Cognitive Spatial Mapping and Its Neural Mechanisms

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Date: 2024-08-24T00:00:00+00:00

Abstract

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Full Text

Cognitive Space Mapping and Its Neural Mechanisms

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Abstract: Cognitive maps can map not only physical space but also support cognitive space mapping, forming map-like representations across different information domains, including perceptual space, episodic memory space, conceptual space, and social space. The neural mechanisms underlying cognitive space mapping include the hippocampus's abstraction and generalization of latent structures, support for generating distributed location maps, binding information with contextual structures, and synergy between the hippocampal formation and other brain regions. Future research should focus on predictive cognitive spatial maps, hippocampal representations of information at different precision levels and hierarchies, research gaps at micro and mesoscopic levels of cognitive space mapping, and the common and specific mechanisms underlying physical and cognitive space mapping.

Keywords: cognitive map, grid cell, place cell, hippocampal formation

The concept of "cognitive map" was first proposed by Tolman (Tolman, 1948). He found that rats navigating mazes did not follow stimulus-response rules but instead formed an internal representation resembling a map to aid in completing complex tasks. Tolman considered cognitive maps as systematic organizations of knowledge for cross-domain behavior and the foundation of mental function. The hippocampal formation, which includes the hippocampus (CA subfields, dentate gyrus, and subicular complex) and the entorhinal cortex (Duvernoy, 2005; Schafer & Schiller, 2018), is regarded as the key structure for cognitive map formation. The hippocampus constructs an environment-centered cognitive map through place cells in the hippocampus (O'Keefe & Nadel, 1978) and grid cells in the entorhinal cortex (Hafting et al., 2005).

Specifically, place cells fire when an organism is in a specific location, with different place cells firing for different locations (O'Keefe & Nadel, 1978). Grid cells, in contrast, fire at multiple locations in a hexagonal pattern, providing precise coordinates for physical space (Hafting et al., 2005) and representing vector relationships and distances between locations (Bush et al., 2015). The unique activity characteristics of place cells and grid cells provide a biological foundation for physical space mapping.

Although researchers have reached considerable consensus on physical space mapping and its mechanisms, whether abstract information can be represented in the form of cognitive spatial maps remains to be confirmed. Existing studies have explored the construction of cognitive spatial maps across different species (rats, monkeys, bats, or humans) (Aronov et al., 2017; Julian et al., 2018; Killian et al., 2012; Omer et al., 2018), at different research levels (cellular or brain region) (Aronov et al., 2017; Constantinescu et al., 2016; Kraus et al., 2013), and for different types of information (perception, memory, concept, or social) (Bao et al., 2019; Deuker et al., 2016; Tavares et al., 2015; Theves et al., 2020). These studies suggest that cognitive space mapping possesses cross-domain properties, with cognitive information of varying degrees of abstraction and types being processed to form cognitive maps (Table 1). For instance, perceptual information, episodic memory information, conceptual information, and social information can be processed to form perceptual space cognitive maps, episodic memory space cognitive maps, conceptual space cognitive maps, and social space cognitive maps, respectively. However, whether these studies can mutually support and corroborate each other still needs clarification. Moreover, current explorations of cognitive space mapping mechanisms remain limited to analogies with physical space (Bellmund et al., 2018), lacking in-depth investigation of the true mechanisms underlying cognitive space mapping. Therefore, this article reviews and synthesizes research on perceptual space, episodic memory space, conceptual space, and social space mapping in animals and humans, examines the neural mechanisms of cognitive space mapping at both micro and macro levels, and finally proposes future research directions.

1.1 Perceptual Space Mapping

Perception is the starting point for individuals to understand the world and the foundation of all mental activities. Recent studies have consistently found that the hippocampus can map perceptual space (Aronov et al., 2017; Bao et al., 2019; Killian et al., 2012), binding visual images, sounds, odors, and other information to perceptual spatial contexts defined by basic perceptual attributes (such as sound frequency), demonstrating cross-modal encoding characteristics.

In the visual modality, researchers had monkeys view images on a screen while conducting single-cell recordings and found that grid cells in their entorhinal cortex encoded multiple locations in the visual field using a sixfold rotational symmetry firing pattern (Killian et al., 2012) (Figure 1a [Figure 1: see original paper]). Similarly, Julian et al. (2018) had human participants perform a visual search task during functional Magnetic Resonance Imaging (fMRI) scanning while recording their eye movement directions. They discovered sixfold rotational symmetry blood oxygen level-dependent (BOLD) signals in the entorhinal cortex that corresponded to the sixfold rotational symmetry firing patterns of grid cells. Specifically, when eye movement directions aligned with the grid orientation, they produced greater neural activity signals than misaligned directions, with a periodicity of 60° (Figure 1b). These results suggest the existence of grid cells that respond to visual images and encode directions between "locations." In the auditory modality, when rats were trained to discriminate different sound frequencies to obtain rewards, place cells in their hippocampus fired for single frequencies, covering the entire task frequency space, while grid cells in the entorhinal cortex responded to multiple frequencies (Aronov et al., 2017), effectively representing task sound frequencies using a one-dimensional auditory spatial structure. In the olfactory modality, studies have found that rodents can form cognitive maps of their surroundings based on odors, primarily involving place cells in hippocampal CA1 (Radvansky & Dombeck, 2018). Additionally, Bao et al. (2019) discovered that humans can navigate in a two-dimensional "odor space" (Figure 1c). In this study, when participants continuously sniffed two mixed odors (composed of two single odors), sixfold rotational symmetry BOLD signals emerged in the entorhinal cortex (Bao et al., 2019) (Figure 1b). These findings demonstrate that the hippocampus is not specialized solely for encoding physical spatial locations but may possess a general circuit suitable for encoding cross-modal perceptual spaces.

