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Perspective article

Grid codes underlie multiple cognitive maps in the human brain

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ABSTRACT

Grid cells fire at multiple positions that organize the vertices of equilateral triangles tiling a 2D space and are well studied in rodents. The last decade witnessed rapid progress in two other research lines on grid codes—empirical studies on distributed human grid-like representations in physical and multiple non-physical spaces, and cognitive computational models addressing the function of grid cells based on principles of efficient and predictive coding. Here, we review the progress in these fields and integrate these lines into a systematic organization. We also discuss the coordinate mechanisms of grid codes in the human entorhinal cortex and medial prefrontal cortex and their role in neurological and psychiatric diseases.

> *In order to understand bird flight, we have to understand aerodynamics; only then does the structure of feathers and the different shapes of bird's wings make sense. David Marr - Vision, 1982.*

1. Introduction

The grid cell, located within the rodent entorhinal cortex (EC), was first discovered and named in 2005 and won the Nobel Prize in Physiology or Medicine in 2014 (Hafting et al., 2005). It is one of the key neural substrates for animals to achieve self-localization, displaying distinctive triangular patterns in space and tiling the entire environment (Fig. 1A). Grid codes are not only the basis of spatial memory, but also closely associated with a variety of diseases, with multiple studies reporting their functional degradation in several specific groups, including mice with AD (Ying et al., 2022), young carriers of the AD high-risk gene apoe4 (Kunz et al., 2015), schizophrenia (Convertino et al., 2022), and the elderly (Stangl et al., 2018). Several questions are being intensively investigated by the neuroscience community: Why is the grid cell's tuning pattern in space a triangle lattice and not something else, such as a square lattice? How does the nervous system generate this tuning pattern? How does it exchange information with upstream and downstream brain regions, such as the hippocampus and prefrontal cortex? And what, if anything, is its unique role in humans compared to rodents? The answers to these questions may help decipher the neural mechanisms of spatial memory and its impairment in neurological and psychiatric diseases.

There has been a wealth of progress on grid cells in rodents, including their modular organization in the EC and the characteristics of their interaction with the environment, see reviews (Ginosar et al., 2023; Moser et al., 2014; Rowland et al., 2016). We note that two other parallel lines of related research have been emerging and converging in the last decade. One route is a series of experimental studies related to human grid codes, which contributes two unique points: It extends the distribution of grid codes in the brain to multiple regions within the DMN network; and it describes that grid codes are involved in multiple non-physical spaces. The other route is the proposal of a series of cognitive computational models that attempt to answer the cognitive functions of grid codes and serve as theoretical explanations for the diverse results of human cognitive experiments in route one. These two routes are complementary and mutually reinforcing, suggesting that human grid codes may constitute one of the basic neural modes involved in a wide range of higher cognitive functions. We think it is a good time to integrate this topic, to review the important work that makes up the two lines, and to inspire a picture of future research.

This review is structured as follows: First, we review key findings on grid cells in rodents, providing relevant background knowledge. Since these findings have been extensively described before (Ginosar et al., 2023; Moser et al., 2014; Rowland et al., 2016), this section is relatively brief. Second, we shift our focus from animal to human studies (Fig. 2). We summarise the experimental research on human grid codes into three categories, namely navigation in physical space, navigation in non-physical space, and oscillatory features of distributed grid codes in

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the brain. Third, we turn our attention to cognitive computational models of grid codes. These models follow different principle assumptions but go in the same direction, revealing the superiority of the triangular tuning pattern and the mechanisms of how the pattern emerges from neural networks (Fig. 3). Finally, we briefly describe the clinical translation of grid codes and their inspiration for AI and give directions for future research.

2. Grid cells in rodents

Three parameters have been proposed to characterize the firing pattern of a grid cell in the environment, namely grid scale, grid orientation, and grid phase (Fig. 1B). Grid scale refers to the distance between two adjacent grid fields, i.e., the length of the sides of a triangle. Grid orientation refers to the relative direction of the firing pattern with regard to environmental axes. Grid orientation is mainly affected by environmental cues, especially the geometry. Grid phase describes the specific position coordinates of the grid field in the environment. The anatomical organization of the grid cell in the EC has a certain regularity. Anatomically adjacent grid cells usually exhibit a similar grid scale as well as grid orientation, whereas the grid phase varies (Fig. 1C) (Gu et al., 2018; Stensola et al., 2012). Clusters of these cells are termed to comprise a functional module. Multiple cells from the same module provide complete coverage of the entire environment (Fig. 1C) (Hafting et al., 2005). Grid scale gradually increases along the dorsoventral axis of the EC, i.e., there is a gradient characteristic of grid modules. The ratio of grid scale between modules is constant, approximately 1.4 (Stensola et al., 2012). Recent experiments have found that gradients widely exist in the brain, not just limited to spatial organization, suggesting that it may serve as a general computational mechanism (Wang, 2022, 2020; Wolff et al., 2022).

Grid cells interact with a variety of other spatial signals (Rowland et al., 2016). There is a rich interaction between the grid cell and the boundary. For example, in square enclosures, most grid cells have a convergent grid orientation of about 8 degrees (Krupic et al., 2015; Stensola et al., 2015), which is hypothesized to be advantageous for encoding space (Chen et al., 2018b). This phenomenon has also been confirmed in humans (Julian et al., 2018). Grid patterns exhibit slight

