



Navigational roots of spatial and temporal memory structure

Sang Ah Lee¹

Received: 11 July 2022 / Revised: 18 November 2022 / Accepted: 24 November 2022 / Published online: 8 December 2022
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2022

Abstract

Our minds are constantly in transit, from the present to the past to the future, across places we have and have not directly experienced. Nevertheless, memories of our mental time travel are not organized continuously and are adaptively chunked into contexts and episodes. In this paper, I will review evidence that suggests that spatial boundary representations play a critical role in providing structure to both our spatial and temporal memories. I will illustrate the intimate connection between hippocampal spatial mapping and temporal sequencing of episodic memory to propose that high-level cognitive processes like mental time travel and conceptual mapping are rooted in basic navigational mechanisms that we humans and nonhuman animals share. Our neuroscientific understanding of hippocampal function across species may provide new insight into the origins of even the most uniquely human cognitive abilities.

Keywords Boundary · Hippocampus · Spatial navigation · Temporal · Episodic memory

Introduction

Descartes is often cited and sometimes disdained for his philosophical doctrine of mind–body dualism (Descartes 2008). However, the introspective observation that our minds, unlike our bodies, are not physically constrained and therefore must be distinct and separable from it is entirely relatable, as the flexible mental travel across time and space is a universal human experience. Fortunately, the fact that we can mentally traverse back to the days of our youth growing up in our hometown thousands of miles away, or that we can imagine soaring at the speed of light around the gaseous rings of Saturn, no longer invokes a belief in spirits and souls escaping our physical bodies and can now be explained through our scientific understanding of cognition.

Cognition is what used to be referred to as the "black box" between sensory stimulation and action—the representation, transformation, and storage of information that guides adaptive behavior (Shettleworth 2001). The original formulation of the cognitive map theory (Tolman 1948) was revolutionary because of its suggestion that humans and nonhuman animals alike have mental representations of the

world around them from which they can compute locations and trajectories that they have never physically experienced before. Unlike principles of behaviorism that emphasized learned associations between perceived stimuli and their outcome (e.g., Watson 1913), cognitive models of the mind highlighted the fact that we can store, activate, and manipulate information internally, even in the absence of a physical stimulus or the need for an immediate behavioral response (e.g., Gallistel 1990).

In addition to various compelling early demonstrations of cognitive processes in humans, such as mental rotation (e.g., Shepard and Meltzer 1971) and studies of animal cognition that allowed us to directly measure neural activity (e.g., Georgopolous et al. 1989), research in the field of spatial navigation played a critical role in deepening our understanding of the mind and its shared neural basis across humans and nonhuman animals (O'Keefe and Nadel 1978). The study of spatial cognition has come a long way since then; this review will provide an overview of the comparative literature on the neurocognitive basis of spatial mapping and consider the theoretical view that evolutionarily ancient navigational mechanisms support even the most abstract cognitive abilities, such as episodic mental time travel and the organization of conceptual maps (Epstein et al. 2017; Bellmund et al. 2018). Specifically, I will propose that spatial boundaries, in particular, directly serve to structure and chunk our continuous experiences into discrete

✉ Sang Ah Lee
sangahlee@snu.ac.kr

¹ Department of Brain and Cognitive Sciences, Seoul National University, Gwanak-Ro 1, Gwanak-Gu, Seoul 08826, Korea

and meaningful contexts that, in turn, influence the way we organize our episodic memories.

Mental spaces and their neural representation across vertebrates

Spatial navigation provides a unique window into cognition, due to its ecological validity and the importance of long-term storage and computation of spatial information at a distance. Because our destinations are often perceptually inaccessible when we first set out on our journey, whether we successfully reach it relies heavily on our mental representation—a cognitive map—of the environment based on our memory of previous journeys and our ability to adaptively use that representation to guide us to our goals.

The discovery of the hippocampus as the seat of the cognitive map (O’Keefe and Nadel 1978) and the large body of evidence that vertebrates ranging from fish to humans share this common physiological basis for spatial memory (Rodriguez et al. 2002) opened up an era of cross-disciplinary exchanges of ideas and scientific progress. For the past several decades, animal and human researchers alike have made a concerted effort to reveal the detailed neural mechanisms underlying spatial navigation and memory (e.g., Bellmund et al. 2018; Burgess et al. 2007; Eichenbaum 2017). Research on the rodent hippocampus has resulted in an immense amount of scientific knowledge on spatial representations at the single cell level, culminating in the Nobel Prize to John O’Keefe, May-Britt Moser, and Edvard Moser in 2014 (Burgess 2014). The four main spatially specific cells identified are place cells that respond when the animal is at a single preferred location within an environment (O’Keefe and Dostrovsky 1971), head direction cells that respond whenever the rat is facing a particular direction (e.g., with respect to distal visual cues) (Taube Muller and Ranck 1990a; b), grid cells that respond at multiple locations in the environment in a hexagonal grid-like pattern (Hafting et al. 2005), and boundary/border cells that respond whenever the rat is a particular direction (and in some cases distance) from extended boundary-like environmental structures (Solstad et al. 2008; Lever et al. 2009). Although the evidence is far less extensive in other species, similar representations of space at the single-neuron level have been discovered in bats (e.g., Yartsev and Ulanovsky 2013), birds (e.g., Siegel et al. 2005; Payne et al. 2021), monkeys (e.g., Hori et al. 2005) and humans (e.g., Ekstrom et al. 2003).

Unlike the controversy over the exact role of grid cells on hippocampal place coding (e.g., Brandon et al. 2014; Bush et al. 2014; Schlesiger et al. 2018), there is a general consensus on the importance of boundary representations

and their influence over both place cells (O’Keefe and Burgess 1996) and grid cells (Fyhn et al. 2007; Hardcastle et al. 2015; Krupic et al. 2015; Stensola et al. 2015). For instance, neural recordings in rat pups showed that the development of boundary cells occurs at the same time as place cells and earlier than grid cells (Bjerknes et al. 2014; Wills Muessig and Cacucci 2014), suggesting that the hippocampal place map relies more heavily on boundary cells rather than grid cells, especially in early development. Moreover, when the cognitive map cannot be anchored to a directional cue (e.g., distal landmarks)—whether it is due to damage or inactivation of the head direction system (Harland et al. 2017), inertial disorientation (Knight et al. 2011; Keinath et al. 2017), or unfamiliarity with the environment (Spiers et al. 2015; Grieves et al. 2017)—environmental boundaries have been shown to exert control over the orientation of the hippocampal map.

