

Why Vision is Important to How We Navigate

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ABSTRACT: Place cells are a fundamental component of the rodent navigational system. One intriguing implication of place cells is that humans, by extension, have “map-like” (or GPS-like) knowledge that we use to represent space. Here, we review both behavioral and neural studies of human navigation, suggesting that how we process visual information forms a critical component of how we represent space. These include cellular and brain systems devoted to coding visual information during navigation in addition to a location coding system similar to that described in rodents. Together, these findings suggest that while it is highly useful to think of our navigation system involving internal “maps,” we should not neglect the importance of high-resolution visual representations to how we navigate space. © 2015 Wiley Periodicals, Inc.

KEY WORDS: cognitive map; hippocampus; humans; path integration; spatial navigation; allocentric; egocentric

INTRODUCTION

The Nobel Prize Committee recently recognized the major contributions of John O’Keefe, May-Britt Moser, and Edvard Moser to understanding the neural basis of navigation, and by extension, memory more generally. Starting with recordings by O’Keefe and Dostrovsky demonstrating the presence of place cells in freely moving rats, and continuing with countless empirical discoveries and theoretical models, these three scientists have filled a previously missing gap in understanding how neural activity relates to higher order cognition. Specifically, the discovery of neurons that fire at precise spatial locations as a rat navigates (termed place cells) and cells that fire throughout the environment in an evenly spaced fashion (termed grid cells), suggest a neural basis for not only how we remember where we are but where we have been and where we are going. These findings have wide ranging implications for understanding cognition more generally, and have intriguing implications for

neural diseases that affect memory and navigation, such as Alzheimer’s disease and stroke, which we as a field are just beginning to understand.

This review will focus primarily on place cells and their larger implications for human spatial navigation because of their importance to location coding in a brain structure called the hippocampus (although grid cells are no less impressive and important!) Consistent with a central role for the rodent hippocampus in coding a “cognitive map” of the environment (Tolman, 1948, O’Keefe and Nadel, 1978), when a rat moves to a different spatial environment, place cells alter the location at which they fire (Wilson and McNaughton, 1993). Using the activity of a population of place cells, it is possible to obtain a fairly precise estimate of a rat’s position in space (Wilson and McNaughton, 1993). Consistent with this finding, lesions to the hippocampus impair the ability of a rat to find a hidden location, suggesting the importance of the neural machinery in the hippocampus to navigation (Morris et al., 1982; Lindner et al., 1997). Place cells derive from a combination of self-motion cues and visual input (Moser et al., 2008), although either one alone may be sufficient to drive place-specific firing (Chen et al., 2013). Place cells thus provide a faithful representation of a rat’s location by using information from multiple modalities to represent position during navigation.

A key question that these important findings lead us to and will be the focus of this paper is exactly how place cells in the rodent apply to the human brain and how humans navigate. One interpretation of the neural coding system described above, and favored by the Nobel Prize Committee, is that the human place coding system also has such an “internal global positioning system.” Here, we will review the evidence for place coding in the monkey and human hippocampus as well as other neural systems that code view-related information, like the positions of spatial landmarks. This will set the stage for the idea that, based on location-related and view-related coding, humans can utilize both path integration (updating based on self-motion cues) and visuospatial representations. As we will argue here, while both systems are present in rats and humans, rats utilize the path integration system to a greater extent than us while our

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high-resolution visuospatial representations play a more prominent role during navigation than rats. These discussions will help provide a more complete understanding of why visual coding might be important to consider in humans in light of the major advances provided by the discovery and characterization of the location-coding system in the rat.

From rats to monkeys to humans: Evidence for neural systems dedicated to location and high-resolution visuospatial coding

An early debate in the nonhuman primate literature focused on whether monkey hippocampal neurons responded to the spatial location of the animal's current view or the spatial location the animal currently occupied (Rolls and O'Mara, 1995; Matsumura et al., 1999). Specifically, recording from hippocampus and parahippocampal cortex in head-restrained monkeys who moved about an environment, Rolls and colleagues found cells that increased firing while viewing specific locations (Rolls and O'Mara, 1995). Other studies, however, with head-fixed monkeys navigating a mobile car on a track, demonstrated hippocampal neurons that fired when the monkey occupied specific spatial locations (Matsumura et al., 1999). Finally, studies in freely navigating squirrel monkeys demonstrated several examples of hippocampal neurons firing at specific spatial locations, reminiscent of place cells (Ludvig et al., 2004). This begged the question, was it spatial location or view location?

