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Feature Review

Structuring Knowledge with Cognitive Maps and Cognitive Graphs

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Humans and animals use mental representations of the spatial structure of the world to navigate. The classical view is that these representations take the form of Euclidean cognitive maps, but alternative theories suggest that they are cognitive graphs consisting of locations connected by paths. We review evidence suggesting that both map-like and graph-like representations exist in the mind/brain that rely on partially overlapping neural systems. Maps and graphs can operate simultaneously or separately, and they may be applied to both spatial and nonspatial knowledge. By providing structural frameworks for complex information, cognitive maps and cognitive graphs may provide fundamental organizing schemata that allow us to navigate in physical, social, and conceptual spaces.

Spatial Navigation and Spatial Knowledge

To navigate efficiently from place to place, we rely on internal representations of the spatial structure of the world [1]. These are sometimes referred to as 'cognitive maps' because they play a functional role that is similar to physical maps. The study of cognitive maps has been a central concern of psychology and neuroscience, stretching back to the dawn of the cognitive revolution [2] (Box 1). The importance of these representational structures is emphasized by the fact that they are believed to be used not only for spatial navigation but also for reasoning, inference, and memory in a wide variety of knowledge domains [3–6].

However, what is the nature of the cognitive map? Under the classical conception, a cognitive map encodes environmental elements (places, landmarks, goals) in **Euclidean space** (see Glossary) [7]. However, an alternative conception is that spatial knowledge takes a graph-like form, consisting of locations (nodes) connected by paths (links/edges), but with no information about their orientation relative to a global reference frame [8]. These two ideas are often considered to be in opposition to each other [8,9]. We review evidence suggesting that both map-like and graph-like knowledge structures are encoded by the human brain (Figure 1). We explore the neural basis of both types of representations, and consider how they might be applied to both spatial and nonspatial information.

What Form Does Spatial Knowledge Take?

Cognitive maps are typically conceptualized as encoding environmental elements in terms of their positions in Euclidean space [1,7,10]. A representation of this type enables a navigator to orient toward unseen locations, identify novel shortcuts, and detour around obstacles – tasks that require the flexible use of spatial knowledge. This formulation received major support from the discovery of **grid cells**, which may provide a neural substrate for representing locations on a 2D Euclidean coordinate system [11,12].

However, a challenge to this idea comes from evidence that people seem to form mental representations that violate Euclidean rules. There are many examples in the literature. People

Highlights

Spatial navigation has been suggested to rely either on Euclidean cognitive maps or on graph-like representations of routes between locations.

Instead of being competing hypotheses, cognitive maps and cognitive graphs may coexist in the same individuals, with their availability and use depending on environmental characteristics and navigational demands.

Cognitive maps and cognitive graphs are instantiated by partially distinct but partially overlapping neural systems in the hippocampal formation, frontal lobes, and scene-selective cortical regions.

Both representational systems can likely support abstract thought; Euclidean maps are suited for representing content varying along continuous dimensions, whereas cognitive graphs are suited for representing state transitions and discrete associations between items.

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Box 1. Historical Conceptions of Cognitive Maps

The concept of a cognitive map dates back to Tolman [2], who presented it as an alternative to behaviorist approaches to psychology. Tolman suggested that animals form representations of environments that are more than an interlinked series of associations and whose learning does not depend on immediate reward. The idea that humans and animals have internal spatial representations is now widely accepted, but there has been less consensus about the nature of 'cognitive maps' – their degree of accuracy, the inputs required to form them, and how they integrate separately experienced environments.

In 1978, O'Keefe and Nadel proposed that cognitive maps are Euclidean, and this has become the dominant model for neuroscientists [7]. A precise definition comes from Langille and Gallistel [178]: 'A map is a set of vectors in a 2- or 3-dimensional vector space, on which navigation-relevant vector functions are defined.' Under this definition, the key feature of a map is that it establishes coordinates for each point in space, thus allowing a navigator to associate non-location information (e.g., terrain characteristics, visual snapshots, reward values) with any location, and to set a direct course between different locations [1]. O'Keefe and Nadel contrasted the flexibility of the Euclidean 'locale' system with the inflexibility of the action-based 'taxon' system, which they postulated mediated a habit-like following of routes.

However, in parallel to the Euclidean map hypothesis, other suggestions for very different types of cognitive maps were put forth, some of which have graph-like aspects. Kuipers suggested that, in addition to Euclidean cognitive maps, people store representations that are based on topological knowledge – connectivity between locations through routes and hierarchical organization of locations into regions [42,43]. Subsequent authors have developed other models of graph-like spatial representations [19,26,36,38,41,45,47,179–182], with additional elements such as a skeleton of major routes on which the graph is constructed [44], labels at nodes and edges indicating directions and distances [8,9,30], and node-specific reference frames [37,39]. It remains debated whether spatial knowledge is Euclidean, graph-based, or a combination of both. In this article we use the term cognitive map to refer to Euclidean cognitive maps, while referring to graph-like structures as cognitive graphs.
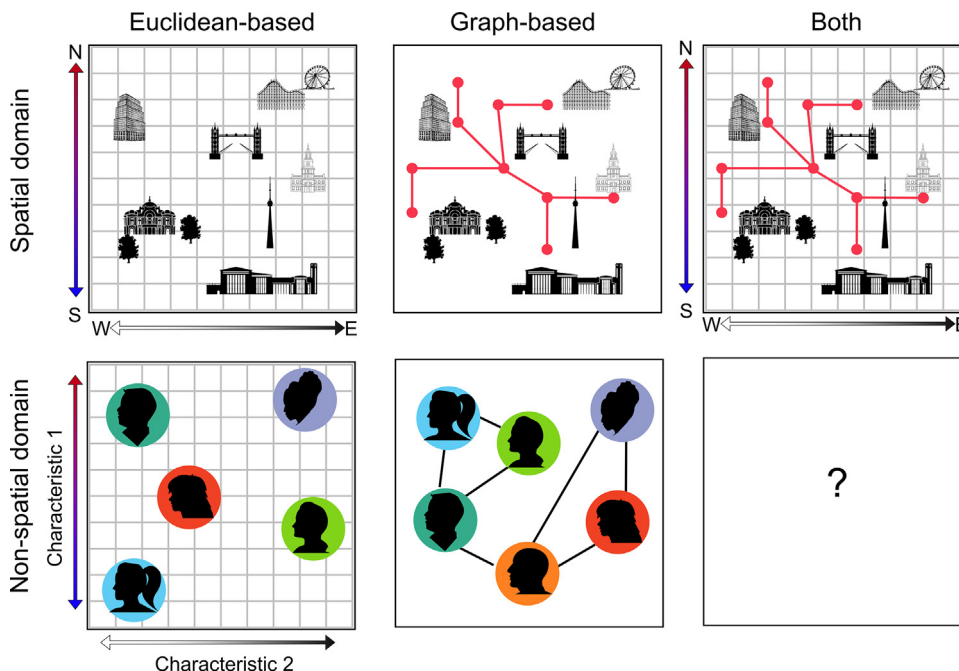

Figure 1. Map-Based versus Graph-Based Representations. In the spatial domain (top row), knowledge can be purely map-based, and locations are coded in terms of Euclidean coordinates (e.g., latitude and longitude), or purely graph-based, where locations are nodes and paths between locations are links. It is also possible for map- and graph-based representations to exist simultaneously, allowing us to switch flexibly between the two. In non-spatial domains (bottom row), knowledge is map-based when information is encoded in terms of continuous dimensions and graph-based when it is encoded in terms of distinct links between items. For example, the individuals in a social group might be represented in terms of their personality characteristics (map-based) or in terms of the social connections within the group (graph-based). It is currently unclear whether a flexible combination of graph- and map-like representations exists in non-spatial domains.

