

The user wants me to translate a Chinese academic text about “认知地图及其内在机制后印本” (Cognitive Maps and Their Intrinsic Mechanisms - Post-print). The text is likely a scientific paper or academic article. Key requirements: 1. Preserve ALL LaTeX commands and placeholders exactly 2. Preserve ALL citation c...

Authors: Wu Wenya, The user has provided a very short input: “王亮” . This appears to be a Chinese name. Let me analyze what needs to be done:

1. The input is just “王亮” - no LaTeX, no citations, no tags
2. According to the instructions, I should translate from Simplified Chinese to English
3. This is a name, so the translation should be the English representation
4. The standard way to translate Chinese names is:
 - Keep the surname first (Wang)
 - Then the given name (Liang)
 - Or use the Western order: Liang Wang

However, looking at the context, this seems to be a name that might appear in an academic paper. In academic contexts, Chinese names are typically: - Written in Pinyin: Wang Liang - Sometimes with the surname first: Wang Liang - Or in Western order: Liang Wang

The most common and standard approach in English academic papers is to use the Pinyin with surname first: Wang Liang.

But wait - the user hasn't provided any tags or other structure. The instructions say: - “Return ONLY the translated text for the given input (no explanations, no quotes, no headings you invent)” - “Keep one output paragraph per input paragraph; do not merge or split paragraphs” - “Maintain exact count and IDs of ...tags”

Since there are no tags in the input, I should just provide the translation directly. The simplest and most accurate translation of “王亮” in an academic context would be “Wang Liang” .

Let me double-check the requirements: 1. Preserve ALL LaTeX commands and placeholders - N/A here 2. Preserve ALL citation commands - N/A here 3. **PRESERVE ALL ...paragraph wrapper tags EXACTLY** - N/A here 4. Maintain academic tone - yes, using standard Pinyin transliteration 5. Use precise technical terminology - N/A 6. Preserve section structure - N/A 7. Translate all content completely - yes, just the name

Since there's no tag, I should just output the translated name directly without any wrapper. The instructions say "if input has N paragraph tags, output must have exactly N paragraph tags with matching IDs". Since N=0 here, I should

Date: 2023-10-09T00:00:00+00:00

Abstract

The user wants me to translate a Chinese academic text about spatial navigation and cognitive maps into English. Let me break down the requirements:

1. Critical Requirements:

- Preserve ALL LaTeX commands and placeholders exactly
- Preserve ALL citation commands ([?], ??, (??), etc.) exactly
- **PRESERVE ALL ...paragraph wrapper tags EXACTLY**
- Maintain academic tone and formal scientific writing style
- Use precise technical terminology (glossary provided)
- Preserve section structure and paragraph organization
- Translate all content completely

2. Output Rules:

- Return ONLY the translated text
- Keep one output paragraph per input paragraph
- Maintain exact count and IDs of ...tags
- Do NOT add Markdown formatting unless present in source
- Preserve original line breaks when meaningful

3. Formatting Guidelines:

- Keep mathematical expressions in original LaTeX format
- Preserve equation numbers and references
- Maintain proper academic paragraph structure
- Use formal scientific language

4. Glossary:

- 机器学习 => machine learning
- 深度学习 => deep learning

Now, let me analyze the input text:

The input is a single paragraph about spatial navigation and cognitive maps. It doesn't contain any LaTeX commands, math placeholders, or citation commands. It also doesn't have any tags in the input. Wait, let me re-read the instructions.

The instructions say "if input has N paragraph tags, output must have exactly N

paragraph tags with matching IDs” . But the input provided by the user doesn't have any tags. This is a bit confusing. Let me check the example again.

Actually, looking at the user's input, it's just plain text without any tags. So according to the rules, I should just translate it as is, without adding any tags. The instructions about preserving tags seem to be for cases where they exist in the input.

Let me translate the content:

“空间导航对于人和动物的生存而言都十分重要，有效的空间表征或认知地图是空间导航的基础。” - Spatial navigation is crucial for the survival of both humans and animals, and effective spatial representation or cognitive maps form the foundation of spatial navigation.

“认知地图的典型属性包括选择性、灵活性以及层级性，海马、场景选择区域以及前额叶等多个脑区都参与认知地图的构建。” - Typical properties of cognitive maps include selectivity, flexibility, and hierarchy, with multiple brain regions such as the hippocampus, scene-selective areas, and the prefrontal cortex all participating in the construction of cognitive maps.

“认知地图的表征形式存在欧式地图和拓扑图两种理论，但各自单独都不能全面解释实际导航中的行为表现，因此有研究者提出了标签图等理论试图调和二者间的矛盾。”

Full Text

Preamble

The Cognitive Map and Its Intrinsic Mechanisms

WU Wenyan, WANG Liang

(CAS Key Laboratory of Mental Health, Institute of Psychology, Chinese Academy of Sciences, Beijing 100101, China)

(Department of Psychology, University of Chinese Academy of Sciences, Beijing 100049, China)

Abstract: Spatial navigation is essential for the survival of humans and animals, and effective spatial representation—or cognitive maps—forms its foundation. Cognitive maps exhibit three prototypical properties: selectivity, flexibility, and hierarchy. Multiple brain regions, including the hippocampus, scene-selective areas, and prefrontal cortex, participate in constructing cognitive maps. The representational format of cognitive maps remains debated, with Euclidean maps and topological graphs representing two theoretical extremes, neither of which can fully explain real-world navigation behavior. Consequently, researchers have proposed theories such as the labeled graph hypothesis to reconcile these contradictions. Future research should examine the dynamic changes in hierarchical organization during cognitive map construction, the expansion of spatial dimensions and categories, and the limitations of the cognitive map hypothesis itself.

Keywords: cognitive map, Euclidean map, topological graph, hierarchy, spatial representation

Spatial navigation represents a crucial cognitive function for humans and other animals inhabiting complex environments (Genzel et al., 2018; Goldshtein et al., 2022). Efficient navigation requires effective mental representation of spatial information—an internal, subjective format of external information and objective knowledge that differs from external objective forms such as cartographic maps or smartphone navigation applications. This internal representation of spatial knowledge is essential for navigation in familiar environments, enabling flexible route planning (Harten et al., 2020) and saving navigation time. Research indicates that long-term reliance on navigation software may degrade spatial memory and navigation abilities (Dahmani & Bohbot, 2020), underscoring the theoretical importance of understanding the mechanisms underlying internal spatial representations.

Because spatial knowledge representations facilitate advanced cognitive behaviors such as route planning and shortcut selection, they are functionally analogous to geographic maps and thus termed “cognitive maps” (Tolman, 1948). Tolman observed that with increased practice, rats in maze tasks gradually optimized their spatial navigation, eventually selecting novel shortcuts not experienced during training. This demonstrated that rats do not merely form simple stimulus-response associations but rather comprehend the overall spatial structure of the environment, actively selecting important cues to construct an allocentric comprehensive map independent of the navigator’s position.

Although Tolman’s concept was rudimentary—functionally demonstrating the necessity of animals forming global environmental knowledge beyond direct experience without detailing specific mechanisms—it spawned numerous subsequent discoveries in spatial navigation research, yielding breakthroughs in both theoretical and experimental studies. Moreover, while originating in psychology, the cognitive map concept has attracted interdisciplinary interest, expanding its scope beyond cognitive psychology and neuroscience into computer science, engineering, economics, management, and behavioral geography (Ruan et al., 2021; He & Yin, 2022).

Given limited understanding of the construction rules, precision, and representational formats of cognitive maps, along with divergent views among researchers, this study reviews relevant theories and experimental research in cognitive neuroscience to provide insights for interdisciplinary investigators. We first summarize the typical properties of cognitive maps from behavioral and functional perspectives, then elaborate on the brain regions involved in cognitive map construction and their mechanisms, subsequently outline theoretical controversies regarding the format of cognitive maps, and finally reflect on this concept while proposing future research directions.

