

# Making our way through the world: Towards a functional understanding of the brain's spatial circuits

Ingmar Kanitscheider and Ila Fiete

## Abstract

Many animals make return trips from a home base to gather food and supplies, mate, or survive the seasons. In a world of unreliable and ambiguous cues, localizing within familiar environments and mapping new environments – functions critical for making successful return trips – is a complex problem requiring memory, integration, and inference. We review some key features of the mammalian brain's navigation system and its computational challenges, as well as the task neuroscientists face in understanding how its components interact and function. We argue that synthesizing the wide body of neural phenomenology requires formalization of the navigation problem as one of sequential probabilistic inference, as done in the robotics field of simultaneous localization and mapping (SLAM).

## Addresses

Department of Neuroscience, The University of Texas, Austin, TX 78712, USA

Corresponding author: Kanitscheider, Ingmar ([ikanitscheider@mail.clm.utexas.edu](mailto:ikanitscheider@mail.clm.utexas.edu))

Current Opinion in Systems Biology 2017, 3:186–194

This review comes from a themed issue on **Mathematical modelling, Dynamics of brain activity at the systems level (2017)**

Edited by **Marcelo O. Magnasco**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 20 May 2017

<http://dx.doi.org/10.1016/j.coisb.2017.04.008>

2452-3100/© 2017 Elsevier Ltd. All rights reserved.

## Keywords

Navigation, Hippocampus, Entorhinal cortex, Computational modelling, Simultaneous localization and mapping, Probabilistic inference.

Keeping track of one's location in space while navigating through it is a high-level cognitive problem handled by areas including the entorhinal cortex and hippocampus, which sit atop the mammalian brain hierarchy. Location coordinates are not simple sensory variables – they are estimated by combining a number of somewhat reliable cues, including self-motion and various external sensory landmarks in visual, tactile, auditory and olfactory space. For accurate localization, these partially informative cues must be integrated over time and fused together according to their reliability, in the context of learned maps of the environment. Navigation further requires goal selection and path planning, which in turn involve balancing exploration of new parts of the world with

exploitation of known venues. Thus, navigation is a wonderfully rich problem domain for understanding how the brain solves hard problems involving time-varying inputs, multisensory fusion, integration, memory, ongoing inference, decision making and optimization. In this review, we will focus on the problems of localization and mapping.

Various neuron populations in the mammalian brain have been discovered to encode spatial variables. However, our understanding of these representations is piecemeal. We propose that models that recognize the localization problem as one of real-time probabilistic inference, and generate neural solutions to challenging versions of this problem, will recapitulate and help to build a functional synthesis of the phenomenology of the brain's navigational circuits.

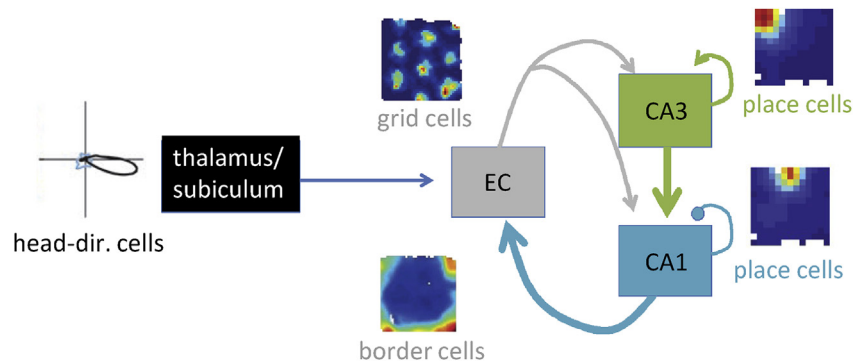
## Neural representations of spatial variables

One way to begin to understand how the brain computes is to characterize how it represents key variables. The classic approach to characterizing neural representations has been to construct tuning curves: the average response of a neuron to different values of an independent variable. Tuning curve-based characterizations of spatially responsive cells are not sufficient for understanding how the brain performs spatial computations, as discussed later. However, they have laid the essential groundwork for understanding how spatial computations are performed in the brain by showing where and how spatial variables are represented.

