

NEUROSCIENCE

Neurons and navigation

György Buzsáki

Where is the geometry of the environment represented in the brain? The entorhinal cortex, where neurons fire repeatedly when an animal's position coincides with the vertices of a grid of triangles, looks like a good bet.

Navigators will be familiar with the principles underlying the question tackled by Hafting *et al.*¹ on page 801 of this issue. The authors' aim was to clarify where in the brain information about an animal's whereabouts is integrated. Their experimental subjects were rats; their approach involved recording from neurons in a part of the brain known as the entorhinal cortex as the rats explored specially designed enclosures.

The simplest navigational method is 'dead reckoning', which requires continuous monitoring of the distance and course taken from some known place. To calculate distance, mechanisms for monitoring both speed and time elapsed are needed. But unless position is recalibrated, errors accumulate over time, hence the need also for celestial or map-based navigation, in which geographical position is determined by 'fixes' of stars or landmarks. A detailed map of the environment can be created through tessellation, which exploits the principle from floor tiling that every part of a surface can be covered by certain polygons of the same size — squares or equilateral triangles — without any gaps or overlaps. Once these polygons are calibrated with the fixed landmarks, they can then provide local reference points (Fig. 1a).

All mammals seem to use both dead reckoning and map-based methods of navigation. To investigate how this information is represented in the brain, researchers have focused on so-called 'place cells' in the hippocampus — a structure that has indirect connections to several areas of the cerebral cortex^{2,3}. But the entorhinal cortex, which occupies a crucial position between the hippocampus and the cortical structures that provide visuo-spatial information, has increasingly come in for attention. Hafting *et al.*¹ now report that information about position, distance and direction can be integrated in the dorsocaudal medial region of the entorhinal cortex (dMEC).

The most striking of their results is the spatial regularity of neuron discharges in the dMEC: activation occurs in a grid-like pattern, with each cell becoming repeatedly active when the rat walks through the vertices of equilateral triangles (Fig. 1b). This grid of virtual triangles covers the entire surface of the recording environment, with the resolution determined by the size of the tiles. Hafting *et al.* found not only that individual entorhinal neurons tessellate a rat's enclosure in a way that corresponds to a grid of triangles, but also that the triangular representation varies from cell to cell.

Like the multiple layers of Marrakech mosaics, representing the evolving styles of different centuries, different neurons can display rotated or displaced versions of the same tessellating structure. Furthermore, neuronal grid size increases from the dorsal to the ventral part of the dMEC from 30 to 70 cm, indicating that the spatial resolution of the environment varies systematically within the entorhinal cortex. By integrating the information from such linearly transformed grids, spatial resolution can, in principle, be increased (Fig. 1c), and the rat's position accurately predicted from the activity of just a handful of dMEC neurons⁴.

Hafting *et al.* also found that the tessellating features of individual neurons persist in environments of different sizes or shapes, and even after the removal of visual cues or when a rat enters a new environment — a strong indication of a rigidly wired representation of spatial metrics. On the other hand, the orientation grid of all dMEC neurons could be altered simultaneously and instantaneously by the coherent rotation of visual landmarks (such orientation information may be supplied by another linear scheme, the previously described head-direction, or 'compass' system⁵).

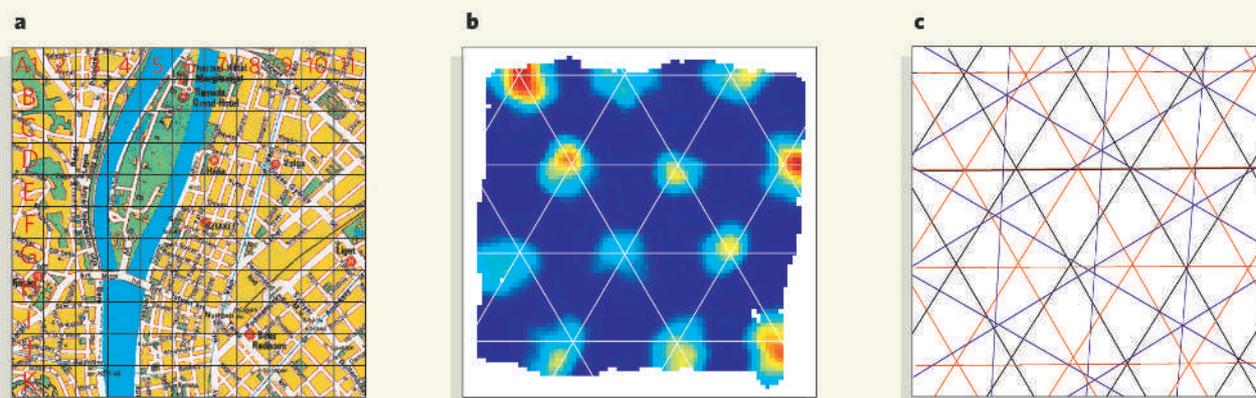


Figure 1 | Tessellation and navigation. **a**, Tessellation of a city map by squares provides information about position, distance and direction, allowing specific places to be easily located. **b**, Hafting *et al.*¹ find that as a rat explores an experimental enclosure, the discharge rate of a neuron in the dorsocaudal medial entorhinal cortex increases at regular intervals

corresponding to the vertices of a triangular grid. **c**, Integration of information from several grid components (that is, from the outputs of several neurons) can increase the spatial resolution of the environment. Three triangular grids are represented here, with red displaced and blue rotated relative to a neuron grid shown in black.

All in all, although neurons in many other systems fire in relation to the animal's position and orientation, Hafting and colleagues' findings suggest that the representation of position, distance and direction may come together in the dMEC. Their observations are compatible with both dead-reckoning and map-based navigation: dMEC neurons showed the same grid-like pattern of activity even in complete darkness, but also followed rearrangements of visible landmarks in the test enclosures.