2. Typical Properties of Cognitive Maps

Cognitive maps do not replicate spatial knowledge with complete fidelity but exhibit distinct psychological properties. They selectively process and store different spatial information according to task demands, leading to distorted representations. Second, to cope with complex and dynamic environments, spatial representations demonstrate flexibility, tolerating redundancy in representational formats for the same information. Additionally, because navigable spaces typically have nested structures, cognitive maps of such spaces exhibit hierarchy, though this hierarchical organization diminishes with increased navigation experience, gradually becoming more coherent.

2.1 Selectivity and Distortion

Cognitive resources are limited, necessitating selectivity in spatial representation to enhance cognitive economy. The standard view across psychology, economics, and artificial intelligence holds that humans form complete and fixed representations for navigation tasks, using heuristics to plan subsequent behavior. However, Ho et al. (2022) found that people flexibly construct specific simplified representations for particular problems, balancing representational complexity with utility.

While spatial knowledge encompasses location, path relationships, and direction, cognitive maps in practical situations may only include subsets of this information. As Borges (1971) illustrated in his science fiction “On Exactitude in Science,” a map containing all information about a geographic environment becomes useless due to its enormous size. Indiscriminately representing all information wastes cognitive resources and fails to efficiently solve specific problems. For instance, when traveling in a city, the appropriate map type depends on transportation mode—cycling requires non-motorized lane maps, driving requires motorized road maps, and satellite imagery alone is unusable.

Selective spatial representation arises from functional demands, with different environments (cultural and geographic) imposing distinct representational requirements. In map-drawing tasks, participants organize hand-drawn maps according to their city’s unique attributes, with personal route usage prominently reflected in their drawings, indicating that spatial representations serve important social functions (Appleyard, 1970). A large-scale cross-cultural study found that people navigate better in environments sharing similar topological features with their native habitat, demonstrating that urban street network design influences residents’ spatial representation tendencies and navigation abilities (Coutrot et al., 2022). These findings suggest that the focus of cognitive maps is shaped by daily needs, with different environments leading to selective representation of different content.

Selective representation implies inherent limitations—compared to real information, distortions inevitably exist, representing the necessary cost for representations to serve specific functions. Path distance estimation is influenced by the

number of location points along the path; when actual distance is controlled, more location points lead to larger distance estimates (Thorndyke, 1981). Paths near city centers are significantly overestimated compared to peripheral paths, and angle estimation shows a bias toward 90° (Byrne, 1979). Linguistic information can also explain specific distortions observed in large-scale geographic map representation tasks, suggesting that natural language experience participates in encoding and forming cognitive maps (Gatti et al., 2022).

Thus, as simplified yet purposeful depictions of environments, practical maps must sacrifice certain details to highlight relevant information. No completely accurate practical map exists; all maps necessarily involve some distortion, depending on their function (Hartley, 2017). Similarly, no completely accurate cognitive map exists; spatial representation distortion accompanies specific functions (Longo, 2021).

2.2 Flexibility and Redundancy

Flexibly applying learned knowledge is crucial for animals to cope with complex environments and unpredictable challenges. Environments are not static—previously accessible paths may be blocked, food resources may disappear—and efficient navigation requires the ability to respond to dynamic changes in environmental cues and structure (Kabadayi et al., 2018). Cognitive map flexibility may underlie this capacity.

As early as 1948, when studying detours and shortcut selection in complex mazes, Tolman observed that rats exhibited strong behavioral flexibility rather than simple stimulus-response sequences. Research has found that flexible cognitive maps and spatial navigation require mental replay, and that stress impairs flexibility (Epsztein, 2022; Brown et al., 2020).

Underlying flexibility is the redundancy of spatial representations and cognitive map formats. To support flexible navigation, the same spatial information may need to be organized and stored in multiple forms simultaneously (Yousif, 2022). The same information or content may have vastly different optimal presentation formats under different conditions or requirements. For example, electronic files have multiple format attributes with distinct functions (PDF files are convenient for viewing, Word documents for editing), and problem formulation significantly affects solution efficiency. Similarly, for the same spatial information, the optimal cognitive map format varies with functional demands, requiring the brain to redundantly represent information in multiple formats for flexible retrieval.

2.3 Hierarchy and Coherence

Navigable spaces are often nested environments containing different sub-regions, such as different buildings on a campus and different rooms within each building. The navigation system may represent different local regions separately, requiring integration of information acquired through discrete learning to form a coherent global cognitive map. Information about different local regions is separated

because navigable spaces include vista space and environmental space (Meilinger et al., 2016). The former encompasses spaces that can be surveyed from a single viewpoint, such as bedrooms or open fields [Figure 1a: see original paper], while the latter requires the navigator to move through obstacles, integrating information learned in each vista space, such as city blocks or mazes [Figure 1b: see original paper].

Within nested environmental spaces [Figure 1c: see original paper], information about different local regions may be organized hierarchically. McNamara (1986) found that spatial priming, direction judgment, and Euclidean distance estimation were all influenced by whether different locations belonged to the same region. In segmented parallel corridors, human spatial memory is organized according to each corridor's local coordinate system, indicating that representations of different local regions are separated (Meilinger et al., 2016). Furthermore, distortions in human spatial relationship judgments support the hierarchical nature of cognitive maps (Stevens & Coupe, 1978). However, hierarchy is not permanent; different local regions may gradually integrate with extensive experience, forming a unified, coherent whole. Early studies showed that common landmarks across regions could facilitate integration of new local information into existing spatial knowledge (Golledge et al., 1993).

3. Neural Mechanisms of Cognitive Maps

Early research on the neural mechanisms of cognitive maps focused on parietal cortex, as patients with parietal damage showed impaired or lost spatial navigation abilities. The subsequent discovery of place cells shifted focus to the hippocampus, leading to further identification of head direction cells and grid cells and border cells in the entorhinal cortex, demonstrating that the hippocampal-entorhinal system is a key region for cognitive maps. Additionally, the medial prefrontal cortex, orbitofrontal cortex, and scene-selective regions also play important roles in cognitive map formation.

3.1 Hippocampal-Entorhinal System

O'Keefe and Dostrovsky (1971) first recorded place cells in rodent hippocampus, which fire only when animals occupy specific locations [Figure 2a: see original paper], indicating that the hippocampus encodes spatial position. Subsequent research identified various cell types in the hippocampal formation encoding direction, environmental boundaries, and other spatial information, including grid cells, head direction cells, and border cells (Hafting et al., 2005; Taube et al., 1990; Lever et al., 2009). Entorhinal grid cells fire at vertices of equilateral triangles tiling the environment [Figure 2b: see original paper], exhibiting sixfold rotational symmetry (Hafting et al., 2005; Doeller et al., 2010). Grid cells provide a regular grid background for spatial representation and can compute directions from current position to navigation goals (Bellmund et al., 2016).

The hippocampal-entorhinal system is crucial for representing both Euclidean

metric information and topological connectivity. Neuroimaging studies have found that the hippocampus and entorhinal cortex encode both Euclidean and path distances between locations, with functional segregation along the hippocampal long axis: the anterior hippocampus correlates with Euclidean distance while the posterior hippocampus correlates with path distance (Morgan et al., 2011; Howard et al., 2014). Hippocampal sensitivity to Euclidean distance originates from entorhinal cortex input, where grid cells' multi-peaked firing fields provide a regular grid background (Hafting et al., 2005), though entorhinal input is not necessary for hippocampal spatial representation reorganization (remapping) (Schlesiger et al., 2018).

