From cognitive maps to spatial schemas

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Abstract | A schema refers to a structured body of prior knowledge that captures common patterns across related experiences. Schemas have been studied separately in the realms of episodic memory and spatial navigation across different species and have been grounded in theories of memory consolidation, but there has been little attempt to integrate our understanding across domains, particularly in humans. We propose that experiences during navigation with many similarly structured environments give rise to the formation of spatial schemas (for example, the expected layout of modern cities) that share properties with, but are distinct from, cognitive maps (for example, the memory of a modern city) and event schemas (such as expected events in a modern city) at both cognitive and neural levels. We describe earlier theoretical frameworks and empirical findings relevant to spatial schemas, along with more targeted investigations of spatial schemas in human and non-human animals. Consideration of architecture and urban analytics, including the influence of scale and regionalization, on different properties of spatial schemas may provide a powerful approach to advance our understanding of spatial schemas.

[H1] Introduction

We learn against the backdrop of past experience[1]. The mammalian hippocampus (HPC) has a crucial role in creating this backdrop to serve mnemonic functions and spatial navigation[2] in the context of a network of specialized neocortical regions. In humans, the hippocampal formation encodes the specific relations contained within experienced events and spaces to support episodic memory[3-6] and spatial navigation[7,8]. Spatial navigation is thought to be guided by the internal representation of spatial relations in a specific environment, referred to as a cognitive map **[G]** [2,9]. The HPC can store unique cognitive maps of different environments or of altered versions of the same environment[2,10-13]. At the same time, similar parts of one environment or multiple environments seem to be represented using generalizable spatial codes[14-19], which refer to a set of abstract spatial relations that can be used flexibly to facilitate navigation. Like a cognitive map, a spatial gist **[G]** is composed of key elements specific to a particular environment, but it may be viewed as a summary of the general layout extracted from experience navigating in that same environment, stripped of its perceptual details[20]. The integration of multiple gists, in turn, could give rise to spatial schemas **[G]** that are independent of a specific environment and the HPC. This Review reexamines the notion of schema as it relates to space, drawing on cognitive neuroscience and urban analytics.

A schema is an abstract knowledge structure that reflects the integration of common patterns that are extracted across multiple events to form a flexible reference template that is used for a particular function[21-26]. The concept of a schema in humans has been largely considered in the context of verbal memory of events, although space is viewed as a defining, and probably crucial, component[27]. Here we consider the possibility of a spatial schema as separate from an event schema **[G]**, instead reflecting learned recurring patterns of spatial relations among key elements of an environment[14,18,28], and facilitated through the act of navigating in that environment[29-32]. For example, whereas an event schema might guide encoding of the events that occur in a particular type of city, a spatial schema would guide encoding of the layout and other spatial elements (that is, the spatial ontology) of such a city. A prominent urban theory identifies these elements of a city as landmarks **[G]**, nodes **[G]**, paths **[G]**, districts **[G]** and edges **[G]**[33-35]. Instances of these elements in Toronto include the CN Tower as a landmark, Yonge

Street as a path, Nathan Phillips Square as a node, the Annex as a district, and Harbourfront as an edge. A spatial schema might be reinstated when one encounters similar elements in a novel environment, or when one must assimilate previously encountered elements with novel elements when a portion of a familiar environment is substantially altered. This process of building on a pre-existing schema may draw on the same cognitive processes and neural interactions involved in schema formation, or it may occur independently. In both cases, spatial schemas would be used to guide navigation by enhancing expectations in predictive coding **[G]** [28].

The concept of a spatial schema is still emerging in the cognitive neuroscience of memory and navigation, with several recent attempts to operationalize[36] and systematically examine spatial schemas in humans[37-39]. There are two aspects to spatial schemas: one that is psychological and relates to using previously formed schemas as reference templates for behaviour, and the other that is also neural and relates to schema formation via HPC–neocortical interaction.

We revisit theoretical frameworks and empirical investigations that are relevant to schemas and potential links between them towards a unified view. Before we do, it is important, first, to distinguish between a spatial schema and a cognitive map. Differences in the behavioural aspects and neural instantiation are highlighted. Next, we review findings from rodent spatial navigation and human event schema studies, comparing them to our notion of spatial schemas in humans. We explore the influence of scale and regionalization in characterizing geometric and surface properties of real-world environments. These facilitate schema construction by helping statistical inferences to be drawn about common elements of different types of environments, such as modern industrial cities[40-44]. We summarize key findings from neuroimaging and computational studies to propose a working neurocognitive framework for understanding the emergence and maintenance of spatial schemas and their application. The heterogeneity of schema operationalizations — which have been proposed to relate to statistical rule learning[1,45-47], associative inference[18,48-52], paired-associate learning[53,54] and prior knowledge retrieval[22,55-57] — highlight the need for a theoretical framework for facilitating future investigations.

[H1] Distinguishing a spatial schema

[H3] Cognitive maps, spatial gists and spatial schemas. Contemporary discussions of how space is represented typically begin with consideration of cognitive maps. A cognitive map is a representation of allocentric **[G]** spatial relations of objects in relation to one another in a specific environment[58]. Tolman coined the term when he observed the ability of rodents to engineer a detour that had never been traversed between two known locations, on the basis of previous experience navigating to each location through another route[58]. Cognitive maps are typically derived from navigating to a rewarded goal destination from multiple start locations. Cognitive maps were given a neurobiological substrate upon the discovery of HPC place cells — first in rodents[59,60] and later in humans[61] — that fire maximally when an animal is occupying a particular location in an environment. Similar to schemas, which were originally described in terms of body representations[62,63] and events or narratives[21-23], cognitive maps took an opposite trajectory, first being described in terms of space[58] but adapted to non-spatial domains such as narratives[2]. Owing to the large scope of the topic, the current review is centred on cognitive maps and schemas as they apply to space.

The gist of an environment may be dissociated from detailed features, and resembles the gist of an experience: just as the gist of an experience refers to the core elements of a particular memory episode[20,64], a spatial gist refers to the core features that characterize a particular environment. Whereas cognitive maps and spatial gists each relate to a particular environment, we argue that a spatial schema is a superordinate spatial representation that supports optimal decision-making in multiple environments that share common geometric and visuospatial properties. As such, a spatial schema could be thought of as a generalizable spatial representation of the category of an environment, formed by integrating overlapping neural representations across similar environments. In this way, schemas may draw on multiple gists and, thus, are not specific to any particular environment or location.

Gists, and the cognitive maps that relate to them, however, are not folded into schemas. They need to remain distinct from one another so that not all environments are viewed as alike — as would be the case if one only relied on schemas. A process known as pattern separation **[G]** [65,66] keeps cognitive maps and gists distinct from one another, but they can work in concert with schemas to aid in navigation[38]. We view this as a bidirectional process: by pointing to elements that are in common, schemas bring into focus what is distinct[67].

