A New View on Grid Cells
Beyond the Cognitive Map Hypothesis

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Abstract. Grid cells in the entorhinal cortex are generally considered to be a central part of a path integration system supporting the construction of a *cognitive map* of the environment in the brain. Guided by this hypothesis existing computational models of grid cells provide a wide range of possible mechanisms to explain grid cell activity in this specific context. Here we present a complementary grid cell model that treats the observed grid cell behavior as an instance of a more abstract, general principle by which neurons in the higher-order parts of the cortex process information.

Keywords: grid cell model, higher-order information processing

1 Introduction

In 1948 Edward Tolman [36] reported on a series of behavioral experiments with rats that led him to hypothesize that the animals had to make use of an internal, map-like representation of the environment. This idea, which came to be known as the *cognitive map hypothesis*, was highly controversial at the time. Accordingly, the discovery of hippocampal *place cells* by O'Keefe and Dostrovsky [25, 27] in the 1970s was met with much excitement as place cells were the first possible direct evidence for such a representation of the environment in the brain [26]. Since then a variety of neurons that exhibit spatially correlated activity were found in the parahippocampal-hippocampal region [35, 15, 11, 13, 32]. In particular the recent discovery of *grid cells* [11, 13] in the entorhinal cortex of rat strengthened the idea that the involved neuronal structures constitute a kind of *metric for space* [23]. Grid cells are neurons that exhibit spatially correlated activity similar to that of place cells with the distinct difference that grid cells possess not just one but multiple, discrete firing fields that are arranged in a regular, hexagonal grid that spans the entire environment (Fig. 1a). Located just one synapse upstream of the hippocampus grid cells are assumed to be an important source of spatial information to place cells [33, 29]. In particular, grid cells are generally considered to be a central part of a path integration system as pointed out by Burgess [5]: *"There has been a surprising rapid and general agreement that the computational problem to which grid cells provide a solution*

is "path integration" within an allocentric reference frame." This consensus is reflected by the fact that all computational models of grid cells proposed so far (except [19]) incorporate mechanisms of path integration as integral parts to explain the hexagonal firing patterns of grid cells. Although existing computational models cover a wide range of possible mechanisms and focus on different aspects of grid cell activity [23, 38, 12, 2, 4, 24], the models share the common approach of explaining grid cells and their behavior as functional components within the cognitive map hypothesis.

Complementary to this common approach this paper presents an alternative grid cell model that treats the observed grid cell behavior as an instance of a more abstract, general principle by which neurons in the higher-order parts of the cortex process information.

2   Model Description

To describe the behavior of grid cells at a more abstract level a computational model is needed that is agnostic to the semantic interpretation of its own state and its respective input space such that the model can provide an explanation of the cell's behavior that does not rely on assumptions based on the putative purpose of that cell, e.g., performing path integration or representing a coordinate system. This way, the observed behavior of grid cells can be treated as just one instance of a more general information processing scheme. To this end we propose to interpret the input signals that a grid cell receives within a small time window as a single sample from a high-dimensional input space. This input space represents all possible inputs to the grid cell and for a certain subset of these inputs, i.e., for inputs from certain regions of that input space the grid cell will fire. The problem of modeling grid cell behavior can then be split into two independent sub-problems. The first problem addresses the question how a cell, given an *arbitrary* input space, chooses the regions of input space for which it will fire. The second problem addresses the question how a *specific* input space has to be structured in order to evoke the actual firing pattern observed in, e.g, grid cells. This paper focuses on the first problem and will touch upon the second problem just briefly.

