Cognitive Maps and Their Intrinsic Mechanisms

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Abstract

Spatial navigation is of great importance for the survival of both humans and animals, and effective spatial representations or cognitive maps constitute the foundation of spatial navigation. The typical attributes of cognitive maps include selectivity, flexibility, and hierarchical organization, with multiple brain regions such as the hippocampus, scene-selective areas, and the prefrontal cortex all involved in the construction of cognitive maps. Concerning the representational format of cognitive maps, there exist two theoretical frameworks: Euclidean maps and topological maps; however, neither alone can comprehensively explain behavioral performance in actual navigation. Therefore, researchers have proposed theories such as labeled graphs to reconcile the contradictions between them. Future research should also attend to changes in hierarchical organization during the construction of cognitive maps, the expansion of spatial scope, and the limitations of the cognitive map hypothesis.

Full Text

Preamble

Cognitive Maps and Their Intrinsic Mechanisms*

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Abstract: Spatial navigation is essential for the survival of humans and animals, and effective spatial representation—or cognitive maps—forms its foundation. Prototypical properties of cognitive maps include selectivity, flexibility, and hierarchy. Multiple brain regions, including the hippocampus, scene-selective areas, and prefrontal cortex, participate in cognitive map construction. Debates persist regarding the representational format of cognitive maps, with Euclidean maps and topological graphs as the two primary theoretical frameworks. Neither framework alone can fully explain navigational behavior, prompting researchers to propose integrative theories such as the labeled graph hypothesis. 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.

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

For humans and other animals inhabiting complex environments (e.g., bats), spatial navigation represents a crucial cognitive function (Genzel et al., 2018; Goldshtein et al., 2022). Efficient navigation requires effective mental representation of spatial information—an internal, subjective form of external information and objective knowledge, distinct from external representations like cartographic maps or smartphone navigation apps (e.g., Gaode Map). Such internal spatial knowledge representations are vital for navigation in familiar environments, enabling flexible route planning and saving navigation time (Harten et al., 2020). 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 internal spatial representation mechanisms.

Because internal spatial representations facilitate advanced cognitive behaviors like route planning and shortcut selection—functionally resembling geographic maps—they are termed cognitive maps. Tolman (1948) first proposed this concept, observing that rats' spatial navigation in mazes improved with practice, enabling them to select novel shortcuts not experienced during training. This suggested that rats did not merely form simple stimulus-response associations but understood the environment' s overall spatial structure, actively selecting important cues to construct an allocentric comprehensive map independent of themselves.

Although Tolman' s concept was rudimentary—functionally describing animals' need to build global environmental knowledge beyond direct experience without detailing specifics—it spawned substantial spatial navigation research, yielding theoretical and experimental breakthroughs. Moreover, while originating in psychology, the concept' s depth and generality attracted interest from other disciplines, 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 cognitive map construction rules, precision, and representational formats—and divergent views among researchers—this review synthesizes cognitive map theories and experimental findings in cognitive neuroscience to inspire multidisciplinary researchers. We first summarize prototypical properties of cognitive maps from behavioral and functional perspectives, then elaborate on relevant brain regions and mechanisms, review theoretical debates about cognitive map formats, and finally reflect on the cognitive map concept while identifying future research directions.

2. Prototypical 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 based on task demands, leading to representational distortions. Second, to cope with complex, dynamic environments, spatial representations exhibit flexibility, tolerating redundant representational formats for the same information. Additionally, because navigable spaces often have nested structures, cognitive maps of such spaces show hierarchical organization, though this hierarchy diminishes with increased navigation experience, gradually becoming coherent.

2.1 Selectivity and Distortion

Cognitive resources are limited, necessitating selective spatial representations to enhance cognitive economy. Standard views across psychology, economics, and AI have held that people form complete, fixed representations for tasks including navigation, using heuristics for planning. However, Ho et al. (2022) found that people flexibly construct specific simplified representations for particular problems, balancing representational complexity and utility.

While spatial knowledge encompasses location, path relationships, and direction, cognitive map content may only include subsets relevant to practical contexts. As Borges (1971) illustrated in "On Exactitude in Science," a map containing all geographic information becomes useless at extreme detail. Representing all information indiscriminately wastes cognitive resources and fails to solve specific problems efficiently. For instance, when traveling in a city, the appropriate map type depends on transportation mode—cycling requires bike lane maps, driving needs road maps, and detailed satellite maps are impractical for direct use.