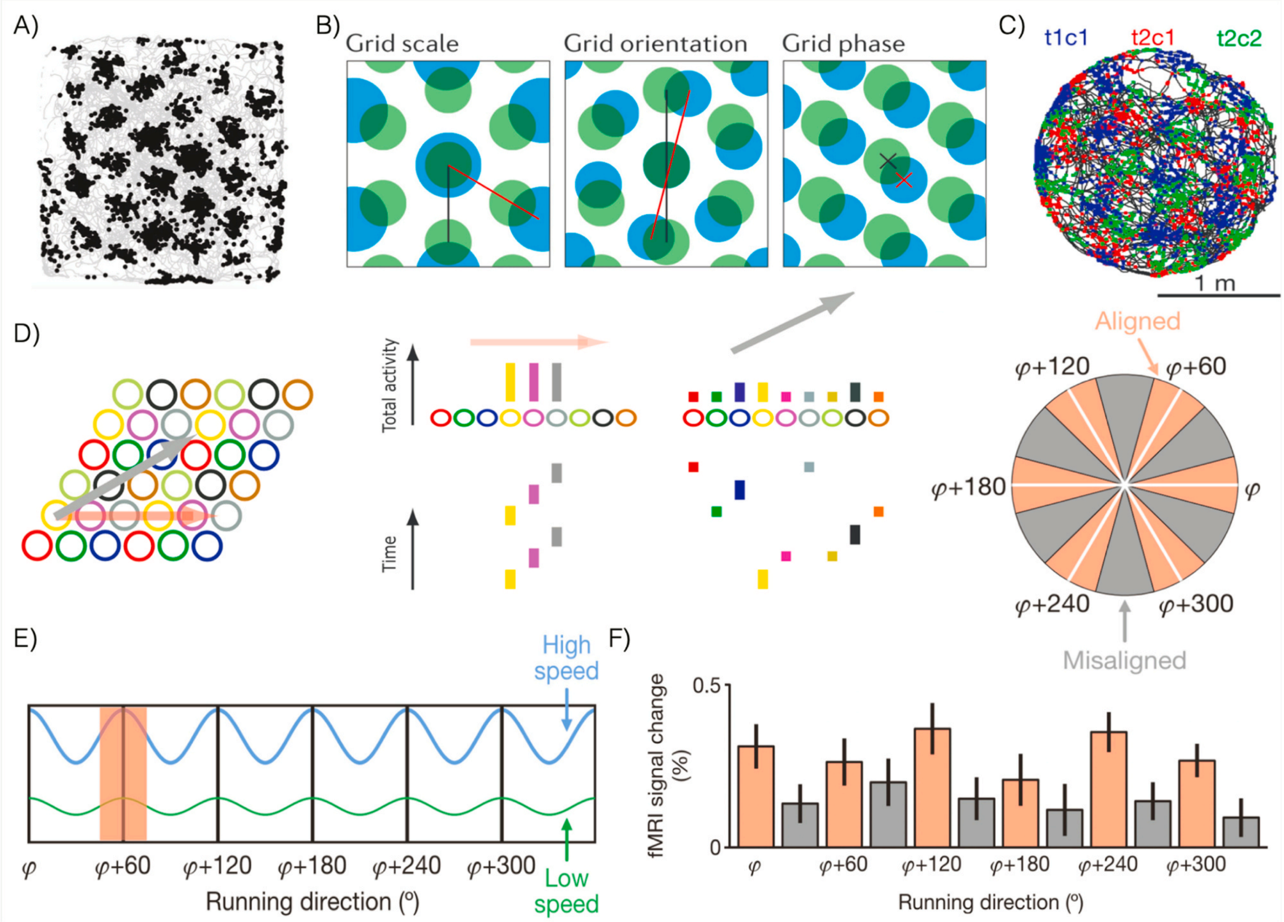


Fig. 1. Properties of grid cells and six-fold modulation. (A) Example grid cell recorded in a square environment. The trajectory of a rat is shown as the grey trace and spikes are shown as black dots. (B) Schematic of two grid cell firing (shown in blue and green), illustrating the differences between grid scale, grid orientation, and grid phase. (C) Grids of three cells, each with a separate color. The three lattices are spatially shifted with each other. These cells are located close to each other in the EC. (D) left: schematic of nine grid cells that consist of one module. The centers of firing fields are shown as open circles with different colors referring to different cells. Middle: the spike number of each cell is indicated by the height of the bars (running through the field center generates twice as many spikes as running through the edge). A run aligned with the grid orientation(red arrow) activates fewer different cells (3 cells shown in this illustration) than a run of the same length aligned at 30° to the grid (grey arrow; 9 cells shown). However, aligned runs have a higher mean activity (see bars) since cells are re-activated more frequently (see bars below, indicating the time course of activation of cells encountered during aligned and misaligned runs). Right: schematic of running directions aligned (red) and misaligned (grey) with the grid. (E) Left: a sinusoidal modulation of brain signal by running direction with six-fold rotational symmetry is predicted because of the constant grid orientation across cells, and a stronger effect for faster (blue) than slower (green) runs. Right: the real data from the human navigation task, which shows the average fMRI signal of all voxels in the EC for all directions of aligned (red) and misaligned (grey) fast runs. Panel A-B adapted from (Moser et al., 2014). Panel C adapted from (Hafting et al., 2005). Panel D-F adapted from (Doeller et al., 2010).

spatial distortions and are most accurate at the edges of the space (Hägglund et al., 2019). As a rat runs across an open arena, spiking errors of the grid cell accumulates since last encountering a boundary, resulting in drift in the grid pattern, and interactions with boundaries yield error correction(Hardcastle et al., 2015). These studies suggest that grid codes receive input from border cells, calibrating the encoding of location. The cue richness of the environment influences grid cell activity (Ulsaker-Janke et al., 2023), and the grid pattern is severely distorted in non-rectangular (e.g., trapezoidal) environments (Krupic et al., 2015), which is assumed to be related to humans' poorer spatial memory in such environments (Bellmund et al., 2019). Further studies are needed to determine how grid cells encode space in complex and polar environments. Grid cells are also related to directional signals. The anterior thalamic nuclei are known to contain head direction (HD) cells (Hulse and Jayaraman, 2020). Inactivated or lesioned anterior thalamic nuclei significantly disrupted the grid (Winter et al., 2015). A recent study reported that individual firing fields of grid cells are tuned to multiple head directions(Gerlei et al., 2020), which may help downstream computations by decorrelating different points of view from the same location. These results suggest that the HD signal is necessary for the generation and function of grid cell activity.

Reward and goals are fundamental elements of spatial navigation and are closely related to grid cell (Nyberg et al., 2022; Sosa and Giocomo, 2021). Two studies reported grid fields moved toward goal location and improved positional decoding near reward, demonstrating that grid cells participate in mnemonic goal coding(Boccara et al., 2019; Butler et al., 2019). Similar to place cells, grid cells also replay the sequence of firing along a spatial trajectory (Ólafsdóttir et al., 2016), and their activities during sleep are shaped by modular organization. Spike-time correlations in sleep are preserved between grid cells that have adjacent grid phases from the same modules, but this correlation is weak across modules, suggesting that grid modules function as independent networks (Gardner et al., 2019; Trettel et al., 2019). A recent paper uses the concept of topology in mathematics to reveal their cluster activity characteristics(Gardner et al., 2022), which is considered one of the promising directions for future neuroscience research(Kanter et al., 2022). Some of the features discovered above have been validated in humans, suggesting cross-species conservation. Next, we turn our attention to human grid studies.

3. Grids in physical space: from animals to humans

In 2013, a virtual navigation task study in neurosurgical patients described the first direct recordings of grid cells in the human brain. Cells in the EC and cingulate cortex exhibiting grid-like firing patterns were identified (Jacobs et al., 2013), suggesting that humans rely on homologous spatial coding schemes as rodents, which was replicated in another single-cell recording study (Nadasdy et al., 2017). Before this, in 2010, a seminal paper described a six-fold modulation of BOLD signals in the EC depending on the direction of movement when humans performed a virtual navigation task, which was interpreted as a network-level proxy of grid cells, although it was an indirect reflection of grid signals (Doeller et al., 2010). Recent computational models have proposed several mechanisms to explain in detail how such macroscopic signal emerge from the populating activity of grid cells (Khalid et al., 2022; Kunz et al., 2019). Here, we briefly describe the simplest one,

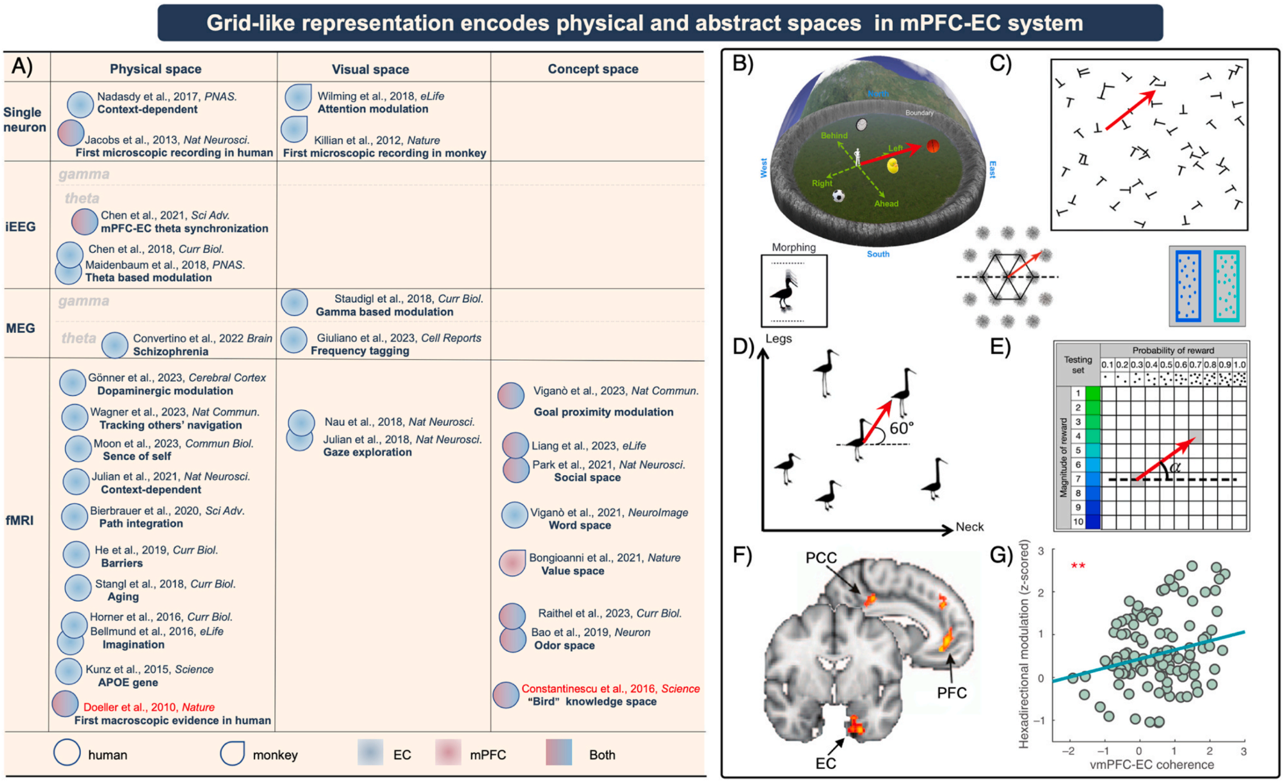


Fig. 2. The grid codes in multiple task spaces and brain regions. (A) Grid codes in the primate brain across multiple cognitive spaces and signal modalities. (B-E) Grid codes in different tasks. The red arrow indicates the running direction in the corresponding task space. (B) Typical experiment paradigms of human virtual navigation, in which subjects learn and recall the locations of several objects. (C) Typical experiment paradigms of human visual exploration, in which subjects find a different letter. (D) Birds space and morphing task(see main text for details). (E) Value space and decision-making tasks (see main text for details). (F) The hexadirectional modulation occurs across the human default mode network, including EC, mPFC, and PCC. This network effect is robust, repeated by two original studies focusing on physical space and abstract space, highlighted in red in (A). (G) Inter-regional coordination of grid codes between mPFC-EC via theta coherence. EC, entorhinal cortex; mPFC, medial prefrontal cortex; PCC, posterior cingulate cortex. Panel F adapted from (Constantinescu et al., 2016). Panel G adapted from (Chen et al., 2021).