The hippocampal formation also represents environmental topology. In constrained mazes composed of connected channels, rodent hippocampal place fields are determined by position relative to maze topology rather than absolute Euclidean location (Dabaghian et al., 2014). Additionally, sequential reactivation of place cells during rest reflects maze topology (Wu & Foster, 2014). During navigation in virtual city streets, human posterior hippocampal signals correlate with the number of path connections likely to be experienced in the future, while anterior hippocampal signals correlate with overall environmental topology (Javadi et al., 2017).

The hippocampal-entorhinal system also implements cognitive map flexibility. Widloski and Foster (2022) recorded hippocampal activity in rats during maze tasks, continuously varying maze structure and food locations by changing obstacle configurations. They found rats could flexibly adjust foraging routes, and hippocampal replay/reactivation during rest could predict future routes and obstacle avoidance. During this process, most place cells maintained stable fields, with only a small proportion changing with obstacle distribution. These "unstable" cells may be closely related to rats' flexible adaptation to spatial layout changes.

The hippocampal-entorhinal system also plays an important role in hierarchical organization of cognitive maps. Different local regions in an environment are represented separately during initial learning, supported by both human behavioral studies and rodent electrophysiological research. For example, human spatial memory is influenced by environmental obstacles, forming local reference frames based on obstacle-segmented environmental shapes (Meilinger et al., 2016). Rodent entorhinal grid cells and hippocampal place cells create independent local maps for local regions, with grid fields and place fields confined within local environments (Alme et al., 2014). However, extensive navigation experience in multi-compartment spaces can weaken or eliminate compartment boundary effects, with grid cell firing fields expanding to global space (Carpenter et al., 2015). Although both rodents and humans initially tend to separate local representations, prolonged, rich experience in multi-region environments causes rodent grid cell firing patterns to shift rapidly from discrete local grid fields to continuous global fields, gradually integrating local region representations to form globally coherent cognitive maps (Wernle et al., 2018). This

phenomenon has not been observed in humans, possibly due to different experimental paradigms (Zhao, 2018).

3.2 Scene-Selective Regions

Visual scenes constitute the primary component of small-scale local environment representation, and correct scene or location identification is crucial for daily life, requiring cortical network participation. The visual scene processing system is not the hippocampal-entorhinal system that represents navigable space but rather the scene-selective regions, which show strong responses when viewing scenes and include three functional sub-regions: the parahippocampal place area (PPA), occipital place area (OPA), and retrosplenial complex (RSC) (Dilks et al., 2022).

Functionally, the mainstream view holds that these three sub-regions directly participate in spatial navigation. OPA represents local spatial layout, environmental boundary constraints, and boundary distances (Henriksson et al., 2019; Julian et al., 2016; Park & Park, 2020). PPA processes visual and geometric features of scenes (Marchette et al., 2015). RSC integrates local representations from the above two regions to form unified global representations (Epstein et al., 2007). fMRI studies have found that sequential appearance of path locations triggers stronger RSC activity (Schinazi & Epstein, 2010), indicating that RSC activity is related to path topology.

Overall, scene-selective regions participate in “stitching” multiple discrete vista spaces to weave a spatial representation fabric for navigators. Current scene information also activates associated representations within the panoramic environment (Robertson et al., 2016). Through this mechanism, scene-selective regions enable dynamic interaction between transient spatial perception and relatively persistent spatial memory, promoting global cognitive map formation. Some researchers term this “stitching” process “mapping,” where retrosplenial cortex extracts cognitive maps from primary sensory information of vista spaces, then adjusts and updates map layout based on recognized environmental landmarks to maintain consistency between cognitive maps and real-world spatial layouts (Liang et al., 2022).

3.3 Prefrontal Cortex

Previous research generally considered the core brain network for cognitive maps and spatial navigation to be composed of the hippocampal-entorhinal system and scene-selective regions, largely ignoring the prefrontal cortex' s (PFC) critical role in adapting to environmental changes, tracking, and advance planning for risk avoidance. Three reasons may explain this neglect: First, PFC damage typically severely impairs executive function (Shallice & Burgess, 1991), naturally degrading performance on most tasks rather than specifically affecting spatial tasks. Second, early studies found that lesioning the medial PFC in rats did not affect performance in navigation tasks such as the water maze (Lacroix

et al., 2002; Sloan et al., 2006). Third, experimental evidence for place cell- and grid cell-like coding in PFC is generally scarcer and emerged relatively later (Park et al., 2021; Jacobs et al., 2013).

Existing research has found functional differences among PFC sub-regions. Dorsolateral PFC (dlPFC) and ventrolateral PFC (vlPFC) are active during detours caused by obstacles and may participate in route replanning (Javadi et al., 2019). Medial PFC (mPFC) is associated with egocentric spatial representation, encoding object-based cognitive maps when navigators remember egocentric target locations (Zhang & Naya, 2020), and can reactivate effective behavioral sequences (Kaefer et al., 2020). Dorsomedial PFC also separates task-relevant from task-irrelevant spatial contexts (Mahmoodi et al., 2023). Orbitofrontal cortex (OFC) represents task state spaces (Schuck et al., 2016) (e.g., value space, feature space), integrating spatial representations of the environment with behavioral value to form decision maps, and participates in compressing representations within the same spatial context (Muhle-Karbe et al., 2023). Dorsal anterior cingulate cortex (dACC) participates in hierarchical encoding of path networks (Anggraini et al., 2018) and can suppress incorrect route selection tendencies (Javadi et al., 2019).

Given the diversity of PFC spatial representation content, Patai and Spiers (2021) summarized that different PFC regions may function at different navigation stages: At navigation onset, mPFC recalls target locations for dmPFC route planning; if detours are needed, dACC searches for alternative routes; lateral PFC then replans routes to avoid incorrect shortcuts; OFC selects specific paths and infers potential outcomes; mPFC represents path distances; and when beyond target range, dACC assists in backtracking.

In summary, as a higher-order brain region, PFC's primary role is as a user and operator of cognitive maps, receiving spatial information from the hippocampus (Nardin et al., 2021) and flexibly applying it to planning, inference, and prediction for efficient spatial navigation.

3.4 Hippocampal-Cortical Interaction

The hippocampus, scene-selective regions, and prefrontal cortex each perform unique functions in cognitive map construction, yet certain advanced properties of cognitive maps require joint action across multiple brain regions and cannot be achieved by single regions alone. Interactions among multiple brain regions may be cooperative or competitive.

The selectivity of cognitive maps may require cooperative interaction between the hippocampus and OFC. In a recent fMRI study combined with computational modeling, stimuli were embedded in multiple relational structures, causing participants to simultaneously form two cognitive maps during learning: one for spatial location relationships and another for predictive relationships (i.e., transition relationships between stimuli). During subsequent selection tasks, only spatial location relationships determined reward magnitude. Modeling re-

sults showed participants' choices became increasingly influenced by spatial location relationships, with behavioral modeling indicating that spatial weights gradually increased while predictive weights gradually decreased. This suggests task demands drive selective strengthening of spatial location cognitive maps and selective weakening of predictive cognitive maps. fMRI results indicated that spatial weight changes were primarily sensitive in the hippocampus, while OFC drove hippocampal updating of task-critical cognitive maps based on reward value (Garvert et al., 2023). However, a recent single-cell recording study in rats proposed the opposite view, suggesting that while both hippocampal formation and OFC participate in cognitive map formation, they operate in parallel rather than in a simple feedforward relationship, and may even compete. Each extracts different features to form distinct cognitive maps: OFC tends to form representations reflecting current task relevance and motivational goals, while hippocampal output hinders "schema cells" in OFC from forming new representations (Zong et al., 2023). That is, the hippocampus tends to be "conservative," extracting existing task schemas and inhibiting new schema formation, whereas OFC tends to dynamically reflect task-relevant goals, forming or flexibly selecting new cognitive maps. Future research must further explore the respective roles of OFC and hippocampus in implementing cognitive map selectivity, their relationship, and whether other brain regions are involved.