In the now famous reorientation paradigm first developed by Ken Cheng (1986), disoriented rats searched for previously found food in locations geometrically symmetrical to the target (defined by the rectangular environmental layout) about half of the time, despite the presence of other visual and olfactory (non-boundary features) cues that broke the room’s symmetry. This effect was strongest in “working-memory”-type tasks that do not involve repeatedly reinforced training at a particular goal location (Cheng 1986). Similar results were obtained with mice (Fellini et al. 2006; Lee et al. 2015a, b, c). When place cells were recorded while animals (mice in this case) performed such a reorientation task, ensembles of hippocampal cells were not only mis-oriented according to the symmetry of the testing space, their activity was sufficient to predict the animals’ behavioral response on a trial-by-trial basis (Keinath et al. 2017), implying that our cognitive map is comprised of boundary-based neural representations of the environment.

Boundary-dependent spatial navigation behaviors have been documented beyond just rodents but across a wide range of animal species, resulting in a treasure trove of comparative studies and converging evidence across the vertebrate phylogenetic tree (Lee 2017). Like rodents, birds (e.g., Kelly et al. 1998) and fish (e.g., Sovrano et al. 2003; see Baratti et al. 2022 for review) exhibit a strong influence of boundary geometry on spatial reorientation behavior. Moreover, just as in rats (Cheng 1986), this effect is stronger in spontaneous, working-memory tasks, with landmarks increasingly contributing to behavior with learning (Vallortigara et al. 1990). Such studies suggested that shared brain structures such as the hippocampus may underlie the shared patterns in boundary-dependent behavior (e.g. Vargas et al. 2004; Fotowat et al. 2019; Mayer et al. 2016; Mayer et al. 2018).

The widespread nature of boundary dependence and its documentation in toddlers and preschool children caught the

interest of developmental researchers in the late 1990s and 2000s as a topic of debate over nature vs. nurture (Newcombe and Ratliff 2007; Spelke 1994; Vallortigara 2009). Children's boundary-based spatial memory shows an impressive early emergence in infants and toddlers (Garrad-Cole et al. 2001; Hermer and Spelke 1994; 1996; Lee Winkler-Rhoades and Spelke 2012), and geometric error patterns (and failure to use non-boundary features and landmarks to disambiguate between symmetric corners) persists until the age of about 5 or 6. Such errors committed even by human adults under certain situations (e.g., verbal shadowing (Hermer-Vazquez et al. 1999; Ratliff and Newcombe 2008), as well as boundary-specific signals in the human brain (Doeller et al. 2008; Lee et al. 2018; Shine et al. 2019).

Such specificities in boundary representations in humans, in turn, stimulated animal researchers to explore questions regarding the origins of spatial cognition in ways that are not possible with human babies. This back-and-forth exchange of ideas and experimental findings kindled a continuing cross-disciplinary debate among researchers on the domain-specificity of the mind, the evolution of cognitive processes, and what it truly means (or not mean) for a cognitive ability to be uniquely human (Spelke and Lee 2012).

Boundaries help structure perceptual space

What constitutes a boundary, and what function does it serve in memory? Despite their importance to hippocampal representations, there is not yet a clear definition of what boundaries *are*, perceptually or functionally. Nevertheless, over the years, various researchers have continued to chip away at this question, bit by bit. The initial discoveries on boundary-based behavior and boundary-coding cells reviewed above were observed only with respect to the walls of the experimental arena—the boundaries of the testing space itself. From such findings, several hypotheses were cast as to what are the critical properties of walls such that they weigh in so heavily on our spatial memory. One class of theories claimed that boundaries are important because they define the surrounding navigable space and that they are obstacles to locomotion (Kosslyn et al. 1974; Muller and Kubie 1987): because walls are affordances to movement, they are important for action and must be mentally noted as such. A second class of theories posited that walls are the most visually salient properties of the environment (i.e., creating highly contrasting edges in the visual field) and that processes such as view matching (Cheng 2008; Sheynikovich et al. 2009) are naturally biased to be guided predominantly by the salient cues while ignoring others that are not as salient (e.g., wall color, small objects etc.). A third class of theories claimed that boundaries are not important in any intrinsic way but learned over the course of development to

be the most stable and useful features of the environment (Newcombe and Ratliff 2007; Xu et al. 2017). These theories emphasize the idea that what is better and more adaptive is weighted more heavily in determining behavior.

Although all of the above views regarding perceptual salience and experienced reliability may be partially true, that does not seem to be the whole part of the story. A series of experiments over the past decade conducted across a variety of species (e.g., chicks, fish, human children, and adults) and environmental conditions have shown that limits or obstacles to movement are neither necessary nor sufficient to elicit boundary-based mapping. For instance, numerous studies on young children and nonhuman animals (i.e., chicks and fish) failed to extract spatial information from a geometric array of objects (Gouteux and Spelke 2001; Lee Shusterman and Spelke 2006; Lee and Spelke 2010a, b; Lee et al. 2012; Lee et al. 2013; Lee et al. 2015a, b, c) or columns (children: Lee and Spelke 2008, 2010a, b, 2011; chicks: Lee et al. 2012; fish: Lee et al. 2015a, b, c), not even when they are closely aligned to prevent movement through them (children: Gianni and Lee 2018), nor when a string is tied around the array to demark the boundary (children: Lee and Spelke 2011). And yet, subtle hill-like terrains (children: Lee and Spelke 2011, chicks: Lee et al. 2012), traversable short walls (children: Lee and Spelke 2008, 2011, 2012; Lourenco and Huttenlocher 2006; Ferrara et al. 2019), chicks: Lee et al. 2012), visual virtual boundaries (including drop-like edges) (human adults: Lee et al. 2018; Negen et al. 2020; Julian et al. 2016; Peer and Epstein 2021), and even perhaps a visual illusion of boundaries at different distances (mice: Twyman et al. 2009; children: Huttenlocher and Lourenco 2007, Lee et al. 2012) guided spontaneous place-finding behavior. These environmental conditions varied widely in their visual salience and were sometimes intentionally designed to make the object arrays and 2D stimuli provide stronger brightness contrasts than the boundary conditions (e.g., Lee and Spelke 2011; Lee et al. 2012). But, even 2 cm-high light-colored “boundaries” against a light-colored floor sufficed, providing no empirical support in favor of accounts based entirely on low-level visual salience.

