Space Bats: Multidimensional Spatial Representation in the Bat

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It is estimated that more than 8 million different species reside on our planet, many of which live a very different lifestyle (1). But whether on the ground, in the ocean depths, or in the sky, all animals must have knowledge of their whereabouts to survive. The possible mechanisms subserving this core function and how these are implemented in the brain have been long-standing questions in neuroscience.

Scientists began studying the neural basis of spatial representation with the report of neurons in the rat dorsal hippocampus that fired when the animal entered a specific location (2). These neurons were called “place cells.” More recently, scientists discovered “grid-cells” in the rat medial entorhinal cortex (MEC), which activate in multiple locations, all arranged on the vertexes of a hexagonal grid (3, 4). Place cells and grid cells are widely considered key elements of the mammalian spatial representation system (5), yet their detailed properties have been studied almost exclusively in rodents. This convergence in choice of an animal model has occluded the understanding of which neuronal mechanisms involved in spatial representation generalize across species and whether different solutions have been reached by different brains. To explore this question and to study the functional properties of these cell types, we used a novel mammalian animal model, the bat. The findings in the bat helped revise our understanding of this important circuitry and show how divergence can powerfully complement convergence in the choice of animal models in neuroscience.

We first asked whether the bat can provide insight into the neural mechanisms giving rise to the grid formation. Two major classes of computational models were proposed to account for this phenomena (6): Attractor-based network models and single-neuron, “oscillatory-interference” models relying on theta-band (5 to 11 Hz) oscillations. The latter class of models received much experimental attention in rodent studies, but all evidences were of a correlative nature (6). We reasoned that, because place cells in bat hippocampus exist in the absence of continuous theta oscillations (7, 8), perhaps grid cells might also exist in their absence. This would causally argue against the validity of the oscillatory-interference class of models or, at least, against their generality across mammals. We recorded the activity of single MEC neurons in bats crawling inside a large arena (8) and found many of them to be grid cells [see the figure (A), left] with properties strikingly similar to those previously described in rats. We further found in the bat MEC all the other spatial cell types previously described in the rat MEC, such as neurons that encode the animal’s head orientation (9) and the borders of its current environment (10). We even found many of the same neural oscillations previously reported in the rat, such as high-frequency “ripple” oscillations (11) and fast and slow gamma oscillations (12). However, as we had hypothesized, theta oscillations in the bat were very different from those in rats. Theta oscillations in the bat were not...
continuous [see the figure (A), middle], and the firing patterns of bat grid cells were not theta-modulated [see the figure (A), right], which put them in striking contrast to pre-requisites of the oscillatory-interference models. Thus, our study in bats (8) allowed for causal examination of a major class of models that were based solely on data from rats.

After establishing the existence of place cells and grid cells in a two-dimensional (2D) environment, we wanted to go one step further and ask: How is the complete 3D volumetric space represented in the mammalian hippocampal formation? This question is pivotal because many animals on our planet, whether in air, in water, or on land, move in 3D environments. However, all studies conducted to date were in either 1D or 2D environments (13), which left this question unresolved. The bat’s flight capability provided us with a unique opportunity to address this question. We focused on the hippocampus and developed the technology to record the activity of single place cells in freely flying bats (14) [see the figure (B), left]. We found that individual place cells provided a stable and nearly isotropic representation of the animal’s position in 3D space. Each place cell fired mainly in a single restricted region of the 3D environment, and all axes were represented with similar resolution [see the figure (B), middle]. Furthermore, each place cell activated in a different location, and the combined activity of multiple place cells represented the 3D environment uniformly [see the figure (B), right]. We further found that the firing patterns of 3D place cells were not theta-rhythmic during flight, which supported our previous findings from the crawling bats and strongly argued against the cross-mammalian generality of oscillatory-based temporal codes for spatial representation (14).

The importance of our findings is fourfold. First, they support the generality of the place-cell and grid-cell phenomena across mammals. Second, they argue in favor of a rate-coding mechanism underlying the formation of spatial firing patterns in these cell types and, by this, constrain the possible computations responsible for their generation. Third, they reveal a coding mechanism for 3D space in the mammalian brain. Finally, they demonstrate that the use of novel animal models in neuroscience can complement existing knowledge and provide insights into the inner workings of the brain.

2013 Grand Prize Winner

The author of the prize-winning essay, Michael Yartsev, received his undergraduate and master’s degrees in biomedical engineering from Ben-Gurion University in 2007. For his Ph.D., he joined the lab of Dr. Nachum Ulanovsky at the Weizmann Institute of Science. There, he recorded the activity of single neurons from the hippocampal formation of freely behaving and flying bats to study the underlying neural mechanisms of spatial memory and navigation in the mammalian brain. Since 2012, Dr. Yartsev is a C. V. Starr Fellow at the Princeton Neuroscience Institute at Princeton University where he is conducting postdoctoral work in the lab of Prof. Carlos Brody studying the neural basis of decision-making.

Finalists

Daniel Bendor for his essay, “Play it again, brain.” Dr. Bendor is a lecturer in the Department of Cognitive, Perceptual, and Brain Sciences and the Institute of Behavioral Neuroscience at University College London. Dr. Bendor received his Ph.D. from Johns Hopkins University under the mentorship of Dr. Xiaojin Wang, studying temporal processing in auditory cortex and the neural correlate of pitch and flutter perception. For his postdoctoral research, he investigated the role of the hippocampus in memory encoding and consolidation, while working with Dr. Matthew Wilson at the Massachusetts Institute of Technology. He has recently started his own lab at University College London, where his research focuses on how neural ensembles encode perceptual and memory-related information. http://scim.ag/_Bendor

Sophie Caron for her essay, “Brains don’t play dice—or do they?” Dr. Caron is currently a postdoctoral fellow in the Department of Neuroscience at Columbia University. Sophie grew up in St-Blaise-sur-Richelieu in Canada and earned a B.Sc. in Biochemistry at the Université de Montréal. She moved to New York City to study the developmental mechanisms behind the diversification of sensory neurons in the laboratory of Dr. Alexander Schier at New York University and, later, Harvard. Having completed her Ph.D., Sophie joined the laboratory of Dr. Richard Axel at Columbia University, where she studies how the information gathered through the senses is represented in higher brain centers; in particular, those involved in memory. http://scim.ag/_Caron

For the full text of finalist essays and for information about applying for next year’s awards, see Science Online at http://scim.ag/ependorf.
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Editor's Summary

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