Figure 1 Perceptual Space Mapping. (a) The firing pattern of a grid cell projected onto visual space. This grid cell tiles the entire visual space with a regular hexagonal firing pattern, showing maximal activation when the monkey's gaze moves to the vertices and centers of the hexagons. Image adapted from Killian et al. (2012). (b) Odor space. The two dimensions of odor space are defined by the intensities of two single odors. Performing odor navigation tasks creates different navigation trajectories in odor space (2). Image adapted from Bao et al. (2019). (c) Sixfold rotational symmetry BOLD signal. This signal has a periodicity of 60°, producing greater neural activity when navigation trajectories align with the grid orientation compared to misaligned trajectories.

In addition to the hippocampus, researchers have discovered place cell and grid cell activity in the primary somatosensory cortex (S1) of foraging rats (Long & Zhang, 2021) and the secondary visual cortex (V2) (Long et al., 2021). Furthermore, the anterior piriform cortex (APC) in humans exhibits sixfold rotational symmetry BOLD signals aligned with entorhinal grid cell directions during olfactory navigation (Bao et al., 2019), suggesting the possible presence of grid cells in this region. These studies indicate that the brain may possess a comprehensive system for mapping perceptual information. However, since the aforementioned studies primarily manipulate non-spatial perceptual stimuli to examine neuronal activity, and these perceptual stimuli have relatively low levels of abstraction, their support for cognitive space mapping is somewhat weak. Further investigation is needed into how the brain represents and maps more abstract cognitive information (such as memory, concept, and social information).

1.2 Episodic Memory Space Mapping

Episodic memory is memory for personal life events. Individuals typically transform these events into appropriate mental representations based on their spatiotemporal characteristics to properly reflect associations between events, thereby facilitating episodic memory retrieval (Ekstrom & Yonelinas, 2020; Gauthier & van Wassenhove, 2016). According to Eichenbaum et al.'s (1997, 1999) memory space theory, continuously occurring or experienced events and their locations constitute episodic memories, with different episodic memories interconnected through overlapping or common elements to form more complex relational memory networks. Here, "continuously occurring or experienced" can be viewed as the temporal dimension of episodic memory, while "location" represents the spatial dimension. Consequently, episodic memory space can be conceived as a specific memory space that encodes events along both temporal and spatial dimensions. The hippocampus provides a general mechanism for integrating temporal and spatial dimensions, placing events within specific spatiotemporal contexts (Cohen & Eichenbaum, 1993; Eichenbaum, 2004, 2014; Eichenbaum et al., 1999).

Researchers have discovered "time cells" in animal hippocampi that function similarly to place cells (Kraus et al., 2015; Kraus et al., 2013; MacDonald et al., 2011; Pastalkova et al., 2008; Salz et al., 2016). These cells fire at specific moments within a temporal structure associated with an event, with different time cells firing at different moments to cover the entire temporal structure, thereby supporting the encoding of event sequences. MacDonald et al. (2011) had rats perform an Object-Delay-Odor Sequences task consisting of two events separated by a time interval. In this task, rats first learned an object (Event 1), then entered a closed narrow channel to experience a time interval (delay), and after exiting the channel, smelled an odor (Event 2) and made a judgment to obtain a reward. The results showed that neurons firing at specific moments could be found in the hippocampus both during event occurrence and during the time interval. Notably, this phenomenon persisted even when controlling for the rat's position, direction, and velocity, indicating that the hippocampus can link discrete events using a "timeline." Researchers further discovered that time-encoding cells in the hippocampus partially overlap with place cells and grid cells, demonstrating that hippocampal neurons possess both temporal and spatial selectivity (Kraus et al., 2015; Kraus et al., 2013; Salz et al., 2016). Additional research suggests that hippocampal neurons encode temporal and spatial information in similar ways, with place cells executing a general and singular algorithm to generate sequences that access and organize sensory experiences distributed across cortical units (Buzsaki & Tingley, 2018; Eichenbaum, 2014; Lisman et al., 2017). Furthermore, Kraus et al. (2013, 2015) found that place cells and grid cells can encode time and space information either separately or in an integrated manner. Kraus et al. (2013) placed rats on a treadmill where, due to the lack of spatial displacement, rats could not activate place cells through changes in movement patterns or environmental cues. Modeling analysis revealed that the firing activity of some hippocampal neurons could be explained by running distance or time alone, while others were jointly explained by both running distance and time. Kraus et al. (2015) employed a similar paradigm and similarly found that the entorhinal cortex contained grid cells that could encode running time or distance separately, as well as grid cells that simultaneously encoded both running time and distance (Kraus et al., 2015). The integration of spatiotemporal information by place cells and grid cells essentially places the running event within a certain spatiotemporal context. These studies collectively corroborate that the hippocampus can encode temporal and spatial dimensions either separately or simultaneously according to task demands.

