Dispatch

Spatial Cognition: Finding the Boundary in the 'Occipital Place Area'

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Summary

Transcranial magnetic stimulation and a virtual reality navigation task reveal that the 'Occipital Place Area' in humans is required to accurately remember where objects are located in relation to boundaries, but not in relation to landmarks.

Main Text

Remembering where you parked your car can be frustrating due to the large number of other parked cars. One solution is to remember where you parked relative to the boundaries of the parking area, another strategy is to locate your car relative to a prominent landmark. Neuroimaging evidence suggests that these two strategies engage different brain circuits. Using a landmark to find a location appears to engage the dorsal striatum, whereas using a boundary recruits the hippocampus [1]. These findings have been used with other discoveries to argue that the hippocampus provides a cognitive map of the environment to store long-term spatial and episodic memories, and the striatum associates actions with discrete stimuli, such as landmarks [2,3]. Increasingly sophisticated experiments have helped characterise these

functional circuits. However, there is still uncertainty about how these systems receive the information needed to form memories and associations. In the case of the hippocampal circuit, there has been particular interest in determining how it receives information about the boundaries in the environment. For the human brain this has remained particularly mysterious. Now, as they report in this issue of *Current Biology*, Julian *et al.* [4] find a region of human occipital cortex that appears to be a potential source of visual information about the boundary.

Three suspects in the search for the boundary

In order to track down the origin of boundary information a useful starting place is to examine the brain regions known to respond preferentially to stimuli that contain boundaries: scenes. Human neuroimaging studies have consistently identified three cortical regions that reliably respond more to scenes than non-scene stimuli. These are the parahippocampal place area (PPA), the retrosplenial complex (RSC). and the occipital place area (OPA). [5-8]. Arguably the most famous of these regions is the PPA, which responds strongly to the presence of boundaries [6,7]. However, it also responds to landmarks and other non-boundary components of scenes, which would argue for a more general role in spatial processing than conveying boundary information [6,7]. The RSC has been found to represent the spatial extent of a bounded region in scenes [7], which would make it a prime suspect. However, it appears to encode more abstract information such as local location and heading information [8, 9], and is also known to play a more general role in memory function [9, 10, 11]. Thus the RSC's candidacy as the provider of boundary information is also

less certain. This leaves the OPA, whose credentials as the potential source of boundary information are stronger due to its more up-stream position in the visual processing hierarchy than the PPA or RSC [5,6,7].

To determine whether the OPA plays a role in processing boundary information Julian *et al.* [4] applied transcranial magnetic stimulation (TMS). above the OPA during a virtual reality spatial memory task. The OPA was identified in each participant using neuroimaging. TMS allowed the researchers to briefly disrupt neural activity in the OPA during the task. The spatial memory task, modelled on a prior study [1], involved learning where several objects were located in a virtual environment composed of a circular boundary wall, a single landmark and distant mountains to orient by, see Fig. 1. The location of each object had to be learned by placing it in the environment and receiving feedback on where it should be correctly located. After an initial learning block the landmark moved to a new location relative to the boundary. Half the objects were now correct relative to the boundary (e.g. the wall section nearest the mountains). and the other half correct relative to the landmark. TMS above the OPA, but not the vertex, disrupted memory for the objects located relative to the boundary and participants showed a bias to using the landmark to locate objects. Demonstrating the specificity of the OPA to boundary information, TMS stimulation had no effect on memory for the objects located relative to the landmark. Various control analyses revealed these effects were not likely due differences in the difficulty of the landmark and boundary tasks. Thus, it appears the OPA is involved in processing information needed for object memory relative to boundaries, but not landmarks.

What is important about this new result is that the effect is causal. The OPA is not just activated by stimuli containing boundaries, but disrupting activity in the OPA disrupts processing of boundary information. Due to the fact most structures involved in spatial memory are located deep in the human brain, there has been little attempt to use TMS to explore causal roles of these brain structures for navigation. Thus, this new result helps provide an important advance in our understanding of the brain regions necessary for spatial navigation.

A visible wall is needed for OPA stimulation to disrupt spatial memory

There are a number of ways in which the OPA might contribute to processing boundaries. It might provide visual information about the wall surface that forms the visible boundary or it could process information about the impediment to movement created by the boundary. To explore these possibilities Julian et al. [4] tested a new group of participants in three different environments. The environments were similar to that used in the first experiment, but participants could only use the boundary for memory because the landmark was absent. Only one the environments contained a visible wall, in the other two the boundary was marked by a change in texture. OPA stimulation was only found to disrupt spatial memory in the environment with the visible wall. This suggests that activity in the OPA is involved in processing visible wall barriers, rather than processing more abstract properties of boundaries; a finding consistent with the OPA playing a perceptual role in the processing environmental information [12].

