

Bond University
Research Repository



Cognitive neuroscience of spatial and geographic thinking

Schinazi, Victor R.; Thrash, Tyler

Published in:
Handbook of Behavioral and Cognitive Geography

DOI:
[10.4337/9781784717544.00016](https://doi.org/10.4337/9781784717544.00016)

Licence:
Other

[Link to output in Bond University research repository.](#)

Recommended citation(APA):
Schinazi, V. R., & Thrash, T. (2018). Cognitive neuroscience of spatial and geographic thinking. In D. R. Montello (Ed.), *Handbook of Behavioral and Cognitive Geography* (pp. 154-174). Edward Elgar Publishing. <https://doi.org/10.4337/9781784717544.00016>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

For more information, or if you believe that this document breaches copyright, please contact the Bond University research repository coordinator.

Cognitive neuroscience of spatial and geographic thinking

Victor R. Schinazi and Tyler Thrash
Chair of Cognitive Science, ETH Zurich, Switzerland

Abstract

Cognitive neuroscience has provided additional techniques for investigations of spatial and geographic thinking. However, the incorporation of neuroscientific methods still lacks the theoretical motivation necessary for the progression of geography as a discipline. Rather than reflecting a shortcoming of neuroscience, this weakness has developed from previous attempts to establish a positivist approach to behavioral geography. In this chapter, we will discuss the connection between the challenges of positivism in behavioral geography and the current drive to incorporate neuroscientific evidence. We will also provide an overview of research in geography and neuroscience. Here, we will focus specifically on large-scale spatial thinking and navigation. We will argue that research at the intersection of geography and neuroscience would benefit from an explanatory, theory-driven approach rather than a descriptive, exploratory approach. Future considerations include the extent to which geographers have the skills necessary to conduct neuroscientific studies, whether or not geographers should be equipped with these skills, and the extent to which collaboration between neuroscientists and geographers can be useful.

Introduction

In 2014, neuroscientists John O'Keefe, May-Britt Moser, and Edvard I. Moser were awarded the Nobel Prize in Physiology or Medicine for their discoveries related to the brain's positioning system. They found place and grid cells in rats' medial temporal lobes that responded to position and orientation information at local and global scales (Hafting, Fyhn, Molden, Moser, & Moser, 2005; O'Keefe & Dostrovsky, 1971). This series of discoveries provided a comprehensive framework for understanding spatial behavior that cognitive scientists had been seeking since Tolman's (1948) original experiments on rat navigation. At the same time, this research referred to three of the four geographic primitives, including location, magnitude, and space-time (i.e., movement; Golledge, 1995). The fourth primitive "identity" has also been studied by neuroscientists in the context of landmark recognition and scene processing (e.g., Epstein & Kanwisher, 1998; Mendez & Cherrier, 2003). These findings suggest that there is potential for collaboration between neuroscience and geography. However, the extent to which these two disciplines have effectively communicated in practice suggests a tenuous relationship at best.

One feature of geographical research is its openness to interdisciplinarity. This is evident in the breadth of topics adopted by various geography departments around the world.

Indeed, geography research ranges from receding Antarctic ice shelves to human spatial thinking and navigation (Kitchin & Blades, 2002; Paglen, 2009). However, this amorphous quality of geography has led to difficulties with establishing the methodological norms that are necessary for its acceptance by other sciences (Couclelis & Golledge, 1983; Smith, 1987). For example, in 1948, the closing of Harvard University's geography department was essentially the result of a perceived lack of academic rigor (Smith, 1987). This event has been characterized as the "death of geography" (Smith, 1987). Over the past few decades, subdisciplines such as behavioral geography and geographic information systems (GIS) have been successful in reacting to this crisis by adopting rigorous methodologies. However, these subdisciplines are not always driven by theory and, as a result, struggle to progress as a science despite their success in industry (Kitchin, 2006).

In contrast, neuroscience has a long history of theory-driven approaches to testing empirical hypotheses, but their findings can sometimes be misinterpreted by scientists in other disciplines. For example, Weisberg, Keil, Goodstein, Rawson, and Gray (2008) found that satisfaction ratings for scientific explanations were significantly higher when presented with neuroimaging data (but see Farah & Hook, 2013). Interestingly, these results were particularly strong for bad explanations presented to novices (even neuroscience students) but not experts (Weisberg et al., 2008). In addition, Fuchs (2006) and Henson (2005) argue that neuroimaging data (e.g., brain activations) are often considered explanations for behavior independent of an underlying theory. However, similar to behavioral measures (e.g., reaction time, accuracy), neuroimaging data represent one of many possible dependent variables that can be used to support or contest a theory (Henson, 2005). In addition, brain localization does not directly indicate the cause of a pattern in behavior (Fuchs, 2006; Henson, 2005). This causal inference requires confirmation or falsification as part of a larger research agenda (Henson, 2005). Indeed, Fuchs (2006) argues that imaging studies are based on probabilistic covariance rather than causal connections (but see Henson, 2005). Neuroscience, as well as cognitive science in general, is also criticized for reductionism (i.e., focusing on one aspect of a complex phenomenon) and overgeneralization from aggregate data to individuals' propensities (Fuchs, 2006).

Geographers interested in neuroscience are susceptible to these same pitfalls. In the last decade, some geographers have argued that localization in the brain can provide support for the role of spatial thinking in education (Gersmehl & Gersmehl, 2006; Lobben & Lawrence, 2015). This research typically aims to develop frameworks of spatial thinking skills that are based on neural correlates. Despite a number of well-motivated investigations into these phenomena, most of these studies still lack a specific theoretical basis, and thus, the neural correlates of spatial thinking are rarely predicted a priori. Given that most geographers are still not experts in neuroscience, these findings risk being misinterpreted and regarded as more credible than purely behavioral research. Part of this challenge is the drive in geography for more advanced technology. Both GIS and neuroimaging technologies can be used by geographers in order to locate

behavioral phenomena in geographic or brain coordinates. However, as is the case with GIS (Kitchin, 2006), there is a tendency for these geographers to adopt an empiricist (i.e., ideographic; fact gathering) but not a positivist (i.e., nomothetic, theory-driven) approach to science.

In this chapter, we provide an overview of research at the intersection of geography and neuroscience. We will focus on the branch of geography that uses neuroscientific techniques rather than the mapping of the structure of the nervous system (i.e., neurogeography). The chapter begins with a discussion of positivism in behavioral geography and neuroscience. We will include a basic guide to the structures and functions of different brain regions and various methods to collect and analyze neuroscientific data. Next, we will report research focused on the neural correlates of spatial thinking and navigation. We will conclude with a critical analysis of the state of the field.

Positivism in geography and neuroscience

The closure of the geography department at Harvard University motivated a methodological shift within the discipline (Couclelis & Golledge, 1983; Golledge, 2008; Kitchin, 2006; Smith, 1987). This quantitative revolution was an explicit attempt to introduce scientific rigor using a positivist approach to the study of spatial phenomena (Golledge, 2008; Kitchin, 2006). Positivists sought the derivation of hypotheses from theory and the (dis)confirmation of these hypotheses using statistical analysis and mathematical modeling (Kitchin, 2006). This epistemological shift was generally well-received within geography but also criticized for simplifying human spatial behavior as rational and economical (Argent & Walmsley, 2009; Golledge, 2008; Kitchin, Blades, & Golledge, 1997). Indeed, behavioral geography (i.e., behavioralism) emerged as a reaction to this concept of homo economicus without abandoning positivism altogether.

Behavioralism is a branch of human geography that investigates the activity of humans in space (Golledge, 2008). Research in this area became more focused on the perceptual and cognitive processes underlying human-environment interaction than the environments themselves (Golledge, 2008; Kitchin et al., 1997). In other words, geographers began to consider the interaction between individuals' cognitive processes and the location and distribution of phenomena (Argent & Walmsley, 2009; Gibson, 1966; Kitchin et al., 1997). For these researchers, the concept of space became, not only physical *or* subjective, but also psychological *and* objective. Psychological space could be considered objective because inferences regarding mental representations could be reproduced by researchers using similar methods. As such, these studies required the aggregation of behavioral data rather than the analysis of any one individual. Consequently, this sometimes required behavioral geographers to adopt and develop data sources (i.e., primary rather than secondary sources; Golledge, 2008), analytical methods (e.g., bidimensional regression; Tobler, 1965, 1994; multidimensional scaling; Golledge & Rushton, 1976; for a review, see Kitchin & Blades, 2002), and

theories (e.g., anchor point theory; Couclelis, Golledge, Gale, & Tobler, 1987; Golledge, 1978) from other disciplines (e.g., cognitive science; Golledge & Stimson, 1997; Golledge, 2008).

Despite behavioralism's general success, this approach received (and continues to receive) a fair amount of criticism (Argent & Walmsley, 2009; Bunting & Guelke, 1979; Kwan & Schwanen, 2009; Rushton, 1979). Much of this criticism developed from a humanist perspective that argues that quantitative methods are incapable of capturing the complexity of human behavior (Bunting & Guelke, 1979; Kitchin, 2006; Kwan & Schwanen, 2009). These critics advocate instead for the use of in-depth, qualitative methods. Notably, these critics often misinterpret aspects of behavioralism's positivist roots (Golledge, 2008; Kitchin, 2006; Smith, 1987). These misinterpretations include the role of the researcher as a dispassionate observer and the challenges with generalizing from aggregate data to individuals (Smith, 1987). The former criticism stems in part from the confusion between the terms "behavioralism" and "behaviorism" (Argent & Walmsley, 2009; Golledge, 2008; Rushton, 1979). The behaviorist approach to psychology emphasized the description of observable behavior independent of any mental process (Schultz & Schultz, 2008). To the behaviorist, this observation required an "objective" researcher detached from the topic of study (i.e., subjects' behavior). However, this definition of objectivity is different from the definition adopted by behavioralists. Because behavioralism acknowledges the underlying mental processes of both research participants and experimenters, this type of objectivity is difficult if not impossible to achieve. Indeed, experimental control may be necessary for obtaining objective results regarding spatial behavior but does not require a dispassionate observer (Kitchin, 2006). In addition, aggregate behavioral data can inform theories regarding the typical individual. Criticisms of this approach often confuse the typical individual with any particular individual or every individual within a population (e.g., Argent & Walmsley, 2009). This misunderstanding also leads to the conclusion that human spatial behavior cannot be studied with rigorous experimental control (e.g., Bunting & Guelke, 1979). However, experimental control is necessary for statistically assessing the extent to which data sampled from a population can generalize to other individuals within that population. Geographers' lack of understanding regarding this analytical approach may be attributable to their lack of training in experimental methods. Indeed, this training would be a necessary first step for the adoption of neuroscientific techniques by geographers.

Another criticism against positivism in geography in general has been its technology-driven (rather than theory-driven) approach to research (Kitchin, 2006; Smith, 1979; Stimson, 2012). For example, there is a pervasive tendency within GIS to adapt research questions to fit the available technology rather than to use this technology to constrain theory (Kitchin, 2006). Because GIS has been extremely successful in transitioning from academia to industry, the contributions of GIS to a foundational understanding of spatial behavior tend to be undervalued and under-investigated (Kitchin, 2006). The same argument could be levied against the potential overconfidence

of behavioral geographers in neuroscientific techniques. Here, behavioral geographers may risk returning to the ideographic approach that they originally sought to avoid. Before using neuroscientific techniques, geographers need to develop a deeper understanding of the anatomy of the brain and the methods used to collect and analyze neuroscientific data.

Neural anatomy and neuroscientific methods

This section will provide a basic guide to neuroanatomy and techniques for the collection and analysis of neuroscientific data. For in-depth resources, we encourage the reader to consult Gazzaniga, Ivry, and Mangun (2014), Poldrack, Mumford, and Nichols (2011), and Ward (2015).

Gross neuroanatomy

Locations in the brain are identified using terms of reference (i.e., directions) and section (i.e., planes of division). Assuming that the person is standing upright, the terms anterior and posterior refer to front and back of the brain, respectively. The terms dorsal and ventral refer to the top and bottom of the brain, respectively. For humans, dorsal and ventral can also be termed superior and inferior. Given that the brain is three-dimensional and symmetrical (i.e., one hemisphere is structurally the mirror-image of the other), the terms medial and lateral are used to refer to the inner and outer surfaces of the brain. Importantly, the term medial can also refer to the center of a brain structure. For example, the medial temporal gyrus is the center of the temporal gyrus but on the lateral surface of the brain. Terms of section include coronal, axial, and sagittal. The coronal plane is perpendicular to the anterior/posterior dimension, and the axial plane is perpendicular to the dorsal/ventral dimension. The sagittal plane divides one hemisphere along the left/right dimension, rather than the medial/lateral dimension. The midline or medial plane is a special case of the sagittal plane that divides the left and right hemispheres of the brain.