Glossary

Cognitive graph: a representation of space in terms of nodes (locations) connected by links (path segments). A cognitive graph can be topological (representing only whether locations are connected to each other or not), or labeled (representing local metric information such as distances and directions of each link, or the angles that links form at a node).

Entorhinal cortex (ERC): a brain region found in both rodents and humans that serves as a major input/output structure for the hippocampus. ERC contains both grid cells and head-direction cells.

Euclidean space: a continuous space defined by reference axes (usually two or three). Locations in a Euclidean space can be specified by coordinates, and relationships between locations can be expressed in terms of distances and angles.

Grid cells: neurons that represent space in a distributed manner by firing in a regular array of locations that tile the environment in a hexagonal lattice.

Head-direction cells: neurons that fire as a function of the direction that the animal is facing, independently of its location, similar to the behavior of a compass.

Hexadirectional modulation: a phenomenon where brain activity is modulated by the subject's current direction of movement, with sixfold symmetry – that is, firing is maximal for headings with angular spacing of 60°. This is believed to be a marker for grid cells, whose fields exhibit a similar sixfold organization.

Local visual scene (or vista space): a space that can be perceived from a single point without the need to navigate. Sometimes contrasted with environmental spaces, which cannot be perceived from a single point of view.

Path integration: a strategy in which a navigator keeps track of the distances and directions they have traveled so as to compute a straight-line vector to the starting point. Path integration is believed to be crucial for learning Euclidean coordinates for locations in the environment, but it can become inefficient in large environments owing to accumulated errors.

Place cells: neurons that represent space in a localized manner by firing when the animal is in a specific location.

tend to distort the angles between path segments in memory toward 90° in a way that can create impossible configurations [13–16]. Distance and direction estimates between locations are warped by the number of turns in the paths connecting them [15,17–21], and can differ between forward and backward path directions [19,21–25]. Moreover, people often maintain only a very schematic and distorted representation of their environment [14,16,26,27], and may be unable to point in the direction of unseen landmarks even after years of experience [28]. Nevertheless, people are often able to confidently and accurately navigate and take novel shortcuts even when they do not possess a full metric mapping of the environment [26,29]. People can even navigate in virtual environments that have an impossible, non-Euclidean structure, while remaining seemingly unaware of those inconsistencies [30–34] (Box 2 and Figure 2).

Results such as these suggest that people might use a non-Euclidean type of spatial knowledge to represent their environment, created by the combination of familiar **routes** into a network of path segments. Memory of how to follow a specific route is often thought to be procedural – an ordered sequence of stimuli and responses ('when seeing X, turn right'), not necessarily incorporating any explicit spatial knowledge [35]. However, learning how routes connect at intersections might allow a navigator to encode a flexible representation of the route network, thus enabling the recombination of path segments in novel ways during navigation [8,19,26,36–39]. Such a flexible representation of path segments is referred to as a **cognitive graph**.

In a graph, only a limited number of spatial locations are represented as nodes. These may be locations of navigational importance (e.g., turns in the road, intersections between routes, prominent landmarks, or locations of prolonged stay) or places with special personal meaning to the navigator [10,36,39]. Spatial relationships between nodes are represented as links that include only the information necessary to travel between the nodes – specific action sequences to take, relevant metric information (e.g., lengths of path segments), or route characteristics

Box 2. Environments – Real, Virtual and Impossible

When the study of cognitive maps began, investigators used real physical environments. In the laboratory, they constructed wooden mazes or filled tubs with milky water. In natural environments, they tracked the countryside over which bees flew or asked students questions about the layout of their campuses. The laboratory environments provided experimental control, whereas the natural environments had the advantage of ecological validity – but both types of environment were 3D layouts that provided a full range of sensory input and in which the participant could move. Along with these strengths came weaknesses. The constructed environments were rarely large in scale, and the natural environments did not allow standardization across studies.

Advances in technology now permit the use of virtual reality (VR) environments in the study of navigation. VR technology comes in a variety of flavors, ranging from desktop computer displays to fully immersive head-mounted displays with body motion tracking, and has been used to study navigation in both humans and non-human animals. Although VR and real navigation differ in some important respects (especially the lack of kinesthetic and proprioceptive feedback in desktop situations [183]), VR navigation experiments have been found to involve many of the same neural mechanisms that are implicated in real-world navigation [184].

One advantage of virtual environments is that they allow participants to experience layouts that are impossible in the real world. For instance, participants can pass through wormholes taking them immediately to spots they would normally take time to get to, or they can go around 'five-sided squares' (Figure 2) [30–34]. Experimenters have often reported that participants do not even notice these impossibilities, and have used this fact to argue against Euclidean cognitive maps [8,30,31]. However, it is also possible that participants expect environments to resemble those they encounter in real life: when faced with difficulty in making sense of their experience, they do their best, attributing their uncertainty to possible lapses of attention or insufficient spatial ability. Indeed, there are sometimes indications that participants are aware of oddities, such as in the swirling notations on sketch maps in a study by Muryy and Glennerster [34]. As that paper notes, future work should directly examine whether people are able to distinguish possible from impossible environments when directly instructed to do so. However, irrespective of the question of whether subjects are aware of the impossible nature of virtual environments, these VR studies suggest that people can form non-Euclidean spatial representations and use them for navigation.

(A) Impossible loops

Zetzsche *et al*. (2009)

(B) Wormholes

Warren *et al*. (2017)

(C) Teleporters

Muryy *et al*. (2018)
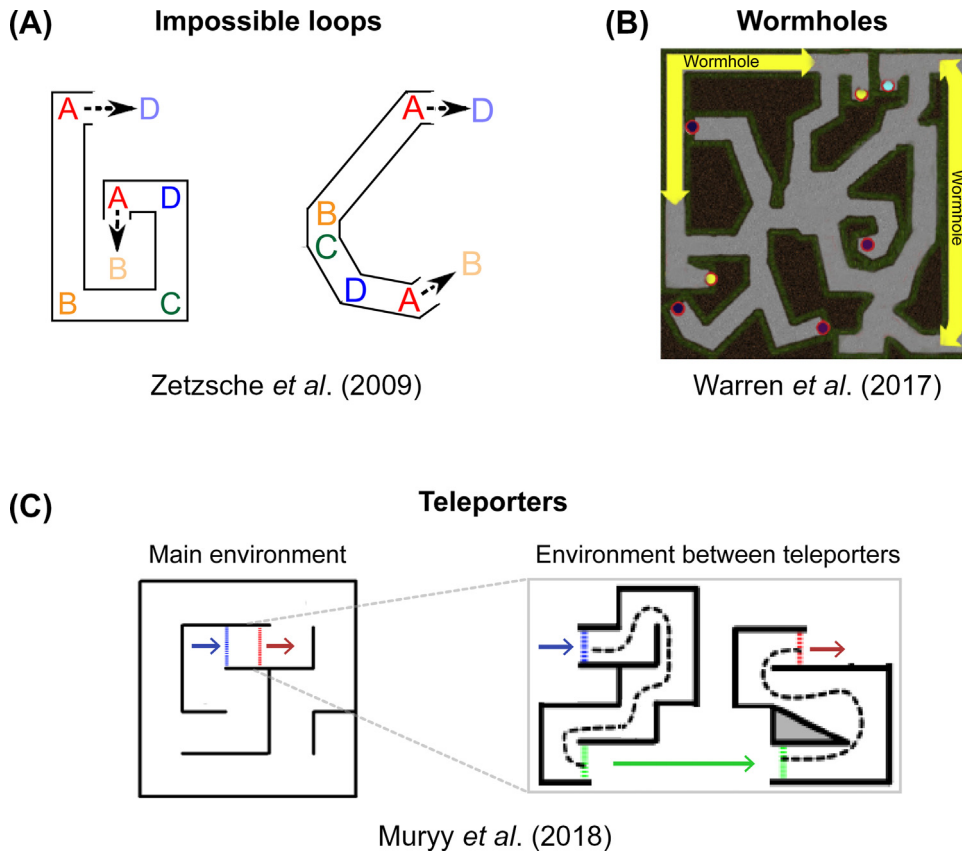
Trends in Cognitive Sciences