Future directions

This discovery raises several questions. How does the information about the wall boundary reach the hippocampus? Which brain regions code for more abstract boundary representations? Given the complexity of the human visual system there are multiple routes that visual representations of the boundary might reach the hippocampus. As Julian *et al.* [4] point out, the functional connections from OPA to PPA [13] may be one such pathway and another may be via anatomical connections to the posterior parietal cortex. Due its depth in the brain the PPA is not a feasible target for future TMS studies. However, sites in the posterior parietal cortex would be. Dorsal and ventral regions of posterior parietal cortex have been shown to provide dissociable contributions to scene processing [14] and thus distinct areas may play a role in processing boundaries. Combining TMS with methods such as high-density electroencephalography would provide a useful means of exploring the role of different regions in the network and their functional inter-relations.

Our understanding of how boundaries are processed by the brain has advanced much further in rodent studies. Cells responding to boundaries have been reported in the entorhinal cortex [15] and the subiculum [16]. While entorhinal cells appear to encode the proximity to boundaries, cells in the subiculum encode the allocentric vectors to boundaries (boundary vector cells). Subiculum and entorhinal cortex differ from posterior cortical areas in that they receive more diverse multimodal input, including highly processed head direction information [17]. Boundary vector cells in the subiculum have recently been shown to respond similarly to boundaries whether they

are a visible wall or created by a drop [18]. Thus the subiculum would appear to be a key brain region for providing a more general abstract code for boundaries. Given that parietal representations of distance appear to straddle spatial, temporal and social dimensions [19], it seems possible that cells encoding abstract boundaries might also be involved in coding the social boundaries which we build the fabric of our societies on.

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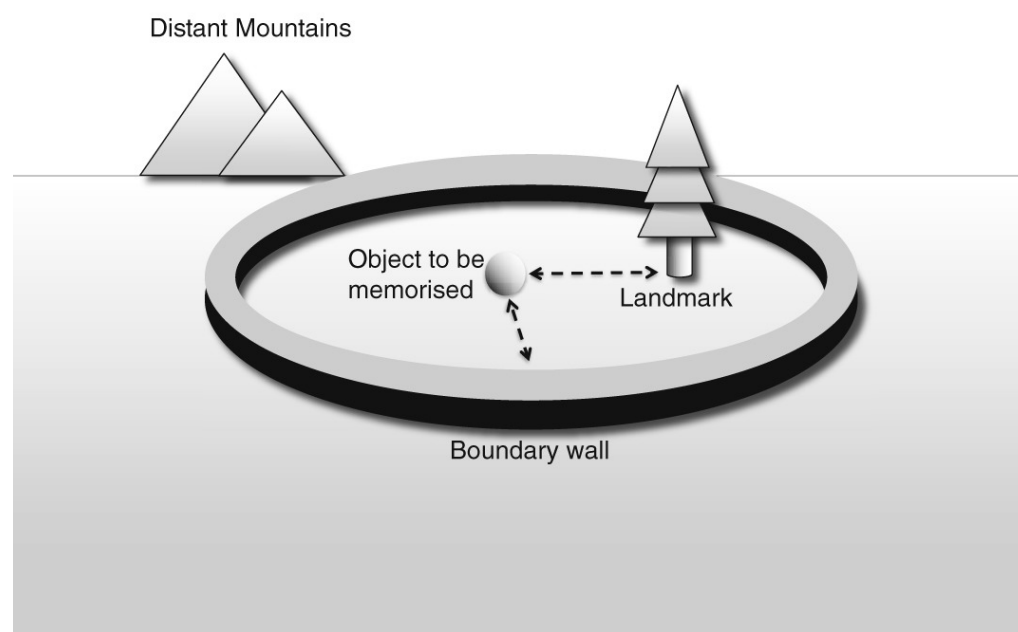
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Figure 1. Spatial memory task used Julian *et al.* [4]. The diagram depicts an example

of the environment in which the participants had to place objects, such as a ball, in

their correct place. The paradigm was adapted from [1]. The environment was viewed

from first person view within the boundary walled region. Dotted lines indicate the

associations that could be formed to help locate the ball either relative to the wall

boundary or the landmark. After placing an object participants were given feedback

about the correct location. Over trials, memory for the location of the objects

improved. TMS stimulation to the OPA specifically disrupted memory for the

association with the wall boundary, but not the landmark association.