

NEUROSCIENCE

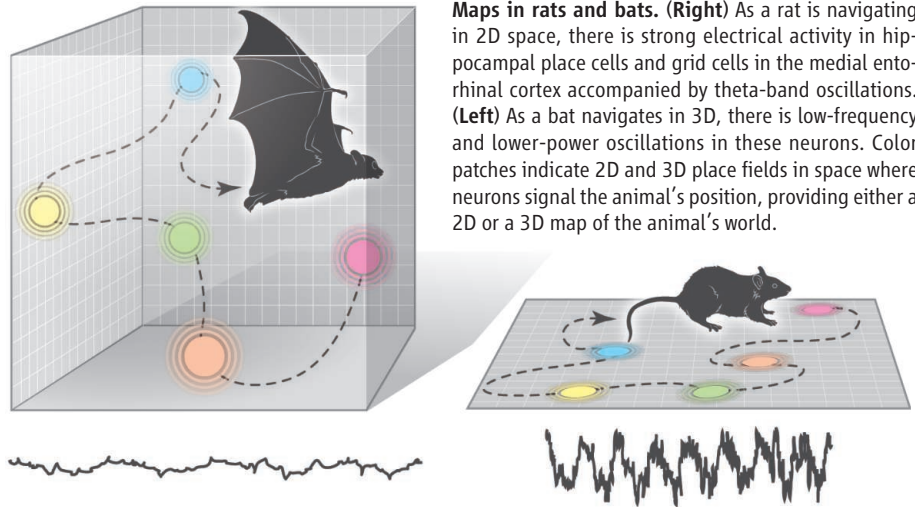
3D Mapping in the Brain

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What's it like to be a bat? If a rat could fly and echolocate, would it navigate and determine its position in the same way? In other words, could the rat truly understand three-dimensional (3D) space? Or is a bat's brain functionally specialized for life in the air? On pages 367 and 363 of this issue, Yartsev *et al.* (1) and Heys *et al.* (2) examine the neural encoding of 3D space and basic neuronal processing in bats and discover fundamental differences in the way species represent their own location.

In the mammalian brain, the ability to remember and navigate through space has been linked to the hippocampus. The best evidence for this association lies with hippocampal neurons called “place cells,” which represent an animal's position (3). However, ground-dwelling rodents have provided the dominant model for such spatial studies, leaving open the question of whether the hippocampal representation of space truly extends into 3D. Furthermore, it is also unknown if the strong theta-band (6 to 12 Hz) modulation of hippocampal electrical activity (4), which is thought to contribute to the spatial response of place cells in rodents (5), plays a similar role in other animals. By describing hippocampal electrical activity in flying bats and in isolated bat medial entorhinal cortical tissue (the entorhinal cortex is a major cortical input to the hippocampus), Yartsev *et al.* and Heys *et al.* find that bats exhibit 3D “place fields,” without any apparent theta-band modulation in the hippocampus or in the membrane potential resonance of specific entorhinal inputs to the hippocampus (see the figure).

Place cells have been characterized in animals as phylogenetically diverse as rats (3), humans (6), and crawling bats (which can move slowly on all fours) (7). Place cells represent an animal's location with spatially selective patterns of electrical activity—each cell “firing” only when the animal is in a specific position, its place field. Typically, place fields are stable and distributed across the environment. A population of place cells



Maps in rats and bats. (Right) As a rat is navigating in 2D space, there is strong electrical activity in hippocampal place cells and grid cells in the medial entorhinal cortex accompanied by theta-band oscillations. **(Left)** As a bat navigates in 3D, there is low-frequency and lower-power oscillations in these neurons. Color patches indicate 2D and 3D place fields in space where neurons signal the animal's position, providing either a 2D or a 3D map of the animal's world.

thus provides a map-like representation of the animal's world (3). This representation is impressively flexible—a new map is quickly generated in a new environment. Attempts with rodents to determine if place cell activity is modulated in 3D could not truly explore volumes of space. Rats trained to climb on a vertical peg board and staircase showed that place cell firing was weakly modulated in the vertical dimension (8), but it was unclear if this constituted a real 3D space code. Yartsev *et al.* tackled this question by recording from fruit bats as they flew around a large cage—a technically impressive feat requiring wireless, light-weight recording equipment and multiple tracking cameras. The authors demonstrate that the hippocampal spatial code is indeed 3D—the bats had place fields that were confined to specific, evenly distributed volumes of the cage with no tendency to be compressed in any one dimension. Although the 3D place fields were stable for several hours, it is unclear if they exhibit the long-term stability of 2D fields and if they can rapidly form new representations when the animals enter a new space.