Hippocampal-cortical information interaction is also important for segmented environmental representation during cognitive map construction. Evidence suggests that when navigating in multi-compartment environments, boundary crossing triggers hippocampal activity peaks, preceded by changes in cortical activity patterns (Baldassano, 2017). In virtual reality three-dimensional multi-room buildings, participants show faster spatial judgments within the same room compared to across rooms, demonstrating behavioral priming effects for same-level spatial representation. fMRI results indicate that hierarchical encoding of three-dimensional spatial information involves hippocampal-cortical coordination: left anterior hippocampus represents local information within rooms, while retrosplenial cortex, parahippocampal cortex, and posterior hippocampus represent room information within broader buildings (Kim & Maguire, 2018). Additionally, the caudate nucleus in the striatum interacts with the hippocampus and prefrontal cortex, participating in encoding environmental transition structures to support flexible navigation (Brown et al., 2012; Gahnstrom & Spiers, 2020).

Since multiple brain regions jointly participate in cognitive map construction, integrating their functions from a neural structural network perspective helps reveal the essence of cognitive maps. Cognitive map construction requires three functional neural loops formed by hippocampal-cortical cooperation (Wang & Wang, 2017). The first loop projects external information (including spatial and non-spatial information) from cortex to hippocampus to form internal representations. The second loop projects hippocampal-entorhinal internal representations via retrosplenial cortex to posterior parietal cortex, guiding prefrontal cortex and supplementary motor areas to transform into behavioral output. The third loop handles goal reward, jointly represented by hippocampus and ventral

striatum.

4. Existential Forms of Cognitive Maps

Current theoretical controversies regarding the format of cognitive maps primarily include Euclidean map and topological graph hypotheses, representing two extremes of representational precision. Euclidean maps require completely accurate representation of spatial coordinates, while topological graphs contain no metric information. Neither alone can fully explain real navigation behavior. Therefore, researchers have attempted to reconcile these theories by integrating Euclidean metric information and topological structure into hybrid cognitive maps.

4.1 Euclidean Map Hypothesis

Building on Tolman's cognitive map concept, O'Keefe and Nadel (1978) proposed that cognitive maps adopt an absolute, unified Euclidean metric structure that facilitates flexible spatial behavior. Primary physiological support for this proposal comes from place cells in the hippocampus and grid cells in the entorhinal cortex. As described above, place cells fire only when animals occupy specific environmental locations (O'Keefe & Dostrovsky, 1971), while grid cells periodically fire at vertices of equilateral triangles tiling the environment (Hafting et al., 2005; Doeller et al., 2010). These cells jointly implement background metric scaling and landmark anchoring for spatial environments.

Euclidean cognitive maps are based on an allocentric reference frame, independent of the navigator's embodied experience [FIGURE:3a, b], similar to cartographic maps that preserve all geometric features including distances and angles between known locations [Figure 3c: see original paper], facilitating novel path and shortcut selection and making navigation highly flexible (Gallistel, 1990). Widdowson and Wang (2022) found that regardless of spatial curvature (Euclidean, hyperbolic, or spherical space), participants' pointing tasks always matched Euclidean directions, suggesting that path integration and spatial updating systems are based on Euclidean geometry.

However, previous research also found that human spatial task performance does not conform to Euclidean geometry assumptions (Beals et al., 1968; Tversky, 1981), challenging the Euclidean cognitive map hypothesis. Necessary conditions for Euclidean metric space include: (1) Non-negativity: distance from point A to itself is 0, distance between different points A and B is >0 ; (2) Symmetry: $AB = BA$; (3) Additivity: if C is a point on line segment AB, then $AB = AC + BC$; (4) Triangle inequality: for any three points A, B, C, $AC + BC \geq AB$ [Figure 3d: see original paper]. Additionally, if A, B, C form a right triangle, the Pythagorean theorem should hold. Experimental evidence shows that distance from a landmark to a non-landmark is judged smaller than the reverse (Burroughs & Sadalla, 1979; Moar & Carleton, 1982), violating symmetry. More location points along a path lead to larger distance estimates (Thorndyke, 1981),

violating additivity. Distance estimates also violate triangle inequality (Byrne, 1979). Furthermore, participants navigating in virtual “wormholes” without detecting spatial distortions or geometric inconsistencies show insensitivity to Euclidean structure (Warren et al., 2017).

Although participants in spatial tasks often show large errors in distance estimation, this does not necessarily falsify the Euclidean map hypothesis—cognitive maps could be Euclidean maps with noise. However, this renders the Euclidean map hypothesis potentially unfalsifiable (Warren, 2019), since if metric maps cannot be completely accurate and moderate errors are acceptable, the tolerable error range becomes difficult to define rigorously.

4.2 Topological Graph Structure Hypothesis

Early opposition to the Euclidean map hypothesis came from Eichenbaum (1997), who argued that hippocampal place cells were insufficient evidence for Euclidean maps because the hippocampus is not specialized for spatial memory alone—hippocampal damage in humans and animals causes broad memory deficits. Therefore, hippocampal cells should participate in representation of broader memory spaces. Eichenbaum et al. (1999) proposed memory space theory, suggesting that cognitive maps essentially record past experiences in memory space. Different events or location node sequences first form episodic memories, which then become linked through repeated or common elements (nodes) to establish memory space [Figure 4a: see original paper]. Representation of physical space is merely a special case of memory space representation (Eichenbaum et al., 1999).

Inspired by memory space theory, subsequent researchers proposed the topological graph hypothesis as an alternative format for cognitive maps. Unlike Euclidean maps’ precise metrics, topological graph theory posits that cognitive maps encode only coarse topological structure. Environmental topology consists of networks formed by nodes and connecting edges, where nodes generally represent locations and edges represent path relationships between locations [Figure 4b: see original paper]. This “place graph” captures location connectivity without embedding positions in a globally consistent coordinate system (coordinate-free). Besides locations, nodes can also represent specific views or local regions (vistas); correspondingly, edges represent actions required to transition between different views or regions (Jacobs & Schenk, 2003; Mallot & Basten, 2009).

Topological graph information content falls between Euclidean maps and route sequence memories. On one hand, graph knowledge is richer than route knowledge. Routes are simple chains linking locations and actions, possibly only part of path networks, supporting navigation along familiar paths but lacking flexibility. Topological graphs can contain multiple paths between two locations, enabling novel paths or detours through recombination of path segments. On the other hand, topological graphs occupy less memory resources than Eu-

clidean maps, with nodes and edges existing in compressed structures without distance metrics or angle information, eliminating the need for detailed coordinate calculations. However, this also prevents explaining humans' ability to select shortcuts to some extent. Therefore, pure topological representation is insufficient for human spatial navigation.

Topological graph representations are common in daily life, such as subway maps [Figure 4c: see original paper], where station names on the same line are placed at equal intervals, emphasizing connectivity rather than actual distances. Central city areas are enlarged compared to peripheral areas, with inter-station distances overestimated (Longo, 2021), reflecting greater passenger flow and higher demand for detailed station information in central areas. Animal route networks also exhibit graph-like properties; for example, capuchin monkeys typically choose different branches at tree junctions for foraging, indicating they can segment path fragments and combine them into useful new paths (Presotto et al., 2018). At the neural level, some hippocampal place cell fields are influenced by environmental topological structure changes (Dabaghian et al., 2014; Widloski & Foster, 2022).

4.3 Compromise or Fusion Hypothesis

If we position different theories of cognitive map format along an axis of metric information precision, Euclidean map and pure topological graph hypotheses occupy the precise and coarse extremes [Figure 5a: see original paper]. However, spatial representations are sensitive to environmental topology while also encoding partial Euclidean information, albeit with some error. Therefore, researchers have attempted to reconcile the two hypotheses into compromise solutions, creating hybrid cognitive maps that moderately fuse topological structure and Euclidean information.