Brain tissue is characterized as either grey or white matter. Grey matter consists of the neural cell bodies and dendrites (i.e., branches of the cell that receive neural signals) and composes the majority of the cerebral cortex and subcortex. White matter consists of support cells (i.e., glial cells) and axons (i.e., branches of the cell that send neural signals) and lies primarily between the cortex and subcortex. The brain also has four ventricles containing cerebrospinal fluid that cushions the brain in case of a collision and maintains a chemical equilibrium in the brain.

Convolutions of grey matter in the cerebral cortex can be characterized as gyri (i.e., the raised surface) and sulci (i.e., the dips or folds). The lateral surface of the cortex is divided into four lobes (i.e., frontal, parietal, occipital, and temporal) distinguished from one another using anatomical landmarks such as sulci. In addition to this division by lobe, there are at least three ways of defining relatively specific regions of the cerebral cortex. First, researchers may refer to specific gyri and sulci (e.g., superior frontal gyrus,

central sulcus). Second, regions may be divided according to sets of cells with different compositions and organization (i.e., their cytoarchitecture). For example, Brodmann distinguished between 52 different brain areas based on the relative distribution of different types of cells. Third, regions of the cortex can be defined with respect to function (e.g., visual cortex, motor cortex). Many of these functions can be localized in one of the four lobes and even related to a specific Brodmann area. However, higher-level functions (e.g., reasoning) can involve multiple Brodmann areas and even cross different lobes.

Different systems within the subcortex include the basal ganglia, the limbic system, and the diencephalon. The basal ganglia is comprised of the caudate nucleus, the putamen, and the globus pallidus. Together, these structures regulate motor activity. The limbic system includes the amygdala, the hippocampus, the cingulate cortex, and the mammillary bodies. These structures regulate learning in and affective responses to the immediate environment. Two primary structures of the diencephalon are the thalamus (responsible for alertness and relaying sensory information to the cortex) and hypothalamus (responsible for a variety of regulatory functions, e.g., hunger, sexual activity). Below the subcortex is the midbrain and hindbrain. The midbrain contains superior and inferior colliculi and the substantia nigra. These regions are primarily responsible for sensory integration, auditory processing, reward, and movement. The hindbrain includes the cerebellum, pons, and medulla oblongata. Collectively, these regions are responsible for movement, dexterity, and the regulation of vital functions (e.g., breathing).

Data collection techniques

Neuroscientific techniques for collecting data regarding the structure and function of the brain can be divided into electrophysiological, imaging, and lesion categories. Each set of techniques has its advantages and disadvantages with respect to invasiveness, temporal resolution, and spatial resolution. Electrophysiological techniques include single- and multiple-cell recordings, electroencephalography (EEG), and magnetoencephalography (MEG). Single- and multiple-cell recordings are typically used for animal studies but have also been used with humans (e.g., Jacobs et al., 2013). These methods involve recording electrical signals (i.e., action potentials) directly at specific neurons (i.e., intracellularly or extracellularly) as they respond to particular stimuli and thus are considered invasive. However, the temporal and spatial resolutions of these techniques are especially precise. EEG is a technique for recording electrical signals that are generated by the brain but recorded at multiple locations on the scalp. This technique is non-invasive with high temporal resolution and low spatial resolution. The spatial resolution is relatively low in part because the signal detected by a particular electrode may reflect activity elsewhere in the cortex. In addition, EEG cannot be used to record subcortical activity. MEG records magnetic (rather than electric) properties of neural activity. Similar to EEG, this technique is non-invasive with high temporal resolution but has much higher spatial resolution. Unfortunately, this technique has not

been widely adopted in spatial thinking and navigation research because of its high cost (but see Cornwell, Johnson, Holroyd, Carver, & Grillon, 2008).

Of these three electrophysiological techniques, EEG is the most popular with research on humans. Nonetheless, the analysis of EEG data poses several unique challenges to the researcher. Because of a low signal-to-noise ratio, the data collected over several trials must be averaged in order to derive an interpretable waveform called an event-related potential (ERP). Detecting an ERP requires the synchronous activation of a set of neurons and the alignment of this set of neurons so that their signal does not cancel out. Important characteristics of ERP data are the timing of peaks relative to stimulus presentation and their amplitude. In order to determine which peaks to analyze, the study must be driven by previous research and specific hypotheses.

In comparison to electrophysiological techniques, imaging techniques tend to have higher spatial resolution and lower temporal resolution. Imaging methods provide structural (i.e., anatomical) and functional (i.e., activation) information. Structural techniques include computerized tomography (CT) and magnetic resonance imaging (MRI). Both of these techniques produce a high-resolution static map that distinguishes between the skull, grey matter, white matter, and cerebrospinal fluid. CT scans are constructed using the absorption of x-rays by different tissues and are mainly used in clinical settings for the detection of gross brain abnormalities (e.g., tumors). MRI scans use magnetic fields to align hydrogen protons and radio wave pulses to change the protons' orientations by 90 degrees. A head coil is then used to detect changes in the magnetic field resulting from the protons' return to their original orientation. Variations in the timing of this realignment are used to distinguish between different types of neural tissue. This procedure is repeated several times for different slices that eventually compose a 3D structural image. MRI is often preferred over CT for research purposes because MRI does not expose the participant to radiation, MRI has better spatial resolution than CT, MRI can better distinguish between white and grey matter than CT, and MRI can be adapted to produce functional images.

Whereas MRI measures changes in the orientation of hydrogen protons, functional magnetic resonance imaging (fMRI) measures changes in levels of oxygenation in the blood. Blood constantly carries oxygen from the lungs to the brain in order to sustain neural activity. As a set of neurons become more active (e.g., while supporting a specific task), the concentration of oxygen in the blood decreases for this area of the brain. Deoxygenated hemoglobin has strong paramagnetic properties and produces distortions in the scanner's magnetic field. Changes in these distortions form the basis of the fMRI signal. This technique of deriving the fMRI signal is termed the blood oxygen-level-dependent (BOLD) contrast. Similar to MRI, this procedure is repeated for different slices of the brain. Compared to electrophysiological techniques, the temporal resolution of fMRI is low because of the delay in changes in the BOLD signal over time (i.e., the hemodynamic response function; HRF). Another functional imaging technique, positron emission tomography (PET), localizes neural activity using a radioactive tracer injected

into the bloodstream. Unlike fMRI, PET scans rely on blood flow rather than changes in oxygenation. One advantage of PET is that it allows for tracing blood flow along specific neural pathways. However, PET is invasive and has lower spatial and temporal resolution than fMRI.

While electrophysiological and imaging techniques provide information regarding the neural correlates that are sufficient for a particular task, lesion techniques can be used to determine which regions are necessary for performing that task. Lesions in animals are often created by the researcher using either surgical or chemical methods. In humans, lesions are either naturally occurring (e.g., resulting from a stroke or accident) or temporarily produced. For example, transcranial magnetic stimulation (TMS) allows the researchers to temporarily disrupt neural function at a particular location on the cortical surface using an electromagnetic current. Although permanent lesions in humans allow for relatively extensive testing, these lesions are rarely focused on a specific region and may even spread beyond the region of interest. On the other hand, the lesions produced by TMS are reversible but can only be induced for a brief amount of time and are restricted to particular regions of the cortex.

Experimental design and analysis of neural data

In order for geographers to make use of these neuroscientific techniques, they must also develop an understanding of experimental design and data analysis. While this challenge is similar for neuroscience as for cognitive science more generally, geographers still need training before they can use neuroscientific methods. Research often attempts to detect patterns in the obtained data. The simplest patterns are relationships between pairs of variables or differences between two conditions of one variable. In neuroscience, cognitive subtraction is used for functional imaging data in order to compare brain activity during a particular task to brain activity during another comparable task (e.g., a baseline task). At least two tasks are necessary for interpreting functional imaging data because the brain is always active. Factorial designs can also be used in order to determine how the effect of one independent variable on the dependent variable is influenced by another independent variable (i.e., a statistical interaction). In addition, parametric designs can be used in order to measure the relationship between brain activity in a specific region and a continuous (rather than categorical) independent variable. When using fMRI, researchers also have to decide how to order the stimuli during the experiment. In block designs, stimuli in the same condition (e.g., faces and places) are presented together, whereas in event-related designs, stimuli from different conditions are interspersed. Block designs have more statistical power for the detection of smaller effects, but some research questions can only be addressed with flexible event-related designs (Amaro & Barker, 2006; Josephs & Henson, 1999).

The raw data of neural analyses are represented by small volumes (e.g., one cubic millimeter) called voxels that correspond to hundreds of thousands of brain cells. Their sizes depend on the resolution of the scanner so that a higher resolution scanner can produce smaller voxels.

There are several steps involved with the analysis of functional imaging data, some of which also apply to structural imaging data. These steps include slice-timing correction, realignment, coregistration of structural and functional images, normalization, spatial smoothing, and statistical comparisons (see Lindquist, 2008). Because slices of the (f)MRI image are acquired sequentially, slice-timing correction is necessary in order to align voxels in time so that they appear to have been collected simultaneously. Realignment (i.e., motion correction) typically involves a rigid body transformation in order to account for possible head and body movements during scanning. In fMRI, the low-resolution functional images must then be coregistered to align with a high-resolution structural image using rigid body or affine transformations. Given that individuals' brains are shaped slightly differently, group comparisons require the normalization with respect to a template brain (e.g., the Talairach or Montreal Neurological Institute brains). Spatial smoothing is then used to enhance the signal-to-noise ratio by applying a low-pass filter. This procedure enhances the apparent activation of voxels surrounded by activated voxels and is particularly useful for group comparisons.

In general, statistical comparisons can be conducted using an exploratory or a confirmatory approach. For neuroscientific data, whole-brain analyses are typically exploratory in that they are not driven by hypotheses regarding specific regions. In contrast, region of interest (ROI) analyses test hypotheses about specific anatomical (e.g., the hippocampus) or functional (e.g., the parahippocampal place area; PPA) regions (Poldrack, 2007). Functional ROIs are typically defined using a localizer scan. For example, in order to localize the PPA, researchers contrast responses to places against responses to objects and consider activation in this region while testing the main hypothesis. In order to test these hypotheses, a statistical map is created in which voxels are associated with a test statistic value (e.g., t , F). In most univariate cases, this procedure involves fitting a general linear model to the HRF of each individual voxel assuming that the stimulus conditions are known. However, multivariate approaches (e.g., multivoxel pattern analysis; MVPA) can also be used to account for dependencies in the activations of different voxels and thus can be sensitive to more fine-grained effects. Connectivity analyses can augment these approaches by investigating the anatomical and functional connections between different brain regions. Whereas functional connectivity describes correlations among seed regions (i.e., the point of departure) and other ROIs, anatomical connectivity (e.g., acquired using diffusion tensor imaging; DTI) describes their physical connections. Voxel-based morphometry (VBM) is another anatomical method used to detect correlations between behavioral and volumetric differences among groups of participants in terms of grey and white matter (Good et al., 2001).

Given the large number of statistical comparisons conducted for each of these methods, corrections for multiple comparisons are critical in order to minimize spurious results. At least two types of correction have been proposed. Family-wise error rate and false discovery rate represent relatively conservative and liberal approaches, respectively.

Nonparametric corrections (e.g., threshold-free cluster enhancement; Smith & Nichols, 2009) can be used when certain assumptions (e.g., normality) are violated while still minimizing alpha inflation. Although a variety of software packages are available and can facilitate the analysis of fMRI data, it is critical for geographers to understand these procedures and the ways in which they interact to produce the final images.

Cognitive neuroscience of geographic spatial thinking

One topic for which geographers have incorporated neuroscientific evidence is the identification and classification of spatial thinking skills (Gersmehl & Gersmehl, 2011; Gersmehl & Gersmehl, 2006, 2007; Gersmehl, 2012; Lobben, Lawrence, & Olson, 2009; Lobben, Lawrence, & Pickett, 2014; Lobben, Olson, & Huang, 2005; Lobben & Lawrence, 2015). Although there is no consensus regarding the precise definition of spatial thinking (Lobben & Lawrence, 2015; Wakabayashi & Ishikawa, 2011), these skills include learning and reasoning about properties of space with internal (e.g., spatial memory) and/or external (e.g., cartographic maps) representations (Mohan, Mohan, & Uttal, 2015; see Chapter 23 in this volume on Geographic Education). “Geospatial” thinking refers specifically to spatial thinking at the environmental (i.e., larger than the body and requiring locomotion) or geographic (i.e., larger than the body and requiring external representations) scales, as opposed to figural (i.e., smaller than the body) and vista (i.e., larger than the body but not requiring locomotion) scales (Golledge, Marsh, & Battersby, 2008; Montello, 1993).