Figure 2. Impossible Virtual Environments Provide Evidence for Non-Euclidean Spatial Representations. Layouts for each experiment are depicted from a survey (bird's-eye) view, although participants only experienced the environments from an eye-level perspective. (A) Impossible looping corridors used Zetzsche *et al.* [31]. Letters indicate distinct corners. Each environment formed a closed, continuous loop from the participants' perspective (that is, walking from A to B to C to D and continuing leads back to A). In the environment on the left, distances were non-Euclidean (e.g., the distance between points A and B was larger than between points C and D); in the environment on the right, angles were non-Euclidean. (B) Maze with wormholes used by Warren *et al,* [30]. Yellow lines indicate the points connected by the wormholes – when participants moved into a wormhole they immediately emerged on its other side. However, the views at the entrance and exit of each wormhole were seamlessly matched such that there was no cue to participants that they had passed into a different part of the environment. (C) Teleporters used by Muryy *et al.* [33]. On the left is the layout of the main environment; two teleporters are marked by blue and red lines. When participants entered a teleporter, they were transported to the environment on the right. After following the route indicated by the dashed line, they emerged back into the main environment from the other teleporter. Therefore, a long and complex route replaced the short Euclidean distance between the blue and red lines. In all three studies (A–C), participants successfully learned to navigate the environments, despite their impossible structure. Furthermore, participants were not informed that the environments were irregular, and many did not report noticing anything amiss (Box 2 for discussion). These findings suggest that people can form non-Euclidean representations of space, possibly taking the form of cognitive graphs.

such as slope and general direction [36,39]. Cognitive graphs can be thought of as a set of state transitions, where specific action sequences lead from one state to another – similar to the mechanisms underlying performance of non-spatial tasks [36,40].

An important aspect of a cognitive graph – distinguishing it in our conception from a cognitive map – is that locations are not referenced to a global coordinate system. Opinions differ, however, as to whether cognitive graphs incorporate local metric information. Some investigators argue for topological graphs that do not use any spatial coordinate system [26,39,41–45]. Supporting this

view is the fact that people usually know the correct topological structure among landmarks (order, containment, and connectivity), even when they have very distorted Euclidean environmental representations [14]. Others have argued for labeled graphs that encode the angles and lengths of the paths extending from each node [8,9,30,37,46]. This type of graph might enable finding novel shortcuts by the sequential summing of local spatial information, explaining how people can make complex navigational maneuvers without possessing a global Euclidean cognitive map [8,30,47].

The evidence we review in the following text suggests that cognitive graphs and cognitive maps do not need to be mutually exclusive. Instead, maps and graphs can be learned in parallel in the same environment (Box 3) [48], and may complement each other.

Neural Systems Supporting Cognitive Maps and Cognitive Graphs

In this section we review the neural systems that support cognitive maps and cognitive graphs. Figure 3A summarizes our conclusions in graphical format.

### Evidence for Euclidean Spatial Representations

The discovery of **place cells** in the rodent hippocampus provided some of the first evidence for a spatial code in the brain [49]. O'Keefe and Nadel [7] hypothesized that these neurons, whose firing depends on the position of the animal, support a Euclidean map. Consistent with this idea, neuroimaging studies have found that the hippocampus exhibits a key feature of a map: encoding distances between locations [3,50–54]. Because Euclidean and path-based distances tend to be correlated in most realistic environments, it has not always been clear whether these distance effects are evidence for map-like or graph-like representations. However, one study that attempted to dissociate these factors found that activity in the anterior hippocampus and entorhinal cortex was related to Euclidean distance, whereas activity in posterior hippocampus was related to path distance [54] (Figure 3B).

Box 3. How Are Cognitive Maps and Graphs Acquired and Lost?

To understand the interplay between cognitive graphs and maps, it is important to consider their order of acquisition. There are two possibilities: graph-first or map-first.

In the first scenario, environments are initially encoded in terms of individual locations and connecting routes. With prolonged experience, more paths in the environment are traversed and more connections are established. This increase in information allows the construction of an integrated representation with a global reference frame that encompasses the entire space, in a manner that is consistent with the classical view of spatial microgenesis ([10]; cf [185]). Evidence for this scenario comes from reports that grid and head-direction cell firing fields are initially anchored by the walls of individual subspaces [186], but with experience extend across boundaries to encompass a larger space [187,188]. In non-spatial domains, this scenario might play out as initial learning of one-to-one associations between stimuli, followed by integration as global organizing principles are discovered.

