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From cortical modules to memories

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Many sensory features are topographically mapped in the mammalian cortex. In each case, features of the external world are systematically represented across the cortical area in a topographic manner, providing a complete representation of stimulus space. The cortex in turn utilizes sets of functionally specific, connected neurons to extract behaviorally relevant features from the incoming sensory information. This organization is perhaps best exemplified by the classical cortical column. The degree to which such networks also exist in high-end association cortices has been unclear. Recently it was shown that the grid map of the entorhinal cortex is organized in a modular fashion. Here, we review the key features of the grid modules and the extent to which the grid modules resemble functional arrangements in other areas of cortex.

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Introduction

The fundamental building block of many areas of sensory and motor cortex is believed to be the column, a set of locally connected neurons that form a functionally specific circuit. The essential columnar structure is established during development when radial glial cells establish a vertically oriented track onto which newborn neurons migrate up to the cortical plate, establishing a clear ontogenetic column [1]. Partly as a consequence of this developmental patterning, intracortical axons are predominately locally confined and vertically oriented, forming a locally connected column in adulthood that spans across all layers of the cortex. In the standard model, this essential unit is repeated over and over across the cortex [2,3]. The precise and orderly mapping of inputs from the thalamus onto the array of columns in the cortex leads to a topographic mapping of stimulus features in many sensory cortices and a degree of functional autonomy of each individual column [4]. The columns in turn transform the incoming sensory data into more behaviorally

relevant information (e.g., detecting lines and edges from spatial receptive fields from the lateral geniculate nucleus). Some striking successes, most notably in the primary somatosensory cortex [5], motor cortex [6] and the visual cortex of cats and monkeys [7,8], have helped the essential tenets of the column model endure for more than half a century. Organizing the cortex as a collection of columns with different tuning allows different features of the sensory environment to be extracted in parallel and passed along to output structures with minimal interference between them [9]. However, whether non-sensory, non-motor regions of the cortex, which lack topographic sensory inputs, also contain topographically organized, functionally autonomous columns has been unclear. In this review we discuss recent evidence that the grid cells of the medial entorhinal cortex (MEC) are modularly organized in a manner that shares some commonality with the columnar organization of the neocortex but also some important differences. We then consider the potential functional implications of this organization and finally discuss how such an organization may form in the absence of patterned inputs.

Organization of an association cortex: the entorhinal cortex

The entorhinal cortex has a similar intrinsic organization as the sensory cortex, including vertically linked cells, tight bundling of dendrites from the deeper layers, and predominantly local connections [10] raising the possibility that it contains functionally autonomous columns. Moreover, the MEC has well-defined spatial responses that allow the cells to be analyzed for topography and modularity in their response properties.

In the MEC four functional cell types have been described: grid cells, conjunctive cells, head direction cells and border cells. Grid cells have multiple firing fields together forming a beautiful hexagonal pattern that repeats over the surface of the environment [11]. The grid cells can be described along three key dimensions: the phase of the grid (i.e. where its vertices are located in any given environment), the scale of the grid, and finally how the grid is oriented in an environment. The presence of several distinctive features makes grid cells an ideal candidate to check for topography and modularity. The phase is not organized in a topographical manner: cells recorded from the same position in the MEC do show very different phases and at any dorsoventral level of the MEC a few grid cells are enough to fully cover an environment. In contrast to this random organization, the scale is organized in a topographical manner. Small grid cells are located close to the dorsal border and the

scale increases from dorsal to ventral MEC. The smallest grid fields are around 30 cm in a rat, but the largest is approximately 3 m in diameter, although the very ventral pole of the MEC has yet to be explored [12]. The most straightforward model predicts that grid cells generate place fields in the hippocampus through the linear summation of aligned grids at different spatial scales [13] and the MEC topographically projects to the hippocampus, and consistent with this, the hippocampus also shows a topographic representation of scale, with exceptionally large place fields of 10 m at the ventral pole [14]. This same topographic organization can be achieved regardless of the precise mechanism of grid cell to place cell transformation [15].