fMRI studies with human participants have also found that the hippocampus can encode not only the temporal dimension of events (Hsieh et al., 2014) but also integrate temporal and spatial dimensions (Deuker et al., 2016; Nielson et al., 2015). Nielson et al. (2015) had participants carry an automatically recording camera for one month to document scenes from their daily lives. During subsequent MRI scanning, participants viewed and recalled photos recorded by the camera, and the results revealed that hippocampal neural activity reflected the proximity of temporal and spatial distances between photos. Deuker et al. (2016) had participants learn the temporal and spatial proximity of objects in a more strictly controlled virtual space. They found that as objects became closer in temporal and spatial distance, the similarity of hippocampal neural activity increased. Both studies discovered hippocampal encoding of spatiotemporal "distance" between events, indicating that the hippocampus constructs a two-dimensional episodic memory space for events. Since invasive research paradigms are difficult to employ for examining cellular activity in the human brain, fMRI results can only serve as macroscopic-level evidence of neural activity. Recently, researchers using intracranial microelectrode recordings have discovered "time cells" in the hippocampus and entorhinal cortex of human epilepsy patients (Reddy et al., 2021; Umbach et al., 2020), providing micro-level validation of human hippocampal encoding of the temporal dimension in memory space.

1.3 Conceptual Space Mapping

Research on conceptual space mapping is primarily divided into two parts: general conceptual space and special conceptual space.

1.3.1 General Conceptual Space

General conceptual space refers to the cognitive space formed by binding abstract concepts to conceptual spatial contexts with different structures. In this context, abstract concepts primarily refer to artificial concepts created by experimenters through combining several attributes, reflecting an abstract form of thinking. For example, representing an object in a two-dimensional feature space composed of two abstract features allows the distance and direction between concepts to be calculated, much like in physical space (Bellmund et al., 2018; Morton & Preston, 2021). Research on general conceptual space has focused on human fMRI studies, primarily examining the mapping functions of the hippocampus and related brain regions such as the medial prefrontal cortex (Constantinescu et al., 2016; Theves et al., 2020; Vigano & Piazza, 2020).

The hippocampus and related brain regions can represent conceptual feature spaces. Constantinescu et al. (2016) postulated a two-dimensional bird space constructed from leg length and neck length, where any bird could transform into another through proportional changes in leg and neck length (Figure 2 [Figure 2: see original paper]). When participants viewed birds with varying proportions of leg and neck length (Figure 2), they formed different trajectories (direction vectors) in the hypothesized two-dimensional bird space. The results revealed sixfold rotational symmetry BOLD signals in the entorhinal cortex and ventromedial prefrontal cortex (Constantinescu et al., 2016), confirming the validity of the two-dimensional bird space and trajectory assumptions. This demonstrates that grid cells can encode directions between concepts, organizing abstract conceptual knowledge (about birds) into a two-dimensional conceptual feature space. Theves et al. (2019) had participants learn objects defined by two abstract dimensions (circle size and square transparency) and found that hippocampal neural activity varied with the distance between objects in this two-dimensional conceptual feature space. Vigano and Piazza (2020) further discovered that individuals can construct two-dimensional conceptual feature spaces for semantic concepts. In their study, participants first learned semantic concepts designed according to two dimensions, and found that sixfold rotational symmetry BOLD signals emerged in the entorhinal cortex during semantic concept stimulation, with more similar semantic concept categories eliciting more similar neural activity (Vigano & Piazza, 2020). This indicates that the entorhinal cortex can compute and encode both direction and distance between semantic concepts. Furthermore, Theves et al. (2020) demonstrated that the hippocampal mapping mechanism is flexible, capable of selecting dimensions relevant to behavior for mapping conceptual feature spaces. In their study, although object concepts were defined by three dimensions (dot frequency, stripe frequency, and transparency), hippocampal BOLD signals were only associated with the dot frequency and transparency dimensions involved in concept classification (Theves et al., 2020).

Figure 2 Conceptual Space Mapping. The bird space hypothesized by Constantinescu et al. (2016). This space is constructed from two dimensions: bird neck length and leg length. Different positions in the two-dimensional bird space correspond to birds with different neck and leg lengths. The researchers set up six Christmas symbols, each corresponding to a bird in the bird space. Trajectories represent transformations from one bird to another according to specific neck-to-leg length ratios. Before the formal experiment, participants explored and learned the hypothesized bird space by freely adjusting the neck-to-leg length ratios. When participants transformed a bird to match a bird corresponding to a specific Christmas symbol, that symbol would appear on the screen. During the formal experiment, participants watched the bird's neck and leg lengths transform according to certain proportions, then imagined whether continuing this transformation would result in a particular Christmas symbol and made a choice. Image adapted from Constantinescu et al. (2016).

In hierarchical conceptual space mapping, researchers have similarly found involvement of the hippocampus and related brain regions. Theves et al. (2021) discovered that the hippocampus is activated during concept learning and updating, while neural activity in the rostrolateral prefrontal cortex reflects "distance" between hierarchical concepts. Morton et al. (2020) found that the hippocampus participates in extracting common and distinctive features of concepts. In the semantic conceptual feature space of Vigano and Piazza (2020) mentioned earlier, hierarchical relationships also exist between individual semantic concepts and semantic concept categories. The results showed that hippocampal distance encoding occurred only between semantic concept categories, not between individual semantic concepts. How the hippocampus participates in representing concepts at different hierarchical levels remains to be further explored.