The most salient feature of grid cells is their firing pattern. The triangular structure resembles the outcome of a number of processes that typically perform some form of error minimization, e.g., the hexagonal packing of circles [37], the Delaunay triangulation [7, 3], or certain kinds of *topology representing networks* [20]. The latter are artificial neural networks that employ forms of *unsupervised competitive learning* to discover the structure of an underlying input space. Among those networks the *growing neural gas* (GNG) introduced by Fritzke [10, 9] stands out as it does not use a predetermined and fixed network topology like, e.g., the well-known self-organizing map (SOM) [18] does. Instead, the GNG uses a data-driven growth process to approximate the topology of the underlying input space resulting in an *induced Delaunay triangulation* of that space. Figure 1b shows an example of a GNG network approximating
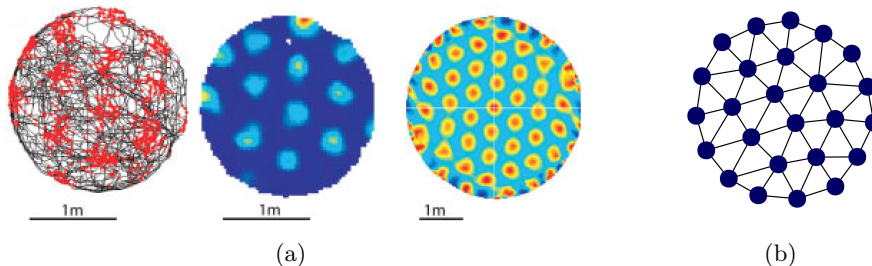
Fig. 1. Comparison of a grid cell firing pattern with a growing neural gas (GNG) network. **(a)** Typical visualization of a grid cell's firing pattern as introduced by Hafting et al. [13]. **Left**: trajoctory (black lines) of a rat in a circular environment with marked locations (red dots) where the observed grid cell fired. **Middle**: color-coded firing rate map of the observed grid cell ranging from dark blue (no activity) to red (maximum activity). **Right**: color-coded spatial autocorrelation of the firing rate map ranging from blue (negativ correlation, -1) to red (positive correlation, +1) highlighting the hexagonal structure of the firing pattern. Figure from Moser et al. [23]. **(b)** Example of a GNG network with 25 units that was fed with inputs from a uniformly distributed, two-dimensional, circular input space. The resulting network forms an *induced Delaunay triangulation* of the input space.

a uniformly distributed, two-dimensional, circular input space. Each GNG unit marks the center of a convex polyhedron representing a local region of this input space. The *relative* size of this region is inversely proportional to the probability of an input originating from that region, i.e., the local *density* of the input space. In addition, the *absolute* size of each local region is determined by the overall number of GNG units that are available to cover the whole input space. The network structure of the GNG, which relates the respective local regions to one another, represents the input space topology.

Given the resemblance between the structure of grid cell firing patterns and the structure of GNG networks for certain input spaces we propose that a *single* grid cell performs an operation that is similar to that of a *whole* GNG, i.e., it is proposed that the objective of a grid cell lies in the approximation of its *entire* input space. This hypothesis differs strongly from the common interpretation of GNGs where the GNG units correspond to individual neurons that each specialize to represent a *single*, specific region of input space. In contrast, this new hypothesis implies that a single neuron represents not only one but *several*, distinct regions of input space. To accomplish this a single neuron would have to recognize several different input patterns. Recent advances in imaging neuronal activity [14, 6] indicate that this is indeed the case.

In addition to their peculiar firing pattern, grid cells exhibit a modular organization in which the firing patterns of neighboring grid cells share a common orientation, spacing, and field size [34]. Furthermore, the distribution of relative grid phases is uniform within each module. To account for these properties we
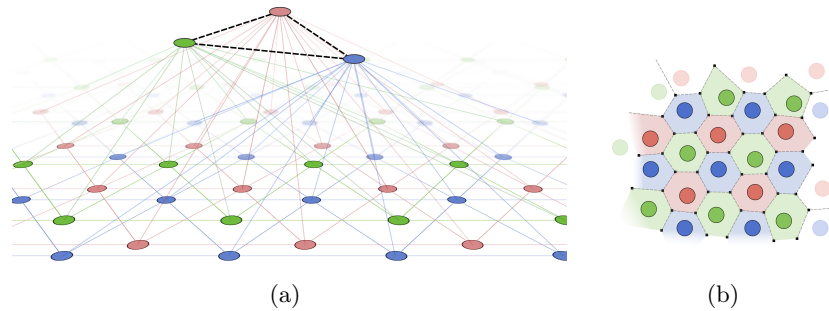
(a)   (b)

Fig. 2. Illustration of the proposed two-layer model. (**a**) The top layer is represented by three units (red, green, blue) connected by dashed lines. The associated sets of connected nodes in the bottom layer are illustrated by corresponding colors. (**b**) Top view on the input space partition induced by the bottom layer sets of nodes.

propose to describe a group of grid cells by a two-layer model[1]. The top layer contains a set of connected units that each represent an individual grid cell. Associated with each top layer unit is a set of connected nodes in the bottom layer representing the set of input patterns that are recognized by the dendritic tree of the grid cell (Fig. 2a). To this end, each node in the bottom layer possesses a *prototype* vector that represents the center of a local input space region. Applying a form of competitive hebbian learning *within* each set of bottom layer nodes (bottom layer competition) arranges the nodes in a triangular pattern that covers the entire input space. In addition, competition *across* the sets of bottom layer nodes (top layer competition) arranges the different triangular patterns in such a way that they share a common orientation and spacing. Furthermore, the top layer competition will also spread the individual triangular patterns uniformly across the input space (Fig. 2b).

