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Running Head: Representing Space for Navigation

Human Spatial Representation:

What We Cannot Learn from the Studies of Rodent Navigation

Mintao Zhao

[1] School of Psychology, University of East Anglia, Norwich, UK

[2] Department of Human Perception, Cognition, and Action, Max Planck Institute for Biological Cybernetics, Tübingen, Germany

Please address correspondence to Mintao Zhao, School of Psychology, University of East Anglia, Norwich NR4 7TJ, UK; E-mail: mintao.zhao@uea.ac.uk.

Abstract

Studies of human and rodent navigation often reveal a remarkable cross-species similarity between the cognitive and neural mechanisms of navigation. Such cross-species resemblance often overshadows some critical differences between how humans and nonhuman animals navigate. In this review, I propose that a navigation system requires both a storage system (i.e., representing spatial information) and a positioning system (i.e., sensing spatial information) to operate. I then argue that the way humans represent spatial information is different from that inferred from the cellular activity observed during rodent navigation. Such difference spans the whole hierarchy of spatial representation, from representing the structure of an environment to the representation of sub-regions of an environment, routes and paths, and the distance and direction relative to a goal location. These cross-species inconsistencies suggest that what we learned from rodent navigation does not always transfer to human navigation. Finally, I argue for closing the loop for the dominant, unidirectional animal-to-human approach in navigation research, so that insights from behavioral studies of human navigation may also flow back to shed light on the cellular mechanisms of navigation for both humans and other mammals (i.e., a human-to-animal approach).

Keywords: navigation, spatial representation, path integration, grid cell, place cell

1. Introduction

Since Tolman's (1948) original concept of a "cognitive map", research on nonhuman animal navigation has long inspired studies of how the human navigation system functions (Lee, 2017; Wang & Spelke, 2002). This *animal-to-human* approach has revealed remarkable similarities between human and nonhuman animal navigation. Specifically, humans and nonhuman animals share the way they form a cognitive map (Ekstrom et al., 2003; Gallistel, 1990; McNaughton, Battaglia, Jensen, Moser, & Moser, 2006; O'Keefe & Nadel, 1978; Shine, Valdés-Herrera, Hegarty, & Wolbers, 2016; Wang, 2016), reorient using the geometric structure of an environment (Cheng, 1986; Cheng & Newcombe, 2005; Hermer & Spelke, 1996; Lee, 2017; Lee & Spelke, 2010), code the sense of direction in the brain (Ekstrom et al., 2003; Jacobs, Kahana, Ekstrom, Mollison, & Fried, 2010; Taube, 2007; Taube, Muller, & Ranck, 1990), represent environmental boundaries (Barry et al., 2006; Julian, Ryan, Hamilton, & Epstein, 2016; Lee, 2017; Solstad, Boccara, Kropff, Moser, & Moser, 2008), and map a navigable space with a grid-like representation (Chen, He, Kelly, Fiete, & McNamara, 2015; Hafting, Fyhn, Molden, Moser, & Moser, 2005; Horner, Bisby, Zotow, Bush, & Burgess, 2016; Jacobs et al., 2013). While such cross-species resemblance underscores the evolutional continuity of neural systems supporting navigation, it also makes us overlook some crucial differences between human and nonhuman animal navigation. It tends to foster an over-optimistic, sometimes illusory, view that the properties of cellular network(s) underlying rodent navigation will effectively predict how humans navigate.

Electrophysiological findings of rodent navigation have often been generalized to human navigation as foundational principles. Such cross-species generalization, however, should be made with caution. To make a cross-species comparison, we need to understand how neural activity is translated into navigation behavior and vice versa. Nonetheless, it remains unsettled how firing properties of cellular networks in the rodent brain are *actually* transformed into navigation behavior and how human navigation behavior can be causally attributed to brain activity (Ekstrom, Huffman, & Starrett, 2017; Geva-Sagiv, Las, Yovel, & Ulanovsky, 2015; Rowland, Roudi, Moser, & Moser, 2016; Spiers & Barry, 2015; Wolbers & Wiener, 2014). The cross-species generalization becomes challenging when we take the substantial differences between human and rodent navigation into consideration. For instance, the rodent visual system is extremely poor and less complex on numerous levels compared to that of humans, necessitating that the navigational system must function in a substantially different manner in humans and rodents (see Ekstrom, 2015, for an elegant review on why vision is important for human navigation). Different methodologies used to investigate human and rodent navigation also make cross-species comparisons difficult. Besides, humans and rodents live and navigate in spaces that are different in nature and scale (e.g., structured vs. wild); they learn space differently (e.g., indirect map learning vs. direct exploration); and they communicate about space differently (e.g., with or without the use of language).

To set a tangible way to contrast navigational mechanisms across different species, I borrowed Marr's (1982) influential framework to categorize navigation research into three levels: *computational*, *algorithmic*, and *implementational*. At the computational or functional level, researchers investigate the principles of how a navigation system works. For instance, to address what makes homing possible after a complicated outbound journey, one can propose a view-based system (by zeroing the difference between current view and stored home view), a self-motion-based path integration system (by zeroing direction and distance of a homing vector that connects current position and home), or any other mechanisms as long as they enable navigators to return home. At the algorithmic or representational level, researchers study what kinds of spatial information support navigation and how they do this. Following the above example, if a path integration system is proposed to support homing, one needs to address how the path integration system encodes information about the outbound path to enable successful homing (e.g., does it continually update a homing vector or does it store the path trajectory and then compute the homing vector only when needed?). Finally, at the implementational or neurophysiological level, researchers aim to reveal how the mind and brain build up spatial representations and make navigational decisions. Continuing with the previous example, to unravel how path integration supports homing, one needs to elucidate how the brain senses a navigator's current location and orientation relative to the immediate surrounding, and how the brain tracks goal locations that may lie out of sight (e.g., McNaughton et al., 2006; Wolbers, Hegarty, Buchel, & Loomis, 2008).

This framework allows the electrophysiological studies of rodent navigation and the behavioral research on human navigation to communicate using the same language: spatial representation (i.e., at the algorithmic level). Studies of rodent navigation aim to identify the firing properties of neurons that are sensitive to orientation, location, distance, speed, and the border of an environment (i.e., at the implementational level). However, to elucidate how a navigation system works, the information sensed by these neurons needs to be translated into a spatial representation, such as representation of homing vector, local space, home view, self-position, and so on (Acharya, Aghajan, Vuong, Moore, & Mehta, 2016; Bush, Barry, Manson, & Burgess, 2015). Merely knowing that Place and the Heading Direction cells are sensitive to the orientation of landmarks is insufficient to explain why rats often home towards a misplaced landmark (e.g., Shettleworth, & Sutton, 2005). To form a theoretical account of such “visual capture”, we often rely on the spatial representations inferred from neural activity rather than the neural activity per se. (e.g., a view-matching hypothesis or a resetting hypothesis, Valerio & Taube, 2012).

