

Opinion

Knowledge Across Reference Frames:
Cognitive Maps and Image SpacesRoberto Bottini^{1,*} and Christian F. Doeller^{2,3}

In human and non-human animals, conceptual knowledge is partially organized according to low-dimensional geometries that rely on brain structures and computations involved in spatial representations. Recently, two separate lines of research have investigated cognitive maps, that are associated with the hippocampal formation and are similar to world-centered representations of the environment, and image spaces, that are associated with the parietal cortex and are similar to self-centered spatial relationships. We review evidence supporting cognitive maps and image spaces, and we propose a hippocampal–parietal network that can account for the organization and retrieval of knowledge across multiple reference frames. We also suggest that cognitive maps and image spaces may be two manifestations of a more general propensity of the mind to create low-dimensional internal models.

Organizing Knowledge in Low-Dimensional Space

Every second, our brains process an amazing amount of information, perceive a dynamic and complex sensory environment, and spontaneously generate countless thoughts. Making sense of this vast amount of data must rely on some structure and organizational principles [1,2]. Determining exactly what these organizational principles are has proved to be a formidable challenge [3–5]. However, convergent evidence from neural, cognitive, and information sciences is pointing toward a fascinating hypothesis: that the human brain may organize knowledge into **low-dimensional spaces** (see [Glossary](#)) that we can easily navigate, explore, and manipulate as we, for example, navigate a familiar environment, explore a picture in a frame, or manipulate an object in our hands [1,2,6,7]. In other words, the neural machinery that evolved to map objects and structure events in the physical world may have been recycled to map and structure knowledge within our minds [6].

Although this idea, broadly taken, has a venerable tradition [8–11], research in cognitive science and neuroscience has only recently provided solid empirical ground for this view. We review here evidence suggesting that the neurocognitive structures and algorithms that are recruited to represent and navigate space are also recruited to represent and navigate (nonspatial) conceptual knowledge. In particular, we focus on, and contrast, world-centered **cognitive maps** (that are usually associated with the hippocampal formation) and self-centered **image spaces** (usually associated with the parietal cortex). We then attempt to integrate cognitive maps and image spaces with the mechanisms of a hippocampal–parietal network, inspired by current models of spatial navigation and based on complementary reference frames (**allocentric** and **egocentric**). Finally, we discuss the role of low-dimensional conceptual spaces in cognition.

World-Centered Cognitive Maps and the Hippocampal Formation

A long history of neuropsychological studies with amnesic patients [12,13] and more recent neuroimaging experiments [14] have shown that the hippocampal formation (i.e., the hippocampus proper and surrounding cortices) is crucial for memory formation and retrieval. However, the

Highlights

Conceptual knowledge is partially organized in low-dimensional geometries – ‘cognitive maps’ – that are analogs of world-centered representations of the environment, and are associated with the hippocampal formation, and image spaces, that are analogs of self-centered spatial relationships and are mostly associated with the parietal cortex.

The complementary activity of cognitive maps and image spaces during conceptual retrieval and manipulation may be akin to the dual system involved in spatial navigation, which is based both on self-centered and world-centered information.

Low-dimensional mental geometries such as cognitive maps and image spaces may play a crucial role in goal-directed cognition, analogical thinking, generalization, and the structuring of abstract conceptual domains.

¹Center for Mind/Brain Sciences (CIMeC), University of Trento, Trento, Italy

²Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

³Kavli Institute for Systems Neuroscience, Centre for Neural Computation, The Egil and Pauline Braathen and Fred Kavli Centre for Cortical Microcircuits, Norwegian University of Science and Technology (NTNU), Trondheim, Norway

*Correspondence: roberto.bottini@unitn.it (R. Bottini).

hippocampal formation is also involved in spatial navigation and perception [7]. Two types of neurons are important for spatial navigation: **place cells** and **grid cells** (Figure 1A). Place cells [15] in the hippocampus fire when an animal traverses a specific location in an environment. Grid cells [16] discovered in the entorhinal cortex (EC) fire instead at multiple locations arranged in a strikingly regular hexagonal grid that tiles the local environment in a map-like fashion. Place cells, grid cells, and other spatially tuned cell types in the hippocampal formation (e.g., border cells, head direction cells) are thought to constitute the navigation system of the brain [17]. Although originally discovered in rats, grid-like coding was later observed with noninvasive brain imaging techniques in humans (fMRI) using an analysis that relies on the symmetrical sixfold periodicity of these spatial representations [18]. Experiments in which participants navigated a virtual reality environment in the MRI scanner (Figure 1B, upper panel) showed a characteristic grid-like modulation of the blood oxygen level-dependent (BOLD) signal in the entorhinal cortex as a function of movement direction [18]. Interestingly, grid-like activity extended beyond the hippocampal formation to portions of the cortex that are usually implicated in conceptual representation and high-level cognition, such as precuneus and medial prefrontal cortex. Grid-like activity has been observed also during imagined spatial navigation [19,20], and the presence of grid cells in human entorhinal and medial prefrontal cortices, as well as of place cells in the hippocampus, has been confirmed via single-cell recordings in implanted epileptic patients [21,22].

