Spatial Knowledge and Navigation

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Abstract

Spatial knowledge is knowledge about where things are in the world and how they are spatially related to each other. One important use of spatial knowledge is to guide navigation from place to place. To accomplish this function, the brain must represent navigationally relevant aspects of the local environment, such as landmarks, scene geometry, and local navigational affordances. It must also form representations of the space beyond the current sensory horizon, which might take the form of a cognitive map or graph. Research to date indicates that representations of the local environmental are supported primarily by scene-responsive regions in higher visual cortex, such as the parahippocampal place area (PPA), occipital place area (OPA), and retrosplenial complex (RSC). Global spatial representations, on the other hand, are supported primarily by the hippocampal formation and the RSC. A key challenge for the field, which this chapter attempts to address, is to understand how the spatial knowledge representations revealed by cognitive behavioral studies are mediated by neural systems.

Main Text

Space, for a navigator, is structured by both the body and the environment. The body is a point that is distinct from all other points. The body faces a specific direction (its *heading*), which determines which way the organism can move without turning and what it can see. Only the immediate environment (*vista space*) can be sensed; the world beyond the sensory horizon (*environmental space*) must be traveled to or recalled from memory (Montello, 1993). Perception and movement are constrained by barriers and facilitated by openings, passageways, and paths. Some objects in the world are stable and thus likely to maintain their location; others are movable and thus might appear in different locations. As these observations indicate, when considering how spatial knowledge is encoded in the mind/brain, it is essential to consider the spatial organization of the world, and how it might facilitate or hinder navigation.

Vista Space: Scenes and Landmarks

A navigating organism must be able to perceive and understand its immediate spatial surroundings (vista space). Of particular importance is the ability to perceive landmarks—items that have a reliable relationship to a location, direction, or point along a path. Landmarks can come in many forms. Some are discrete objects such as buildings, statues, traffic lights, and mailboxes. Others are more distributed entities, such as the arrangement of streets at an intersection, the shape of a room, or the topography of a landscape. Indeed, in many cases the surroundings as a whole (the "local scene") act as a kind of landmark.

Psychological research suggests that several qualities make some items more useful as landmarks than others (Burnett, Smith, & May, 2001; Jansen-Osmann, 2002; Janzen, 2006). First, good landmarks are perceptually salient: they are easy to perceive and easy to distinguish from other landmarks. Second, good landmarks are stable: they are reliably associated with certain locations or bearings. Third, good landmarks are located in navigationally relevant places—for example, an intersection or other decision point. Consider, for example, a church on a town square: this is an ideal landmark because it is distinctive and visible, always in the same location, and in the center of the road network of the town.

Objects that have landmark-suitable qualities appear to hold a special status in the cognitive system of animals and humans. Consider stability. Rats will use an object that is fixed in space as a reference from which to encode the distance and direction to a goal, but they will not use an equivalent object that is not fixed (Biegler & Morris, 1993). Spatial position also has an effect on whether objects are encoded as landmarks. Janzen (2006) asked participants to learn a path through a virtual reality environment. Objects were placed in various locations along the path. After training, participants were presented with the same objects in isolation, intermixed with foils, and asked to report whether each item was familiar or not. Reaction times were faster for objects that had been at navigational decision points than for objects that had been at other locations along the path. This suggests that the decision point objects had obtained a special status in memory.

An especially salient and stable aspect of the perceptible environment is the geometric layout of a local space—for example, the shape of a room or the arrangement of streets at an intersection. A prominent line of research suggests that this geometric information might play a special role in spatial orientation (Cheng, 1986). When rats are trained to dig for a buried food reward in one location in a rectangular chamber and then removed from the chamber, disoriented, and placed back in the chamber, they will search for the reward in either the correct location or the diagonally opposite location. This behavior is notable because these two locations are equivalent in terms of the geometric shape of the chamber. Geometric errors are observed even in chambers that include visual markings on the walls or corners that could, in theory, disambiguate the two conflated locations. Thus, the animals appear to preferentially use the geometry of the chamber to reorient themselves. These results spawned the idea—much debated—that reorientation is mediated by a *geometric module* that is impenetrable to nongeometric cues (see Cheng, Huttenlocher, & Newcombe, 2013). In any case, several lines of evidence suggest that

environmental boundaries act as important references for spatial memory (Hartley, Trinkler, & Burgess, 2004; Lee, 2017).