In the second scenario, environments are initially encoded using a Euclidean map, which might be created through path integration. Graph representations are formed later as part of a consolidation process that involves the identification of key locations, and the storing of paths between these locations in memory, such that they can be directly retrieved rather than being computed anew each time they are required. Consistent with this scenario are findings indicating that activity during navigation shifts from the hippocampus to cortical regions, especially RSC, as an environment becomes familiar [189–191]. The graph-like nature of these cortical representations can be inferred from examination of patients with hippocampal damage. When these patients are asked to draw sketch maps of neighborhoods they have lived in for decades, the maps tend to be schematic, only including the main roads and the few most prominent landmarks [192]. In one particularly illuminating case, a former London taxi driver was able to navigate along primary roads in virtual London, but tended to get lost when the route involved more side streets, suggesting that only a skeleton of primary locations and routes remained [193]. Although there is no direct connection to non-spatial domains, these findings are reminiscent of observations in semantic dementia patients, who retain a skeleton of core concepts with a shrinking network of specific exemplars as the disease progresses [194].
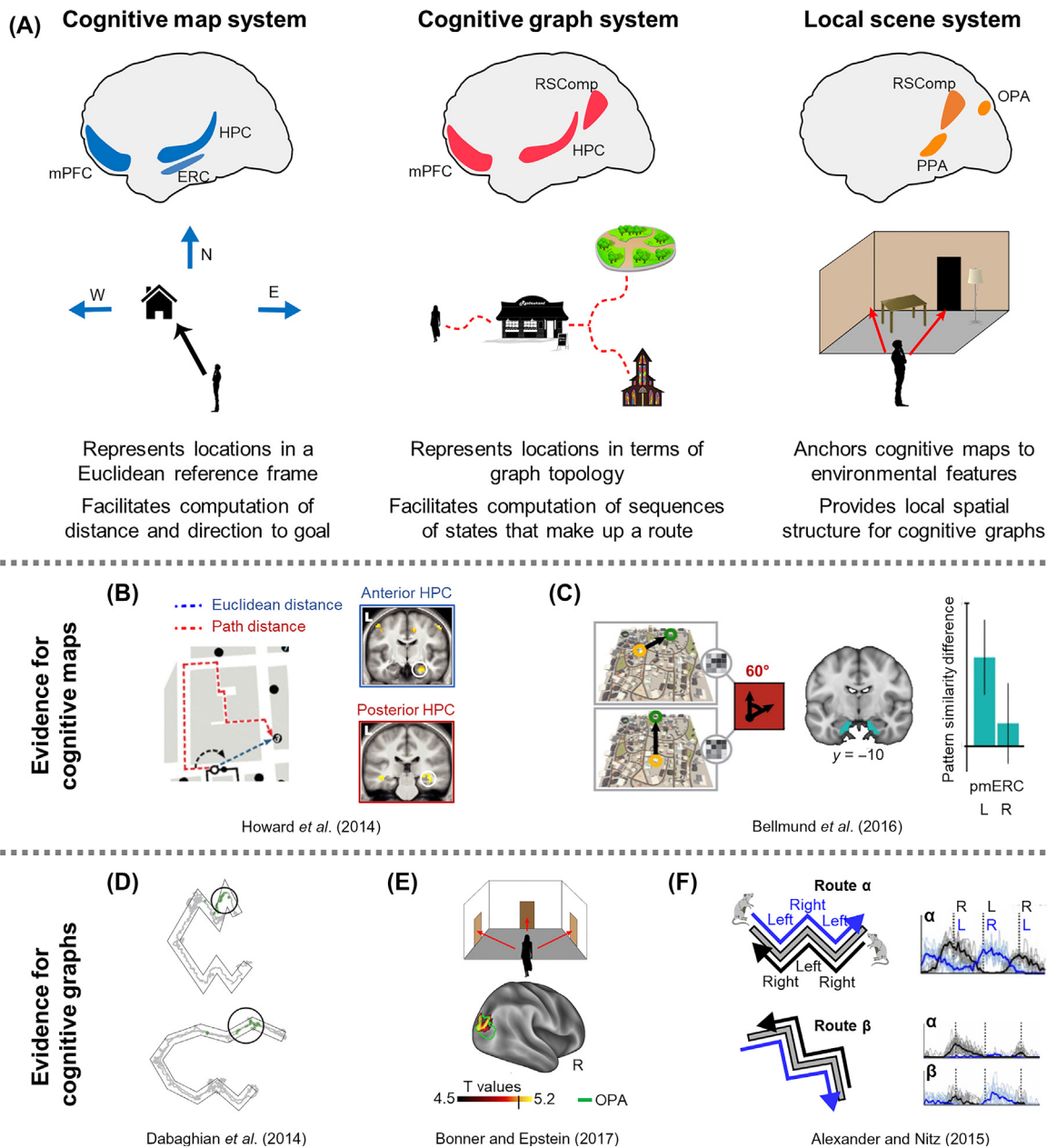
Figure 3. Neural Systems Supporting Map-Based and Graph-Based Representations. (A) Putative brain systems supporting each type of representation, and their suggested functions. (B–F) Evidence for cognitive map and cognitive graph representations. (B) Results from an fMRI study showing Euclidean distance representations in the anterior hippocampus and path distance representations in the posterior hippocampus (Howard *et al.* [54]). Participants learned the layout of London's Soho district and navigated toward different goal locations. Activity in the anterior hippocampus scaled with Euclidean distance to the current navigational goal, whereas activity in the posterior hippocampus scaled with path distance to the goal. (C) Results from an fMRI study showing representation of Euclidean direction to goal (Bellmund *et al.* [86]). Subjects learned the layout of a virtual city, and then on each trial they were asked to imagine themselves standing in front one building while facing in the direction of another building. Activity patterns in ERC exhibited a sixfold symmetry with respect to the imagined vector, demonstrating the existence of a direction code related to entorhinal grid cells. (D) Example of a topological representation in the rat hippocampus (Dabaghian *et al.* [94]). Rats navigated a U-shaped route, which could be folded such that the angles between route segments and their positions within the surrounding room were changed, without changing the overall route length. Hippocampal place cells fired at the same route segments regardless of the manipulation, demonstrating that the firing is sensitive to route topology and not to absolute Euclidean location in space. (E) Results of an fMRI study showing sensitivity to the navigational affordances of scenes (Bonner and Epstein [115]). Participants viewed rooms with exits (doors) at

(Figure legend continued at the bottom of the next page.)

The spatial metric underlying these distance codes is believed to be implemented not in the hippocampus itself, but upstream in the **entorhinal cortex (ERC)**. This region contains grid cells whose multi-peaked firing fields provide a regular grid for representing space [11]. Evidence for grid-cell-like representations has also been reported in human fMRI [55], single neuron activity [56], and intracranial theta oscillations [57], suggesting a cross-species Euclidean representational mechanism. The integrity of these grid-cell-like patterns relates to navigational ability and is reduced in individuals at genetic risk of developing Alzheimer's disease and in older adults [55,58,59]. Interestingly, grid-cell-like patterns in humans have also been observed outside the ERC, notably in the medial prefrontal cortex (mPFC) [55,56,60], suggesting that frontal lobe regions also support the encoding of continuous spatial dimensions. Within the ERC, grid cells are organized into discrete modules along the dorsal–ventral axis, and more ventral modules exhibit larger grid fields [61]; a similar organization by scale is observed in hippocampal place cells in rodents [62] and hippocampal fMRI signals in humans [63–65]. The use of multiple scales may allow the hippocampal/entorhinal system to support maps of different sizes, and also to encode locations with greater robustness by combining information across scales [66].

Recording and modeling studies suggest that the grid system uses its own internal attractor dynamics to support a representation of a continuous 2D manifold [67]. Activity in this manifold might be updated based on inputs from **head-direction cells** [68] and speed cells [69], thus providing a mechanism for **path integration** [12]. However, it is worth noting that grid patterns often exhibit distortions from regularity, and these are tied in a predictable manner to the geometry of the environment as defined by its boundaries [70–72]. Behavioral studies in humans have shown that spatial memories exhibit biases that are consistent with the geometry-based distortions observed in rodent grid cells [73–75]. According to one theory, grid cells may provide accurate measures of distance to the most recently encountered boundary, but only an approximate reference system for the environment as a whole [76]. Interactions with environmental boundaries or with distal cues can reduce navigational errors by correcting the drift in spatial codes that is inevitable when grid and place fields are updated solely from internal self-motion cues [77–80]. These findings suggest that path integration may rely primarily on a Euclidean grid signal, but goal-directed navigation ultimately relies on representations that are a compromise between this Euclidean signal and information obtained from local spatial features such as boundaries and landmarks.