Over the past 20 years, a variety of governmental and academic initiatives have focused on improving geospatial thinking skills in the United States (Downs & de Souza, 2006), Europe (Kavouras et al., 2014), and Asia (Wakabayashi & Ishikawa, 2011) because of their importance for scientific progress and everyday life (e.g., for giving and following directions). Indeed, geospatial thinking skills have been linked to competence and innovation in STEM disciplines (i.e., science, technology, engineering, and mathematics; (Uttal, Miller, & Newcombe, 2013; Wai, Lubinski, & Benbow, 2009) and the social sciences and humanities (Goodchild & Janelle, 2010). These initiatives are motivated by shortcomings in both the availability of programs for geographic education and the underperformance of students from primary school through the university level (Dunn, 2011; Golledge, 2008). For example, Dunn (2011) found that university students from a geography course in the United States had difficulties reporting the latitude and longitude of New York City (i.e., latitudes above 90 degrees north and longitudes in the Eastern Hemisphere).

Some researchers have argued that an important step towards addressing these challenges is developing frameworks for identifying and classifying geospatial thinking skills (e.g., Gersmehl & Gersmehl, 2006; Golledge, 2008; Lobben & Lawrence, 2015). According to this argument, these frameworks can provide a more inclusive and effective geographic curriculum. To date, two research programs have attempted to connect their frameworks to neuroscientific evidence. First, Gersmehl and Gersmehl (2006, 2007,

2011) and Gersmehl (2012) have identified between eight and ten different geospatial thinking skills (including spatial comparisons, influences, groups, transitions, hierarchies, analogies, patterns, and associations) and their potential neural correlates. For example, Gersmehl and Gersmehl (2011) attribute skills related to spatial comparisons (i.e., the ability to discriminate between quantities) to “a small area of the brain above and behind the left ear” (p. 51). Similarly, skills related to spatial transitions (i.e., slopes gradients, and sequences) are linked to “a specific area of the brain above the left eye” (p. 54), and spatial hierarchies are suggested to “involve structures on the right side of the brain” (p. 55; Gersmehl & Gersmehl, 2011). This framework specifically considers geospatial thinking skills to be malleable, occurring in parallel, and somewhat independent. According to this position, the malleability of these skills suggests that early training can benefit learning and application later in life (Gersmehl, 2012). Because these skills occur in parallel and are relatively independent, geographic curriculum can also be designed to address more complex skills at an earlier age (Gersmehl & Gersmehl, 2011).

Despite these efforts and a large number of citations (e.g., Lobben et al., 2009, 2014; Lobben & Lawrence, 2015; Manning, 2014; Mohan et al., 2015; Wakabayashi & Ishikawa, 2011), the framework provided by Gersmehl and Gersmehl (2006) has failed to provide clear descriptions of the precise neural localizations and underlying mechanisms of geographic concepts. This lack of clarity may be a result of oversimplification and overgeneralization with respect to existing neuroscientific evidence and terminology. Indeed, these articles often use behavioral evidence in order to infer the roles of different brain structures without recourse to electrophysiological, imaging, or lesion studies. For cases in which neural evidence is described accurately, these descriptions remain imprecise. Here, the authors do not adhere to typical neuroscientific terms (e.g., as found in a brain atlas) and use vague oversimplifications for localizing brain regions and their function. For example, the intraparietal sulcus (Cohen Kadosh et al., 2005) and the caudate nucleus (Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Schinazi, Nardi, Newcombe, Shipley, & Epstein, 2013) could have been used in their descriptions of spatial comparisons and transitions, respectively. In addition, the authors overgeneralize from established neuroscientific evidence in one content area (e.g., reading) to geographic concepts (e.g., map reading). Without empirical neuroscientific evidence to support each of these geospatial thinking skills and the distinctions between them, their framework is speculative at best. However, using concrete tasks specifically designed to tap each of the individual geospatial thinking skills, neuroscientific evidence may be obtained to confirm or disconfirm their existence.

To date, at least two studies have empirically (but not neuroscientifically) investigated the framework from Gersmehl and Gersmehl (2006). Gersmehl (2012) developed and tested new instructional materials at several primary schools in New York City. Students were instructed to perform several tasks that involved spatial reasoning, geographic sequencing, regionalization, and geographic pattern recognition. Gersmehl (2012) suggest that participation in these activities corresponded to an improvement in standardized reading and math tests. However, as noted by the author, lack of a control

group and systematic variation precludes a causal interpretation of this effect. In addition, Bednarz and Lee (2011) developed a 16-item questionnaire in order to assess various frameworks of geospatial thinking skills (including Gersmehl & Gersmehl, 2006). The results of a factor analysis on responses to these questionnaire items revealed that there were multiple distinct modes of spatial thinking but did not provide any support for the existing frameworks.

The second framework that uses neuroscience in order to inform the classification of geospatial thinking skills was proposed by Lobben and Lawrence (2015). Based on a review of neuroscientific research related to perceptual grouping and visual attention (Lobben et al., 2009) and two empirical studies (Lobben et al., 2014, 2005), this framework organizes geospatial thinking skills hierarchically along three continuous dimensions (i.e., attribute, space, and time) of a geographic data cube. These dimensions are based on the geographic primitives (i.e., identity, location, space-time, and magnitude) proposed by Golledge (1995) and the ways in which primitives can be combined into more complex skills with learning (see Golledge, 2008). According to Lobben and Lawrence (2015), the reorganization of skills from existing frameworks was needed in order to allow for the generation and testing of novel hypotheses regarding the relationships among these skills. Similar to Gersmehl and Gersmehl (2006), Lobben and Lawrence (2015) use neuroscientific concepts and findings in order to inform the initial placement of these skills along the three dimensions of the cube. Specifically, these dimensions are mapped onto the distinction between dorsal (i.e., where) and ventral (what) streams of information processing (Goodale & Milner, 1992). Here, the spatial dimension is associated with the dorsal stream, and the attribute dimension is associated with the ventral stream. Time is associated with the different scales at which information is processed in either stream, and more complex skills require processing further along both streams.

While Lobben and Lawrence (2015) provide a model that represents a synthesis of existing frameworks, it is unclear to what extent this model contributes (beyond existing models) to the generation and testing of novel hypotheses. First, they overgeneralize from one principle of visual processing (i.e., the what/where distinction) to geospatial thinking skills that are influenced by additional modalities (e.g., proprioception; Loomis et al., 1993; Schinazi, Thrash, & Chebat, 2015). Although Lobben and Lawrence (2015) note that this what/where distinction is somewhat outdated (Milner & Goodale, 2008), they do not elaborate the manner in which their framework is connected to more modern interpretations of the behaviors resulting from dorsal and ventral streams. Indeed, both streams can be characterized as representing what and where information but differ in terms of the observer's awareness of that information (i.e., explicit versus implicit knowledge). Second, the contribution of neuroscience to this framework is unclear given that the authors do not propose any specific hypotheses regarding the localization or function of geospatial thinking skills. The only provided example investigates the neural localization of mental rotation for a specific type of geographic stimulus (i.e., cartographic maps; Lobben et al., 2014).

In two studies, Lobben and colleagues (2014, 2005) have investigated spatial behaviors that require geospatial thinking but are not explicitly connected to any specific skills. Lobben and colleagues (2005) compared map memory (i.e., recognizing routes on maps), map rotation (i.e., determining whether two maps are flipped and rotated from each other or only rotated), and sleuthing (i.e., determining a location on a map given a picture from the first-person perspective) in terms of both behavioral and neuroimaging data. Results from the behavioral data revealed that sleuthing required more time than either of the other tasks and that performance on sleuthing and map rotation tasks were correlated. Results from fMRI data (from one participant) indicated that more voxels were activated for the sleuthing task than for the map rotation task, that there was a right-hemisphere bias for the map rotation task, and that there were differences in the specific regions activated by the two tasks. While this study represents one of the first attempts at incorporating neuroscientific evidence into cartography, there are several possible criticisms for this study specifically and for this approach to neuroscience. Overall, inferential statistics are often used incorrectly, and the connections between these analyses and their conclusions are unclear. For the behavioral data, nonsignificant correlations are considered “weak relationships,” and response time is used as an indication of relative difficulty across the three tasks. This use of response time is inappropriate because the tasks vary along several confounded dimensions (e.g., stimulus type, instructions). For the neural data, the extremely small sample size (i.e., N=1) does not allow for any generalization to human spatial thinking. In addition, the analysis of the neuroimaging data was entirely exploratory (i.e., no ROI analysis), and the resulting table of different neural activations across the two tasks is uninterpretable. In general, the approach of counting voxels across the entire brain (especially without distinguishing positive and negative activations) does not indicate the relative importance of two different tasks (Cohen & DuBois, 1999). Furthermore, an appropriate control task (e.g., a same-different judgment with unrotated maps) would have facilitated their interpretation of the activated voxels.

Lobben and colleagues (2014) is the first neuroscientific article conducted by geographers and published in a geography journal (i.e., *Annals of the Association of American Geographers*). This article extends their previous effort by investigating the behavioral and neural activation differences between the mental rotation of maps with text, maps without text, and simple geometric figures. They hypothesized that the regions activated by the mental rotation of maps (contrasted against a same-different judgment for unrotated maps) would be distinct from the regions activated by the mental rotation of simple geometric figures because of maps' function and the scale of space that they represent. The results from a factor analysis on the behavioral data suggested that responses were more consistent within stimulus conditions than between stimulus conditions. The neuroimaging data revealed both similarities in and differences between the activations associated with map conditions and the simple geometric figures. Specifically, the superior parietal lobule and the middle frontal gyrus were activated in all conditions. The authors interpret this similarity as reflecting the previously established

neural correlates of mental rotation (Cohen et al., 1996). In addition, there were specific activations for the precentral gyrus and the lateral occipital cortex for the map conditions and simple geometric figures, respectively. The authors interpret this difference as representing two strategies (i.e., motor or visual) related to the mental rotation of different stimuli (i.e., maps or simple geometric figures, respectively). Despite the advances of Lobben and colleagues (2014), there remain several shortcomings. First, although the researchers did use a same-different task with unrotated stimuli as the control conditions, the simple geometric figures were not sufficiently similar to the map stimuli to be properly contrasted. The initial behavioral experiment with complex geometric stimuli (containing map-like elements) suggest that such a control would have been possible, and it is unclear why this approach was not adopted. Finally, the researchers again report whole-brain analyses rather than focusing on their specific hypotheses. Whole-brain analyses are often coupled with ROI analyses because nearly any activation can be interpreted in a post-hoc manner, especially for novel stimuli such as maps.

The quality of neuroscientific evidence so far obtained with respect to these geospatial thinking frameworks suggests that establishing a neurologically defensible model may be implausible at this stage. Until geographers have the necessary training or establish solid collaborations with neuroscientists, the development of a pedagogically defensible model may be a more worthwhile endeavor (Manning, 2014). In contrast, neuroscientific research on navigation is relatively mature. While this research has been conducted mostly by cognitive scientists, navigation is a skill that requires geospatial thinking (Bednarz & Lee, 2011). Because of the large amount of neuroscientific research on navigation, we will focus on studies that are methodologically and theoretically sound.

Cognitive neuroscience of navigation

Navigation refers to the actions and decisions used to acquire and manipulate spatial information (e.g., views of scenes, an abstract coordinate system) in order to maintain orientation or find the location of a goal. The majority of neuroscientific studies that investigate navigation have attempted to draw inferences regarding behavior at environmental and geographic scales. Given the restrictions imposed by electrophysiological and neuroimaging techniques, researchers have used small-scale representations (e.g., static images, videos, interactive virtual environments) of large-scale environments and/or probed spatial memory for externally acquired knowledge. Although small-scale representations can be useful for studying navigation (e.g., Chrastil, Sherrill, Hasselmo, & Stern, 2015; Ekstrom et al., 2003; Marchette, Vass, Ryan, & Epstein, 2015; Shelton & Gabrieli, 2002), some researchers have suggested that the elicited responses constitute only a subset of navigation behaviors at larger scales (Wolbers & Wiener, 2014). Others argue that neuroimaging studies employing virtual reality may be neglecting the interoceptive cues typically involved in real-world navigation (Taube, Valerio, & Yoder, 2013). However, studies using virtual reality tend to

converge with those using lesion or intracellular recordings, suggesting that there is some overlap in the representation of small- and large-scale spaces at the neural level.