Similarly, to pinpoint what underlies human navigation behavior (e.g., how we take a detour when a familiar route is blocked), the functional principles of our navigation system also need to be decomposed into cognitive or neural representations (e.g., goals, routes, the structure of explored environment, etc.; Chrastil & Warren, 2015; Ekstrom, & Isham, 2017; McNamara, Rump, & Werner, 2003; Viard, Doeller, Hartley, Bird, & Burgess, 2011). By translating both neural firing and navigation behavior into spatial representations and their computations, we may bridge the gap between the functional-level analysis of human navigation behavior and the implementational-level analysis of rodent brain activity during navigation. This translation process, as suggested by Ekstrom et al. (2017), may involve non-obvious neural coding schemes like those emerged in the hidden layers of neural networks.

This review focuses on how spatial information is represented in memory, in particular, how spatial representations inferred from the behavioral characteristics of human navigation are *different* from those suggested by the firing properties of cells in rodents’ brain. I argue that a navigation system requires a storage system (i.e., spatial representation) in addition to a positioning system (i.e., spatial perception) in order to operate (Section 2). Then I review the fundamental differences between spatial representation revealed by cellular activity recorded in rodent brain and spatial representation informed by human navigation behavior. I argue that the difference spans the whole hierarchy of spatial representation; representation of environmental structure (Section 3), representation of sub-regions of an environment (Section 4), representation of paths and routes (Section 5), and representation of distance, direction, and location (Section 6). Finally, the review highlights that behavioral research on human navigation may also shed light on the cellular mechanism of mammal navigation (Section 7).

2. A Positioning System versus a Navigation System

Electrophysiological studies of rodent navigation have revealed an inner positioning system in the brain (for recent reviews, see Grieves & Jeffery, 2017; Moser, Kropff, & Moser, 2008; Moser et al., 2014; Rowland et al., 2016; Taube, 2007; Cullen & Taube, 2017). This neural positioning system consists of different types of cells that are sensitive to various aspects of spatial information, such as location (i.e., place cells, O'Keefe & Dostrovsky,1971; O'Keefe & Nadel, 1978), orientation (i.e., Heading Direction cells, Ranck, 1984; Taube et al., 1990a, 1990b; see also Jacobs et al., 2017; Olson, Tongprasearth, & Nitz, 2017), distance and scale of space (i.e., grid cells, Hafting et al., 2005; Kjelstrup et al., 2008; Sargolini et al., 2006), velocity of movement (i.e., speed cells, McNaughton, Barnes, & O'Keefe, 1983; Hinman, Brandon, Climer, Chapman, & Hasselmo, 2016; Kropff, Carmichael, Moser, & Moser, 2015), and spatial boundary (i.e., border cells, Solstad et al., 2008; or boundary vector cells, Barry et al., 2006). A similar neural positioning system has also been found in the human brain (Ekstrom et al., 2003; Jacobs et al., 2013; see also Doeller, Barry, & Burgess, 2010, for indirect evidence from an fMRI study). In theory, these cells could serve as a cellular odometer and a neural compass, allowing a navigator to localize oneself within the immediate environment, remain orientated, and reach a goal (Barry & Burgess, 2014; Epstein, Patai, Julian, & Spiers, 2017; Valerio & Taube, 2012).

However, a positioning system that merely specifies one's *current* location and orientation cannot completely support navigation—getting from *here* to *there (*see also Geva-Sagiv et al., 2015; Rowland et al., 2016; Wang, 2016). A functioning navigation system requires both a "compass" (i.e., an orienting and positioning system) and a "map" (i.e., a storage system), so that it can denote both "here" and "there" as well as specify the way to get there from here. The "map" could store all learned spatial information in a globally coherent way (i.e., a cognitive map or survey knowledge). It could also be a graph-node representation of all traveled routes and visited places without them being knitted together consistently (i.e., route knowledge; Chrastil, 2013; Siegel & White, 1975). It may also be a collection of stimulus-response associations based on visual, odor, or geomagnetic senses (Frost & Mouritsen, 2006). The "map" can be internal (e.g., spatial memory), external (e.g., navigational aid), or a mixture of both. Without such a storage component in a navigation system, a rat would be unable to find an unseen feeding site it visited before, and a bird could not migrate thousands of kilometers to the same place year after year (except following a leader). Thus, to unravel how a navigation system works, we need to understand not only how and what kind of spatial information is *sensed*, but also how and what kind of sensed information is *stored*.

A sensing-and-storage system for navigation has many advantages over a positioning system alone. With both sensing and storage components, a navigation system can fulfill the three elementary functions of navigation: self-localization and reorientation, goal monitoring, and path planning. The sensing component can support the spatial perception that is occurring now and mostly within the immediate visual boundary, whereas the storage component can extend it temporally to the past/future and spatially beyond the visible boundary (e.g., Byrne, Becker, & Burgess, 2007). A storage component also allows a navigation system to build up high-order spatial knowledge, such as the sequence of visited places, the connection and relationship between walked trajectories, the topographical network of learned paths and areas, or even the geometric structure of a known environment. Such spatial knowledge enables a navigation system to guide complex navigation behavior (e.g., to take a detour or a shortcut). This sensing-and-storage system for navigation is consistent with the intertwining role of the hippocampus in spatial cognition and episodic memory (Burgess, Maguire, & O'Keefe, 2002; Eichenbaum, 2000, 2017b; Eichenbaum & Cohen, 2014; Ekstrom & Ranganath, 2017; Howard, Fotedar, Datey, & Hasselmo, 2005; Knierim, 2015; Miller et al., 2013; Olton, Becker, & Handelmann, 1979). It is also in line with the primary approach used to implement an artificial navigation system (e.g., Llofriu et al., 2015; Milford, 2008; Milford & Schulz, 2014; Thrun, 2008).

A sensing-and-storage system also helps address the challenging questions a positioning system faces. For instance, a positioning system that continuously tracks location and orientation is computationally expensive and error-prone, whereas a sensing-and-storage system is not. The storage component would allow insects and rodents to use visual memory to navigate without continuously monitoring self-motion and orientation (Collett, 2010; Schwarz, Mangan, Zeil, Webb, & Wystrach, 2017; Shettleworth, & Sutton, 2005; Sturzl, Zeil, Boeddeker, & Hemmi, 2016; Valerio & Taube, 2012). Note that a complete reliance on visual memory for navigation would be less resilient against environmental perturbations than a continuous tracking system. Another challenge is how a positioning system maps a large-scale space. It has been shown that place and grid cells along the dorsal-ventral axis of the hippocampus and the medial entorhinal cortex (MEC) are sensitive to the scale of space (Brun et al., 2008; Hafting et al., 2005; Kjelstrup et al., 2008). However, how these cells map large-scale environments remains to be elucidated (Geva-Sagiv et al., 2015; Mouritsen, Heyers, & Gunturkun, 2016; see also). Sensing and mapping the space around hundreds to thousands of kilometers is even more challenging (e.g., long-distance migration of birds or sea turtles; Lohmann, Hester, & Lohmann, 1999; Mouritsen et al., 2016; Vardanis, Klaassen, Strandberg, & Alerstam, 2011). By enabling various navigation strategies (e.g., memory of a series of navigational decisions and actions along the journey), a storage component can make such continuous mapping unnecessary for long-distance navigation in insects (Menzel & Greggers, 2015; Sturzl et al., 2016), birds (Mouritsen et al., 2016), and mammals (Tsoar et al., 2011).

