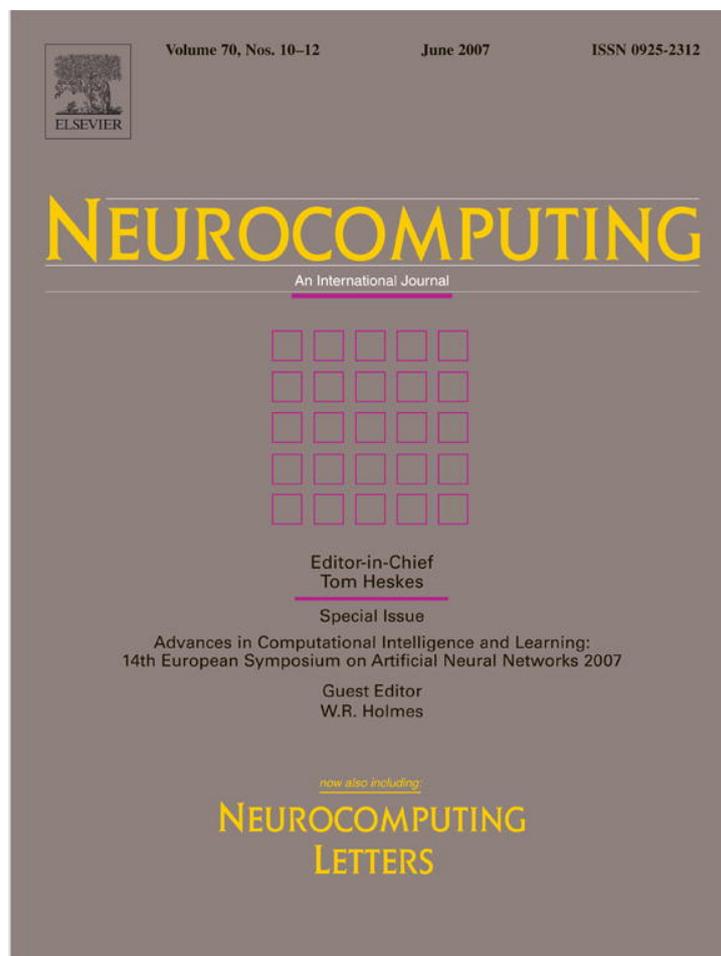


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Quantified symmetry for entorhinal spatial maps

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Abstract

General navigation requires a spatial map that is not anchored to one environment. The firing fields of the “grid cells” found in the rat dorsolateral medial entorhinal cortex (dMEC) could be such a map. dMEC firing fields are also thought to be modeled well by a regular triangular grid (a grid with equilateral triangles as units). We use computational means to analyze and validate the regularity of the firing fields both quantitatively (using summary statistics for geometric and photometric regularity) and qualitatively (using symmetry group analysis). Upon quantifying the regularity of real dMEC firing fields, we find that there are two types of grid cells. We show rigorously that both are nearest to triangular grids using symmetry analysis. However, type III grid cells are far from regular, both in firing rate (highly non-uniform) and grid geometry. Type III grid cells are also more numerous. We investigate the implications of this for the role of grid cells in path integration.

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1. Introduction

Place cell representation is context [24,13] and task-specific [12], while general navigation requires a more abstract map that is not anchored to one environment. It has been hypothesized that there exists a representation upstream of the rat hippocampus that is context-independent [20,18,23]. This general spatial map is just a component of a distributed network [18] which is the basis for navigation [25,15]. One potential possibility for such a map is the multi-peaked firing field found in dorsolateral medial entorhinal cortex (dMEC), which accurately represent the rat’s position [5] in a near-regular grid [7]. This is in sharp contrast to place cells’ one-peak firing fields [15,16]. The regularity of these firing fields and their context-independence have been used in recent models of path integration. Using symmetry analysis [10,9], we investigate to what degree dMEC firing fields are regular grids. (see also [2]). We show that there are in fact two types of grid cells, one that is strikingly regular, and another a greater departure from regularity. Both types of firing fields are

shown to be nearest to a $p6m$ symmetry group (a triangular grid). However, the departure from regularity of the majority of grid cells analyzed means that the role of dMEC in path integration must be rethought.