In addition to real and imaged navigation, place and grid cells also support the exploration of visual scenes [23]. Spatial view cells (similarly to place cells) increase their firing rate when a particular environmental location is observed, and have been recorded in the primate hippocampus [24,25]. Grid cells also encode the location of gaze during free viewing of visual scenes, both in monkeys [26] and humans [27,28]. The involvement of the hippocampal formation in spatial perception (beyond memory and navigation) is also known from neuropsychological studies showing that amnesic patients with hippocampal damage are also impaired in recognizing scenes, compared with faces, objects, or colors [29]. More specifically, the spatial perception of patients with hippocampal damage seems to be particularly impaired when processing multiple spatial relationships [30] or when information gathered from several fixations needs to be bound into a cohesive percept [31,32]. In sum, the hippocampal formation (especially the hippocampal-entorhinal system) seems to provide a world-centered and relational map of the surrounding environment [16,18] and of perceptual landscapes [26–28] to guide both navigational and viewing behavior [23].

Crucially, conceptual (nonspatial) processing also seems to rely on the same place- and grid-like organization. When rats were trained to distinguish between different sound frequency levels in exchange for food [33], place cells in the hippocampus fired for particular frequencies, and grid cells in the EC fired for multiple frequencies (paralleling the single-place and multiple-place receptive fields in spatial environments for place and grid cells, respectively). Crucially, in a second experiment in which rats navigated an enclosure, the same exact cells that fired for sound frequencies also fired for spatial locations, showing that place and grid cells are recruited to represent both spatial and nonspatial information. In humans, evidence that conceptual knowledge can be organized spatially into cognitive maps comes from an experiment in which participants learned to associate arbitrary Christmas symbols with different bird silhouettes [34]. The birds differed between each other in terms of neck and leg length (Figure 1B, lower panel). Thus, learning bird-symbol associations could be seen as placing the symbols in 2D 'bird space', defined by neck length and leg length. However, this conceptual space was never made explicit, and the participants did not realize the possibility of such a representational framework [34]. Nonetheless, when participants entered the MRI and performed different tasks involving the Christmas symbols, the authors were able to track the 'movements' from one symbol to the other in the conceptual

Glossary

Alloentric: an alloentric reference frame is a coordinate system that is referenced to spatial landmarks and encodes the relationships between objects in the environment. Alloentric representations are independent of the subject's point of view.

Analogy: in its more general sense analogy concerns the ability to compare features and relational patterns across different conceptual domains.

Cognitive map: originally intended as spatial representations encoding locations and objects in Euclidean space from an alloentric point of view, the term has been extended to a general low-dimensional organization of information along selected feature dimensions.

Egocentric: an egocentric reference frame is a coordinate system centered on one's own body, part of it, or a given vantage point (also known as self-centered reference). Egocentric representations change depending on the point of view of the subject.

Grid cells: entorhinal neurons that fire in several locations that tile the environment according to a regular hexagonal lattice.

Grounded: conceptual knowledge that is grounded is represented according to internal models that have been learned during sensorimotor interactions with the environment.

High-dimensional spaces: mental representations in which concepts are seen as points in a space that is determined by several dimensions.

Image space: low-dimensional, self-centered, and flexible spatial configuration of mental resources that is maintained to organize knowledge and facilitate behavior.

Low-dimensional spaces: mental representations in which concepts are seen as points in a space that is determined by a few (e.g., 1 or 2) selected dimensions.

Mental number line: conceptual organization in which numbers (or magnitude in general) are represented according to a scalar linear schema that can be oriented along the horizontal (left/right) or vertical (bottom/up) axis.

Mental timeline: conceptual organization of the succession of events according to a line that can be oriented along the sagittal (back/front), horizontal (left/right), or vertical (e.g., top/down) axes.