Both Euclidean and topological maps are necessary for spatial representation, but their specific construction and use depend on environmental features and task demands (Peer et al., 2021). By restricting metric information to limited local regions, hybrid models avoid cognitive overload while better explaining spatial representation imprecision or errors. These fusion hypotheses reconcile theoretical disputes between Euclidean and topological maps and can better explain existing experimental evidence, but they are not fundamentally innovative.

4.4 Unified or Integrated Hypothesis

Many environments in physical and abstract relational spaces share identical underlying structures despite different sensory stimuli. For example, different physical environments follow Euclidean rules but have different internal location organizations; different family genealogies share the same branching structure but have different members. If generalization can occur across environments

with similar internal structures but different stimuli, spatial representation efficiency in new environments can be improved.

Based on this idea, Whittington et al. (2020) proposed the TEM (Tolman-Eichenbaum Machine) model as a unified framework integrating Euclidean maps and topological graphs. The model's name commemorates Tolman and Eichenbaum, scholars associated with these two representational formats. TEM's basic assumption is that generalization of environmental or task abstract structures provides great convenience for spatial representation and reasoning. Both hippocampal spatial memory and relational memory follow the common principle of structural generalization, including structural abstraction and binding of specific sensory information. The key to structural generalization lies in factorization and recombination—separating different types of knowledge (e.g., underlying structure and specific sensory stimuli) into independent factors for flexible recombination in new situations. Structural abstraction occurs in medial entorhinal cortex, with abstracted structures generalizable across different sensory stimuli to enable remapping; specific sensory binding occurs in the hippocampus.

After learning and training based on these principles, TEM-simulated entorhinal cortex exhibits properties of multiple cell types, such as grid cells, border cells, and object vector cells; TEM-simulated hippocampal cells also show place cell properties. These TEM-simulated cell activity patterns match experimental results from both physical and abstract spaces well, indicating that structural generalization principles are effective and may underlie both Euclidean maps and topological graphs, suggesting the two may be two sides of the same coin in mental representation.

Successor representation (SR) theory also views Euclidean and topological representations as different manifestations of the same underlying neural code. SR proposes that the hippocampus may not only encode current position and state but may emphasize encoding future successor states valuable for navigation (Stachenfeld et al., 2017; de Cothi et al., 2022). By encoding distributions of likely future reachable positions, it constructs cognitive maps of the environment. In topological graphs, each state is a node and transition probabilities between states are connection weights; in Euclidean maps, each state is a key Euclidean location, with state transitions corresponding to paths between locations.

4.5 Hierarchical Theory

In the Euclidean map and topological graph theories described above, different locations in cognitive maps are represented at undifferentiated levels without hierarchical relationships. However, as mentioned in Section 2.3, environmental spaces often have nested structures, so representations of different regions in cognitive maps may have hierarchical organization, with information about different spatial scales or geographic units represented at different levels (Zhao, 2006).

Specifically, early hierarchical theory proposed that different regions of an environment exist on different branches of a tree structure—spatial knowledge is not represented at the same level, but more detailed spatial knowledge is stored at lower levels while more abstract knowledge corresponds to higher levels. Boundaries between regions may be objectively present or subjectively defined (Hirtle & Jonides, 1985). Compared to within-region spatial representations, spatial relationships or distance representations across region boundaries have lower precision (Wang & Brockmole, 2003).

Hierarchical theory generally applies to environments with relatively large spatial scales or complex internal structures, where complexity may arise from physical factors (e.g., wall barriers) or human causes (e.g., administrative divisions). Simple small-scale spaces generally lack obvious multi-region branching structures (e.g., vista spaces), so hierarchy is not prominent in these space types. Hierarchical theories can be divided into strongly hierarchical and partially hierarchical theories based on how spatial relationships are encoded in memory (McNamara, 1986).

Strongly hierarchical theory holds that no spatial relationship encoding exists between locations on different branches at the same hierarchical level; their spatial relationships must be derived from higher-level spatial knowledge [Figure 6: see original paper]. For example, spatial relationships between two cities in the same province are not directly encoded but are indirectly obtained by comparing each city's position within the province. Strongly hierarchical theory is more memory-efficient for storing spatial knowledge but clearly sacrifices flexibility.

In contrast, partially hierarchical theory holds that spatial relationships between locations in different regions of an environment can be encoded (Stevens & Coupe, 1978) [Figure 6: see original paper]. This is relatively more memory-demanding (more spatial relationships to encode), but the advantage of this redundancy is faster and more accurate spatial judgment, as direct use is more efficient than derivation. McNamara (1986) found that spatial task performance was influenced by which regions locations belonged to, supporting partially hierarchical theory. However, hierarchical theory has received less attention in recent years, and Euclidean map and topological graph research has not incorporated cognitive map hierarchy.

5. Future Directions

5.1 Dynamic Changes in Cognitive Map Hierarchy

Cognitive map hierarchy manifests when spatial environments have nested structures, a problem not considered by Euclidean map and topological graph formats. We hypothesize that hierarchy is closely related to spatial scale, emerging when representing large-scale spaces, while Euclidean and topological representations exist within relatively smaller sub-levels. However, since cognitive map construction is dynamic, large-scale spaces are not static. As cognitive maps gradually expand, boundaries between different regions may gradually overlap, leading to

corresponding integration of spatial representations. Consequently, the hierarchy initially present in large-scale space representation may gradually diminish or even disappear during this process, forming a globally uniform cognitive map containing both Euclidean and topological information and establishing new path relationships connecting sub-regions that originally belonged to different superordinate levels [Figure 7: see original paper].

Hierarchical representations across different scales are organized along the posterior-to-anterior hippocampal axis, with PFC cells having larger predictive horizons and hippocampal cells having relatively smaller horizons (Brunec & Momennejad, 2022). Therefore, PFC may occupy superordinate levels in hierarchical representation, encoding high-level planning, as confirmed by a recent subway map navigation study (Liang et al., 2022). Scene-selective regions, sensitive to scenes (e.g., local location points), may bridge the representational gap between PFC and the hippocampal-entorhinal system by “stitching” local regions into global cognitive maps.

However, cognitive map expansion potential is limited because human spatial cognitive resources are constrained. The scale range of cognitive maps necessarily has an upper limit, which may differ across individuals. Future research should examine whether hierarchy reduction occurs during dynamic cognitive map construction, further investigate human cognitive map scale limitations, and explore how Euclidean and topological maps integrate during cognitive map formation and whether capacities for the two representations are related.

5.2 Expansion of Spatial Dimensions and Scope

Traditional spatial representation research has focused primarily on conventional two-dimensional physical space, leading to flattened understanding (e.g., analogizing to two-dimensional maps). As navigation cognition advances, innovative paradigms have emerged, with navigable spaces in experiments including more novel forms.

On one hand, physical spaces have expanded in dimensionality and curvature manipulation. In terms of Euclidean space dimensionality, expansion from two to three dimensions has occurred. For example, Kim and Doeller (2022) had participants explore three-dimensional spaces composed of planes and curved surfaces through ground movement or flying, followed by distance estimation tests. They found better Euclidean distance estimation when participants could have a bird’s-eye view (i.e., direct exposure to three-dimensional structure), indicating that spatial representation is not limited to two-dimensional planes but adapts to behavioral experience and task demands. Moreover, in non-Euclidean spaces such as hyperbolic or spherical spaces, participants’ pointing tasks still matched Euclidean rules, suggesting that spatial representation may extend daily experience to virtual spaces with different curvatures (Widdowson & Wang, 2022). However, when Euclidean space is distorted (e.g., with “wormholes” enabling instantaneous travel between locations), participants may show behavioral bi-

ases without detecting distortions (Warren et al., 2017). These studies focus on behavioral performance without examining how relevant brain regions such as hippocampus and entorhinal cortex represent these unusual physical spaces or whether mechanisms differ from conventional space representation. Future research should combine these innovative spatial paradigms with neural measurement techniques.