2. Methods

A symmetry g of a geometric set S is a distance-preserving transformation that keeps S setwise invariant (i.e. $g(S) = S$). All symmetries of S form a group G [3] and is called the symmetry group of S . Thus the symmetry group of a lattice is a collection of all transformations which leave the representation invariant. The lattice can be generated by a single tile. This tile can be translated in 2D such that it produces a *covering* (no gaps) and a *packing* (no overlaps) of the plane [6]. There are only five unit lattice shapes, which can generate all possible 2D lattice forms [3], one of which is the hexagonal lattice unit, which has a pair of equilateral triangles as units. Each hexagonal unit thus has two equilateral triangles and the lattice that it generates is then called a triangular grid. A triangular grid has equilateral triangles as units.

Fyhn et al. [5] presented that the firing fields of grid cells deviate from geometric and photometric regularity. To

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quantify the amount of deviation from regularity, Liu et al. have devised a taxonomy of near-regular textures (NRTs). A type I NRT has geometric regularity but lacks photometric (color/amplitude) regularity. A type II texture deviates from regular geometry and has photometric regularity. A type III texture departs further from geometric and photometric regularity than any other NRT type [10]. More formal definitions are used for analysis of images, and are as follows. The equation for the *geometric regularity* G of the lattice is

$$G = \sum_{i=1}^{N_i} \frac{(l_i - \|T_1\|)^2}{\|T_1\|^2} + \sum_{j=1}^{N_j} \frac{(l_j - \|T_2\|)^2}{\|T_2\|^2} + \sum_{k=1}^{N_k} \frac{(l_k - \|T_1 + T_2\|)^2}{\|T_1 + T_2\|^2} + \sum_{m=1}^{N_m} \frac{(l_m - \|T_1 - T_2\|)^2}{\|T_1 - T_2\|^2}, \quad (1)$$

where $l_i, l_j, l_k,$ and l_m are the lengths of the links in the lattice D_L corresponding to links in the regular lattice R_L along the directions of $T_1, T_2, T_1 + T_2,$ and $T_1 - T_2,$ respectively. N_i, N_j, N_k, N_m are the total number of links in $D_L,$ and θ is the angle between T_1 and T_2 [10]. Vectors T_1 and T_2 form the boundary of a generating tile and can be used to generate the entire lattice.

The *appearance regularity* A is the average standard deviation of all corresponding pixels in all lattice tiles. Regular textures have $G = 0$ and $A = 0.$ type I textures have G close to zero and $A > 0.$ Type II textures have $G > 0$ and A closer to zero. Type III textures have G and A scores

much further from zero [10]. See Fig. 1 for examples of the different types of NRTs.

Geometric regularity is inversely proportional to the texture’s distortion (from a regular texture). If we fit a lattice structure onto the texture, the value G depends on the amount we must deform this lattice in order to make it fit the nearest regular pattern. Photometric or appearance regularity can be thought of as quantifying the differences in amplitude of the peaks in the firing field. A type II grid cell is more regular than a type III grid cell, in the sense that the distance of the grid cell lattice from a regular lattice is smaller for type II cells. We also applied a lattice regularization algorithm that computes the nearest regular lattice to a NRT. The algorithm takes a user-specified deformed lattice D_L and finds the nearest regular lattice via optimization by minimizing this energy functional:

$$E_D = \sum_{i=1}^{N_i} (l_i - \|T_1\|)^2 + \sum_{j=1}^{N_j} (l_j - \|T_2\|)^2 + \sum_{k=1}^{N_k} (l_k - \|T_1 + T_2\|)^2 + \sum_{m=1}^{N_m} (l_m - \|T_1 - T_2\|)^2.$$

With all of the symbols being identical to those defined for the geometric regularity measure (Eq. (1)).

To fully explore the grid cell representation, it is necessary to examine the conditions under which the dMEC grid remains invariant. That is, under what transformations (or symmetry group) is the dMEC grid