In this section, we will present evidence regarding the neural correlates involved in the acquisition and manipulation of spatial information during navigation. While previous neuroscientific research on navigation provides evidence for some of the geospatial thinking skills highlighted by various frameworks, this evidence does not entirely support any particular framework. Navigation relies on a variety of brain regions that include the hippocampus (Burgess, Maguire, & O'Keefe, 2002; O'Keefe & Nadel, 1978), parahippocampus (Aguirre, Detre, Alsop, & D'Esposito, 1996; Hassabis et al., 2009), retrosplenial cortex (Epstein, 2008; Maguire, 2001; Wolbers & Büchel, 2005), parietal cortex (Howard et al., 2014; Spiers & Maguire, 2007; Whitlock, Sutherland, Witter, Moser, & Moser, 2008), prefrontal cortex (Ciamelli, 2008; Hartley, Maguire, Spiers, & Burgess, 2003; Maguire, Frith, Burgess, Donnett, & O'Keefe, 1998), and caudate nucleus (Bohbot, Lerch, Thorndyck, Iaria, & Zijdenbos, 2007; Packard & Knowlton, 2002). We will organize the literature in terms of coexisting networks of brain regions that support scene-processing, path integration, place learning and goal-directed navigation, and response-based navigation. These regions include cells that are specialized for basic aspects of spatial information (e.g., location, direction, boundary) that are critical for navigation.

Navigation at the cellular level

Place and grid cells in the medial temporal lobe serve distinct (but complementary) functions with respect to the navigator's location (for a review, see Moser, Kropff, & Moser, 2008). A place cell responds when an animal is at a specific location (i.e., the cell's place field) in the local environment (O'Keefe & Dostrovsky, 1971). Place fields are relatively stable over time. A set of place fields will cover the entire local environment but will remap when the animal moves to a different environment or when the local environment substantially changes. One function of remapping is to encode new spatial representations that are sufficiently different from existing representations (McNaughton, Battaglia, Jensen, Moser, & Moser, 2006). This process provides a flexible system for navigating within and between a variety of environments. Place cells rely primarily on visual cues (e.g., boundaries, distant landmarks; Jeffery, 2007) but are not necessarily visual cells in that they may respond to locations in the dark (e.g., by using olfactory cues; Save, Nerad, & Poucet, 2000). These cells were originally discovered in the rat hippocampus (O'Keefe & Dostrovsky, 1971) but have also been found in humans (Ekstrom et al., 2003). Ekstrom and colleagues (2003) recorded from multiple cells in the hippocampus and elsewhere (i.e., the parahippocampus, amygdala, and frontal lobes) while epileptic patients played a taxi driver game. They found cells (primarily in the hippocampus) that responded to specific locations in the virtual environment (Ekstrom et al., 2003). More recently, Hassabis and colleagues (2009) used MVPA to show that the hippocampus can distinguish between different locations within the same virtual environment.

Unlike place cells, grid cells in the entorhinal cortex respond to multiple locations in the environment (Hafting et al., 2005; Moser et al., 2008). Grid fields are regularly spaced, forming a triangular grid that spans the local environment. The spacing of a grid field does not change with respect to changes in environmental boundaries and landmarks, but the spacing and orientation of different grid fields vary systematically from dorsal to ventral layers of the entorhinal cortex (Hafting et al., 2005). This organization provides a coordinate system for the spatial representations encoded by place cells in the hippocampus (Whitlock et al., 2008) and may provide the basis of path integration (Hafting et al., 2005; Moser et al., 2008). In humans, Jacobs and colleagues (2013) collected data from multiple-cell recordings in epileptic patients while the patients learned the locations of four invisible objects in a virtual environment. They found a large concentration of cells in the entorhinal cortex (and also in the hippocampus) that responded to multiple locations in the virtual environment and formed a triangular grid-like pattern (Jacobs et al., 2013). Notably, Jacobs and colleagues found similar cells for which the grid-like pattern was sensitive to movement direction (i.e., conjunctive grid-by-direction cells).

In order to orient within a larger environment, navigators need to know the direction they are facing in addition to their location. Head direction cells respond to an animal's head direction independent of the animal's location or body orientation relative to the head (Taube, Muller, & Ranck, 1990a). Collectively, the preferred directions represented by these cells can be evenly distributed over a 360 degree angle (Taube et al., 1990a). The preferred directions and peak firing rates of head direction cells remain stable over time and depend largely on vestibular input but not necessarily geomagnetic cues (Taube, Muller, & Ranck, 1990b). However, the preferred directions of these cells may be tuned using visual landmarks while learning a new environment (Taube et al., 1990b). Head direction cells were originally found in the presubiculum (Taube et al., 1990a) but have also been found in other areas of the Papez circuit (e.g., retrosplenial cortex, entorhinal cortex), as well as outside of the Papez circuit (e.g., lateral dorsal thalamus, dorsal striatum; Taube, 2007). To date, there has not been direct evidence of head direction cells in humans, but their existence is consistent with evidence of orientation coding in scene processing and navigation (Marchette, Vass, Ryan, & Epstein, 2014). Indeed, Vass and Epstein (2016) found that the retrosplenial complex and entorhinal cortex can code for the observer's imagined heading although these regions may prefer particular headings (e.g., facing north or facing east/west, respectively).

A variety of other cells have been found to contribute to spatial navigation. Border cells (Solstad, Boccara, Kropff, Moser, & Moser, 2008; sometimes referred to as boundary vector cells, Lever, Burton, Jeewajee, O'Keefe, & Burgess, 2009) respond when an animal is close to the border of an environment (e.g., walls, sheer drops) independent of head direction. These cells have been found in different layers of the medial entorhinal cortex together with head direction and grid cells (Solstad et al., 2008). In addition, speed cells (also found in the medial entorhinal cortex; Kropff, Carmichael, Moser, & Moser, 2015) perform a distinct role from grid, border, and head direction cells by

providing the speed profile of an animal during movement. Conjunctive cells combine properties of these different cell types by, for example, responding to both location and head direction (Sargolini et al., 2006). Together, these cells support at least four operations that are fundamental for navigation behavior.

Scene-processing network

The scene-processing network involves the identification of, localization of, and orientation with respect to visual cues learned from a first-person perspective (Epstein, 2008; Epstein & Vass, 2014). Processing of the local scene (e.g., cityscapes, landscapes) is a first step towards navigating between locations. There are at least three functional regions that have been associated with the scene-processing network, including the parahippocampal place area (PPA; Epstein, Harris, Stanley, & Kanwisher, 1999; Epstein & Kanwisher, 1998), retrosplenial complex (RSC; Epstein, Parker, & Feiler, 2007; Maguire, 2001), and occipital place area (OPA; Dilks, Julian, Paunov, & Kanwisher, 2013). All of these regions respond preferentially to scenes than to objects or faces and perform complementary but distinct roles in navigation (Epstein, 2008).

The PPA is located at the boundary of the posterior parahippocampal cortex and the anterior lingual gyrus (Epstein, 2008). Activity in the PPA is similar for scenes with or without discrete objects (i.e., a room containing furniture versus an empty room) and is reduced when the scene's surfaces are reorganized (Epstein & Kanwisher, 1998). This finding suggests that the PPA primarily encodes the local scene with respect to a set of connected surfaces rather than discrete objects within the scene. Indeed, a PET and fMRI studies in which participants navigated virtual environments from a first-person perspective found that activity in the parahippocampal gyrus (not exclusively the PPA) was reduced for environments without objects or textured surfaces (Aguirre et al., 1996; Maguire, Frith, et al., 1998). Using MVPA, Hassabis and colleagues (2009) also found that this region can distinguish between two different virtual rooms. Although studies of the PPA typically use visual stimuli, the PPA has been found to respond to verbal cues (Epstein & Higgins, 2007; Vass & Epstein, 2016). In addition, activity in the PPA is similar for novel and familiar scenes (Epstein, Graham, & Downing, 2003; Epstein et al., 1999; but see Köhler, Crane, & Milner, 2002), but a weak effect has been found for differences in the activation of the PPA during the first presentation of a scene (Epstein et al., 2007). As scenes become more familiar, their representations in the PPA tend to shift from viewpoint-specific (i.e., encoding the local scene from a particular perspective) to viewpoint-invariant, as evidenced by a reduction in the MR signal (i.e., adaptation) to visual stimuli (Epstein, Higgins, & Thompson-Schill, 2005). Indeed, this shift has been correlated to self-reported navigation ability using the Santa Barbara Sense of Direction scale (Epstein et al., 2005; Hegarty, Richardson, Montello, Lovelace, & Subbiah, 2002).

The parietal cortex has been associated with egocentric processing (i.e., with reference to the observer; Burgess, 2006), and the posterior parietal cortex has been correlated with egocentric direction to the goal (Spiers & Maguire, 2007). Specifically, the RSC is functionally located in the medial parietal lobe along the parietal-occipital sulcus and

includes the (structural) retrosplenial cortex proper (Brodmann areas 29 and 30; Epstein, 2008; Epstein & Vass, 2014). While the PPA represents the structure of the local scene, the RSC situates the local scene within the larger, extended environment (Epstein, 2008). For example, Park and Chun (2009) presented portions of panoramic images to participants and found that the PPA considered each portion as a separate scene and that the RSC exhibited adaptation to different portions. Adaptation can also occur for both the PPA and RSC with respect to changes in place, view, and heading (Sulpizio, Committeri, & Galati, 2014), but differences among similar tasks in terms of activation only occurs for the RSC (Epstein et al., 2007). Specifically, Epstein and colleagues (2007) presented views of scenes to participants that differed with respect to location, orientation, and familiarity. They found that the RSC was able to discriminate between these three tasks (in terms of differences in neural activity) but that the PPA responded to these three tasks similarly (Epstein et al., 2007). Recently, Vass and Epstein (2013) instructed participants to judge the heading from which images of a familiar university campus were taken and found that the pattern of activity in the RSC corresponded to the locations from which these images were taken. The relationship between RSC activity and orientation tasks has also been established by another MVPA study using judgments of relative direction (JRDs; Vass & Epstein, 2016). Here, activity in the RSC distinguished between scenes imagined from different headings (Vass & Epstein, 2016). Similarly, Gomez, Cerles, Rousset, Remy, and Baciú (2014) found that the retrosplenial cortex proper (Brodmann area 30) responded to changes in orientation while learning the locations of objects from a video. Marchette and colleagues (2014) found that the RSC codes for both imagined location and heading. In this study, participants learned the locations of objects in museums during navigation through a large virtual park and later performed JRDs towards objects in these museums. The pattern of activity in the RSC corresponded to the geometry of the museum rather than the orientation of the museum within the large park, suggesting that the RSC is particularly tuned to features of the local environment.

Schinazi and Epstein (2010) investigated the roles of the PPA and the RSC with respect to the acquisition of spatial knowledge during large-scale navigation. Participants first learned the buildings along a three-kilometer route and were later scanned while performing a recognition task with those buildings. During the recognition task, the presentation of these buildings was preceded by the presentation of buildings that occurred either immediately beforehand or afterwards along the route (indicating the direction of travel). The results revealed that both the PPA (see also Janzen & van Turennout, 2004; Janzen & Weststeijn, 2007) and RSC responded more strongly to buildings at decision points (e.g., intersections) than to other buildings. In addition, the RSC encoded the direction of travel at decision point buildings, but these effects were driven by the least familiar buildings. Consistent with Montello (1998), Schinazi and Epstein (2010) provide evidence that spatial knowledge acquisition does not occur in discrete stages (i.e., landmark, route, and survey knowledge; see Siegel & White, 1975) but that some of these stages can occur in parallel (see Chrastil, 2013, for an alternative framework based on neural evidence).

A variety of lesion studies largely corroborate these roles for the PPA and RSC in scene processing during navigation (for reviews, see Aguirre & D'Esposito, 1999; Maguire, 2001). In general, damage to the parahippocampal gyrus results in difficulties in encoding novel building landscapes but not drawing a familiar neighborhood from a top-down perspective, suggesting these two tasks tap different navigation systems (Takahashi & Kawamura, 2002). In another study, Mendez and Cherrier (2003) describe a patient with damage to the right medial occipitotemporal region who had difficulties recognizing scenes without prominent landmarks but could navigate using prominent landmarks. Interestingly, damage to the retrosplenial cortex proper does not necessarily affect landmark recognition but does impair the use of landmarks for orientation in a larger environment (Ino et al., 2007; Maguire, 2001). Given these findings, several researchers have concluded that the RSC performs a critical role in shifting between different modes of spatial learning (e.g., egocentric versus allocentric representations; (Epstein, 2008; Vann, Aggleton, & Maguire, 2009).

Studies using temporary lesions (induced with TMS) to a region near the transverse occipital sulcus (i.e., the OPA) impaired the discrimination of scenes but not faces or objects (Dilks et al., 2013). In another TMS study, Julian and colleagues (2016) found that temporary lesions to the OPA disrupts the relationships between boundaries and landmarks, suggesting that the OPA may be important for the representation of scene boundaries. We speculate that the OPA may provide the boundary information necessary for the definition of local scene geometry represented by the RSC.