These studies showed that the critical properties of successful boundary utilization in both children and nonhuman animals consisted of 3D, opaque, extended surfaces (not freestanding objects). And while this characterization is not mutually exclusive with adaptive learning theories (clearly, spatial behavior is also subject to learning), the proficiency of controlled-reared chicks and fish in boundary-based navigation (Brown et al. 2007; Chiandetti and Vallortigara 2010) and the early development of boundary cells in rat pups on their first days shortly following eye-opening (Bjerknes et al. 2014) suggest that, while

boundary representations may have been evolutionarily adaptive for the very reasons described above (e.g., stability, reliability), adaptive *learning* cannot be the main driver of their early effects on spatial cognition. Moreover, adult human failures to discriminate between real and illusory boundaries in their behavioral search patterns (Negen et al. 2020) reveal that even as adults our adaptively learning is not immediate.

Although the hippocampal spatial map is generally thought of as modality-free, the interpretation that is most consistent with the data is that what we have been referring to as boundaries are actually visual representations of environmental structure (i.e., terrain). In fact, simple reorientation studies have demonstrated that transparent walls are difficult to use for spatial mapping in both younger children (Gianni et al. 2018) and nonhuman animals such as fish (Lee et al. 2013). Neuroimaging studies have shown that the geometric structure of scenes is represented in both the parahippocampal and occipital scene-processing regions of the human high-level visual cortex (Park et al. 2011; Ferrara and Park 2016), and spatial cognitive deficits in neurological disorders such as Alzheimer's Disease or Williams Syndrome are also associated with visual boundary-processing deficits (Bird et al. 2010b; Ferrara et al. 2019; Julian et al. 2016). The visual representation of the 3D terrain has been reported to occur even in the occipital cortex and plays a causal role in navigation (Julian et al. 2016). In both rodents and human epilepsy patients, visual boundaries in virtual navigation tasks are sufficient to elicit boundary-specific responses in the hippocampal formation (boundary cells in mice: Aronov and Tank 2014; human intracranial recordings: Lee et al. 2018; human fMRI: Shine et al. 2019). Some boundary-coding neurons in the rodent subiculum have been shown to fire not just at the boundaries but also from a range of distances away from them (Lever et al. 2009; Stewart et al. 2013). In some cases, such representations are memory-driven and are activated even in the absence of the physical stimulus itself (Poulter et al. 2021).

Visual representation of boundaries allows animals to map out the space without having to actively transverse the environment. In fact, it seems hardly adaptive for an animal who has vision not to use it to map out its surroundings from a distance. Mapping space means that geometric relations are extracted, rather than just stored as a visual template of the scene: in other words, when we look out into the vast space before us, its visual boundary structure allows us to divide it into smaller regions and places. We may adaptively utilize this organization or chunking of continuous spaces to induce a switching of hippocampal “maps” when we cross a boundary to a new “context” (Brunec et al. 2018; Muller and Kubie 1987; Savelli et al. 2008). This chunking of space may induce a characteristic trade-off between efficiency and precision. For instance, memories formed on the same side

of a boundary may be better associated with one another (e.g., Horner et al. 2016a, b), while traversing a boundary in the middle of a sequence of events may perturb memory at the point of crossing (e.g., Radvansky and Copeland 2006).

Navigational basis of episodic space and time

So far, we have laid out a mechanism by which animals and humans alike use perceptual boundary layouts to map continuous space into discrete locations. Given the intimate connection between spatial mapping and episodic memory, however, could boundary representations also help structure our continuous temporal experiences into discrete points in time as well?

Although much of the literature fails to make this distinction explicit, an important difference between mapping out relative spatial locations and actual navigation is that navigation requires the binding of space (e.g., places) across time. Over the years, animal researchers have heroically shown that the basic what–where–when binding that characterizes episodic memory is not a uniquely human ability but a widely shared cognitive function that serves an adaptive purpose across a variety of species (see Clayton et al. 2001; Crystal 2010 for review). Electrophysiological studies in the rodent hippocampus have shown that some hippocampal place cells are also “time cells” which exhibit a preferred temporal firing field rather than just a spatial one (Eichenbaum 2014). More recent findings of cells in the entorhinal cortex show a variety of firing patterns, such as ramping up or down of firing rates or a context-dependent phasic increase across time, sometimes “resetting” its timing with a change in spatial context (Tsao et al. 2018). Converging evidence for temporal information coding has been reported in the human medial temporal lobe (Bellmund et al. 2019; Montchal et al. 2019). Such findings, in combination with the vast literature on sequential place cell replay and preplay (see Foster 2017 for review) implies that rodents may also be able to both cognitively re-experience and plan spatiotemporal events through the sequential activation of hippocampal place cells, even in the absence of movement.

The sequential activation of memories has been proposed to be fundamental to the role of the hippocampus in episodic mental simulation (Buzsáki and Tingley 2018). One study with young children showed that in a task involving the sequential placement of objects into boxes distributed around the testing space, even 3-year-old children can pick out the correct boxes and the correct objects (i.e., recognition memory) but perform very poorly at putting them in the correct order (i.e., what–where–when episodic memory) (Mastrogiuseppe et al. 2019). Interestingly,

young children first develop the ability to reliably bind together a sequence of locations (where-when) several years before they can recall the sequence of objects (what-when), which occurs around the age of 6 when they are also able to bind together the entire what-where-when sequence (Lee et al. 2015a, b, c). Around 6 years is the age when children begin to exhibit signs of adult-like episodic memory (e.g., using various measures of associative memory and autobiographical memory), and this change is attributed to the maturation of the hippocampus and its connectivity with the prefrontal cortex (DeMaster and Gheiti 2012; Blankeship et al. 2016; Olson and Newcombe 2014). This point in development is also, and probably not coincidentally, the same age at which children begin to show flexibility in their boundary representations, reliably incorporating landmarks (Hermer and Spelke 2016; Learmonth et al. 2003), object arrays (Gianni and Lee 2018), and 2D forms (Ferrara and Landau 2015) into their spatial search behavior.