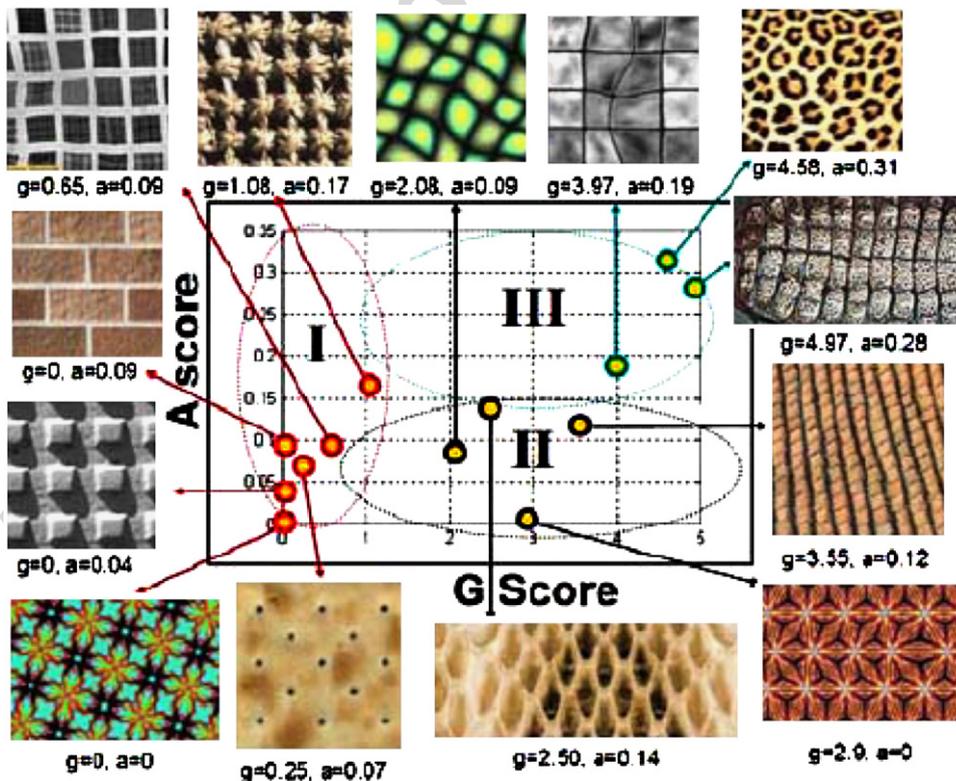


Fig. 1. This is a figure from Liu et al. [10] illustrating the different types of near-regular textures.

approximately unchanged? A preliminary response is that the pattern has distinct 2D periodicity. To formally study the regularity of the dMEC grid, it is necessary to describe the geometry of the grid. Hafting et al. [7] concluded that the grid was a regular lattice by looking at the autocorrelogram of each cell's firing field without analyzing its symmetry groups. The form of the regular lattice was hexagonal, with six peaks being equidistant from the central peak. Some aspects of this lattice form are that its tiles are composed of two equilateral triangles [7] and the angular separation of the inner vertices of the hexagon is always a multiple of 60° [7].

3. Analysis and results

Hafting et al.'s data on grid cells suggests that dMEC firing fields are near-regular [7]. Accordingly, we applied Liu et al.'s [10] algorithm on Hafting et al.'s [7] data (from the 2m diameter circular enclosure) to quantify such regularity qualitatively (symmetry group type) and quantitatively (nearest regular lattice). The results of using Liu et al.'s lattice regularization algorithm on the firing fields are illustrated in Fig. 2. To the left (in Fig. 2) are the firing fields, whose deformed lattice is fitted by hand using the same user interface that was developed in Liu et al. [10]. To the right (in Fig. 2) is the regularized lattice, with image

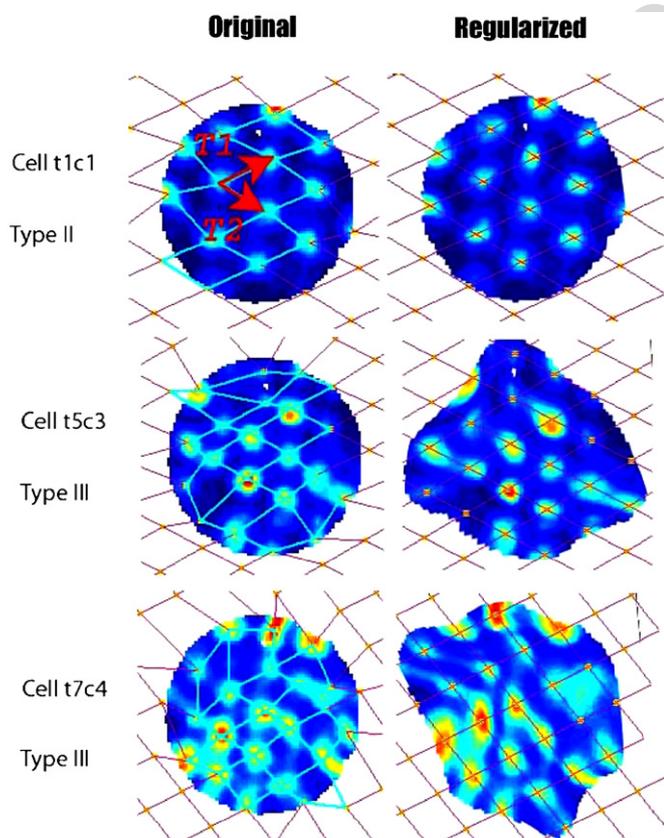


Fig. 2. These are the firing field lattices of three different grid cells. The generating vectors T_1 and T_2 are indicated in red.