Selective spatial representations arise from functional demands, with different environments (cultural and geographic) imposing different representational requirements. In map-drawing tasks, participants organize hand-drawn maps according to their city' s characteristics, with personal route usage prominently reflected, demonstrating strong social functional significance (Appleyard, 1970). A large-scale cross-country study found that people navigate better in environments with topological features similar to their upbringing, showing that urban street network design influences residents' spatial representation tendencies and navigation abilities (Coutrot et al., 2022). Thus, cognitive map focus is shaped by daily needs, with selective content varying across environments.

Selective representation implies limitations—distortions relative to ground truth, representing the cost of serving specific functions. Path distance estimation is influenced by the number of locations along the path; with actual distance controlled, more locations yield larger distance estimates (Thorndyke, 1981).

Paths near city centers are overestimated compared to peripheral paths, and angle estimates show bias toward 90° (Byrne, 1979). Linguistic information also explains specific distortions in large-scale geographic map tasks, suggesting natural language experience participates in encoding cognitive maps (Gatti et al., 2022).

Thus, as purposeful simplifications, practical maps must sacrifice some details to highlight relevant features. No perfectly accurate practical map exists; all maps necessarily contain distortions determined by their functions (Hartley, 2017). Similarly, no perfectly accurate cognitive map exists; spatial representation distortions accompany specific functions (Longo, 2021).

2.2 Flexibility and Redundancy

Flexibly applying learned knowledge is crucial for animals to cope with complex, unpredictable environments. Survival conditions change—paths become blocked, food sources disappear—and efficient navigation requires adapting to dynamic environmental cues and structures (Kabadayi et al., 2018), likely enabled by cognitive map flexibility.

In 1948, Tolman observed rats' flexible behavior in complex mazes during detouring and shortcut selection, not simple stimulus-response sequences. Research shows flexible cognitive maps and spatial navigation require mental replay, with stress impairing flexibility (Epsztein, 2022; Brown et al., 2020).

Underlying flexibility is representational redundancy—same spatial information may be organized and stored in multiple formats simultaneously (Yousif, 2022). Optimal representational formats vary across conditions or demands, just as electronic files have multiple format attributes (PDFs for viewing, Word documents for editing) and problem phrasing affects solution efficiency. For spatial information, optimal cognitive map formats vary with functional needs, requiring the brain to redundantly represent information in multiple formats for flexible deployment.

2.3 Hierarchy and Coherence

Navigable spaces are often nested environments containing subregions (e.g., different buildings on campus and rooms within each building). Representations of different local areas may be separate, requiring integration of discretely learned local information to form a global cognitive map. Local information is separated because navigable spaces include vista space and environmental space (Meilinger et al., 2016). Vista spaces (e.g., bedrooms, open fields) can be surveyed from a single viewpoint [Figure 1a: see original paper], whereas environmental spaces (e.g., neighborhoods, mazes) require movement between obstacles to integrate information from multiple vista spaces [Figure 1b: see original paper].

In nested environmental spaces [Figure 1c: see original paper], local area information may be organized hierarchically. McNamara (1986) found spatial priming, direction judgment, and Euclidean distance estimation were affected by whether locations were in the same region. In segmented parallel corridors, human spatial memory organized according to each corridor’ s local coordinate system, indicating separate representations of different local areas (Meilinger et al., 2016).

Additionally, distortions in spatial relationship judgments support cognitive map hierarchy (Stevens & Coupe, 1978). However, hierarchy is not permanent; different local areas may gradually integrate to form a unified, coherent whole. Early research showed that common landmarks across regions facilitate integration of new local information into existing spatial knowledge (Golledge et al., 1993).

3. Neural Mechanisms of Cognitive Maps

Early cognitive map research focused on the parietal cortex, with damage causing impaired or lost spatial navigation. Subsequent discovery of place cells shifted focus to the hippocampus, leading to further identification of head direction cells, entorhinal grid cells, and border cells, establishing the hippocampal-entorhinal system as critical for cognitive maps. Additionally, medial prefrontal, orbitofrontal, and scene-selective regions 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], demonstrating hippocampal spatial location coding. Beyond location, subsequent research identified diverse cell types coding direction, boundaries, and other spatial information: 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 symmetry (Hafting et al., 2005; Doeller et al., 2010). Grid firing positions form periodic hexagons in open fields, providing a metric scaffold for spatial representation and computing directions from current location to navigation goals (Bellmund et al., 2016).