Does the bat hippocampus use the same mechanisms to construct space as the rodent hippocampus? A key functional difference revealed by Yartsev *et al.* is that bat place cells exhibit no theta-band modulation of their spike trains—in rodents, this rhythmic modulation of neuronal firing is evident whenever the animals are in motion (4). Indeed, several computational models describe the spatial activity of grid cells (9), an input to the

hippocampus, in terms of theta-band oscillators (5). Grid cells are neurons in the medial entorhinal cortex, and like place cells, exhibit stable spatially constrained firing, but tessellate the environment with an array of regularly distributed firing fields. Again, grid cells appear to be a mammalian phenomenon—they are found in rodents (9), and similar spatial representations exist in humans (10). The spatial grid array can be described as an interference pattern occurring between theta-band oscillations in grid cells or their inputs, the frequencies of which track the animal's velocity (5). Such a configuration generates regular grid cell firing and provides a mechanism by which information about self-motion—speed and direction—can update a representation of location, a process known as path integration.

An absence of theta-band modulation of bat grid cells had been reported (11); however, the results were debated because the cells of the slowly crawling bats emitted too few spikes for a conclusive analysis (12). To address this, Heys *et al.* directly examined the membrane dynamics of bat medial entorhinal stellate cells in brain slices. In rodents, these neurons show subthreshold membrane potential resonance and oscillate at theta-band frequency—good evidence for interference models. However, the authors found no theta-band resonance in the bat stellate cells. It is therefore unlikely that the spatial firing of bat grid cells is produced by theta-band membrane potential resonance in medial entorhi-

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nal cortex—as envisaged in one formulation of the interference model (13).

Different implementations of the interference model have placed the velocity-controlled oscillators in other brain regions, such as the medial septum (14), and do not necessarily require membrane potential oscillations to be present in the entorhinal cortex (some degree of theta-band modulation of grid cell firing would be expected). Heys *et al.* did observe membrane potential oscillations of medial entorhinal cells, but at frequencies below the normal theta range (1 to 2 Hz), raising the possibility that oscillatory interference might be occurring at lower frequencies. These findings may be indicative of differences in the nature of neuronal oscillations between species. For instance, hippocampal theta-band oscillations in humans have a much lower frequency than in rats (15). Alternatively, a shift to lower-frequency

oscillations might avoid unwanted interactions with the processing of bat echolocation epochs which occur at 6 to 12 Hz. Indeed, at least one species of bat shows theta-like modulation in hippocampal neurons when echolocating (7).

It may be that the adaptations that allow bats to function in, and encode, 3D space have dramatically altered the way they path integrate—as such, their grid cells may be functionally different from those in rodents and humans. Characterizing grid cells in flying bats will help to answer some of these questions.

References and Notes

1. M. M. Yartsev, N. Ulanovsky, *Science* **340**, 367 (2013).
2. J. G. Heys, K. M. MacLeod, C. F. Moss, M. E. Hasselmo, *Science* **340**, 363 (2013).
3. J. O'Keefe, L. Nadel, *The Hippocampus as a Cognitive Map*. (Oxford Univ. Press, ed. 1, 1978).
4. G. Buzsáki, *Neuron* **33**, 325 (2002).