The difference between spatial gists and spatial schemas should be revealed at a neuroanatomical level. Spatial gists may be mediated by the anterior HPC (Fig. 1), although there is lesion evidence reviewed below to suggest that they do not depend on it, at least in humans. It is possible that spatial schemas are accessed through an HPC index formed by HPC–neocortical interactions that gave rise to the schemas, but extrapolating from event schemas[22], which do not rely on the HPC, we believe spatial schemas do not depend on the HPC for their maintenance or retrieval.

An important question is whether geometric resemblance **[G]** between different navigation experiences facilitates or interferes with the acquisition of a cognitive map for a novel environment that shares common local and global properties with existing cognitive maps of previously learned environments[38]. Evidence suggests that an acquired cognitive map of a particular environment interferes with learning a novel environment that possesses features that are inconsistent with previous knowledge. In one study, experienced London taxi drivers were asked to learn the layout and scenes of a novel version of London using a reconstruction that included photographs of buildings with similar architectural style and historical period to those in London, but from another UK city[68]. Performance on spatial memory tests, such as drawing the layout of the novel environment in a sketch map and recognizing scenes from photographs, indicated that, unlike non-expert controls, the taxi drivers had considerable difficulty learning a novel version of London that differed from their previously learned version of London[68]. A more recent study similarly showed proactive interference in participants who were navigating novel virtual reality environments that contained segments that overlapped with familiar environments learned the day before. However, interestingly, experience with the familiar environment facilitated navigation in the segments of the novel environment that did not overlap with the familiar environment[37]. These findings provide indirect evidence that prior knowledge can interfere with the acquisition of spatial knowledge for schema-incongruent elements of a novel environment. The interfering effects of the original environment might suggest that a cognitive map or gist of the environment had formed, as is suggested by additional evidence that proactive interference increases as a function of cognitive mapping and self-reported sense of direction[37]. A schema, by contrast, might facilitate learning of a novel environment that resembles a familiar one. We return to the roles of geometric resemblance and local versus global scale in describing possible mechanisms of schema formation.

[H3] Spatial schemas in rodents. As was the case for early work on cognitive maps, the neurobiological mechanisms of schemas have been primarily studied in rodents using spatial learning paradigms[2,14,26], which serve as models of human episodic memory. In an influential study, rats were trained on a paired-associate memory task in which they learned the spatial arrangement of several flavour–place associations in a testing environment[53] (Fig. 2a). New paired associates that were consistent with learned associations were acquired in only a single trial. HPC lesions more than 24 hours after paired-associate learning did not disrupt the recall of original or novel paired associates. However, HPC lesions did disrupt initial acquisition if they were applied before the representation had an opportunity to undergo rapid consolidation; that is, before 24 hours. In a follow-up study, upregulated expression of immediate early genes in several regions of neocortex, including the medial prefrontal cortex (mPFC) and retrosplenial cortex (RSC), was associated with more rapid acquisition of novel paired associates in (non-lesioned) rats that were exposed to the original paired associates[54]. The more recently developed 'HexMaze', a large-scale, complex, gangway maze experienced by mice for different durations, has been used to show that the passage of time, rather than the frequency of training, is responsible for the accumulation of spatial knowledge into a long-term representation[69]. The observed learning gains in these studies were attributed to the formation of a spatial schema[53,54] (for a recent theoretical framework based on these findings, see ref. [36]).

An earlier study used a 'village maze' (Fig. 2b): a two-story, enriched environment that contains multiple rewards, which may enable the formation of a spatial schema[70]. After a few weeks' experience in the village maze, the ability of rats to learn to flexibly navigate to different rewarded locations within the maze was tested. Rats with HPC lesions but extensive experience with the village acquired those associations as quickly as controls did, whereas inexperienced HPC-lesioned rats took much longer. Such rapid updating as seen in the experienced HPC-lesioned rats is consistent with the embedding of the novel paths to a goal into a schema of the environment, rather than with completely new learning of novel paths. One possibility is that the rapid adoption of novel paths is mediated by schema-information-guiding circuits in the dorsal striatum, which are used to update a stored transition structure (choices at junctions) that is linked to a particular goal[71]. The roles of other extra-HPC structures in schema formation and use also require specification (Fig. 1).

[H3] Spatial schemas in humans. The few studies explicitly designed to examine the presence of spatial schemas in humans were largely adaptations of earlier rodent studies. In a human analogue of the paired-associate memory task, participants acquired object–location associations over a period of 302 days[72]. Consistent with previous findings[73-75], functional MRI (fMRI) data showed an activity shift from HPC to ventromedial prefrontal cortex (vmPFC) for retrieval of learned associates after 24 hours, but that with overlearning (by 90 days), retrieval responses shifted to ventrolateral PFC (vlPFC), representing a process of semanticization. Once knowledge was semanticized, the vmPFC was found to be active during retrieval of subsequently learned novel associates (from day 91 to 105) that were congruent with previously learned associates. This was accompanied by a more rapid shift of activity from HPC to vlPFC, reflecting reduced forgetting and accelerated systems consolidation.

Other human studies have used associative inference **[G]** tasks to assess the degree to which neural representations for novel inferences and prior knowledge are integrated in posterior HPC and vmPFC[22,49]. Representational similarity analyses **[G]** indicate that the representations of learned associations, particularly those that are previously established in memory, are integrated in anterior HPC and posterior mPFC, but remain distinct in the posterior HPC and anterior mPFC[49]. These findings are consistent with a fine-to-coarse detail gradient for encoding information along the posterior-to-anterior axis of the HPC[76-78] (Fig. 1). Human HPC representations for context–item associations that are accumulated over multiple learning trials also seem to generalize across events that share similar item–context associations[79]. However, specific experimental paradigms for schemas of space are needed to determine whether and how spatial schemas that arise from routine navigational experience in real-world environments differ from event schemas, and what the precise role of the vmPFC is in learning, accessing and maintaining them (Box 1).

Human studies of remote spatial memories for familiar environments offer a starting point for investigating gist-like or 'schematized' spatial representations[25,27,80]. Schematic aspects of remote spatial memories are those features that survive HPC damage and continue to support navigation[27,80]. This was demonstrated in the case K.C., an individual with bilateral HPC damage, who could produce accurate sketch maps of the overall layout of his hometown (Fig. 3) and judge relative distances and directions between its major landmarks[27,81,82]. K.C. was impaired, however, in remembering minor landmarks and perceptual details of familiar environments, despite having largely intact visuoperceptual processing abilities and semantic knowledge of those same places. Notably, K.C. and other individuals with hippocampal amnesia were still able to navigate familiar environments using only a schematic form of their spatial representation[81,82].

