

Cognitive Maps and the Hippocampus

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Following a familiar route and finding a novel route in a familiar environment depend on different cognitive processes and representations. A recent study by Hartley et al. begins to identify the neural basis of route following and wayfinding in humans. Their study also raises important questions about the functions of the hippocampus.

It is easy to identify at least two kinds of navigation in our day-to-day experiences. One is exemplified on a small-scale by the quick trip to the refrigerator and back during a television commercial, and on a large-scale by the drive from home to work and back each day. This type of navigation involves following a familiar route, and at times, seems to be performed almost unconsciously. The other is exemplified by trying to find a new way to work because of street construction or by searching for a new restaurant in a familiar city. This kind of navigation, sometimes referred to as wayfinding, is deliberate, consciously controlled, and may depend on knowing or inferring the global spatial relations among locations in the environment. Researchers of human spatial memory and navigation have long suspected that these two kinds of navigation depend on different cognitive processes and representations of the environment [1, 2], and behavioral studies have confirmed this hypothesis [3]. But until recently, little was known about the neural basis of route following and wayfinding in humans. In the first experiment of its kind, Hartley, Maguire, Spiers, and Burgess cleverly employed virtual environments and functional neuroimaging to examine whether these two types of navigation are supported by different networks in the human brain [4].

Route vs. survey knowledge

Following a familiar route has been thought to rely on route knowledge—knowledge of ordered sequences of locations, or landmarks, and actions to be taken at each landmark (e.g., go straight, turn right, etc.). Finding novel routes through a familiar environment has been thought to rely on survey knowledge—knowledge of the spatial layout of landmarks defined in a common reference system. Analogous distinctions have appeared in the animal learning literature. Indeed, Tolman [5] coined the term “cognitive map” to refer to survey knowledge acquired by rats in maze-learning experiments. In O’Keefe and

Nadel's [6] seminal theory of spatial memory in the rat, the *taxon* system uses learned associations between environmental stimuli and locomotor responses to create "routes" from starting points to destinations, whereas the *locale* system uses map-like representations of the environment to compute geodesic paths between locations.

Imaging the brain during route following and wayfinding

Hartley and colleagues created two distinct but structurally similar towns in desktop virtual reality. Subjects learned each town under different conditions: One was explored freely, with minimal direction from the experimenter. In the other, subjects repeatedly followed the same route from starting point to destination. BOLD (blood oxygen level dependent) activity was then measured using fMRI while subjects engaged in three tasks: The *wayfinding* task was performed in the town that had been explored freely. Subjects had to find their way between successively presented target locations (9 in all including the starting point). Hartley and colleagues assumed that good performance in this task depended on survey knowledge of the town. The *route-following* task was performed in the town in which subjects had only learned one route. Subjects just had to follow this route repeatedly. The *trail-following* task, which served as a control for the other two, required subjects to follow a trail defined by green markers on the virtual ground plane.

The authors hypothesized that successful wayfinding would preferentially engage the hippocampus, whereas route-following would be more dependent on the caudate nucleus. Support for these relationships was obtained from three key results. First, an analysis of navigation performance within subjects showed that better trial-by-trial performance on the wayfinding task was associated with greater activation in the right posterior hippocampus. Second, participants were assigned a global measure of performance on wayfinding, which was then correlated with brain activation differences between wayfinding and route following. The results indicated that good navigators showed greater wayfinding activation than poor navigators in the perirhinal cortex and marginally in the hippocampus. The head of the caudate showed the opposite pattern, with greater wayfinding activation for poor compared to good navigators. Finally, overall performance on wayfinding was positively correlated with brain activation differences between wayfinding and trail following in the left hippocampus (albeit this result does not speak directly to differences between wayfinding and route following). Together, these results suggested that successful navigation was associated with greater activation in medial temporal lobe regions during wayfinding and with greater activation in the caudate during route following.

Hartley and colleagues' results are intriguing but may be limited in certain respects. One potential limitation is that subjects received no proprioceptive or vestibular feedback during navigation. Many individuals have difficulty staying oriented when they navigate virtual environments under such conditions [7, 8]. Extensive practice in the virtual environment seems to mitigate these effects to some extent [9]. All of Hartley and colleagues' subjects were experienced "first-

person gamers”, and therefore, were probably less affected by the absence of proprioceptive and vestibular cues. It would be interesting to investigate whether gamers learn special navigation strategies to compensate for impoverished locomotion cues. Another possible limitation is that different learning conditions were used for the two navigation tasks. The intentional pairing of free exploration with later wayfinding and of route learning with later route following guarantees that learning of one type will not influence performance of the other type. However, this feature of the design also limits inferences about the extent to which observed patterns of brain activation are due to a particular type of representation that has been stored in the brain or to the inferences required to perform the particular navigation task.