The hippocampal-entorhinal system is crucial for representing both Euclidean metric information and topological connectivity. Neuroimaging studies show hippocampus and entorhinal cortex encode Euclidean and path distances between locations, with functional segregation along the hippocampal long axis—anterior hippocampus correlates with Euclidean distance, posterior with path distance (Morgan et al., 2011; Howard et al., 2014). Hippocampal sensitivity to Euclidean distance originates from entorhinal cortex input, where grid cells’ multiple firing fields provide a regular metric scaffold (Hafting et al., 2005), though entorhinal input is not necessary for hippocampal remapping (Schlesiger et al., 2018). The hippocampus also represents environmental topology. In constrained mazes with connected corridors, rodent place fields are determined by relative maze topology rather than absolute Euclidean positions (Dabaghian et al., 2014), and sequential reactivation during rest reflects maze topology (Wu & Foster, 2014). During virtual street navigation, human posterior hippocampus signals correlate with the number of possible path connections, while anterior hippocampus signals relate to global topological properties (Javadi et al., 2017).

Differential representation of environmental scales relies on segregation of place cell firing fields along the hippocampal long axis (Evensmoen et al., 2013; Brunec et al., 2018) and grid cell firing fields along the entorhinal dorsoventral axis (Stensola et al., 2012). Anterior hippocampus represents coarse, global environmental information, while posterior hippocampus supports fine-grained local representations. In entorhinal cortex, more ventral cells have larger grid fields, representing coarse information in large-scale environments, whereas more dorsal cells represent fine-grained spatial information in small-scale environments.

Environmental geometry (e.g., boundary shape) affects grid cell firing patterns. Transforming a square environment into a trapezoid severely distorts rodents' regular grid firing patterns (Chen et al., 2015), with grid pattern degradation potentially related to cognitive map distortion. Virtual reality studies with humans show that location memory accuracy decreases in trapezoidal versus square environments, particularly in the narrow portion (Bellmund et al., 2020). Thus, entorhinal grid cells' geometric metric deformation may be the primary cause of cognitive map distortion.

The hippocampus implements cognitive map flexibility. Widloski and Foster (2022) recorded hippocampal activity in rats during maze tasks with changing obstacle configurations and food locations. Rats flexibly adjusted foraging routes, and hippocampal replay during rest predicted future routes and obstacle avoidance. Most place cells maintained stable firing fields, while a minority changed with obstacle distribution. These "unstable" cells may be closely related to flexible behavioral adaptation to spatial layout changes.

The hippocampal-entorhinal system also contributes to hierarchical cognitive map organization. Different local areas are represented separately during initial learning, supported by human behavioral studies and rodent electrophysiology. Human spatial memory is influenced by environmental obstacles, forming local reference frames based on obstacle-defined region boundaries (Meilinger et al., 2016). Rodent entorhinal grid cells and hippocampal place cells create independent local maps for different regions, with firing fields confined within local environments (Alme et al., 2014). However, extended navigation in multi-compartment spaces can weaken or eliminate compartment boundary effects, with grid cell firing fields expanding globally (Carpenter et al., 2015). Although rodents and humans initially tend to separate local representations, after extensive experience in multi-region environments, rodent grid cells rapidly shift from discrete local to continuous global firing patterns, integrating local representations into a unified global cognitive map (Wernle et al., 2018). This phenomenon has not been observed in humans, possibly due to different experimental paradigms.

3.2 Scene-Selective Regions

Visual scenes are primary components of small-scale local environment representation, and correctly identifying scenes or locations is crucial for daily life. Scene processing involves a cortical network distinct from the hippocampal-entorhinal system: scene-selective regions, which respond strongly to scene viewing. These include the parahippocampal place area (PPA), occipital place area (OPA), and retrosplenial complex (RSC) (Dilks et al., 2022).

Functionally, these subregions are thought to directly participate in spatial navigation. OPA represents local spatial layout, environmental boundaries, and boundary distances (Henriksson et al., 2019; Julian et al., 2016; Park & Park, 2020). PPA processes visual and geometric scene features (Marchette et al., 2015). RSC integrates local representations from the other two regions into a unified global representation (Epstein et al., 2007). fMRI studies show sequential appearance of path locations elicits stronger RSC activity (Schinazi & Epstein, 2010), indicating RSC activity relates to path topology.

