Cognitive Neural Mechanisms of Boundary-Enhanced Spatial Navigation

Authors: Hao Xin, Yuan Zhongping, Lin Shuting, Shen Ting, Hao Xin

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Abstract

Boundaries refer to obstacles that occupy a large proportion of the visual field and possess three-dimensional extended planes, which play a crucial facilitative role in spatial navigation behaviors of humans and animals. Cognitive developmental research has found that in early childhood (1.5-2 years), children achieve object localization by processing the spatial geometric structure of boundaries, and with age development, gradually learn to utilize boundary height information (3.1-4.7 years), length information (4-5 years), visual barrier information (5 years), and other features to complete spatial navigation. Based on these cognitive processes, neuroimaging research, primarily using adults as subjects, has discovered that the medial temporal lobe and parietal brain regions in the brain have distinct functional roles in boundary processing. Specifically, the spatial geometric structure and constituent elements of boundaries (height, length, and angle) are represented by the parahippocampal place area and retrosplenial complex in the brain; the navigational affordances of boundaries are represented by the occipital place area; and the learning and retrieval of object locations bound to boundaries are mediated by the hippocampus. However, several research questions remain worthy of in-depth exploration in the future. First, to expand and deepen the understanding of the cognitive processes through which boundaries facilitate navigation and their developmental patterns. Second, to comprehensively reveal the brain functional basis extensively involved in boundary-facilitated spatial navigation, particularly the functional interactions between the medial temporal lobe and posterior parietal lobe. Third, to closely examine the psychological or neural representations of environmental boundaries versus environmental centers encoded by the brain, and their distinctions and connections. Fourth, to intensively investigate behavioral impairments in boundary-based navigation among populations genetically susceptible to Alzheimer' s disease. Finally, to extend the exploration of the influence mechanisms of boundaries in domains such as long-term memory, time perception, visuospatial processing, and social networks.

Full Text

The Cognitive Neural Mechanisms of Boundary-Enhanced Spatial Navigation

Hao Xin[1],[2], **Yuan Zhongping**[1],[2], **Lin Shuting**[1],[2], **Shen Ting**[1],[2]

[1]Key Laboratory of Adolescent Cyberpsychology and Behavior (Central China Normal University), Ministry of Education, Wuhan 430079, China
[2]School of Psychology, Central China Normal University, Wuhan 430079, China

Abstract

Boundaries are obstacles with extended surfaces that occupy a large proportion of the visual field and play a crucial role in facilitating spatial navigation for both humans and animals. Cognitive developmental research has revealed that children as young as 1.5 to 2 years of age can successfully reorient themselves and locate objects by processing the spatial geometry of boundaries. With increasing age, children gradually learn to utilize additional boundary features for navigation, including height information (around 3.1 to 4.7 years), length information (4 to 5 years), and visual opaqueness (by age 5). Building upon these cognitive processes, neuroimaging studies conducted primarily with adult participants have identified distinct functional roles for the medial temporal lobe and parietal cortex in boundary processing. Specifically, the parahippocampal place area (PPA) and retrosplenial complex (RSC) jointly represent boundary geometry and its constituent elements (height, length, and angle). The occipital place area (OPA) encodes navigational affordances of boundaries, while the hippocampus is responsible for learning and retrieving object locations bound to boundaries. However, several important questions remain for future investigation. First, research should expand and deepen our understanding of the cognitive processes underlying boundary-enhanced navigation and their developmental trajectories. Second, studies should comprehensively reveal the broader neural functional basis, particularly the functional interactions between the medial temporal lobe and posterior parietal cortex. Third, greater attention should be paid to the psychological and neural distinctions and connections between encoding of environmental boundaries versus the environmental center. Fourth, research should specifically examine behavioral impairments in boundary-based navigation among individuals with genetic susceptibility to Alzheimer’ s disease. Finally, future work should extend to explore boundary influence mechanisms in domains such as long-term memory, time perception, visuospatial processing, and social networks.