On the other hand, spatial knowledge has begun to refer broadly to abstract cognitive spaces, including social relationship space, concept space, value space, and semantic space, rather than being limited to physical space (Schafer & Schiller, 2018). Spatial metaphors are common in daily life—descriptions of social hierarchy and interpersonal relationships are closely related to spatial expressions (e.g., “climbing high,” “sitting above,” “distant,” “close”). Social relationship perception, in turn, influences physical space representation, with closer relationships shortening subjectively represented distances (Kerkman et al., 2004). Social information is encoded similarly to spatial information, representing each social individual as coordinates and establishing evaluation dimensions for social space based on features or attributes (e.g., power, popularity) (Park et al., 2020), enabling social inference and decision-making. Humans can encode potential social relationship patterns in abstract feature spaces and flexibly construct social networks (Son et al., 2021). Brain networks including hippocampus, precuneus, dorsolateral PFC, and insula jointly participate in social space navigation (Zhang et al., 2022). However, many elements in social space cannot be clearly mapped to physical space—for example, boundaries of social situations cannot be clearly defined, and distance metric dimensions in interpersonal relationship space have no upper limit. Future research must further clarify these ambiguities.

5.3 Limitations of the Cognitive Map Hypothesis

The cognitive map is an intuitive metaphor for spatial representation with high face validity, describing complex abstract spatial representation as simple, vivid maps that are easily accepted and understood. However, it may involve a “representationalist fallacy”—the illusion that such a map exists independently of the navigator, possibly arising from the prevalence of practical maps in daily life and researchers’ blind analogies (Warren, 2019). Neural system activity related to spatial navigation does not need to copy the physical environment but rather helps humans and other animals maintain effective associations with their environments to enhance survival (Sung et al., 2021).

Tversky (2005) previously proposed using cognitive collages and spatial mental models in simple environments to replace the cognitive map metaphor. Recently, Farzanfar et al. (2023) further proposed the concept of spatial schema, hypothesizing that similar navigation experiences in similar environments form spatial schemas (e.g., cities with similar layouts). Specifically, the gist and details of environmental spatial information are represented separately, corresponding to spatial gist and cognitive maps. Spatial gist refers to core features of specific en-

vironments, represented in anterior hippocampus, while detailed information is represented in posterior hippocampus—both specific to particular environments. Spatial schema, however, is a superordinate spatial representation extracted from multiple spatial gists, participating in optimizing navigation decisions by extracting generalizable similar features across similar environments (e.g., geographic, visual spatial features), primarily represented in medial PFC.

The theoretical assumptions and early evidence for cognitive maps originated from rodent behavioral and electrophysiological research. However, human brain information representation differs from rodents, with differences spanning all aspects of spatial representation, including environmental structure, sub-regions, routes, directions, and distances (Zhao, 2018). Therefore, future research should focus more on human navigation behavior rather than directly cross-species theoretical transplantation.

Furthermore, the unclear concept of cognitive maps leads to ambiguous and overly broad scope. As an analogical concept, cognitive maps have many vague aspects, such as map scale, detail, precision, and representational format. This may result in two studies with substantially different content both being labeled as cognitive maps, ranging from simple conditioning tasks (Costa et al., 2023) to complex spatial navigation (Epstein et al., 2017), with vastly different variables and requirements indiscriminately grouped under the cognitive map umbrella. Future research must examine the scope of the cognitive map concept to avoid overgeneralization and focus on the essence, characteristics, and neural dynamic mechanisms of spatial representation processes.

The philosophical origin of cognitive map thought lies in Kant's views on the nature of spatial representation. Kant (1781/2004) proposed in *Critique of Pure Reason* that spatial representation is innate and therefore a priori. Building on Kant's theory of spatial representation innateness and Tolman's (1948) cognitive map concept, O'Keefe and Nadel (1978) explicitly stated that spatial nature is absolute, making cognitive maps Euclidean maps with physiological basis in hippocampal cells representing absolute positions (and subsequently discovered grid cells in entorhinal cortex providing metric scaling), opposing relative (or relational) space theories. However, hippocampal function is not limited to physical space but participates in broad memory space representation, leading Eichenbaum et al. (1999) to propose memory space theory and topological graph theory representing relative connections.

Both Euclidean map and topological graph hypotheses have validity and limitations. Both have received some validation at the neural mechanism level and are necessary for certain basic properties of cognitive maps. Recent attempts to combine or unify them aim to describe cognitive maps more completely. Although these theories accommodate features of both Euclidean and topological maps, they neglect the role and influence of spatial hierarchy in cognitive map construction.

Hierarchical organization in nested space representation has been frequently ob-

served behaviorally, and hierarchical theory was proposed early on. However, research on how such spaces are represented in the brain is scarce (Kim & Maguire, 2018), and Euclidean and topological studies have not incorporated cognitive map hierarchy. Both may be constructed in nested spaces, but this may not be because they lack hierarchical representation capability, but because previous research paradigms focused more on features after cognitive map completion rather than examining the dynamic construction process. Hierarchy may gradually decrease during cognitive map construction through learning. Future research must further explore and test this hypothesis.

Additionally, trends in cognitive map research suggest future attention should focus on expanding spatial dimensions and categories, comparing differences and commonalities between social space, semantic space, and traditionally studied physical space. Multiple behavioral, modeling, and neural phenomena reveal that cognitive maps have basic properties including selectivity, distortion, and flexibility. Future research must further refine theoretical construction based on these properties and reflect on potential limitations of the cognitive map hypothesis.

References

- Beals, R., Krantz, D. H., & Tversky, A. (1968). Foundations of multidimensional scaling. *Psychological Review*, 75(2), 127-142.
- Bellmund, J. L., de Cothi, W., Ruiter, T. A., Nau, M., Barry, C., & Doeller, C. F. (2020). Deforming the metric of cognitive maps distorts memory. *Nature Human Behaviour*, 4(2), 177-188.
- Bellmund, J. L., Deuker, L., Navarro Schröder, T., & Doeller, C. F. (2016). Grid-cell representations in mental simulation. *Elife*, 5, e17089. <https://doi.org/10.7554/eLife.17089.001>
- Brunec, I. K., Bellana, B., Ozubko, J. D., Man, V., Robin, J., Liu, Z. X., ... Moscovitch, M. (2018). Multiple scales of representation along the hippocampal anteroposterior axis in humans. *Current Biology*, 28(13), 2129-2135.
- Brunec, I. K., & Momennejad, I. (2022). Predictive representations in hippocampal and prefrontal hierarchies. *Journal of Neuroscience*, 42(2), 299-312.
- Burroughs, W. J., & Sadalla, E. K. (1979). Asymmetries in distance cognition. *Geographical Analysis*, 11(4), 414-421.
- Byrne, R. W. (1979). Memory for urban geography. *The Quarterly Journal of Experimental Psychology*, 31(1), 147-154.
- Carpenter, F., Manson, D., Jeffery, K., Burgess, N., & Barry, C. (2015). Grid cells form a global representation of connected environments. *Current Biology*, 25(9), 1176-1182.
- Chen, X., He, Q., Kelly, J. W., Fiete, I. R., & McNamara, T. P. (2015). Bias in

human path integration is predicted by properties of grid cells. *Current Biology*, 25(13), 1771–1780.

Coutrot, A., Manley, E., Goodroe, S., Gahnstrom, C., Filomena, G., Yesiltepe, D., ...Spiers, H. J. (2022). Entropy of city street networks linked to future spatial navigation ability. *Nature*, 604(7904), 104–110.