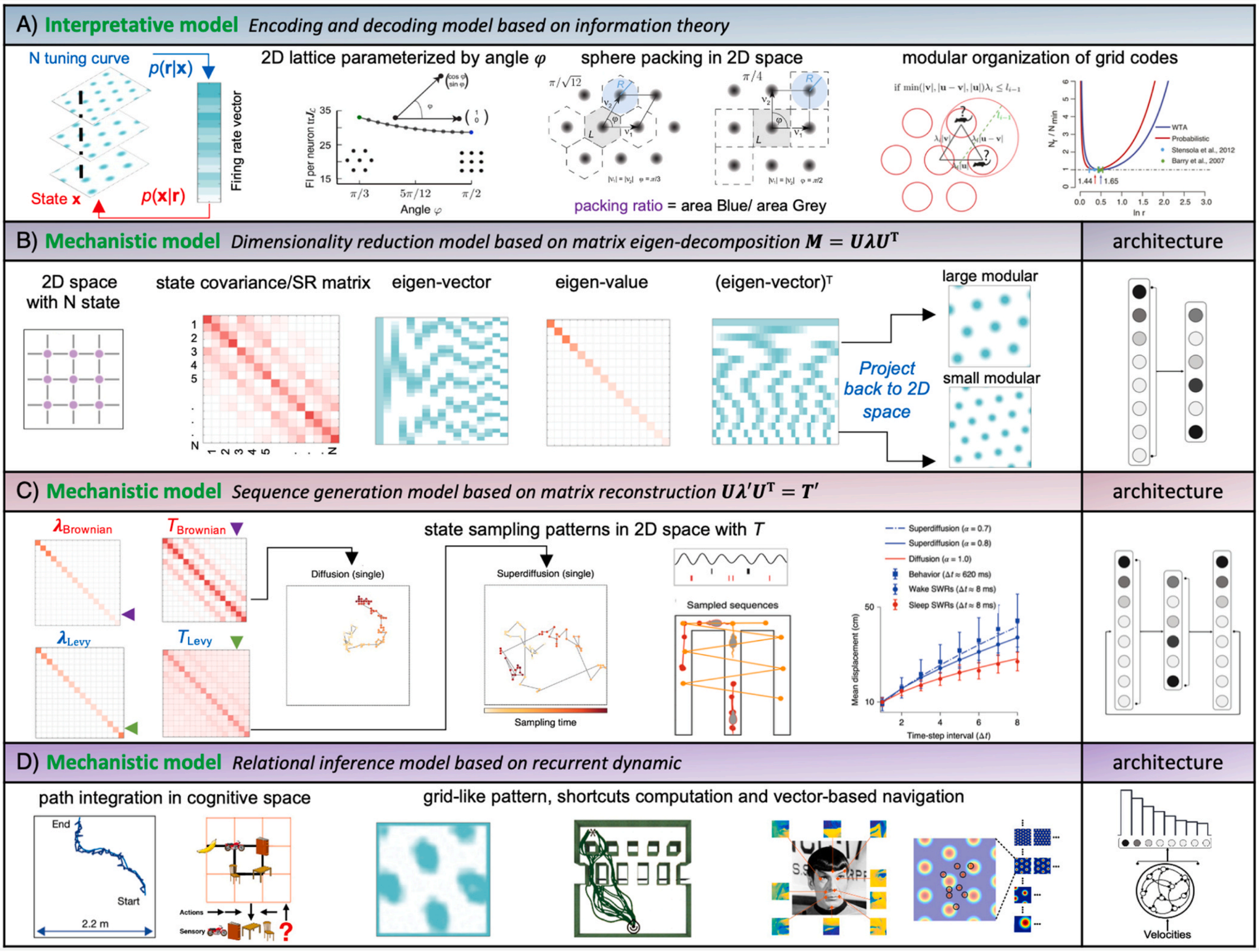


Fig. 3. Cognitive computational models of grid codes. (A) Encoding and decoding models. State x is encoded by r according to 2D-tuning curves. The inverse process is to decode x using r. A triangular lattice has the largest Fisher information, optimal packing ratio, and thus the smallest decoding error. To eliminate ambiguity, the diameter of grid fields from the next module (large red circles) must be smaller than the grid scale of the preceding module (distance between two small red circles). The optimal scale ratio is close to the experimental data. Adapted from (Mathis et al., 2015; Wei et al., 2015). (B) Dimensionality reduction models. Given N states (place cells), eigenvectors of the place codes' covariance matrix or SR matrix exhibit grid-like patterns when projected back into 2D space. Eigenvectors of different eigenvalues correspond to the modular organization of grids. (C) Sequence generation model. Increasing weights of larger eigenvalues induces a preference for local transitions (purple arrow). The sampling sequence resembles diffusion-like Brownian motion. Increasing weights of smaller eigenvalues induces a preference for remote transitions (green arrow). The sampling sequence resembles super-diffusion Levy motion. A third mode called "minimum autocorrelation sampling" resembles cycling representations of the left/right track. The pattern of place sequence replay during wakefulness and sleep in experiments and models. Adapted from (McNamee et al., 2021). (D) Relational inference models. Both physical and abstract space for path integration tasks require relational inference. Activities of RNN units exhibit grid-like patterns in 2D space. Neural networks with grid codes can perform shortcut and one-shot face recognition based on vector navigation. Adapted from (Banino et al., 2018; Bicanski and Burgess, 2019; Whittington et al., 2020).

which originated in the 2010 seminal study.

The key factor is that the grid orientation of the grids relative to the environment appears to be constant across cells and thus creates systematic variation in neural population dynamics for runs aligned or misaligned with the main axes of the grids (Fig. 1D). The authors predicted that the brain activity should exhibit a six-fold rotational symmetry modulated by running direction (Fig. 1E). They found the strong effect in the EC (Fig. 1F), which is termed grid-like representation. In addition, similar effects were found in the medial prefrontal cortex (mPFC) and posterior cingulate cortex (PCC). This study demonstrates the ability to infer cellular representations in humans using non-invasive fMRI, promoting a coherent understanding of spatial behavior at the neural and systems levels. This landmark work opened the door for a series of subsequent human grid code studies. Many studies replicated this effect across multiple cognitive spaces, signal modalities, and distributed brain regions (Fig. 2A).

In this section, we review human studies about navigation in physical space. These studies mainly use VR-based object-location memory tasks, in which participants collected and replaced objects found within the arena, similar to the water maze in rodents (Fig. 2B). Two studies explored whether the human grid is involved in spatial imagery. Subjects imagine moving to the locations of each object before actively navigating to get it. Grid-like representation is present in periods of both active navigation and imagination (Bellmund et al., 2016; Horner et al., 2016), suggesting that grid codes are utilized during imagined movements, potentially underpinning our ability to simulate routes mentally. Three studies explored the effects of environmental cues and rewards on grid codes. Grid-like representations were abolished when environments were compartmentalized by barriers (He and Brown, 2019). This result is similar to that of rat's grid cells in the hair maze (Derdikman et al., 2009), suggesting a diversity of grid codes in fragmented environments. Human grid-like representations showed realignment (i.e., different grid orientations) between two distinct environments (Julian and Doeller, 2021), which is termed remapping in rodent literacy (Jun et al., 2020). In a third ambiguous context, trial-by-trial realignment could predict context-dependent behavior. A recent study found that levodopa suppresses grid-like activity and impairs spatial learning in novel environments in healthy young adults (Gönner et al., 2023), suggesting that dopamine signaling may play a role in shaping ongoing spatial representations. Two papers examined the effect of the sense of self and others on grid codes. Grid-like representation is decreased when a body-shaped avatar is seen by participants (Moon et al., 2022). Meanwhile, grid codes can track other individuals navigating through space (Wagner et al., 2023), thus contributing to socio-spatial navigation, which is a flourishing subfield in rat and bat research (Geva-Sagiv et al., 2015; Omer et al., 2018).

Two other studies found that grid-like representations are reduced in young carriers of the AD high-risk gene apoe4 and that this representation predicts behavioral performance during path integration tasks (Bierbrauer et al., 2020; Kunz et al., 2015). Compromised grid-like representations were also observed in healthy aging and associated with larger path integration errors(Stangl et al., 2018). Distance estimation during human path integration is sensitive to geometric deformations of a familiar environment and this bias can be predicted by the rescaling properties of grid cells (Chen et al., 2015). These studies support the contribution of grid codes to path integration, see review (Segen et al., 2021).

4. Grid in non-physical space: from visual to concept

We process a variety of information in our daily lives, not just limited to navigating in physical space (Box 2). For example, during visual exploration, we locate the position of objects in visual space and calculate distances. In this process, the saccade generates trajectories and can be tracked by an eye-tracker. In socialization, we can feel close to or far from people, i.e., have a "distance" from others. A pioneering study found that hippocampal formation tracks ongoing changes in social relationships using functional neuroimaging (Tavares et al., 2015). In this study, participants engaged in a role-playing game in which they were to find a new home and a job through interactions with virtual cartoon characters. Participants who reported better social skills showed stronger covariance between hippocampal activity and ’’movement’’ through ’’social space.’’ More generally, the encoding and retrieval of associative memories between different items can be viewed as navigating and searching in a concept space. Representations of some items are more similar, i.e., closer proximity in this space. Thus, free recall can be seen as wandering through that space and generating trajectories. Recently, the method of word embeddings has been used to measure distance in this space (Kahana, 2020; Nour et al., 2023; Solomon et al., 2019). Supervised, we exhibit similar behavioral characteristics in these different spaces, which are thought to be related to optimal search strategies (Zaburdaev et al., 2015) (see Box 2 and the section on cognitive computational models for levy flight).