Keywords: boundary, spatial navigation, cognitive development, functional basis, medial temporal lobe

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Corresponding Author: Hao Xin, E-mail: psyhaoxin@ccnu.edu.cn

1 Introduction

In the natural world, animals require robust spatial navigation abilities to return safely to their nests after foraging and to avoid predators. For humans, navigating from one location to another is a daily challenge. Spatial navigation —the process of moving between different locations based on judgments about oneself and environmental cues—represents a fundamental adaptation for both animal survival and human functioning. This complex ability involves multiple cognitive and perceptual processes, including vision, proprioception, and kinesthesia. Extensive research indicates that successful spatial navigation relies on two primary information sources: external environmental cues (such as visual, auditory, and olfactory information, with visual cues—particularly boundaries and landmarks—being most extensively studied) and internal self-motion information (Chen et al., 2017). The 2014 Nobel Prize in Physiology or Medicine awarded to John O' Keefe, May-Britt Moser, and Edvard I. Moser for discovering place cells and grid cells that form the brain' s spatial positioning system marked a major advance in our understanding of the neural basis of navigation. Critically, this discovery shifted researchers' focus toward environmental cues that play essential roles in navigation, particularly boundaries. Mounting evidence consistently demonstrates that the representation of spatial cells used to construct cognitive maps is strongly controlled by boundary information (Häglund et al., 2019; He et al., 2019; Keinath et al., 2017; Krupic et al., 2015). Moreover, numerous behavioral studies have identified a boundary advantage effect in spatial navigation, where individuals show smaller response errors when using boundary cues compared to landmark cues (Doeller & Burgess, 2008; Lee, 2017; Mou et al., 2013).

Boundaries are defined as obstacles with extended surfaces that occupy a large proportion of the visual field, such as walls, glass panels, and ledges (Lee, 2017; Lew, 2011). Behavioral research demonstrates that boundaries effectively guide path integration and object localization, with both humans and animals consistently showing a preference for using boundaries to locate objects (Lee, 2017). Early neurophysiological studies in rodents identified boundary vector cells in the hippocampal subiculum that encode boundary position and direction, as well as border cells in the medial entorhinal cortex that respond specifically to nearby boundaries (Barry et al., 2006; Lever et al., 2009; Savelli et al., 2008; Solstad et al., 2008; Stewart et al., 2014). Notably, border cells respond only to boundaries that block movement, whereas boundary vector cells also respond to traversable obstacles such as gaps (Bicanski et al., 2020). Recent research has discovered numerous egocentric boundary cells in the rat retrosplenial cortex, dorsomedial striatum, postrhinal cortex, parahippocampal region, and lateral entorhinal cortex that encode the position and direction of boundaries relative to the self (Alexander et al., 2020; Gofman et al., 2019; Hinman et al., 2019; van Wijngaarden et al., 2019; Wang et al., 2018). Similar cells have been found in the macaque hippocampus, which shows high homology with humans (Mao et al., 2021). Information from these boundary-responsive cells is transmitted to egocentric boundary cells to accomplish the transformation from an environment-centered to a self-centered reference frame, thereby guiding subsequent navigation (van Wijngaarden et al., 2020). Although boundary-encoding neurons have not yet been identified in humans, a recent *Nature* study using intracranial electrodes in epilepsy patients observed strong theta oscillations in the medial temporal lobe when individuals approached boundaries during real navigation, with similar neural oscillations occurring when watching others near walls (Stangl et al., 2021). These findings support previous research on boundary-specific neural responses in the human subiculum (Lee et al., 2018) and demonstrate that the brain anchors both self and other localization to boundaries.

Most research on the neural representation of boundaries in humans has employed functional magnetic resonance imaging (fMRI). For example, Shine et al. (2019) had participants learn the locations of landmarks positioned in four directions within a virtual environment containing four differently oriented boundaries. Participants then viewed movement through the virtual environment and, based on cue objects appearing near boundaries, selected which landmark was located in that direction. By varying movement paths, the researchers could dissociate boundary orientation from other factors. Using support vector machine (SVM) analysis, they found that the human entorhinal cortex and posterior subiculum could discriminate boundary orientation above chance level, indicating that these regions encode boundary direction. These studies not only open a window into the mechanisms underlying boundary-enhanced navigation but also highlight the critical importance of boundary cues in spatial navigation. It is worth noting that discrete objects or multiple landmarks can also provide environmental or self-referential information for navigation, though less stably than boundaries. In rodents, researchers have identified allocentric object vector cells in the medial entorhinal cortex, landmark vector cells in the hippocampus, and egocentric object bearing cells in the lateral entorhinal cortex (Andersson et al., 2021; Deshmukh et al., 2013; Høydal et al., 2019; Wang et al., 2018). Whether vector coding for boundaries, landmarks, and objects follows a unified model remains unknown.