Path integration

In contrast to scene processing, path integration largely relies on idiothetic (i.e., self-movement) rather than allothetic cues (Taube, 2007; Vann et al., 2009). Path integration refers to the maintenance of the orientation and location of an observer in relation to a larger environment. This process involves the integration of self-motion cues (e.g., optic flow, vestibular input) and the maintenance of this information in working memory (Kim, Sapiurka, Clark, & Squire, 2013; Taube, 2007). Many animals rely heavily on path integration while searching for food and finding their way back home (Gallistel, 1990; Müller & Wehner, 1988). In rats, this system has been associated with grid cells in the entorhinal cortex (Hafting et al., 2005; McNaughton et al., 2006), but in humans, path integration can rely on several other regions, including the hippocampus (e.g., Chrastil et al., 2015; Gomez et al., 2014), prefrontal cortex (PFC; Spiers & Gilbert, 2015), and human motion complex (hMT+; Wolbers, Wiener, Mallot, & Büchel, 2007).

In humans, path integration has been studied using both visual and nonvisual cues. Electrophysiological and neuroimaging studies typically involve videos (or interactive virtual environments) that require the participants to integrate optic flow information over time (e.g., Chrastil et al., 2015; Gramann et al., 2010). For example, Wolbers and colleagues (2007) trained participants to point to the starting location after walking two

legs of a triangle and found a negative correlation between pointing error and activation in the right hippocampus (but see Arnold, Burles, Bray, Levy, & Iaria, 2014). Notably, these authors also report activation in the PFC and hMT+, suggesting that these two regions are involved in the monitoring and updating of hippocampal output (Wolbers et al., 2007). Chrastil and colleagues (2015) extended this finding by comparing homing distance (i.e., vector-based) and degree-based models of path integration. They found that activity in the (bilateral) hippocampus, left parahippocampus, and right retrosplenial cortex proper increased with homing distance and path integration performance (Chrastil et al., 2015). Consistent with these studies, Sherrill, Erdem, Ross, Brown, Hasselmo, and Stern (2013) found that activity in the posterior hippocampus was related to performance on a first-person navigation task that required path integration. In many of these studies, homing (i.e., finding the start location) is used to infer the mechanisms underlying path integration. In such cases, activity in the hippocampus may correspond to the maintenance of any goal location in spatial memory (see subsection on Place learning and goal-directed navigation). In addition, path integration for simple routes and expectation violations during navigation (i.e., detours) may depend in part on spatial working memory and attentional processes supported by the PFC (Arnold et al., 2014; Spiers & Gilbert, 2015).

In contrast, lesion studies often have participants estimate walked distances and turns while blindfolded (e.g., Worsley et al., 2001). These studies partially support the role of the hippocampus in path integration. For example, Worsley and colleagues (2001) tested blindfolded patients with right or left temporal lobectomies using triangle completion and route reproduction tasks. They found that the right temporal lobe may be critical for estimating turns (but not distances; Worsley et al., 2001). However, Philbeck, Behrmann, Levy, Potolicchio, and Caputy (2004) found that damage to the right medial temporal lobe can affect the maintenance of distance information during path integration. In a comparative study involving both humans and animals, Kim and colleagues (2013) argued that the involvement of the medial temporal lobe for humans may depend on the complexity of the outward path. In this case, patients with medial temporal lobe damage (compared to rats with hippocampal damage) were able to successfully integrate shorter outward paths with fewer turns (Kim et al., 2013). These discrepancies between studies may support the idea that the hippocampus is particularly responsible for a specific aspect of path integration such as learning a goal location.

Place learning and goal-directed navigation

Place learning and goal-directed navigation includes the embedding of locations into flexible spatial representations. Place learning is often differentiated from learning sequences of actions that are tied to specific stimuli (i.e., response learning; Hartley & Burgess, 2005; Packard & McGaugh, 1996). In this section, we focus specifically on the neural correlates of place learning and other types of goal-directed navigation. In the next section, we will discuss the way in which place and response learning interact to support navigation. Place learning has been primarily associated with the medial

temporal lobe (e.g., the hippocampus, parahippocampus, and entorhinal cortex; Aguirre et al., 1996; Doeller, Barry, & Burgess, 2010; Howard et al., 2014; O'Keefe & Nadel, 1978) and the PFC (Ciaramelli, 2008; Spiers & Gilbert, 2015). Other regions have also been implicated, including the precuneus (Ghaem et al., 1997), insula (Hartley et al., 2003), and retrosplenial cortex proper (Wolbers & Büchel, 2005).

Since the discovery of place cells in the hippocampus (O'Keefe & Dostrovsky, 1971), several researchers have focused on this region as critical for goal-directed navigation and place learning (O'Keefe & Nadel, 1978). One early study using PET compared London taxi drivers' (i.e., expert navigators) abilities to recall the shortest route between two locations and to describe the appearance of famous landmarks and found activation in the right hippocampus (Maguire, Frackowiak, & Frith, 1997). In another PET study, Maguire, Burgess, Donnett, Frackowiak, Frith, and O'Keefe (1998) also found activity in the right hippocampus as participants navigated towards different familiar goals in a virtual town compared to following a trail (but see Aguirre et al., 1996, for fMRI evidence implicating the parahippocampal gyrus in a similar task). Maguire and colleagues (1998) also found that the hippocampus preferentially responded to the comparison of successful to unsuccessful trials. In addition, Wolbers and Büchel (2005) scanned participants while they watched a video of a route through a virtual environment and later had them report the relative positions of landmarks along this route. Here, the hippocampus was specifically recruited during initial encoding.

Structural imaging has also indicated that grey matter volume in the hippocampus (analyzed using VBM) corresponds with navigation expertise (Maguire et al., 2000; Maguire, Woollett, & Spiers, 2006; Woollett & Maguire, 2011). Maguire and colleagues (2000) found that the posterior hippocampi of London taxi drivers were significantly larger than those of control participants, but the anterior hippocampi were larger in controls than in taxi drivers. Indeed, in a longitudinal study, Woollett and Maguire (2011) found a larger increase in the grey matter volume of the posterior hippocampus in taxi driver trainees who successfully completed the training program compared to unqualified trainees and other controls. Maguire, Woollett, and Spiers (2006) suggest that larger grey matter volumes in the posterior hippocampus of taxi drivers may be attributable to their flexible use of spatial representations during navigation. Specifically, Maguire and colleagues (2006) found that taxi drivers had larger hippocampi than bus drivers who tend to follow predefined routes. Together, these authors suggest that these findings may reflect a tradeoff between goal-directed navigation ability and other spatial memory abilities (e.g., the delayed recall of complex figures; Maguire et al., 2006; Woollett & Maguire, 2011).

fMRI (e.g., Howard et al., 2014) and EEG (e.g., Vass et al., 2016) studies have also implicated the hippocampus in the encoding of distances relative to a goal (Spiers & Barry, 2015). Vass and colleagues (2016) demonstrated that this relationship is indeed attributable to distance metrics rather than travel time and independent of proprioceptive or visual cues. However, different parts of the hippocampus correspond to different

distance metrics (i.e., Euclidean versus route; Howard et al., 2014; Morgan, Macevoy, Aguirre, & Epstein, 2011). Morgan and colleagues (2011) scanned participants while viewing familiar landmarks on a university campus and found a linear relationship between activity in the left anterior hippocampus and the Euclidean distance between consecutively presented landmarks. Notably, this activity was also correlated with subjective ratings of these distances (Morgan et al., 2011). In addition, Howard and colleagues (2014) scanned participants while viewing a video of a previously walked route. At some decision points, participants were asked to report which direction to go. Howard and colleagues (2014) found that activity in the posterior hippocampus was related to route distance between their current location in the video and the goal, whereas activity in the anterior hippocampus was related to Euclidean distance between their current location in the video and the goal. In contrast, Sherrill and colleagues (2013) found that activation in the posterior hippocampi was related to Euclidean distance to a goal during navigation. Other regions of the medial temporal lobe (primarily the entorhinal cortex) may also be related to the representations of Euclidean distances (Howard et al., 2014; Spiers & Barry, 2015). For example, Howard and colleagues (2014) found a relationship between entorhinal activity and changes in Euclidean distances to the goal. Indeed, Doeller and colleagues (2010) found evidence for grid cell-like activity in the entorhinal cortex and elsewhere underlying goal-directed navigation (see also Jacobs et al., 2013).

Most lesion studies support the idea that the medial temporal lobe (in particular the right hemisphere) is critical for place learning (Abrahams, Pickering, Polkey, & Morris, 1997; Holdstock et al., 2000; Holdstock, Mayes, Cezayirli, Aggleton, & Roberts, 1999) and goal-directed navigation (Astur, Taylor, Mamelak, Philpott, & Sutherland, 2002; Maguire, Nannery, & Spiers, 2006; Spiers, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2001). In general, damage to this region impairs spatial memory but not object memory (Abrahams et al., 1997; Spiers et al., 2001). With respect to navigation, Astur and colleagues (2002) found that patients with bilateral medial temporal lobe lesions were unable to locate a hidden platform in a virtual version of the Morris water maze task (see Morris, Garrud, Rawlins, & O'Keefe, 1982). Similarly, Spiers and colleagues (2001) described one patient with bilateral hippocampal pathology who could not navigate towards a location, recognize previously visited locations, or draw maps of a learned virtual reality environment. However, Maguire and colleagues (2006) suggested that the hippocampus may be more critical for encoding fine-grained details such as small streets rather than main arteries during navigation.

While the hippocampus may be necessary for goal-directed navigation, the PFC appears to be necessary for maintaining the location of a goal in working memory (Ciaramelli, 2008). Ciaramelli (2008) described one patient with bilateral damage to the ventromedial prefrontal cortex who had difficulties navigating his hometown but no impairment of landmark and route knowledge. However, this patient's performance would improve when reminded of or asked to rehearse the destination during navigation (Ciaramelli, 2008). Consistent with Ciaramelli (2008), an fMRI study by Spiers and

Maguire (2006) decomposed navigation into several categories using retrospective think aloud data and found that activity in the PFC was related to route planning. In a different analysis, the same data indicated a positive correlation between activity in the PFC and proximity to the goal (Spiers & Maguire, 2007), suggesting that this region is involved with actively maintaining goal information (Spiers, 2008). The differential recruitment of the hippocampus and PFC may reflect different strategies for navigation (Burgess et al., 2002) and result in gender differences (Grön, Wunderlich, Spitzer, Tomczak, & Riepe, 2000), but these findings are somewhat inconclusive.

Electrophysiological studies have also associated the theta band with goal-directed navigation (Bischof & Boulanger, 2003; Caplan et al., 2003; Kober & Neuper, 2011; Vass et al., 2016; White, Congedo, Ciorciari, & Silberstein, 2012). Using both EEG at the scalp and intracranial EEG (iEEG), these authors have related patterns of theta activity to determining the shortest path between two landmarks (Kober & Neuper, 2011) and navigating through a familiar virtual town (White et al., 2012), virtual T-junction mazes (Caplan et al., 2003), and complex virtual mazes (Bischof & Boulanger, 2003). Given the low spatial resolution of EEG, connecting these results to the imaging studies described above can be difficult. However, future experimental designs may exploit the high temporal resolution of EEG in order to study the dynamics of spatial processing during navigation. Another possibility is for researchers to capitalize on the higher spatial resolution of techniques such as MEG. For example, Cornwell and colleagues (2008) used a combination of MEG and MRI in order to investigate the role of theta oscillations in the hippocampus and parahippocampus during goal-directed navigation through a virtual Morris water maze task. These results were also consistent with the role of the hippocampus specifically in early learning (Iaria et al., 2003; Wolbers & Büchel, 2005) and the relationship between hippocampal theta oscillations and navigation (Vass et al., 2016).

Response-based navigation

Response-based navigation consists of associations between sequences of actions and local environmental cues (i.e., turn left at the mosque). Compared to place learning, response-based representations are relatively rigid and have been primarily associated with the basal ganglia, particularly the caudate nucleus (Hartley & Burgess, 2005; Packard & Knowlton, 2002). The relationship between place and response learning has been characterized in terms of competition, cooperation, or compensation (Hartley & Burgess, 2005). Competition between these two systems occurs when these two types of learning are placed into conflict. For example, Bohbot and colleagues (2007) asked participants to learn locations within a radial arm maze. Landmarks were present during learning but absent during testing, resulting in a task that favored response-learning (Bohbot et al., 2007). VBM analyses revealed a positive correlation between the number of errors in the maze and grey matter volume in the hippocampus and a negative correlation between number of errors and grey matter volume in the caudate nucleus (Bohbot et al., 2007). In contrast, Schinazi and colleagues (2013) found that errors in

JRDs (i.e., inferences regarding the relative locations of landmarks in a large-scale environment) were positively correlated with grey matter volume in the caudate nucleus and negatively correlated with grey matter volume in the hippocampus. These findings helped explain individual differences from previous research in geography that used a similar method (Ishikawa & Montello, 2006; see also Chapter 7 of this volume on Learning the Environment). Similarly, Marchette, Bakker, and Shelton (2011) dissociated hippocampal and caudal activity in terms of place (i.e., shortcutting) and response (i.e., route reproduction) strategies.