Are grid cells involved in the encoding of these non-physical spaces?

Box 1
Glossary.

Action transition matrix $P(s,a,s')$: the probability of a direct transition from state s to s' under action/relationship a.

Grid cell: cell with multiple firing fields at the vertices of equilateral triangles tiling a 2D space.

Cognitive computational model: computational program performing cognitive tasks to explain neuronal or behavioral data.

Cognitive space: mental models in which sets of relationships describe the transitions between objects and events based on their positions in an internal map/graph.

Efficient coding: a hypothesis that stimuli should be represented in the least redundant code to best make use of limited resources and that the number of spikes/neurons needed to transmit a given signal is minimized.

Feedforward network: network with only unidirectional connections. Information flows in a forward direction—from input nodes through hidden nodes to output nodes.

Internally generated sequence: an ordered sequence of neural activity generated based on internal dynamics that reflect past/future behavioral sequences.

Interpretative model: addresses why the brain operates as it does. For example, why do triangular tuning pattern but not squares emerge?

Mechanistic model: addresses how the brain operates based on its anatomy and physiology. For example, how does the triangular tuning pattern arise from neural networks?

Modular organization of grid cell: grid scales are grouped into 5–7 discrete modules such that the cells in each module share similar scales. The scale ratio of two adjacent modules is ~1.4.

Policy$\pi(a|s)$: the probability of taking an action a at state s. For example, in a lattice world with up, down, left, and right actions, a random policy is to choose one of these actions with a probability of 0.25.

Policy transition matrix $T(s,s')$: the one-step expected transition probability of state s to s' under a given policy. $T(s,s') = \sum_a \pi(a|s)P(s,a,s')$.

Predictive coding: a hypothesis that the brain constructs and updates mental models of the world based on prediction errors from comparisons between bottom-up sensory inputs and top-down prior predictions.

Relational inference: A process of generating new relationships based on manipulation of known relationships.

Recurrent neural network: connections between nodes can form a loop, allowing output from nodes as input to the same nodes. The loop may generate rich temporal dynamics.

Sphere packing: arranging non-overlapping spheres within a space as tightly as possible.

Successor representation $M(s,s')$: Matrix of all direct and indirect transitions between states under a given policy weighted by a discount factorγ. $M(s,s') = \sum_{t=0}^{\infty}\gamma^t T(s,s')^t$

Box 2

Brownian walks, Levy walks, and information search efficiency.

Random walks are basic concepts in physics and are widely used to model diffusion processes. Two classic random walks, i.e.*, Brownian walks and Levy walks, are receiving attention in cognitive neuroscience to describe behavioral and neural patterns. The difference between the two is the distribution of diffusion step sizes. Brownian walks follow a Gaussian distribution, and Levy walks have heavy tails. Thus, Levy walks represent a super-diffusion process that can travel farther from its starting state than Brownian walks within the same duration.*

Here we focus on the links of random walks to navigation in cognitive spaces. In physical space, ecological studies have found that the foraging trajectory patterns of many animals, from insects to mammals, are related to Levy walks. Similar patterns were observed in human behavior of individual mobility across geographic scales. In visual space, trajectories of saccade exploration of pictures are also consistent with Levy's walks. In memory space, the duration between consecutively retrieved items in a free memory retrieval task corresponds well with Levy walks [108]. Brownian walks and Levy walks are also present in neural activity. The dynamics of neural activation in resting-state fMRI and gamma activity of local field potentials can be modeled by Levy walks. The replay trajectories of hippocampal place cells during wakefulness resemble a Levy-like super-diffusion process, while they are closer to more locally constrained Brownian diffusion processes during sleep. Studies are starting to investigate the mechanisms that generate Levy walks in neural circuits], and these mechanisms may underlie the same macroscopic Levy walk behavioral patterns in different cognitive spaces. Why are Levy walks ubiquitous in many domains? They are related to a concept called exploration efficiency in the foraging literature, which is defined as the fraction of environmental states visited relative to the cumulative distance traversed. Levy walks with long jumps provide a more efficient strategy to search random distributions in unknown environments compared to Brownian walks, which tend to oversample local regions.

This question is hard to investigate in rodents, especially in conceptual space. Two fMRI papers and two MEG papers analyzed grid codes in visual space. The typical experimental paradigm is that subjects explore pictures, for example, finding the letter L in a pile of letters T (Fig. 2C), and recording the trajectories of eye movements. BOLD responses in the EC exhibited the six-fold periodic modulation by gaze-movement direction (Nau et al., 2018b). Furthermore, the grid orientation was determined by the boundary (Julian et al., 2018), which is similar to rodents. Grid-like representation was also observed in human high-frequency activity, both in MEG and iEEG recordings (Staudigl et al., 2018). A recent study reported that movements of covert attention can elicit grid-like representation using frequency tagging in humans (Giari et al., 2023). Monkey single-cell recording study directly recorded grid cells in EC during the monkeys' exploration of pictures (Killian et al., 2012; Wilming et al., 2018). All these results indicate that the human EC represents visual space using grids, suggesting that vision and navigation share several key components to solve overlapping computational challenges (Nau et al., 2018a).

A study published in 2016 extends grid codes into the abstract conceptual space of knowledge (Constantinescu et al., 2016). The stimulus material was a set of cartoon pictures of birds. Notably, the birds had different neck and leg lengths, forming different concepts such as ducks and swans. Thus bird knowledge can be organized in a two-dimensional space, with one dimension being the length of the neck and the other the length of the legs (Fig. 2D). However, the experiment did not explicitly ask subjects to do so, and subjects mentioned that they did not organize the birds in this way after the experiment. The subject's task was instead to watch the bird's morphing and continue to imagine it. In a single trial, the pre-morphing and post-morphing birds formed a straight-line trajectory in this latent space, thus defining a "direction of motion". BOLD signal in mPFC and EC show a six-fold rotation symmetry modulation of the direction of motion. The authors therefore concluded that we can organize conceptual knowledge in grid codes. This outstanding study demonstrated the potential uniqueness of human grids, such as participation in imagination, reasoning, etc., and inspired subsequent research on other abstract spaces.

Two studies created a two-dimensional odor space composed purely of odor stimuli to mimic how people encounter smells in a natural environment (Bao et al., 2019; Raithel et al., 2023). During navigation, fMRI responses in EC, mPFC, and posterior piriform cortex take the form of grid-like representations and entorhinal grid strength scaled with behavioral performance across subjects. Another study taught humans the meaning of novel words as arbitrary labels for a set of audio-visual objects varying orthogonally in size and sound and similarly observed grid-like representations (Viganò et al., 2021). Similar results were found in the field of social neuroscience. Two studies found that inferences on a multidimensional social hierarchy recruited grid-like codes (Park et al., 2021; Zilu et al., 2023). Participants engaged in a role-playing game in which they learn the rank of individuals organized into a 2D social hierarchy defined by competence and popularity. One recent paper reported the grid-like signal changed as a function of goal proximity, being relatively weaker for trajectories that were far apart from goal locations and stronger close to the goal during conceptual navigation in humans (Viganò et al., 2023). The above studies found grid codes in multiple cognitive spaces, however, causal manipulation was lacking.

In 2021, a monkey study took a step forward. The study trained monkeys to complete a classical decision-making experiment in which the stimulus was a pattern composed of dots (Bongioanni et al., 2021). Dots varied in reward magnitude cued by color and in reward probability cued by the number (Fig. 2E). Monkeys had to learn to integrate these two dimensions to make optimal choices. Clearly, the stimuli constitute a two-dimensional value space, which is never explicitly shown to the monkey. Any two stimuli can form a linear trajectory and produce a "direction of motion". As expected, an mPFC grid code was observed to integrate this value space. Meanwhile, the authors examined the effect of focal mPFC disruption on choice behavior with transcranial ultrasound stimulation. This operation impaired behavioral performance, suggesting that grid codes are indeed used to integrate two dimensions.

5. Coordination of grid codes in distributed brain regions

We summarized the experimental literature on grid codes in humans (and monkeys) to date. Two features that distinguish them from rodents emerge clearly. One is that grid codes are identified in multiple non-physical spaces. A rat study reported that grid cells can respond to different sound frequencies (Aronov et al., 2017). However, whether they are activated in more complex two-dimensional abstract spaces is still unknown (O'Keefe and Krupic, 2021). Another feature is that multiple fMRI studies, particularly those related to conceptual space, found sixfold-rotation modulation in the mPFC as well (which also includes the PCC but is less stable than the mPFC) (Fig. 2F), suggesting that grids in this region may participate in more abstract processing. To the best of our knowledge, no grid cells were reported in the mPFC of rodents, which may be explained by the fact that they are dominated by navigation of physical space.