5. N. Burgess, C. Barry, J. O'Keefe, *Hippocampus* **17**, 801 (2007).
6. A. D. Ekstrom *et al.*, *Nature* **425**, 184 (2003).
7. N. Ulanovsky, C. F. Moss, *Nat. Neurosci.* **10**, 224 (2007).
8. R. Hayman, M. A. Verriotis, A. Jovalekic, A. A. Fenton, K. J. Jeffery, *Nat. Neurosci.* **14**, 1182 (2011).
9. T. Hafting, M. Fyhn, S. Molden, M.-B. Moser, E. I. Moser, *Nature* **436**, 801 (2005).
10. C. F. Doeller, C. Barry, N. Burgess, *Nature* **463**, 657 (2010).
11. M. M. Yartsev, M. P. Witter, N. Ulanovsky, *Nature* **479**, 103 (2011).
12. C. Barry, D. Bush, J. O'Keefe, N. Burgess, *Nature* **488**, E1 (2012).
13. L. M. Giocomo, E. A. Zilli, E. Fransén, M. E. Hasselmo, *Science* **315**, 1719 (2007).
14. A. C. Welday, I. G. Shlifer, M. L. Bloom, K. Zhang, H. T. Blair, *J. Neurosci.* **31**, 16157 (2011).
15. R. Kaplan *et al.*, *PLoS Biol.* **10**, e1001267 (2012).

Acknowledgments: C.B. is supported by a University College London Excellence Fellowship and a Wellcome Trust Principal Fellowship (awarded to N. Burgess). C.F.D. is supported by the European Research Council (ERC-StG RECONTEXT).

10.1126/science.1237569

CLIMATE CHANGE

Climate's Dark Forcings

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The black soot coming out of the tailpipes of diesel trucks is a nuisance familiar to every highway traveler. Soot also endangers the health of untold numbers of women and their families exposed to smoke from traditional cookstoves burning biofuels and coal. But in addition to irritating our noses and lungs, this pollutant, also known as black carbon (BC), is the strongest absorber of solar radiation in the atmosphere. The magnitude of global warming from BC, as well as its regional effects, has been the subject of intense debate. In a recent comprehensive assessment, Bond *et al.* (1) have synthesized available model results and observations, and propose a “best estimate” for BC's global climate forcing. Their estimate is almost twice as high as values commonly discussed (2). What causes such large discrepancies between estimates, and what are the implications for the global and regional climate effects of BC?

Unlike greenhouse gases, BC is not a single, chemically defined substance with constant physical properties. In addition to the aggregates of nanometer-scale carbon spher-

ules traditionally thought of as BC, the atmosphere contains light-absorbing organic or “brown” carbon (BrC) (3). BrC may account for 15 to 50% of light absorption in the atmosphere and in snow and ice (1, 4, 5) and has different optical properties and source and sink patterns from BC. In addition to combustion sources, especially biomass burning, BrC is also produced by atmospheric chemical reactions, a source not considered in emission inventories.

BrC is sometimes included implicitly in climate models constrained by BC measurements, because different BC measurement techniques may include some or all BrC. However, most models have ignored BrC absorption and, as a result, concluded that the combination of BC and nonabsorbing organic carbon leads to net cooling. This has been challenged by two recent studies (5, 6). It is essential to improve measurement techniques for BrC and to include it explicitly in models.

BC (including BrC) influences climate through numerous mechanisms. In addition to causing atmospheric heating and surface dimming, BC-containing aerosols affect cloud optical properties and precipitation behavior. This in turn affects the energy budget of the atmosphere (7). The global net BC forcing is obtained by integrating over

Uncertainties about the properties and amounts of atmospheric black carbon complicate efforts to understand its regional and global effects on climate.

all mechanisms. Because most earlier studies have included only a subset of mechanisms, one must be very careful when making comparisons.

Bond *et al.*'s “all mechanisms” forcing estimate of +1.1 W m⁻² (with a large uncertainty) is about twice as high as that of UNEP/WMO (2), mostly because of higher values for the absorption by BC in the atmosphere. Yet, their estimate of 0.88 W m⁻² for the forcing from light absorption by present-day BC is almost identical to that from a previous study (0.9 W m⁻²) (8). This agreement is instructive, because the two studies use atmospheric models, but are otherwise based on very different approaches.

Ramanathan and Carmichael's estimate (8) is based on satellite and ground-based light absorption data from the AERONET network of more than 140 sites around the world. In contrast, Bond *et al.* derive absorption estimates from emission inventories and atmospheric models. They initially obtain values lower than supported by observations; only when they scale up their results to agree with the AERONET data do the two studies converge. This suggests that underestimation of atmospheric BC absorption by as much as a factor of three is the primary culprit for the lower forcing estimates in most earlier models. Either the models are missing a major BC

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