Behavioral and Brain Sciences Commentary on Jeffery et al "Navigating in a 3D world" Grid maps for spaceflight, anyone? They are for free! --Manuscript Draft--

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Grid maps for spaceflight, anyone? They are for free!

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Abstract. We show that, given extensive exploration of a 3D volume, grid units can form with the approximate periodicity of a face-centered cubic crystal, as the spontaneous product of a self-organizing process at the single unit level, driven solely by firing rate adaptation.

In the target article, Jeffery et al. suggest that a fully three-dimensional representation of space may have not been found, in a number of studies, because of the intrinsic computational complexity of 3D representations, which would make the cost of setting them up too high, and not because of anything to do with the spatial behaviour of the species, like rats and primates, used in those studies. If so, genuine representations of 3D volumes would be unlikely to be revealed even when moving beyond surface-dwelling species, towards flying or marine animals, who appear capable of experiencing 3D space more thoroughly, through 3D navigation.

Clearly, managing directional information in 3D space offers more challenges than on the plane (Finkelstein, Derdikman, Foerster, Las, & Ulanovsky, 2012). Nevertheless, how this may affect the development of a grid representation in 3D depends on the mechanisms at work to generate it. If such mechanisms were to rely heavily on head direction inputs, then Jeffery et al. would have a point. If not, there might be space for surprises.

We have been analysing since 2005 a model for grid cell formation (Kropff & Treves, 2008; Treves, Kropff, & Biswas, 2005) based on a self-organisation process driven solely by firing rate adaptation (head direction information and recurrent connections are needed only to align the grids along common axes, (Si, Kropff, & Treves, 2012)). The model produces grids in 2D spontaneously. Individual grid cells average in time the content of spatially modulated inputs, which can be very generic and need not require any specific computation. The emergence of a grid structure in the firing rate is induced by the animal exploration of space, and the final appearance of the grid, its structure, depends on the way the environment is explored (Si et al., 2012), and on the topology of the space itself (Stella, Si, Kropff, & Treves, 2012).

What would this model predict in 3D, if the units receive broad spatial inputs modulated also in the third dimension? Individual grids are expressed by the feedforward inputs in the basic model, and the same inputs could "carry" both 2D crawling grids and 3D flying grids. We have looked at how the very same model behaves, when expanding the original square environment into a cubic one, and allowing the simulated animal to fly around the time usually required for the 2D exploration to generate good grid units.



Figure 1. The 3D autocorrelogram of a sample unit developing an approximate fcc 3D firing rate map.

As in 2D, the model produces a regular tiling of space: its units develop grid fields positioned at the vertices of a lattice uniformly filling the available volume. By computing the 3D autocorrelogram of the spatial activity of these units (Figure 1), it is apparent that the configuration reached by the fields is the so-called face centered cubic (fcc). In this configuration each field is surrounded by 12 other fields, and all pairs of neighbouring fields have roughly the same distance.

Our model shows how grids in two and three dimensions (or in any number of dimensions) may be produced starting from the very same principles of auto-organization, without increasing costs in higher dimensions. Adaptation provides the means to shape regular forms out of rough and unpolished spatial inputs, and it does it regardless of the topology of the external environment. Without a spatial behaviour engaging the full three-dimensional environment, however, no 3D grid units would appear, since there is no hardwired or ad hoc designed structure, in our model, to support them.

In the words of the authors of the target article, our model seems to indicate that the absence of three-dimensional grids in rats has an *ontogenetic* cause: rats do not possess three-dimensional grids because, alas, they have never learned to fly.

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