Children's ability to bind together where-when is required for their successful binding together of what-where-when and is mediated by the binding of objects to locations (what-where) (Mastrogiuseppe et al. 2019). In other words, episodic binding may ride on a more purely navigational representation of spatiotemporal sequences. When an identical experiment was conducted in a population of young adults with Williams Syndrome (WS), a neurodevelopmental disorder characterized by abnormal parieto-hippocampal development and severe deficits in spatial cognition (Ferrara and Landau 2015; Lakusta et al. 2010; Udwin and Yule 1991), researchers found that they were significantly impaired in where-when memory binding relative to mental age-matched controls (Mastrogiuseppe et al. 2019; see also Vicari et al. 1996). These results suggested that impaired hippocampal function may induce much greater deficits in spatiotemporal binding—the navigational "event-like" aspect of memory—than the standard place recognition memory. If such is the case, could such difficulties be a strong indicator of hippocampal degeneration, as in Alzheimer's disease (AD)?

AD patients tested on a similar task were severely impaired in binding together memory components but not as impaired in place recognition memory, once again affirming the importance of temporal information in hippocampal disorders (e.g., Bellassen et al. 2011; El Haj and Kapogiannis 2016). In a scene-based episodic memory task that tested what, where, and when separately (and without requiring elderly participants to actually move around the room), subjects saw a sequence of scenes and were asked to identify: (1) an object that was removed from one of the scenes (what), (2) the correct location in the scene (where), and (3) the scene (out of the two) that had come earlier in the encoding sequence (when). AD patients were not significantly impaired in their what memory, but were significantly

impaired in their where and when memory. Interestingly, we found that performance in when memory had the highest level of specificity, even more so than standardized memory assessments, while performance in their where memory had the highest level of sensitivity in classifying the participants into AD vs. age-matched controls (Park and Lee 2021).

Boundaries help chunk time into event memories

If episodic memory is cognitively akin to navigation in the sense that one must mentally traverse through time and space, how does the structure of one's spatial cognitive map constrain the organization of one's temporal event memory? To explore this question, we can once again invoke the case of boundaries, given their strong influence on spatial mapping, as reviewed above.

Human studies have demonstrated that contextual change is detrimental to memory in general (e.g., Radvansky and Copeland 2006). Studies of temporal memory have further added that sequential order of items is more difficult to remember if a spatial boundary is crossed in between the items (e.g., from one room to another) than if they were experienced on the same side (Horner et al. 2016a, b). A recent finding suggests that this effect of boundaries on spatiotemporal sequence memory occurs in young children and is contingent upon their development of boundary representations (Rah et al. 2022). In younger children up to about 5 years old, only wall-like surface layouts—those that we characterized above as the basic drivers of spatial mapping that children successfully reorient by various featural cues at that age—influence their temporal sequence memory. Non-canonical boundaries, such as object arrays and 2D lines, do not affect sequence memory until the age of about 5 or 6, which is around the time these same structures begin to guide spatial mapping (e.g., Gianni and Lee 2018, Ferrara and Landau 2015).

Although further converging research in nonhuman animal cognition and neuroscience is needed, the fact that the development of the temporal structure of event memories depends on the child's representations of space strongly suggests that mental time travel is intimately connected to navigational processes. Furthermore, the existence of hippocampal neurons that fire in sequence both spatially and temporally (Macdonald et al. 2013; Eichenbaum 2014), and the potential anchoring effect of spatial boundaries on hippocampal and entorhinal neural activity (see Giocomo 2015), provide a promising outlook on the detailed characterization of neural mechanisms underlying spatiotemporal navigation and memory.

Looking beyond space and time

The view that I have proposed above partly reconciles spatial theories of hippocampal function with those emphasizing episodic, relational memories—nevertheless, it only partially resolves the theoretical discrepancy that, in some cases, runs much deeper (e.g., Eichenbaum 2017; Ekstrom and Ranganath 2018; Robin 2018). For instance, some researchers have proposed that the main function of the hippocampus, in humans and nonhumans animals alike, is not constrained to any domain or type of information at all and that the overrepresentation of the spatial domain in studies of the hippocampus arises from the importance of space in the experimental designs traditionally used with nonhuman animals (e.g., mazes, recording chambers, memory tasks) (Eichenbaum et al. 1999; Eichenbaum 2017).

In the past decade or so, a completely domain general approach to the hippocampus has gained momentum, based predominantly on neuroimaging studies in human adults. The initially sensational reports of grid-cell-like six-fold symmetry in human brain signals have now been shown not only in virtual or imagined navigation (Horner et al. 2016a, b; Jacobs and Lee 2016), but also in tasks requiring navigation through any highly abstract space defined by any quantifiable features—ranging from mapping relative lengths of the leg and neck in taxonomy to mapping social attributes such as popularity and power (Constantinescu et al. 2016; Park et al. 2021). This general mapping view of hippocampal function has been eagerly adopted into computational models such as in the Tolman-Eichenbaum Machine (Whittington et al. 2020), describing memory mechanisms and generalized knowledge structures in terms of the interaction between grid cells and place cells.

The question of whether hippocampal function is fundamentally spatial or not may be an evolutionarily relevant one, depending on what selection pressures it was originally sculpted by 300 million years ago and what changed over time, as species diverged along their own evolutionary path. Some studies have shown that the rodent hippocampal cells can represent a variety of nonspatial information such as tone frequency (e.g., Aronov et al. 2017), but such evidence is sparse and often confounded with other information such as time. One potentially important piece of the puzzle is that although grid cells have only been recorded from the medial temporal lobe in rodents, a six-fold grid-like symmetry in human fMRI signals has been reported in the parietal and prefrontal (e.g., orbitofrontal) cortex, in addition to the medial temporal lobe (Horner et al. 2016a, b; Constantinescu et al. 2016; Park et al. 2021).

