

Dispatch

## Spatial Cognition: Goal-Vector Cells in the Bat Hippocampus

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A new study recording from the hippocampus of flying bats has revealed populations of neurons tuned to the egocentric direction of the goal, the distance to the goal or their conjunction during spatial navigation.

The ability to navigate space depends on the hippocampus and neighbouring brain regions. Each brain region contains cells that code for distinct spatial properties. These cells include hippocampal ‘place cells’ which map current location in the environment; ‘head-direction cells’ which provide a signal akin to an internal compass; and medial entorhinal ‘grid cells’ which provide a grid-like system to map space [1–3]. Numerous computational models have sought to explain how such cells might be used for navigation [4], but these models have faced a challenge: the spatial cells discovered so far can tell you where you are and which direction you are facing, but do not directly signal the direction or distance to a future goal. Without this information, the animal is doomed to wander aimlessly through the world. Computational models have so far explored ways such information could be extracted from the known properties of place, head-direction and grid cells [4]. But a new study by Sarel *et al.* [5] has revealed populations of neurons in the hippocampus with distinct properties: they are tuned to the egocentric direction and distance to the goal. These ‘goal-vector cells’ may underlie our capacity to know how far our goal is and in what direction it lies.

Previous research examining goal coding in rats has found that place cells can pre-activate before navigation begins, coding for locations ahead of the rat on the path to intended destinations [6–9]. This is akin to retrieving the route prior to setting off on a journey. Single unit recordings in humans navigating a virtual environment have revealed neurons that are selective to specific goals, or active in particular places *en route* to a specific goal: goal x location cells [10]. But such goal coding

on its own is insufficient to signal the direction and distance to travel to a goal. One potential limitation of past studies was that they did not fully sample the range of different distances and directions to the goal over many different trajectories, making it difficult to detect the presence of cells coding for the distance or direction to the goal. To overcome this sampling problem, Sarel *et al.* [5] examined the hippocampus of Egyptian fruit bats; a species capable of carrying a neural recording device whilst covering a large range of distances and directions to a goal during flight.

To study the coding for spatial goals, Sarel *et al.* [5] had the bats fly in a 72m<sup>3</sup> room in search of food on a platform (Figure 1A). The platform was placed either in the centre of the room or hidden in a randomised location behind an opaque curtain that blocked sight and echolocation. Because the bats' trajectories were largely confined to a narrow range of heights, a two-dimensional horizontal projection of the flight-paths was used for the analyses. As the bats flew around the room 309 cells in the hippocampal area CA1 were recorded from. Many of these cells displayed firing consistent with place cells and were not tuned to the location of the goal. However, of the cells recorded, 19% were shown to be significantly tuned to the angle between the central goal and the bats heading direction (goal-direction cells, see Figure 1B). This proportion increased to 27% for the sessions when the goal was hidden. The goal-direction cells were stable within behavioural sessions and the distribution of preferred goal-direction spanned the entire 360°, with an overrepresentation of angles close to 0° (directly ahead from the bat). Furthermore, most goal-direction cells (81%) were significantly tuned to only one of the two goal locations. Despite 55% of the goal-direction cells also displaying signs of place dependent activity, part of the study's criteria for a goal-direction cell was that it must exhibit a stronger goal-direction tuning than place tuning in a reconstruction analysis. A similar reconstruction analysis aiming to disassociate the goal-direction signal from a head-direction signal revealed that the activity of the majority of cells were better explained by goal-direction.

In addition to goal-direction cells, 16% of CA1 cells were shown to be modulated by the distance between the goal and the bat's location (goal-distance cells). Many of these cells were more tuned to the path-distance to the goal than the Euclidean distance (see Figure 1A,C), and although the distribution of preferred path-distances spanned 0–10 m, the majority fired maximally at 0–2 m.

Interestingly, some cells displayed a conjunctive representation of both goal-direction and goal-distance, thus displaying a vectorial encoding of the goal.

