movement trajectories for each path length are shown in Fig. 6B. Fourth box in Fig. 6A corresponds to results of simulations of learning for paths of length $S = 172L$ with raw (not normalized) input signals. It can be seen from these experiments that large size fields ($\sigma_r > 0.25L$) with relatively high positive gridness score ($> 0.1$) could be formed with high probability (8 of 14) after relatively short experience of navigation in a new environment (Fig. 6B, upper trace). Quality of fields learned with normalized input signals was usually higher as it could be seen from comparison of gridness score statistics for normalized (3d bar in Fig. 6A) and not normalized cases (4th bar).

Learning of smaller size grid fields generally requires significantly longer paths, but we observed that this requirement can be significantly weakened. This could be achieved by introducing restrictions on a maximal and minimal weight of each synapse. For example, by setting minimal and maximal weight of synapses to -0.002 and 0.01, respectively, we obtain a model which can extract grid fields from experience of navigation along the paths as short as $S = 13L$. Example of such offline learning experiment results is shown in Fig. 7. Trajectory of animal movement had length $S = 12.8L$ and is shown in Fig. 7D. We observe that in these experiments probability to obtain fields with gridness score higher than 0.1 for short paths (mean $S = 13L$) was high (7 of 14, gridness score Mean $\pm SD = 0.24 \pm 0.59$, statistics is shown in fifth bar in Fig. 6A).

It is possible to modify equation (21) by different ways to obtain online learning version of the model. An example of learning in such a model is shown in Fig. 8. Learning equations were:

$$\dot{w}_{it} = -\eta_- x_{it} y_t + \eta_+ x_{it}^2 y_t - C w_{it}^3 H(x_{it} - \Theta) \quad w_{it} \geq w_{min}$$

$$\dot{w}_{it} = 0 \quad w_{it} < w_{min}$$

Parameters of the model were: $\eta_+ = 100$, $\eta_- = 200$, $C = 1$, $w_{min} = -0.4$, $\sigma_r = 0.14L$, $\Theta = 0$ Learning in this model was relatively slow and quality of grid fields was lower than it was for offline learning models.

IV. DISCUSSION

In this work we have described formation of grid-like spatially selective sensory fields in the group of models of EC neuron with linear activation function which recieves spatially modulated input from place cells or from neurons of different sensory systems.

We have shown that learning of hexagonaly symmetric fields in these models is a result of complex action of several simple biologically motivated synaptic plasticity rules. These rules include rules for associative synaptic plasticity similar to those widely used for description of linear LTD and an LTP rule with supralinear dependence on presynaptic activity or a combination of BCM-like rule for LTP with sublinear LTD rule. We observed that even
purely LTD rule with nonlinearity of dependence of LTD rate on presynaptic activity or a rule with very small LTD component in comparison to LTP is sufficient for robust grid-like fields formation.

From the perspective of pattern formation theory the role of rules for associative synaptic plasticity with linear dependence on synaptic weights in learning is selection of patterns composed of a group of waves with similar wavelengths. This critical wavelength determinate size of grid fields. Additional plasticity rules with nonlinear dependence on synaptic weights are required for selection of subgroup consisting of six waves whose wavevectors compose hexagon from the group of waves with critical wavelength. These rules can be result of restrictions on maximal or minimal synaptic weights, of a small supralinearity of the dependence of synaptic plasticity rate on the synaptic weight or of nonlinearity of a neuron activation rule. BCM-like LTP term nonlinearly depends on synaptic weights and as result it can play a role both in critical wavelength waves selection in combination with sublinear LTD term and in consequent hexagonal symmetric pattern formation.

In addition to these results we have shown that some variants of grid fields selforganisation models described in this work are capable for a fast offline learning of grid fields after very short experience of navigation in a novel environment. The possibility of online learning was shown for some sets of model parameters.

The model discribed in this work differ from other published models of grid fields formation based on synaptic plasticity in PC-GC synapses. At first it do not required additional firing rate adaptation process as it is supposed to be important for grid fields learning in the model of Korpff and Treves [3, 4]. As result the learning in the proposed model is not sensitive to the changes in speed of animal movement. In addition it allowed learning on the basis of reactivation of episodic memory of navigation without requirment for recall of continuous fragments of movement trajectory.

The speed of grid fields formation in some modifications of proposed model is similar to those observed for the model described in work of Castro and Aguiar [6], but learning rules used in our model have more general form and are better biologically motivated.

Some of the models described in this work allowed detailed mathematical analysis. This property could be useful for the analysis of possible selforganization mechanism of modular structure of grid cell networks observed in

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**FIG. 6:** Statistics of the quality of grid fields observed in offline learning simulations.

**A.** Statistics of gridness scores for the grid fields formed in different conditions. First three statistical bar plots correspond to learning of a basic model of EC neuron with animal’s movement paths of three different lengths (mean lengths was 61L, 86L and 172L, N=14 for each path length). In these computational experiments, input signals in each location in environment were normalized by means of division of each input signal on the sum of square roots of this signal over whole trajectory. Gridness scores of fields learned without this normalization were systematically lower (compare 3d and 4th bars obtained for paths with mean length 172L, N=14). Last statistical bar corresponds to the modified model with additional limit imposed on the minimal synaptic weight. For this modified model mean length of animal’s path was 13L (N=14).

**B.** Examples of paths that were used in experiments described in A, corresponding to the mean path lengths 61L (top), 86L (middle) and 172L (down).
FIG. 7: Offline learning of grid fields after short period of navigation in the model of GC neuron with bounded synaptic weights. 
A Grid fields formed after 8000 time steps of offline learning. Length of traveling path used for learning was 12.8L. B. Synaptic weights as a function of spatial position of the centers of presynaptic PCs fields. C Wave amplitudes as a function of wavectors (This is Fourier transform of weights distribution shown in B). D Travelling path that was used for learning

In conclusion we suggest that learning on the basis of simple and biologically plausible synaptic plasticity rules could result in formation of grid-like fields on neurons in EC which receives synaptic inputs from place cells in hippocampus and spatially modulated sensory inputs from different sensory systems. It is likely that such learning contributes to the formation of grid fields in early development and to maintainence of normal grid cells activity patterns in familiar environments.

FIG. 8: Online learning of grid fields in a model of EC neuron during random exploration of diamond-shaped environment. The length of movement path simulated in this experiment was 183L. Panels are the same as in Fig. 7.
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