While abstract and imagined representations of boundaries have also been reported (Bird et al. 2010a, b; Brunec et al. 2018; Robin 2018), detailed and specific interactions

between abstract grid and boundary signals (that are analogous to spatial grid and spatial boundary representations) have yet to be reported. Such discrepancies might indicate that the human hippocampus (and with its elaborate interaction with the prefrontal cortex) is different from the rodent hippocampus in its ability to code and generalize information in their episodic memories. Furthermore, the traditionally “spatial” signals in regions like the PFC may arise across development, similar to the emergence of abstract spatial and geometric concepts in children (Spelke et al. 2010). If this is true, a domain-generalized function of the hippocampus may be a unique feature of the human mind that is founded upon but eventually surpasses the limitations of core cognitive systems that we share with other animals (Spelke and Lee 2012). As the fascinating story of our cognition and mind continues to unfold, the road is well-paved for 25 more years of fruitful, synergistic exchanges between human and animal cognition researchers.

Acknowledgements This research was supported by government-funded grants to SAL from IITP (Grant No. 2019-0-01371-003) and NRF (Grant No. 2021M3E5D2A01023891).

Data availability Data availability statement: Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

References

- Aronov D, Tank DW (2014) Engagement of neural circuits underlying 2D spatial navigation in a rodent virtual reality system. *Neuron* 84:442–456
- Aronov D, Nevers R, Tank DW (2017) Mapping of a non-spatial dimension by the hippocampal/entorhinal circuit. *Nature* 543:719–722
- Baratti G, Potrich D, Lee SA, Morandi-Raikova A, Sovrano VA (2022) The geometric world of fishes: a synthesis on spatial reorientation in teleosts. *Animals* 12:881
- Bellassen V, Iglói K, de Souza LC, Dubois B, Rondi-Reig L (2011) Temporal order memory assessed during spatiotemporal navigation as a behavioral cognitive marker for differential Alzheimer's disease diagnosis. *J Neurosci* 32:1942–1952
- Bellmund JLS, Gärdenfors P, Moser EI, Doeller CF (2018) Navigating cognition: spatial codes for human thinking. *Science* 362:eaat6766
- Bellmund JLS, Deuker L, Doeller CF (2019) Mapping sequence structure in the human lateral entorhinal cortex. *Elife* 8:e45333
- Bird CM, Capponi C, King JA, Doeller CF, Burgess N (2010a) Establishing the boundaries: the hippocampal contribution to imagining scenes. *J Neurosci* 30:11688–11695
- Bird CM, Chan D, Hartley T, Pijnenburg YA, Rossor MN, Burgess N (2010b) Topographical short-term memory differentiates Alzheimer's disease from frontotemporal lobar degeneration. *Hippocampus* 20:1154–1169
- Bjerknes TL, Moser EI, Moser MB (2014) Representation of geometric borders in the developing rat. *Neuron* 82:71–78
- Blankenship SL, Redcay E, Dougherty LR, Riggins T (2016) Development of hippocampal functional connectivity during childhood. *Hum Brain Mapp* 38:182–201