The discovery of these cells is important, not only because it fills a missing piece in the puzzle regarding how the brain supports spatial navigation, but also because it helps explain the results of several recent human functional magnetic resonance imaging (fMRI) studies investigating navigation in virtual environments. These fMRI studies [11–16] found that activity in the hippocampus / subiculum correlates with the distance to the goal during navigation. Because Sarel *et al.* [5] discovered that goal-distance cells tuned to locations close to the goal were more abundant, this would predict that the global activity of the hippocampus should increase with proximity to the goal. This was indeed the case in many of the fMRI studies [12–14,16] (assuming that the fMRI BOLD signal is a marker for local demands on neural activity). Furthermore, in addition to the goal proximity signal, the over-representation of goal-direction cells that were tuned to smaller angles would predict greater global hippocampal activity when the goal is directly ahead of the navigator. This is exactly what Howard *et al.* [14] observed when they examined brain activity at path-decision points during navigation: a negative correlation between hippocampal activity and ‘goal-distance x egocentric direction to the goal’. Thus, it could be that the bat brain has helped uncover what might be occurring in the human brain.

Observation of egocentric direction coding in the hippocampus is surprising given the vast number of studies reporting allocentric spatial coding in the hippocampus [1–4]. Egocentric coding has consistently been found to be the preserve of the posterior parietal cortex [3,4,17]. However, studies in which rats run back and forth on linear tracks have consistently reported unidirectional place cells which become selectively active when the rat is running in a particular track direction [18]. Might this directional selectivity explain the findings of Sarel *et al.* [5]? This seems unlikely, as the bats appear to take highly irregular paths through the space, and do not follow overly-stereotypical trajectories which could lead to such unidirectional firing. Nonetheless, it is possible that circulation around a goal location gives rise to these particular cell coding properties and it will be exciting to discover how such cells operate when bats fly at much greater distances. It is quite possible that the way in which these cells code distance and direction changes at different operational stages of

navigation [3], such as when determining the initial orientation towards a goal or when maintaining heading direction during the long flight to a distant goal [19].

Another question raised by the results of Sarel *et al.* [5] is whether, in addition to egocentric direction cells, there might exist cells that code for the allocentric direction to the goal (for example, firing when south east of the goal). A recent fMRI study [17] in which participants had to judge the direction to hidden goals indicates that such cells might exist, but points to the entorhinal region as the locus of such a cell population rather than the hippocampus. Considering the findings of Sarel *et al.* [5], important future steps will be to replicate the existence of goal-vector cells in other species and update computational models of navigation. Furthermore, since goal-distance coding has been observed in the human hippocampus during imagined navigation of subway networks [16], it may be that goal vector cells are used in humans to do more than navigate space, such as helping us to navigate the complexities of social networks [20].

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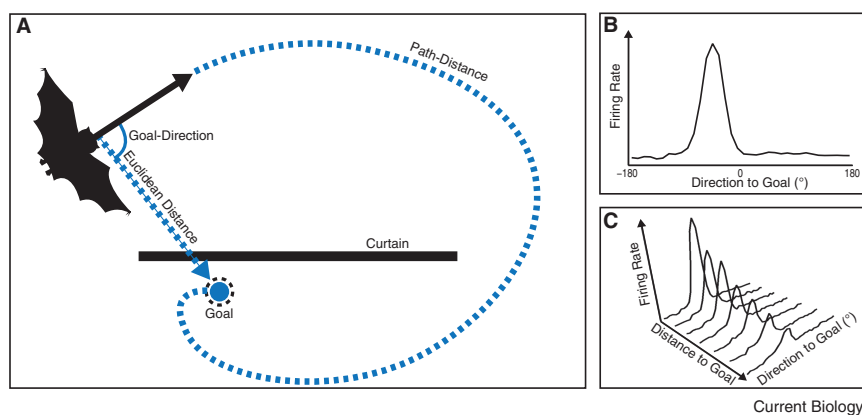


Figure 1. The Task and Key Results from Sarel *et al.* [5].

(A) Plan view of the experimental set up with bat (not shown to scale) and one of the potential goal locations shown. (B) Illustrative example of a goal-direction neuron with activity plotted against egocentric goal direction. (C) An illustrative example of a conjunctive distance x direction goal-vector cell.

In Brief:

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