The answer, as suggested in these studies and subsequent ones in humans, appeared to be both. An early observation using noninvasive functional magnetic resonance imaging (fMRI) suggested an area in posterior parahippocampal cortex that responded strongly when participants viewed spatial landmarks during navigation (Aguirre et al., 1996; Janzen and van Turennout, 2004). Tying together view and place coding, in a study in 2003, we found evidence for both location and landmark responsive cells in the human medial temporal lobes. In this study, we investigated patients undergoing extracellular recordings during seizure monitoring who freely navigated virtual environments on a laptop computer. We found neurons in the hippocampus that fired at specific spatial locations, independent of the angle at which they entered the place field or what they viewed on the screen (Ekstrom et al., 2003). We also found cells in the parahippocampal cortex that responded when patients viewed landmarks, regardless of the angle that they looked at them (Ekstrom et al., 2003). These studies, along with noninvasive fMRI studies, suggested the presence of both location and view coding responses during navigation in humans (Aguirre et al., 1996; Hartley et al., 2003).

Are human location-responsive cells the same as what is observed in rats?

Several issues are worth considering regarding location-responsive cells in humans. One concern that could point to differences between rats and humans is that the observed human place responses differed in their selectivity. Location-specific firing rates in the patients we tested typically increased

2–5 times above baseline, ranging from about 1 to 15 Hz within field. This is less selective than place cells in the hippocampus of rodents, where firing rates often increase 100 times above baseline or more within a place field. Nonetheless, human location responsive cells fired well above chance in our study (Ekstrom et al., 2003) and in subsequent studies confirming the presence of human place cells (e.g., Miller et al., 2013). Furthermore, a neural coding scheme does not require much more than a statistically significant change in firing rate to convey relevant information (Rieke et al., 1999). Thus, although less selective, human hippocampal neurons code location-specific information.

Could selectivity differences relate in some form to differences in how we code space? Of course, other factors could be relevant in why human place cells fire at a lower peak rate than those in rats, including the fact that human recordings do not involve moveable electrodes. It is intriguing, though, to consider this issue from an ecological standpoint: humans undergo a multitude of different cognitive demands that might be expected to enrich what our hippocampus does while rats undergoing place cell recordings are reared for precisely this function. Consistent with this argument, in addition to responding to locations, neurons in the human hippocampus respond to other stimuli, such as famous faces (Quiroga et al., 2005) and conjunctions of locations, views, and goals (Ekstrom et al., 2003), likely supporting episodic memory (Miller et al., 2013). Similarly, when trained and tested on tasks requiring coding of odors and their position, rat hippocampal neurons respond to these task demands as well as conjunctions of locations and odors (Wood et al., 1999). Thus, place cells are one of many different types of responses present in both rat and human hippocampus, and their relative prominence in rats might be a product of their rearing and training (and possibly evolutionary specialization toward navigation).

Is there something about our visual system that makes us special?

Beyond differences in how we are “reared” before testing in the lab, the presence of view-coding neurons in both monkeys and humans raises an important question regarding how we treat visual input compared to rats. The rat retina is primarily made up of rods (not high-acuity cones), lacks a fovea (Euler and Wässle, 1995), and is low acuity compared to other mammalian species (Douglas et al., 2005). Rats lack orientation columns, the backbone for complex visual processing in primates, and their visual cortex is $\sim 1/10$ the size of that in squirrels, who are more visually oriented overall (Van Hooser et al., 2005). Finally, it appears unlikely that rats have a specific brain system devoted to object processing that is comparable to our high-resolution ventral stream, which contains numerous steps for processing fine-grained details of objects (Kravitz et al., 2013). Yet, as we will discuss shortly, high-resolution visual processing appears critical to many of our navigational abilities, including using cartographic maps to infer spatial location.

Analysis of eye fixations in freely moving rats further demonstrates that their visual system may be “oriented”

differently than humans. Eye tracking in rats during navigation demonstrates that rather than converging on a single location in front of them (like humans), rat eyes often move out of synch. Instead of fixating on a location in front of them, rodent eye movements appear optimized to converge at locations *above* them (Wallace et al., 2013), a possible adaptation to predators such as hawks and owls. In contrast, our eye movements appear particularly optimized to fixate in front of us, with binocular alignments outside of 1–2 degrees resulting in double vision and failure to fuse images. These differences in visual processing suggest one reason why rat navigation in VR might be impoverished compared to actual navigation (Chen et al., 2013) and support the prediction that vision is a more important factor in how we navigate than rats.

These dissimilarities in rat and human visual systems also relate to differences in navigation using vision. Rats that undergo retinal enucleation (blind rats) show surprisingly little impairment at navigating the Morris Water Maze (Lindner et al., 1997). In contrast, blind humans, particularly congenitally blind individuals, suffer profound navigational impairments (Thinus-Blanc and Gaunet, 1997). In fact, a major endeavor in the field of blind navigation is to develop GPS devices that can help substitute for visual-deficits during navigation (Loomis et al., 2001). In the case of rats, head-direction and proprioceptive information may provide sufficient input (via a mechanism termed “path integration”), along with information provided by whisking, to update their position when lacking vision (Etienne and Jeffery, 2004). While blind individuals can certainly employ path integration mechanisms to navigate, in many cases, better than sighted individuals (Loomis et al., 2001), there is little debate that vision forms a central part of everyday navigation in humans. This may be particularly evident in sighted humans when path integration, which accumulates errors as a function of distance, breaks down in the absence of visual cues (Foo et al., 2005).