'bird space' by using hexagonal symmetry, and grid-like activity was seen in most of the areas previously observed during spatial navigation. Such a grid-like coding of nonspatial conceptual knowledge has also been demonstrated in studies where human participants navigate an olfactory space composed of a combination of odor stimuli [35] and a feature space defined by the size and pitch of fictional objects [36]. Beyond a specific grid-like code, evidence that the hippocampal–entorhinal circuit organizes nonspatial experience into a relational and metric configuration that is well captured by low-dimensional geometries extends to several cognitive domains such as statistical regularities of events [37], their temporal duration and succession [3,38,39], concepts in abstract feature spaces [40], semantic relationships [41], the structure of episodes in complex narratives [42] and the relationship between characters in social interactions [43]. In sum, there is evidence that nonspatial conceptual knowledge can be organized in low-dimensional cognitive maps akin to the spatial representation that supports navigation in the physical world [2].

Place cells: hippocampal neurons that are active when the animal occupies a particular location in an environment.

Primary conceptual metaphor: a cognitive process in which a conceptual domain (e.g., time) is represented by borrowing features (and/or relations between features) from another conceptual domain (e.g., space), based on straightforward experiential correlation (moving for longer time = moving for longer space). Usually, the source (donor) domain is more concrete and has stronger sensorimotor bases than the target domain.

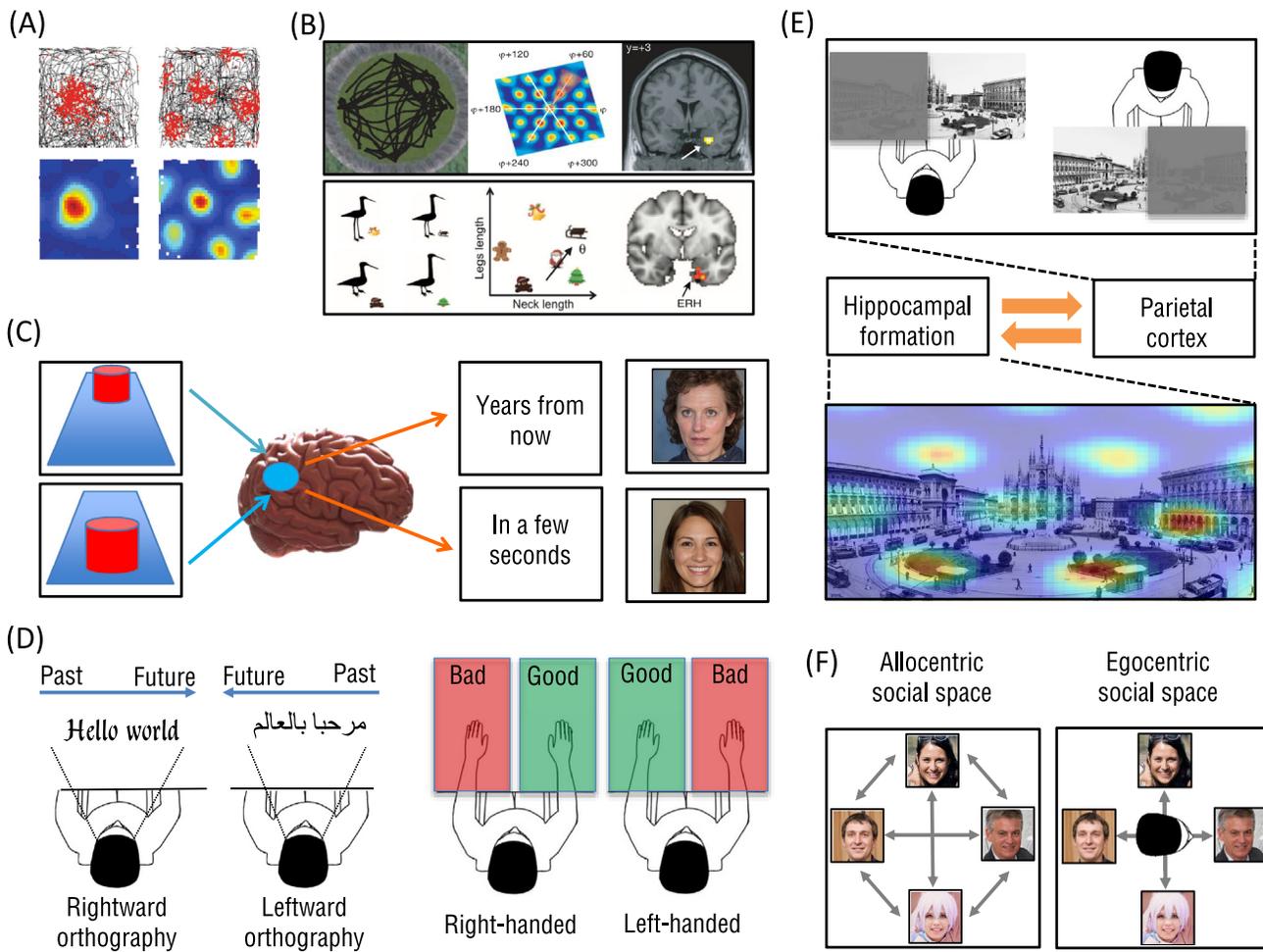
Self-Centered Image Spaces and the Parietal Cortex