A spatial schema reflects the integration of spatial gists across multiple environments that have shared features, identified via statistical abstraction. Schematized spatial memories primarily include geometric properties **[G]**, rather than surface properties **[G]** [27,70,80,83]. As described above, in rats with pre-lesion experience in the complex village maze, allocentric navigation abilities are preserved after HPC lesions[70]. Navigation ability in these animals was impaired after manipulating distal cues (for example, pictures on walls surrounding the maze), however, indicating that stable room geometry determined success. The village maze is a rare example of an animal task, designed on the basis of findings in K.C., that serves as an experimental animal model of the use of pre-existing spatial schemas in humans (Fig. 2b). It provided converging evidence that semantic-like spatial representations or spatial schemas exist independently of the HPC[70]. It remains to be determined if new schemas can be acquired and/or updated by individuals with HPC lesions; findings in an individual with developmental amnesia (owing to early HPC damage)[82] and in another individual with adult-onset HPC damage[84] suggest that this may indeed be possible.

[H1] Mechanisms of spatial schema formation

[H3] Memory consolidation, generalization and hippocampal replay. The idea of schemata[21,23,62,74] or schemas[22,63] was first introduced by Henry Head in 1926 as a psychological–neurological construct to explain the organization of knowledge accumulated throughout one's lifetime[22,85-87]. Contemporary neurobiological theories of schemas[22,88,89] are based on the initial empirical observation that pre-existing knowledge accelerates the rate of systems consolidation[26,53,54] via the formation of new synapses[53,54] and laminar reorganization[90], whereby transient memories originating in the HPC become stabilized in neocortical regions, including the mPFC and vmPFC, the posterior parietal cortex (PPC), the anterior cingulate cortex and the RSC[22,25,26,90] (Fig. 1). It is important to keep in mind that, in this consolidation process, memories are transformed from highly specific instances to more generalized representations, losing specificity in the process[91]. The process of generalization, by contrast, probably relies on the formation and use of gist-based representations in the HPC rather than on the formation and use of schemas per se. For example, the generalized representations formed by rodents in the studies reviewed above seem to rely on gist-like representations rather than schemas[18,53,54]. Gist-like representations in the HPC may feed into schematic ones elsewhere in the brain, such as the mPFC in rodents and vmPFC in humans (Box 1).

However, some spatial memories retain their detailed HPC representations in perpetuity, along with their schematic representation, and these representations interact with each other, with one or the other dominating depending on various conditions, including time since acquisition, task demands and retrieval cues[92,93]. This interplay is similar to that between event schemas and representations of event details, which co-exist in both the HPC and neocortex[94]. Future work is needed to determine where and how detailed and schematic spatial (and event) representations co-exist and the conditions that influence whether they compete and/or cooperate in storage and retrieval.

A plausible physiological mechanism by which schemas develop is through the integration of repeated memories with overlapping elements during HPC replay **[G]** during slow-wave sleep (SWS)[89,95-98], through the coordination of neural network oscillations that facilitate HPC–neocortical interactions[99,100]. In rodents and humans, sleep has been found to enhance gist extraction from memory[89], HPC spatial representations[101] and explicit knowledge of regions in space[29] — mechanisms that have been attributed to schema learning[22,63]. Disruption of replay of HPC neuronal sequences in rodents during SWS[101,102] severely impairs the retrieval of spatial representations[103], suggesting that replay mechanisms are needed for the consolidation of spatial memories. On one hand, sleep enhances specific instances via HPC circuitry[101,102]. On the other hand, sleep enables the extraction of regularities across instances, the loss of contextual information and the retention of gist, as seen in representations in extra-hippocampal regions[89,97]. The focus of schema research in humans has been almost exclusively on event schemas. Although spatial schemas in humans may be instantiated through similar neurophysiological mechanisms to those underlying event schema formation, the neural substrates for the integration of spatial representations learned through navigational experience remain to be fully understood.

[H3] Geometric resemblance. The extraction of the meaning of stimuli beyond their superficial sensory properties may be the first step in capturing the essence of a schema[14,20,22], possibly mediated by gist representations. Human 'concept cells' seem to encode a stable representation of a specific person or landmark, regardless of size or viewing angle[104,105], providing sparse codes **[G]** for visually invariant abstractions related to personal events[106]. Analogous to the selectivity of concept cells, the receptive fields of place cells in the rodent HPC are sensitive to specific locations in space[60,61].

Geometric resemblance guides the generalization of spatial learning of locations from one environment to another[14-18,53,107]. Geometric features are the 3D structural features of an environment, such as the arrangement of walls, whereas surface properties include 2D features, such as visual patterns, textures and colours. These two forms of spatial features have been described in the context of core systems of intuition (such as Euclidean geometry, natural numbers and symbols) in developmental studies[108-111]. Geometric resemblance might explain findings that people are less likely to detect changes in surface properties than geometric properties of highly familiar and extensively experienced landmarks and scenes, whether tested directly by recognition or indirectly by eye-movements; if such changes are detected, the changes are at a global or coarse level[112].

When geometric or surface features are modified, the firing patterns of HPC place cells can change in a process known as remapping[11,113]. Geometric modifications are accompanied by more substantial changes in the firing patterns of place cells than are surface modifications[15,113,114], suggesting that HPC remapping actively supports the role of geometry in the stability of spatial representations[115]. Remapping is thought to underlie the ability of the HPC to store multiple unique representations of similar environments or altered states of the same environment[12]. Such remapping has been proposed to be conceived as the HPC performing 'hidden state inference', whereby sensory information is integrated with stored representations to create a 'belief' about current occupancy in the environment[116]. One possibility is that many repeated experiences with environments with a particular geometry may bias the stored representations that are used to drive the hidden state inference[117]. Such biases could form part of the mechanism by which spatial schemas influence the encoding of novel environments. For example, repeated experience with similarly configured towns might lead to biases in the states stored in the HPC, in turn leading to a more effective remapping of HPC cells when visiting a novel town that is very similar to the other towns than when visiting a novel, dissimilar town. This process of biasing stored representations is akin to how schemas supported by the mPFC facilitate pattern separation to disambiguate overlapping representations: HPC cell remapping by modifying spatial firing patterns may enable the differentiation of similar experiences or locations. In line with these ideas, Zheng et al. showed that the mPFC represents a common spatial structure across environments that have shared and unique elements[38] (see also Box 1). In this way, the HPC, guided by schemas, could extract the particular gist of the environment without attention to specific details.

Cells in the macaque HPC, termed 'schema cells,' have been found to encode task representations that encompass spatial and cognitive dimensions, dissociated from immediate visual properties of the environment[14]. The increasing similarity between firing patterns of schema cells was not driven by visual similarity between environments, as indicated by point-of-gaze maps[14,118], but by their common spatial geometry[14], and by past and future actions within the task structure[14,105]. The latter links value-based judgements to specific spatial features, enabling rewards to guide the development of spatial schemas, particularly early in their formation. These putative schema cells in the macaque may be homologous to concept cells in humans, although it is not clear whether these schema cells differ from concept cells in their stimulus selectivity[98,99]. Multivoxel pattern similarity analyses in a recent fMRI study in which participants learned item–context associations showed that HPC responses to items that share a similar context, a likely requisite for schema formation, are more likely to occur in overlapping regions than responses to items that do not share a context[79]. Overlapping item–context associations may serve as the building blocks for schemas, or for gists that combine to form schemas. Geometric resemblance could help drive spatial schema construction via HPC remapping[115]. However, schemas themselves may be better represented by cell assemblies outside of the HPC than by single schema cells, at least in humans.