Additionally, researchers have proposed a predictive cognitive map hypothesis, suggesting that place cells can represent not only an organism's current location but also future possible locations and their likelihood distributions (de Cothi et al., 2022; Stachenfeld et al., 2017). Stoewer et al. (2023) successfully simulated this firing pattern of place cells in multidimensional semantic conceptual space using a “successor representation” algorithm. This result suggests that conceptual space may be mapped through predictive cognitive maps.

1.3.2 Special Conceptual Space

Special conceptual space primarily refers to reward space, which is the cognitive space formed by binding the concept of “reward” to physical or abstract spatial contexts. Reward is a form of abstract cognitive information—an abstraction and generalization of things with reward value. Organisms need to understand the meaning of rewards much like they understand concepts, in order to respond to rewards incorporated into physical or abstract spaces. Research shows that when animals obtain rewards in physical or abstract spaces, their hippocampal place cells and grid cells exhibit unique representations of both the reward and its environment (Baraduc et al., 2019; Butler et al., 2019; Hok et al., 2007; Poucet & Hok, 2017). Therefore, reward space can be considered a special type of conceptual space.

Studies have found that place cells increase their firing at locations where rats obtain rewards (Poucet & Hok, 2017), with place fields clustering toward reward locations (Hok et al., 2007). When reward locations change, some place cells in the macaque hippocampus continue to fire for that reward, and these cells are called schema cells (Baraduc et al., 2019; Wirth et al., 2017). Schema cells provide high-level conceptual knowledge about task structure. In the human hippocampus, “concept cells” with functions similar to schema cells also exist (Quiroga, 2012; Quiroga et al., 2005). These cells selectively encode photographs of celebrities from different perspectives. Due to the existence of “concept cells,” humans can recognize celebrities without placing them in specific contexts. In addition to place cells, grid cell activity is also influenced by rewards. Grid cells in the rat entorhinal cortex respond to rewards incorporated into physical space by distorting their regular hexagonal grid firing fields (Boccara et al., 2019) or scaling grid spacing (Butler et al., 2019).

However, Quiroga (2019) notes that different species exhibit different responses to rewards in space. Rats tend to respond to rewards bound to the environment, representing an “AND” conjunction (responding to rewards in specific environments). Humans possess concept cells and thus demonstrate a more abstract “OR” representation independent of the environment (responding invariantly to rewards in one or another environment). Monkeys, meanwhile, employ a mixed (AND/OR) representation (Quiroga, 2019). Humans’ ability to separately represent rewards and environments allows them to bind rewards with different contexts, enabling rapid learning and knowledge generalization when environments change.

From a broader perspective, place cells and grid cells responding to rewards can be viewed as encoding a concept within cognitive space. Thus, “concept cells” and place cells actually share the same mapping function, responding to specific individuals and precise locations, respectively (Quiroga, 2012; Quiroga et al., 2005). A recent study found that macaques can construct a three-dimensional "reward space" (Knudsen & Wallis, 2021). Researchers had macaques view three images while continuously changing their reward values, and discovered "value place cells" in the hippocampus that encoded different positions in the three-dimensional "reward space" (with each dimension defined by the reward value of one image) (Figure 3 [Figure 3: see original paper]). When the three images changed (sensory stimulation changed while the background structure remained constant), these "value place cells" could undergo remapping (Knudsen & Wallis, 2021). In summary, "reward space" essentially binds the concept of "reward" within physical or abstract spatial contexts, representing a special type of conceptual space.

Value change trajectory Value place cells Figure 3 Reward Space Mapping. In Knudsen & Wallis (2021), macaques viewed three images on a screen that could have different reward values and constructed a three-dimensional reward space in their brains. The black trajectory represents the value change trajectory formed in reward space as the reward values of the three images continuously changed, while colored dots represent firing hippocampal neurons. Image adapted from Knudsen & Wallis (2021).

1.4 Social Space Mapping

Social interaction is an important activity in human life. Studies have found that the brain can map "social space," binding others to social spatial contexts to support social reasoning and decision-making (Behrens et al., 2018; Schafer & Schiller, 2018). Making appropriate social inferences and decisions is crucial for individual survival and development, so social spatial contexts are often associated with social environments and typical social attributes such as reputation, power, and intimacy.

Researchers have discovered "social place cells" in the hippocampus of bats (Omer et al., 2018) and rats (Danjo et al., 2018) that encode the locations of conspecifics in physical space, and these cells partially overlap with place cells that encode the animal's own location. Studies with human participants have further explored how the hippocampus and related brain regions bind others to abstract social spatial contexts. Tavares et al. (2015) designed a virtual social interaction game in which participants interacted with different characters. The results showed that participants could egocentrically represent others in a two-dimensional social space constructed from power and intimacy (Figure 4a [Figure 4: see original paper]). The left hippocampus tracked the vector angle formed between the individual and others during each interaction, while the posterior cingulate cortex tracked the vector distance between them. The combination of vector angle and distance represented how participants dynamically tracked the outcomes of social interactions with others within their own social space. This study also found that participants' hippocampal neural activity correlated with their social abilities, reflecting the unique social attributes of social space. This research was replicated and validated by Zhang et al. (2022).