In addition to encoding distances, another key aspect of a Euclidean map is that it allows calculation of the direction to the navigational goal. Theoretical work suggests that grid cells can perform such computations [81–83]. Neuroimaging studies have found evidence for encoding of direction to a navigational goal in the ERC and presubiculum. In two studies, multivoxel patterns in these regions distinguished uniquely between directions in a manner reminiscent of rodent head-direction cells [84,85], while in another study these patterns exhibited a sixfold symmetry that is characteristic of grid cells [86]. Notably, the latter study used a complex virtual city where the straight-line vectors between various locations did not correspond to the navigational paths (Figure 3C). When taken together with the evidence for distance coding, these findings point to a Euclidean representational system in the brain, centered on ERC and hippocampus.

different locations, as well as naturalistic scenes. Information about navigational affordances (i.e., pathways for movement) in both types of scenes could be decoded from multi-voxel patterns in the OPA. (F) Examples of route information encoding in the rat retrosplenial cortex (Alexander and Nitz [126]). Rats navigated two W-shaped routes located in different parts of a room, in both route directions. Some retrosplenial neurons encoded route action sequences (e.g., right-left-right turn) while distinguishing the direction of route movement, while other retrosplenial neurons additionally distinguished between the two routes. Abbreviations: ERC, entorhinal cortex; HPC, hippocampus; L, left; mPFC, medial prefrontal and orbitofrontal cortex; OPA, occipital place area; PPA, parahippocampal place area; R, right; RSComp, retrosplenial complex.

Evidence for Graph-Based Spatial Representations

In contrast to the flexible navigation afforded by a cognitive map, route-based navigation is often conceptualized as a rigid, procedure-bound strategy. Consistent with this view, numerous studies report a distinction between map-based navigation supported by the hippocampus and route following supported by the caudate nucleus [87–90]. However, graph-based navigation can go beyond merely following an overlearned trajectory to enable flexible recombination of path segments in planning. This type of navigation is unlikely to involve the caudate, but instead may recruit brain networks that partially overlap with the cognitive map system [91].

Proposals that the hippocampal formation represents graph-like spatial codes, instead of (or in addition to) cognitive maps, have existed in parallel with cognitive map theory for some time [38,92]. Although they did not use the term, Eichenbaum and Cohen [93] characterized the hippocampus as encoding relational elements (e.g., A is east of B) that could form the elements of a spatial graph. Recent evidence from rodent neurophysiology suggests that hippocampal place fields in constrained mazes are determined by position relative to the topological structure of the maze, rather than by distance along the path or position in Euclidean space [94] (Figure 3D). More broadly, hippocampal place cells have been shown to divide space and time into segments [95,96], encode the hierarchical structure of experience [97], and represent schematic relationships between environmental elements [98], all of which can be conceptualized in terms of graph coding.

During navigational planning, hippocampal place cells are believed to support a path-based mechanism that respects environmental topology [92,99–101], and the firing rates of place cells are modulated by past and future paths [102–104]. Evidence for such a path-based planning mechanism has been observed in both rodents [105] and humans [54,106]. Hippocampal replay (i.e., sequential reactivation of place cells when the rodent is stationary) also appears to be sensitive to maze topology, and reversal of replay direction is observed at intersections [107]. Related results have been reported in human neuroimaging: as participants entered a new street in a virtual environment, their posterior hippocampal signal reflected the number of network connections possible for future travel, whereas anterior hippocampal signal reflected the global network topology of the environment [108]. These data are consistent with the idea that the hippocampus supports a graph-like representation of locations in the environment and the links connecting them.

The Role of Scene Regions

As discussed previously, behavioral studies suggest that people might not only encode topological graphs of which nodes are connected to each other – they might also encode labeled graphs that contain local spatial information about the distance and direction of the links or the angles that the links form at each node. What are the neural mechanisms that would give graphs this type of local spatial structure?

To our knowledge, no studies have directly investigated this question. That said, a relevant observation is that there is an intimate relationship between these local spatial features of a graph node and the spatial features of the **local visual scene**. This fact is well known to roboticists, who have exploited it when building artificial navigation systems [109]. Thus, we hypothesize that global topological representations, supported by the hippocampus, are given local spatial structure by the network of cortical regions that represents the local scene. These **scene-selective regions** include the parahippocampal place area (PPA), occipital place area (OPA), and retrosplenial complex (RSComp) [110]. In previous reviews we discussed a possible role for these regions in anchoring cognitive maps by providing geometric and contextual inputs to the hippocampal/

entorhinal system [3,111]. We argue here that they may also play a central role in representing elements of cognitive graphs.

Both OPA and PPA respond strongly during the viewing of spatial scenes such as landscapes, cityscapes, and rooms [110]. Several lines of recent work suggest that OPA may be particularly important for processing information about the spatial layout of the local scene [111,112]. For example, OPA has been shown to represent scene geometry as defined by environmental boundaries [113,114], as well as the navigational affordances of the scene as defined by the locations of egress points and pathways through the scene [115] (Figure 3E). The latter result is particularly relevant because the egress points define the structure of the local environment within a labeled graph (e.g., a room with two exits on opposite walls has a different graph structure than a room with two exits on adjoining walls or a room with three exits). PPA, on the other hand, appears to process the visual features, geometric features, and objects that define a scene as a specific place or context [116,117]. In map-based navigation, these representations of the geometric structure (OPA) and identifying features (PPA) of the local scene provide the perceptual inputs that allow a navigator to determine their orientation and location within the reference frame of the cognitive map. In graph-based navigation, these same representations would allow a navigator to understand the angles between the links converging on a node (using the OPA) and the discriminating features that give a node its unique identity (using the PPA).

These local representations might be integrated into the larger graph by RSComp, a region that encompasses retrosplenial cortex proper (BA 29/30) and adjoining territory in the parieto-occipital sulcus. Like OPA and PPA, RSComp responds strongly when people view scenes, and recent work suggests that its posterior portion may contain a retinotopic map similar to those found in OPA and PPA [118]. However, RSComp is also implicated in global spatial processes that may be crucial for understanding the relationship between the local scene and the wider world [119].

In real-world or realistic virtual environments, RSComp represents spatial quantities such as location and heading [120–122] that are defined relative to stable environmental features such as environmental boundaries and landmarks [123–125]. In linear mazes, neurons in rodent retrosplenial cortex represent path elements that could potentially be used to construct a graph, such as turns, position along the path, and path identity ([126–128]; [129] for related results in monkeys). These cells also represent relationships between path elements [130] and the allocentric location of the path within the broader environment [126] (Figure 3F). These integrative functions of RSComp contrast with the egocentric and route-centered coding observed in lateral parietal cortex neurons, which fire in response to specific route actions (e.g., turning left or right) and route positions, but do not incorporate information about the allocentric location of the route within the larger spatial context [131]. In an fMRI study, we observed that RSComp was sensitive to the order that buildings were encountered along a newly learned route through an urban neighborhood, and responded more when buildings were presented in the correct order than when they were presented in the reverse order [132]. Notably, this effect was only found for buildings at intersections, suggesting that RSComp might be encoding routes in a graph-like manner with the intersections as nodes.

Taken together, this evidence suggests that graph-based navigation is supported in part by a network of cortical regions typically thought of as being scene-selective, with OPA and PPA primarily involved in representing the nodes, and RSComp primarily involved in representing the links. The functions of these regions in graph-based navigation are related to their functions in map-based navigation, but they are not always directly analogous. The role of RSComp is particularly instructive. In map-based navigation, RSComp is believed to mediate between scene-based codes in the cortex and map-based codes in the hippocampal/entorhinal system [133].