[H3] Pattern recognition and gist versus detail. Pattern recognition is a neural mechanism for gist extraction and schema formation in mice[1] and humans[119,120]. In a water-maze paradigm, mice exposed to platform locations that were moved across trials according to selections from a normal distribution were able to acquire a generalized representation of the spatial distribution that was disrupted by pharmacological inhibition of the mPFC[1]. Given the known role of the mPFC in monitoring the contents of memory retrieval[22], this finding suggests that the mPFC is involved in monitoring the degree of consistency between existing schemas and novel information[1,53,121]. A recent study that used a similar distributional learning paradigm during spatial navigation suggests that statistical pattern recognition also underlies spatial gist extraction and navigation search patterns in humans[119].

Neuropsychological evidence in individuals with bilateral HPC damage, such as K.C. described above[80], indicates that the gist or overall layout of a familiar environment learned before the onset of HPC damage is preserved[3,80-82,122-124], whereas memory for details or surface properties is lost[80-82,123,124]. This distinction is similar to that found in rodents with HPC lesions and extensive pre-lesion experience in an environment: they are able to use the overall layout of the learned environment, or its spatial gist, and take detours to reach goal locations, although often not the most optimal ones[70,125,126]. Thus, whereas the (posterior) HPC seems to support detailed cognitive maps, a network of extra-HPC regions, including the parahippocampal cortex

(PHC), RSC and PPC, seems to support cognitive maps that have been transformed over repeated experiences navigating in a particular environment to form a 'spatial gist' — a summary of a specific environment[25,27,127,128]. Human and rodent lesion studies suggest that although the anterior HPC may help to generate and support a spatial gist, anterior HPC is not necessarily required to maintain or retrieve spatial gists. A collection of multiple gists makes up a spatial schema, which we argue is probably supported by the mPFC, possibly together with the HPC and a network of posterior regions (Fig. 1). It remains for future work to determine if, and to what extent, amnesic individuals with HPC damage can rely on statistical pattern recognition to guide navigation in novel environments that geometrically resemble spatial gists and schemas formed long ago.

[H3] Regionalization of space. The role of geometry in spatial schemas extends to complex human settlements[129]. Real-world spaces are segmented by physical barriers that yield various substructures or regions[41,130-133]. Recent findings indicate that a city's spatial structure is characterized by multiple subregions (such as urban zoning areas) connected via distribution networks (such as streets)[40,43,134,135]. However, regions and boundaries are determined not only by the physical structure of the built environment, but also by the way we process the environment in relation to stored knowledge in semantic memory. For example, Toronto's financial district is bounded by Lake Ontario as a natural barrier to the south, and by 'Hospital Row' to the north-west, the latter distinguished by its tree-lined boulevard as well as the style and purpose of its buildings.

The influence of stored knowledge on segmentation of environments into subregions is suggested by studies showing that human spatial representations are prone to systematic biases[136,137] and may be hierarchically organized, similar to semantic and event knowledge[133,138,139]. For example, distances between two locations are overestimated if they are separated by a barrier or boundary (such as state borders), and angles of intersections are remembered as being closer to 90 degrees[138]. Familiarity with an environment produces other biases: distances from less familiar places to more familiar places are often underestimated compared with estimates of distances from more familiar to less familiar places[136,140], and familiar locations are drawn larger on maps than are unfamiliar locations[141] (Box 1). In a virtual maze task, landmarks belonging to a semantic category (vehicles, animals or buildings) were clustered to form implicit semantic regions that exerted an influence on navigation decisions. Specifically, individuals prefer to take routes that cross fewer semantic regions, even if they are the same length as routes that contain more regions[29]. These findings suggest that semantic cues influence spatial judgements, and that heuristic-based decisions in relation to space are based on parcellating the environment into semantic regions.

Sensitivity to region boundaries may reflect a neurophysiological mechanism by which variations in different visuospatial forms in the environment are identified. Rodent HPC cells show repeated firing in multicompartment environments, with increased clustering of activity when the animal is near open doorways[15,16]. Consolidation mechanisms, such as sleep, seem to facilitate the explicit knowledge and retrieval of semantic regions and their boundaries[29]. A study in mice navigating environments with repeating connectivity patterns further shows that sleep contributes greatly to the development of spatial schemas[69]. These consolidation mechanisms might act on place cells in the HPC and on grid cells in the entorhinal cortex (ERC), which show repeating patterns of activity in an arrangement comparable to equilateral triangles that tile the environment[11]. As discussed below, the involvement of grid cells in the extraction of a gist, and ultimately a schema, is supported by fMRI evidence showing that the presence of barriers that segment an environment modulates activity in several brain regions, including human ERC[131]. The ERC may work with the HPC and occipital place area, which represent local geometry common across segments, and with the RSC, which integrates segments into a superordinate map, to give rise to a gist in the service of schema formation[39].

[H1] Networks and hubs for spatial schemas

Interacting networks of brain regions including specialized ‘hubs’ help to support navigation and spatial memory[61,142-144] (Fig. 1). Several brain regions have been implicated in neuroanatomical models of navigation, including the HPC, RSC, ERC, PHC, PPC, mPFC and inferior temporal cortex (ITC)[145]. According to one model[145], the HPC and RSC are hubs of two largely overlapping networks that preferentially support allocentric and egocentric spatial representations, respectively (see also ref.[146]). fMRI studies indicate that many of the same extra-HPC regions involved in the initial acquisition of spatial knowledge for large-scale environments are also involved in the retrieval of schematized spatial memory[27,83,128] and event schemas[22], suggesting that the core elements of spatial schemas may be laid down at acquisition[92,147-150]. Given the importance of scale and regionalization for spatial schemas, this section focuses on key regions that encode these properties.

Neural mechanisms exist outside of the HPC to represent similar substructures of an environment that may give rise to spatial schemas. For example, RSC neurons encode common features of routes with repeating segments, periodically firing across segments of routes that share a similar shape[151]. Although this finding supports the importance of a global code in capturing similar spatial contexts, the repetition-activation patterns reflect similarity between metric distances travelled in different directions from specified spatial boundaries, akin to a local code for the space traversed[151]. In either case, regionalization using physical barriers or metric distance travelled are both determined by the global properties of the environment.

The RSC has also been shown to integrate egocentric and allocentric spatial frames of reference[146,152] and to generalize local codes (that is, codes for specific regions, such as the south-west corner of a specific room) across geometrically similar environments (in this example, to the south-west corner of various rooms)[19,39,152]. In participants who learned the location of objects in geometrically similar but visually distinct (virtual) buildings[152], the representation of facing direction (for example, south-west) was generalized across environments with similar geometry, as indicated by fMRI activity pattern similarity in the RSC across multiple trials. In a follow-up study[19], when asked to navigate to a target object, participants were more likely to navigate to an equivalent location in an incorrect building rather than navigate to an incorrect location in the correct building. Similar findings have been reported in a virtual outdoor environment segmented into subspaces by a natural barrier (a river)[39].