How do grid codes in EC and mPFC communicate? It is assumed that in general, the brain's communication is realized through neural oscillations (Buzsáki and Vöröslakos, 2023; György Buzsáki and Moser, 2013; Wang, 2010). In rodents, grid cells are thought to rely on theta oscillations (Brandon et al., 2011; Koenig et al., 2011). Recently, three studies investigated oscillatory features of grid codes using invasive EEG recordings in epilepsy patients while they performed spatial navigation tasks. One study reported that the power of entorhinal theta oscillations showed a six-fold modulation and the strength of this modulation correlated with spatial memory performance (Maidenbaum et al., 2018). Another study found similar results and additionally described the spatio-temporal dynamics of grid-like representations (Chen et al., 2018a). In the temporal domain, the modulation was stronger during later stages of the experiment, i.e. stabilized over the course of the navigation. In the spatial domain, the modulation was stronger in the boundary region, showing sensitivity to the environmental boundary. One study found a decrease in EC theta activity during movement onset in schizophrenia, accompanied by a decline in grid-like representations (Convertino et al., 2022). A study analyzed subjects with both mPFC and EC electrodes and described grid-like representation based on mPFC theta oscillations. Grid orientations of mPFC and EC were similar and related to the coherence of the two regions (Fig. 2G), revealing that theta oscillations coordinate grid information in the mPFC-EC system (Chen et al., 2021).

An important function of mPFC-related theta is cognitive control (Cavanagh and Frank, 2014; Eichenbaum, 2017; Helfrich and Knight, 2016), which is defined as the ability to guide behavior toward achieving internally maintained goals. A great deal of mPFC-related theta research comes from EEG, which is referred to as frontal midline theta. Converging evidence suggests that frontal midline theta can be source-localized to areas 32 of mPFC (Cavanagh and Frank, 2014), where grid codes were described (Bongioanni et al., 2021; Chen et al., 2021; Constantinescu et al., 2016; Doeller et al., 2010). Cognitive control requires phase synchronization of theta oscillations between mPFC and remote brain areas to select context-specific representations (Eichenbaum, 2017; Place et al., 2016). Indeed, an fMRI study found that human grid-like representations were realigned between two environments (Julian and Doeller, 2021), and we thus speculate that this function is accomplished by the mPFC through theta synchronization with the EC, which needs to be supported by future studies.

6. Cognitive computational models of grid codes

The above studies have found that grid representations are involved in "navigation" of both physical and non-physical spaces. This naturally raises the fundamental question–what function do these distributed grids play across multiple cognitive spaces? Besides these empirical studies, another research line along cognitive computational models of grid codes also developed rapidly in the last decade. These models focus on three central aspects of grid codes: Why does triangular lattice tuning exist? Why do grid cell systems constitute discrete modules? How does the nervous system generate the pattern? In this section, we discuss these questions. Before diving into these models, we briefly introduce the concept of navigation and reinforcement learning.

The concept of navigation has recently undergone a shift and it can be defined as an active process of information sampling and searching in any space (Behrens et al., 2018; Hunt et al., 2021; Whittington et al., 2022). Goal finding in the physical world, scanning over pictures, and free recall in word space can all be viewed as navigation processes. Similar behavioral patterns are exhibited in all these spaces (Zaburdaev et al., 2015). This process has been formalized by reinforcement learning theory (Behrens et al., 2018; Wise et al., 2023). The basic elements of reinforcement learning are an agent, actions, and an environment. The environment is defined by states and the transitions between them, called action transition matrix P. The goal of an agent is to learn the policy that maximizes long-term rewards. Under the guidance of this policy, the agent samples a sequence of states and identifies the statistical features governing the transition between states, called policy transition matrix T. Since the number of real-world task states is huge, we must have effective ways to compress states and identify more abstract (i.e., generalizable) properties of their relationships (Niv, 2019; Radulescu et al., 2021). Compression of states involves segmenting our continuous stream of experience into meaningful units (Buzsáki and Tingley, 2018; György Buzsáki and Moser, 2013). For example, we are good at segmenting and grouping features from visual space, which can be done by sampling several saccades in a second. We are also good at organizing information from the environment hierarchically, for example, by grouping closely connected streets into blocks (i.e., hidden states) (Balaguer et al., 2016; Collin et al., 2015; Farzanfar et al., 2022). It has been proposed that grid codes are necessary for compressing and inferring hidden states in cognitive spaces and thus serve the goals of efficient information searching and knowledge generalization based on the above empirical studies.

Based on these insights, several influential cognitive computational models of grid codes have been proposed. We divide these models into four categories (Fig. 3). However, these models are not mutually exclusive but closely linked. Guided by the principles of efficient coding and predictive coding, these models argue that grid representations are involved in various operations in cognitive space, such as low-dimensionality embedding, modulating internally generated sequences, and relational inference.

6.1. Encoding and decoding models based on information theory

Several interpretative models have studied the optimal representation of states guided by accounts of efficient coding from information theory (Mathis et al., 2012; Stemmler et al., 2015; Wei et al., 2015). Suppose there are N neurons with specific tuning curves. Each state is encoded by an N-dimensional firing rate vector r, the elements of which are obtained through the tuning curves with added noise. Through this encoding, states in cognitive space are mapped onto neural space. Decoding then refers to estimating the state inversely from r (Fig. 3A). Assuming that the neurons are independent, it can be shown that tuning curves that are organized in a triangular lattice pattern across state space minimize the decoding error derived from Fisher information (Mathis et al., 2012; Wei et al., 2015).

Intuitively, this can be related to the sphere packing in mathematics (Mathis et al., 2015). For example, consider storing as many oranges as possible in a given 2D space. Arranging them such that their centers are positioned at the vertices of equilateral triangles minimizes the gaps and thus maximizes packing density (Fig. 3A). Thus, for each given neuron, organizing its spike at the vertices of equilateral triangles tiling a state space optimizes the coverage of this space (i.e., leaves minimal "gaps" in which no firing occurs) and a combination of neurons with randomly distributed firing locations in this space would provide information about all locations.

However, the information provided by spatially periodic firing fields is equivocal: When a given neuron fires, we can only infer our location at one of these firing fields, without any chance to disentangle between them. This confusion can be eliminated by a modular organization of grid coding schemes in which the joint information from neurons corresponding to smaller and larger modules provides unequivocal information about one given location, see Box 3 for detail (Stemmler et al., 2015). Several modeling works predict the optimal ratio between modules, which is close to the experiment data (i.e., about 1.4) (Stemmler et al., 2015; Wei et al., 2015). Some studies extend this framework to discuss the optimal number of cells in different modules (Mosheiff et al., 2017) and the optimal tuning curves of 3D grid cells (Ginosar et al., 2021; Mathis et al., 2015; Stella and Treves, 2015).

6.2. Dimensionality reduction models based on eigen-decomposition

The studies reviewed in this part and the next have features of both

Box 3
Nested coding framework of grid cell.

Since the discovery of the modular organization of grid cells, computational neuroscientists have explored its advantage with great enthusiasm, and they have referred to this coding framework as "Nested coding framework". Here, we use a 1D track as an example to help build an intuitive explanation of why this framework could help infer spatial location from spatially periodic firing fields.

Consider coding N positions in a 1D track with neurons. We assume the system has 20 cells with periodic fire fields and consists of four modules (M1, M2, M3, M4). Every module contains five cells represented by different colors, i.e., *blue, red, yellow, purple, and green. The period of each module is denoted by scale 1, scale 2, scale 3, and scale 4. If only cells from M1 are used, the precision could be high, since the narrow Gaussian field. However, because the field of the same cell is repeated five times, the ambiguity is also high. For example, consider coding position 25, indicated by the black line. The blue cell has the highest firing rate here, after the winner-take-all rule, by which it encodes the location 25 (for simplicity, we use the winner-take-all rule; the population vector rule yields similar results, see (*Wei et al., 2015; Mathis et al., 2015*)). However, when observing the blue cell's activation, we infer that we could be at positions 25, 50, 75, or 100. That is, when a given neuron fires, we can only infer our location at one of these firing fields, without any chance to disentangle between them. Thus position coding with small-scale modules is high precision but also high ambiguity. If only cells from M4 are used, for example, again to code location 25, the red cell has the highest activation here and encodes this location. Note that the coding precision is low due to the wide Gaussian field and we can only infer the position located, maybe, between range [10–40]. However, the ambiguity is low because the scale is beyond the range of the track. Thus position coding with large-scale modules that exceed the environmental boundary is low precision but high ambiguity.*

Starting at the M4, one can gradually refine the position coding. As seen in the figure, by taking the intersection of the shaded portions of the different modules, we can accurately and uniquely determine position 25. The same idea can be easily extended to a 2D map, as studied by Mathis et al. (2012), Wei et al. (2015) *and* Mathis et al. (2015).

interpretative and mechanistic models and explain why triangular tuning curves emerge and how they arise from neural systems. Early models have proposed that grid cells in EC serve as input to the hippocampus to generate place cells (McNaughton et al., 2006). Several experiment studies reported conflicting results. Input from EC to hippocampus is necessary for place activity (Colgin et al., 2009; Fernández-Ruiz et al., 2021; Liu et al., 2023; Yamamoto and Tonegawa, 2017). When blocking hippocampus, however, grid activity disappeared(Bonnevie et al., 2013). Furthermore, the development of place cells precedes that of grid cells in rats (Bjerknes et al., 2014; Ulsaker-Janke et al., 2023). These

Box 4
Successor representation model.

To build an intuitive understanding of the successor representation (SR) model, we use the 1D track as an example. Consider seven place cells and a track with seven states/locations. The color circles in figure denote different states.