Cooperation between these two systems occurs when participants shift from reliance from one system to another (Hartley & Burgess, 2005). For example, Hartley and colleagues (2003) asked participants to follow a well-known route and wayfind through a virtual town. For good navigators, the caudate nucleus was active during the route-following task, and the hippocampus was active during the wayfinding task. Based on self-reported strategies, Iaria and colleagues (2003) distinguished between place and response learners in a virtual radial arm maze. They found that place learners had more activation in the right hippocampus only during the early stages of learning (consistent with Wolbers & Büchel, 2005) and for response learners, activity in the caudate nucleus increased with learning (Iaria et al., 2003). Together these results are consistent with animal studies in which healthy rats shift from a place learning to a response learning strategy over time (Packard & McGaugh, 1996).

Compensation occurs when damage to or inhibition of one system leads to the recruitment of the other system. For example, Packard and McGaugh (1996) found that rats with selective chemical lesions (i.e., lidocaine injections) to the hippocampus or caudate nucleus exhibited different patterns of spatial learning. Specifically, damage to the caudate nucleus resulted in a preference for place learning in a cross maze over learning. Damage to the hippocampus resulted in no preference for a specific strategy during early trials but a preference for response learning during later trials (Packard & McGaugh, 1996). In humans, gradual increases in dysfunction of the caudate nucleus caused by Huntington's disease leads to compensation by the hippocampus (Voermans et al., 2004). Voermans and colleagues (2004) scanned participants while recalling previously experienced turns at specific intersections inside a virtual house. These researchers found that the progression of the disease decreased recruitment of the caudate nucleus and increased recruitment of the hippocampus. This compensatory change did not result in a change in navigation performance (Voermans et al., 2004).

Conclusions and outlook

Behavioral geography is traditionally open to different disciplines, adopting their methods and ways of thinking. At the same time, geographic research has struggled to incorporate neuroscientific methods appropriately. This challenge may be related to past difficulties with the establishment of behavioral geography as a positivist science and result from a lack of training in experimental approaches more generally. In this chapter,

we have argued that the bridging of these two disciplines requires a theory-driven approach and more focused training in neuroscientific methods. Towards this end, we have also provided a primer on neural anatomy and neuroscientific techniques. This primer serves as a basic introduction to the discipline and also highlights some of the complexities involved in conducting neuroscientific research. We also reviewed previous research on geospatial thinking (largely conducted by geographers) and navigation (largely conducted by neuroscientists). Despite geographers' initial efforts, research in geospatial thinking has not extended beyond an exploratory approach. In contrast, navigation research is relatively well-developed and theoretically driven.

Given this perspective, there are at least three ways to proceed. If geographers wish to pursue neuroscientific research, additional training or experienced collaborators are necessary. This training should include experience in a neuroscience department for the development of both theoretical concepts and practical laboratory skills. Geographers could also involve collaborators from neuroscience in the initial development of experimental designs and not just post hoc analyses or interpretations. These two options could help shift neuroscience research in geography to a more hypothesis-driven model that can be used to investigate unresolved questions (e.g., individual differences in geospatial thinking skills). However, these two options have so far proven difficult to pursue. Another alternative is using neuroscientific knowledge for informing and interpreting research in behavioral geography. Although we consider positivist research in behavioral geography important, geographers may address their questions more efficiently by applying skills in geography and exchanging possible solutions with neuroscientists.

References

- Abrahams, S., Pickering, A., Polkey, C. E., & Morris, R. G. (1997). 'Spatial memory deficits in patients with unilateral damage to the right hippocampal formation'. *Neuropsychologia*, **35**(1), 11–24.
- Aguirre, G. K., & D'Esposito, M. (1999). 'Topographical disorientation: a synthesis and taxonomy'. *Brain*, **122**(9), 1613–1628.
- Aguirre, G. K., Detre, J. A., Alsop, D. C., & D'Esposito, M. (1996). 'The parahippocampus subserves topographical learning in man'. *Cereb Cortex*, **6**(6), 823–9.
- Amaro, E., & Barker, G. J. (2006). 'Study design in fMRI: basic principles.'. *Brain and Cognition*, **60**(3), 220–32.
- Argent, N. M., & Walmsley, D. J. (2009). 'From the inside looking out and the outside looking in: Whatever happened to “behavioural geography”?'. *Geographical Research*, **47**(2), 192–203.
- Arnold, A. E. G. F., Burles, F., Bray, S., Levy, R. M., & Iaria, G. (2014). 'Differential neural network configuration during human path integration.'. *Frontiers in Human Neuroscience*, **8**, 263.

- Astur, R. S., Taylor, L. B., Mamelak, A. N., Philpott, L., & Sutherland, R. J. (2002). 'Humans with hippocampus damage display severe spatial memory impairments in a virtual Morris water task.'. *Behavioural Brain Research*, **132**(1), 77–84.
- Bednarz, R. S., & Lee, J. (2011). 'The components of spatial thinking: empirical evidence'. *Procedia - Social and Behavioral Sciences*, **21**, 103–107.
- Bischof, W. F., & Boulanger, P. (2003). 'Spatial navigation in virtual reality environments: an EEG analysis.'. *Cyberpsychology & Behavior: The Impact of the Internet, Multimedia and Virtual Reality on Behavior and Society*, **6**(5), 487–95.
- Bohbot, V. D., Lerch, J., Thorndyraft, B., Iaria, G., & Zijdenbos, A. P. (2007). 'Gray matter differences correlate with spontaneous strategies in a human virtual navigation task'. *J Neurosci*, **27**(38), 10078–83.
- Bunting, T. E., & Guelke, L. (1979). 'Behavioral and perception geography: A critical appraisal'. *Annals of the Association of American Geographers*, **69**(3), 448–462.
- Burgess, N. (2006). 'Spatial memory: how egocentric and allocentric combine'. *Trends in Cognitive Sciences*, **10**(12), 551–557.
- Burgess, N., Maguire, E. A., & O'Keefe, J. (2002). 'The human hippocampus and spatial and episodic memory'. *Neuron*, **35**, 625–641.
- Caplan, J. B., Madsen, J. R., Schulze-Bonhage, A., Aschenbrenner-Scheibe, R., Newman, E. L., & Kahana, M. J. (2003). 'Human theta oscillations related to sensorimotor integration and spatial learning.'. *Journal of Neuroscience*, **23**(11), 4726–36.
- Chrastil, E. R. (2013). 'Neural evidence supports a novel framework for spatial navigation.'. *Psychonomic Bulletin & Review*, **20**(2), 208–27.
- Chrastil, E. R., Sherrill, K. R., Hasselmo, M. E., & Stern, C. E. (2015). 'There and Back Again: Hippocampus and Retrosplenial Cortex Track Homing Distance during Human Path Integration.'. *Journal of Neuroscience*, **35**(46), 15442–52.
- Ciaramelli, E. (2008). 'The role of ventromedial prefrontal cortex in navigation: a case of impaired wayfinding and rehabilitation'. *Neuropsychologia*, **46**(7), 2099–105.
- Cohen Kadosh, R., Henik, A., Rubinsten, O., Mohr, H., Dori, H., van de Ven, V., ... Linden, D. E. J. (2005). 'Are numbers special? The comparison systems of the human brain investigated by fMRI'. *Neuropsychologia*, **43**(9), 1238–1248.
- Cohen, M. S., & DuBois, R. M. (1999). 'Stability, repeatability, and the expression of signal magnitude in functional magnetic resonance imaging.'. *Journal of Magnetic Resonance Imaging: JMRI*, **10**(1), 33–40.
- Cohen, M. S., Kosslyn, S. M., Breiter, H. C., DiGirolamo, G. J., Thompson, W. L., Anderson, A. K., ... Belliveau, J. W. (1996). 'Changes in cortical activity during mental rotation. A mapping study using functional MRI.'. *Brain: A Journal of Neurology*, **119**(1),

89–100.

Cornwell, B. R., Johnson, L. L., Holroyd, T., Carver, F. W., & Grillon, C. (2008). 'Human hippocampal and parahippocampal theta during goal-directed spatial navigation predicts performance on a virtual Morris water maze.'. *Journal of Neuroscience*, **28**(23), 5983–90.

Couclelis, H., & Golledge, R. G. (1983). 'Analytic research, positivism, and behavioral geography'. *Annals of the Association of American Geographers*, **73**, 331–339.

Couclelis, H., Golledge, R. G., Gale, N., & Tobler, W. (1987). 'Exploring the anchor-point hypothesis of spatial cognition'. *Journal of Environmental Psychology*, **7**, 99–122.

Dilks, D. D., Julian, J. B., Paunov, A. M., & Kanwisher, N. (2013). 'The occipital place area is causally and selectively involved in scene perception.'. *Journal of Neuroscience*, **33**(4), 1331–6a.

Doeller, C. F., Barry, C., & Burgess, N. (2010). 'Evidence for grid cells in a human memory network.'. *Nature*, **463**(7281), 657–61.

Downs, R., & de Souza, A. R. (2006). *Learning to think spatially: GIS as a support system in the K-12 curriculum*. Washington, DC.

Dunn, J. M. (2011). 'Location knowledge: Assessment, spatial thinking, and new national geography standards'. *Journal of Geography*, **110**(2), 81–89.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). 'Cellular networks underlying human spatial navigation'. *Nature*, **425**(6954), 184–8.

Epstein, R. A. (2008). 'Parahippocampal and retrosplenial contributions to human spatial navigation'. *Trends Cogn Sci*, **12**(10), 388–96.

Epstein, R. A., & Higgins, J. S. (2007). 'Differential parahippocampal and retrosplenial involvement in three types of visual scene recognition.'. *Cerebral Cortex (New York, N.Y. : 1991)*, **17**(7), 1680–93.

Epstein, R. A., Higgins, J. S., & Thompson-Schill, S. L. (2005). 'Learning places from views: variation in scene processing as a function of experience and navigational ability'. *J Cogn Neurosci*, **17**(1), 73–83.

Epstein, R. A., Parker, W. E., & Feiler, A. M. (2007). 'Where am I now? Distinct roles for parahippocampal and retrosplenial cortices in place recognition'. *J Neurosci*, **27**(23), 6141–9.

Epstein, R. A., & Vass, L. K. (2014). 'Neural systems for landmark-based wayfinding in humans.'. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **369**(1635), 20120533.

Epstein, R., Graham, K., & Downing, P. E. (2003). 'Viewpoint specific scene representations in human parahippocampal cortex'. *Neuron*, **37**, 865–876.

Epstein, R., Harris, A., Stanley, D., & Kanwisher, N. (1999). 'The parahippocampal place area: recognition, navigation, or encoding?'. *Neuron*, **23**(1), 115–25.

Epstein, R., & Kanwisher, N. (1998). 'A cortical representation of the local visual environment'. *Nature*, **392**(6676), 598–601.

Farah, M. J., & Hook, C. J. (2013). 'The Seductive Allure of “Seductive Allure”'. *Perspectives on Psychological Science: A Journal of the Association for Psychological Science*, **8**(1), 88–90.

Fuchs, T. (2006). 'Ethical issues in neuroscience.'. *Current Opinion in Psychiatry*, **19**(6), 600–7.

Gallistel, C. R. (1990). *The Organization of Learning*. Cambridge, MA: MIT Press.

Gazzaniga, M. S., Ivry, R. B., & Mangun, G. R. (2014). *Cognitive Neuroscience: The Biology of the Mind* (Fourth edi). New York, NY, USA: W.W. Norton & Co.

Gersmehl, P., & Gersmehl, C. (2011). 'Spatial thinking: Where pedagogy meets neuroscience'. *Problems of Education in the 21st Century*, **27**, 48–66.

Gersmehl, P. J. (2012). "“Wormholes” in the common core: Spatial reasoning, literacy, and mathematics education'. *Anekumene*, **1**(2), 37–53.

Gersmehl, P. J., & Gersmehl, C. A. (2006). 'Wanted: A concise list of neurologically defensible and assessable spatial thinking skills'. *Research in Geographic Education*, **8**(1), 5–38.

Gersmehl, P. J., & Gersmehl, C. A. (2007). 'Spatial thinking by young children: Neurologic evidence for early development and “Educability”'. *Journal of Geography*, **106**(5), 181–191.

Ghaem, O., Mellet, E., Crivello, F., Tzourio, N., Mazoyer, B., Berthoz, A., & Denis, M. (1997). 'Mental navigation along memorized routes activates the hippocampus, precuneus, and insula'. *Neuroreport*, **8**(3), 739–744.

Gibson, J. J. (1966). *The Senses Considered as Perceptual Systems*. Boston: Houghton-Mifflin.

Golledge, G. R. (1978). 'Representing, interpreting and using cognized environments'. *Papers and Proceedings, Regional Science Association*, **41**, 169–204.