The RSC has also been implicated in the instantiation and reinstatement of event schemas in a neuroanatomical model of schemas[22]. In our recent research, the RSC was found to code distance to goals in well-known, real-world environments, but not in recently learned environments[153]. This is consistent with the RSC providing a long-term store of the spatial structure of the environment, such as the distance between locations in an integrated spatial map of a segmented environment[39]. Such a representation might take a schematic form, such that similar distances across different environments are processed similarly or by the same neural populations in the RSC[153,154].

The ERC is another candidate for a hub involved in the formation of spatial schemas. Grid cells in the ERC are posited to provide a structural scaffold for episodic events and spatial representations[7], with ERC acting as a mediator between HPC and neocortex by providing a geometric code for the global properties of the environment[155,156]. The ERC achieves this outcome by learning the transition structure of an environment and the regularities that occur within it, offering a more generalized code that is optimal for spatial schema instantiation[157]. Recent fMRI research has revealed that, like rodent grid cells, human ERC grid-cell-like activity shifts from 6-fold rotational symmetry in an open arena to 4-fold rotational symmetry in an environment compartmentalized by barriers[131] indicating that the structure of the environment has a strong impact on how the brain organizes its representation of space.

Determining how networks that support spatial navigation, event schemas and spatial memory relate to one another is necessary to gain a better understanding of the neural underpinnings of spatial schemas in humans. fMRI repetition suppression **[G]** effects in several brain regions, including the RSC, HPC and PHC in participants navigating to target landmarks in rooms within a virtual multi-level building revealed that the repetition suppression effect was similar across rooms that had the same layout, suggesting generalization of neural representations[130]. The posterior HPC showed abstraction over different views of a room across the building, suggesting that the posterior HPC might help build a more global map of the building. This contrasts with fMRI data from participants navigating city streets presented in film footage[158]. In this context, the anterior HPC provided a more global code (tracking global street connections), while the posterior HPC provided a more local code (tracking local street connections)[158]. One possible explanation for the different engagement of the posterior and anterior HPC in generalization relates to spatial scale, with the posterior HPC encoding room or junction spaces, and the anterior HPC encoding large-scale (outdoor) spaces[76].

Representations of navigation plans[159], the regionalization of physical environments and the neural representations of physical environments[29,160] are all typically hierarchical — whereby a high-level structure encompasses multiple mid-level or low-level features. The PFC and PPC (particularly the angular gyrus) may sit atop such a functional cortical hierarchy and integrate low-level features with high-level categorical concepts to facilitate decision making. Thus, it is likely that these regions are involved in integrating statistical regularities of visual percepts with high-level semantic concepts about spatial environments to aiding hierarchical structuring of the knowledge. Investigating possible spatial processing roles of regions such as the vmPFC and angular gyrus[22,45,105] is important in filling the knowledge gap in this area. Regions implicated in scene-processing, such as the parahippocampal place area and RSC, have a role in the integration of common local properties such as surface features. A posterior region, such as AG, may bind the contents and the structure of experience at a higher level of abstraction than does the HPC[161] and, thus, is probably an important area for relating spatial gists to spatial schema (summarised in Fig. 1).

[H1] Insights from urban data analytics

Above, we have presented behavioural and neurobiological evidence to suggest that spatial schemas are a type of extra-HPC spatial representation. We suggest that schema instantiation involves pattern recognition and the regionalization of previously encountered spaces to extract a common geometric structure. In this section, we draw on ideas from other disciplines to hypothesize about the forms of spatial schemas in real-world human environments (for example, urban and rural regions).

'Form follows function' is an influential design principle often followed by architects; the structure (or geometry) of an artifact is determined by the function it is meant to serve[162-164]. For example, a building regulates the flow of air and individuals across its boundaries, similar to a living system[165]. Buildings also establish social importance and 'meaning' through embellishments and modifications to their surface properties and structural features[165]. Buildings are similar to many objects, in that they are constructed by assembling smaller parts into a whole, whereas buildings differ from many objects in that buildings create volumes of space through the arrangement of objects, such as walls[166,167]. The structures in the built environment have arisen mainly through collective activity of humans sharing a common goal. This drive to make buildings for humans comes with its own evolved functions in humans just as in other species, such as termites, which create structures in their mounds. Future research may help us understand the links between the schemas created to navigate the built environment and the schemas that drive the constructions of the urban realm.

One approach to understanding how the built environment is organized and related to human behaviour is through the field of space syntax[166]. Space syntax aims to identify the series of construction steps or local rules that result in a global spatial pattern. For example, if a small square cell is adjoined by other squares on three sides, and the process is repeated, a 'courtyard complex' scheme is generated[166]. Local rules often define the topological relations of containment and boundary[165]. These local rules give rise to the global form of real human settlements. For example, the global form of 'beady-ring' settlements of Les Yves in southern France results from a recursive addition of spatial units according to a local rule[165]. Space syntax theorists have identified other elementary formulae besides the courtyard complex and the beady-ring templates, such as central spaces, blocks and ring streets. These investigations have shown that variations in local rules lead to different probabilities for different global spatial forms[166]. Different classes of spatial configurations are associated with differences in the connectedness of regions of space and thereby influence the movement and interactions of individuals in space[168,169].

Graph-theoretic measures of street networks have also been used to operationalize the essential urban elements that characterize a city form, as theorized by the urban theorist Kevin Lynch[33,34]. Through qualitative analysis of verbal descriptions of Boston residents, Lynch found that the presence of these essential elements in their descriptions was associated with the ease with which navigators understand the spatial coherence of their environment[33]. Five elements — landmarks, paths, nodes, edges and districts – have been identified as building blocks of a common understanding of the space that is shared amongst people with extensive experience of the region. In a more recent computational study, the original sketch map of Boston consisting of elements collectively described by its residents, was recreated using graph-network indices such as betweenness centrality **[G]**, incidence angle of vertices and modularity optimization[34]. As mentioned in the section on regionalization of space, findings from spatial cognition studies in humans show that semantic knowledge and language cues exert a powerful influence on human spatial judgements[29,138] and may contribute to spatial schemas. Spatial forms have also been proposed to be a 'fossil' the reflects the social and psychological characteristics of a group of people that share common linguistic and cultural values[166,170]. Similarly, virtual landmarks may help in navigating electronic space (such as the world-wide web) by influencing the frequency of visits and connectivity between related webpages[171].