What does the hippocampus do?

A fundamental question raised by this research is what the functions of the hippocampus really are. Hartley and colleagues conclude that it is specifically involved in navigation via novel paths, and imply that it is responsible for creating a cognitive map of the environment. This conclusion has its historical roots in O’Keefe and Nadel’s [6] most influential—and controversial—claim: That the locale system was the province of the hippocampus. One of the strongest lines of evidence in support of this claim was the existence of “place cells” in rat hippocampus [10]. Place cells are neurons that are location selective; they respond maximally when the rat’s head is in a particular location in the environment. Research over the past thirty years has confirmed that the rat hippocampus has an important role in spatial memory and navigation; however, characterizing the functions of the hippocampus is a matter of controversy [11].

There is little question that the hippocampus plays a role in many non-spatial processes [12-14]. At issue is the disproportionate role that the hippocampus seems to have in spatial tasks and what this fact implies about the functions of the medial temporal lobes. According to several contemporary theories of hippocampal function [15, 16], the hippocampus is not specifically designed for creating and storing cognitive maps. One such theory claims that the primary function of the hippocampus is to associate information in ways that allow flexible use of past experiences to benefit future behaviors (“flexible memory expression”; [17]). Spatial tasks preferentially recruit the hippocampus because they often depend on novel uses of learned associations. Such flexibility would be required for tasks such as wayfinding (at least when survey knowledge was still being acquired) but not for tasks such as route following, which can be accomplished by rigidly applying previously learned associations.

This nonspatial theory of hippocampal function can account for effects of hippocampal damage on spatial memory performance [15; but see 18, 19]. For instance, in the Morris water maze, rats with hippocampal damage can find the goal when conditions do not require flexible use of past learning but fail when conditions require inference [20]. This theory makes the novel prediction that wayfinding in a very familiar environment—one for which survey knowledge is well-developed—will require little hippocampal involvement because successful navigation would not depend as heavily on novel uses of learned associations.

Consistent with this prediction, Teng and Squire [21] found that patient EP had intact memory for a familiar environment learned long before his brain injury, despite extensive damage to the medial temporal lobes [also see 22]. Notably, EP was unimpaired not only on route-following tasks but also on tasks akin to the wayfinding task used by Hartley and colleagues, suggesting that with extensive experience, the topographical representation is complete (and perhaps represented cortically) and no longer requires the inferencing capabilities of the hippocampus.

Although Hartley and colleagues depict their results as reflecting different representations of the environment, their findings are largely consistent with this alternative characterization of the functions of the hippocampus. The route-following task requires only simple direct access to or reinstatement of information that is already stored. Such reinstatement of a stored representation would not be expected to preferentially engage the medial temporal lobe structures if those structures are involved in the flexible transfer of previous experiences to novel problems. Alternatively, the wayfinding task taps into memories of the space that are still under construction and cannot be solved by a mechanism that supports simple, direct reinstatement of a previously learned route. Survey knowledge is still being inferred from the routes experienced during learning and explored during retrieval. Inferring global spatial relations from experienced routes and applying this newly formed knowledge are examples of the kinds of flexible processing that have been linked to the hippocampus.

The survey view (or big picture)

Scientific progress is often greatest when competing theories can be integrated. Certainly in primates, and perhaps even in rodents, the hippocampus has many functions other than purely spatial ones; however, it may be solely responsible for *building* cognitive maps [22-24]. Nonspatial theories of hippocampal function, such as flexible memory expression, may describe the mechanisms involved in these constructive processes. Viewed in this way, one can see that Hartley and colleagues' findings provide crucial new insights about how route and survey knowledge are processed in the brain, and at the same time, frame this new understanding in the broader context of the memorial functions of the medial temporal lobes. Navigation by well-learned routes does not require the flexible application of past experiences, and therefore does not recruit the hippocampus. In contrast, finding novel paths in a recently learned environment depends precisely on the memorial functions for which the hippocampus may be specialized. Hartley and colleagues' results provide a foundation for more detailed hypotheses about specific processes involved in different types of encoding, retrieval, and inference and help to bridge the gap between alternative theories of the hippocampus. A beautiful aspect of their experimental approach is that spatial and nonspatial theories of hippocampal function can be contrasted within a common spatial context.

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