Another important navigational cue is the overall visual appearance of the local scene, which is determined not only by geometric but also by nongeometric features, such as color, texture, and the spatial distribution of visual features. Insects use this kind of raw visual information to identify specific locations (Collett, Chittka, & Collett, 2013), and humans have the ability to use a similar strategy (Gillner, Weiss, & Mallot, 2008). Notably, this viewpoint-dependent "snapshot" appears to differ from representations of the spatial structure of the local environment, with visual appearance used primarily for place recognition and geometry used primarily for spatial orientation (Burgess, Spiers, & Paleologou, 2004; Valiquette & McNamara, 2007; Waller & Hodgson, 2006). Consistent with this idea, in a recent study we found that disoriented rodents use nongeometric visual cues, such as a visual pattern along a wall, to identify their overall navigational context (i.e., the experimental chamber they are in) while using local geometry to recover their heading direction within this context (Julian, Keinath, Muzzio, & Epstein, 2015). This suggests the existence of a mechanism for appearance-based place recognition that is behaviorally dissociable from the mechanism for geometry-based reorientation.

Scenes and Landmarks in the Brain

fMRI studies have identified three brain regions that exhibit greater response when subjects view scenes (landscapes, street scenes, rooms, or buildings) than when they view other meaningful visual stimuli, such as artifacts, animals, vehicles, bodies, or faces: the parahippocampal place area (PPA), the retrosplenial complex (RSC), and the occipital place area (OPA; Epstein, 2014). The PPA encodes multiple aspects of the scene that might be useful for identifying it as a particular place or category of place, including the spatial expanse of the scene (Kravitz, Peng, & Baker, 2011; Park, Brady, Greene, & Oliva, 2011), the individual objects within it (Harel, Kravitz, & Baker, 2013), and the global scene structure (Walther, Chai, Caddigan, Beck, & Fei-Fei, 2011). The RSC shows similar responses but, additionally, codes explicitly spatial quantities such as the implied heading and location of the observer relative to both local scene geometry (Marchette, Vass, Ryan, & Epstein, 2014) and the wider environment (Baumann & Mattingley, 2010; Shine, Valdés-Herrera, Hegarty, & Wolbers, 2016; Vass & Epstein, 2013). Damage to the PPA leads to a deficit in recognizing scenes and landmarks—a syndrome that has been labeled *landmark agnosia*—while damage to the RSC leads to a deficit in the ability to use scenes and landmarks to recover one's heading and orient oneself in space (Aguirre & D'Esposito, 1999).

The OPA may process visual features that are essential for both scene/landmark recognition and spatial perception. When processing in the OPA is disrupted by transcranial magnetic stimulation (TMS), impairments are observed in the ability to visually categorize scenes (Ganaden, Mullin, & Steeves, 2013), discriminate scenes based on their spatial layout (Dilks, Julian, Paunov, & Kanwisher, 2013), and perceive environmental boundaries in scenes (Julian, Ryan, Hamilton, & Epstein, 2016). Complementing this TMS work, a recent fMRI study from our

lab suggests that the *navigational affordances* of the local environment might be processed in the OPA (Bonner & Epstein, 2017). Participants in the study viewed artificial rooms or natural scenes, which varied in terms of the direction that one could move to egress the scene. For example, one scene might depict a room with a door on the left wall, while another might depict a room with a door on the right wall. Multivoxel activation patterns within the OPA contained information about these navigational affordances, even when other visual and spatial features of the scenes were strictly controlled. Navigational affordances and environmental boundaries are complementary aspects of the spatial structure of scenes: affordances are where one can go in the local environment, and boundaries are where one's movement is blocked.