- Brandon MP, Koenig J, Leutgeb JK, Leutgeb S (2014) New and distinct hippocampal place codes are generated in a new environment during septal inactivation. *Neuron* 82:789–796
- Brown AA, Spetch ML, Hurd PL (2007) Growing in circles: rearing environment alters spatial navigation in fish. *Psychol Sci* 18:569–573
- Brunec IK, Moscovitch M, Barense MD (2018) Boundaries shape cognitive representations of spaces and events. *Trends Cogn Sci* 22:637–650
- Burgess N (2014) The 2014 Nobel Prize in physiology or medicine: a spatial model for cognitive neuroscience. *Neuron* 84:1120–1125
- Burgess N, Maguire EA, O’Keefe J (2007) The human hippocampus and spatial and episodic memory. *Neuron* 35:625–641
- Bush D, Barry C, Burgess N (2014) What do grid cells contribute to place cell firing? *Trends Neurosci* 37:136–145
- Buzsáki G, Tingley D (2018) Space and time: the hippocampus as a sequence generator. *Trends Cogn Sci* 22:853–869
- Cheng K (1986) A purely geometric module in the rat’s spatial representation. *Cognition* 23:149–178
- Cheng K (2008) Whither geometry? Troubles of the geometric module. *Trends Cogn Sci* 12:355–361
- Cheng K, Huttenlocher J, Newcombe NS (2013) 25 years of research on the use of geometry in spatial reorientation: a current theoretical perspective. *Psychon Bull Rev* 20:1033–1054
- Chiandetti C, Vallortigara G (2010) Experience and geometry: controlled-rearing studies with chicks. *Anim Cogn* 2013:463–470
- Clayton NS, Griffiths DP, Emery NJ, Dickinson A (2001) Elements of episodic-like memory in animals. *Philos Transact* 356:1483–1491
- Constantinescu AO, O’Reilly JX, Behrens TEJ (2016) Organizing conceptual knowledge in humans with a gridlike code. *Science* 352:1464–1468
- Crystal JD (2010) Episodic-like memory in animals. *Behav Brain Res* 215:235–243
- DeMaster DM, Gheiti S (2012) Developmental differences in hippocampal and cortical contributions to episodic retrieval. *Cortex* 49:1482–1493
- Descartes R (2008) *Meditations on first philosophy: with selections from the objections and replies* (m. moriarty trans.). Oxford University Press, Oxford
- Doeller CF, King JA, Burgess N (2008) Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proc Natl Acad Sci* 105:5915–5920
- Eichenbaum H (2014) Time cells in the hippocampus: a new dimension for mapping memories. *Nature Rev Neurosci* 15:732–744
- Eichenbaum H (2017) The role of the hippocampus in navigation is memory. *J Neurophysiol* 117:1785–1796
- Eichenbaum H, Dudchenko P, Wood E, Shapiro M, Tanila H (1999) The hippocampus, memory, and place cells: is it spatial memory or a memory space? *Neuron* 23:209–226
- Ekstrom AD, Ranganath C (2018) Space, time, and episodic memory: the hippocampus is all over the cognitive map. *Hippocampus* 28:680–687
- Ekstrom AD, Kahana MJ, Caplan JB, Fields TA, Isham EA, Newman EL, Fried I (2003) Cellular networks underlying human spatial navigation. *Nature* 425:184–187
- El Haj M, Kapogiannis D (2016) Time distortions in Alzheimer’s disease: a systematic review and theoretical integration. *Npj Aging Mech Dis* 2:16016
- Epstein RA, Patai EZ, Julian JB, Spiers HJ (2017) The cognitive map in humans: spatial navigation and beyond. *Nat Neurosci* 20:1504–1513
- Fellini L, Schachner M, Morellini F (2006) Adult but not aged C57BL/6 male mice are capable of using geometry for orientation. *Learn Mem* 13:472–481
- Ferrara K, Landau B (2015) Geometric and featural systems, separable and combined: evidence from reorientation in people with Williams syndrome. *Cognition* 144:123–133
- Ferrara K, Park S (2016) Neural representation of scene boundaries. *Neuropsychologia* 2016(89):180–190
- Ferrara K, Landau B, Park S (2019) Impaired behavioral and neural representation of scenes in Williams syndrome. *Cortex* 121:264–276
- Foster D (2017) Replay comes of age. *Annu Rev Neurosci* 40:581–602
- Fotowat H, Lee C, Jun JJ, Maler L (2019) Neural activity in a hippocampus-like region of the teleost pallium is associated with active sensing and navigation. *Elife* 8:e44119
- Fyhn M, Hafting T, Treves A, Moser MB, Moser EI (2007) Hippocampal remapping and grid realignment in entorhinal cortex. *Nature* 446:190–194
- Gallistel CR (1990) *The organization of learning*. MIT Press, Cambridge
- Garrad-Cole F, Lew AR, Bremner JG, Whitaker CJ (2001) Use of configurational geometry for spatial orientation in human infants (*Homo sapiens*). *J Comp Psychol* 115(3):317–320
- Georgopoulos A, Lurito JT, Petrides M, Schwartz AB, Massey JT (1989) Mental rotation of the neuronal population vector. *Science* 243:234–236
- Gianni E, Lee SA (2018) Defining spatial boundaries: a developmental study. In: Fogliarini P, Ballatore A & Clementini E (eds) *Proceedings of Workshops and Posters at the 13th International Conference on Spatial Information Theory. Lecture Notes in Geoinformation and Cartography*. Springer
- Gianni E, de Renzi L, Lee SA (2018) The developing role of transparent surfaces in children’s spatial representation. *Cogn Psychol* 105:39–52
- Giocomo LM (2015) Environmental boundaries as a mechanism for correcting and anchoring spatial maps. *J Physiol* 594:6501–6511
- Gouteux S, Spelke ES (2001) Children’s use of geometry and landmarks to reorient in an open space. *Cognition* 81:119–148
- Grieves RM, Duvelle E, Wood ER, Dudchenko PA (2017) Field repetition and local mapping in the hippocampus and the medial entorhinal cortex. *J Neurophysiol* 118:2378–2388
- Hafting T, Fyhn M, Molden S, Moser MB, Moser EI (2005) Microstructure of a spatial map in the entorhinal cortex. *Nature* 436:801–806
- Hardcastle K, Ganguli S, Giocomo LM (2015) Environmental boundaries as an error correction mechanism for grid cells. *Neuron* 86:827–839
- Harland B, Grieves RM, Bett D, Stentiford R, Wood ER, Dudchenko PA (2017) Lesions of the head direction cell system increase hippocampal place field repetition. *Curr Biol* 27:2706–2712
- Hermer L, Spelke ES (1994) A geometric process for spatial orientation in young children. *Nature* 370:57–59
- Hermer L, Spelke E (2016) Modularity and development: the case of spatial reorientation. *Cognition* 61:195–232
- Hermer-Vazquez L, Spelke ES, Katsnelson A (1999) Sources of flexibility in human cognition: dual-task studies of space and language. *Cogn Psychol* 39:3–36
- Hori E, NishioY KK, Umeno K, Tabuchi E, Sasaki K, Endo S, Ono T, Nishijo T (2005) Place-related neural responses in the monkey hippocampal formation in a virtual space. *Hippocampus* 15:991–996
- Horner AJ, Bisby JA, Wang A, Bogus K, Burgess N (2016a) The role of spatial boundaries in shaping long-term event representations. *Cognition* 154:151–164
- Horner AJ, Bisby JA, Zotow E, Bush D, Burgess N (2016b) Grid-like processing of imagined navigation. *Curr Biol* 26:842–847
- Huttenlocher J, Lourenco SF (2007) Coding location in enclosed spaces: is geometry the principle? *Dev Sci* 10:741–746