In summary, an increasing number of scholars worldwide have recognized the critical importance of boundaries in spatial navigation, and the integration of cognitive neuroscience has accumulated substantial findings. However, these studies are scattered across different perspectives, and a systematic summary of the cognitive processes and neural basis of how boundaries facilitate spatial navigation is lacking. Therefore, this article systematically reviews relevant research from the past decade, clarifying the cognitive neural mechanisms of boundaries in spatial navigation from two perspectives: cognitive developmental processes and neural foundations. Finally, based on existing research, we propose future directions to provide references for upcoming studies and applications. A glossary of specialized terms is provided in Table 1.

Table 1. Glossary of Specialized Terms

Full Term	Abbreviation
Parahippocampal place area	PPA
Retrosplenial complex	RSC
Occipital parietal area	OPA
Transverse occipital sulcus	TOS
Functional magnetic resonance imaging	fMRI
Support vector machine	SVM
Transcranial magnetic stimulation	TMS

2 The Cognitive Developmental Process of Boundary-Enhanced Spatial Navigation

Cheng' s (1986) geometric module theory represents the initial and most influential framework for understanding boundary processing, later expanded by Spelke and Lee (Lee, Sovrano & Spelke, 2012; Lee, Winkler-Rhoades & Spelke, 2012; Spelke & Lee, 2012). This theory proposes that humans and animals possess a dedicated cognitive module for recognizing spatial geometric layout that operates independently of other spatial cues (Cheng, 1986; Cheng et al., 2013; Hermer & Spelke, 1996). The geometric module is considered a priori knowledge with cross-species consistency (Lee, 2017; 费广洪, 潘晓敏, 2013). Evidence for object localization using boundary geometry has been robustly demonstrated in animals including poultry, rats, and toads (Lee et al., 2020; Sotelo et al., 2020).

Importantly, the geometric module theory has received strong support from numerous behavioral studies with human participants (see Table 2), primarily focusing on children aged 1.5 to 5 years in real-world environments using the reorientation paradigm. In this paradigm, participants are disoriented within rectangular or other shaped boundary environments and must locate a hidden object using either geometric or non-geometric cues (color, texture). Successful use of spatial geometry is determined by comparing search frequencies at the correct corner versus the geometrically equivalent corner, or by assessing whether the combined search proportion at these two corners exceeds chance level. Hermer and Spelke (1994) first applied this paradigm to test 18-24-month-old children and adults, requiring them to find a hidden object in a rectangular room with either all white walls or one blue wall after disorientation. Results showed that children searched the correct and equivalent corners equally often in both conditions, whereas adults could distinguish between them when one wall was blue. This indicates that while 1.5- to 2-year-old children can use boundary geometry for reorientation, they cannot use feature cues like adults.

Recent advances in geometric module theory have focused on how the extended surface properties of boundaries and their refined features facilitate object localization. For example, Lee and Spelke (2010) manipulated the size, stability, and relationship to circular boundaries of two rectangular columns while hiding stickers behind them for 3-year-old children to find after disorientation. Results showed that regardless of size changes or column movement, children successfully located the stickers above chance level only when columns were attached to the circular boundary. Performance dropped to chance when columns were detached or became flat markers on the boundary, demonstrating that only three-dimensional extended surfaces effectively promote children’ s reorientation.

Researchers have further investigated how children perceive boundary surfaces, finding that they encode height, length, and visual opaqueness. First, Lee and Spelke (2008) tested 46-56-month-old children (approximately 4-5 years) with boundaries of different heights, finding that only walls forming spatial geometry effectively guided reorientation (even 30 cm high walls), whereas line segments forming flat rectangles did not. This indicates that children encode object location using the vertical height of boundaries. Notably, Lee and Spelke (2011) created rectangles formed by 2 cm high white poles or flat black paper, finding that 38-51-month-old children (approximately 3-4 years) performed above chance only with the white poles, showing they can detect heights as low as 2 cm for reorientation.

Second, Gianni and Lee (2017) manipulated boundary length in 4-5-year-old children, finding that performance exceeded chance with 100 cm boundaries but not with 50 cm boundaries. This suggests that children process boundary length, with shorter boundaries likely perceived as landmarks rather than effective navigation aids. Thus, with age, children show developing cognitive processing of both boundary height and length, though length processing appears to develop slightly later than height processing.

