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Social Spaces: Place Cells Represent the Locations of Others

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How does the brain represent the location of others? Recordings in rats and bats show that, along with representing self-location in an environment, some hippocampal neurons are modulated by the position of another individual.

As well as knowing one's own location, being able to recognize the position of others in space is a crucial skill for hunting, escaping a predator, finding a mate, or socializing. Two recent papers, by Danjo *et al.* [1] and Omer *et al.* [2], report that some cells within the hippocampus of the rat and the bat, which support self-localization, also fire in response to the location of a conspecific.

The hippocampus constructs a representation of self-location via the activity of the spatially sensitive 'place cells' [3,4], but it has been speculated that place cells might also encode the location of other individuals. Increasing evidence suggests a role for social processing in hippocampus. For example, social stimuli induce alterations in place cell activity [5], and ventral hippocampus has been implicated in memory for individuals [6], while neuroimaging studies in humans have revealed hippocampal involvement in social rank processing [7]. Also, Mou and Ji [8] recently found place cell reactivation in a rat observing another rat at the relevant locations. There has, however, hitherto been no clear evidence of neurons encoding the position of another individual *per se*. But now Danjo *et al.* [1] and Omer *et al.* [2] have reported such activity in the place cells of rats and bats, respectively.

Both groups [1,2] used paradigms in which an observer animal attended to the location of another 'demonstrator' animal

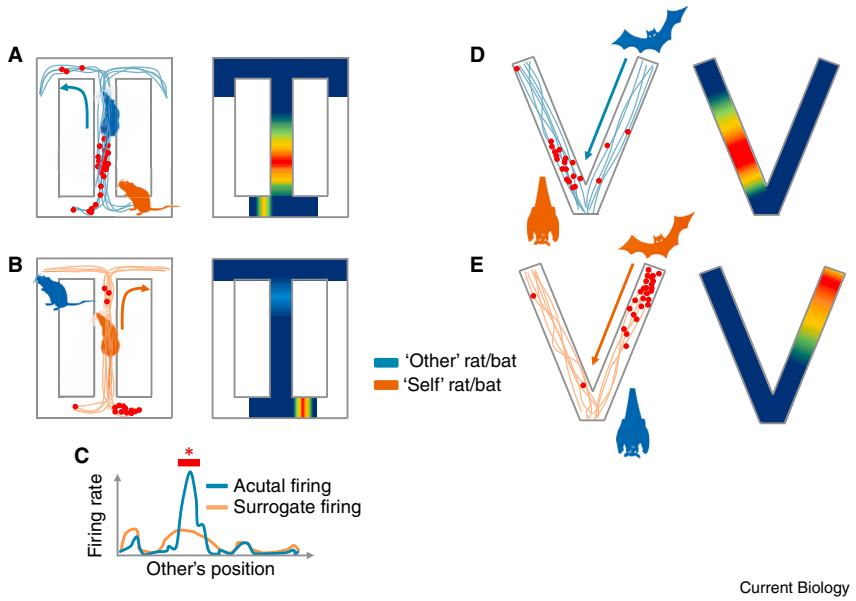

Figure 1. Hippocampal cells encode the spatial location of other individuals.
(A,B) The two-choice rat task [1]. The 'self' observer rat (orange) watches the 'other' demonstrator rat (blue) run up the central stem and make a choice, and then goes to the same or opposite location (depending on task rule). (A) The data plotted in the reference frame of the other. Left: spike plot of a place cell from the self rat, where spikes (red dots) are shown plotted over the other rat's trajectory (blue lines). The spike's from the self's place cells are emitted when the other rat is at particular places on its trajectory. Right: the same data plotted as a firing-rate map (red, max firing; blue, min/no firing) showing the place field in the other reference frame. (B) Left: the same data plotted in the reference frame of the self rat (trajectory, orange lines), showing activity clustered where the self rat was waiting in the right-hand start arm. Right: corresponding rate map. (C) Firing in the 'other' reference frame (blue line), compared with predicted firing constructed using the cell's firing under the hypothesis that it only depends on the self's positions (orange line). The red line and asterisk show significant 'other' firing, over and above that predicted by the self's location. (D,E) The two-choice bat task [2], illustrated as for (A,B), using in-flight data in one travel direction, showing a cell with one place field in the 'other' reference frame and a different one in the 'self' frame.

to solve a two-choice spatial task. In the Danjo *et al.* [1] experiment, observer rats watched a demonstrator rat take random left or right trajectories on a T-maze and then either followed the demonstrator or took the opposite route, depending on task condition. In the Omer *et al.* [2] experiment, bats watched another bat fly to food located either to the left or to the right, before flying to that same location and back. In both experiments, when cell firing was correlated with the animal's own position then most cells produced 'place fields', that is location-specific activity, in the usual way. However, a subset of the cells showed activity that was also modulated by the position in space of *another* individual (Figure 1). In the bat experiment, where trajectories went in both directions, cells were directional and usually preferred only one of the two possible trajectories, ruling out simple encoding of distance or time [9].