- Jacobs J, Sav L (2016) Spatial cognition: grid cells support imagined navigation. *Curr Biol* 26:R277–R279
- Julian JB, Ryan J, Hamilton RH, Epstein RA (2016) The occipital place area is causally involved in representing environmental boundaries during navigation. *Curr Biol* 26:1104–1109
- Julian JB, Kamps FS, Epstein RA, Dilks DD (2019) Dissociable spatial memory systems revealed by typical and atypical human development. *Dev Sci* 22:e12737
- Keinath AT, Julian JB, Epstein RA, Muzzio IA (2017) Environmental geometry aligns the hippocampal map during spatial reorientation. *Curr Biol* 27:309–317
- Kelly DM, Spetch ML, Heth CD (1998) Pigeons' (*Columba livia*) encoding of geometric and featural properties of a spatial environment. *J Comp Psychol* 112:259–269
- Knight R, Hayman R, Ginzberg LL, Jeffery K (2011) Geometric cues influence head direction cells only weakly in nondisoriented rats. *J Neurosci* 31:15681–15692
- Kosslyn SM, Pick HL, Fariello GR (1974) Cognitive maps in children and men. *Child Dev* 45:707–716
- Krupic J, Bauza M, Burton S, Barry C, O'Keefe J (2015) Grid cell symmetry is shaped by environmental geometry. *Nature* 518:232–235
- Lakusta L, Dessalegn B, Landau B (2010) Impaired geometric reorientation caused by genetic defect. *Proc Natl Acad Sci USA* 107:2813–2817
- Learmonth AE, Nadel L, Newcombe NS (2003) Children's use of landmarks: implications for modularity theory. *Psychol Sci* 13:337–341
- Lee SA (2017) The boundary-based view of spatial cognition: a synthesis. *Curr Opin Behav Sci* 16:58–65
- Lee SA, Spelke ES (2008) Children's use of geometry for reorientation. *Dev Sci* 11:743–749
- Lee SA, Spelke ES (2010a) A modular geometric mechanism for reorientation in children. *Cogn Psychol* 61:152–176
- Lee SA, Spelke ES (2010b) Two systems of spatial representation underlying navigation. *Exp Brain Res* 206:179–188
- Lee SA, Spelke ES (2011) Young children reorient by computing layout geometry, not by matching images of the environment. *Psychon Bull Rev* 18:192–198
- Lee SA, Shusterman A, Spelke ES (2006) Reorientation and landmark-guided search by young evidence for two systems. *Psychol Sci* 17:577–582
- Lee SA, Sovrano VA, Spelke ES (2012a) Navigation as a source of geometric knowledge: Young children's use of length, angle, distance, and direction in a reorientation task. *Cognition* 123:144–161
- Lee SA, Spelke ES, Vallortigara G (2012b) Chicks, like children, spontaneously reorient by three-dimensional environmental geometry, not by image matching. *Biol Lett* 8:492–494
- Lee SA, Winkler-Rhoades N, Spelke ES (2012c) Spontaneous reorientation is guided by perceived surface distance, not by image matching or comparison. *PLoS ONE* 7:e51373
- Lee SA, Vallortigara G, Fiore M, Spelke ES, Sovrano VA (2013) Navigation by environmental geometry: the use of zebrafish as a model. *J Exp Biol* 216:3693–3699
- Lee SA, Ferrari A, Vallortigara G, Sovrano VA (2015a) Boundary primacy in spatial mapping: evidence from zebrafish (*Danio rerio*). *Behav Processes* 119:116–122
- Lee SA, Tucci V, Sovrano VA, Vallortigara G (2015b) Working memory and reference memory tests of spatial navigation in mice (*Mus musculus*). *J Comp Psychol* 192:189–197
- Lee JK, Wendelken C, Bunge SA, Ghetti S (2015c) A time and place for everything: Developmental differences in the building blocks of episodic memory. *Child Dev* 87:194–210
- Lee SA, Miller JF, Watrous AJ, Sperling MR, Sharan A, Worrell GA, Berry BM, Aronson JP, Davis KA, Gross RE, Lega B, Sheth S, Das SR, Stein JM, Gorniak R, Rizzuto DS, Jacobs J (2018) Electrophysiological signatures of spatial boundaries in the human subiculum. *J Neurosci* 38(13):3216–3217
- Lee SM, Jin SW, Park SB, Park EH, Lee CH, Lee HW, Lim HY, Yoo SW, Ahn JR, Shin J, Lee SA, Lee I (2021) Goal-directed interaction of stimulus and task demand in the parahippocampal region. *Hippocampus* 3:717–736
- Leonard K, Vasyukiv V, Kelly DM (2020) Reorientation by features and geometry: effects of healthy and degenerative age-related cognitive decline. *Learn Behav* 48:124–134
- Lever C, Burton S, Jeewajee A, O'Keefe J, Burgess N (2009) Boundary vector cells in the subiculum of the hippocampal formation. *J Neurosci* 29:9771–9777
- Lourenco SF, Huttenlocher J (2006) How do young children determine location? Evidence from disorientation tasks. *Cognition* 100:511–529
- Macdonald CJ, Carrow S, Place R, Eichenbaum H (2013) Distinct hippocampal time cell sequences represent odor memories in immobilized rats. *J Neuroscience* 33:14607–14616
- Mastrogioseppe M, Bertelsen N, Bedeschi MF, Lee SA (2019) The spatiotemporal organization of episodic memory and its disruption in a neurodevelopmental disorder. *Sci Rep* 9:18447
- Mayer U, Pecchia T, Bingman VP et al (2016) Hippocampus and medial striatum dissociation during goal navigation by geometry or features in the domestic chick: an immediate early gene study. *Hippocampus* 26:27–40
- Mayer U, Bhushan R, Vallortigara G, Lee SA (2018) Representation of environmental shape in the hippocampal formation of the domestic chick (*Gallus gallus*). *Brain Struct Funct* 223:941–953
- Montchal ME, Reagh ZM, Yassa MA (2019) Precise temporal memories are supported by the lateral entorhinal cortex in humans. *Nat Neurosci* 22:284–288
- Mullally SL, Maguire EA (2013) Memory, imagination, and predicting the future: a common brain mechanism? *Neuroscientist* 20:220–234
- Muller RU, Kubie JL (1987) The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. *J Neurosci* 7:1951–1968
- Negen J, Sandri A, Lee SA, Nardini M (2020) Boundaries in spatial cognition: looking like a boundary is more important than being a boundary. *J Exp Psychol Learn Mem Cogn* 46:1007–1021
- Newcombe NS, Ratliff KR (2007) Explaining the development of spatial reorientation: modularity-plus-language versus the emergence of adaptive combination. In *The Emerging Spatial Mind*, Plumer J, Spencer J (eds) Oxford University Press, Oxford
- O'Keefe J, Burgess N (1996) Geometric determinants of the place fields of hippocampal neurons. *Nature* 381:425–428
- O'Keefe J, Dostrovsky J (1971) The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Res* 34:171–175
- O'Keefe J, Nadel L (1978) *The hippocampus as a cognitive map*. Clarendon Press, Oxford
- Olson IR and Newcombe NS (2014) Binding together the elements of episodes: relational memory and the developmental trajectory of the hippocampus. *The Wiley Handbook and the Development of Children's Memory*, Volume I/II. Patricia J. Bauer and Robyn Fivush.
- Park JH, Lee SA (2021) The fragility of temporal memory in Alzheimer's disease. *J Alzheimer's Dis* 79:1631–1646
- Park S, Brady TF, Greene MR, Oliva A (2011) Disentangling scene content from spatial boundary: complementary roles for the parahippocampal place area and lateral occipital complex in representing real-world scenes. *J Neurosci* 31:1333–1340
- Payne HL, Lynch G, Aronov D (2021) Neural representations of space in the hippocampus of a food-caching bird. *Science* 373:343–348
- Peer M, Epstein RA (2021) The human brain uses spatial schemas to represent segmented environments. *Curr Biol* 31:4677–4688