1. *Motivation for the model proposal.*

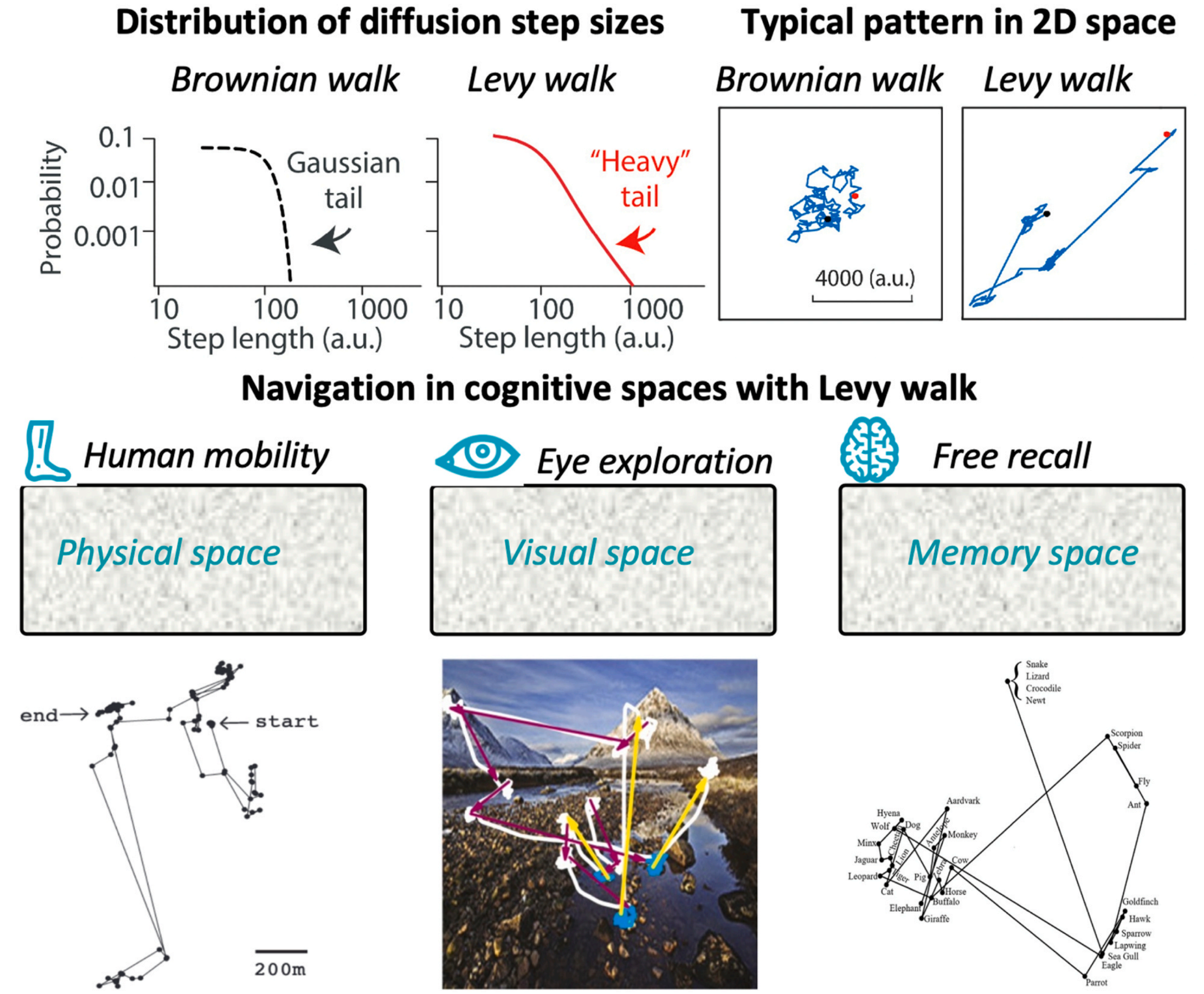
Traditionally, the firing pattern of place cells is explained by the "distance model" that has a Gaussian shape. That is to say, the activation of place cells is modulated by spatial distance and independent of the animal's behavioral strategy, i.e., *whether the animal explores the environment randomly or "always runs to the right". However, experimental data suggest that behavioral strategy influences the activity of place cells. When newly exposed to the environment, place cell activity is symmetrical. As the rat is trained to run repeatedly in a preferred direction, initially symmetric place cells (red) begin to skew (blue) opposite the direction of travel. The SR model proposes that the hippocampus learns a predictive map that encodes each state in terms of its successor states. SR argues that given the policy to explore the environment, the firing rate of cell j (encoding state j) in state i represents the expected probability of transition from i to j, defined as the weighted sum of all direct and indirect transitions from i to j (one step,two step,three step and so on). For example, cell 4's firing rate in S3 represents the expected probability of moving from S3 to S4. Since S3 is closer to S4 than S2, the transfer probability should be larger. In the case of a random strategy, the probability of S5 to S4 is the same as S2 to S4. Therefore, the firing field of cell 4 is a Gaussian function, the same as the distance model. However, if the animal always runs to the right, it only samples the experience of "transfers from S3 to S4" but not "transfers from S5 to S4". Thus firing field of cell 4 in S5 is 0——the symmetry is broken.*

2. *Successor matrix M and state value computing.*

The column ID of M represents the cells and the row ID represents the states. M(i,j) characterizes the firing rate of cell j in state i, which encodes the expected transfer probability from state i to state j. Under the random strategy, the M is a symmetric matrix. Under the "always run to the right" strategy, M is a triangular matrix. The column of M denotes the place field of one cell, e.g. *M(:,4) represents the field of cell 4 (firing rate of cell 4 in S1 to S7). The row of M denotes the firing rate vector at one state, e.g., M(4,:) represents the firing rate of cells 1–7 in S4 (transition probability from S4 to S1-S7). The benefit of SR is that animals can use it to compute state value quickly. For example, when the animal is at S4, by reading M(4,:) and the reward vector R (which may be encoded in the striatum), They can compute the value of S4 with the dot product of the two vectors. The intuitive explanation is like this: the value of a state depends on the probability that it will reach a rewarded state.*

3. *Relationship between eigenvectors of the SR and grid cells.*

Combining this idea with the SR, Stachenfeld et al. argued that grid fields reflect a low-dimensional eigendecomposition of the SR matrix M. The eigenvectors of the M of 1D track exhibit periodic tuning across a range of spatial scales reminiscent of grid cells. The larger the eigenvalue, the larger the spatial scale, reminiscent of the modules. The eigenvectors of the M of the 2D map exhibit hexagonal shapes (also see Fig. 3 *in the main text). In structured environments, planning can be achieved more efficiently by decomposing the task into subgoals, but the discovery of good subgoals is a difficult problem. The eigenvectors of the M of a structured environment can be used for subgoal discovery. As the figure shows, the eigenvectors with large eigenvalues partition the task space, with boundaries between the partitions producing useful subgoals. This suggests a role for grid cells in spatial planning and maybe a more general role for grid cells in hierarchical planning.*



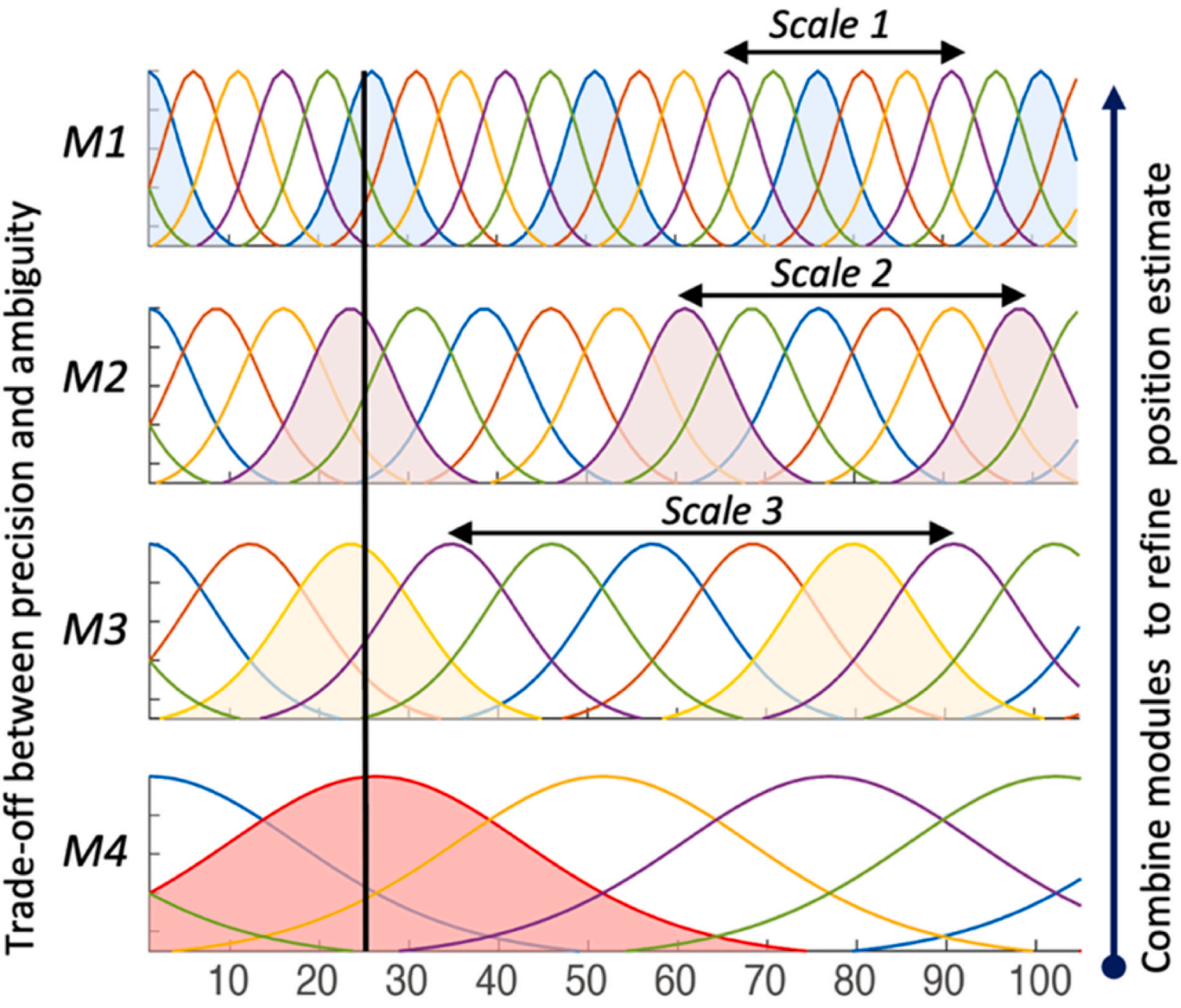
Box 2 Figure. Random walk in multiple cognitive spaces.