While human navigation studies have long investigated how spatial information is stored in memory, research on rodent navigation often focuses on the mechanistic system of how spatial information is sensed by a positioning system (Eichenbaum, 2017b; Epstein, Patai, Julian, & Spiers, 2017; McNamara, 1986; Siegel & White, 1975). These two lines of research seem to paint different pictures about the way the sensed spatial information is represented in memory. In the following sections, I review different hypotheses about how humans and rodents may represent the structure of an environment, sub-regions of an environment, traversed routes, and distance and direction.

3 Representation of an Environment: Metrical or Topological?

How are the geometrical properties of an environment stored in memory? One prevailing hypothesis postulates that spatial information about an environment is represented in a metric way (McNaughton et al., 2006; Moser & Moser, 2008; Rowland et al., 2016). Both the original concept of a "cognitive map" and the recent discovery of grid cells suggest a metric representation of environmental space, in which the Euclidean distance and angle between places are specified with a globally consistent coordinate system. An alternative hypothesis proposes that environmental space is represented in a topological manner (Chrastil & Warren, 2014b; Dabaghian, Brandt, & Frank, 2014; Ekstrom et al., 2017; Ekstrom & Ranganath, 2017; Muller, Stead, & Pach, 1996; Montello, 1998; Remolina & Kuipers, 2004). Like a subway map, a topological representation registers an environmental space as a network of nodes (i.e., unique places) and edges (i.e., paths connecting nodes). It stores the topological relations between places, such as continuity and connectivity, but does not necessarily maintain veridical metric information in a globally consistent way.

Arguments for a metric cognitive map are based primarily on two lines of findings. At the functional level, a variety of animal species can directly return to its nest (i.e., homing) after a complex outbound journey and can navigate between two places that have not been traversed before (Menzel & Greggers, 2015; Menzel et al., 2005; Collett & Collett, 2000; Mittelstaedt & Mittelstaedt, 1980; Tsoar et al., 2011). Ants, bees, pigeons, and bats all show this homing ability after being displaced to a new location that has no visual access to its nest (Cheeseman et al., 2014; Etienne & Jeffery, 2004; Gallistel, 1990). Such remarkable homing ability is consistent with Tolman's (1948) original view of a "comprehensive map" and with the theory of a "locale system" in a cognitive map (O'Keefe & Nadel, 1978). The near-perfect calculation of a homing direction indicates that the metric information of an environment is recorded in, and can be read out from, a “mental map” (e.g., McNaughton et al., 2006).

At the implementational level, the discovery of grid cells uncovers a potential neural metric for an environmental space, providing another support for a metric representation (Hafting et al., 2005; Kjelstrup et al., 2008; Sargolini et al., 2006; see also Doeller et al., 2010; Jacobs et al., 2013). The grid cells in the MEC show a spatially periodic firing pattern consisting of a hexagonal array (Hafting et al., 2005; Jacobs et al., 2013). Such spatially regular firing patterns tile the entire space available to the navigator (i.e., forming grids), thereby providing a universal and intrinsic neural metric for space. Furthermore, the grid cells situated along the dorsal-ventral axis of MEC tune to space of increasing scale. The further away the grid cells are located from the anatomical border of the dorsal MEC, the larger the size of the grids (Brun et al., 2008; Hafting et al., 2005; Kjelstrup et al., 2008). These findings strongly advocate the view that a mental map built with information sensed via grid cells is metric (Bush et al., 2015; McNaughton et al., 2006; Moser & Moser, 2008).

Nonetheless, none of the evidence that supports a metric spatial representation is conclusive. At the functional level, while a metric map entitles direct homing, the direct homing (or the ability to take a shortcut) does not necessarily prove a metric representation (Gallistel, 1990). Navigation behavior that is consistent with a metric representation can be achieved without actually storing a metric cognitive map (e.g., using guidance strategies based on familiar visual landmarks, Bennett, 1996; Cheung et al., 2014; Collett, Chittka, & Collett, 2013; Srinivasan, 2015). Non-metric spatial representation also allows for homing or taking a shortcut. For instance, a topological representation with local metric information (i.e., a labeled graph) also enables a navigator to take a shortcut or a detour, despite the potential for local metric information to be noisy and geometrically inconsistent (Babichev, Cheng, & Dabaghian, 2016; Chrastil & Warren, 2014b, 2015; Ekstrom, Arnold, & Iaria, 2014; Remolina & Kuipers, 2004).

At the implementation level, the firing pattern of grid cells is modulated by the geometry, novelty, and visual accessibility of an environment, which undermines its role as a universal, environment-independent metric of space (Figure 1; Barry, Ginzberg, O'Keefe, & Burgess, 2012; Barry, Hayman, Burgess, & Jeffery, 2007; Chen, Manson, Cacucci, & Wills, 2016; Krupic, Bauza, Burton, Barry, & O'Keefe, 2015; but see Carpenter & Barry, 2016). For instance, the same set of grid cells can yield different firing patterns for a square and a trapezoid environment (Krupic et al., 2015). The essential geometric properties of the grid pattern observed with a square environment —the orientation, scale, symmetry, and homogeneity of the hexagonal structure — were disrupted in a trapezoid environment (Figure 1A). When the visual input is blocked by exploring a familiar square environment in complete darkness, the firing pattern of grid cells is also significantly disrupted (Figure 1B Chen et al., 2016). The grid cells also showed expanded firing grids when exploring a novel environment in comparison with navigating in a familiar space (Figure 1C, Barry et al., 2012). Moreover, when a square environment was parametrically changed into a horizontal rectangle, a vertical rectangle, or a smaller square, the grid patterns stretched and shrank accordingly (Figure 1D, Barry et al., 2007). These findings indicate that the visual environment determines the firing pattern of grid cells. That is, the ruler and protractor used to measure the metrics of an environment vary with the environment it measures. Hence, grid cells may function as a neural metric for a *local* space at a given moment

(Carpenter & Barry, 2016; Rowland et al., 2016), but may not serve as a universal metric across different environments and the change of the same environment across time.

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How, then, is an environment represented in memory? An alternative possibility is that the locally metric but globally nonmetric spatial relations are stored with a topological representation, such as a cognitive graph (Chrastil & Warren, 2014b; Ekstrom et al., 2014; Muller, Stead, & Pach, 1996; Montello, 1998; Remolina & Kuipers, 2004). In a cognitive graph, places are represented as nodes and the path connecting places are represented as edges between nodes. In addition, approximate distance information between places can be represented as a label to the edges (i.e., edge weights), whereas angular relations between edges can be represented as a label to the node. Note that although this labeled graph metaphor still implies some form of metric representation, it does not have to (Babichev, et al., 2016; Ekstrom et al. 2014). More importantly, the approximate metric information labeled to the graph is only limited to the local space and does not necessarily require a global frame of reference (Chrastil & Warren, 2014b, 2015; Ekstrom et al. 2014; Remolina & Kuipers, 2004).

