A world away from reality

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Technology that involves VR has obvious advantages for studies of simple sensorimotor computations, in which a defined set of inputs, such as those corresponding to an animal's movement, is associated linearly with neural output. However, some pressing concerns are raised when VR technology is used to study higher-order computations such as spatial navigation. Navigation reflects the integration of many sensory inputs. The resulting outputs are not linearly related to sensory perception, but rather express cognitive abstractions.

Goal-driven navigation relies on several cell types in the brain, including place cells (which fire when an animal is in a particular location), grid cells (which fire at periodically spaced positions across the entire environment) and border cells (which fire selectively along local borders)[7,8]. By fixing an animal's head in place, investigators can monitor the activity of these neurons at high resolution while the animal runs between specific locations in virtual space. But do animals navigate in the same way in VR as in real life?

Navigating in the real world is a multisensory process that integrates visual, olfactory and tactile stimuli with vestibular information and information about the activity of moving body parts. But in VR, these elements are often not coordinated, and the animal's sensory experience is largely reduced to a combination of visual inputs and locomotion, which are easy to control. The animal must overcome discrepancies between visual cues that follow movements and cues that are static in VR, such as smell or head direction. Conflicts between movement and sensory inputs might alter the activity of space-encoding neurons to reflect only information coordinated to motion, such as visually changing landmarks and accumulated distance[1,2], at the expense of other cues. This could lead researchers to overestimate the contribution of visual inputs to navigation and, in the most extreme cases, might lead to the loss of computation altogether[2].

A particular concern is whether the loss of vestibular input that accompanies movement restriction affects animals' computation of their position. A continuous mismatch between vestibular and visual inputs might not be detrimental in linear environments. When an animal runs in a straight line, visual inputs are repeatedly and stereotypically paired to the same locomotor information, which may, with continued training, allow the animal to compensate for mismatches. However, such a mismatch might have a greater effect in two-dimensional or 3D VR arenas.

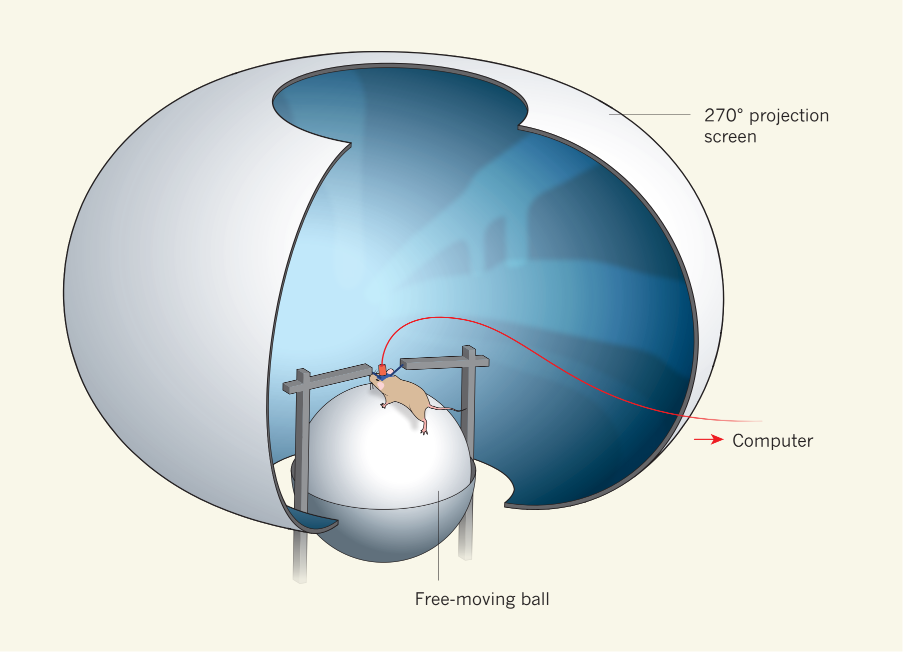

Figure 1 | A mouse explores a virtual world. In most typical virtual-reality experiments, a mouse is head-fixed above a ball. Its legs are free, allowing it to move the ball in all directions. By moving the ball, the mouse navigates around a virtual world that is projected onto a 270° doughnut-shaped screen in front of it. Head fixing enables neural activity to be measured and correlated with the motor actions that drive movement.

Indeed, if movement is unrestrained, the position-coding activity of place and grid cells is similar in 2D VR to that in the real world[5]. In stark contrast to this, position coding is disrupted and a new coding emerges when body movement is restricted, or if the head is fixed[2]. These data cast doubt on whether the way animals interpret 2D or 3D space can ever be understood using VR under conditions of head or body restriction. Strategies that compensate for the loss of synchrony between vestibular information and the animal's behaviour would be a welcome advance.

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Finally, are all types of position-coding cell represented in VR-based navigation? It is unclear if and how border, speed and head-direction cells are activated when movement is restricted. Moreover, cells might not fire in the same way in the two worlds. In one analysis[2], 60% of the place cells activated in the real world were silent in VR. Whereas studies typically check that VR-activated cells are represented in real-world sessions, the opposite direction of investigation lags behind — although there are exceptions to this[3].

More than 40 years ago, the neuroscientist John O'Keefe changed our understanding of the physiology of navigation by studying rats freely foraging for food. By allowing the natural sensory–motor interactions required for the formation of an internal representation of space, O'Keefe discovered the first element of the 'cognitive map' — the place cell[9]. VR can extend that ecological approach to higher cognitive functions. But to do so successfully, the technology needs further development and validation. ■

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