

Spatial Cognition: Grid Cell Firing Depends on Self-Motion Cues

H. Freyja Ólafsdóttir and Caswell Barry*

Department of Cell and Developmental Biology, University College London, Gower Street, London WC1E 6BT, UK

*Correspondence: caswell.barry@ucl.ac.uk
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A recent study has found that the periodic spatial activity of grid cells is completely degraded when animals are moved passively around an enclosure, strengthening the view that grid-firing is generated on the basis of self-motion information.

Grid cells, found in the medial entorhinal cortex and parasubiculum, exhibit remarkable periodic firing patterns spanning an animal's environment [1]. Because this regularity is (broadly speaking) independent of the animal's environment, grid-firing is widely thought to be driven by the animal's perception of its own movements. Indeed, most mainstream models of grid cells describe their activity in terms of the integration of such self-motion cues (for example [2–5]). Surprisingly, direct evidence in support of this belief is scant and the relative importance of different sources of self-motion information — such as optic flow, motor efference copy or vestibular information — is unknown. The paper by Winter *et al.* [6] in this issue of *Current Biology* speaks to these questions, showing that grid-patterns break down, losing all reliable spatial structure, when rats are passively moved through space in a transparent cart. The clear implication is that visual and vestibular information alone are insufficient to support grid firing.

Do Grid Cells Need Self-Motion Cues?

Investigation of the brain's spatial system has revealed a number of cell types that signal different but complementary aspects of an animal's representation of self-location. The best known examples are place cells [7], which respond when an animal occupies specific regions of space; head direction cells [8], which signal the animal's direction of facing; and more recently, grid cells [1]. As an animal moves through space it has access to two distinct sets of cues which inform its current location and drive the activity of these cells: information about its own

motion and environmental information, such as the location of visually detected landmarks. Place cell firing is known to be strongly influenced by environmental cues; manipulating the configuration of the animal's environment produces predictable changes in the cells' spatial responses [9]. Conversely, grid cells have attracted a great deal of theoretical and experimental interest precisely because their periodic firing patterns appeared to be more strongly dependent on self-motion cues [1,10].

To understand the role of self-motion and environmental cues in generating grid-patterns, Winter *et al.* [6] analysed grid cell activity in two movement conditions. In the first, 'active' (Figure 1a) condition, animals were allowed to freely forage in a familiar square enclosure while entorhinal and parasubicular grid cells were recorded with extracellular electrodes. In the second, 'passive' condition (Figure 1b), rats were moved through the same environment in a transparent cart; eliminating self-motion cues originating from proprioception and motor systems, while preserving vestibular and visual cues. Winter *et al.* [6] found that passive movement completely abolished the regular grid-pattern; the cells continued to fire at a reduced rate but were spatially unstable, not firing reliably as the animal was moved through previously visited positions. An important control was provided by concurrently recorded head direction cells, which maintained their directional activity in the passive condition, albeit with some attenuation of their directional tuning. Normal head direction function is known to depend upon an intact vestibular system and also requires environmental cues to stabilise the cells' activity [11,12];

information that must be accessible to rats in the cart.

Are Grid Cells Influenced by Environmental Cues?

Although the hexagonal firing of grid cells appears to require self-motion cues, accumulating evidence also indicates a robust influence of the environment on grid-firing. For example, Barry *et al.* [13] found that an established grid-pattern will stretch or squash to follow changes made to the shape of a familiar enclosure, and it is known that grid cell activity is disrupted in highly repetitive environments [14]. Similarly, Krupic *et al.* [15] and Stensola *et al.* [16] recently showed that environmental geometry, the borders and walls of an enclosure, exerted a strong influence over grid cell symmetry.

Is it possible to reconcile these seemingly opposing findings? A simple suggestion is that grid-patterns are established in each novel enclosure on the basis of self-motion cues and subsequently become anchored to environmental cues. This does not seem to capture the whole picture though, not least because grid firing becomes increasingly regular with experience [17,18].

How Do Environmental and Self-Motion Cues Interact to Form Grids?

A more comprehensive account of grid cell activity is one that assumes both environmental and self-motion cues continually play a role in determining grid-firing, the balance between the two depending on the availability of the different cue types. This 'dual control' was nicely demonstrated by Hardcastle *et al.*

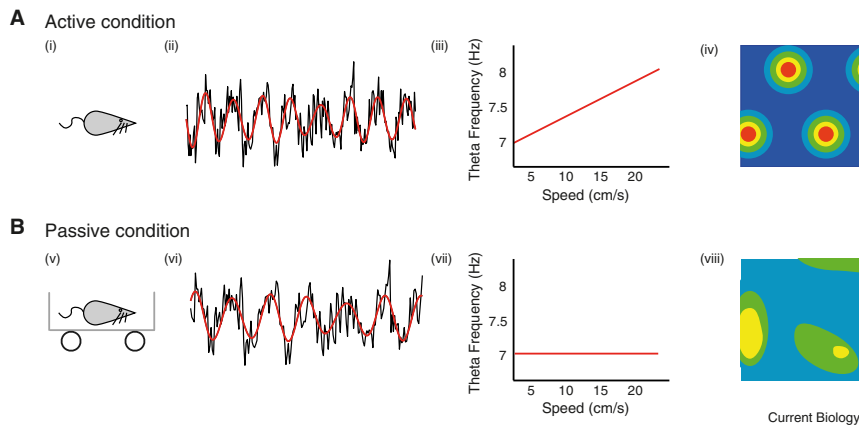


Figure 1. Grid cells require active movement.