Beyond their role in processing scenes, several studies suggest that the PPA, RSC, and OPA may play a broader role in processing landmarks, including object-like landmarks. These regions respond more strongly to objects if they have intrinsic qualities that would make them more useful as landmarks (Troiani, Stigliani, Smith, & Epstein, 2014), such as being large and stable (Auger, Mullally, & Maguire, 2012; Konkle & Oliva, 2012) or distant from the viewer (Amit, Mehoudar, Trope, & Yovel, 2012). This preference for large, stable objects is even observed in blind participants making size judgments in response to auditory cues (He et al., 2013). There is also evidence for a neural correlate of the decision point effect, in the form of greater response to decision point objects compared to non–decision point objects, when they are viewed in isolation outside of the navigational context (Janzen & van Turennout, 2004). Multivoxel codes in the PPA, RSC, and OPA contain information about landmarks that generalizes across different views (Marchette, Vass, Ryan, & Epstein, 2015), and all three regions respond during the retrieval of information about specific familiar landmarks even when no picture of the landmark is provided (Fairhall, Anzellotti, Ubaldi, & Caramazza, 2013). Taken as a whole, these results suggest that the PPA, RSC, and OPA may play a role in the processing of landmarks that goes beyond mere visual perception.

Environmental Space: Cognitive Maps and Structured Representations

I now turn to a discussion of environmental space—the space that one can locomote to, typically extending beyond the current sensory horizon. Essential to any discussion of this topic is the concept of a cognitive map. This idea was first proposed by Tolman (1948) to account for aspects of the navigational behaviors of rats that could not be easily explained by behaviorist theories. Tolman observed, for example, that when animals were faced with a situation in which a familiar (but roundabout) path to a goal was blocked, they would often choose an alternative strategy of moving directly toward the goal. Such findings indicated that the animals must have some kind of internal representation of space—akin to a map—that could be flexibly used to guide behavior.

In a later formulation, which has become the "classic" view, O'Keefe and Nadel (1978) argued that the cognitive map is a Euclidean representation of navigational space—that is, a representation of space in terms of spatial coordinates. It is clear, however, that cognitive maps must be more complex than a single sheet of mental graph paper. At a minimum, an organism

would need separate maps for different environments: it is highly unlikely that my cognitive map of Philadelphia picks up uninterrupted when I get off the plane in San Francisco. Even within the same city or campus, environmental spatial knowledge is structured in multiple ways. As a qualitative illustration of this, Lynch (1960) asked people to describe their experiences of their home cities (figure 69.1). From these accounts he identified five elements that made up their "image" of the city, including paths (streets, highways, bridges), edges (linear boundaries such as a riverbank), districts (regions with geographical and conceptual cohesion), nodes (strategic foci, often junctions of paths), and landmarks. Clearly, their mental map of the environment was more than just a collection of labeled coordinates.

Results from human psychological experiments support the idea that spatial knowledge is structured. Environmental spaces are often represented in a hierarchical manner, with locations grouped together into clusters or regions (Hirtle & Jonides, 1985; McNamara, Hardy, & Hirtle, 1989). For example, Wiener and Mallot (2003) taught subjects a virtual maze containing several objects that were grouped into regions based on conceptual similarity between the objects (e.g., all objects in one region were cars). When asked to navigate through this environment, participants chose paths that minimized the number of regions they had to pass through, even when an equivalent path had the same physical distance. The existence of hierarchical and regional structure may account for long-standing observations that spatial knowledge is distorted relative to metric truth, as evidenced by the fact that people make systematic errors in their estimates of distances and directions between locations (Tversky, 1993).

Relevant to this discussion of spatial structure is the notion of a spatial reference frame. To define coordinates, one must have reference axes. Much of what we know about how these axes are coded comes from studies using the judgment of relative direction (JRD) task. Participants in these experiments first learn an environment containing several objects. Later, after being removed from the environment, they are asked to imagine they are standing at one object while facing a second; from that imagined position and heading they are asked to indicate the remembered bearing to a third object. A consistent result from these experiments is that performance is orientation-dependent; that is, accuracy varies as a function of imagined facing direction (McNamara, Sluzenski, & Rump, 2008). The preferred direction is often aligned with the geometric shape of the environment or with the direction the subject was facing when first entering the environment (Shelton & McNamara, 2001). These results suggest that we assign spatial axes to environments when we first encounter them, which are used to lay down spatial memories. Memory retrieval is more accurate for imagined headings that are aligned rather than misaligned to these spatial axes.