Additionally, other studies have demonstrated that the hippocampus and related brain regions participate in social space construction. Park et al. (2020) had participants learn hierarchical differences of two groups of virtual characters along reputation and ability dimensions. The results revealed that neural activity in the hippocampus, entorhinal cortex, and medial prefrontal cortex reflected the Euclidean distance between virtual characters in the two-dimensional feature space constructed from reputation and ability, indicating that the two groups of virtual characters were integrated and represented within a unified space. Park et al. (2021) not only validated hippocampal and related brain regions' encoding of distances between virtual characters but also found that when participants performed character reasoning, sixfold rotational symmetry BOLD signals emerged in the entorhinal cortex, medial prefrontal cortex, orbitofrontal cortex, superior temporal sulcus, and temporoparietal junction (Figure 4b-c), indicating that grid cells participate in the organization and mapping of social space.

Post-interaction character position (x,y) Character's initial position Intimacy (x) Figure 4 Social Space Mapping. (a) Schematic diagram of "social space" from Tavares et al. (2015). This example shows a character's movement trajectory relative to the participant during four social interactions. Image adapted from Tavares et al. (2015). (b-c) Park et al. (2021) found that when participants completed social reasoning tasks, they formed direction vectors in the hypothesized social space, eliciting sixfold rotational symmetry BOLD signals in the brain.

2 Neural Mechanisms of Cognitive Space Mapping

The aforementioned animal research has focused on hippocampal place cell and grid cell activity, while human studies have found neural signals in the hippocampus resembling place cell and grid cell activity, indicating that the hippocampus is a key structure for cognitive space mapping. Additionally, brain regions such as sensory cortex, medial prefrontal cortex, orbitofrontal cortex, and cingulate cortex exhibit similar neural activity and functional coupling with the hippocampus, suggesting that cognitive space mapping is not accomplished by the hippocampus alone but may involve coordination with multiple brain regions at the network level. A comprehensive review of relevant research is detailed in Table 1.

2.1 Hippocampal Mechanisms Supporting Cognitive Space Mapping

The hippocampus may support cognitive space mapping through three potential mechanisms: First, the hippocampus abstracts and generalizes the latent structures of cognitive spaces. Different cognitive spaces can be abstracted into various latent structures, including spatial structures with different dimensions, such as one-dimensional (Aronov et al., 2017), two-dimensional (Bao et al., 2019; Deuker et al., 2016; Park et al., 2021; Park et al., 2020; Tavares et al., 2015), or even multidimensional (Knudsen & Wallis, 2021) structures. These structures can also include Euclidean spaces (Park et al., 2021; Park et al., 2020) and topological maps (Theves et al., 2021) with different information precision, as well as hierarchical (Morton et al., 2020; Theves et al., 2021) structures. These structures can be manifested within the same space, essentially organizing complex knowledge into abstract relational structures (Peer et al., 2021). For example, hierarchical concepts and genealogical diagrams, though belonging to conceptual and social spaces respectively, are fundamentally abstract hierarchical structures. The generation of cognitive spatial maps with different structures may stem from functional requirement differences, reflecting the flexibility and selectivity of cognitive spatial maps (Wu Wenya & Wang Liang, 2023). Two recent rodent studies have further confirmed that the hippocampus can encode latent structures formed through computation (Nieh et al., 2021; Sun et al., 2020). Sun et al. (2020) had mice run laps in a maze, receiving rewards only after every four laps. They found that some cells in hippocampal CA1 encoded maze locations while others encoded lap numbers, demonstrating that hippocampal neurons can encode sequences of discrete events and maintain representations of complex spatial and non-spatial structures. The abstraction and generalization of structural information in cognitive maps may be related to the medial entorhinal cortex—the primary information input region to the hippocampus—where grid cells cluster into modules that maintain stable spatial phase structures across different environments. Specifically, grid cells within the same module that are adjacent in one environment remain adjacent in another environment (Fyhn et al., 2007; Whittington et al., 2022). However, existing research lacks exploration of information precision and hierarchy within latent structures. Human fMRI studies often use "distance" encoding to represent relationships between locations in cognitive space, but distance encoding cannot specify whether the distance is Euclidean or topological connectivity, nor can it reflect information precision. Furthermore, how information at different hierarchical levels is represented in hierarchical cognitive spaces remains to be answered.

Second, the hippocampus supports the generation of distributed location maps to represent relationships between objects. Place cells in the hippocampus fire for single locations, covering the entire "space" to form location maps of different cognitive spaces. Grid cells in the entorhinal cortex fire at multiple locations, with grid cells of different orientations overlapping to provide precise coordinates for space (Hafting et al., 2005), enabling the computation of vector relationships and distances between different locations (Bush et al., 2015). Research has found that distributed location maps can be manifested in highly abstract latent spaces. Nieh et al. (2021) had mice perform an Accumulating Towers task in a T-maze, where mice had to attend to towers appearing on both sides of the maze while running, with rewards appearing on the side with more towers. Mice needed to compute which side would contain the reward. The number of towers on the right side minus those on the left side was termed "evidence." The results revealed place cells in the hippocampus that encoded different "locations" in a two-dimensional “evidence space” composed of both “evidence” and physical space (Nieh et al., 2021).