Overall, scene-selective regions "stitch" multiple discrete vista spaces into a 360° panoramic view encompassing both visible and non-visible space, with current scene information activating associated representations in the panoramic environment (Robertson et al., 2016). This process enables dynamic interaction between transient spatial perception and relatively persistent spatial memory, facilitating global cognitive map formation. Some researchers term this "mapping" —RSC extracts cognitive maps from primary sensory information of vista spaces, then adjusts and updates map layouts based on recognized environmental landmarks to maintain consistency between cognitive maps and real space (Liang et al., 2022).

3.3 Prefrontal Cortex

Previous research generally considered the core spatial network to comprise hippocampal-entorhinal and scene-selective regions, neglecting 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 impairs executive functions (Shallice & Burgess, 1991), causing poor performance across most tasks rather than specific spatial deficits. Second, early studies found medial PFC lesions in rats did not affect performance in water maze navigation tasks (Lacroix et al., 2002; Sloan et al., 2006). Third, evidence for place cell- and grid cell-like coding in PFC is scarcer and emerged later (Park et al., 2021; Jacobs et al., 2013).

Research reveals functional differences among PFC subregions. Dorsolateral PFC (dlPFC) and ventrolateral PFC (vlPFC) activate during obstacle-induced detouring, possibly participating in route replanning (Javadi et al., 2019). Medial PFC (mPFC) relates to egocentric spatial representation, encoding object-based cognitive maps when remembering egocentric target locations (Zhang & Naya, 2020), reactivating effective behavioral sequences (Kaefer et al., 2020), and representing topologically organized environmental space (Sauer et al., 2022). Dorsomedial PFC separates task-relevant from task-irrelevant spatial contexts (Mahmoodi et al., 2023). Orbitofrontal cortex (OFC) represents task state spaces (e.g., value space, feature space), integrating spatial representation 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) encodes path network hierarchies and suppresses incorrect route tendencies (Javadi et al., 2019).

Given PFC' s diverse spatial representations, Patai and Spiers (2021) proposed that different PFC regions function at different navigation stages: At navigation onset, mPFC recalls target locations for dorsomedial PFC route planning. If detouring is needed, dACC searches for alternative routes, then lateral PFC replans routes while avoiding incorrect shortcuts. During this process, OFC selects specific paths and infers potential outcomes, mPFC represents path distances, and dACC assists in backtracking when beyond target range.

In summary, as a higher-order region, PFC primarily serves as cognitive map user and operator, receiving spatial information from the hippocampus (Nardin et al., 2021) and flexibly applying it to planning, inference, and prediction for efficient navigation.

3.4 Hippocampal-Cortical Interactions

The hippocampus, scene-selective regions, and PFC each perform unique functions in cognitive map construction, yet certain advanced properties require multi-region interactions, either cooperative or competitive.

Cognitive map selectivity may involve hippocampal-OFC cooperation. A recent fMRI and computational modeling study embedded stimuli in multiple relational structures, where participants formed both spatial location and predictive (transition) cognitive maps during learning. In a subsequent selection task, only spatial relationships determined reward value. Modeling showed participants' choices became increasingly influenced by spatial relationships, with spatial weights increasing and predictive weights decreasing, indicating task demands drove selective strengthening of spatial maps and weakening of predictive maps. fMRI revealed spatial weight changes were hippocampally mediated, while OFC updated task-relevant cognitive maps based on reward value (Garvert et al., 2023).

Conversely, a recent rodent single-unit recording study proposed that hippocampus and OFC operate in parallel, even competitively, rather than in simple feedforward fashion. Each region extracts different features to form distinct cognitive maps: OFC tends to form representations reflecting current task relevance and motivational goals, while hippocampal output inhibits OFC "schema cells" from constructing new representations (Zong et al., 2023). The hippocampus appears more "conservative,"extracting existing task schemas and inhibiting new schema formation, whereas OFC dynamically reflects task-relevant goals, forming or flexibly selecting new cognitive maps. Future research must further explore each region' s role in selectivity and their relationship.