This brings up an important question: If spatial knowledge is hierarchical, what is the relationship between the local reference frame (perhaps encompassing vista space but perhaps extending beyond it) and the groups or regions that constitute the higher level of the hierarchy? One possibility is that local reference frames are connected to each other by stored vectors to make a "network of reference frames" akin to a graph (Meilinger, 2008). Indeed, the idea that spatial knowledge is organized like a graph is one that recurs throughout the literature (Poucet, 1993;

Trullier, Wiener, Berthoz, & Meyer, 1997; Warren, Rothman, Schnapp, & Ericson, 2017). Another possibility—not mutually exclusive—is that each local reference frame is a separate "map," which can be retrieved by a separate context recognition mechanism (Julian et al., 2015; Marchette, Ryan, & Epstein, 2017). We consider both of these possibilities in the next section.

Neural Systems for Representing Environmental Space

Some of the strongest evidence for the existence of a cognitive map comes from neuroscience. O'Keefe and Dostrovsky (1971) were the first to report the existence of neurons in the rodent hippocampus that fire when the animal is in specific locations in the world. O'Keefe and Nadel (1978) hypothesized that these *place cells* were the neural instantiation of the cognitive map. Extensive work over the past few decades has fleshed out this picture by showing that place cells are complemented by other classes of spatial cells in the hippocampal formation and related structures that support a neural mechanism for cognitive map-based navigation (Hartley, Lever, Burgess, & O'Keefe, 2014). These include grid cells (which provide a distance metric for the cognitive map), head direction cells (which provide a measure of the animal's orientation), and border/boundary cells (which allow cognitive maps to be anchored to environmental boundaries). Although initially identified in rodents, similar cells have since been found in humans (Ekstrom et al., 2003; Jacobs et al., 2013).

Neuroimaging studies support the idea that the hippocampus and entorhinal cortex play an important role in mediating a cognitive map in humans (see Epstein, Patai, Julian, & Spiers, 2017 for a review). Distances between locations—a key feature of a metric map—are reflected in fMRI adaptation effects (Morgan, Macevoy, Aguirre, & Epstein, 2011) and dissimilarities between multivoxel activation patterns (Deuker, Bellmund, Schröder, & Doeller, 2016; Nielson, Smith, Sreekumar, Dennis, & Sederberg, 2015). Moreover, the size of the right posterior hippocampus predicts participants' abilities to form allocentric representations of the environment (Hartley & Harlow, 2012; Schinazi, Nardi, Newcombe, Shipley, & Epstein, 2013), and this structure increases in volume in London taxi drivers as they acquire "the knowledge" of city streets and landmarks (Woollett & Maguire, 2011). These findings from humans indicate that the hippocampus is involved in memory for large-scale, real-world environmental spaces, not just the small-scale, single-chamber spaces commonly used in rodent-recording experiments.

Neuropsychological studies indicate that spatial memories for premorbidly learned environments are not obliterated by hippocampal damage (Teng & Squire, 1999), though they do become less detailed (Rosenbaum et al., 2000) and more schematic (Maguire, Nannery, & Spiers, 2006). This suggests that neocortical structures may also play a role in mediating environmental spatial knowledge. The retrosplenial/medial parietal region encompassing the RSC may be especially important for this function. This region is highly active in fMRI studies when spatial knowledge is retrieved (Epstein, Parker, & Feiler, 2007; Rosenbaum, Ziegler, Wincour, Grady, & Moscovitch, 2004). Moreover, fMRI activity in this region correlates with the amount of survey knowledge that a navigator has acquired about the environment (Wolbers & Buchel, 2005), and

the number of spatially responsive cells in rodent retrosplenial cortex increases as an environment becomes more familiar (Smith, Barredo, & Mizumori, 2012).