Third, researchers have examined boundary transparency. Gianni et al. (2018) tested 22-95-month-old children (approximately 2-8 years) in rectangular structures made of opaque or transparent glass, requiring them to find hidden stickers after disorientation. Results showed that from age 2, children performed above chance with opaque boundaries, but required until age 5 to exceed chance with transparent boundaries. This indicates early cognitive processing of visual blocking features, with the ability to use transparent boundary geometry developing gradually with age.

Additionally, researchers have investigated how adults represent boundary geometry, proposing the shape-segment hypothesis. This hypothesis suggests that during boundary-based navigation, individuals first form a representation of the overall boundary shape, then select local boundary segments to encode target locations (Zhou & Mou, 2019b). This hypothesis has been validated in a series of studies by Mou' s team. For instance, Zhou and Mou (2018) created virtual environments where participants learned four object locations relative to boundaries that were either complete circular walls, four arc segments, or one arc segment. Results showed significantly larger response errors with complete circular walls compared to four or one arc segment, with no difference between the latter two conditions. This indicates that individuals segment boundaries and perform better with local boundary information. Whether children similarly perceive and segment boundary shapes remains an open question for future research.

In summary, boundary surfaces with extended three-dimensional structure help individuals perceive spatial layout, form mental representations of spatial geometry, and flexibly perform mental segmentation as needed, providing self-orientation and location information. Critically, by early childhood (1.5-2 years), humans can recognize spatial geometric structures formed by boundaries, gradually learning to use height (3.1-4.7 years), length (4-5 years), and visual opaqueness (by age 5) to facilitate navigation. However, although children can use boundary information for localization, their effectiveness and precision remain inferior to adults, with mature and accurate boundary use potentially not achieved until after adolescence (Bullens et al., 2010; Glöckner et al., 2021; Hao et al., 2021).

Table 2. Summary of Cognitive Developmental Studies on Boundary-Enhanced Spatial Navigation

Study	Age Range (Mean)	Sample Size	Key Findings
Hermer & Spelke (1994)	18-24 months	Children: 16; Adults: 16	Children: C = G in both white and blue wall conditions; Adults: C = G in white wall condition, C > G in blue wall condition
Lee & Spelke (2010)	~3 years	29 children	Columns attached to boundary: performance > 0.5; Detached columns: performance = 0.5; Flat markers: performance = 0.5

Study	Age Range (Mean)	Sample Size	Key Findings
Lee & Spelke (2008)	46-56 months	16 children	30 cm or 90 cm walls: C + G $>$ 0.5; Flat rectangle: C + G $<$ 0.5
Lee & Spelke (2011)	38-51 months	16 children	2 cm high rectangle: C + G $>$ 0.5; Flat rectangle: C + G $<$ 0.5
Gianni & Lee (2017)	4-5 years	16 children	50 cm boundary: C + G $<$ 0.5; 100 cm boundary: C + G $>$ 0.5
Gianni et al. (2018)	22-95 months	86 children	Ages 2-4: transparent boundary C + G $<$ 0.5, opaque boundary C + G $>$ 0.5; Age 5: both transparent and opaque boundaries C + G $>$ 0.5
Bullens et al. (2010)	5-20 years	18 children, 18 adults	Boundary-based localization: 5 years = 7 years $<$ adults
Julian et al. (2019)	Children: 6-17 years; Adults: 20-35 years	18 children, 18 adults	Boundary-based distance error: children $>$ adults
Glöckner et al. (2021)	Children: 6-10.33 years; Adults: 18-50 years	29 children, 16 adults	Boundary model matching: significant differences for 6-13 years, no difference for 15-17 years
Zhou & Mou (2018)	Adults	29 adults	Response error: 4 segments = 1 segment $<$ complete boundary

Note: C = Correct corner; G = Geometrically equivalent corner; WS = Williams syndrome

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3 The Neural Basis of Boundary-Enhanced Spatial Navigation

How does the brain represent boundaries and learn object locations bound to them? Neuroimaging research (see Table 3), primarily with adult participants using task-based fMRI, has revealed distinct functional roles for the medial temporal lobe and parietal cortex in boundary processing (Julian, Keinath, Marchette & Epstein, 2018). Specifically, boundary geometry and its constituent elements are processed by the parahippocampal place area (PPA) and retrosplenial complex (RSC). Navigational affordances of boundaries are encoded by the occipital place area (OPA), while boundary-related learning is mediated by the hippocampus.