Dabaghian, Y., Brandt, V. L., & Frank, L. M. (2014). Reconceiving the hippocampal map as a topological template. *Elife*, 3, e03476. <https://doi.org/10.7554/eLife.03476>

Dahmani, L., & Bohbot, V. D. (2020). Habitual use of GPS negatively impacts spatial memory during self-guided navigation. *Scientific Reports*, 10(1), 6310.

de Cothi, W., Nyberg, N., Griesbauer, E.-M., Ghanamé, C., Zisch, F., Lefort, J. M., ...Spiers, H. J. (2022). Predictive maps in rats and humans for spatial navigation. *Current Biology*, 32(17), 3676–3689.

Dilks, D. D., Kamps, F. S., & Persichetti, A. S. (2022). Three cortical scene systems and their development. *Trends in Cognitive Sciences*, 26(2), 117–127.

Doeller, C. F., Barry, C., & Burgess, N. (2010). Evidence for grid cells in a human memory network. *Nature*, 463(7281), 657–661.

Eichenbaum, H. (1997). Declarative memory: Insights from cognitive neurobiology. *Annual Review of Psychology*, 48(1), 547–572.

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(2), 209–226.

Epstein, R. A., Parker, W. E., & Feiler, A. M. (2007). Where am I now? Distinct roles for parahippocampal and retrosplenial cortices in place recognition. *Journal of Neuroscience*, 27(23), 6141–6149.

Epstein, R. A., Patai, E. Z., Julian, J. B., & Spiers, H. J. (2017). The cognitive map in humans: Spatial navigation and beyond. *Nature Neuroscience*, 20(11), 1504–1513.

Epsztein, J. (2022). Mental replays enable flexible navigation. *Nature*, 605(7908), 35–36.

Evensmoen, H. R., Lehn, H., Xu, J., Witter, M. P., Nadel, L., & Håberg, A. K. (2013). The anterior hippocampus supports a coarse, global environmental representation and the posterior hippocampus supports fine-grained, local environmental representations. *Journal of Cognitive Neuroscience*, 25(11), 1908–1925.

Farzanfar, D., Spiers, H. J., Moscovitch, M., & Rosenbaum, R. S. (2023). From cognitive maps to spatial schemas. *Nature Reviews Neuroscience*, 24(2), 63–79.

Gahnstrom, C. J., & Spiers, H. J. (2020). Striatal and hippocampal contributions to flexible navigation in rats and humans. *Brain and Neuroscience*

Advances, 4, 1-7.

Gallistel, C. R. (1990). *The organization of learning*. Cambridge: The MIT Press.

Garvert, M. M., Saanum, T., Schulz, E., Schuck, N. W., & Doeller, C. F. (2023). Hippocampal spatio-predictive cognitive maps adaptively guide reward generalization. *Nature Neuroscience*, 26(4), 615-626.

Gatti, D., Marelli, M., Vecchi, T., & Rinaldi, L. (2022). Spatial representations without spatial computations. *Psychological Science*, 33(11), 1947-1958.

Genzel, D., Yovel, Y., & Yartsev, M. M. (2018). Neuroethology of bat navigation. *Current Biology*, 28(17), R997-R1004.

Goldshtein, A., Harten, L., & Yovel, Y. (2022). Mother bats facilitate pup navigation learning. *Current Biology*, 32(2), 350-360.

Golledge, R. G., Ruggles, A. J., Pellegrino, J. W., & Gale, N. D. (1993). Integrating route knowledge in an unfamiliar neighborhood: Along and across route experiments. *Journal of Environmental Psychology*, 13(4), 293-307.

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), 801-806.

Harten, L., Katz, A., Goldshtein, A., Handel, M., & Yovel, Y. (2020). The ontogeny of a mammalian cognitive map in the real world. *Science*, 369(6500), 194-197.

Hirtle, S. C., & Jonides, J. (1985). Evidence of hierarchies in cognitive maps. *Memory & Cognition*, 13(3), 208-217.

Ho, M. K., Abel, D., Correa, C. G., Littman, M. L., Cohen, J. D., & Griffiths, T. L. (2022). People construct simplified mental representations to plan. *Nature*, 606(7912), 129-136.

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*, 24(12), 1331-1340.

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), 1188-1190.

Jacobs, L. F., & Schenk, F. (2003). Unpacking the cognitive map: The parallel map theory of hippocampal function. *Psychological Review*, 110(2), 285-315.

Javadi, A.-H., Emo, B., Howard, L. R., Zisch, F. E., Yu, Y., Knight, R., ...Spiers, H. J. (2017). Hippocampal and prefrontal processing of network topology to simulate the future. *Nature Communications*, 8(1), 14652.

- Javadi, A.-H., Patai, E. Z., Marin-Garcia, E., Margolis, A., Tan, H.-R. M., Kumaran, D., ... Spiers, H. J. (2019). Prefrontal dynamics associated with efficient detours and shortcuts: A combined functional magnetic resonance imaging and magnetoencephalography study. *Journal of Cognitive Neuroscience*, 31(8), 1227-1247.
- 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*, 26(8), 1104-1109.
- Kabadayi, C., Bobrowicz, K., & Osvath, M. (2018). The detour paradigm in animal cognition. *Animal Cognition*, 21(1), 21-35.
- Kaefer, K., Nardin, M., Blahna, K., & Csicsvari, J. (2020). Replay of behavioral sequences in the medial prefrontal cortex during rule switching. *Neuron*, 106(1), 154-165.
- Kerkman, D. D., Stea, D., Norris, K., & Rice, J. L. (2004). Social attitudes predict biases in geographic knowledge. *The Professional Geographer*, 56(2), 258-269.
- Kim, M., & Doeller, C. F. (2022). Adaptive cognitive maps for curved surfaces in the 3D world. *Cognition*, 225, 105126. <https://doi.org/10.1016/j.cognition.2022.105126>
- Kim, M., & Maguire, E. A. (2018). Hippocampus, retrosplenial and parahippocampal cortices encode multicompartement 3D space in a hierarchical manner. *Cerebral Cortex*, 28(5), 1898-1909.
- Lacroix, L., White, I., & Feldon, J. (2002). Effect of excitotoxic lesions of rat medial prefrontal cortex on spatial memory. *Behavioural Brain Research*, 133(1), 81-91.
- 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), 9771-9777.
- Liang, Q., Li, J., Zheng, S., Liao, J., & Huang, R. (2022). Dynamic causal modelling of hierarchical planning. *NeuroImage*, 258, 119384. <https://doi.org/10.1016/j.neuroimage.2022.119384>
- Longo, M. R. (2021). Distortion of mental body representations. *Trends in Cognitive Sciences*, 26(3), 241-254.
- Mahmoodi, A., Nili, H., Harbison, C., Hamilton, S., Trudel, N., Bang, D., & Rushworth, M. F. (2023). Causal role of a neural system for separating and selecting multidimensional social cognitive information. *Neuron*, 111(7), 1152-1164.
- Mallot, H. A., & Basten, K. (2009). Embodied spatial cognition: Biological and artificial systems. *Image and Vision Computing*, 27(11), 1658-1670.