Grid cells are organized in modules

The topographic arrangement of grid cells in the MEC surprisingly resembles the topographic arrangement seen in many primary sensory and motor cortices, suggesting that the MEC may use similar principles as the sensory and motor cortex. However, another feature of the sensory and motor cortex is its organization as a set of functionally specific circuits. These circuits can take the form of anatomically discrete units, like in the barrel cortex, or continuously graded organizations, like in the orientation selectivity of the visual cortex of cats and monkeys. Since the precise firing patterns of grid cells are likely to arise from continuous attractor networks in the MEC [16,17] and cells of the same attractor network should have the same spacing and orientation [18,19,20,21], it follows that grid cells could show a modular arrangement corresponding to multiple attractor networks.

This prompted Stensola *et al.* [22] to examine the issue more completely by densely sampling of grid cells along the entire dorsoventral axis of the MEC. Using this approach, Stensola *et al.* found discrete jumps in grid spacing, with a scale ratio of 1.42 (square root of 2, thus, a near perfect doubling of the area within the hexagon). Moreover, several other features of the grid were co-modular with spacing, including orientation, ellipticity and theta frequency, suggesting that the modules are collections of interconnected neurons with similar selectivity.

Are the modules anatomically segregated (like in sensory and motor cortex)? The MEC has a few anatomical features that suggest that anatomically discrete modules should exist. For example, entorhinal neurons show locally confined axonal projections [10] and cytochrome oxidase stains shows discrete patches or islands within the MEC [23]. However, Stensola *et al.* found a relatively small number of modules (approximately 5) compared to the hundreds observed in cytochrome oxidase staining, suggesting that the modules do not follow the boundaries defined by cytochrome oxidase staining. Furthermore,

the modules are organized as a set of overlapping bands with blurry anatomical boundaries between them (see Figure 1), such that cells of the different modules can be recorded at the same dorsoventral location or even the same tetrode, though the most dorsal part of the MEC contains only cells of the smallest scale. The modules are therefore anatomically intermingled, yielding an unusual paradox wherein the cells of different modules are functionally discrete but anatomically overlapping.

To test whether the modules were functionally independent, Stensola *et al.* compressed the environment along one axis and measured the amount of rescaling in the grid cells. Cells in the smallest module did not rescale with the environment, while cells in all other modules re-scaled roughly in proportion to the rescaling of the environment. These data suggest that the modules are functionally independent and form a discrete, rather than graded, representation of space, similar to the functional divisions between the individual barrels of the barrel cortex.

One of the great mysteries of the columnar organization of cortex is whether or not the columnar organization has any functional implications for perception, cognition or behavior [24]. In the next section, we propose that the functionally independent modules may help minimize the interference between competing memories, providing a clear functional relevance for such an arrangement.

Does the modular organization of the entorhinal grid map have functional implications?

The hippocampal–entorhinal circuit is critical for the formation of new episodic memories, or memories for events that occur in a particular spatial and temporal context. Memory retrieval has two inherent challenges. One is that an episode will never exactly re-occur and objects, people, stories are constantly changing. If so, then how can the network recall a memory based on only partial or degraded information? Second, if distinct episodes are too similar at the time of encoding, they might be intermixed and increase the risk of errors in the retrieval process. These problems have motivated two core concepts in memory research: pattern separation and pattern completion [25–27]. Pattern separation allows two closely related but distinct patterns to be differentiated from one another. Conversely, pattern completion fills in gaps when information is incomplete. A key challenge for memory research is to understand exactly how pattern completion and pattern separation are accomplished within the hippocampal–entorhinal circuit.

Place cells can increase the separation of two maps through global remapping, whereby individual cells turn on, turn off or shift their firing fields to an unpredictable location. The separation is so complete that the population of active cells in two different environments is

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