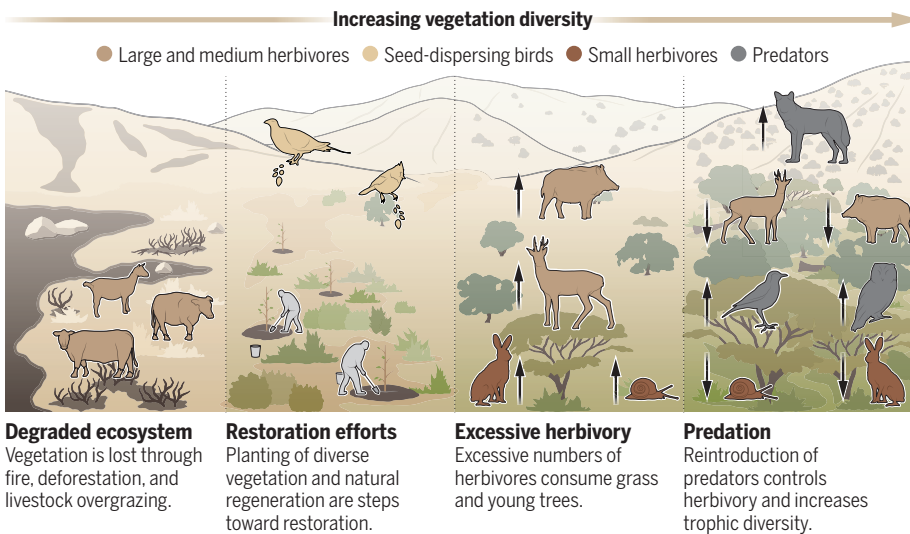


This conclusion challenges the common perception that vegetation restoration often results in faunal restoration through passive re-colonization (6) and highlights that ecosystem disassembly and reassembly are not symmetrical. In terrestrial systems, for example, many wild animals are not likely to recolonize (relatively small) restored vegetation patches that are embedded in highly fragmented landscapes. This could be due to barriers to movement (7) or to local, re-

restrial ecosystems, where wildlife, in general, and predators, in particular, are slowly returning (10). The findings suggest that this could accelerate vegetation regeneration. In tropical and subtropical systems, predator and herbivore species whose numbers are declining (9) could be reintroduced for concomitant restoration of vegetation and trophic structure. Yet empirical field studies need to be conducted to validate this hypothesis.

## Restoring food webs to regenerate vegetation

Restoration of ecosystems such as forests can be initiated by the active planting of vegetation or by natural processes such as seed dispersal by birds. However, excessive numbers of herbivores and imbalances in the composition of herbivore communities can limit regeneration through high levels of herbivory. Reintroducing predators to the ecosystem can control herbivory and facilitate restoration.



gional, or functional extinctions (1, 8).

An established principle in ecology is that, through trophic and behavioral cascades, predators limit herbivore densities, which reduces consumption of vegetation and thus increases vegetation biomass (9). Xu *et al.* reviewed the few available studies of the impact of predator reintroductions on vegetation restoration. The results suggest that predator reintroduction might be as effective for vegetation restoration as removing herbivores (through physical enclosures, insecticides, or deterrents) or plant-centered solutions (such as decreasing plant competition or promoting facilitation), indicating that the presence of predators in an ecosystem plays a critical role in the restoration of its vegetation (see the figure). A major benefit of this nature-based solution is that it enables vegetation restoration while also restoring the trophic structure and potentially the composition and food webs of degraded ecosystems.

All predator reintroduction studies analyzed by Xu *et al.* come from temperate ter-

Although the study of Xu *et al.* supports the importance of trophic cascades and the key role of trophic rewilding in ecosystem restoration, the specific restoration solutions applied should also consider local contingencies and the broader socioeconomic context. Their work also emphasizes that restoration of the diversity in Earth's ecosystems is intrinsically linked to the restoration of their biostructure. ■

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## NEUROSCIENCE

# The neural basis of mental navigation in rats

## A brain-machine interface demonstrates volitional control of hippocampal activity

By Michael E. Coulter<sup>1</sup> and Caleb Kemere<sup>2</sup>

Complex behaviors such as navigation often require chains of decisions that can be mentally simulated ahead of carrying out the behavior. The activity of spatially coding neurons (place cells) in the hippocampus and associated cortical regions has been posited as the expression of a "cognitive map," which could serve as a substrate for generating these complex behaviors (1). On page 566 of this issue, Lai *et al.* (2) report that rats can navigate through a virtual reality (VR) environment using a brain-machine interface (BMI) that estimates the rat's mental location from the ongoing activity of neurons in its hippocampus. This finding is an exciting expansion of BMI implementation from sensorimotor functions to a more cognitive domain and suggests that hippocampal activity is under volitional control. In addition, the BMI approach provides a new tool for probing the circuit-level mechanisms of mental navigation and spatial imagination.

Since neuroprosthetic BMIs emerged about two decades ago (3), a basic paradigm has been used: Animals, which have been surgically implanted with cortical recording electrodes, engage in a sensorimotor task—for example, moving a joystick to control a cursor on a screen. Initial trials are used to train a "decoder," which maps neural activity to the task space. Once trained, the task interface is switched to be controlled by decoded ongoing neural activity rather than the animal's physical movements. This approach has provided information on the neural circuits that plan and control limb movements (4) as well as enabling devices that restore communication function in individuals with severe paralysis (5). So far, BMIs have largely targeted neurons from

regions whose activity strongly correlates with movement and so might be expected to be under natural volitional control.