Human fMRI studies primarily validate the generation of distributed location maps through hippocampal encoding of distance and direction between objects (or locations represented by objects). Specifically, distance encoding refers to encoding the proximity between two objects in cognitive space, while direction encoding refers to encoding the direction vector formed by connecting two objects in cognitive space. According to the characteristics of distributed location maps, a particular location in cognitive space is encoded by one or more place cells. When two locations are relatively close, the place fields of the place cell populations encoding these two locations exhibit more overlap, resulting in more similar neural activity for proximal locations (Bellmund et al., 2018; Gärdenfors, 2000), which is considered distance encoding. “Moving” from one location to another forms a direction vector connecting the two locations. If this direction vector aligns with the grid orientation of grid cells, it elicits greater neural activity compared to misaligned vectors, producing sixfold rotational symmetry BOLD signals that can be considered direction encoding. It is worth noting that the relationship between distributed location maps constructed by micro-level neurons and the distance and direction encoding manifested in macro-level brain region BOLD signals is indirect. How micro-level neurons coordinate to support macro-level brain region functions remains to be further explored.

Third, the hippocampus binds information with contextual structures. This phenomenon follows the principle of structural generalization and conforms to the rules of hippocampal remapping. Specifically, in perceptual space, the hippocampus binds perceptual stimuli to perceptual spatial contexts; in episodic memory space, it binds events to spatiotemporal contexts; in general conceptual space, it binds abstract concepts to conceptual spatial contexts; in reward space, it binds rewards to physical or abstract spatial contexts; and in social space, it binds others to social spatial contexts. The hippocampal binding of information and context aligns with the principle of structural generalization (Mark et al., 2020; Whittington et al., 2018; Whittington et al., 2020). Based on this principle, Whittington et al. (2018) proposed that cognitive maps can be decomposed into two factors: sensory stimuli and latent structure. Different sensory stimuli and latent structures can be recombined to form different cognitive maps. Regardless of how sensory stimuli change, as long as the underlying relational structure is mastered, flexible judgments and reasoning can be performed (Figure 6 [Figure 6: see original paper]). This mechanism involves, on one hand, the transmission of relational structure information to the hippocampus via grid cells in the medial entorhinal cortex, and on the other hand, the transmission of sensory stimuli to the hippocampus via the lateral entorhinal cortex. The hippocampus integrates these two information streams, embedding specific sensory information within the latent structure, with place cells representing “locations” in cognitive space. Indeed, two distinct information streams exist in the entorhinal cortex that separately transmit spatial and object information (Manns & Eichenbaum, 2006), while hippocampal cells that integrate information only fire when specific objects correspond to specific locations. Such conjunctive signals encode "what happens where" (Komorowski et al., 2009). This information transmission circuit may similarly apply to binding specific information to specific cognitive spatial contexts. The joint representation of sensory stimuli and latent structure also conforms to the rules of hippocampal remapping (Colgin et al., 2008), where grid cells, being less susceptible to sensory stimulation, can provide structural information, while place cells change their firing locations in response to sensory stimulation changes, allowing different sensory stimuli to be represented within the same relational structure (Whittington et al., 2022). The ability of "time cells" (MacDonald et al., 2011) and "value place cells" (Knudsen & Wallis, 2021) to undergo remapping supports this conception. Researchers have also trained a machine learning model called TEM (The Tolman-Eichenbaum Machine) based on the principle of structural generalization, finding that the simulated hippocampus and entorhinal cortex in TEM indeed exhibited properties of various spatial cells including place cells and grid cells (Sanders et al., 2020; Whittington et al., 2020).

2.2 Hippocampal Collaboration with Other Brain Regions

Cognitive space mapping is not accomplished by the hippocampus alone but also involves coordination between the hippocampus and sensory cortex (Bao et al., 2019; Poo et al., 2022), between the hippocampus and medial prefrontal cortex (Constantinescu et al., 2016; Mack et al., 2020; Park et al., 2021), and between the hippocampus and orbitofrontal cortex (Park et al., 2021; Park et al., 2020; Vigano & Piazza, 2020), among other brain regions.

First, the hippocampus integrates information from sensory cortex. In animal studies, Poo et al. (2022) found that neurons in the posterior piriform cortex (PPC) of rats could not only discriminate odors but also encode spatial information, helping the brain form an odor-location association map, and that functional coupling exists between the PPC and hippocampus. Human fMRI studies have found that the anterior piriform cortex exhibits sixfold rotational symmetry BOLD signals aligned with entorhinal grid cell directions during olfactory navigation (Bao et al., 2019). These studies suggest that the hippocampus may receive and integrate information from sensory cortex to accomplish cognitive spatial map construction.