A *cognitive graph* representation is superior to a cognitive map representation in many aspects. Firstly, it is computationally economic and energetically less demanding. If a graph representation can approximate multiple spaces with small adjustments and heuristics, storing a representation for every traversed area will be unnecessary (see also Ekstrom et al. 2017). This addresses the concern of mapping large-scale space (Geva-Sagiv et al., 2015; Mouritsen, Heyers, & Gunturkun, 2016). Secondly, it incorporates imprecise and inconsistent geometric relations in the representation of both local space and the global environment (Friedman, 2009; Moar & Bower 1983; Tversky, 1981; for a review, see Ekstrom et al., 2014). Thirdly, it readily accounts for the influence of space stretching (which does not change topological geometry) and darkness (i.e., which may disrupt topological properties of spatial enclosure) on the firing of grid cells (Barry et al., 2007; Chen et al., 2016). Finally, it allows map-like guidance (e.g., taking a shortcut or detour) for both a biological and an artificial navigation system (Babichev, et al., 2016; Hübner & Mallot, 2007; Mair et al., 2014; Remolina & Kuipers, 2004).

The cognitive graph hypothesis gains support from studies of human navigation behavior (Chrastil & Warren, 2014b, 2015; Moar & Bower 1983; Warren, Rothman, Schnapp, & Ericson, 2017; Tversky, 1981; for reviews, see Ekstrom et al., 2014, 2017) and neural activity of hippocampal place cells (Dabaghian et al., 2014; OKeefe & Burgess, 1996). For instance, Warren et al. (2017) asked human participants to learn a virtual environment containing “wormholes”, which could covertly teleport participants from one place to another, thereby creating a non-Euclidean environment where the same place is situated in two different parts of the same environment. They found that spatial knowledge acquired in such an environment violates metric postulates (e.g., the path connecting three locations did not form a closed triangle; human participants went to entirely different places when aiming at the same goal location). However, the relative length and rough orientation between places were preserved in memory (see also Chrastil & Warren, 2014b). Consistent with this observation, Vass et al (2016) also found that human hippocampal low-frequency oscillations carry information about the teleported distance even without visual and idiothetic input. Dabaghian et al. (2014) demonstrated the topological encoding of space in the rodent brain. They used a morphable running track to dissociate geometric from topological properties of space and found that place cells represent the topological properties of a walking path (e.g., connectivity between places) more than the geometric properties (distances and angles).

4 Representation of Sub-regions of an Environment: Integrated or Separated?

Environmental spaces are often nested and consist of different sub-regions (e.g., different areas in a city, various buildings in an area; or different stories/rooms in a building). How does a navigation system stitch together the local maps of these separated compartments in memory? This question has been investigated by both behavioral studies of human navigation (Foo, Warren, Duchon, & Tarr, 2005; Han & Becker, 2014; Ishikawa & Montello, 2006; Meilinger, Strickrodt, & Bülthoff, 2016; Moeser, 1988; Wang & Brockmole, 2003a, 2003b; Zhang, Mou, McNamara, & Wang, 2014) and electrophysiological studies of rodent navigation (Alme et al., 2014; Derdikman et al., 2009; Spiers, Hayman, Jovalekic, Marozzi, & Jeffery, 2015; Wernle, Waaga, Morreaunet, Treves, Moser, & Moser, 2018). Both lines of research share the view that newly-learned environments are represented separately. However, they differ in whether the separated representations are integrated into a coherent global representation or not.

Recent studies of rodent navigation suggested that newly-learned compartmental space is represented separately. When a square-shape environment was fragmented into multiple hairpin-like compartments, the grid cells no longer showed a continuous grid representation of the entire environment. Instead, it showed repeated grid representations across different compartments with the same running direction (Derdikman et al., 2009). This finding demonstrates that the grid cells in the entorhinal cortex create independent local maps for individual local regions, even these regions are physically next to each other. The hippocampal place cells also show repeated firing at the same locations across alleys of the fragmented space (see also Grieves, Jenkins, et al., 2016; Spiers et al., 2015). Moreover, Alme et al. (2014) showed that hippocampal place cells could form independent maps for multiple local environments, even when these local environments share nearly identical geometrical properties of global space (i.e., rooms of same shape and size) and local space (i.e., square-shape recording arena). These results indicate that the development of a neural code for a newly learned environment does not substantially change the existing neural representation of a known place (see also Muller & Kubie, 1987; Wilson & McNaughton, 1993). Therefore, both the grid cells and the place cells initially form discrete representations for different compartments of an environment.

Humans also represent different regions of a newly learned space separately. When the space in a hall is fragmented into interconnected parallel corridors, human spatial memory is organized with a local coordinate system that is specific to the corridor (Meilinger et al., 2016, see also McNamara, 1986; McNamara et al., 2003). When the walls that formed the corridors were removed, the memory of the same space was represented within a global frame of reference. These findings show a remarkable resemblance to the fragmented grid-cell representation of compartmental space (Derdikman et al., 2009; Wernle et al., 2018). Kyle et al. (2015) demonstrated that the human hippocampal spatial code is also environment-specific, consistent with the view that local spaces are independently represented. Recently, Marchette, Vass, Ryan, and Epstein (2014) found that human retrosplenial cortex encodes self-location and orientation concerning a local space (i.e., different museums in a park) but not a global space (i.e., the park). Such location and orientation encoding can be generalized to other local spaces of the same geometry (i.e., repetitive across compartmental spaces). This finding mimics the repetitive hippocampal place cell maps for fragmented spaces of identical geometry in rodents (Derdikman et al., 2009; Grieves, Jenkins, et al., 2016; Spiers et al., 2015), indicating that newly learned regions of an environment are represented independently in human memory.

Are newly-learned compartments integrated into a unified and coherent environment in memory? The electrophysiological studies of rodent navigation suggest that the answer is yes (Figure 2). For instance, Carpenter, Manson, Jeffery, Burgess, and Barry (2015) showed that a prolonged experience with multi-compartment space leads the grid cells to form a unified and coherent global representation for the whole space. Similar to Derdikman et al. (2009), they found repetitive grid patterns for adjacent compartments during early recording sessions (Figure 2A-B, upper row). However, after two to three weeks of experience with the setting, the firing pattern of grid cells transitioned from representing individual local compartments to representing the whole space, tiling over the two adjacent compartments without a discontinuity (Figure 2A-B, lower row). Recently, Wernle et al. (2018) found that the merging of two local grid maps into a coherent one occurs almost immediately when the wall that separates two adjacent compartments was removed (Figure 2C). They showed that individual grid fields nearby the location of the partition wall rapidly shifted their positions after wall removal, forming a continuous grid map that covered the newly merged space (Figure 2D; see Spiers et al., 2015, for different remapping of hippocampal place cells). These results suggest that rodents can rapidly combine the representation of different sub-regions, either by extensive experience or by the removal of physical boundaries.