- 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), 14896-14908.
- McNamara, T. P. (1986). Mental representations of spatial relations. *Cognitive Psychology*, 18(1), 87-121.
- Meilinger, T. (2008). The network of reference frames theory: A synthesis of graphs and cognitive maps. In C. Freksa, N. S. Newcombe, P. Gärdénfors, & S. Wölfl (Eds.), *Spatial Cognition VI. Learning, Reasoning, and Talking about Space* (pp. 344-360). Springer.
- Meilinger, T., Strickrodt, M., & Bühlhoff, H. H. (2016). Qualitative differences in memory for vista and environmental spaces are caused by opaque borders, not movement or successive presentation. *Cognition*, 155, 77-95.
- Moar, I., & Carleton, L. R. (1982). Memory for routes. *The Quarterly Journal of Experimental Psychology Section A*, 34(3), 381-394.
- 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), 1238-1245.
- 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.
- Muhle-Karbe, P. S., Sheahan, H., Pezzulo, G., Spiers, H. J., Chien, S., Schuck, N. W., & Summerfield, C. (2023). Goal-seeking compresses neural codes for space in the human hippocampus and orbitofrontal cortex. *bioRxiv*, 2023-01. <https://doi.org/10.1101/2023.01.12.523762>
- Nardin, M., Kaefer, K., & Csicsvari, J. (2021). The generalized spatial representation in the prefrontal cortex is inherited from the hippocampus. *bioRxiv*, 2021-09. <https://doi.org/10.1101/2021.09.30.462269>
- 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(1), 171-175.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford: Oxford University Press.
- Park, J., & Park, S. (2020). Coding of navigational distance and functional constraint of boundaries in the human scene-selective cortex. *Journal of Neuroscience*, 40(18), 3621-3630.
- Park, S. A., Miller, D. S., & Boorman, E. D. (2021). Inferences on a multi-dimensional social hierarchy use a grid-like code. *Nature Neuroscience*, 24(9), 1292-1301.

- Park, S. A., Miller, D. S., Nili, H., Ranganath, C., & Boorman, E. D. (2020). Map making: Constructing, combining, and inferring on abstract cognitive maps. *Neuron*, 107(6), 1226-1238.
- Patai, E. Z., & Spiers, H. J. (2021). The versatile wayfinder: Prefrontal contributions to spatial navigation. *Trends in Cognitive Sciences*, 25(6), 520-533.
- Peer, M., Brunec, I. K., Newcombe, N. S., & Epstein, R. A. (2021). Structuring knowledge with cognitive maps and cognitive graphs. *Trends in Cognitive Sciences*, 25(1), 37-49.
- Presotto, A., Verderane, M. P., Biondi, L., Mendonça-Furtado, O. D., Spagnoletti, N., Madden, M., & Izar, P. (2018). Intersection as key locations for bearded capuchin monkeys (*Sapajus libidinosus*) traveling within a route network. *Animal Cognition*, 21(3), 393-405.
- Robertson, C. E., Hermann, K. L., Mynick, A., Kravitz, D. J., & Kanwisher, N. (2016). Neural representations integrate the current field of view with the remembered 360° panorama in scene-selective cortex. *Current Biology*, 26(18), 2463-2468.
- Ruan, X., Chai, J., Wu, Y., Zhang, X., & Huang, J. (2021). Cognitive map construction and navigation based on hippocampal place cells. *Acta Automatica Sinica*, 47(3), 666-677.
- Sauer, J.-F., Folschweiller, S., & Bartos, M. (2022). Topographically organized representation of space and context in the medial prefrontal cortex. *Proceedings of the National Academy of Sciences*, 119(6), e2117300119. <https://doi.org/10.1073/pnas.2117300119>
- Schafer, M., & Schiller, D. (2018). Navigating social space. *Neuron*, 100(2), 476-489.
- Schinazi, V. R., & Epstein, R. A. (2010). Neural correlates of real-world route learning. *Neuroimage*, 53(2), 725-735.
- Schlesiger, M. I., Boubilil, B. L., Hales, J. B., Lehn, H., Xu, J., Witter, M. P., Nadel, L., & Häberg, A. K. (2013). The anterior hippocampus supports a coarse, global environmental representation and the posterior hippocampus supports fine-grained, local environmental representations. *Journal of Cognitive Neuroscience*, 25(11), 1908-1925.
- Schuck, N. W., Cai, M. B., Wilson, R. C., & Niv, Y. (2016). Human orbitofrontal cortex represents a cognitive map of state space. *Neuron*, 91(6), 1402-1412.
- Shallice, T., & Burgess, P. W. (1991). Deficits in strategy application following frontal lobe damage in man. *Brain*, 114(Pt 2), 727-741.
- Sloan, H. L., Good, M., & Dunnett, S. B. (2006). Double dissociation between hippocampal and prefrontal lesions on an operant delayed matching task and a

water maze reference memory task. *Behavioural Brain Research*, 171(1), 116–126.

Son, J.-Y., Bhandari, A., & FeldmanHall, O. (2021). Cognitive maps of social features enable flexible inference in social networks. *Proceedings of the National Academy of Sciences*, 118(39), e2021699118. <https://doi.org/10.1073/pnas.2021699118>

Stachenfeld, K. L., Botvinick, M. M., & Gershman, S. J. (2017). The hippocampus as a predictive map. *Nature Neuroscience*, 20(11), 1643–1653.

Stensola, H., Stensola, T., Solstad, T., Frøland, K., Moser, M.-B., & Moser, E. I. (2012). The entorhinal grid map is discretized. *Nature*, 492(7427), 72–78.

Stevens, A., & Coupe, P. (1978). Distortions in judged spatial relations. *Cognitive Psychology*, 10(4), 422–437.

Sung, J. Y., Harris, O. K., Hensley, N. M., Chemero, A. P., & Morehouse, N. I. (2021). Beyond cognitive templates: Re-examining template metaphors used for animal recognition and navigation. *Integrative and Comparative Biology*, 61(3), 825–841.

Taube, J. S., Muller, R. U., & Ranck, J. B. (1990). Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *Journal of Neuroscience*, 10(2), 420–435.

Thorndyke, P. W. (1981). Distance estimation from cognitive maps. *Cognitive Psychology*, 13(4), 526–550.

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, 55(4), 189–208. <https://doi.org/10.1037/h0061626>

Tversky, B. (1981). Distortions in memory for maps. *Cognitive Psychology*, 13(3), 407–433.

Tversky, B. (1993). Cognitive maps, cognitive collages, and spatial mental models. In A. U. Frank & I. Campari (Eds.), *Spatial Information Theory: A Theoretical Basis for GIS* (pp. 14–24). Springer.

Wang, R. F., & Brockmole, J. R. (2003). Human navigation in nested environments. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 29(3), 398–404.

Wang, L., & Wang, L. (2017). Neural circuit basis of cognitive maps. *Biochemistry and Biophysics Advances*, 44(3), 187–197.

Warren, W. H. (2019). Non-euclidean navigation. *Journal of Experimental Biology*, 222(Suppl_1), jeb187971. <https://doi.org/10.1242/jeb.187971>

Warren, W. H., Rothman, D. B., Schnapp, B. H., & Ericson, J. D. (2017). Wormholes in virtual space: From cognitive maps to cognitive graphs. *Cognition*, 166, 152–163.

Wernle, T., Waaga, T., Mørreaunet, M., Treves, A., Moser, M.-B., & Moser, E. I. (2018). Integration of grid maps in merged environments. *Nature Neuroscience*, 21(1), 92-101.

Whittington, J. C., Muller, T. H., Mark, S., Chen, G., Burgess, N., & Behrens, T. E. (2020). The Tolman-Eichenbaum machine: Unifying space and relational memory through generalization in the hippocampal formation. *Cell*, 183(5), 1249-1263.

Widdowson, C., & Wang, R. F. (2022). Human navigation in curved spaces. *Cognition*, 218, 104923. <https://doi.org/10.1016/j.cognition.2021.104923>

Widloski, J., & Foster, D. J. (2022). Flexible rerouting of hippocampal replay sequences around changing barriers in the absence of global place field remapping. *Neuron*, 110(9), 1547-1558.

Wu, X., & Foster, D. J. (2014). Hippocampal replay captures the unique topological structure of a novel environment. *Journal of Neuroscience*, 34(19), 6459-6469.

Yousif, S. R. (202

Note: Figure translations are in progress. See original paper for figures.

Source: ChinaXiv –Machine translation. Verify with original.