This translation function allows a navigator to anchor their cognitive map to the local scene and understand directional relationships to unseen locations. Indeed, an inability to understand the relationship between the local scene and distal locations is an oft-reported consequence of the 'heading disorientation' observed after RSComp damage [134]. Graph-based navigation, on the other hand, might utilize vectors (i.e., links) that are stored directly in RSComp instead of being recalculated through hippocampus–ERC–RSComp interactions each time they are required (Box 3). In this way, a brain region that is used for active computation during map-based navigation might also come to support graph knowledge.

Factors That May Affect the Encoding and Use of Maps and Graphs

Although cognitive maps and cognitive graphs can develop in parallel, different factors may influence the genesis and use of each. Consideration of these factors may help to clarify previous findings that appeared to support one type of representation over the other.
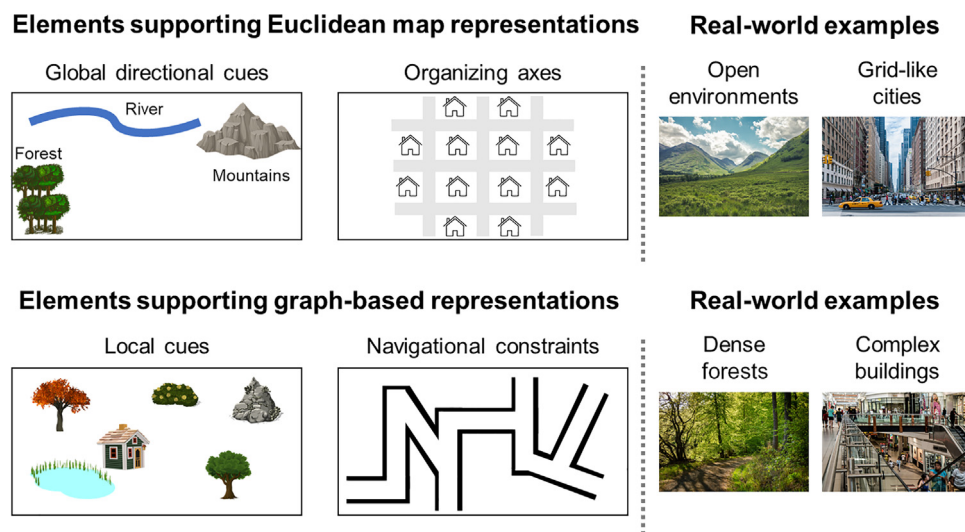
Environmental Constraints

To keep track of their location in a Euclidean coordinate system while moving about the world, navigators must maintain a sense of direction within a consistent reference frame. This task is easier in environments that contain clear global directional cues, such as prominent distal landmarks or slopes, and clear organizing axes, such as prominent straight routes (Figure 4). Thus, map-like codes are more likely to be used in open arenas or in cities with a grid-like street structure, especially when prominent landmarks such as large buildings or mountains are visible. By contrast, graph-based navigation is aided by distinct local landmarks that help to identify nodes or trigger route action sequences [24,135], and may be more efficient than map-based navigation in environments where movement is constrained to a small number of routes [19,21,26,31,32,36]. Prototypical environments that would facilitate graph-like navigation include complex buildings, cities with limited visibility and curving streets, natural cave systems, and dense forests; in such environments, people may learn to navigate by following and combining path segments, without being aware of their global orientation or metric location [28,29].

Spatial Scale

Navigable spaces vary in scale, from small rooms to large cities. These different scales may require different navigational strategies [136,137] that rely on partially separable neural systems [64,65]. Smaller environments (such as single rooms) might be easily coded as a Euclidean reference frame, especially if they are entirely co-visible. By contrast, larger spaces containing several subcompartments or subregions have an inherent hierarchical structure that lends itself to representation as a graph, and boundaries between these subcompartments may limit visibility and movements, making it difficult to create a global Euclidean map [18,138,139]. Indeed, several theories of spatial cognition emphasize the coding of a Euclidean reference frame for small environments, and a graph of connecting routes for larger environments [8,37,39,42,43]. The scale of space, by itself, need not be the only determinant of the form of representation – a large open park with clear axes and boundaries might be represented using a Euclidean coordinate frame, whereas a small building with several corridors might be represented as a cognitive graph. However, all other things being equal, smaller spaces may tend to be represented as Euclidean maps, whereas larger spaces may tend to be represented as cognitive graphs.

Individual and Cultural Variability

People appear to vary in their ability (and tendency) to form Euclidean and route-based representations. Most individuals can learn to follow specific routes, but many perform poorly when they are asked to point in the direction of unseen landmarks (i.e., create a Euclidean representation)

Elements supporting Euclidean map representations

Global directional cues

Organizing axes

Real-world examples

Open environments

Grid-like cities

Elements supporting graph-based representations

Local cues

Navigational constraints

Real-world examples

Dense forests

Complex buildings

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Figure 4. Environmental Features Supporting Map-Based and Graph-Based Representations. Euclidean map representations are supported when the environment contains global directional cues (e.g., distal landmarks, slopes) or prominent defining axes. Map-based representations may be favored in open environments, small covisible spaces such as single rooms, and in cities with a grid-like structure. By contrast, graph-based representations are supported by the presence of local landmarks and may be optimal when navigation is constrained to specific routes. Graph-based representations might be favored in dense forests, complex buildings, and cities without clear organizing axes.