Could differences in vision relate to differences in the brain systems involved in how we navigate? Potentially, yes. While the parahippocampal cortex contains neurons that respond to spatial landmarks (Ekstrom et al., 2003) and the posterior parahippocampal cortex responds strongly to landmarks during navigation (Janzen and van Turenout, 2004), no such homolog exists in the rat, at least that has been shown so far. In fact, both rat postrhinal cortex and retrosplenial cortex are different than their human homologs and are overall less well developed (Maguire, 2001; Witter, 2002). On the basis of the above considerations, it is reasonable to consider that human retrosplenial and parahippocampal cortices receive significantly stronger visual input in humans than rats. Thus, compared to a rodent, our brain navigation system puts a heavy emphasis on visual input.

But how might our high-resolution visual system result in a behaviorally different spatial representation from a rodent? One example of the importance of vision to how we navigate is our ability to use cartographic maps as a small-scale representation of the locations of objects in our larger environment. It remains unclear if cartographic maps are useful in any form to

a rat. In humans, the brain systems involved in using a cartographic map also do not appear to be the same ones involved in place coding (Zhang et al., 2012) and may derive, in part, from our ability to represent objects in high resolution (Shelton and Gabrieli, 2002). As human participants learn a new environment, activation in retrosplenial cortex, and not hippocampus, tracks improvements in the accuracy of cartographic maps that they draw (Wolbers and Buchel, 2005). Furthermore, applying a recently learned overhead map to navigation recruits a network of different areas, including retrosplenial cortex, parahippocampal cortex, and precuneus, with the hippocampus active only when the map must be used flexibly (Zhang and Ekstrom, 2013). Finally, patterns of retrosplenial activation (and not hippocampal activation) provide a fairly precise readout of our position and heading (Marchette et al., 2014). Thus, cartographic maps are one example of how our high-resolution visual system plays a critical role in how we learn and navigate space.

Why do we use GPS in the first place? View often trumps location in human spatial navigation

Cartographic maps are an excellent means of deriving the exact position of objects or places in an environment, provided we can orient ourselves accurately relative to their position. Despite our ability to use cartographic maps to navigate and remember spatial locations, though, these do not appear to translate into precise “map-like” knowledge. Specifically, we often use past experience to substitute for detailed perceptual information about the world, often referred to in the visual perceptual literature as heuristics or grouping laws. In one particularly compelling study, participants had to make judgments about the relative positions of cities on a map following completion of a geography class. When asked to judge whether Seattle or Montreal was further north, despite having just completed a class in geography, participants consistently made the error that Canadian cities were further north (Friedman and Montello, 2006). One would have expected, though, if our location-specific coding mechanisms were GPS-like and our knowledge map-like, that we would have accurately encoded the positions of cities on the map. Thus, while we certainly can employ what we have learned from cartographic maps to estimate distances and directions, it is also clear that we reconstruct our memories of maps to be consistent with what is often true about the world (e.g., Canadian cities are further north).

One might easily argue that geographic-scale maps represent an entirely different level of abstraction from the scale of space involved with place cells, despite their obvious similarity to “cognitive maps.” Even the representations derived from smaller-scale, navigable space (most often used in studies of rodent navigation), however, show biases based on visual representations. For example, when pointing to locations in a recently navigated environment, although participants can often point to objects and locations fairly accurately (within about

20–30 degrees error), previously experienced viewpoints and geometrically salient features distort map-like knowledge (McNamara et al., 2003). In one of many examples of this, participants in a highly familiar city pointed more accurately when oriented northward than when oriented in any other direction, presumably because they had encoded viewpoints of the city, in part, via a cartographic map (Frankenstein et al., 2012). This has led some to argue that we do not use location-specific information particularly well to estimate the position of objects in an environment and that we instead favor viewpoint and orientation dependent coding schemes over cognitive maps (Wang and Spelke, 2002). In fact, viewpoint updating can theoretically account for a range of our navigational abilities, including our ability to use shortcuts when navigating (Wang and Spelke, 2002; Ekstrom et al., 2014). Thus, view information, rather than absolute location, is likely a more critical determinant of how humans represent space.

CONCLUSION

The aforementioned discussion stresses a critical piece of the navigational code that we often neglect when we focus on rodent place cells: the importance of visual coding mechanisms to human spatial navigation. Although, like rats, we employ both path integration and visual-based strategies when navigating, high-resolution visuospatial representations are a more prominent component of how we represent space than rodents. Consistent with this idea, in contrast to the rodent, hippocampal lesions in humans result in inconsistent effects on navigation (for a review and in depth discussion, please see: Ekstrom et al., 2014). This is further consistent with the greater involvement of visually-responsive brain areas like parahippocampal and retrosplenial cortex in human spatial navigation. Thus, while place cells represent an extremely important piece of a larger puzzle involved in navigation, much remains to be learned about how high-resolution visually-based representations relate to location coding systems in humans.

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