3.1 Neural Representation of Boundary Geometry

Boundary geometry and its features (height, length, and angle) are primarily represented by the PPA and RSC, with RSC showing greater specificity for overall spatial geometry and PPA demonstrating greater sensitivity to individual geometric elements. Unlike traditionally anatomically-defined regions, PPA and RSC are functionally-defined areas involved in scene recognition (Epstein, 2008; Epstein et al., 1999). The PPA is located in the posterior parahippocampal cortex, extending into the lingual gyrus, covering the collateral sulcus and extending to the fusiform gyrus. The RSC is situated in the retrosplenial cortex, extending posteriorly to the parietal-occipital sulcus (Bar & Aminoff, 2003; Epstein & Baker, 2019; Epstein & Kanwisher, 1998; Zhen et al., 2017).

Kamps et al. (2016) found that when participants viewed images of intact wall layouts versus scrambled layouts, both PPA and RSC showed significantly greater activation for intact layouts, indicating processing of boundary geometry. Similarly, Harel et al. (2013) presented images with or without boundary geometry and found greater PPA and RSC activation for geometric images. However, when presenting images with or without objects, PPA activation was higher for object-containing scenes while RSC activation did not differ, suggesting that PPA represents both spatial geometry and objects, whereas RSC represents only spatial geometry. Thus, RSC may be more specialized for spatial geometry than PPA.

Subsequent research has investigated how PPA and RSC process boundary geometry. First, both regions show sensitivity to boundary height. Ferrara and Park (2016) presented images of scenes with different boundary heights and found that PPA activation was highest for walls, intermediate for 5 cm curbs, and lowest for textured mats, with significant differences between all conditions. RSC activation was significantly higher for walls than for curbs or mats, but did not differ between the latter two conditions. This indicates that while both regions are sensitive to height, PPA can discriminate small height differences, whereas RSC requires greater height differences to show significant activation changes. Ferrara et al. (2019) provided stronger evidence for PPA' s fine-grained boundary representation by combining fMRI with a reorientation paradigm. While typical individuals successfully reoriented using flat textures, curbs, and walls, individuals with Williams syndrome could only use walls. Imaging results showed that typical participants' PPA activation differed significantly across all three conditions, whereas Williams syndrome participants' PPA showed greater activation for walls only, with no difference between curbs and textures. This suggests that impaired PPA function in Williams syndrome prevents fine-grained boundary height discrimination necessary for navigation.

Second, researchers have examined the neural basis of boundary length and angle. Dillon et al. (2018) presented participants with pairs of images that were identical, differed in wall length or angle, or were completely different scenes. They found that PPA activation changes were significantly greater for length or angle changes compared to identical images, with activation patterns similar to completely different scenes. In contrast, RSC activation changes did not differ across these conditions, indicating that boundary length and angle changes are primarily represented by PPA rather than RSC. In summary, PPA provides a more fine-grained representation of boundary geometry, whereas RSC provides a coarser representation. PPA detects changes in boundary geometry by identifying variations in height, length, and angle, while RSC primarily uses height changes to detect geometric transformations. However, research on RSC remains limited, requiring further investigation into how it processes boundary geometry.

3.2 Neural Basis of Boundary Navigational Affordance

Neuroimaging research has primarily focused on physical navigational affordances of boundaries, distinguishing between passable and impassable (blocking) properties. Studies using diverse neuroscientific methods have identified the OPA as the key region processing boundary navigational affordances. Like PPA and RSC, OPA is a functionally-defined region located in the dorsal occipital lobe (Dilks et al., 2013), also known as the transverse occipital sulcus (TOS) due to its location near this anatomical landmark (Grill-Spector, 2003). A crucial causal study by Julian et al. (2016) used transcranial magnetic stimulation (TMS) over OPA while participants learned object locations bound to boundaries or landmarks in virtual environments. TMS to OPA significantly impaired boundary-based navigation but not landmark-based navigation, establishing a causal role for OPA in boundary processing. In a subsequent island scenario surrounded by water, OPA stimulation increased reaction times without affecting accuracy, leading researchers to hypothesize that OPA processes boundary navigational affordances.