or integrate intersecting routes (i.e., create a cognitive graph). These capacities depend on factors such as mental rotation ability and associative memory [140,141]. In addition, people have consistent individual tendencies to either follow familiar routes or go straight in the general direction of their goal [29,89,142]. Social and cultural factors may also have an effect. For example, Americans rely more on global (cardinal) directions and less on local landmarks than Europeans when giving route descriptions [143,144], and men use cardinal directions and global directional cues (such as slopes) more than women when navigating and giving directions (and this ratio also varies by country) [145–150].
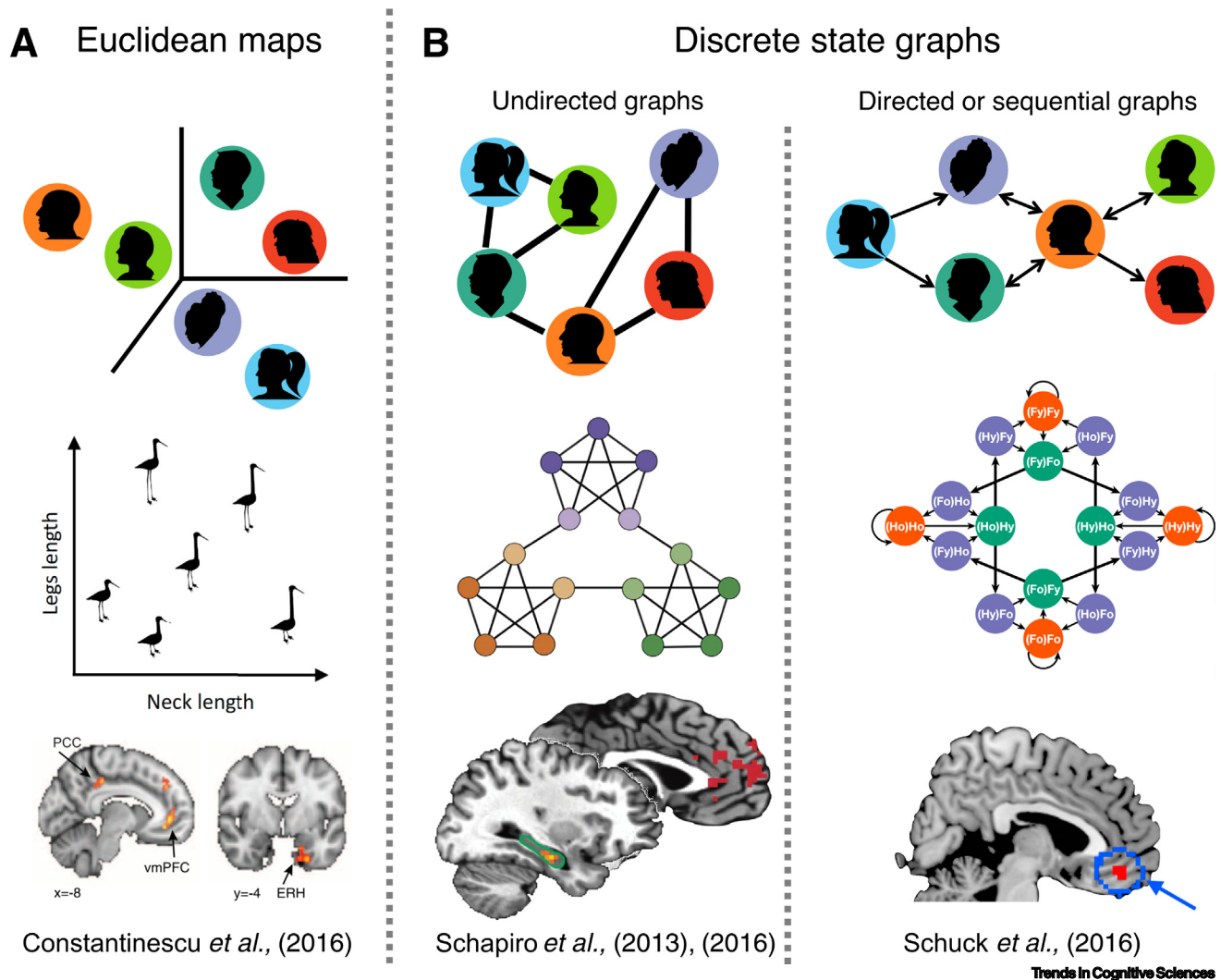
Despite the previously-mentioned factors, in many environments people can maintain both map and graph representations, and use them interchangeably. The differential use of each may depend on the type of problem encountered [29,142]. For example, in a city built as a grid but with one-way streets, a route-based representation may be used when driving, but Euclidean navigation may be more useful when walking. Different types of problems will require different types of representations – and this parallels the different types of knowledge organization used in other types of problems that are outside the spatial domain.

Beyond Space: Maps and Graphs in Abstract Domains

To what extent does the map–graph distinction extend to domains that are not inherently spatial, such as social or semantic knowledge? An increasing number of researchers have argued that spatial cognitive maps can be generalized to form maps of nonspatial information (reviewed in [3–6]). By contrast, parallels between spatial and nonspatial graphs have been less discussed.

In our everyday lives, we are likely to use a wide variety of map-like and graph-like knowledge structures [4,151]. For example, we may represent the people we know in terms of continuous variables

such as various abilities that are naturally encoded as a map-like attribute space (Figure 5A), or we may represent them in terms of discrete relationships between individuals that are naturally encoded in graph-like formats (e.g., social networks or family trees; Figure 5B). Similarly, we might represent living creatures in terms of continuous variables such as size and ferociousness, or in terms of a semantic network of discrete associations [152]. In experimental settings, the details of the paradigm may determine whether participants form map-like or graph-like representations: some tasks require participants to organize information along continuous dimensions, whereas others involve ordered transitions between discrete states. To date, most experiments

A Euclidean maps

B Discrete state graphs

Undirected graphs

Directed or sequential graphs

Legs length

Neck length

PCC

vmPFC

x=-8   y=-4   ERH

Constantinescu *et al.,* (2016)

Schapiro *et al.,* (2013), (2016)

Schuck *et al.,* (2016)

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Figure 5. Maps and Graphs in Abstract Spaces. (A) Some types of nonspatial knowledge might be organized into Euclidean spaces based on continuous feature dimensions. For example, the people working together on a project may be represented as points in a space based on their abilities or characteristics. Entorhinal cortex and medial prefrontal cortex have been shown to represent such non-spatial maps of continuous dimensions – for example, the length of bird legs and necks in a shape space [160] (panel reproduced, with permission, from Constantinescu *et al.* [5]). (B) Other types of nonspatial knowledge might be organized into graphs representing connections or transitions between states. The middle column shows an example of an undirected graph indicating which people in the group know each other socially. The hippocampus and medial prefrontal cortex have been implicated in representing such undirected graphs (Schapiro *et al.* [169,171]). The right column shows an example of a directed graph, indicating a set workflow in which tasks are passed from particular team members to other team members. A representative study investigating this type of knowledge structure implicated the orbitofrontal cortex as the locus of 'task space' graphs that contain the transitions between different nodes in the graph (Schuck *et al.* [172]). Note that the relationships contained in the graphs in panel B can be independent of the placement of the individuals in Euclidean space in panel A. Abbreviations: ERH, entorhinal cortex; PCC, posterior cingulate cortex; vmPFC, ventromedial prefrontal cortex.

have used only one task at a time, leading to an intriguing discrepancy between the spatial and nonspatial literatures: whereas spatial results can often be explained equally well by Euclidean or graph-based representations, nonspatial results usually come from paradigms that constrain the participant to use one representation or the other. However, despite this difference, the observed neural substrates from spatial and nonspatial experiments are similar.

Several studies have examined the coding of continuous representational dimensions in nonspatial domains. These studies have revealed a remarkable correspondence between the neural systems involved in the coding of spatial and nonspatial maps. Hippocampal cells in rodents have been shown to encode several linear dimensions, including time [153–155] and auditory pitch [156]. In fMRI studies, hippocampal activity has been shown to track Euclidean vectors along experimentally defined dimensions, including the angle of a power versus affiliation vector derived from social interactions [157], distance within a 2D social attribute space defined by popularity and competence [158], and distance in a 2D stimulus space defined by visual size and opacity [159]. Entorhinal activity has also been shown to track Euclidean distance [158], and grid-like signals (in the form of **hexadirectional modulation**) have been found in ERC for several abstract spaces, including a continuous shape space defined by bird beak and leg length [160] (Figure 5A), an olfactory space defined by the blending of two odors [161], and a semantic space in which symbolic labels were used to parse two continuous stimulus dimensions into categorical regions [162]. Grid cells in monkey ERC have been shown to encode the visual space on a display screen [163], and a similar effect has been observed in human ERC [164,165]. As previously observed for physical spaces, neuroimaging studies have observed grid-like signals in mPFC [160–162]. Taken together, these results provide strong evidence for a common neural system that represents Euclidean spaces across a wide variety of physical and abstract domains.