Second, information exchange between the hippocampus and medial prefrontal cortex supports efficient and flexible cognitive space mapping. The medial prefrontal cortex receives input from the hippocampus regarding task context information, abstracts and generalizes cognitive information based on the current context, and in turn shapes hippocampal representations. Studies have found that the hippocampus can select dimensions relevant to behavior for mapping conceptual space (Morton & Preston, 2021; Theves et al., 2020), which may involve the medial prefrontal cortex. Other research has shown that the medial prefrontal cortex can perform goal-directed information filtering and dimensionality reduction during concept learning, with functional coupling to the hippocampus during this process (Mack et al., 2020), indicating that the medial prefrontal cortex transmits information to the hippocampus and helps it form conceptual spatial representations associated with task goals. Furthermore, the reciprocal connections and functional coupling between the hippocampus and medial prefrontal cortex play a role in relational processing and memory integration, supporting the abstraction, generalization, and organization of experiences to form memory spaces (Kumaran et al., 2009; Schlichting et al., 2015; Zeithamova et al., 2012).

Third, functional coordination between the hippocampus and orbitofrontal cortex shapes representations at different information levels. The hippocampus and orbitofrontal cortex describe information at different levels of cognitive space, with the former involving relational representations of abstract knowledge and the latter involving “state space” representation and value evaluation (Niv, 2019; Schuck et al., 2016; Stalnaker et al., 2015; Wikenheiser & Schoenbaum, 2016). When tasks require both types of information, they are co-activated and exhibit similar neural activity. Wikenheiser and Schoenbaum (2016) noted that information input from the orbitofrontal cortex modulates location-selective hippocampal neurons with additional information, generating representations sensitive to factors such as reward, goals, and motivation. Conversely, the hippocampus transmits relational information to the orbitofrontal cortex, linking its outcome expectations to specific abstract relationships. Wikenheiser et al. (2017) found that suppressing hippocampal information output impairs orbitofrontal cortex encoding of task structure.

However, relevant research suggests that grid cells may exist throughout the neocortex, with higher-level cognitive tasks being learned and represented through a location-based framework (Hawkins et al., 2018). Moreover, grid cell coding in the hippocampus is flexible and should be understood as part of the collective pattern of brain neural activity (Ekstrom et al., 2020). Future research should further explore how the hippocampus coordinates with the medial prefrontal cortex, orbitofrontal cortex, and other brain regions at the larger network level.

Table 1 Literature Review of Cognitive Space Mapping

Information Abstraction Level	Information Content	Spatial Background	Other Brain Regions Involved	Structure Type
Low	Sensory stimuli	Perceptual space defined by basic perceptual attributes (e.g., sound frequency)	Piriform cortex, ventromedial prefrontal cortex	Distributed location map
High	Events with spatiotemporal characteristics	Spatiotemporal context	Orbitofrontal cortex, medial prefrontal cortex, posterior cingulate cortex, temporoparietal junction	Distributed location map
High	Abstract concepts (mainly artificial concepts); “reward” concepts	Varies according to concept characteristics and task requirements	Rostrolateral prefrontal cortex, ventromedial prefrontal cortex, medial orbitofrontal cortex	Two-dimensional Euclidean space structure, distance and direction encoding
High	Others in social contexts	Associated with social environment and social attributes (reputation, power, intimacy)	Medial prefrontal cortex, orbitofrontal cortex, superior temporal sulcus, temporoparietal junction	Two-dimensional Euclidean space structure, distance and direction encoding

3 Research Prospects

The above synthesis of relevant research attempts to reveal the neural mechanisms of cognitive space mapping and has identified several issues and limitations. For example, place cells and grid cells may employ other neural computation and coding methods, cognitive space cannot reflect information precision and hierarchy, and there is a disconnect between micro-level and macro-level research on cognitive space mapping. Future research can focus on the following aspects.

3.1 Predictive Cognitive Spatial Maps

The most prominent function of cognitive maps is to help individuals perform flexible navigation and decision-making (Whittington et al., 2022; Zhang et al., 2021). Research on cognitive space mapping reveals a high degree of association between hippocampal neural activity, spatial representation, and navigational behavior in decision-making (Boorman et al., 2021; Constantinescu et al., 2016; Morton et al., 2020; Park et al., 2021). This has led to the assumption that there is a strict correspondence between the metric properties of grid cells, metric representations of space, and metric navigation behavior, allowing for mutual inference. However, this assumption may be neither necessary nor flexible (Ekstrom et al., 2020). The predictive cognitive map hypothesis may address this issue. The “successor representation” (Dayan, 1993) is a typical representative and computational model of this hypothesis. This model proposes that the function of cognitive maps is to predict future valuable states based on the current state, suggesting that the hippocampus primarily constructs predictive maps of the environment by encoding subsequent possible locations and their likelihood distributions. This model can better predict the non-uniform distribution of place cells near rewards after reward incorporation (de Cothi et al., 2022; Stachenfeld et al., 2017). This theory provides a new perspective on the relationship between neural activity and behavior, enabling researchers to move beyond the assumption of strict correspondence between grid coding, spatial representation, and navigation behavior (Ekstrom et al., 2020). Successor representation has been preliminarily explored in some non-spatial tasks (Garvert et al., 2017; Stoewer et al., 2022) and semantic conceptual spaces (Stoewer et al., 2023). Future research should consider the possibility and rationality of applying this neural coding mechanism to cognitive space mapping and explore how common computational and coding schemes in cognitive space mapping compete and cooperate with models such as successor representation.