What about the issues raised by this discovery of tessellation patterns? The superficial layer of the dMEC monitored by Hafting *et al.* is only a small part of the entorhinal cortex — do neurons in other layers and parts of this brain region show similar grid patterns or operate in a qualitatively different manner? If they do possess tessellation features, what functions do these neurons serve? How are the grid patterns described by Hafting *et al.* formed in the first place? Is the 30–70-cm metric specific to the rat and the environment in which it was reared, or is it universal in mammals? Is the flexible representation of position that is evidently encoded in the hippocampus crucial in setting up and modifying the rigid grid system of the entorhinal cortex? Finally, how do these results relate to the non-spatial responses of neurons observed in the lateral entorhinal cortex⁶?

There is also the long-standing issue of the relationship between navigation and memory. Ample clinical evidence indicates that the hippocampus and entorhinal cortex are involved in encoding and recalling memories, in particular episodic memories^{7–9} — events that are specific to an individual and that are embedded in both a spatial and a temporal context. Are such memories processed by different neuronal mechanisms from those in the dMEC, or do the tessellation features described by Hafting *et al.* play a part? One potential link is the 'distance' relations (the coupling strengths) between the adjacent elements of an episode, which allow for recollection of the exact sequence of what happened where and when.

However, the map-based navigation supported by the dMEC grid patterns does not require a time component, whereas the key feature of episodic memories is their temporal context⁷. So another organizational feature of the hippocampal–entorhinal system might be involved. This is the 'theta oscillation' of collective neuronal activity, which has a frequency of 5–10 Hz, and which may provide the temporal metrics needed for both dead-reckoning navigation and the temporal ordering of the elements of episodic memory. This mechanism could conceivably bring grid cells with different sizes and orientations into temporal register with each other. If it does, we may begin to think about how elementary mechanisms such as space tessellation and temporal coordination, which initially

supported dead-reckoning navigation, evolved to represent memories¹⁰.

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MAGNETOSPHERIC PHYSICS

Turbulence on a small scale

Melvyn L. Goldstein

The four-spacecraft Cluster mission has identified small-scale vortices in Earth's magnetosphere. The observation reveals processes that transfer energy and momentum from the solar wind to the magnetosphere.

Turbulence is ubiquitous. It can be seen by gently stirring cream into coffee, or by observing the white caps and surf at the beach, and it causes the drag on cars and aeroplanes. The phenomenon is also widespread in magnetized plasmas — ionized gases that contain a magnetic field — such as the interstellar and intergalactic media, the solar wind and Earth's magnetosphere.

Although magnetic fields complicate the description of turbulence, certain characteristics, among them vortices, can arise in fluid and magnetofluid turbulence. On page 825 of

this issue, Sundkvist *et al.*¹ report the detection of small vortices in the 'dayside cusp' of Earth's magnetosphere by the four-spacecraft Cluster, a joint European Space Agency and NASA mission. The authors describe their observations as evidence for a phenomenon known as drift-kinetic Alfvénic turbulence.

The solar wind is the extension of the corona, the hot outer atmosphere of the Sun, into interplanetary space. Near Earth, the speed of the solar wind is typically around 400 kilometres per second, with variations of a couple of hundred kilometres per second that

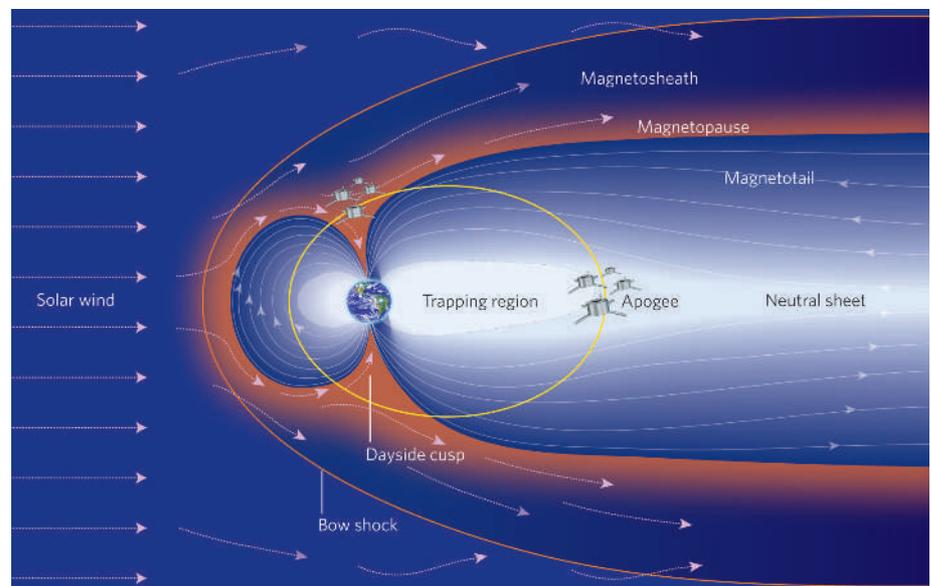


Figure 1 | Transverse cut of Earth's magnetosphere. A two-dimensional cut through the magnetosphere, with the Sun to the left. Solar-wind plasma is heated as it passes through the bow shock caused by its encounter with Earth's magnetic field. Some of the plasma is funnelled down the dayside cusps into the Northern and Southern Hemispheres. The Cluster orbits are shown as they appear in February/March of each year, the time period of the observations reported by Sundkvist *et al.*¹. When the four spacecraft are on the dayside, they pass through the cusp regions; when near apogee on the nightside, they cross the magnetotail and neutral sheet. (The diagram is not to scale; in reality, the apogee of Cluster's orbits occurs at some 19 Earth radii.)