Space syntax has been used to study prototypical spatial patterns on a global scale (for example, across different street grids)[166,172]. First, a city street network is transformed into a network of lines using its topological properties[34,173-175]. For example, a long straight main road can be represented as a single axial line **[G]** or as a large set of connected street segments **[G]**. Space syntax-derived segment and axial maps can then be analysed as various types of graphs to derive spatial measures, such as connectivity (measured using the graph-theoretic index of degree centrality), integration (closeness centrality) and choice (betweenness centrality)[175]. A city street network can thus be represented as a graph in which street segments or axial lines are the units rather than the nodes. 'Integration' measures the extent to which a street is close to the topological centre of the network and is typically measured on an axial map, whereas 'connectivity' measures the number of immediately connected streets. 'Choice' measures the likelihood that a street segment would be traversed when all paths through the network are considered, and it typically includes a measurement of the angular displacement between segments[173-175].

To understand how such space syntax measures might be reflected in neural dynamics during navigation, researchers have used fMRI to track responses to connectivity, integration and choice during the simulated navigation of a real city[158]. When navigating recently learned city streets in London, UK, activity in the anterior HPC increases when entering streets with greater global connections (that is, with higher integration) and decreases when entering streets that are less globally connected[176]. Such responses probably reflect the activity of neurons that, during exploration, learn the important, highly connected streets that maximally enable navigation across the network of city streets. The posterior HPC is also responsive on entering streets, but rather than signalling a global code, it reacts to the connectivity (for example, showing higher activity when entering a road with many connections than a road with dead-end). The different functional responses of the anterior and posterior HPC may reflect the role of these brain regions in simulating future routes through the street network.

Urban data analytics further show that industrial cities can be classified using characteristic spatial patterns and common principles, such as an organization centred around nodes of economic activity[42,43,129,177]. Industrial cities in different regions of the world are suggested to exhibit scale-invariant structural characteristics (for example, road networks)[40,129], whereas the number of nodes and their configuration depends on infrastructure development, size and other sociocultural factors[40].

Interestingly, the mobility patterns of individuals towards and away from nodes of economic activity in cities are consistent over time. Analysis of daily travel patterns of individuals using origin–destination matrices indicates stable movement patterns between functionally distinct regions (such as residential and commercial regions) in different cities[177]. Given that these statistical commonalities of mobility patterns characterize the underlying structure of a city[41,43] and navigational behaviours[34,117,178,179], they provide support for the notion of a spatial schema for an environment with key elements that can be generalized to other environments that belong to a superordinate category[159].

The observation that local rules drive global form in human settlements[166] suggests a link between gestalt **[G]** notions of grouping (or assembling parts into a unit) and configuration (or positioning the units in space)[180]. For example, the topological relations of containment and boundary resemble the gestalt grouping rules that organize visual percepts at a neuronal and behavioural level[180-183]. Similarly, studies of fractal geometries in urban scenes, in which smaller units reflect the statistical properties of the global geometry[129,183,184], may help determine whether variations in fractal dimensions affect spatial judgements and navigation performance[185].

Alongside the allocentric graph-theoretic indices such as integration and choice, measures that involve egocentric information have been derived within the from space syntax framework to characterize spatial relationships in scenes (also known as vista spaces). For example, viewshed analysis (which uses 2D polygons known as isovists to represent the visible area from a given vantage point) have been used to characterize local scenes[186]. Future studies that combine fMRI and 3D simulations of real-world environments in virtual reality are needed to examine how the relationship between local indices, such as isovists, and global connectivity measures might be reflected in brain activity. Recent work has shown that the connectivity of a space in view is reflected in the activity of the occipital place area[18], but how this connectivity extends to active navigation is not known. Longitudinal studies are also needed to investigate the interactions between early navigation experiences and individuals' spatial cue preferences (for example, for geometric versus surface features) over the course of development[108-111].

Recent evidence from testing virtual navigation ability in about 3.9 million people worldwide with the game Sea Hero Quest[117,178] has revealed that people who report having grown up in the cities of countries with 'grid-like' cities (such as the United States and Argentina; Fig. 4) are generally worse navigators than people who grow up in cities with disorganized layouts (such as Prague, London or Paris)[117] or outside cities entirely. However, people who grew up in 'griddy' cities had a slight advantage at navigating grid-like virtual environments in Sea Hero Quest (Fig. 4c), suggesting that experience of gridded cities does not have a purely negative effect on navigation skill[117]. These findings suggest that our early-life experiences with environments lead to the formation of spatial schemas that support particular navigational approaches that prepare us to variable extents for navigating different novel terrains[187].

[H1] Conclusions

We have reviewed an interdisciplinary body of work to encourage future studies on the topic of spatial schemas. A cognitive map can vary in precision from a highly detailed map to a gist, whereas a schema is a knowledge structure that is extracted from multiple gist-like cognitive maps in a way that is similar to how schemas form from events. Schemas may be built through specific expectations on the basis of a store of many repeated cognitive maps, culminating in a meta-map prediction of what lies ahead in the environment in which we are navigating. We propose that the integration of overlapping features of similar environments results in prototypical spatial forms that act as templates for wayfinding behaviour in novel contexts. We have presented evidence from animal and human studies that suggests that geometric resemblance is a key feature of environments that gives rise to generalizable spatial representations. We have discussed the distinction between geometric and surface properties as two forms of spatial representation that parallel the dissociable gist and detailed aspects of remote spatial memories.

Several questions remain to be addressed. For example, do spatial schemas form along a posterior-to-anterior axis outside of the HPC, representing gradient of detail similar to what has been found within the HPC[76-78]? How are schemas used to guide current navigation in novel and familiar environments, and when might schemas impede navigation? How might neural oscillations facilitate communication among the HPC and PFC via RSC to instantiate spatial schemas[188]? To what extent does a spatial schema, once instantiated, interact with rewards and goals?

Future studies that are needed to address these questions require the convergence of computational techniques (Box 2) with theoretical frameworks of memory consolidation and spatial navigation in familiar, real-world environments. There is potential for the application of urban-data-analytic methods, such as those involving space syntax and agent-based modelling[189] in paving the way for systematic investigations of navigational experience in real-world environments (Box 3). These techniques are needed to quantify geometric and surface properties of spaces at different scales. An interdisciplinary approach to the study of spatial schemas may inform urban planning policies of future human cities that better respond to the needs of diverse populations, including individuals vulnerable to memory-system — and, thus, navigational — deterioration.