Bonner and Epstein (2017) further tested this hypothesis by presenting indoor scenes with or without doors that manipulated boundary navigational affordances. They found that OPA representational similarity was significantly correlated for scenes containing doors, indicating OPA encodes navigational affordances. Moreover, OPA automatically identified navigational passages formed by boundaries in real-world scenes. Recent fMRI research shows that OPA represents self-referenced passable distances (how far one can move forward) based on boundary affordances. Park et al. (2020) presented indoor scenes with transparent curtains (passable) or glass (impassable) at near, medium, or far distances. Using SVM classification, OPA could distinguish near, medium, and far scenes with curtains but not with glass. Since glass was impassable at all distances (making passable distances identical across scenes), OPA could not differentiate them. However, curtains' navigational affordances created different passable distances, enabling OPA discrimination. This aligns with previous findings that OPA processes egocentric distance (Persichetti & Dilks, 2016). Additionally, OPA shows greater activation for dynamic first-person perspective videos than static images (Kamps, Lall & Dilks, 2016), suggesting OPA primarily supports self-referenced representations by tracking navigational affordances and distance changes relative to the self.

Building upon physical affordance research, Lee' s team has innovatively separated visual from physical properties of boundaries. They define "look-like boundaries" as visually appearing as boundaries without physical impediment (e.g., virtual boundaries or curtains), arguing that visual properties are more critical than physical properties for localization and navigation. In one study comparing visual-plus-physical boundary (plywood), visual-only boundary (passable), and landmark (cones) conditions, they found no performance differences between physical and visual boundary conditions, but both differed from the landmark condition in response bias (Negen et al., 2019). This suggests individuals localize objects based on visual rather than physical navigational affordances. However, neuroimaging research has focused exclusively on physical affordances, leaving open whether OPA also represents visual navigational affordances—a question for future investigation.

3.3 Learning Mechanisms for Boundary Representation

Multiple studies indicate that boundary learning is incidental, with the hippocampus serving as the core neural substrate (Bird et al., 2010; Doeller et al., 2008). Doeller et al. (2008) used a desktop VR paradigm and found that learning object locations bound to boundaries activated the right posterior hippocampus, whereas learning landmark-bound locations activated the striatum. This suggests a specific relationship between the hippocampus and boundary-based location encoding, and between the striatum and landmark-based learning. Developmental research has shown similar patterns: younger adults performed better on boundary learning and showed greater hippocampal activation, while older adults performed better on landmark learning and showed greater striatal activation (Schuck et al., 2015). This implies that age-related hippocampal decline may impair boundary-based learning, suggesting a causal relationship.

Further evidence comes from Julian et al. (2019), who found that adults with

Williams syndrome showed worse boundary-based learning than children, consistent with evidence of early hippocampal dysfunction in this population (Meyer-Lindenberg et al., 2005). Additionally, Guderian et al. (2015) demonstrated a direct causal relationship between hippocampal structure and boundary learning. Using Doeller' s (2008) paradigm with individuals having hippocampal volume reduction and healthy controls, they found that those with severe hippocampal atrophy made significantly more errors in boundary-based navigation. Thus, hippocampal function and structure constitute the neural foundation for boundary-based learning; damage to this region impairs the ability to effectively encode and remember object locations using boundaries.

4 Summary and Future Directions

In summary, using boundary cues for spatial navigation is a complex cognitive process. Developmental research demonstrates that by early childhood (1.5-2 years), humans can recognize spatial geometric structures formed by boundaries, gradually learning to use height (3.1-4.7 years), length (4-5 years), and visual opaqueness (by age 5) to facilitate navigation. Neuroimaging research with adults shows that boundary geometry is represented by PPA and RSC, with different preferences for geometric features; physical navigational affordances are encoded by OPA; and boundary-based learning and memory are mediated by the medial temporal lobe hippocampus. While these studies provide initial insights, several limitations and unanswered questions warrant deeper investigation:

First, future research should expand exploration of cognitive processes underlying boundary-enhanced navigation and their developmental trajectories. Previous studies on boundary geometry may have overlooked confounding factors such as salience. Boundaries in typical research (large circles or rectangles) occupy substantial area and may capture attention more than other cues, causing spontaneous neglect of alternative information sources (Buckley et al., 2015; Newcombe & Huttenlocher, 2007; Wang & Mou, 2020). Most desktop VR studies show that removing boundaries impairs performance while removing landmarks does not. However, when landmark size is increased, participants use both boundaries and landmarks, with no significant impairment from removing either cue (Doeller & Burgess, 2008; Honbolygó et al., 2014), demonstrating that boundary salience influences cue selection. Although some research has examined other boundary features (e.g., color), empirical work remains limited and developmental trajectories unknown. Future studies should construct integrated cognitive networks or computational models to clarify the role of these processes in boundary-based navigation.