Were cells responding to the other animal itself or to the future trajectory of the self? Danjo *et al.* [1] decoupled self and other trajectories by switching tasks from the opposite-side to the same-side rule, or by considering error trials, finding that many cells were self-trajectory-dependent (Figure 2A), reminiscent of the path-sensitive activity typical of place cells in stereotyped tasks [10,11]. However, some cells were tuned to the other rat's trajectory independently of the observer (Figure 2B).

Do these other-tuned place cells care about the animacy of the other animal, or only about its location? Omer *et al.* [2] found that some hippocampal neurons encoded the position of an inanimate object, even one that did not signal reward. Interestingly, responses to the objects were less directional. Perhaps animate and inanimate stimuli are differentiated, or perhaps the difference is due to the inherent directionality of an animal's body *versus* the objects.

Do these findings mean that place cells come in two flavours, representing the self's-place or another's-place? Not quite — a purely other-place cell would fire *whenever* the other animal was in the relevant place, irrespective of the observer's location, but these experiments were not set up for such observations. In the Danjo *et al.* [1] study, in which the moving observer had a more variable location with respect to the demonstrator rat, such activity was rarely seen, and nor has this been observed previously [12]. Thus, in both experiments, most other-frame encoding occurred while the observer animal was

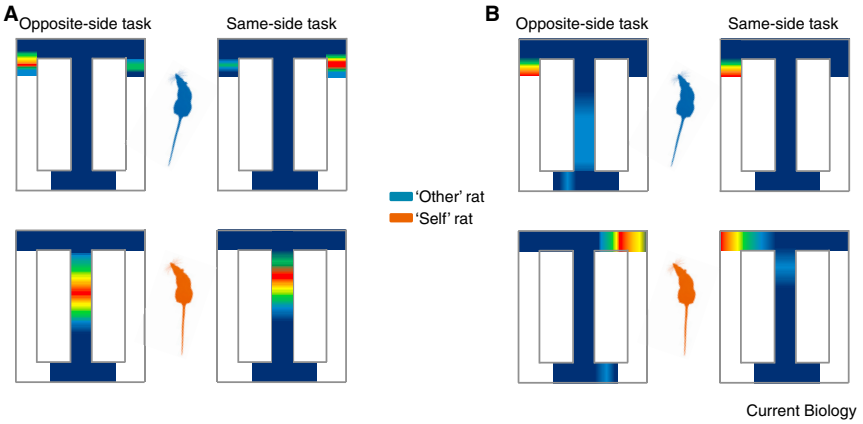

Figure 2. Two forms of beyond-self-location encoding.
(A) A cell tuned to the self's future trajectory, independent of the other rat. Top: firing rate map in the 'other' reference frame. Bottom: same cell's rate map in the 'self' reference frame. The cell's firing in the 'other' reference frame was firing-rate-modulated (hot colors, higher rate) by the self's future goal. (B) A cell tuned to the location of the other rat, independent of the self's trajectory; reference frames as in (A). The cell always fired when the other rat was at the left goal.

stationary or following at a stereotypical distance, and so constitutes a self's place field that is modulated by the observer's position.

This type of dual encoding — modulation of a place field by factors other than the animal's own location — often occurs when the additional factor becomes a reliable and relevant descriptor of a situation. However, the finding that not just the presence, but the *location* of another animal can be one such factor is surprising and important – other animals are dynamic, and computing where they are is a complex problem. This finding then raises a number of questions. How does the observer's brain compute the other's position in the absence of the spatial stimuli, such as directional, odometric and boundary information, that contribute to self-place field formation? Does the animal care about the characteristics of the other animal (identity, social rank, etc.) or only its location? Could *two* different individuals' positions be simultaneously represented, and how would downstream structures untangle the various signals? Is an experimenter's position represented during experiments, and how has this affected previous place cell experiments? And, most importantly, what is the function of such 'social coding' of space?

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Infection Models: Novel Potato Blight-like Pathogens in Worms

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Oomycetes are best known as plant pathogens, causing for example potato blight. Other oomycetes are deadly yet less well studied pathogens of animals including humans. Osman and colleagues now present the nematode *C. elegans* as a new, genetically tractable host model that should enhance our general understanding of oomycete infections.

Potato blight has had devastating effects on potato harvest, repeatedly causing serious famines in human populations. The most infamous example is the Great Irish Famine in the middle of the 19th century, in which potato blight accounted for a death toll of more than one million, leading another two million to emigrate to the United States. Potato blight is caused by a pathogen with a fateful name, *Phytophthora infestans*, meaning the plant-ruining infestation. This pathogen belongs to an unusual group of organisms, the oomycetes, that were long thought to be fungi, but which are in fact more closely related to brown algae and diatoms [1]. Phytophthora and other oomycetes are still considered to pose a serious threat to economically relevant plants and are thus of particular interest to agricultural research [2]. It is less well known that oomycetes can also infect animals and cause disease in humans. One example includes pythiosis caused by *Pythium insidiosum*, which is now considered an emerging human pathogen with high morbidity and significant