Golledge, R. G. (1995). 'Primitives of spatial knowledge'. In T. L. Nyerges, D. M. Mark, R. Laurini, & M. J. Egenhofer (Eds.), *Cognitive Aspects of Human-Computer Interaction for Geographic Information Systems* (pp. 29–44). Dordrecht, Netherlands: Kluwer Academic Publishers.

Golledge, R. G. (2008). 'Behavioral geography and the theoretical/quantitative revolution'. *Geographical Analysis*, **40**(3), 239–257.

Golledge, R. G., & Rushton, G. (1976). 'Spatial Choice and Spatial Behavior'.

- Golledge, R. G., & Stimson, R. J. (1997). *Spatial Behavior: A Geographic Perspective*. New York: Guilford Press.
- Golledge, R., Marsh, M., & Battersby, S. E. (2008). 'A conceptual framework for facilitating spatial thinking'. *Annals of the Association of American Geographers*, **98**(2), 285–308.
- Gomez, A., Cerles, M., Rousset, S., Rémy, C., & Baciú, M. (2014). 'Differential hippocampal and retrosplenial involvement in egocentric-updating, rotation, and allocentric processing during online spatial encoding: an fMRI study.'. *Frontiers in Human Neuroscience*, **8**, 150.
- Good, C. D., Johnsrude, I. S., Ashburner, J., Henson, R. N., Friston, K. J., & Frackowiak, R. S. (2001). 'A voxel-based morphometric study of ageing in 465 normal adult human brains.'. *NeuroImage*, **14**(1), 21–36.
- Goodale, M. A., & Milner, A. D. (1992). 'Separate visual pathways for perception and action.'. *Trends in Neurosciences*, **15**(1), 20–5.
- Goodchild, M. F., & Janelle, D. G. (2010). 'Toward critical spatial thinking in the social sciences and humanities.'. *GeoJournal*, **75**(1), 3–13.
- Gramann, K., Onton, J., Riccobon, D., Mueller, H. J., Bardins, S., & Makeig, S. (2010). 'Human brain dynamics accompanying use of egocentric and allocentric reference frames during navigation.'. *Journal of Cognitive Neuroscience*, **22**(12), 2836–49.
- Grön, G., Wunderlich, A. P., Spitzer, M., Tomczak, R., & Riepe, M. W. (2000). 'Brain activation during human navigation: gender-different neural networks as substrate of performance'. *Nature Neuroscience*, **3**, 404–408.
- Hafting, T., Fyhn, M., Molden, S., Moser, M. B., & Moser, E. I. (2005). 'Microstructure of a spatial map in the entorhinal cortex'. *Nature*, **436**(7052), 801–6.
- Hartley, T., & Burgess, N. (2005). 'Complementary memory systems: competition, cooperation and compensation'. *Trends Neurosci*, **28**(4), 169–70.
- Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). 'The well-worn routed and the path less traveled: Distinct neural bases of route following and wayfinding in humans'. *Neuron*, **37**, 877–888.
- Hassabis, D., Chu, C., Rees, G., Weiskopf, N., Molyneux, P. D., & Maguire, E. A. (2009). 'Decoding Neuronal Ensembles in the Human Hippocampus'. *Current Biology*, **19**(7), 546–554.
- Hegarty, M., Richardson, A. E., Montello, D. R., Lovelace, K., & Subbiah, I. (2002). 'Development of a self-report measure of environmental spatial ability'. *Intelligence*, **30**, 425–447.
- Henson, R. (2005). 'What can functional neuroimaging tell the experimental psychologist?'. *The Quarterly Journal of Experimental Psychology Section A*, **58**(2),

193–233.

Holdstock, J. S., Mayes, A. R., Cezayirli, E., Aggleton, J. P., & Roberts, N. (1999). 'A comparison of egocentric and allocentric spatial memory in medial temporal lobe and Korsakoff amnesics'. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, **35**(4), 479–501.

Holdstock, J. S., Mayes, A. R., Cezayirli, E., Isaac, C. L., Aggleton, J. P., & Roberts, N. (2000). 'A comparison of egocentric and allocentric spatial memory in a patient with selective hippocampal damage'. *Neuropsychologia*, **38**(4), 410–425.

Howard, L. R., Javadi, A. H., Yu, Y., Mill, R. D., Morrison, L. C., Knight, R., ... Spiers, H. J. (2014). 'The hippocampus and entorhinal cortex encode the path and Euclidean distances to goals during navigation.'. *Current Biology : CB*, **24**(12), 1331–40.

Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. D. (2003). 'Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: variability and change with practice'. *Journal of Neuroscience*, **23**(13), 5945–52.

Ino, T., Doi, T., Hirose, S., Kimura, T., Ito, J., & Fukuyama, H. (2007). 'Directional disorientation following left retrosplenial hemorrhage: a case report with fMRI studies.'. *Cortex*, **43**(2), 248–54.

Ishikawa, T., & Montello, R. D. (2006). 'Spatial knowledge acquisition from direct experience in the environment: Individual differences in the development of metric knowledge and the integration of separately learned places'. *Cognitive Psychology*, **52**, 93–129.

Jacobs, J., Weidemann, C. T., Miller, J. F., Solway, A., Burke, J. F., Wei, X.-X., ... Kahana, M. J. (2013). 'Direct recordings of grid-like neuronal activity in human spatial navigation.'. *Nature Neuroscience*, **16**(9), 1188–90.

Janzen, G., & van Turenout, M. (2004). 'Selective neural representation of objects relevant for navigation'. *Nature Neuroscience*, **7**(6), 673–677.

Janzen, G., & Weststeijn, C. G. (2007). 'Neural representation of object location and route direction: An event-related fMRI study'. *Brain Research*, **1165**, 116–125.

Jeffery, K. J. (2007). 'Integration of the sensory inputs to place cells: what, where, why, and how?'. *Hippocampus*, **17**(9), 775–85.

Josephs, O., & Henson, R. N. (1999). 'Event-related functional magnetic resonance imaging: modelling, inference and optimization.'. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **354**(1387), 1215–28.

Julian, J. B., Ryan, J., Hamilton, R. H., & Epstein, R. A. (2016). 'The Occipital Place Area Is Causally Involved in Representing Environmental Boundaries during Navigation.'. *Current Biology : CB*, **26**(8), 1104–9.

Kavouras, M., Kokla, M., Tomai, E., Darra, N., Baglatzi, A., Sotiriou, S. A., & Lazoudis, A. (2014). 'The GEOTHNK platform: Connecting spatial thinking to secondary

education'. In *2014 IEEE 14th International Conference on Advanced Learning Technologies* (pp. 754–758). Athens, Greece: IEEE.

Kim, S., Sapiurka, M., Clark, R. E., & Squire, L. R. (2013). 'Contrasting effects on path integration after hippocampal damage in humans and rats.'. *Proceedings of the National Academy of Sciences of the United States of America*, **110**(12), 4732–7.

Kitchin, R., & Blades, M. (2002). *The Cognition of Geographic Space*. London: Taurus.

Kitchin, R. M. (2006). 'Positivist geographies and spatial science'. In S. Aitkin & G. Valentine (Eds.), *Approaches to Human Geography* (pp. 20–29). London, UK: SAGE Publications Ltd.

Kitchin, R. M., Blades, M., & Golledge, R. G. (1997). 'Relations between psychology and geography'. *Environment & Behavior*, **29**(4), 554–573.

Kober, S. E., & Neuper, C. (2011). 'Sex differences in human EEG theta oscillations during spatial navigation in virtual reality.'. *International Journal of Psychophysiology*, **79**(3), 347–55.

Köhler, S., Crane, J., & Milner, B. (2002). 'Differential contributions of the parahippocampal place area and the anterior hippocampus to human memory for scenes.'. *Hippocampus*, **12**(6), 718–23.

Kropff, E., Carmichael, J. E., Moser, M.-B., & Moser, E. I. (2015). 'Speed cells in the medial entorhinal cortex'. *Nature*, **523**(7561), 419–24.

Kwan, M.-P., & Schwanen, T. (2009). 'Quantitative revolution 2: The critical (re)turn'. *The Professional Geographer*, **61**(3), 283–291.

Lever, C., Burton, S., Jeewajee, A., O'Keefe, J., & Burgess, N. (2009). 'Boundary vector cells in the subiculum of the hippocampal formation.'. *Journal of Neuroscience*, **29**(31), 9771–7.

Lindquist, M. A. (2008). 'The statistical analysis of fMRI data'. *Statistical Science*, **23**(4), 439–464.

Lobben, A. K., Lawrence, M., & Olson, J. M. (2009). 'fMRI and human subjects research in cartography'. *Cartographica*, **44**(3), 159–169.

Lobben, A. K., Lawrence, M., & Pickett, R. M. (2014). 'The map effect'. *Annals of the Association of American Geographers*, **104**(1), 96–113.

Lobben, A. K., Olson, J. M., & Huang, J. (2005). 'Using fMRI in cartographic research'. In *Proceedings of the 22nd International Cartographic Conference* (pp. 1–10). A Coruna, Spain.

Lobben, A., & Lawrence, M. (2015). 'Synthesized model of geospatial thinking'. *The Professional Geographer*, **67**(3), 307–318.

Loomis, J. M., Klatzky, R. L., Golledge, R. G., Cicinelli, J. G., Pellegrino, J. W., & Fry, P.

- A. (1993). 'Nonvisual navigation by blind and sighted: Assessment of path integration ability'. *Journal of Experimental Psychology, General*, **122**, 73–91.
- Maguire, E. A. (2001). 'The retrosplenial contribution to human navigation: a review of lesion and neuroimaging findings'. *Scand J Psychol*, **42**(3), 225–38.
- Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S. J., Frith, C. D., & O'Keefe, J. (1998). 'Knowing where and getting there: A human navigation network'. *Science*, **280**, 921–924.
- Maguire, E. A., Frackowiak, R. S. J., & Frith, C. D. (1997). 'Recalling routes around London: Activation of the right hippocampus in taxi drivers'. *The Journal of Neuroscience*, **17**, 703–7110.
- Maguire, E. A., Frith, C. D., Burgess, N., Donnett, J. G., & O'Keefe, J. (1998). 'Knowing where things are: Parahippocampal involvement in encoding object locations in virtual mental imagery'. *Journal of Cognitive Neuroscience*, **10**, 61–76.
- Maguire, E. A., Gadian, D. G., Johnsrude, I. S., Good, C. D., Ashburner, J., Frackowiak, R. S. J., & Frith, C. D. (2000). 'Navigation-related structural change in the hippocampi of taxi drivers'. *Proceedings of the National Academy of Science*, **97**(8), 4398–403.
- Maguire, E. A., Nannery, R., & Spiers, H. J. (2006). 'Navigation around London by a taxi driver with bilateral hippocampal lesions.'. *Brain*, **129**, 2894–2907.
- Maguire, E. A., Woollett, K., & Spiers, H. J. (2006). 'London taxi drivers and bus drivers: a structural MRI and neuropsychological analysis'. *Hippocampus*, **16**(12), 1091–1101.
- Manning, A. (2014). 'Gersmehl and Gersmehl's "Wanted: A concise list of . . . spatial thinking skills"'. *Geography*, **99**(2), 108–110.
- Marchette, S. A., Bakker, A., & Shelton, A. L. (2011). 'Cognitive mappers to creatures of habit: differential engagement of place and response learning mechanisms predicts human navigational behavior.'. *Journal of Neuroscience*, **31**(43), 15264–8.
- Marchette, S. A., Vass, L. K., Ryan, J., & Epstein, R. A. (2014). 'Anchoring the neural compass: coding of local spatial reference frames in human medial parietal lobe.'. *Nature Neuroscience*, **17**(11), 1598–606.
- Marchette, S. A., Vass, L. K., Ryan, J., & Epstein, R. A. (2015). 'Outside Looking In: Landmark Generalization in the Human Navigational System.'. *Journal of Neuroscience*, **35**(44), 14896–908.
- McNaughton, B. L., Battaglia, F. P., Jensen, O., Moser, E. I., & Moser, M.-B. (2006). 'Path integration and the neural basis of the "cognitive map".'. *Nature Reviews Neuroscience*, **7**(8), 663–78.
- Mendez, M. F., & Chierri, M. M. (2003). 'Agnosia for scenes in topographagnosia.'. *Neuropsychologia*, **41**(10), 1387–95.