There has been interest in BMIs that decode cognitive states (for example, affect or preference) for neurofeedback or closed-loop modulation (6, 7). Critically, unlike BMIs that use naturally volitional regions, cognitive neurofeedback requires the user to practice to achieve the desired patterns of neural activity. Although there have been some reports that hippocampal activity might precede motor actions (8, 9), the activity patterns of hippocampal place cells are thought to be largely generated from action by the integration of sensory information with internal feedback on limb position and movement. Whether the population code in the hippocampus

hippocampus can be volitionally controlled without training.

Spatial navigation can be thought of as model-based control (10): By using a predictive model of the world, actions are planned. Executing these actions changes the relationship of the individual to the world. This, in turn, updates sensory information, which finally updates predictions from the world model. This process is fundamentally a loop, but it critically involves motor action and sensory feedback. In addition to physically traversing the world, humans can mentally navigate—for example, choosing routes by imagining traveling through them. This imagined navigation coarsely activates the same temporal lobe brain regions as actual navigation (11). However, a deeper circuit-

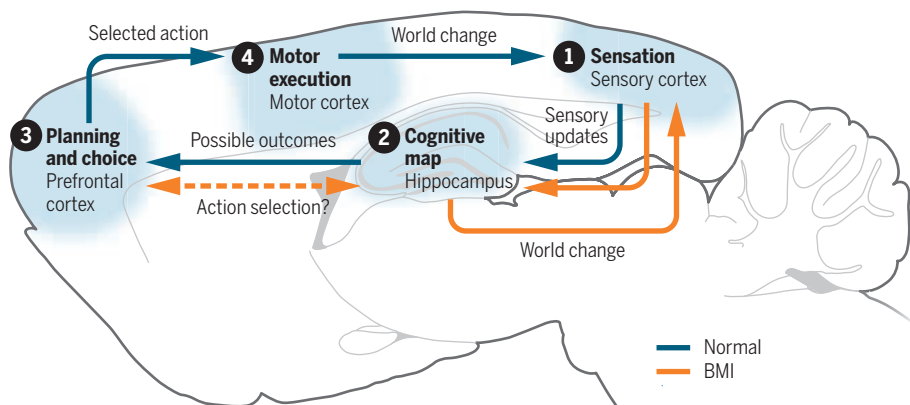
themselves moving in space, or whether they were directly representing the location of a distinct object by activating recently reported hippocampal neurons associated with object locations (12) (which would be less akin to mental navigation).

Can animals be trained to perform imagined navigation—to volitionally activate representations of remote locations—in the real world? Previous work suggests that representations of space by the activity of hippocampal neurons are similar in VR and real environments (13), so it is likely that the findings of Lai *et al.* also apply outside of VR; future experiments can test this hypothesis.

The hippocampus is known to exhibit bursts of ensemble activity in sequences that seem to represent locations away from the animal's current position. These bursts take place during sharp wave ripples (SWRs), which occur during periods of rest and sleep, and theta sequences, which are synchronized by oscillations in activity present during ongoing exploration. Both types of burst sequences have been given hypothetical roles in mental navigation (14), but the BMI approach of Lai *et al.* presents an opportunity to test this directly. They observed periods of SWRs and theta oscillations during performance of the BMI task. Strong theta oscillations were observed during all trials, when the rat was moving and still. This latter observation is consistent with rats mentally moving through the environment. Although post hoc analyses found equivalent navigation ability when SWRs were excluded, the 1.5 to 5 s decoding windows used in the BMI were too long to assess whether theta sequences are present or how they might be used by the animal to navigate. Developing faster online decoding algorithms and/or using higher-density neural recording techniques might address this issue and enable experiments to uncover the timescale of the ensemble activity that enables mental navigation. ■

## Investigating the neural basis of mental navigation

To enable spatial navigation, sensory information (1) is used to generate a predictive model of the world [cognitive map (2)], which enables actions to be planned (3). Execution of the planned action (4) changes the relationship of the individual to the world, which updates sensory information. A brain-machine interface (BMI) was trained to decode place cell activity from the hippocampus of rats navigating in virtual reality. The animals were able to control their location through the BMI, thus enabling changes to their relationship with the world in the absence of motor execution. This approach facilitates investigation of the neural circuits underlying mental navigation.



could be volitionally generated naturally (without training) remained uncertain.

The BMI system developed by Lai *et al.* decodes the activity of sparsely firing hippocampal place cell ensembles. The authors used a task in which rats initially navigate through a VR environment to a visually cued reward location by running on a spherical treadmill. A decoder is trained on the ensemble neural activity recorded during this initial training period. Then, control of the visual scene is transferred from the treadmill to the signal that is decoded in real time from hippocampal activity. Unexpectedly, they found that under BMI control, the rat continues to navigate through the VR environment to reward locations. This observation provides evidence that the ensemble activity in the

level understanding of mental navigation has been prevented by an inability to instruct a nonhuman subject to imagine a navigational path.

By directly tying changes in the VR environment to the output of the hippocampus, the approach taken by Lai *et al.* may enable the study of mental navigation in animal models (see the figure). Indeed, while rats primarily ran on the treadmill during BMI control, on many trials they successfully navigated the VR while remaining still. Moreover, if the decoded signal was used to move an object in a stationary three-dimensional environment, the animals were capable of directing this movement with their hippocampal activity. Unfortunately, the authors could not distinguish between the hypothesis that the animals are continuing to mentally navigate as if they were the object that was moving, as a human might look at a picture and imagine

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