Hippocampal-cortical interactions are also crucial for segmented environmental representation in cognitive map construction. Evidence shows boundary crossing in multi-compartment environments elicits hippocampal activity peaks, preceded by changes in cortical activity patterns (Baldassano, 2017). In virtual 3D multi-room buildings, participants show faster spatial judgments within versus across rooms, demonstrating behavioral priming for same-level spatial representation. fMRI reveals hierarchical encoding of 3D space involves hippocampal-cortical cooperation: left anterior hippocampus represents local room information, while retrosplenial, parahippocampal cortices, and posterior hippocampus represent room information within broader building contexts (Kim & Maguire, 2018). Additionally, caudate nucleus in the striatum interacts with hippocampus and PFC to encode environmental transition structures, supporting flexible navigation (Brown et al., 2012; Gahnstrom & Spiers, 2020).

Given multi-region involvement, integrating these functions from a neural network perspective may reveal cognitive map essence. Cognitive map construction requires three functional neural loops formed by hippocampal-cortical cooperation (Wang & Wang, 2017). The first loop processes external information (including spatial information)···

4. Theoretical Debates on Cognitive Map Formats

4.1 Euclidean Map Hypothesis

The Euclidean map hypothesis posits that cognitive maps are metric maps encoding precise Euclidean information (coordinates, distances, angles), enabling accurate spatial calculations. This hypothesis is supported by hippocampal place cells coding absolute positions and entorhinal grid cells providing metric scaffolds. However, Euclidean maps must satisfy three geometric axioms: symmetry (distance A→B = B→A), additivity (A→B + B→C = A→C), and triangle inequality (direct distance ≤ sum of indirect distances). Empirical evidence shows human cognitive maps violate these axioms: distance estimates are asymmetric (Burroughs & Sadalla, 1979; Moar & Carleton, 1982), increase with more intermediate locations (Thorndyke, 1981), and violate triangle inequality (Byrne, 1979). In virtual "wormhole" environments with spatial distortions, participants navigate without detecting geometric inconsistencies, showing insensitivity to Euclidean structure (Warren et al., 2017).

Although participants show large distance estimation errors in spatial tasks, this does not necessarily refute the Euclidean map hypothesis, as cognitive maps could be noisy Euclidean maps. However, this renders the hypothesis potentially unfalsifiable (Warren, 2019): if metric maps cannot be perfectly precise and moderate errors are acceptable, what error range is tolerable? This is difficult to define strictly.

4.2 Topological Graph Hypothesis

Early opposition to Euclidean maps came from Eichenbaum (1997), who argued hippocampal place cells insufficiently support Euclidean maps because the hippocampus is not specialized for spatial memory—hippocampal damage causes broad memory deficits in humans and animals. Thus, hippocampal cells likely represent a broader memory space.

Eichenbaum et al. (1999) proposed memory space theory, suggesting cognitive maps essentially record past experiences in memory space. Episodic memories form sequences of events or locations, which become linked through repeated or common elements (nodes) to establish memory space [Figure 4a: see original paper]. Physical space representation is merely a special case of memory space representation.

Inspired by this, researchers proposed the topological graph hypothesis as an alternative format. Unlike Euclidean maps' precise metrics, topological graphs encode coarse topological structure as networks of nodes (locations) and edges (path relationships) [Figure 4b: see original paper]. This "place graph" captures connectivity without embedding locations in a global coordinate system (coordinate-free). Nodes can also represent specific views or vista spaces, with edges as actions needed for transitions (Jacobs & Schenk, 2003; Mallot & Basten, 2009).

Topological graphs contain more information than route sequences but less than Euclidean maps. Routes are simple chains of locations and actions, supporting only familiar path navigation without flexibility. Topological graphs contain multiple paths between locations, enabling novel routes through path recombination. However, they occupy less memory than Euclidean maps, storing compressed structures without distance or angle metrics, yet cannot fully explain humans' ability to select shortcuts. Pure topological representation is insufficient for human navigation.

Topological representations are common in daily life, such as subway maps [Figure 4c: see original paper], where stations on the same line are equally spaced, emphasizing connectivity over distance, with central areas enlarged and inter-station distances overestimated (Longo, 2021), reflecting higher demand for detailed station information downtown. Animal route networks also show graph-like properties; capuchin monkeys select different branches at intersections for foraging, indicating they can segment and combine path fragments into useful novel routes (Presotto et al., 2018). Neurally, some hippocampal place cell firing fields are influenced by environmental topology (Dabaghian et al., 2014; Widloski & Foster, 2022).