Fewer studies have directly investigated graph coding in nonspatial domains, but evidence for graph-based coding comes from studies that present participants with sequences of items corresponding to transition matrices that have an underlying graph structure (Figure 5B). Behaviorally, the learning of such graphs can be demonstrated by evaluating participant response times in terms of distances within the graph [166–168], or by testing their ability to parse items into 'communities' of closely linked stimuli [169,170]. These studies have found evidence for graph coding and hierarchical organization using both explicit [168,170] and implicit [166,167,169] measures. Neuroimaging studies suggest that the hippocampus, PFC, and RSComp support the ability to extract graph structure [166,168,169], but the pattern of results differs depending on specific task requirements. In a virtual subway network where participants made navigational decisions, but in the absence of first-person navigation experience, the hippocampus and ventromedial PFC jointly tracked proximity to goal as the number of stops along the route, whereas dorsomedial PFC tracked distance to goal in terms of the number of subway lines [168]. Interestingly, although not emphasized by the authors, this study also found effects of graph distance in RSComp. Similarly, in a network structure that participants learned by observing sequences of items corresponding to possible transitions between graph nodes, mPFC and hippocampal patterns were more similar for items closer together in the underlying structure [169,171]. However, another study found that activation patterns in a different frontal region adjacent and connected to the mPFC – orbitofrontal cortex – distinguished between nodes of a directed graph that represented the hidden states of a behavioral task [172]. Interestingly, this ability to represent the contingencies between abstract states seems to depend crucially on intact communication between the hippocampus and the orbitofrontal cortex [173]. This evidence is broadly consistent with the idea that the orbitofrontal cortex represents tasks as an abstracted graph of the goal-directed transitions between actions or states [40,174].

Studies using multivoxel pattern analyses have not typically found evidence for graph-like coding in ERC (e.g., [171]). However, in one study where participants viewed objects in temporal sequences governed by a specific graph structure, ERC exhibited fMRI adaptation related to link distance and other graph measures [166]. This finding suggested that objects associated with nearby nodes in the graph recruit more overlapping neural populations relative to objects associated with nodes that are further apart. This result is consistent with theoretical views that the hippocampus and ERC work together as a system that represents both the details and the structural regularities of the environment [175–177]. Under this perspective, the hippocampus establishes a set of states that can be linked to perceptual inputs, whereas ERC represents general geometric rules that govern transitions from one state to another – rules that could potentially take either a map-like or graph-like form. This intriguing idea suggests the possibility that maps and graphs may be variants of an underlying representational continuum rather than categorically different knowledge structures (Box 4).

Concluding Remarks and Future Perspectives

Cognitive maps and cognitive graphs provide two powerful methods for organizing spatial and nonspatial knowledge. Although cognitive maps have been a topic of extensive discussion in the literature, cognitive graphs have garnered comparatively less attention – there is much still to be learned about how they operate and how they are instantiated by neural systems (see Outstanding Questions). Meanwhile, the issue of whether true Euclidean maps exist [8,26,36,47] and how they might support nonspatial knowledge remains a topic of intense debate.

One crucial unresolved issue is whether cognitive maps and cognitive graphs can truly be distinguished. As we have highlighted, most studies in spatial cognition use paradigms that can lead participants to develop both graph and map representations of the same environment. Participants may then use these representations interchangeably and according to their individual preferences, complicating the interpretation of the results. An important avenue for future research would be to develop experimental paradigms that are specifically designed to tease apart graph and map representations, both in space and in abstract domains. For example, different spatial environments could be constructed that are balanced for most features, but

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Box 4. Are Maps and Graphs Fundamentally Different?

Are maps and graphs truly different, or are they only different manifestations of the same underlying neuronal code? Some recent proposals suggest that all representations in the hippocampal/entorhinal system are fundamentally graph-like. One influential idea draws on reinforcement learning to argue that the hippocampus does not primarily code for one's current state (i.e., location), but instead encodes the distribution of possible states that could be visited in the future, termed the successor representation (SR) [177]. Knowledge of the available state space is acquired via exploration [195], and includes the likelihood of visiting each state and the probability of transitioning between specific states [196]. SRs therefore correspond to graph structure learning, where each state is a node, and the transition probability between any pair of adjacent states determines the weight of the connecting link. These transition probabilities can be affected by both spatial factors (such as boundaries) and non-spatial factors (such as the current goal). This approach has been used to explain hippocampal responses ranging from rodent electrophysiology to human conceptual learning [177]. In this scheme, grid fields in the entorhinal cortex are argued to represent principal components of hippocampal state representations [177,197], which can support planning across multiple spatial scales.

How might the brain build a Euclidean representation out of this inherently graph-like structure? A relevant observation is that the SR is agnostic about how states and transitions between them are defined. Existing models assume that spatial information is inherent in this definition; for example, by defining states in terms of their Euclidean locations [177] or transitions in terms of compass directions [175]. One possibility is that this information is provided by cell types whose firing is inherently spatial, such as head-direction cells and boundary vector cells (BVCs) [198,199]. These neural responses to one's immediate environment (and additional local scene input from scene-selective areas) can thus be used to compute SR states. An open question is whether non-spatial inputs (perhaps from image spaces in the posterior parietal cortex [200]) might be used in a similar way to define states and transitions for abstract spaces.

Outstanding Questions

- Are maps and graphs fundamentally distinct forms of representation, or are they two facets of the same underlying code (Box 4)? For example, can Euclidean maps be conceptualized as very dense graphs – or, alternatively, can cognitive graphs be conceptualized as maps that have higher-dimensional topologies?

- How do individual differences in maps versus graphs use manifest across the population? Are people who are better at Euclidean navigation also better at graph-based navigation, or do people tend to favor one representation or the other? Do preferences for map-like or graph-like codes when navigating in space transfer to non-spatial tasks?

- Many studies have investigated the neural systems that support cognitive maps. By contrast, the neural basis of cognitive graphs is less well established. To what extent are the hypotheses presented here about the neural basis of cognitive graphs borne out by studies that specifically investigate this question?

- Physical space has three orthogonal dimensions that are continuous and equipotential. By contrast, semantic 'spaces' typically have many more dimensions, and these may not be orthogonal and are often more categorical than continuous. Do these differences have implications for understanding how cognitive maps and graphs are used to represent non-physical spaces?

- How extensive is the overlap between the brain systems that encode spatial versus nonspatial knowledge? Do non-spatial representations rely on additional systems beyond those used in spatial navigation, for example linguistic or compositional codes? To what extent does non-spatial thinking use other 'spatial' cell types beyond place cells and grid cells – for example, head-direction cells or boundary cells?

have different geometries that encourage the formation of either graph or map representations. Alternatively, behavioral and fMRI similarity measures could be used to identify competing representations of cognitive graphs and Euclidean maps in the same environment, for example by contrasting coding of path distances and Euclidean distances between locations (e.g., [54]). The same procedures could be used in non-spatial domains, for example by investigating representations of items connected as a graph (e.g., social network connectivity between people) versus coding of the same stimuli on a Euclidean space (e.g., people's location on a coordinate system defined by continuous personality traits).

Irrespective of whether maps and graphs turn out to be fundamentally different or two sides of the same coin, the distinction between these knowledge structures provides a useful framework for thinking about how complex information is represented in the mind-brain. Future investigations of these structures will be important not only for understanding not only how neural systems mediate spatial navigation, a core cognitive ability that is essential for survival and human flourishing, but also other fundamental elements of thought, including reasoning, memory, and prospection.

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