- Poulter S, Lee SA, Dachtler J, Wills TJ, Lever C (2021) Vector trace cells in the subiculum of the hippocampal formation. *Nat Neurosci* 24:266–275
- Radvansky GA, Copeland DE (2006) Walking through door—ways causes forgetting: situation models and experienced space. *Mem Cognit* 34:1150–1156. <https://doi.org/10.3758/bf03193261>
- Rah YJ, Kim J, Lee SA (2022) Effects of spatial boundaries on episodic memory development. *Child Dev* 93:1574–1583
- Ratcliff KR, Newcombe NS (2008) Is language necessary for human spatial reorientation? Reconsidering evidence from dual task paradigms. *Cogn Psychol* 56:142–163
- Robin J (2018) Spatial scaffold effects in event memory and imagination. *Wiley Interdiscip Rev* 9:e1462
- Rodriguez F, López C, Vargas JP, Broglio C, Gómez Y, Salas C (2002) Spatial memory and hippocampal pallium through vertebrate evolution: insights from reptiles and teleost fish. *Brain Res Bull* 3–4:499–503
- Savelli F, Yoganarasimha D, Knierim JJ (2008) Influence of boundary removal on the spatial representations of the medial entorhinal cortex. *Hippocampus* 18:1270–1282
- Schlesiger MI, Boublil BL, Hales JB, Leutgeb JK, Leutgeb S (2018) Hippocampal global remapping can occur without input from the medial entorhinal cortex. *Cell Rep* 22:3152–3159
- Shepard R, Meltzer J (1971) Mental rotation of three-dimensional objects. *Science* 171:701–703
- Shettleworth S (2001) Animal cognition and animal behaviour. *Anim Behav* 61:277–286
- Sheynikhovich D, Chavarriaga R, Strössl T, Arleo A, Gerstner W (2009) Is there a geometric module for spatial orientation? Insights from a rodent navigation model. *Psychol Rev* 116:540–566
- Shine JP, Valdés-Herrera JP, Tempelmann C, Wolbers T (2019) Evidence for allocentric boundary and goal direction information in the human entorhinal cortex and subiculum. *Nat Commun* 10:4004
- Siegel JJ, Nitz D, Bingman VP (2005) Spatial specificity of single-units in the hippocampal formation of freely moving homing pigeons. *Hippocampus* 15:26–40
- Solstad T, Boccara CN, Kropff E, Moser MB, Moser EI (2008) Representation of geometric borders in the entorhinal cortex. *Science* 322:1865–1868
- Sovrano VA, Bisazza A, Vallortigara G (2003) Modularity as a fish (*Xenotoca eiseni*) views it: conjoining geometric and nongeometric information for spatial reorientation. *J Exp Psychol Anim Behav Process* 29:199–210
- Spelke ES (1994) Innate knowledge: six suggestions. *Cognition* 50:431–445
- Spelke ES, Lee SA (2012) Core system of geometry in animal minds. *Philos Trans R Soc B* 367:2784–2793
- Spelke E, Lee SA, Izard V (2010) Beyond core knowledge: natural geometry. *Cogn Sci* 34:863–884
- Spiers HJ, Hayman RMA, Jovalekic A, Marozzi E, Jeffrey KJ (2015) Place field repetition and purely local remapping in a multi-compartment environment. *Cereb Cortex* 25:10–25 (**More Doorways**)
- Stensola T, Stensola H, Moser M-B, Moser EI (2015) Shearing-induced asymmetry in entorhinal grid cells. *Nature* 518:207–212
- Stewart S, Jeewajee A, Wills TJ, Burgess N, Lever C, Lever C (2013) Boundary coding in the rat subiculum. *Philos Trans R Soc B* 369:20120514
- Taube JS, Muller RU, Ranck JB (1990a) Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *J Neurosci* 10:420–435
- Taube JS, Muller RU, Ranck JB (1990b) Head-direction cells recorded from the postsubiculum in freely moving rats. II. Effects of environmental manipulations. *J Neurosci* 10:436–447
- Tolman EC (1948) Cognitive maps in rats and men. *Psychol Rev* 55:189–208
- Tsao A, Sugar J, Lu L, Wang C, Knierim JJ, Moser MB, Moser EI (2018) Integrating time from experience in the lateral entorhinal cortex. *Nature* 561:57–62
- Twyman AD, Newcombe NS, Gould TJ (2009) Of mice (*Mus musculus*) and toddlers (*Homo sapiens*): evidence of species-general spatial reorientation. *J Comp Psychol* 123:342–345
- Udwin O, Yule WA (1991) A cognitive and behavioral phenotype in Williams syndrome. *J Clin Exp Neuropsychol* 13:232–244
- Vallortigara G (2009) Animals as natural geometers. In: Tommasi L, Peterson MA, Nadel L (eds) *Cognitive biology: evolutionary and developmental perspectives on mind, brain, and behavior*. MIT Press, Cambridge
- Vallortigara G, Zanforlin M, Pasti G (1990) Geometric modules in animals' spatial representations: a test with chicks (*Gallus gallus domesticus*). *J Comp Psychol* 104:248–254
- Vargas JP, Petruso EJ, Bingman VP (2004) Hippocampal formation is required for geometric navigation in pigeons. *Eur J Neurosci* 20(7):1937–1944
- Vicari S, Brizzolara D, Carlesimo GA, Pezzini G, Volterra V (1996) Memory abilities in children with Williams syndrome. *Cortex* 32:503–514
- Watson JB (1913) Psychology as the behaviorist views it. *Psychol Rev* 20:158–178
- Whittington JCR et al (2020) The Tolman-Eichenbaum machine: unifying space and relational memory through generalization in the hippocampal formation. *Cell* 183:1249–1263
- Wills TJ, Muessig L, Cacucci F (2014) Development of spatial behaviour and the hippocampal neural representation of space. *Phil Trans Roy Soc B* 369:20130409
- Xu Y, Regier T, Newcombe NS (2017) An adaptive cue combination model of spatial reorientation. *Cognition* 163:56–66
- Yartsev MM, Ulanovsky N (2013) Representation of three-dimensional space in the hippocampus of flying bats. *Science* 340:367–372

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.