## Discovery of spatial tuning

The tuning curve approach has led to the discovery of cells involved in computing a broad assortment of spatial and navigation-related quantities ([Figure 1](#)): A place cell in the hippocampus fires whenever the animal is in a specific spatial location [\[2\]](#); a grid cell in medial entorhinal cortex (MEC) fires at multiple locations arranged on a regular triangular grid [\[3\]](#); a head direction cell in the postsubiculum, retrosplenial cortex, entorhinal cortex or thalamus [\[4–6\]](#) fires whenever the animal's head is pointing in a given direction (relative to some external reference); border [\[1,7\]](#) and boundary vector cells [\[8\]](#) in the entorhinal cortex and subiculum respond at or parallel to environment boundaries; speed cells in the medial entorhinal cortex [\[9\]](#) are sensitive to the animal's running speed; and landmark cells in lateral entorhinal cortex respond to local objects in a space based on their identity and the local reference frame [\[10,11\]](#).

Figure 1



Neural representations for spatial navigation. Summary of notable types of neural tuning for navigation-related variables; the brain areas where they appear; and major anatomical connections between areas. Head direction and border cell data from Ref. [1] (Reprinted with permission from AAAS). Grid cell data from Boccara, C.N., Sargolini, F., Thoresen, V.H., Solstad, T., Witter, M.P., Moser, E.I., Moser, M.-B. Grid cells in pre- and parasubiculum, *Nat Neurosci* 13 (8), 987–94 (2010) (Reprinted by permission from Macmillan Publishers Ltd). Place cell data from Colgin, L.L., Leutgeb, S., Jezeq, K., Leutgeb, J.K., Moser, E.I., McNaughton, B.L., Moser, M.-B. Attractor-map versus autoassociation based attractor dynamics in the hippocampal network, *J Neurophysiology* 104 (1), 35–50 (2010) (Reprinted with permission from APS).

### Mechanisms of spatial tuning in individual neural populations

The discoveries of neural tuning motivated the development of circuit models capable of generating such representations. Continuous attractor models of head direction cells [12], place cells [13,14] and grid cells [15,16] show how forgetful neurons could collectively represent and store spatial variables while integrating motion inputs to update these representations. These models, which were constructed to recapitulate individual tuning curves, have met with substantial recent successes in tests of their circuit-level predictions about cell–cell relationships constrained by internal dynamics rather than external inputs [5,6,17–19].

### Gaps between mechanistic models and observed tuning in homogeneous populations

We may arguably have a first-order understanding of the mechanisms of spatial tuning in groups of cells with homogeneous (but spatially offset) tuning curves, through hand-designed network models. However, even within this framework, there are notable gaps between our understanding and observed phenomena.

Examples of such gaps include understanding how multiple subnetworks of grid cells with different spatial periods [20,21] could emerge and modularize through plasticity and development; what drives the consistent skew in the grid cell response across familiar square enclosures [22] and the distortion of grid tuning in non-square environments [23,24]; whether periodic [16,25] or aperiodic attractor networks [15,16] or some combination of feedforward/oscillatory and attractor dynamics [26] underlies the grid cell response. Filling these gaps requires an elaboration of existing types of models, coupled with experimental study and data analysis for testing the elaborated models.

### More complex realities and questions

The realities of representation and requirements for computation in the navigation circuit are more complex than models that generate homogeneous tuning curves capture. Further, the description of neurons based on spatial tuning is a static view that neglects temporally changing responses, versions of which are required for navigational computations and are richly observed in spatial circuits.

#### Sparse location tuning

Only a fraction of cells across navigation-related circuits display clearly discernible tuning to a navigation-relevant variable [27]. Even among spatially tuned cells, strong location specificity seems sparse [28]: high spatial information appears to reside in a small subset of neurons across environments [29]. From a coding-theoretic perspective, which would support maximally whitened representations with equalized information-sharing of the encoded variable across neurons, this is a puzzling result – why not dispense with the cells that, across environments, fail to exhibit strong location specificity? Are the less discriminating cells sidelined in spatial computations or essential to some other aspect of the computation? Mechanistically, are the low- and high-spatial information cells part of the same recurrent network or uncoupled populations?

#### Mixed (conjunctive) representations and remapping

The navigation circuits contain various examples of mixed selectivity or conjunctive tuning: when a cell is tuned to one navigation-related variable, it is frequently jointly tuned to another. On the most basic level, the joint representation of grid cells (or place cells) to both spatial coordinates is a form of conjunctive coding. Cell in layers III–V of medial entorhinal cortex exhibit

Download English Version:

<https://daneshyari.com/en/article/8918163>

Download Persian Version:

<https://daneshyari.com/article/8918163>

[Daneshyari.com](https://daneshyari.com)