

Opinion

Grid Cells and Place Cells:
An Integrated View of their
Navigational and Memory
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Much has been learned about the hippocampal/entorhinal system, but an overview of how its parts work in an integrated way is lacking. One question regards the function of entorhinal grid cells. We propose here that their fundamental function is to provide a coordinate system for producing mind-travel in the hippocampus, a process that accesses associations with upcoming positions. We further propose that mind-travel occurs during the second half of each theta cycle. By contrast, the first half of each theta cycle is devoted to computing current position using sensory information from the lateral entorhinal cortex (LEC) and path integration information from the medial entorhinal cortex (MEC). This model explains why MEC lesions can abolish hippocampal phase precession but not place fields.

Much has been learned about the cell types in the hippocampal region that underlie the sense of place, culminating in the 2014 Nobel Prize. The first cell type discovered was the place cells of the hippocampus [1]. These fire when an animal is in a particular location of a given environment (Figure 1A). More recently, investigation of the medial entorhinal cortex (MEC), a cortical region that provides input to the hippocampus, led to the discovery of cells with various response properties. Of these, the best known are grid cells. These fire when the animal is in any of multiple locations that form a triangular grid [2] (Figure 1B). Other cell types include conjunctive grid cells (these fire only when the animal is on a vertex of the grid and when the animal moves in a particular direction) [3], head-direction cells [4–6], speed cells [7], and boundary vector cells [8] (Figure 1C). The lateral entorhinal cortex (LEC) also provides input to the hippocampus and contains cells that carry sensory information about the current position [9]. These cell types are pieces of the puzzle, but a framework for understanding how these cell types work together to produce the sense of place and access memory information is still needed.

A core question is the function of grid cells. It had generally been assumed that grid cells are an obligatory precursor of place cells [10–13]. However, such models have been called into question by results showing that place cells exist after elimination of grid cells [14–18]. Recent reviews have suggested why place cells do not require grid cells; namely, place cells also receive sensory information about position from the LEC, information that is sufficient to define the place field [19,20]. This leaves unresolved the question of what the special role of grid cells might be and, more generally, how the identified pieces of the puzzle fit into a functional framework. Before suggesting such a framework, we first review what is known about **path integration** and **theta sequences** (**phase precession**; see [Glossary](#)), two phenomena central to the framework that we will develop.

Trends

Previous models of place cell generation by summing of grid cell inputs have been called into question by recent results.

The phase precession of place cells depends on the MEC and thus probably grid cells.

Phase precession is an expression of theta sequences, in which place cells fire in order during a single theta cycle.

The theta cycle can be broken into two parts: during the first half of the theta cycle, current position is represented; during the second half of the theta cycle, the system performs mind-travel to upcoming locations.

Mind-travel during the second half of theta is hypothesized to be driven by grid cells given their universal representation of spatial adjacency.

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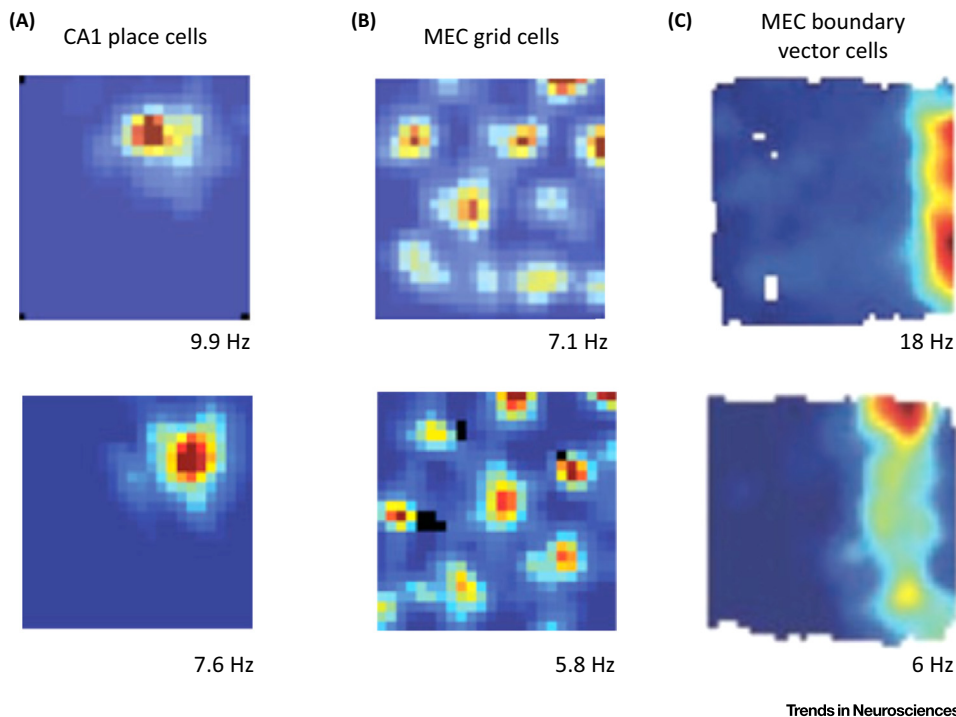