- Milner, A. D., & Goodale, M. A. (2008). 'Two visual systems re-viewed.'. *Neuropsychologia*, **46**(3), 774–85.
- Mohan, L., Mohan, A., & Uttal, D. (2015). 'Research on thinking and learning with maps and geospatial technologies'. In M. Solem, N. Huynh, & R. Boehm (Eds.), *Learning Progressions for Maps, Geospatial Technology, and Spatial Thinking* (pp. 9–21). New York, New York, USA: Cambridge University Press.
- Montello, D. R. (1993). 'Scale and multiple psychologies of space'. In A. U. Frank & I. Campari (Eds.), *Spatial information theory: A theoretical basis for GIS* (pp. 312–321). New York: Springer-Verlag.
- Montello, R. D. (1998). 'A new framework for understanding the acquisition of spatial knowledge in large-scale environments'. In J. M. Egenhofer & G. R. Golledge (Eds.) (pp. 143–154). New York: Oxford University Press.
- Morgan, L. K., Macevoy, S. P., Aguirre, G. K., & Epstein, R. A. (2011). 'Distances between real-world locations are represented in the human hippocampus.'. *Journal of Neuroscience*, **31**(4), 1238–45.
- Morris, R. G., Garrud, P., Rawlins, J. N., & O'Keefe, J. (1982). 'Place navigation impaired in rats with hippocampal lesions.'. *Nature*, **297**(5868), 681–3.
- Moser, E. I., Kropff, E., & Moser, M.-B. (2008). 'Place cells, grid cells, and the brain's spatial representation system.'. *Annual Review of Neuroscience*, **31**, 69–89.
- Müller, M., & Wehner, R. (1988). 'Path integration in desert ants, *Cataglyphis Fortis*'. *Proceedings of the National Academy of Sciences of the United States of America*, **85**, 5287–5290.
- O'Keefe, J., & Dostrovsky, J. (1971). 'The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat'. *Brain Research*, **34**, 171–175.
- O'Keefe, J., & Nadel, L. (1978). *The Hippocampus as a Cognitive Map*. Oxford: Clarendon Press.
- Packard, M. G., & Knowlton, B. J. (2002). 'Learning and memory functions of the Basal Ganglia'. *Annual Review of Neuroscience*, **25**, 563–593.
- Packard, M. G., & McGaugh, J. L. (1996). 'Inactivation of Hippocampus or Caudate Nucleus with Lidocaine Differentially Affects Expression of Place and Response Learning'. *Neurobiology of Learning and Memory*, **65**(1), 65–72.
- Paglen, T. (2009). 'Experimental geography: From cultural production to the production of space'. In N. Thompson (Ed.), *Experimental Geography: Radical Approaches to Landscape, Cartography, and Urbanism* (pp. 27–33). New York, NY, USA: Melville House.
- Park, S., & Chun, M. M. (2009). 'Different roles of the parahippocampal place area (PPA) and retrosplenial cortex (RSC) in panoramic scene perception.'. *NeuroImage*, **47**(4), 1747–56.

- Philbeck, J. W., Behrmann, M., Levy, L., Potoicchio, S. J., & Caputy, A. J. (2004). 'Path integration deficits during linear locomotion after human medial temporal lobectomy.'. *Journal of Cognitive Neuroscience*, **16**(4), 510–20.
- Poldrack, R. A. (2007). 'Region of interest analysis for fMRI.'. *Social Cognitive and Affective Neuroscience*, **2**(1), 67–70.
- Poldrack, R. A., Mumford, J. A., & Nichols, T. E. (2011). *Handbook of Functional MRI Data Analysis*. New York, NY, USA: Cambridge University Press.
- Rushton, G. (1979). 'Commentary on behavioral and perception geography'. *Annals of the Association of American Geographers*, **69**, 463–474.
- Sargolini, F., Fyhn, M., Hafting, T., McNaughton, B. L., Witter, M. P., Moser, M.-B., & Moser, E. I. (2006). 'Conjunctive representation of position, direction, and velocity in entorhinal cortex.'. *Science (New York, N.Y.)*, **312**(5774), 758–62.
- Save, E., Nerad, L., & Poucet, B. (2000). 'Contribution of multiple sensory information to place field stability in hippocampal place cells.'. *Hippocampus*, **10**(1), 64–76.
- Schinazi, V. R., & Epstein, R. A. (2010). 'Neural correlates of real-world route learning'. *Neuroimage*, **53**(2), 725–35.
- Schinazi, V. R., Nardi, D., Newcombe, N. S., Shipley, T. F., & Epstein, R. A. (2013). 'Hippocampal size predicts rapid learning of a cognitive map in humans'. *Hippocampus*, **23**(6), 515–528.
- Schinazi, V. R., Thrash, T., & Chebat, D.-R. (2015). 'Spatial navigation by congenitally blind individuals'. *Wiley Interdisciplinary Reviews: Cognitive Science*, n/a–n/a.
- Schultz, D. P., & Schultz, S. E. (2008). *A History of Modern Psychology*. Belmont, CA: Thomson Wadsworth.
- Shelton, A. L., & Gabrieli, J. D. (2002). 'Neural correlates of encoding space from route and survey perspectives'. *J Neurosci*, **22**(7), 2711–7.
- Sherrill, K. R., Erdem, U. M., Ross, R. S., Brown, T. I., Hasselmo, M. E., & Stern, C. E. (2013). 'Hippocampus and retrosplenial cortex combine path integration signals for successful navigation.'. *Journal of Neuroscience*, **33**(49), 19304–13.
- Siegel, A. W., & White, S. H. (1975). 'The development of spatial representations of large-scale environments'. *Adv Child Dev Behav*, **10**, 9–55.
- Smith, N. (1979). 'Geography, science, and post-positivist modes of explanation'. *Progress in Human Geography*, **3**(3), 356–383.
- Smith, N. (1987). "Academic War Over the Field of Geography": The Elimination of Geography at Harvard, 1947–1951'. *Annals of the Association of American Geographers*, **77**(2), 155–172.

- Smith, S. M., & Nichols, T. E. (2009). 'Threshold-free cluster enhancement: addressing problems of smoothing, threshold dependence and localisation in cluster inference.'. *NeuroImage*, **44**(1), 83–98.
- Solstad, T., Boccara, C. N., Kropff, E., Moser, M.-B., & Moser, E. I. (2008). 'Representation of geometric borders in the entorhinal cortex.'. *Science (New York, N.Y.)*, **322**(5909), 1865–8.
- Spiers, H. J. (2008). 'Keeping the goal in mind: prefrontal contributions to spatial navigation'. *Neuropsychologia*, **46**(7), 2106–8.
- Spiers, H. J., & Barry, C. (2015). 'Neural systems supporting navigation'. *Current Opinion in Behavioral Sciences*, **1**, 47–55.
- Spiers, H. J., Burgess, N., Hartley, T., Vargha-Khadem, F., & O'Keefe, J. (2001). 'Bilateral hippocampal pathology impairs topographical and episodic memory but not visual pattern matching.'. *Hippocampus*, **11**(6), 715–25.
- Spiers, H. J., & Gilbert, S. J. (2015). 'Solving the detour problem in navigation: a model of prefrontal and hippocampal interactions.'. *Frontiers in Human Neuroscience*, **9**, 125.
- Spiers, H. J., & Maguire, E. A. (2006). 'Thoughts, behaviour, and brain dynamics during navigation in the real world'. *Neuroimage*, **31**, 1826–1840.
- Spiers, H. J., & Maguire, E. A. (2007). 'A navigational guidance system in the human brain'. *Hippocampus*, **17**, 618–626.
- Stimson, R. J. (2012). 'You don't need sight to have vision: Reginald G. Golledge was a giant in analytical human geography'. *Annals of the Association of American Geographers*, **102**(1), 234–243.
- Sulpizio, V., Committeri, G., & Galati, G. (2014). 'Distributed cognitive maps reflecting real distances between places and views in the human brain.'. *Frontiers in Human Neuroscience*, **8**, 716.
- Takahashi, N., & Kawamura, M. (2002). 'Pure topographical disorientation--the anatomical basis of landmark agnosia.'. *Cortex*, **38**(5), 717–25.
- Taube, J. S. (2007). 'The head direction signal: origins and sensory-motor integration.'. *Annual Review of Neuroscience*, **30**, 181–207.
- Taube, J. S., Muller, R. U., & Ranck, J. B. (1990a). 'Head-direction cells recorded from the postsubiculum in freely moving rats: I. Description and quantitative analysis.'. *Journal of Neuroscience*, **10**(2), 420–35.
- Taube, J. S., Muller, R. U., & Ranck, J. B. (1990b). 'Head-direction cells recorded from the postsubiculum in freely moving rats: II. Effects of environmental manipulations'. *Journal of Neuroscience*, **10**(2), 436–447.
- Taube, J. S., Valerio, S., & Yoder, R. M. (2013). 'Is navigation in virtual reality with fMRI really navigation?'. *Journal of Cognitive Neuroscience*, **25**(7), 1008–19.

- Tobler, W. R. (1965). 'Computation of the corresponding of geographical patterns'. *Papers of the Regional Science Association*, **15**, 131–139.
- Tobler, W. R. (1994). 'Bidimensional regression'. *Geographical Analysis*, **26**(3), 187–212.
- Tolman, E. C. (1948). 'Cognitive maps in rats and men'. *The Psychological Review*, **55**(4), 189–208.
- Uttal, D. H., Miller, D. I., & Newcombe, N. S. (2013). 'Exploring and enhancing spatial thinking: Links to achievement in science, technology, engineering, and mathematics?'. *Current Directions in Psychological Science*, **22**(5), 367–373.
- Vann, S. D., Aggleton, J. P., & Maguire, E. A. (2009). 'What does the retrosplenial cortex do?'. *Nat Rev Neurosci*, **10**(11), 792–802.
- Vass, L. K., Copara, M. S., Seyal, M., Shahlaie, K., Farias, S. T., Shen, P. Y., & Ekstrom, A. D. (2016). 'Oscillations Go the Distance: Low-Frequency Human Hippocampal Oscillations Code Spatial Distance in the Absence of Sensory Cues during Teleportation'. *Neuron*, **89**(6), 1180–6.
- Vass, L. K., & Epstein, R. A. (2013). 'Abstract representations of location and facing direction in the human brain.'. *Journal of Neuroscience*, **33**(14), 6133–42.
- Vass, L. K., & Epstein, R. A. (2016). 'Common Neural Representations for Visually Guided Reorientation and Spatial Imagery.'. *Cerebral Cortex (New York, N.Y. : 1991)*.
- Voermans, N. C., Petersson, K. M., Daudey, L., Weber, B., Van Spaendonck, K. P., Kremer, H. P., & Fernandez, G. (2004). 'Interaction between the human hippocampus and the caudate nucleus during route recognition'. *Neuron*, **43**(3), 427–35.
- Wai, J., Lubinski, D., & Benbow, C. P. (2009). 'Spatial ability for STEM domains: Aligning over 50 years of cumulative psychological knowledge solidifies its importance.'. *Journal of Educational Psychology*, **101**(4), 817–835.
- Wakabayashi, Y., & Ishikawa, T. (2011). 'Spatial thinking in geographic information science: a review of past studies and prospects for the future'. *Procedia - Social and Behavioral Sciences*, **21**, 304–313.
- Ward, J. (2015). *The Student's Guide to Cognitive Neuroscience* (Third edit). East Sussex, UK: Psychology Press.
- Weisberg, D. S., Keil, F. C., Goodstein, J., Rawson, E., & Gray, J. R. (2008). 'The seductive allure of neuroscience explanations.'. *Journal of Cognitive Neuroscience*, **20**(3), 470–7.
- White, D. J., Congedo, M., Ciorciari, J., & Silberstein, R. B. (2012). 'Brain oscillatory activity during spatial navigation: theta and gamma activity link medial temporal and parietal regions.'. *Journal of Cognitive Neuroscience*, **24**(3), 686–97.

Whitlock, J. R., Sutherland, R. J., Witter, M. P., Moser, M.-B., & Moser, E. I. (2008). 'Navigating from hippocampus to parietal cortex.'. *Proceedings of the National Academy of Sciences*, **105**(39), 14755–62.

Wolbers, T., & Büchel, C. (2005). 'Dissociable retrosplenial and hippocampal contributions to successful formation of survey representations'. *Journal of Neuroscience*, **25**(13), 3333–40.

Wolbers, T., & Wiener, J. M. (2014). 'Challenges for identifying the neural mechanisms that support spatial navigation: the impact of spatial scale.'. *Frontiers in Human Neuroscience*, **8**, 571.

Wolbers, T., Wiener, J. M., Mallot, H. A., & Büchel, C. (2007). 'Differential recruitment of the hippocampus, medial prefrontal cortex, and the human motion complex during path integration in humans'. *J Neurosci*, **27**(35), 9408–16.

Woollett, K., & Maguire, E. A. (2011). 'Acquiring “the Knowledge” of London’s Layout Drives Structural Brain Changes'. *Current Biology*, **21**(24), 2109–2114.

Worsley, C. L., Recce, M., Spiers, H. J., Marley, J., Polkey, C. E., & Morris, R. G. (2001). 'Path integration following temporal lobectomy in humans'. *Neuropsychologia*, **39**(5), 452–464.