4.3 Compromise or Fusion Hypotheses

If we position cognitive map theories on a continuum from precise to coarse, Euclidean and pure topological hypotheses occupy opposite extremes [Figure 5a: see original paper]. However, spatial representations are sensitive to both topological structure and partial Euclidean information (with some error). Researchers have attempted reconciliation through hybrid cognitive maps combining topological structure with limited Euclidean information.

Meilinger (2008) first proposed the network of reference frames theory, where each local area has a small metric reference frame as graph nodes, connected by edges representing viewpoint transformations between frames [FIGURE:5b, top]. Notably, local reference frames need not integrate into a unified global frame; novel paths require sequential viewpoint transformations from current to target location. This theory posits precise Euclidean maps at small local scales but coarse topological maps at large global scales.

This theory relaxes Euclidean maps'strict global consistency constraint, reducing memory load while permitting representational errors and distortions, better fitting actual navigation behavior. However, precise metric representation in every local area remains cumbersome, and inter-regional path relationships (lengths, angles) are ambiguous. Warren (2019) proposed the labeled graph hypothesis as a simplification.

Labeled graphs [FIGURE:5b, bottom] de-emphasize precise local representation, instead supplementing inter-regional nodes with metric information: edge weights represent approximate path lengths, and node labels indicate approximate angles between adjacent paths at intersections. Like the reference frame network, labeled graphs need not represent all spatial information within a unified global reference frame.

Both Euclidean and topological maps are necessary, with usage depending on environmental features and task demands (Peer et al., 2021). Restricting metric information to limited local areas avoids cognitive overload while explaining spatial representation imprecision. These fusion hypotheses reconcile theoretical debates and better explain experimental evidence, though they essentially⋯

4.4 Unified or Integration Hypotheses

Many environments share identical underlying structures despite different sensory stimuli—different physical environments follow Euclidean rules but have different organizations; different family trees share branching structures but have different members. Generalizing across structurally similar but stimulus-different environments could improve representation efficiency. Based on this, Whittington et al. (2020) proposed the Tolman-Eichenbaum Machine (TEM) model as a unified framework integrating Euclidean and topological formats, named to honor scholars associated with each representation.

TEM' s core assumption is that generalizing environmental or task abstract structures greatly facilitates spatial representation and reasoning. Both hippocampal spatial memory and relational memory follow structural generalization principles, including structural abstraction and binding to specific sensory information. Structural generalization' s key is factorization and recombination—separating different knowledge types (latent structure vs. specific sensory stimuli) into independent factors for flexible recombination in novel situations.

Structural abstraction occurs in medial entorhinal cortex, enabling generalization across different sensory stimuli and remapping; specific sensory binding occurs in the hippocampus. After training, TEM-simulated entorhinal cortex exhibits diverse cell properties (grid cells, border cells, object vector cells), and simulated hippocampal cells show place cell properties. These activity patterns match experimental results in physical and abstract spaces, suggesting structural generalization may be the common underlying mechanism for Euclidean and topological maps, making them two sides of the same representational coin.

Successor representation (SR) theory also views Euclidean and topological maps as different expressions of the same neural code. SR proposes that the hippocampus encodes not just current location but future-valued successor states (Stachenfeld et al., 2017; De Cothi et al., 2022), building cognitive maps by encoding likely future locations. In topological graphs, each state is a node with transition probabilities as edge weights; in Euclidean maps, each state is a key Euclidean location with transitions corresponding to inter-location paths.

4.5 Hierarchical Theories

In the above theories, all locations occupy undifferentiated representational levels without hierarchical relationships. However, as discussed in Section 2.3, environmental spaces often have nested structures, suggesting hierarchical organization in cognitive maps—information about different scales or geographic units is represented at different levels (Zhao, 2006).

Early hierarchical theories proposed that different environmental regions are stored in different branches of a tree structure, with spatial knowledge represented at varying levels of abstraction rather than uniformly. More detailed knowledge is stored at lower levels, more abstract knowledge at higher levels. Regional boundaries may be objective or subjective (Hirtle & Jonides, 1985), with cross-boundary spatial relationships represented less accurately than within-region relationships (Wang & Brockmole, 2003).