Formally, the proposed model consists of a set of units $u \in U$ and a set of connections $c \in C$ located in the top layer, as well as a set of parameters θ. Each connection c is described by a tuple:

$$c := (P, t) \in C, \quad P \subseteq U \wedge |P| = 2, \;\; t \in \mathbb{N},$$

with units $p \in P$ linked by the connection and the connection's *age* t. Each unit u is described by a tuple:

$$u := (V, E) \in U,$$

containing a set of nodes $v \in V$ and a set of edges $e \in E$ located in the bottom layer. Each node v is described by a tuple:

$$v := (w, a_{\mathrm{err}}, \epsilon_{\mathrm{ref}}) \in V, \quad w \in \mathbb{R}^n, \;\; a_{\mathrm{err}} \in \mathbb{R}, \;\; \epsilon_{\mathrm{ref}} \in \mathbb{R},$$

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[1] A preliminary version of this idea was presented by Kerdels and Peters [16].

with the *prototype* w, the *accumulated error* a_{err}, and a refractory factor ϵ_{ref}. Each edge e is described by a tuple:

$$e := (S, t) \in E, \quad S \subseteq V \wedge |S| = 2, \ t \in \mathbb{N},$$

with nodes $s \in S$ linked by the edge and the edge's *age* t. The set of parameters θ consists of:

$$\theta := \left\{ \epsilon_b, \epsilon_n, \epsilon_r, \tau_t, M_t, \epsilon_{\mathrm{b.start}}, \epsilon_{\mathrm{b.end}}, \epsilon_{\mathrm{n.start}}, \epsilon_{\mathrm{n.end}}, \tau_b, M_b, \lambda, \alpha, \beta, \gamma, t_r \right\}.$$

The model is initialized with M_t fully connected top level units u each starting with two nodes v that have random prototype vectors as well as accumulated errors and refractory factors set to zero. An input $\xi \in \mathbb{R}^n$ at time t is processed as follows:

– For each top layer unit $u \in U$:
  - Find the two nodes s_1 and s_2 in $u.V$ whose prototypes w have the smallest Euclidian distance to the input ξ. Node s_1 is called the *best matching unit* (BMU) of u.
  - Increment the age t of all edges connected to s_1 by one.
  - If no edge between s_1 and s_2 exists, create one.
  - Reset the age t of the edge between s_1 and s_2 to zero.
  - Add the squared distance between ξ and the prototype w of s_1 to the accumulated error a_{err} of s_1.
  - Adapt the prototype of s_1 and all prototypes of its direct neighbors:

$$s_1^{t+1}.w := s_1^t.w + \epsilon_b^t \left(1 - s_1^t.\epsilon_{\mathrm{ref}} \right) \left(\xi - s_1^t.w \right),$$
$$s_n^{t+1}.w := s_n^t.w + \epsilon_n^t \left(1 - s_1^t.\epsilon_{\mathrm{ref}} \right) \left(\xi - s_n^t.w \right),$$

  with

$$\epsilon_b^t := \epsilon_{\mathrm{b.start}} \left(\frac{\epsilon_{\mathrm{b.end}}}{\epsilon_{\mathrm{b.start}}} \right)^{\frac{t}{t_r}}, \quad \epsilon_n^t := \epsilon_{\mathrm{n.start}} \left(\frac{\epsilon_{\mathrm{n.end}}}{\epsilon_{\mathrm{n.start}}} \right)^{\frac{t}{t_r}},$$
$$s_n \in \left\{ k \mid \exists (S, t) \in E, \ S = \{s_1, k\}, \ t \in \mathbb{N} \right\}.$$