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In contrast, representation of local space in human memory is not integrated in the same manner shown by the remapping of grid cells. Humans are often unable to accurately extract the geometric relations between locations learned from different regions of an environment, suggesting that each area is independently represented and is not integrated into a coherent global representation (Foo et al., 2005; Han & Becker, 2014; Ishikawa & Montello, 2006; Schinazi, Nardi, Newcombe, Shipley, & Epstein, 2013; Weisberg, Schinazi, Newcombe, Shipley, & Epstein, 2014; but see Mou, McNamara, & Zhang, 2013). Moreover, extensive navigation experience with a multi-region environment does not necessarily lead to a merging of local maps. This even includes environmental spaces that people have learned or lived in for weeks, months, or even years (e.g., different rooms within a complex building, or different regions within a campus or large neighborhood area), humans often do not integrate fragmented space into a coherent global space in memory (Ishikawa & Montello, 2006; Meilinger et al., 2016; Moeser, 1988; Weisberg et al., 2014). It has also been shown that humans may acquire global spatial knowledge in parallel to route knowledge, rather than building it stage by stage (Ishikawa & Montello, 2006; Montello, 1998; Zhang, Zherdeva, & Ekstrom, 2014). These findings cast doubt on the view that local grid maps are integrated into a global grid map to support large-scale navigation (see also Geva-Sagiv et al., 2015; Wolbers & Wiener, 2014).

Therefore, concerning the representation of compartmental space, what we have inferred from the remapping of grid or place cells (i.e., implementation-level analysis) is different from that indicated by the studies of human spatial memory (i.e., functional-level observation). The former suggests that memory of sub-regions is organized with a globally consistent metrical system (i.e., consistent with the cognitive map hypothesis), whereas the latter suggests that the representations of local spaces are stored with independent and often inconsistent frames of reference (i.e., in line with the topological representation hypothesis).

5 Representation of Routes Traveled: Path-Dependent or Path-Irrelevant?

Directly exploring an environment facilitates humans to acquire spatial knowledge and offers probably the only way for nonhuman animals to build up spatial representations. How does a navigation system represent the route information sensed during such exploration? One mechanism that processes the route information during navigation is path integration, a process that keeps tracking one’s position and orientation by integrating translational and rotational components of self-motion (Etienne & Jeffery, 2004; Loomis et al., 1993; Müller and Wehner, 1988). Spatial and self-motion information sensed during navigation can be used to form a mental map of an environment via path integration (McNaughton et al., 2006; Moser and Moser, 2008; Wang, 2018). Both human and rodent navigation studies have attempted to unveil how the brain implements the function of path integration (e.g., Chrastil et al., 2015; 2016; Gil et al., 2018; McNaughton et al., 2006; Wolbers, Wiener, Mallot, & Büchel, 2007). Whereas many studies have investigated how humans represent the routes they traveled, little is known about whether rodents store information about their traveled paths and, if so, what aspects of path information are stored in memory.

Studies of rodent navigation often focus on path-independent encoding of location and orientation. The firing properties of place cells, head direction cells, grids cells, and boundary cells, by definition, are determined by where an animal is located (i.e., place, grid, and boundary cells) or which direction it faces (i.e., head direction cells), regardless of which path leads them there and which path they will take next. Thus, the cellular positioning system is assumed to function in a path-irrelevant way. Similarly, behavioral studies often investigate the process of path integration using path-irrelevant indexes, such as whether a navigator accurately reaches a goal, returns to home, or senses self-location or orientation (for a review, see Etienne & Jeffery, 2004). Although such path-independent neural codes are capable of integrating path information (Bush et al., 2015; McNaughton et al., 2006), they cannot tell us how the route information is represented in memory. That is, much path integration research has investigated how path information is integrated without questioning how the path information is represented.

In contrast, studies of human navigation suggest a path-dependent encoding of space. One such example is the orientation-dependent representation of space. Humans often use the walking direction of routes as a reference direction (i.e., a cognitive "north") to represent spatial relations of places, landmarks, and objects (McNamara et al., 2003; Meilinger, Riecke, & Bülthoff, 2014; Meilinger et al., 2016; Mou & McNamara, 2002; Mou et al., 2013; Shelton & McNamara, 2001, 2004). It means that spatial information (e.g., a goal location) is not equally accessible from different orientations (see also McNamara & Diwadkar, 1997). This orientation-specific encoding of space cannot be easily explained by a path-independent positioning system. Another support for a path-dependent representation comes from the findings of neurons that are sensitive to the direction of walking routes (Ekstrom et al., 2003; Jacobs et al., 2010; Page, Sato, Froehler, Vaughn, & Duffy, 2015). For instance, Ekstrom and colleagues (2003) found that the firing fields of human place cells changed when the navigation trajectories led to different goals (i.e., remapping; Figure 3A). Similarly, Jacobs et al. (2010) showed that neurons in the human entorhinal cortex are activated only when the walking direction is clockwise or is counterclockwise around a square route (Figure 3B). Therefore, humans represent more than just the location and orientation information during navigation; how we experience an environment also shapes how we represent it in memory.

-------------------[Insert Figure 3 about Here] -------------------

The challenge to the path-independent encoding also comes from studies of rodent navigation (Frank, Brown, & Wilson, 2000; Nitz, 2006; Pfeiffer & Foster, 2013; Wood, Dudchenko, Robitsek, & Eichenbaum, 2000). The brain networks supporting rodent navigation may also encode certain aspects of path information. For instance, the place cells in the CA1 region of rat hippocampus fire differently depending on the turning direction of the trajectory, suggesting that these cells encode information specific to individual routes (Frank et al., 2000; Wood et al., 2000). Nitz (2006) elegantly demonstrated that parietal neurons and hippocampal CA1 neurons might encode a specific type of route (e.g., the first segment, or the segment start with a left turn and then followed by a right turn). Moreover, the route-specific firing of CA1 places cells is not due to the encoding of goal locations (i.e., reward sites). When rats learned two different routes that shared the same starting path and led to an identical goal location, these place cells still fire on one trajectory but not both, suggesting that they encode information about the trajectories but not the goal (Figure 3C; Grieves, Wood, et al., 2016; see also Ito, Zhang, Witter, Moser, & Moser, 2015). Pfeiffer and

Foster (2013) showed that CA1 place cells could encode future path information ahead of locomotion. They found that ensembles of place cells can generate a temporal sequence of firing fields, which may be used to plan a route between a rat's current location and a known goal location (see also Davidson, Kloosterman, & Wilson, 2009; Johnson & Redish, 2007). These results suggest that the firing of place cells may carry information about individual routes, rather than being entirely determined by the local spatial information.

In comparison with whether or not route information is encoded in memory, it is more challenging to address what aspects of route information are represented. One critical element of route information is its geometric shape or path configuration. Humans seem to be able to encode path configuration of the routes travelled (He & McNamara, 2017; McNamara et al., 2003; Wiener, Berthoz, & Wolbers, 2011), though the encoding of path configuration may require attention (Chrastil et al., 2015; Zhao & Warren, 2015a). For nonhuman animals, it is hard to draw a decisive conclusion. Humans can demonstrate whether the geometric properties of traveled trajectories are encoded in memory by describing, illustrating, or reproducing the routes they have traversed. However, none of these apply to nonhuman animals. Therefore, while the different firing of place cells indicates that different neural representations between left- and right-turn routes (Frank et al., 2000; Wood et al., 2000), precisely what information leads to these different neural responses remains unknown (e.g., it could be the decision to turn left or right, the episodic memory of a left or right turn, or the planning of path to the goal, etc.).