Hierarchical theories apply to relatively large-scale or complex environments, where complexity may arise from physical barriers or human factors (e.g., administrative divisions). Simple small-scale spaces (e.g., vista spaces) lack obvious multi-region branching structures and thus show less hierarchy. Hierarchical theories subdivide into strong and partial versions based on how spatial relations are encoded in memory (McNamara, 1986).

Strong hierarchical theories posit no direct spatial relation encoding between locations on different branches at the same level; their relations must be derived from higher-level knowledge [Figure 6: see original paper]. For example, spatial relations between two cities in the same province are not directly encoded but derived by comparing their positions within the province. This approach saves memory resources but sacrifices flexibility.

Partial hierarchical theories, by contrast, allow spatial relation encoding between locations in different regions (Stevens & Coupe, 1978) [Figure 6: see original paper]. This redundancy requires more memory storage but enables faster, more accurate spatial judgments. McNamara (1986) found spatial task performance was affected by location regions, supporting partial hierarchy. However, hierarchical theory has received less recent attention, and Euclidean/topological research has not incorporated cognitive map hierarchy.

5. Future Directions

5.1 Hierarchical Changes in Cognitive Maps

Cognitive map hierarchy emerges in nested spatial environments, yet neither Euclidean nor topological theories address hierarchy. We hypothesize that hierarchy is closely related to spatial scale, emerging in large-scale space representation, while Euclidean and topological representations exist within relatively smaller-scale levels. Because cognitive map construction is dynamic, large-scale space is not static. As cognitive maps expand, boundaries between different regions may gradually overlap, leading to representational fusion. Consequently, the hierarchy initially present in large-scale space representation may gradually diminish or disappear, forming a global, uniform cognitive map containing both Euclidean and topological information and establishing new path connections between previously hierarchically separated subregions [Figure 7: see original paper].

Hierarchical representation across scales is organized along a posterior-to-anterior hippocampal-PFC axis, with PFC cells having larger predictive horizons than hippocampal cells (Brunec & Momennejad, 2022). Thus, PFC may occupy higher hierarchical levels, encoding high-level planning, as confirmed by a recent subway map navigation study (Liang et al., 2022). Scene-selective regions, sensitive to local scenes, "weave" local areas into global cognitive maps, potentially bridging the representational gap between PFC and hippocampal-entorhinal systems.

However, cognitive map expansion potential is limited because spatial cognitive resources are constrained, with individual differences in scale limits. Future research should examine whether hierarchy decreases during dynamic cognitive map construction, investigate human cognitive map scale limitations, and explore how Euclidean and topological representations integrate during development and whether their capacities are related.

5.2 Expansion of Spatial Dimensions and Range

Traditional spatial representation research has focused on conventional two-dimensional physical space, leading to flattened understanding (e.g., analogizing to 2D maps). As navigation cognition advances, innovative paradigms have introduced novel navigable space forms.

First, physical spaces have expanded in dimension, curvature, and distortion rules. Euclidean spaces have extended from 2D to 3D. Kim and Doeller (2022) had participants explore 3D spaces composed of planes and arcs via ground movement or flight, finding better Euclidean distance estimation when participants had bird' s-eye views, indicating spatial representation adapts to behavioral experience and task demands. In non-Euclidean spaces (hyperbolic or spherical), participants' pointing tasks still matched Euclidean rules, suggesting they generalize everyday experience to virtual spaces with different curvature (Widdowson & Wang, 2022). However, when Euclidean space is distorted (e.g., "wormholes"enabling instantaneous teleportation), participants may show behavioral biases without detecting distortions (Warren et al., 2017). These studies focus on behavior without examining how hippocampus and entorhinal cortex represent these unusual spaces or whether mechanisms overlap with conventional space representation—an important future direction.

Second, spatial knowledge has expanded to abstract cognitive spaces beyond physical space, including social relationship space, concept space, value space, and semantic space (Schafer & Schiller, 2018). Spatial metaphors are common in daily life—social hierarchies and relationships are described using spatial terms ("climbing," "upper seat," "distant," "close"). Social relationship perception affects physical space representation, with closer relationships shortening subjective distances (Kerkman et al., 2004). Social information is encoded similarly to spatial information, representing individuals as coordinates along dimensions like power and popularity (Park, Miller, et al., 2020), enabling social inference and decision-making. Humans encode latent social relationship patterns in abstract feature spaces to flexibly construct social networks (Son et al., 2021). A brain network including hippocampus, precuneus, dlPFC, and insula participates in social space navigation (Zhang et al., 2022). However, many social space elements lack clear physical space correspondences (e.g., social occasion boundaries, unlimited distance metric dimensions), requiring future clarification.