  - Set the refractory factor ϵ_{ref} of s_1 to one.
  - Remove all edges with an age above threshold τ_b and remove all nodes that no longer have any edges connected to them.
  - If an integer-multiple of λ inputs has been processed and $|u.V| < M_b$, add a new node v. The new node is inserted "between" the node j with the largest accumulated error a_{err} and the node k with the largest accumulated error among the direct neighbors of j. Thus, the prototype w of the new node is initialized as:

$$v.w := (j.w + k.w) / 2.$$

  The existing edge between nodes j and k is removed and edges between nodes j and v as well as nodes v and k are added. The accumulated

errors of nodes j and k are decreased and the accumulated error of the new node v is set to the decreased accumulated error of node j:

$$\Delta j\text{.}a_{\mathrm{err}} = -\alpha j\text{.}a_{\mathrm{err}}, \quad \Delta k\text{.}a_{\mathrm{err}} = -\alpha k\text{.}a_{\mathrm{err}},$$

$$v\text{.}a_{\mathrm{err}} := j\text{.}a_{\mathrm{err}} .$$

- Finally, decrease the accumulated error of all nodes as well as their refractory factors:

$$\Delta v\text{.}a_{\mathrm{err}} = -\beta\, v\text{.}a_{\mathrm{err}},$$

$$\Delta v\text{.}\epsilon_{\mathrm{ref}} = -\gamma\, v\text{.}\epsilon_{\mathrm{ref}}, \quad \forall v \in V.$$

- Identify the two units u_1 and u_2 whose BMUs were closest to input ξ.
- Increment the age t of all connections to u_1 by one.
- If no connection between u_1 and u_2 exists, create one.
- Reset the age t of the connection between u_1 and u_2 to zero.
- Adapt the BMUs of u_1 and u_2 as well as their neighbors:

$$u_1\text{.}s_1^{t+1}\text{.}w := u_1\text{.}s_1^t\text{.}w + \epsilon_b\left(\xi - u_1\text{.}s_1^t\text{.}w\right),$$

$$u_1\text{.}s_n^{t+1}\text{.}w := u_1\text{.}s_n^t\text{.}w + \epsilon_b\epsilon_r\left(\xi - u_1\text{.}s_n^t\text{.}w\right),$$

$$u_2\text{.}s_1^{t+1}\text{.}w := u_2\text{.}s_1^t\text{.}w + \epsilon_n\left(\xi - u_2\text{.}s_1^t\text{.}w\right),$$

$$u_2\text{.}s_n^{t+1}\text{.}w := u_2\text{.}s_n^t\text{.}w + \epsilon_n\epsilon_r\left(\xi - u_2\text{.}s_n^t\text{.}w\right).$$

- Remove all edges with an age above threshold τ_t.

In the present model each set of bottom layer nodes behaves essentially like a growing neural gas. To accommodate sequential input, e.g., a sequence of animal positions, the original GNG algorithm [10, 9] is extended by a successive reduction of the learning rates ϵ_b and ϵ_n to capture a more uniform distribution of inputs, as well as a refractory factor ϵ_{ref} that reduces the impact of equal or similar consecutive inputs. The connected top layer units track the neighborhood relations of the corresponding bottom layer node sets. The additional adaption step of the top layer establishes a competition across the bottom layer node sets resulting in an even distribution and alignment of these sets.

3   Example of Grid Cell Activity

To generate a grid like firing pattern, the proposed model requires an input space that is a uniformly distributed, two-dimensional, periodic representation of possible animal locations. A possible neuronal mechanism that results in a representation of location with these properties consists of two orthogonal, one-dimensional attractor networks. Attractor networks were first introduced as a computational model of *head direction* cells [39] and later used in models of place and grid cells [21, 22, 28]. Here we use two orthogonal, one-dimensional attractor networks as described in a previous work [16]. During an initial learning phase the model is fed with randomly generated locations. After the model has settled into a stable configuration, recorded movement data provided by Sargolini et
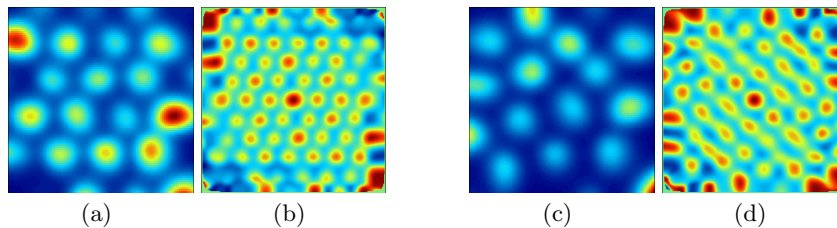
(a)   (b)   (c)   (d)