3.2 Hippocampal Representation of Information at Different Precision Levels and Hierarchies

The hippocampus exhibits a prominent characteristic at the cellular level: the existence of place cells and grid cells at different scales. Specifically, place cell place fields increase in size along the dorsoventral axis of the rodent hippocampus (Brunec et al., 2018), while grid cell firing fields and spacing increase along the dorsoventral axis of the rodent entorhinal cortex (Stensola et al., 2012). Physical space research has found that the anterior hippocampus represents Euclidean distance, while the posterior hippocampus represents path distance (Howard et al., 2014). Farzanfar (2023) also noted that spatial summaries are represented by the anterior hippocampus, while detailed information is represented by the posterior hippocampus. This cellular-level characteristic of the hippocampus may provide representations of information at different precision levels and hierarchies for cognitive space (Strange et al., 2014), such as identifying a Ferrari as a vehicle or as the more specific category of racing car, enabling individuals to flexibly use different types of information. Vigano and Piazza (2020) attempted to examine human hippocampal representation of hierarchical information in conceptual space but found no relevant evidence, possibly due to fMRI signal precision and analysis of the hippocampus as a whole. Therefore, future research can explore hippocampal information representation by designing research paradigms targeting different cognitive spaces, improving fMRI signal precision, and deeply investigating the gradient topological patterns along the hippocampal axis.

3.3 Micro and Mesoscopic Level Research on Cognitive Space Mapping

Currently, research at the micro and mesoscopic levels of cognitive space mapping is limited. Future research in this area can help researchers gain deeper understanding of the intrinsic mechanisms of cognitive space mapping. A large number of current studies focus primarily on micro-level research of single neurons in animals (Killian et al., 2012; Kraus et al., 2015) and macro-level research on human fMRI brain networks (Bao et al., 2019; Julian et al., 2018), while micro-level research on single neurons in humans mostly uses patients as subjects (Reddy et al., 2021; Umbach et al., 2020). Differences in brain evolution between animals and humans prevent simple analogies, and animal single-neuron research cannot substitute for micro-level human neuron research. Similarly, caution is needed when generalizing findings from patient studies to normal individuals. Moreover, existing research lacks attention to the mesoscopic level between the micro-level of single neurons and the macro-level of fMRI brain networks. Notably, research at the single-neuron level and brain network level are not isolated; the distributed location maps at the micro-level and the distance and direction encoding at the macro-level require mesoscopic-level investigation of neuronal connectivity and coordination to bridge the gap (Kunz et al., 2019). Future research should pay more attention to cognitive space mapping processes in normal humans and attempt to use techniques such as cellular recording, intracranial EEG, and magnetoencephalography to explore the activity of spatial cells and resulting neural oscillations in the human brain during different types of cognitive space mapping, clarifying the activity patterns of neuronal populations. This will help fill the research gaps at the micro and mesoscopic levels of human cognitive space mapping.

3.4 Analogies Between Physical and Cognitive Space Mapping

Inspired by physical space mapping, research on cognitive space mapping is gradually deepening. Existing studies have found that physical and cognitive space mapping rely on the same spatial cells and activate overlapping brain regions, including the hippocampus, medial prefrontal cortex, and orbitofrontal cortex (Zhang Jiaxin et al., 2019; Constantinescu et al., 2016; Doeller et al., 2010). Therefore, physical and cognitive space mapping may employ the same neural architecture. However, whether physical and cognitive space mapping can be directly analogized still requires consideration of many issues. For example, how features such as landmarks, boundaries, and environmental geometry are manifested in cognitive space (Epstein et al., 2017), whether place cells undergo remapping in conceptual and social spaces (Schafer & Schiller, 2018), and how information about location, time, reward, and society can be integrated into a unified representation of "lived space" (Schafer & Schiller, 2018). Furthermore, the same activity of spatial cells in physical and cognitive spaces may serve different functions. For instance, in irregular physical environments, grid cell grid fields become distorted, causing individuals to have greater difficulty remembering target locations and leading to disorientation (Bellmund et al., 2020). In reward space, however, distortion of grid cell grid fields serves to better respond to rewards and goals (Boccara et al., 2019). Future research should conduct comprehensive analogies between cognitive and physical space mapping, clarifying their common and specific mechanisms to construct an integrated research framework for cognitive maps.

4 Conclusion

Cognitive maps are representations of physical space and, more importantly, internal world models constructed based on experience. Like an invisible navigation chart, they support flexible behavior and decision-making in organisms. Investigating the construction of cognitive maps and their intrinsic mechanisms can deepen our understanding of how organisms comprehend and adapt to their surroundings. Existing research has explored the construction of cognitive spatial maps from different types of information—perception, memory, concept, and society—using various species (rats, monkeys, bats, and humans) as subjects and examining different research levels (cells and brain regions). The findings obtained mutually support and corroborate each other, validating Tolman's conception of cross-domain cognitive maps. Mechanistically, the activity of place cells and grid cells in the hippocampus, along with coordination between the hippocampus and multiple brain regions, provides support for cognitive space mapping. However, research on cognitive space mapping requires further deepening. Future research directions include the neural computation methods of place cells and grid cells, hippocampal representation of information at different precision levels and hierarchies, and exploration of neural activity at micro and mesoscopic levels. Only by gaining profound insight into the intrinsic mechanisms of cognitive space mapping and combining them with the operational principles of physical space mapping can we draw the complete picture of cognitive map research.

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