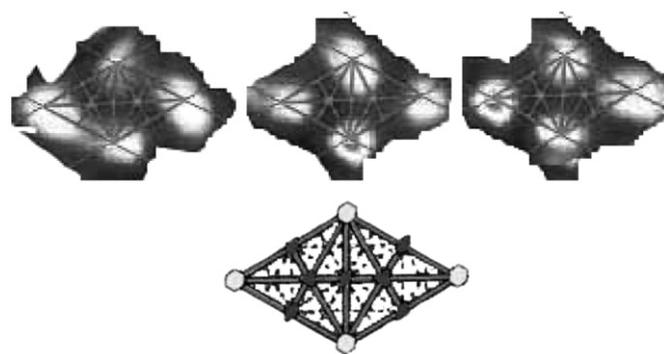


Fig. 3. These are the first, fourth, and seventh tiles of cell t5c3 and the p6m symmetry group tile which we fit onto grid cell firing fields. The three tiles from t5c3 are highly bilaterally symmetric, as can be seen by the similarity of both sides with respect to the axes demarcated by the lines overlaid on the firing field. A p6m tile has outer vertices that are invariant under 60° rotation, and is bilaterally symmetric along all of the solid lines. Both of these combined imply that the grid is triangular.

pixels morphed accordingly. The figure shows three of the 11 firing field lattices fitted using this algorithm.

As can be seen in Fig. 2, the grid cells analyzed are nearest to a lattice which is hexagonal. In agreement with the triangular grid hypothesis [7], we demonstrate that the symmetry group of this firing field is actually p6m using the wallpaper group classification algorithm outlined in Liu et al. [9]. As can be seen by Fig. 3, this is true of the regular tiles recovered by Liu et al.'s algorithm [10]. The claims made by Hafting et al. that grid cells can act as a triangular grid [7] are thus further justified geometrically and algebraically. However, dMEC firing fields are still a departure from the perfect regularity of triangular grids. To analyze how close different grid cells are to a lattice with p6m symmetry group, we quantify the regularity of the firing fields as follows:

We compute the **G** and **A** scores for all 11 of the grid cell lattice tiles. They form two clusters in **G**–**A** space (see Fig. 4). In Liu's classification of NRTs, the two clusters fall squarely within type I (geometrically regular) and III NRT's. Grid cells of type I are well-described by a lattice with p6m symmetry group (hexagonal or triangular grid). If all grid cells were of type I, then the hypothesis that the grids from these cells are used like a conventional map would be quite strong. However, this is not the case. A more prevalent kind of grid cell is that of type III. Grid cells of type III nearest to a p6m regular pattern are significant departures from the geometric and firing rate uniformity needed to call them strictly regular. Each unit of a type III grid cell firing field has markedly non-uniform firing rate at all vertices of triangles which are not equilateral.

4. Summary and discussion

Using Liu et al.'s symmetry group classification [10,9] algorithm, we are able to identify the symmetry group of