Figure 1. Firing Properties of Cell Types. Rats forage for food in a square-shaped environment. Whenever a spike occurs, the location of the animal is recorded. The heat map shows the spike rate of a given cell as a function of location. The color scale ranges from no activity in dark blue to the maximum rate in red (shown below maps). (A) CA1 place cells [17]. (B) MEC layer II grid cells, adapted from [17]. (C) MEC boundary vector cells, adapted from [8].

Path Integration (Dead-Reckoning)

As noted above, both the LEC and MEC provide information about position. However, this information is derived in different ways. The process of spatial localization can use sensory information about landmarks in the environment, information that is thought to come from the LEC [21]. However, these landmarks may be few and far between; information about intermediate positions is provided by a process termed ‘path integration’ that is thought to come via the MEC [22]. This computation takes a past estimate of the position of the animal and adds to it the change in position during the intervening time, thereby forming an estimate of current position. The change in position can be computed by integrating a velocity vector (direction and speed of the animal) that is based on vestibular information, sensorimotor information about self-motion, and optic flow [23]. Experiments demonstrate that information about path integration is present in place cells [24,25] and grid cells [26]. A major advance in theoretical neuroscience has been the understanding that a network of grid cells is capable of performing path integration. If activity bumps are moved in proportion to a velocity vector, bump position is determined by the integration of velocity and therefore provides an estimate of current position [22,27–30] (see [Box 1](#) for further explanation). Several influential models have thus assumed that grid cells perform path integration and that the results are then passed on to place cells [13,28,31–33]. However, we will argue below that the primary function of grid cells is integration of a different type of information: an **artificial velocity vector** (AVV) that represents the direction of imagined motion.

Theta Sequences and Phase Precession

Population activity in the rodent hippocampal system exhibits theta-frequency oscillations (5–10 Hz), particularly during movement [34]. Recordings reveal ‘theta sequences,’ in which place cells fire during a theta cycle in order of the position of their place fields ([Figure 2A–C](#))

Glossary

Artificial velocity vector (AVV):

consists of a direction of interest and a distance of interest. This vector is integrated by the grid cell network to generate mind-travel in the appropriate direction.

Grid cell modules: the grid cell network consists of several discrete modules. The grid cells in each module have a consistent spatial scale, a scale that differs between modules. The grid cells in each module move coherently when introduced into a new environment.

Mind-travel: the process of internally generating a sequence of place cell activations without corresponding motion.

Path integration: also known as ‘dead-reckoning.’ Starting with an identified position, adding the change in position derived from self-motion cues provides a new estimate of position.

Phase precession: single-cell manifestation of theta sequences observed as a negative correlation between position and the theta phase of spiking.

Rate place field: the area in which a place cell fires. This is the standard method for defining a place field in the literature.

Theta sequence: within a theta cycle, an internally generated sequence of place cells fire corresponding to a sequence of locations. This sequence is time-compressed compared to the length of time it would take to traverse this path in space. See mind-travel.

True place field: small part of the place field corresponding to region that cell actually represents. Firing outside that small region can be understood as predictive firing during mind-travel.

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