Whereas studies of human navigation highlight the importance of route-based information in spatial representation, research on animal path integration often focuses on the processes of integration rather than the representation of paths. A path-independent encoding of space faces challenges from accumulating research on both human and nonhuman animal navigation. It is also worth noting that although human and other mammals are assumed to share the same cognitive and neural mechanism of path integration, damage to the hippocampal structure tends to have different influences on navigation behavior (Shrager, Kirwan, & Squire, 2008; Kim, Sapiurka, Clark, & Squire, 2013).

6 Representation of Distance and Direction: Continuous or Categorical?

How well do humans and nonhuman animals sense the distance and direction between two places? Accurate sensing of distance and direction is vital for the survival of nonhuman animals. They need it to precisely calculate the location of a pray or a predator and to head back to their resting place after a feeding excursion (Galistel, 1990). The positioning system discovered in the rodent and primate brain not only provides a mechanism of self-localization but also offers an intrinsic metric for measuring the distance and relative direction between different locations (Bush et al., 2015; McNaughton et al., 2006). As mentioned in previous sections, rodents seem to represent distance and direction in a reasonably precise way. The firing fields of grid cells regularly tile the space enclosed by the visual boundaries, providing a biological odometer and protractor for an accurate measurement of distance and direction. Accurate representation of distance and direction is even more evident in navigation behavior. For a local small-scale space, they were able to home directly after a complex outbound feeding journey (Collett & Collett, 2000; Etienne & Jeffery, 2004). For long migration journeys, they can swim or fly for thousands of miles to arrive at the same place they visited before (Lohmann et al., 1999; Mouritsen et al., 2016; Vardanis et al., 2011).

Human estimation of distance and direction is often biased and inconsistent (Ishikawa & Montello, 2006; Loomis et al., 1993; McNamara & Diwadkar, 1997). Even after a short outbound path, our estimation of homing direction can be as bad as chance level (Chrastil & Warren, 2013; Zhao & Warren, 2015a, 2015b). When asked to point to the direction of a known place, we often exhibit angular errors greater than 20° (Ishikawa & Montello, 2006; Meilinger et al., 2014; Meilinger et al., 2016; Mou et al., 2013; Mou, Zhao, & McNamara, 2007). Without rich environmental cues (e.g., walking in a desert), we even struggle to maintain a straightforward direction of walking (Souman, Frissen, Sreenivasa, & Ernst, 2009). When vision is blocked, we cannot keep our walking direction in an open field after five to ten minutes of walking (Souman et al., 2009). Such distortion is not limited to spatial representation acquired via direct learning (i.e., exploration). Humans also show significant errors in representing the relative direction of geographic places (e.g., cities in North America) —spatial knowledge obtained from map learning (Friedman, 2009; Zhang et al., 2014).

The neural mechanism of human direction representation appears to differ from that in rodents as well. For rodents, since each heading direction cell is tuned to a different direction, the population of heading direction cells are thought to encode a continuous direction of 360° range (Cullen & Taube, 2017; Taube, 2007). Such continuous representation of heading direction has not yet been found in the human brain. Human brain imaging studies suggest that the retrosplenial cortex and subiculum are involved in encoding the facing direction (Chadwick, Jolly, Amos, Hassabis, & Spiers, 2015; Chrastil, Sherrill, Hasselmo, & Stern, 2016; Shine et al., 2016; Vass & Epstein, 2013). Specifically, the subicular region encodes geocentric orientation relative to the environment (Chadwick et al., 2015;

Vass & Epstein, 2013, but see Spiers & Maguire, 2007), whereas the retrosplenial cortex may represent both geocentric orientation (Chadwick et al., 2015; Shine et al., 2016) and egocentric orientation relative to oneself (Chrastil et al., 2016; Marchette, et al., 2014). Nonetheless, these brain areas are often sensitive to the categorical shift of facing direction (e.g., from facing north to facing west or from facing one street to facing another), suggesting that human representation of heading direction may be regularized and categorical.

Human distance representation also shows poor correspondence with physical distance. Although distance estimation is relatively accurate in local space (e.g., Wu, Ooi, & He, 2004), it is often distorted in large-scale space. Many factors can cause such distortion, such as the presence and the number of junctions and turns (Kuipers, 1983), spatial boundaries (Friedman & Montello, 2006; Sinai, Ooi, & He, 1998), and even the perceived salience of places (McNamara & Diwadkar, 1997). Moreover, how we sense the distance (e.g., walking vs. galloping; or walking vs. sitting in a car) also affects how we represent and reproduce it (Arnold, Iaria, & Ekstrom, 2016; Brunec, Javadi, Zisch, & Spiers, 2017; Chrastil & Warren, 2014a; Waller, Loomis, & Haun, 2004). Together, these results indicate that human distance representation does not always correspond to the extrinsic physical metrics. Thus, the accurate sensing of distance at the cellular level, as observed in rodent navigation, may not apply to the distance representation in human memory.

The neural network supporting human navigation (e.g., hippocampus, parahippocampus, and retrosplenial cortex) can encode both egocentric distance toward a goal and allocentric distance between familiar places (Balaguer, Spiers, Hassabis, & Summerfield, 2016; Chrastil, Sherrill, Hasselmo, & Stern, 2015; Chrastil et al., 2016; Howard et al., 2014; Morgan, MacEvoy, Aguirre, & Epstein, 2011; Spiers & Barry, 2015; Vass et al., 2016; Viard et al., 2011). For instance, Morgan et al. (2011) showed that the human left hippocampus encodes the relative distance between real-world familiar locations. It exhibits more similar neural activities to familiar landmarks that are close to each other as opposed to landmarks far apart. Howard et al. (2014) found that the neural activity in the posterior part of hippocampus significantly correlates with the length of a route to a goal, whereas neural activity in the entorhinal cortex correlates with the Euclidean distance between current and goal locations. This finding is consistent with Spiers, Olafsdottir, and Lever (2017), who found a significant correlation between rat hippocampal activity and the distance to a goal; the firing of CA1 place cells decreased with increased proximity to a goal. Chrastil and colleagues (2015) also showed that the hippocampus and retrosplenial cortex can represent the Euclidean distance between the start and current locations. These correlations imply that humans may encode distance with a continuous metric, as suggested by the grid system used to measure distance by rodents.

The correlations between neural activity and physical distance are open to alternative explanations. For instance, although Howard et al. (2014) demonstrated that human hippocampal activity is related to the route and the Euclidean distance to a goal, it is hard to discern whether such distance representation was based on sensory odometer or visuospatial memory of a map (because participants learned the layout by both studying maps and walking tours). Furthermore, given that hippocampal neurons encode both space and time (Eichenbaum, 2017a; Kraus, Robinson, White, Eichenbaum, & Hasselmo, 2013), it remains to be elucidated whether the tracking of distance is supported by the neural coding of spatial metrics or temporal metrics. As for the hippocampal encoding of short versus long distance between familiar locations (Morgan et al., 2011), it remains unknown whether such distance encoding is continuous, ordinal, or categorical.