Experiment paradigm used by Winter *et al.* [6]. (A) During active movement, a 6–12 Hz (theta) oscillation dominates the local field potential of the medial entorhinal cortex (ii), which is modulated by the running speed of the animal (iii), and is associated with normal grid cell firing (iv). During passive movement (B), theta is still present (vi) but its speed modulation is abolished (vii), as well as grid firing (viii).

[19], who analysed grid cell activity while rodents were close-to and away-from the walls of a large environment. Grid-patterns were found to be less precise and less stable when animals were further away from the walls; particularly so after long excursions without wall contact. The authors suggested that, as the animals moved around the interior of the enclosure, grid-firing was mainly supported by self-motion cues, which inherently accumulate error. Conversely, when the animals were close to the walls, grid-firing was also supported by environmental cues. Specifically, the authors found grid contact with the walls stabilised the grid-pattern, implying that environmental cues, such as boundaries, may provide grid cells with an error correction mechanism.

Do the combined effects of self-motion and environmental cues on grid-firing impact our understanding of Winter *et al.*'s work [6]? It is clear that the transparent cart eliminated some self-motion cues but it also prevented the animals from contacting the enclosure boundaries, limiting the possibility for error correction. The contribution of these factors cannot be completely teased apart in the current experiment. In Hardcastle *et al.*'s work [19], however, even after long periods away from the walls, grid-patterns were still clearly present, their stability being slightly ameliorated. In contrast, Winter *et al.*'s passive movement condition entirely

abolished the regular periodic firing [6]. In other words, it seems to be the proprioceptive and motor efference self-motion cues, which were absent in the cart, that are necessary for normal grid cell activity.

The Neural Mechanism for Integration of Self-Motion

Although self-motion information is clearly important for grid firing, the neural mechanism by which this integration occurs to generate grid-patterns is less clear and somewhat contentious. Broadly speaking, two main classes of computational model seek to explain grid cell firing, though some hybrid models combine elements of both classes. Continuous attractor models (for example [4,5]) see grid firing as emerging from an interconnected network of cells. The alternative, oscillatory interference models (for example [2,3]) describe grid-patterns in terms of the interactions between multiple neuronal oscillations, in particular the 6–12 Hz theta-band oscillations that dominate hippocampal and entorhinal local field potentials. Crucially, in the latter case, the difference in frequency between the interfering oscillations must vary with the animal's velocity.

In line with this view, in rats, theta frequency is known to increase linearly with running speed [20]. Winter *et al.* [6] observed this effect in their active condition but in the passive condition, with animals in the cart, theta frequency did not

vary with movement speed. Although strictly a correlational result, the absence of grid-patterns in conjunction with an absence of theta-velocity modulation adds to evidence linking theta and grid cell firing. More specifically though, it suggests that modulation of theta-band frequencies by running speed is the mechanism by which self-motion cues are integrated to generate grid-patterns.

Combining Cues to Support Grid Firing

While Winter *et al.*'s study [6] establishes the importance of self-motion cues for normal grid cell activity, it is less clear what the outcome would be in the total absence of environmental cues; would normal grid-patterns form but be unstable relative to the environment, slowly drifting around? In a similar vein, Hardcastle *et al.*'s [19] analysis nicely shows how the relative efficacy of self-motion and environmental cues on grid firing is modulated by the availability of those cues. Indeed, a similar transition has also been reported over much longer timescales, with grid-patterns moving from a local map, defined by environmental cues, to a global map established on the basis of self-motion cues, over the course of several days [18]. However, the neural mechanism by which this modulation is achieved and how it relates to plasticity in the entorhinal cortex and hippocampus remains to be explored.

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Animal Memory: Chimpanzees Anticipate What Comes Next in Short Movies

Michael J. Beran

Department of Psychology and Language Research Center, Associate Professor, Georgia State University, University Center, Atlanta, GA 30302-5010, USA

Correspondence: mjberan@yahoo.com

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A recent study shows that chimpanzees remember a movie they viewed one day earlier, and their eye movements show that they anticipate certain actions in that movie before those actions occur by looking to parts of the scene that are about to become relevant to the storyline.

One of my favorite movies, *Office Space*, is about a software engineer who does not like his job; among the many reasons for this is that even getting into the office requires touching a door handle that shocks him every day. Later in the movie, he has had enough of that door, and he grabs a drill from a workman standing on a ladder, and unscrews the entire door handle to end this problem. Each time that I see this movie, I anticipate this grabbing of the drill, and my eyes drift to where it is located in the scene even before the actor reaches for it. The reason, of course, is that I remember the scene, and I know what is coming next, and I am preparing for it by locating the drill that the actor soon will grab. This

happens all of the time when we re-watch movies, advertisements, or even our own home videos. We look to where we expect certain actions to occur, and we anticipate those actions, all presented on a two-dimensional monitor or screen. And, often we do this after only one experience watching the scene previously. A new study [1] reported in this issue of *Current Biology* shows that chimpanzees and bonobos, like humans, remember videos they saw only once, and when shown that video again, they anticipate exciting and salient parts of a scene and look in anticipation to where in the scene those events will occur.

In the study of Kano and Hirata [1], the apes first watched a highly salient scene

(the reader can find these scenes online as part of the article's Supplemental Information). In the scene, a human is attacked by a gorilla (played by another human in a costume), and the attacking gorilla emerges from one of two doors. When shown the same video a second time the next day, and with eye-tracking technology monitoring where the apes were looking through the video, the researchers found that the chimpanzees clearly anticipated what was going to happen next. They looked more often toward the door where the gorilla character would eventually emerge during the few seconds before his emergence than they did toward another door or toward that same door during the original viewing of the video