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Figure 1 | Neurocognitive framework of spatial gist and schema. Schemas are dynamic knowledge structures formed by extracting generalizable common features of particular detailed episodic events. It follows that spatial representations may also reflect the accumulation of 'spatial gists' of an environment type (for example, a grid-like city) that are extracted from multiple experiences navigating similar or different environments. A spatial schema is a term used to describe the representation of a particular type of environment (such as a city central square or waterfront area; part **d**) rather than a specific environment (such as Nathan Phillips Square or Harbourfront in Toronto; part **c**). A spatial schema is a consolidated distribution of spatial gists for a given prototype (panels **a,d**). 'Spatial gist' is a term used to refer to abstract spatial elements that, if removed, alter the identity of a specific environment. This concept is depicted in panels **b** (scene level) and **e** (street level). A hippocampus (HPC)-based representation of an environment is highly linked with detailed perceptual features of episodic events (panels **c**,**f**). The medial prefrontal cortex (mPFC) facilitates schema development by linking spatial features with goal-relevant actions and behaviours. A network of posterior regions, including parahippocampal cortex (PHC) and posterior parietal cortex (PPC), is involved in representing perceptual features and spatial relations. The RSC serves as a hub for translating information between two orthogonal frames: detailed or local cues versus coarse or global cues, and egocentric versus allocentric. Environment geometry input is received by the entorhinal cortex (ERC). Statistical learning of spatial context is integrated in the angular gyrus (AG) and mPFC into spatial schemas and is continuously updated through reciprocal connections with HPC and other posterior regions. Importantly, although the various posterior regions play specialized roles in representing components of surface properties and their relations and/or coding of these properties within local or global scales, it is the interaction of hubs with networks of regions that eventually gives rise to spatial schemas. AG, angular gyrus; aHPC, anterior hippocampus; EC; entorhinal cortex; mPFC, medial prefrontal cortex; PHC, parahippocampal cortex; pHPC, posterior hippocampus; RSC, retrosplenial cortex. Photo of Toronto waterfront credit: rabbit75_ist/Getty.

Figure 2 | Spatial navigation paradigms. **a |** The event arena[53] contains a 7x7 grid of potential sandwell locations, from which a map of 6 distinct flavour–location associations are formed over time (left). The lines between the wells represent an overall schema that the flavour-location pairs constitute. Four start boxes are located around the maze along with intra- and extra-maze cues (star, hexagon). In an individual trial (centre panel), the rat is given a flavoured pellet (such as a banana-flavoured pellet) in the start box, and it has to go directly to one of the six sandwells for additional banana pellets (red dashed arrow; repeated for the remaining five flavours). With extensive practice across 3 months, the rats show improved performance, indicated by increased digging time in the correct location and fewer errors when choosing the location in which to dig first. After 9 weeks (right panel), an update to the flavor–place associations is made, with two new flavours placed in new locations, represented by red symbols on the maze. This update can be learned following a single exposure[36]. **b |** In the village maze paradigm[70], rats were reared and trained to find rewards located in a multi-level environment over an extended period of time. Following lesions to the hippocampus (HPC group) or sham lesions (control groups), rats were tested over the course of 10 days in the original environment (not shown) or in a modified version of the pre-operative environment. The effect of HPC lesions on remote spatial memory in rats navigating altered environments was measured based on errors in finding reward locations. Experimental manipulations included moving the village apparatus to a different room with novel distal cues but the same room geometry (left graph), changing the identity of distal cues in the original room (middle graph) and rotating the village apparatus by 180 degrees in the same room (right graph). Errors in rats' ability to find reward locations were measured over the course of 10 days in HPC-lesioned rats (HPC) and sham-lesioned (control) groups. HPC-lesioned rats were severely impaired in room change and village rotation conditions, but performed well in the cue distortion condition. These findings indicate that HPC-lesioned rats used stable room geometry rather than distal or surface cues to navigate to correct goal locations. Therefore, geometric cues, rather than surface properties, seem to facilitate allocentric navigation in a highly familiar environment, despite HPC lesions[70]. Part **a** is adapted with permission from ref. [36], Sage Publications. Part **b** is adapted from ref. [70], Springer Nature Ltd.

Figure 3 | Sketch map test of remote spatial memory. Sketch map of a highly familiar neighbourhood drawn by an individual with amnesia (known as K.C.; left) and a control participant who grew up in the same neighborhood (right)[213]. Although the overall spatial configuration of K.C.'s sketch map was intact, he included fewer streets and landmarks than did control participants. Sketch maps drawn by other individuals with amnesia relating to bilateral hippocampal damage are similarly accurate in terms of overall layout yet similarly impoverished in detail[81,82]. This pattern of performance suggests that the hippocampus is needed for detailed spatial representations, similar to its role in episodic memory[4-6,20]. Figure reprinted with permission from ref [213], Elsevier.

Figure 4 | Examples of street networks and their association with the development of navigation ability. **a |** Street networks for the centres of the 10 most populous cities in Argentina and Romania; two countries that differ most in terms of the organized versus disorganized orientations of their streets[115]. **b |** Screen shots from the virtual navigation task Sea Hero Quest, in which participants navigate a boat to checkpoints. Trajectory data was collected from 3.9 million participants to estimate the population performance from 38 countries. **c |** Example trajectories (overlaid density plots of thousands of participants) for nine environments tested , at increasing levels of difficult in the game Sea Hero Quest. **d |** Calculation of the street network entropy (SNE), which measures the extent to which streets are misaligned with one another. Polar plots of the frequency of street misalignment in Prague (high SNE, 3.6) and Chicago (low SNE, 2.5). **e |** Association between SNE and the effect size for the negative impact of growing up in a city compared to non-city participants, and also the identification of two clusters of countries (with high and low SNE). Argentina and the USA have the largest gap in performance between those who grew up inside cites versus those who grew up outside cities, whereas Romania lies at the other end of the scale. **f |** Participants who reported growing up in cities from the low-SNE countries were most impacted by environments in Sea Hero Quest with a high SNE, and marginally better at navigating grid-like environments with a low SNE. The repeated exposure to street network patterns during development are proposed to cause generalizations mediated through a learned spatial schema (for example, of what to expect in griddy or non-griddy environments)[117]. Figure adapted from ref. [117], Springer Nature Ltd.

Box 1 | Contributions of ventromedial prefrontal cortex to spatial schemas

The ventromedial prefrontal cortex (vmPFC) features prominently in the literature on event schemas in humans[22,190]. Similar to a cognitive map, the vmFPC may support a flexible representation of the world, providing structure to make sense of an ongoing stream of sensory input to enable relational inferences[191]. The vmPFC and orbitofrontal cortex have been implicated in reward valuation, decision-making, social cognition and monitoring the contents of memory retrieval. It is unclear whether and how these processes link together and factor into spatial schemas. One possibility is that these processes may interact with a spatial schema as it forms and acts as a scaffold for the unfolding of events[20]. Similar to the contents of an event schema, the contents of a spatial schema might take on value. This value attribution may be reflected in the finding that familiar places are drawn larger than unfamiliar places[141], as well-known places are most likely to be valued or to contain reward.