Second, research should deeply investigate the broader neural functional basis, particularly functional cooperation between brain regions, and examine developmental changes in children' s brains. Previous studies have focused on the ventral visual pathway' s medial temporal lobe, neglecting dorsal pathway regions such as frontal and parietal cortex, and have primarily examined single-region activation rather than inter-regional interactions. However, frontoparietal regions participate in spatial navigation (Freedman & Ibos, 2018; Zhang & Naya, 2020), and recent theories propose functional interactions between ventral and dorsal visual pathways (Pitcher & Ungerleider, 2021). Early work by Kravitz et al. (2011) suggested a functional pathway between dorsal parietal and ventral medial temporal regions for navigation. Future research should examine activation in frontal and parietal regions during boundary-based navigation and investigate functional connectivity between medial temporal and posterior parietal regions to fully reveal the neural mechanisms. Additionally, since most neural research uses adult participants, developmental studies collecting multimodal data (structural, resting-state, task-based) are needed to characterize the dynamic developmental trajectory of boundary processing. Combining non-invasive TMS or transcranial electrical stimulation with other neuroimaging techniques to establish causal relationships between cognitive processes and brain regions represents another important future direction.

Third, research should address the psychological and neural distinctions and connections between encoding environmental boundaries versus the environmental center. Corresponding to boundary cues, geometric center points also play a special role in navigation and localization (Gallistel, 1990; LaChance et al., 2019). LaChance et al. (2019) recorded neural signals in rats foraging freely in square arenas and identified egocentric center-encoding cells in the postrhinal cortex (homologous to human parahippocampal region), including center-bearing cells, center-distance cells, and head direction cells. This suggests that the environmental center may contribute to cognitive map formation through interactions with the environment-centered reference frame. Additionally, path cells in the human entorhinal cortex show significant activity when epilepsy patients navigate along square paths (Jacobs et al., 2010), potentially linking to center representation. These findings imply independent processing of center and boundary information, though some argue against functional separation (Alexander, Robinson et al., 2020), suggesting that center perception depends on boundary knowledge. A recent study in epilepsy patients with intracranial electrodes identified anchor cells in the parahippocampal region that encoded both boundaries and center points relative to self-direction, with different directional preferences for boundary- versus center-anchored cells (Kunz et al., 2020). This suggests both separation and connection in boundary and center representations, but research remains limited to egocentric reference frames. Future studies should clarify the distinctions and connections between boundary and center representations and how they support transformations between egocentric and allocentric reference frames.

Fourth, research should extend boundary-based navigation studies to Alzheimer’ s disease populations. With rapidly increasing global prevalence, using spatial navigation tasks for prevention and identification of at-risk individuals has become a hot topic (Coughlan et al., 2018, 2019; 张家鑫 et al., 2019). Recent research with APOE4 carriers found that boundary-based navigation performance positively predicted episodic memory decline over 18 months (Coughlan et al., 2020), highlighting the relationship between Alzheimer' s disease and boundary-based navigation. Since preclinical Alzheimer' s disease involves damage to entorhinal cortex and hippocampus—key regions for boundary-based navigation (Coughlan et al., 2018)—future studies should integrate genetics, electrophysiology, and neuroimaging to comprehensively investigate specific impairments in boundary-based navigation among at-risk and preclinical populations, providing new avenues for precision prevention and screening.

Finally, space and time are inseparable in human experience, so boundary research should extend beyond spatial dimensions to memory, time perception, visuospatial processing, and social networks (Brunec et al., 2020; Julian et al., 2018; Pellencin et al., 2018). For example, event boundaries segment continuous experience into discrete episodes, shaping long-term memory representations (Horner et al., 2016; Jeunehomme & D' Argembeau, 2020; Logie & Donaldson, 2021; 邵意如 & 周楚, 2019). Since spatial boundaries segment space during navigation, boundary mechanisms in time may parallel those in space (Brunec et al., 2018). Systematic research is lacking, so future studies should examine how different boundary types affect event memory and compare these mechanisms to spatial boundary processing to clarify similarities and differences across domains.

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