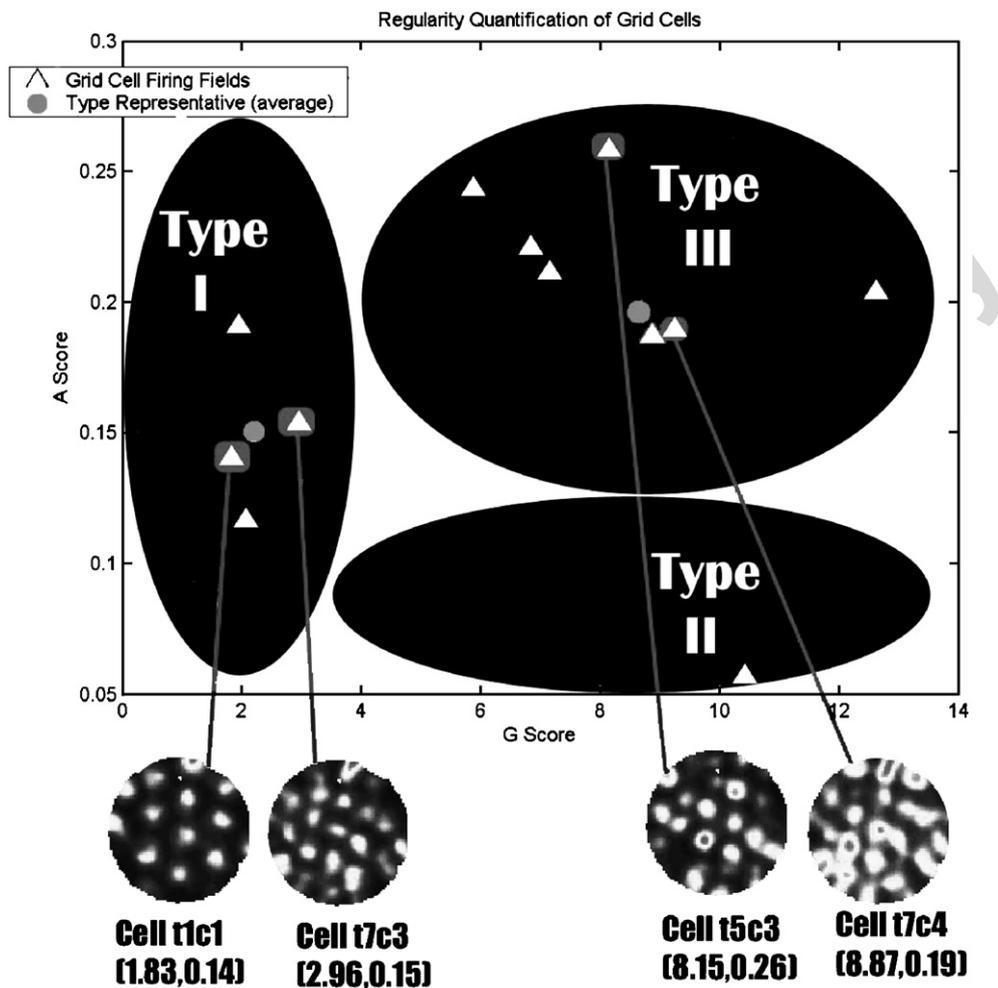


Fig. 4. A plot of the G and A scores of all 11 grid cells fitted with regularized lattices. Clustering was done using k-means. The first (leftmost) cluster of grid cells falls within type I near-regular lattices, and the second cluster of grid cells is of type III, according to Liu's classification of near-regular lattices and textures [10].

the firing fields as $p6m$, and quantify grid cells into two types of regularity. Because the statistical regularity of the grids found in dMEC is of two kinds: one highly regular (type I), the other much further from regularity (type III), we can speculate what this means for path integration. Our findings indicate that not all grid cell firing fields are well-described by a regular triangular grid. The many accounts of path integration which rely on this hypothesis (such as [1,8,14]) thus do not reflect the firing field regularity statistics. What is a possible alternative?

The two types of cells can be treated like regular lattices with fixed additive Gaussian noise added (both to the firing rates and geometry of the vertices). Type I grid cells are more regular, and type III grid cells are significantly more noisy. Consistent with this view of grid cells is a model in which place cells integrate information from grid cells of both types and do a form of maximum likelihood estimation to find the rat's current position. The increased variability of type III grid cells resolves much of the ambiguity about the rat's position that comes from the

uniformity of type I grid cells. At the same time, type I grid cells could be used as a baseline which is relatively constant.

Finally, it has been shown that attractor networks can be created which implement a computation equivalent to maximum likelihood estimation [4,26]. Attractor network models have been proposed to model the path integration properties of place cells [19,21,27] (specifically, head direction cells, which project to place cells and are thought to be the basis of place cells' path integration properties). Therefore, the proposed model is equivalent to having many type III grid cells and some type I grid cells projecting to a place cell, which determines the rat's most likely position from that set of grid cells. The specific framework in which this could be understood is that outlined in Pouget et al. [17].

Whatever the model, the statistical analysis of regularity in grid cells would not be possible in a rigorous fashion without recourse to group theory. The lessons to be learned from the varieties of regularity in grid cells is that simple

map-like navigation using grids is not only statistically infeasible but also suboptimal for estimation of the rat's position.

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