results prompted researchers to rethink their relationship (for a recent review, see Morris and Derdikman, 2023).

One theory argued that the function of grid codes may be to provide a low-dimensional embedding of cognitive space, with place codes providing a higher-dimensional, more explicit representation of this space (Behrens et al., 2018; Whittington et al., 2022). Specifically, one study proposes that the transformation of place-to-grid codes reflects a dimensionality reduction similar to PCA (Dordek et al., 2016). Under two constraints—non-negative decomposition and zero-mean activity of place codes, the eigenvectors of the covariance matrix of place codes have grid-like patterns when projected into 2D space (Fig. 3B). A two-layer feedforward network (mimicking connections from hippocampus to EC) with Hebbian synaptic learning provides a biologically plausible microcircuit that performs PCA. Inspired by this work, studies proposed different biological mechanisms to achieve these constraints, such as phase precession (Monsalve-Mercado and Leibold, 2017) and spike-rate adaptation (D'Albis and Kempter, 2017). With the additional constraint——the output neuron should capture the minimal variance of encoding neurons, a model gives a straightforward explanation of the experimental evidence of grid cells remapping under transformations of environmental cues (Anselmi et al., 2020). Recent rigorous mathematical analysis has unified these mechanisms (Sorscher et al., 2022).

The "successor representation" (SR) model based on the above work offered novel insights into place-grid codes by linking them to theories of predictive coding and reinforcement learning (Stachenfeld et al., 2017). The model argues that place codes provide predictive representation of future states in cognitive space, rather than representing states per se, see Box 4 for detail. The SR model unites the advantages of both model-free and model-based algorithms because the value can be computed faster than via model-based algorithms while allowing for a more flexible updating than via model-free algorithms(Gershman, 2018; Russek et al., 2017). Given a policy to explore the environment, SR supposes that the firing rate of cell j (encoding state j) in state i represents the expected probability of transition from i to j, defined as the weighted sum of all direct and indirect transitions from i to j. Grid codes encode a low-dimensional embedding of this predictive SR matrix M, that is, the eigenvector of M (Stachenfeld et al., 2017). M and the covariance matrix of place codes under random policies are mathematically equivalent. However, their cognitive explanations are very different. At any moment, the product of the place code vector (one row of M) and the reward vector can quickly compute the state value (Box 4). Because of their multiple modules, grid codes can be used for extracting multiscale structures during hierarchical planning (Stachenfeld et al., 2017). Recent empirical evidence at both the behavioral and neural levels is consistent with predictions from the SR model (Brunec and Momennejad, 2022; de Cothi et al., 2022; Garvert et al., 2023; Mattar and Daw, 2018).

For different physical spaces that we are faced with every day, we may represent compressed structural knowledge that is common to various environments via grid codes. These codes form a priori



Box 3 Figure. Nested coding framework of grid cell

templates that are used for rapid generalization when encountering new environments (Whittington et al., 2022). One model argues that the grid codes are default representations of SR, which in most cases, are eigenvectors of **M** under the random policy (Piray and Daw, 2021). During navigation, the brain combines prior representations from this default grid (maybe from mPFC)with representations of the current task grid (maybe from EC) to infer context and states.

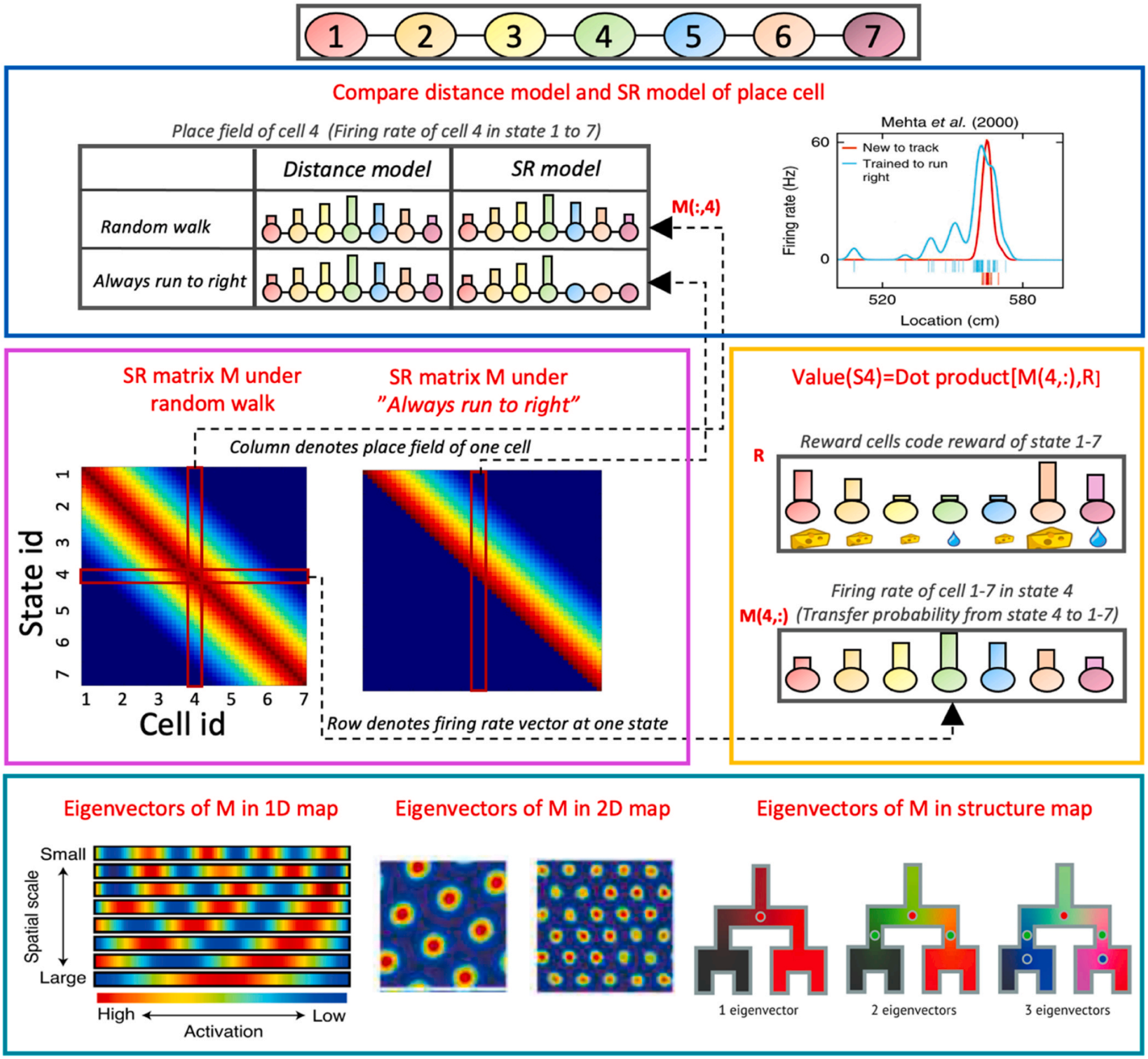
6.3. *Sequence generation model based on matrix reconstruction*

Recent studies assert that grid cells are important for the sequential firing of place cells (Yamamoto and Tonegawa, 2017). The sequential replay of place codes has multiple patterns in 2D space. It is closer to Brownian walks during sleep and Levy walks during waking (Pfeiffer and Foster, 2015; Stella et al., 2019) (Box 2). Do grid codes contribute to the generation of these patterns? A study addressed this question by assuming a model whereby grid cells serve the inverse operation of dimensionality reduction (McNamee et al., 2022, 2021). Mathematically, the transition matrix T can be reconstructed using matrix multiplication based on eigenvectors and eigenvalues (Fig. 3C). Cognitively, this indicates that grid codes can be used to infer transitions within cognitive spaces. Agents navigate space by multiplying the initial state vector with this reconstructed T iteratively to sample a sequence of states. Modulations on eigenvalues can generate diverse sequence patterns of place codes. By up-weighting large eigenvalues, the reconstructed T prefers nearby states and the sampled sequence is close to a Brownian walk, which reflects fundamental statistical structure and thus can be used during an offline period to help consolidate details of the world (Stella et al., 2019). By up-weighting small eigenvalues, the transfer probability to non-local states in T will increase, and the sequence will sample large jumps occasionally (Pfeiffer and Foster, 2013). The pattern is similar to a Levy walk and has higher exploration efficiency (Zaburdaev et al., 2015), which is useful for planning during online task periods (McNamee et al., 2021; Qi and Gong, 2022).