7 Summary

To understand the cognitive and neural mechanisms of navigation, knowing how spatial information is represented in memory is as important as knowing how a neural positioning system senses spatial information. While many studies have demonstrated the remarkable resemblance between how human and nonhuman animals represent space, this review highlights some of the critical cross-species inconsistencies. Such inconsistency spans the whole hierarchy of spatial representation, from the encoding of distance and direction (continuous vs. categorical) to the representation of routes (path-relevant vs. path-independent encoding), sub-regions of an environment (separated vs. integrated), and the geometric structure of environmental space (metric vs. topological). Although navigation is one of the most primitive skills found across animal species, these inconsistencies demonstrate that what we learned from the electrophysiological studies of rodent navigation does not necessarily apply to human navigation. These inconsistencies also highlight the importance of closing the loop for the dominant animal-to-human approach in navigation research, so that insights from behavioral studies of human navigation may also flow back to shed light on the cellular mechanism of navigation for humans and other mammals (i.e., a human-to-animal approach).

Figure Captions

Figure 1. Grid patterns are sensitive to environment geometry, novelty, and visual input.

(A). Grid pattern observed in square arena was distorted in trapezoids (adapted with permission from Krupic et al., 2015). Rows 1 and 3 are example of rate maps of two representative grid cells; rows 2 and 4 show corresponding spatial autocorrelograms.

(B). Grid patterns observed in light condition were disrupted in complete darkness (adapted with permission from Chen et al., 2016 under the CC BY License 4.0). Columns 1 and 3 are example of rate maps of three representative grid cells; columns 2 and 4 show corresponding spatial autocorrelograms.

(C). Grid patterns observed in familiar environments expand in novel environments (adapted with permission from Barry et al., 2012). Rows 1 to 3 show the raw data (locations of firing in green and animal's path in black), rate maps, and spatial autocorrelograms, respectively. Data were from one grid cell in five different trials, trials 1 and 5 were recorded in a familiar arena whereas trials 2 to 4 were recorded in a novel arena (shown with red outline).

(D). Grid patterns observed in a square arena stretched and shrank with environmental deformation (adapted with permission from Barry et al., 2007). The upper panel shows raw data (locations of firing in green and animal's path in black) when a square arena was changed to a vertical rectangle, horizontal rectangle, and a smaller square arena. The lower panels show corresponding rate maps (left) and spatial autocorrelograms (right).

Figure 2. Integration of grid patterns for local compartments.

(A-B) Integration of adjacent compartmental space into a coherent global space following extensive experience (adapted with permission from Carpenter et al., 2015 under the CC BY License 4.0). The similarity between grid patterns for the two compartments was high during early exposure (Panel A, upper row), which was reduced by weeks of exploration experience during later exposure (Panel A, lower row). Similarly, during early exposure, a local model with repetitive grid patterns showed a better fit to the rate maps than a global model, in which grid patterns tile across the compartments (Panel B, upper row). The opposite fitting results were obtained during late exposure (Panel B, lower row).

(C-D) Combination of adjacent compartmental space into a coherent global space following the removal of the partition wall (adapted with permission from Wernle et al., 2018). (C) Examples of grid patterns before (left) and after (right) the removal of partition wall from two representative grid cells (one in each row). (D) Grid patterns for two compartments were integrated rapidly into a global one during the first trial after wall removal. Column 1 show grid maps of two grid cells (one in each row) before the removal of the partition wall; columns 2 to 4 show grid maps observed 5, 10, 20, and about 40 minutes after the wall removal, respectively.

Figure 3. Path-specific encoding of spatial information.

(A). Path-specific encoding of spatial information by a right hippocampal cell in the human brain (adapted with permission from Ekstrom et al., 2003). The firing-rate map of this cell showed significant place selectivity when the participant looked for one goal location (i.e., shop Sc, left panel) in a virtual navigation task, but not when the participant searched for other shops (right panel). Red lines denote the participant's navigation trajectory; black squares indicate areas where the cell fired with high rate.

(B). Route-direction-dependent firing of hippocampal place cells in the human brain (reproduced with permission from Jacobs et al., 2010). Each row shows the firing-rate map of one place cell when participants navigated the virtual town in a clockwise direction (left column) and in a counterclockwise direction (middle column). Gray lines indicate participants' trajectory. The right column shows the computed place field of the place cell in each row. Red and blue place fields indicate the cell fired specifically during clockwise and counterclockwise movements, respectively.

(C). Trajectory-dependent firing of place cells is not due to the encoding of goal location (adapted with permission from Grieves, Wood, et al., 2016 under the CC BY License 4.0). The left most panel shows a schematic illustration of the four trained routes through the maze. Note that some of the segments were shared by either four or two trained routes. The right four panels show firing-rate maps of four representative cells, which demonstrate differential firing in the start arena, the lower central segments shared by all four routes, the left and the right arms shared by two routes. Note that one cell shows different firing at the central shared segments even though two inner routes lead to the same goal location.

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Figure 1

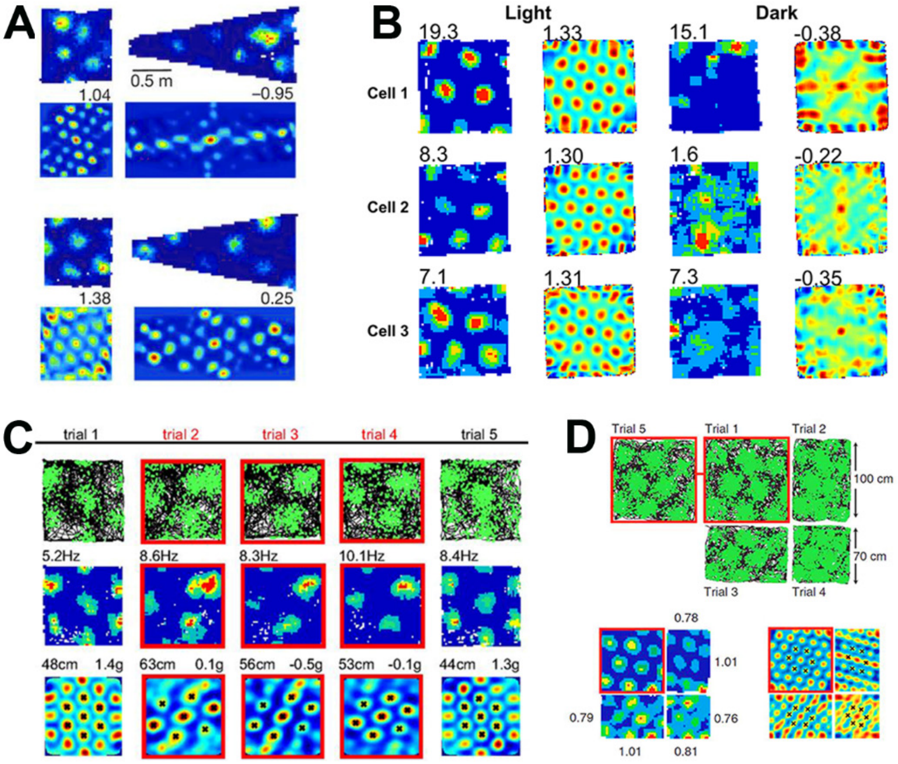

A
0.5 m
1.04
−0.95
1.38
0.25
B
Light
Dark
19.3
1.33
15.1
-0.38
Cell 1
8.3
1.30
1.6
-0.22
Cell 2
7.1
1.31
7.3
-0.35
Cell 3
C
trial 1
trial 2
trial 3
trial 4
trial 5
5.2Hz
8.6Hz
8.3Hz
10.1Hz
8.4Hz
48cm
1.4g
63cm
0.1g
56cm
-0.5g
53cm
-0.1g
44cm
1.3g
D
Trial 5
Trial 1
Trial 2
100 cm
70 cm
Trial 3
Trial 4
0.78
1.01
0.79
0.76
1.01
0.81