But what kind of knowledge is encoded in the hippocampal formation and the RSC? As I noted above, we have many cognitive maps, not just one, and individual cognitive maps might be hierarchical or fragmented. The well-established phenomenon of remapping is likely to be the mechanism by which multiple maps are supported by the hippocampal-entorhinal system (Colgin, Moser, & Moser, 2008). Within any given environment, about a quarter of the hippocampal place cells exhibit place fields, while the remainder are quiescent. When an animal changes its environment—for example, if it is moved from an experimental chamber in one room to a different experimental chamber in another room—the set of active versus quiescent cells changes in an unpredictable manner, and even cells that are active in both environments change their firing locations relative to each other dramatically. Thus, the rodent hippocampal formation appears to have mechanisms for representing multiple maps as distinct pages within a larger "cognitive atlas."

What about hierarchical or fragmented structure within a map? The majority of neurophysiological recording studies are performed in open field environments. Thus, it is not surprising that the responses in these environments—for example, the regular tessellation of grid fields—reflects something that looks very much like a Euclidean map. However, when the environment becomes more structured, the place and grid representations become structured as well (figure 69.2*A*). For example, when an open field is divided by barriers into smaller subchambers, grid fields are observed to reflect the geometry of each subchamber, resetting their phase as the animal moves from one subchamber to another, rather than representing the environment as a whole (Derdikman et al., 2009). A similar effect of field repetition has been observed in hippocampal place cells (Spiers, Hayman, Jovalekic, Marozzi, & Jeffery, 2013) . In related fMRI studies in humans, the RSC exhibits repeated use of the same spatial schema across geometrically similar subchambers (Marchette et al., 2014; figure 69.2*B*).

Beyond compartmentalization, two recent studies provide some evidence for the coding of graph-like structure when rats navigate through mazes consisting of constrained paths. In one study the animals navigated in the dark through a maze consisting of 10 path segments, which were connected flexibly to each other so that the angle between them could be varied (Dabaghian, Brandt, & Frank, 2014). Hippocampal place fields reflected the animal's position relative to the topography of the path rather than its position in Euclidean space. In another study, rats were trained to run paths through a maze consisting of three arms connected at a central choice point (Wu & Foster, 2014). When the animals rested at the end of the arms, "replay" activity was observed during sharp-wave-ripple events. Notably, these replay sequences reflected the connectivity structure of the maze, with the direction of replay reversing at the choice point. In humans, activity in the hippocampus has been observed to reflect both Euclidean measures of space (e.g., the total size of the space or the Euclidean distance to a destination) and graph-like measures of space (e.g., the complexity of the space, the path distance to a destination, the global connectivity; Baumann & Mattingley, 2013; Howard et al., 2014; Javadi et al., 2017). Evidence

for the graph-like coding of space has also been observed in rodent retrosplenial cortex (Alexander & Nitz, 2017) and human RSC (Schinazi & Epstein, 2010).

Conclusion

Although there is now a burgeoning cognitive neuroscience literature on spatial navigation, the knowledge structures that underlie navigation are relatively unexplored. As with any topic in cognitive neuroscience, spatial knowledge can be studied in terms of the cognitive representations that underlie it and the neural systems that support it. Until recently, these investigations have largely been the province of different fields: cognitive psychologists and animal behavior researchers on the one hand; neuroimagers and electrophysiologists on the other. In this chapter I have made a preliminary attempt to link these two literatures, but the field is ripe for further exploration.

Acknowledgment

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Figure Legends

Figure 69.1 A cognitive map of Boston, Massachusetts, containing many structural elements (paths, edges, nodes, districts, and landmarks). Compiled by Lynch (1960) from resident reports.

Figure 69.2 Spatial representations in structured environments. *A*, Grid cells code a regular triangular grid in open environments, but this pattern fragments into repetitive local fields when the environment is segmented into smaller subchambers (*white lines indicate walls*). A similar effect of pattern fragmentation is observed in hippocampal place cells. *B*, In a multichamber environment, RSC represents local geometric organization. Participants imagined facing an object along the wall at each location indicated by a circle. Colors and numbers indicate the similarity of multivoxel patterns for each view compared to the reference view (*red circle*). There is a high degree of similarity between views facing "local north" (i.e., away from the entrance) in different subchambers. (See color plate 82.)