Another possibility is that spatial schemas are instantiated separately from event schemas, in a more dorsal region of the mPFC, which has been associated with planning, goals and attention[192]. This possibility is further suggested by evidence of grid-like coding in mPFC similar to that observed in entorhinal cortex[193]. The proximity and strong interconnectedness of dorsomedial prefrontal regions with premotor and supplementary motor cortex[194] might help to facilitate the integration of planning and goals with locomotive aspects of navigation. Once formed, the spatial schema might interact with rewards and motivations via connectivity with more ventral regions of prefrontal cortex, which, in turn, play a role in dimensionality reduction **[G]** to enhance goal-relevant landmarks[195]. In this way, a schema may be necessary to make the goals more apparent for a particular task and to monitor attainment of a goal, where the goal is a spatial destination. Studies of consolidation and remote spatial memory in rodents have focused on more dorsal regions, particularly anterior cingulate cortex[196,197], but evidence in humans is sparser. There is some functional MRI evidence of increased activation of the dorsomedial prefrontal cortex in highly familiar environments that had been navigated extensively over many years[127,154], even following bilateral hippocampal lesions[198], but the precise conditions in which this region is activated is unclear. Targeted studies asking individuals with mPFC lesions to describe a spatial schema are needed. In one such study, the difficulty that an individual with vmPFC damage, who was known as L.G., had in navigating in a familiar environment was found to relate to L.G.'s inability to maintain a goal in mind, rather than to a loss of schema representations per se[199]. L.G.'s knowledge of the routes and of the locations of landmarks along them were intact; he needed only to be reminded of the goal for the representation to be expressed appropriately during navigation.

Box 2 | Computational approaches to understanding spatial schemas

To establish whether a spatial schema of a real-world environment (such as a city) is formed, the degree of generalization of spatial learning across different environments must be systematically investigated. However, systematic measurement of quantitative differences in the spatial organization of real-world environments, which often have varied layout patterns and route morphologies, is a major challenge[40-42,44,132,176,200].

Unravelling the complexities of the cognitive structure and neural basis of spatial schemas requires modern computational approaches, such as deep learning and urban analytics, to ascertain how perception and memory interact with built environments. Neural network models are powerful tools for understanding pattern recognition mechanisms that underlie visual perception, whereas Bayesian generative models explain how abstract prior knowledge is used to make inferences about familiar and novel stimuli[28,201-203].

Computational approaches have also provided converging evidence of a core network of brain regions that enable schemas, as identified in patient-lesion and fMRI studies. A neural network model of brain regions underlying spatial schemas, consisting of an HPC-supported indexing stream and a neocortex-dominant representation stream[201], replicates early experiments in rodents[53,54]. A deep neural network that mimics the computational mechanisms in the primate posterior parietal cortex suggests that high-dimensional sensory inputs from scenes (that is, global properties) are projected onto low-dimensional inputs (that is, local properties) according to a learned spatial structure, akin to a spatial schema in this region[160].

Formal artificial intelligence models provide flexibility in planning and account for a range of biological processes at neural and behavioural levels[204]. A model-based algorithm **[G]** has been designed to plan optimally the shortest route between two points in a network by partitioning the environment into modules and planning first across modules and then within modules. Studies of navigation support the idea that navigation planning follows a hierarchical representation of space that consist of a series of contexts that, in humans, is mediated by the dorsomedial PFC[128,133,159,204]. The regionalization of space provides an efficient heuristic for planning actions in spatial navigation[29,131,159,205,206], and computational models are particularly useful in understanding the correlations between physical regions and substructures, and their representations in the brain. A helpful approach in future work will be the comparison of different simulated agents with rats and humans in an identical navigation task, which would enable the integration of human and rodent neuroscience methods with the study of artificial intelligence agents[207].

Box 3 | Topology and urban analytics

Topology **[G]** is a mathematical concept that provides a quantitative measure of equivalence between different geometrical forms such that they can be continuously morphed into each other using scale-invariant transformations. For example, sections of the urban fabric of Mumbai can be deformed using topological transformations into the suburban neighbourhoods of Las Vegas or into the regular grid structure of New York city blocks[208]. Studies that focus on mathematical analyses of topology have helped us gain insight into spatial patterns that characterize different types of environments[43,135,208]. For example, a dominant model of modern city form is the clustering of economic activities in urban hubs, known as polycentricity[43,209]. The patterns of individuals' movement to and from urban hubs across cities can be collected using GIS (geographic information system) tools and phone-usage data[40,43,177,210]. The pattern of an individual's movements around a city seems to be highly consistent over an observational period of 6 months[177]. Moreover, mobility patterns of 90 percent of the population in different countries can be captured by repeating 'motifs' of individuals' movements over time[177]. It is interesting to consider whether these motifs represent routine navigational behaviours or spatial regularities that constrain individual decisions. Spatial schemas are stable neural representations of such environmental regularities, similar to how statistical regularities form priors or expectations in visual perception[28,47,211,212].

Glossary

Cognitive map

A representation of relationships among allocentric spatial elements or features in a particular or single environment.

Spatial gist

Essential elements of a particular environment.

Spatial schema

A generalizable spatial representation derived from experiencing many similar environments.

Event schema

A structured body of prior knowledge that captures common patterns across related experiences of events.

Landmarks

Defined physical elements, such as objects and buildings, that are salient and/or hold functional or navigational meaning.

Nodes

Strategic points of crossing or convergence.

Paths

Channels along which observers move, such as streets or walkways.

Districts

Large-scale sections with a common identifying character, into which observers can enter.

Edges

Boundaries between two regions that breaks line continuity, such as a waterfront.

Predictive coding

A neural process by which expectations or 'mental models' of the external world based on prior experience are compared against sensory input.

Allocentric

A frame of the representation of spatial relationships among objects in an environment, that is irrespective of an observer's point of view.

Pattern separation

A process by which overlapping patterns of neural activity that represent highly similar items or events are made more distinct as they are encoded in memory.

Geometric resemblance

Similarities in geometry within an environment or across multiple environments, such as highly similar arrangements of buildings at two different intersections.

Associative inference

Assesses learning of a third latent association B–C following direct learning of overlapping associations A–B and A–C.

Geometric properties

Three-dimensional structural features of an environment, such as the arrangement of buildings at an intersection.

Representational similarity analyses

Characterizations of the neural representation of a stimulus presentation through direct pairwise comparisons of imaged activity patterns associated with each experimental condition in selected brain regions of interest.

Surface properties

Two-dimensional features, such as visual patterns, textures and colours.

HPC replay

Reactivation of the sequence of neuronal firing within the HPC that occurred during a previous experience, believed to contribute to the long-term storage and reconsolidation of memories.

Sparse codes

Activation of a small subset of neurons representing a distinct item or event.

Repetition suppression

Reduced neural activity in response to repeated presentation of a stimulus.

Centrality

In network analyses, measures such as degree, betweenness and closeness that provide indices of connectivity.

Axial line

The longest straight line representing the maximum extension of a point of space.

Street segments

All the unique sections of a street between junctions that make up a street.

Gestalt

Principles to explain how individual elements are perceived as an organized whole.

Dimensionality reduction

A technique that is widely used in machine learning to reduce the number of attributes in a dataset while maintaining similar information.

Topology

Mathematical property of geometric objects that are unaffected by continuous change of size and shape.

TOC blurb

Schemas are structured bodies of prior knowledge that reflect common patterns of information from related experiences. In this Review, Farzanfar et al. discuss evidence for spatial schemas, how they form and how they differ from cognitive maps.