Figure 2

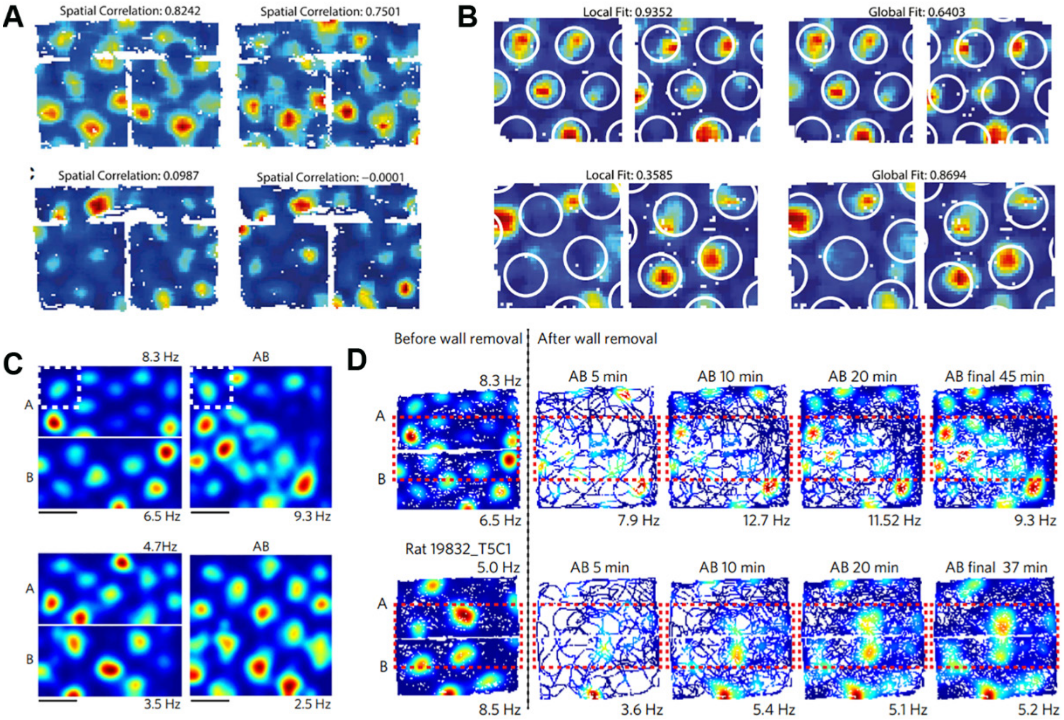
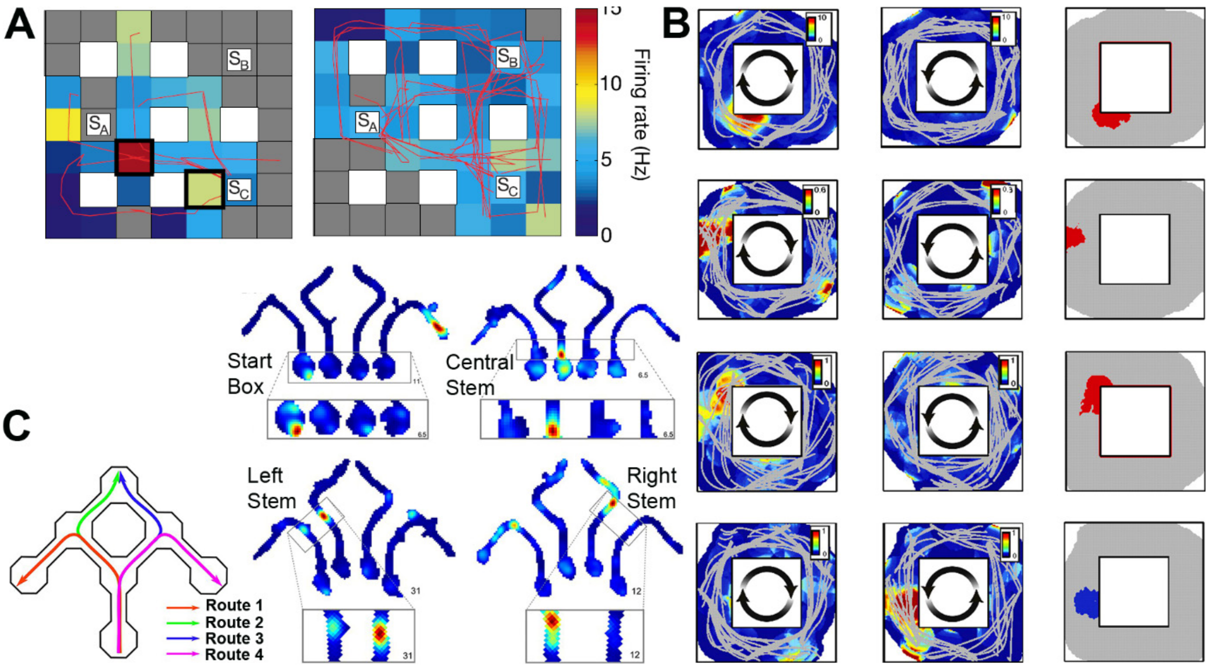

A
Spatial Correlation: 0.8242
Spatial Correlation: 0.7501
Spatial Correlation: 0.0987
Spatial Correlation: −0.0001
B
Local Fit: 0.9352
Global Fit: 0.6403
Local Fit: 0.3585
Global Fit: 0.8694
C
8.3 Hz
AB
A
B
6.5 Hz
9.3 Hz
4.7Hz
AB
A
B
3.5 Hz
2.5 Hz
D
Before wall removal
After wall removal
8.3 Hz
AB 5 min
AB 10 min
AB 20 min
AB final 45 min
A
B
6.5 Hz
7.9 Hz
12.7 Hz
11.52 Hz
9.3 Hz
Rat 19832_T5C1
5.0 Hz
AB 5 min
AB 10 min
AB 20 min
AB final 37 min
A
B
8.5 Hz
3.6 Hz
5.4 Hz
5.1 Hz
5.2 Hz

Figure 3


A
S_B
S_A
S_C
S_B
S_A
S_C
15
10
5
0
Firing rate (Hz)
B
10
10
0.6
0.3
1
1
Start
Box
Central
Stem
11
6.5
6.5
6.5
C
Left
Stem
Right
Stem
31
31
12
12
Route 1
Route 2
Route 3
Route 4