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 representations as simple maps. However, it may commit "representationalist fallacy" —the illusion that an independent map exists for reference, perhaps arising from everyday map use and researchers' blind analogy (Warren, 2019). Spatial navigation neural activity need not copy physical environments but should help maintain effective organismenvironment associations for survival (Sung et al., 2021).

Tversky (2005) proposed cognitive collages (tolerating systematic errors) and spatial mental models (for simple environments) as alternatives. Recently, Farzanfar et al. (2023) introduced spatial schemas, hypothesizing that similar environmental structures (e.g., similarly laid-out cities) form schemas through separate representation of gist and detail. Spatial gist (core environmental features) is represented in anterior hippocampus, while details are represented in posterior hippocampus—both environment-specific. Spatial schemas are higher-level representations extracted from multiple spatial gists, capturing generalizable features across similar environments to optimize navigation decisions, primarily represented in medial PFC.

Cognitive map theory and early evidence originated from rodent behavior and electrophysiology, but human brain representation differs fundamentally across aspects including environmental structure, subregions, routes, directions, and distances (Zhao, 2018). Future research should focus more on human navigation rather than direct cross-species theory transfer.

Additionally, the cognitive map concept is unclear and overly broad. As an analogical concept with ambiguous aspects (scale, detail, precision, format), studies with vastly different content may both claim to investigate cognitive maps, from simple conditioning tasks (Costa et al., 2023) to complex navigation (Epstein et al., 2017). Future research should examine the concept' s scope to avoid overgeneralization and focus on spatial representation' s essence, characteristics, and neural dynamics.

5.4 Conclusion

The cognitive map concept has philosophical roots in Kant' s view that spatial representation is innate and a priori. Building on Kant and Tolman (1948), O' Keefe and Nadel (1978) argued that spatial nature is absolute, making cognitive maps Euclidean, with physiological basis in hippocampal cells coding absolute positions (and later entorhinal grid cells providing metric scales), opposing relative/relational space theories. However, hippocampal functions extend beyond physical space to broad memory space representation, leading Eichenbaum et al. (1999) to propose memory space theory and subsequent topological graph theories.

Both Euclidean and topological hypotheses have validity and limitations, receiving partial neural mechanism support and being necessary for certain cognitive map properties. Recent attempts to combine or unify them more completely describe cognitive maps but neglect hierarchy's role in nested space representation. Hierarchy has been behaviorally observed and theoretically proposed, but neural representation research is scarce (Kim & Maguire, 2018). Euclidean and topological theories have not incorporated hierarchy, possibly because paradigms focus on completed cognitive map features rather than dynamic construction processes. During learning, hierarchy may gradually decrease—a speculation requiring future exploration.

Additionally, future research should examine spatial dimension and range expansion, comparing cognitive maps across social, semantic, and physical spaces. Multiple behavioral, modeling, and neural phenomena reveal cognitive maps’ selectivity, distortion, and flexibility. Future work should refine theoretical construction based on these properties and reflect on cognitive map limitations.

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The cognitive map and its intrinsic mechanisms*

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Abstract: Spatial navigation is vital for the survival and reproduction of humans and other animals living in complex environments. Effective spatial representation, also known as the cognitive map, is the basis of efficient spatial navigation. Prototypical properties of the cognitive map include selectivity, flexibility and hierarchy. Several brain regions such as the hippocampus, the scene-selective areas and the prefrontal cortex are involved in the construction of the cognitive map. There are two theoretical contradictions in the representational format of the cognitive map, namely Euclidean map and topological graph, neither of which can fully account for the navigational behavior. Therefore, some researchers had put forward theories to reconcile this controversy such as the labeled map hypothesis, the reference frame network theory, etc. Future researchers are suggested to focus on the dynamic changes of the hierarchical organization during the process of constructing the cognitive map, the expansion of spatial dimensions and categories, and the limitations of the cognitive map.

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

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