Fig. 3. Exemplary rate and autocorrelation maps of simulated grid cells. (**a,b**) Simulated grid cell with 20 bottom layer nodes. (**c,d**) Simulated grid cell with 16 bottom layer nodes.

al. [31] of a rat foraging for food in a square environment is used. Figure 3 shows exemplary rate and autocorrelation maps of two top layer units with either 16 or 20 bottom layer nodes exhibiting grid like firing patterns. In this example, the following set of parameters θ was used:

$$
\begin{aligned}
&\epsilon_b && = 0.05, && \epsilon_n && = 0.005, && \epsilon_r && = 0.001, && \tau_t && = 1000, && M_t = 50, \\
&\epsilon_{b.start} = 0.05, && && \epsilon_{b.end} = 0.0005, && \epsilon_{n.start} = 0.01, && \epsilon_{n.end} = 0.0001, && \tau_b && = 300, \\
&M_b && = \{16, 20\}, && \lambda && = 1000, && \alpha && = 0.5, && \beta && = 0.0005, && \gamma && = 0.2, \\
&t_r && = 500000.
\end{aligned}
$$

4   Discussion

The proposed model describes a putative general principle by which neurons in higher-order parts of the cortex process information of arbitrary input spaces:

> Each neuron aspires to represent its input space as well as possible while being in competition with its peers.

This assumed behavior contrast the behavior of "classic" perceptrons [30] in interesting ways. A perceptron can be interpreted as a linear classifier where the input weights define a hyperplane that divides the input space into two regions. The output of the activation function then indicates from which of the two regions the respective input pattern originated. Combining the output of several perceptrons successively divides the input space into a smaller and smaller subregion (Fig. 4a). In contrast, the top layer units of our model compete with each other and generate a tiled, periodic partition of the input space (Fig. 2b). If the output of top layer units from *separate* neuron groups or modules with *different* spatial scales and/or orientations is combined, they can collectively identify a specific, individual subregion of the input space by coinciding only in that region (Fig. 4b). In case of grid cells, this mechanism was successfully used to explain the formation of place cells from grid cell activity [29, 33, 8, 1].
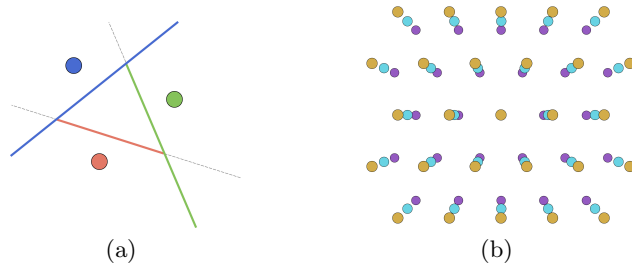
(a)   (b)

Fig. 4. Comparison of strategies to identify specific subregions in input space. (**a**) Multiple perceptrons successively partition the input space to identify a specific subregion (the middle triangle). (**b**) Top layer units from *separate* grid cell groups with *different* spatial scales identify a specific subregion by coinciding in that region.

Both, a population of perceptrons as well as a population of top layer units in our model represent a form of input space encoding that allows to identify individual subregions of input space. The use of periodic input space partitions as basic elements of such an encoding may have a number of advantages over a linear partition of input space:

- Representing the entire input space in each neuron averages the activity of all neurons in a group independently of the particular input and may be metabolically beneficial.
- Sequences of inputs are split into repeating subsequences. For example, if a rat runs in a given direction, a small number of grid cells will be activated in sequence repeatedly increasing the probability that this subsequence will be learned.
- If a set of periodic input space partitions across several spatial scales identifies a specific region of input space, the size of this region depends on which subset of partitions are choosen.

In particular the latter two points require further investigation, as they may yield new approaches to the problem of learning complex sequences and to the problem of learning hierarchical representations.

5   Conclusion and Outlook

We presented a computational model that can explain the behavior of grid cells in terms of two independent sub-problems: the information processing performed by the cells and the structure of their input space. We argue that neurons in higher-order parts of the cortex pursue a general information processing scheme in which the neurons try to represent their input space as well as possible. In future research, we will investigate if this general information processing scheme can be used to explain the behavior of neurons other than grid cells. For example,

Killian et al. [17] report on entorhinal neurons with grid-like firing patterns in response to saccadic eye movements.

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