Has a fully three-dimensional space map never evolved in any species? A comparative imperative for studies of spatial cognition

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Abstract: I propose that it is premature to assert that a fully three-dimensional map has *never* evolved in any species, as data are lacking to show that space coding in all animals is the same. Instead, I hypothesize that three-dimensional representation is tied to an animal's mode of locomotion through space. Testing this hypothesis requires a large body of comparative data.

The target article by Jeffery et al. reviews the literature on three-dimensional spatial navigation and highlights important considerations for interpreting both behavioral and neurobiological data on this topic. In their review, they lay the foundation for the hypothesis that three-dimensional spatial navigation is "bicoded" – that is, based on different encoding mechanisms for horizontal and vertical space. Furthermore, they argue that a fully three-dimensional map has never evolved in any species.

The "bicoded" model is based on studies of animals that move along surfaces to navigate, which constrains the design of experiments and the data used to build theory. For a complete theory of three-dimensional spatial navigation, a wider range of animals must be studied. In particular, data from animals that freely navigate three-dimensional volumetric space will help determine whether a single model can account for three-dimensional spatial navigation in terrestrial, aerial, and aquatic species. Counter to the model proposed by the authors of the target article, I hypothesize that a fully three-dimensional volumetric map has evolved in species that are not limited to navigating along surfaces. More broadly, I hypothesize that three-dimensional spatial representation depends upon an animal's mode of locomotion and the navigational tasks it encounters in the natural environment.

Another point I would like to make is that models of three-dimensional spatial navigation must be grounded in behavioral and neurobiological studies of animals engaged in biologically relevant and natural tasks. For example, rodents have conveniently served as animal models for a wide range of studies, including spatial navigation. Many rodent maze studies are, however, highly artificial, requiring that animals perform tasks they are unlikely to encounter in a natural setting, and in spaces far more restricted than they would navigate in the wild. The study of inbred rodents that have not navigated the natural environment for many generations raises additional concerns.

Research traditions have limited the study of spatial navigation, and advances in the field require a comparative approach. The importance of choosing the right animals for the questions under study, first articulated by Nobel Laureate August Krogh (1929), is widely recognized in the field of Neuroethology, but is less influential in the broad field of Systems Neuroscience. It is important that the spatial navigation research community interested in problems of three-dimensional spatial navigation turn to the study of animals that have evolved to solve this problem.

Echolocating bats present an excellent model system to pursue questions about three-dimensional spatial navigation. Bats belong to the order Chiroptera, many species of which use biological sonar systems to represent the spatial location of targets and obstacles. In turn, this spatial information is used to build a cognitive map that can guide navigation in the absence of sensory cues. Anecdotal reports and laboratory studies of echolocating bats provide evidence that bats rely strongly on spatial memory (Griffin 1958; Jensen et al. 2005), and field studies show that bats use memory on many different spatial scales (Schnitzler et al. 2003; Tsoar et al. 2011). Importantly, bats use an absolute-space–based (allocentric) navigational strategy that is hippocampus-dependent, and place cells have been identified and characterized in the bat hippocampus (Ulanovsky & Moss 2007; Yartsev & Ulanovsky 2013). Furthermore, grid cells have been recently described in the medial entorhinal cortex (MEC) of the Egyptian fruit bat (Yartsev et al. 2011). Therefore, echolocating bats are particularly well suited for researchers to use in behavioral, neurobiological, and computational studies of three-dimensional spatial navigation.

Neural recording data from the MEC and hippocampus of bats have raised questions about the generality of the rodent model in spatial representation. Although neural recordings from awake, behaving rats and bats show that neurons in the hippocampus and MEC represent two-dimensional space in a similar way (Ulanovsky & Moss 2007; Yartsev et al. 2011), there is one noteworthy difference, namely an absence of continuous theta oscillations in hippocampal recordings from the big brown bat (Ulanovsky & Moss 2007) and the MEC and hippocampus in the Egyptian fruit bat (Yartsev et al. 2011; Yartsev & Ulanovsky 2013). Whole cell patch clamp studies of the MEC of the big brown also demonstrate differences in subthreshold membrane potential resonance between bats and rats (Heys et al. 2013). These reported species differences challenge a fundamental assumption of the oscillatory interference model of spatial coding (e.g., Burgess et al. 2007; Hasselmo et al. 2007). By extension, comparative data could raise questions about the generality of three-dimensional spatial coding mechanisms in the brains of animals that have evolved to navigate along surfaces, compared with those that move freely through three-dimensional volumetric spaces, such as air and water.

In summary, I propose that it is premature to assert that a fully three-dimensional map has *never* evolved in any species, as empirical data are lacking to support the notion that three-dimensional space coding in all animals is the same. Recent findings from Yartsev & Ulanovsky (2013), demonstrating three-dimensional space representation in the hippocampus of the free-flying Egyptian Fruit bat, are consistent with the hypothesis that space representation is tied to an animal's mode of locomotion. To fully test this hypothesis requires a large body of comparative data.

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Making a stronger case for comparative research to investigate the behavioral and neurological bases of three-dimensional navigation

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Abstract: The rich diversity of avian natural history provides exciting possibilities for comparative research aimed at understanding three-dimensional navigation. We propose some hypotheses relating differences in natural history to potential behavioral and neurological adaptations possessed by contrasting bird species. This comparative approach may offer unique insights into some of the important questions raised by Jeffery et al.