This model predicts that grid codes, especially different modules, are involved in hippocampal sequence generation, which will be a hot spot for future experiment research. The model also mentions a third mode that supports value computation called “minimum autocorrelation sampling” (Fig. 3C), which has been experimentally verified recently (Kay et al., 2020).

6.4. *Relational inference models based on recurrent dynamics*

The above models propose that grid codes compress transition relationships between states. Potentially, this could form the basis for relational inference. The continuous attractor network model of grid cells derives from this, proposing that it is the neural substrate for path integration (relational inference in physical space)(Burak and Fiete, 2009; McNaughton et al., 2006). It is a kind of recurrent neural networks (RNN) with hand-designed weights and has been reviewed elsewhere (Khona and Fiete, 2022). Benefiting from technical advances in machine learning, recent work directly trains RNNs on path integration tasks, and



Box 4 Figure. Successor representation model.

grid-like weights can spontaneously emerge (Fig. 3D) (Banino et al., 2018).

Path integration requires predicting a final position given an initial position and a series of relationships (e.g., velocity vectors). This requirement is to construct the relationship between two positions, that is, to perform vector-based navigation (Bush et al., 2015). Grid codes enable the RNN to generate shortcuts reminiscent of those conducted by mammals (Banino et al., 2018). Similar tasks and results exist in non-physical spaces. For example, in a family tree, knowing that Lisa and Bob are mother and son, and Bob and Ben are brothers, one predicts that Lisa is Ben's mother (Whittington et al., 2020). The exact constraints necessary for the emergence of grids in RNNs are still under debate. A recent model applied vector computation of grids to face recognition to achieve one-shot recognition (Fig. 3D) (Bicanski and Burgess, 2019). Combined with experimental findings of grid codes in visual space, this may shed light on the mechanism of prosopagnosia.

We reviewed the cognitive computational models of grid codes and we now briefly discuss how mPFC and EC may relate to these models. Any grid code-generating brain region is likely to recruit a combination of these mechanisms. We speculate that grid codes in EC, which are more receptive to velocity input, are biased toward the recurrent dynamics based on local circuits (Garcia and Buffalo, 2020; Rueckemann et al., 2021). Information with insufficient prior knowledge is more likely to first enter the hippocampus to form abstract spaces, such as value (Knudsen and Wallis, 2021; O'Keefe and Krupic, 2021) and latent state (Schuck et al., 2016; Schuck and Niv, 2019; Vaidya and Badre, 2022; Wilson et al., 2014), and is then compressed by the mPFC-EC system for inference and generalization. Meanwhile, tasks faced by humans are arguably more complex and often involve high-dimensional cognitive spaces. For example, when choosing a restaurant for dinner, you may consider various factors including physical distance, taste of the food, and the restaurant ambiance. Both physical and abstract task variables are jointly mapped in the hippocampus (Nieh et al., 2021), and primate hippocampal neurons show schema-like activities that integrate goal-centered and task-related information (Baraduc et al., 2019; Peer and Epstein, 2021). Thus, the hippocampus can abstract concepts from various dimensions of the environment. We propose that the mPFC-EC system flexibly selects and reduces the dimensions of hippocampal cognitive spaces according to task demands. A new perspective argues that grid codes represent the order of events in space based on their temporal contiguity (Rueckemann et al., 2021). Our proposal favors this view and advocates that mPFC-EC grid codes build a compressed transition representation rooted in the temporal sequence of experiences. Grid codes learn a predictive transfer map, rather than a rigid metric system that is bound to physical space.

7. Application of grid codes

Two grid coding-inspired artificial intelligence models have recently been proposed (Banino et al., 2018; Whittington et al., 2020). As we reviewed above, grid-like units may emerge when RNNs are trained on path integration tasks, and these networks can also compute goal vectors and generate shortcuts (Fig. 3D). Another work extended this to other cognitive spaces and generate an “inference machine”. The model factorizes cognitive maps into stimuli and structures. The same relationship structures underlying various tasks are encoded within an RNN. Stimuli are stored within an attractor network. After the agent receives sensory stimuli and relationships (actions), it combines two pieces of information to infer states. This is similar to path integration and landmark navigation strategies used in physical navigation. Humans can optimally integrate the two, an ability that matures after age ten and declines with aging (Bruns and Röder, 2023; Nardini et al., 2008; Segen et al., 2021). We speculate that grid codes of the elderly and children may be limited, and a recent study indeed provided evidence for the former effect (see below) (Stangl et al., 2018).

The brain regions showing tau-related neurodegeneration in Alzheimer’s disease (AD) highly overlap with those showing grid codes (Coughlan et al., 2018; Igarashi, 2023; Jagust, 2018). Several human studies have linked grid codes with AD. Reduced grid codes were found in young adults with high genetic risk for AD and in normal healthy older adults (Bierbrauer et al., 2020; Kunz et al., 2015; Stangl et al., 2018). Young adults’ spatial memory performance did not differ from the performance of a control group, but navigation trajectories tended to be attracted to borders (Kunz et al., 2015). A similar behavioral pattern was found in subsequent studies (Coughlan et al., 2019). Based on the grid models reviewed above, we speculate that the goal state may still be accurately retrieved, but impaired grids cause a less precise reconstruction of the transition matrix M, which participants attempt to compensate via stable environmental cues——boundary.

Although grid codes are mostly studied in 2D spaces, they can easily be applied to reconstruct transition matrices in 1D (Jacob et al., 2019; McNamee et al., 2021; Yoon et al., 2016). Many studies have found that interactions between hippocampus, EC, and mPFC, in particular via theta synchronization is important for 1D relational inference task(A-B, B-C, infer A-C) (Backus et al., 2016; Barron et al., 2020; Koster et al., 2018; Park et al., 2020); but see contrasting result from (Basile et al., 2020). Furthermore, neural replay and transition relationships are impaired in schizophrenia (Nour et al., 2021), which again is related to impaired grid codes (Convertino et al., 2022). Because of the critical role of grid codes for relational inference, sequence generation, and reconstruction of cognitive spaces, we believe that more sensitive cognitive markers based on grids, such as Levy walk-eye movement patterns and neural sequence sampling patterns, can be developed in the future.

8. Concluding remarks and future directions

In this manscript, we first reviewed experimental research on human grid codes, which uncovered their diverse roles in physical space and non-physical space and their oscillatory features of distributed grid codes in the brain (Fig. 2). We also summarize cognitive computational models of grid codes, which revealed the superiority of the triangular tuning pattern and the mechanisms of how the pattern emerges from neural networks (Fig. 3). Finally, we briefly describe the clinical translation of grid codes and their inspiration for AI. There are some future important questions about human grid we list below.

Can we identify grid codes in abstract spaces at the single-unit level and a modular organization of grids in the human brain? And How are grid codes of physical and non-physical spaces related?

Can hexadirectional modulation be detected in behavior? Or why behavior is not hexadirectionally affected.

Can the mPFC-EC system organize any continuous abstract variables into grid codes? Where are the boundaries and dimensional limits of the abstract space that a grid can encode?

How can we probe reactivation of grid codes and their oscillatory properties during offline waking and sleep stages? Does this reactivation differ in mPFC and EC? And how is it related to replay recently observed in human (Liu et al., 2019)?

How are grid representations in theta (iEEG) and gamma (MEG) frequencies related? Can closed-loop deep brain stimulation be developed to adaptively modulate theta/gamma activity to improve grid representations and improve performance during navigation in cognitive space?

Returning to the opening quote, as David Marr says, understanding aerodynamics is the only way to understand the flight of a bird, rather than just staring at the wings (Marr, 2010). Similarly, constructing cognitive models of the grid and combining them with empirical data is a promising path to reveal its mysteries. We thus strongly call for research on grid codes via both experimental and modeling approaches in order to integrate domains of cognitive neuroscience and unravel the mysteries of the mind.

CRediT authorship contribution statement

Dong Chen: Conceptualization, Visualization, Writing – original draft, Writing – review & editing. **Axmacher Nikolai:** Writing – review & editing. **Wang Liang:** Conceptualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no competing interests.

Data Availability

No data was used for the research described in the article.

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