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**Abstract:** The target article does not consider neural data on primate spatial representations, which we suggest provide grounds for believing that navigational space may be three-dimensional rather than quasi-two-dimensional. Furthermore, we question the author's interpretation of rat neurophysiological data as indicating that the vertical dimension may be encoded in a neural structure separate from the two horizontal dimensions.

The neurophysiological data presented by Jeffery et al. in the target article in support of the view that spatial representations for navigation by surface-travelling mammals are quasi-planar come from just one animal: the rat. There is no consideration of neural data from primates. We suggest here that when primate neural data are examined, it raises the possibility that primates have three-dimensional volumetric spatial representations for navigation, not quasi-planar ones. Furthermore, we question the author's interpretation of rat physiological data as suggesting that the encoding of the vertical dimension occurs in a different neural structure from the horizontal dimensions, "in an as yet undiscovered region" (sect. 5.1, para. 5).

One indication of possible differences in spatial representations between rats and primates comes from comparing allocentric responses in the hippocampus. Rat hippocampal place cells fire only when a rat is located at a particular place. On the other hand, macaque monkeys also have hippocampal cells that respond when a monkey is merely looking from a distance at a particular spot, whose location has both horizontal and vertical components (Georges-François et al. 1999; Rolls 1999).

Although neurophysiological studies of navigation in rats have focused on the hippocampus, neurophysiological and functional magnetic resonance imaging (fMRI) studies in macaque monkeys and humans have highlighted other structures as also important during navigation. Among them are the posterior parietal cortex, posterior parahippocampus, and retrosplenial cortex (RSC), together with the nearby posterior cingulate cortex (PCC) (Epstein 2008; Kravitz et al. 2011). RSC and PCC appear to be part of a network that transmits spatial information for navigation from the posterior parietal cortex to medial temporal lobe structures, in particular the parahippocampus and hippocampus.

In addition to being the ultimate source of spatial information for navigation, the posterior parietal cortex is also involved in spatial representations for the control of action (which may be distinct from spatial representations for object recognition and memory [Sereno & Lehky 2011]; see also earlier work by Goodale & Milner 1992). Control of action includes control of 3D eye movements and 3D visually guided reaching and grasping by the arm and hand (Blohm et al. 2009; Breveglieri et al. 2012; Hadjidimitrakis et al. 2012). Spatial representations for the control of action in primates operate in a 3D volumetric space, and not a quasi-2D multiplanar space. Furthermore, recent physiological studies in monkeys of populations of posterior parietal cells (Sereno & Lehky 2011) show evidence for a 3D representation of space in primates even when simply fixating.

As the posterior parietal cortex in primates appears to be a source of spatial information both for control of action and for navigation, it seems a reasonable conjecture that known parietal 3D spatial representations for control of action could also be used for navigation. While the dimensionality of space representation for navigation in primates is an important topic that has not been well studied, there are physiological reasons to believe that it may be three-dimensional.

## Monkeys in space: Primate neural data suggest volumetric representations

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It is also not clear that the representation of space in the rat is quasi-two-dimensional, as Jeffery et al. claim, in the sense that information about the vertical dimension is processed by different neural circuitry. The authors cite physiological evidence of neural activity in navigation circuits that is modulated by the vertical dimension; for example, elongated vertical (relative to horizontal) place-cell and grid-cell receptive fields for vertically arranged spatial layouts. It doesn't follow from those response anisotropies that medial temporal lobe structures are not encoding the vertical dimension. Computational studies, for example, might establish that observed properties of rat grid and place cells are sufficient to account for behavioral abilities within the vertical dimension without postulating other unknown neural centers for vertical spatial representations. Indeed, there is a debate within the theoretical literature about whether narrowly tuned or coarsely tuned cells provide better representations within a population (Lehky & Sereno 2011; Pouget et al. 1999; Zhang & Sejnowski 1999). As the authors themselves state, "much remains to be determined about vertical processing in the navigation system" (sect. 4.1, para. 10). Therefore, the conclusion of the target article that space for navigation is quasi-two-dimensional for all surface-travelling mammals may be premature.