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Grid cells: Reading the neural code for space

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The cognitive map for spatial navigation is thought to rely on grid cells. Scientists at Ludwigs-Maximilians-Universitaet in Munich and Harvard University have now put forward a mathematical theory that explains key grid-cell features and how these give rise to a neural metric for space.

One year ago, the Nobel Prize in Physiology or Medicine went to the discoverers of the mammalian "GPS system" for spatial navigation. Measuring neural activity in cortex, these researchers had found that some cells represent space in a highly surprising manner: As the animal moves through its environment, distinct sets of cells are sequentially activated. Each individual "grid cell" responds to multiple positions in space that form a virtual hexagonal lattice tessellating the environment. This strikingly periodic and beautiful spatial pattern has caught the imagination of experimental and theoretical neuroscientists alike, and has been proposed to constitute the brain's metric for space.

Theoretical neuroscientists at LMU Munich and the Bernstein Center for Computational Neuroscience in Munich, and at Harvard University, have now put forward a comprehensive mathematical theory that explains many features of grid cell activity that had remained mysterious, and makes specific predictions that can be tested in neurophysiological and behavioral experiments. The framework proposed by Martin Stemmler (LMU), Alexander Mathis (Harvard) and Andreas V.M. Herz (Professor of Computational Neuroscience at LMU) exploits and extends a computational principle well known from sensory systems and the brain's motor cortex - population-vector decoding: physical quantities such as the angle of a visual stimulus or the direction of a movement can be easily read out from the activity of a population of neurons with different tuning properties if the neurons' activities are combined in a particular, vector-like manner.

However, the theory proposed by Stemmler and colleagues goes far beyond these previous schemes in that the decoded quantity - the animal's position - is not a circular variable. "Animals move on two-dimensional surfaces or in three-dimensional spaces, so their position is not a one-dimensional variable either. In addition, population-vector averages across different grid scales need to be combined," explains Andreas Herz. Yet, the overall conceptual similarity of the new scheme to conventional population-vector decoding suggests that there exist overarching computational principles that operate throughout the brain. "This raises hopes that, in spite of the brain's complexity, a thorough understanding of the neural basis of many cognitive processes is possible."

Thanks to the new theory, three basic questions can now be readily answered: Why are grid cells organized into discrete modules, within which all grid lattices share the same spatial scale and orientation, but have different spatial offsets? Why do the spatial scales of the grid lattices form a geometric progression? And why is the observed scale ratio close to 3/2? "If grid cells were not organized into modules with fixed grid scale and orientation, the brain could not use population vectors to represent spatial position," explains Martin Stemmler. "The geometric progression in the grid scales maximizes the spatial resolution of the neural code, based on just a few bursts of neural activity. Finally, the scale ratio should be close to 3/2 to avoid large-scale errors when information from different grid modules is combined to calculate a single quantity, the animal's position estimate."

The theory also shows that grid cells can be used not only to estimate position in world-centered coordinates, but also to tell the direction to some goal - for example, a food source or the animal's home - in self-centered coordinates, a key requirement for navigation. "Transiently silencing individual grid modules should lead to specific types of navigational errors - a prediction that can be tested in future research", says Alexander Mathis. Perhaps most importantly, the new work translates the hitherto rather hazy notion of "a neural metric for space" into a precisely defined mathematical framework. The results have already helped to settle a recent controversy in the field - whether the observed distortions of grid patterns falsify the proposed role of grid cells as a metric for space (no, they don't) - and will, most probably, also guide future experiments.

More information: Connecting multiple spatial scales to decode the population activity of grid cells, *Science Advances*, dx.doi.org/10.1126/science.1500816

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