Another crucial brain region for spatial cognition is the parietal cortex, which is known to represent the location of objects according to an egocentric frame of reference (e.g., whether something is left/right, up/down, or far/close relative to the body [44–47]). Neurons in the parietal cortex support both bottom-up and top-down shifts of attention towards different parts of space [48] and encode the spatial distance of objects from the self [49].

Interestingly, recent studies have found evidence that the inferior parietal cortex also encodes emotional and temporal 'distance', from an egocentric point of view [49]. Indeed, a machine-learning algorithm trained to classify spatially close and distant objects based on neural activity in the inferior parietal lobule (IPL) is able, without further training, to classify close or distant events in time (e.g., the sentences 'in a few seconds', 'a year from now' or pictures of emotionally 'close' and 'distant' friends [50], Figure 1C). Similarly, in another study, the right IPL was activated when participants engage in both mental space travel (positioning oneself in a given city, and moving east or west) and in mental time travel (positioning oneself in a given year, and move past or future), encoding both the spatial and temporal distance traveled [51].

The idea that not only spatial relationships but also other conceptual domains can be represented in an egocentric spatial frame of reference has been largely investigated in behavioral and neuropsychological studies [52]. Time is a paradigmatic example. Temporal succession is represented in a **mental timeline** along the horizontal left–right axis (Figure 1D, left panel). Participants in behavioral experiments are faster to categorize earlier events by pressing a left key and later events pressing a right key compared with vice versa [53], people spontaneously gesture according to their mental timeline when talking about temporal relationships [54], and patients with left spatial neglect also neglect the 'left side' of time: in a task where they learned a fictional person's past and future preferences ('used to like lasagna', 'will enjoy pizza'), they selectively misremembered the past preferences [55].

Both temporal and numerical knowledge are represented spatially. Numbers are represented along a **mental number line**, where lower numbers are associated with the left side of space and higher numbers are associated with the right side [56]. For instance, when asked to generate random numbers, participants move their eyes according to the magnitude they have in mind, and spontaneously look to the right before saying a larger number word (relative to the previous word) and to the left before saying a smaller number word [57]. Similar effects are found for other examples of ordered domains (such as days of the week, or letters of the alphabet), and for random lists of items temporally ordered in memory [58,59], as well as for several other cognitive domains. For instance, higher and lower pitches are spontaneously associated with higher and



Trends In Cognitive Sciences

Figure 1. Allocentric and Egocentric Organization of Spatial and Nonspatial Conceptual Domains. (A) Firing of a place cell (left) and a grid cell (right) recorded from the rat hippocampus and entorhinal cortex, respectively (adapted, with permission, from [17]). (Upper panel) Spike locations (red dots) are shown on the animal's path (black line) through a square enclosure. (Lower panel) Autocorrelation firing fields reveal the unique spatial field of place cells (left) and the regular hexagonal field of grid cells (right). (B) (Upper panel) Hexadirectional blood oxygen level-dependent (BOLD) signal emerging in the entorhinal cortex, measured by fMRI during navigation in a virtual circular arena (adapted, with permission, from [18]). (Lower panel) A hexadirectional BOLD signal, also emerges in the entorhinal cortex during navigation of an abstract 'bird space' (adapted, with permission, from [34]). (C) A machine-learning algorithm trained on distinguishing between spatially far or close objects based on fMRI activity in the inferior parietal lobe (IPL) can also distinguish between sentences referring to the close or far future, and between pictures of emotionally close or far friends [50]. (D) (Left panel) Spatialized representation of the flow of time along the horizontal axis is modulated by the egocentric experience of rightward or leftward orthography. (Right panel) The spatialized representation of valence along the horizontal axis is instead modulated by the egocentric experience of spatial fluency: 'right is good' for right-handed people, 'left is good' for left-handers. (E) Graphic representation of the experiment conducted by Bisiach and Luzzatti in two neglect patients [84]. The egocentric representation of Piazza Duomo (upper panel), which depends on parietal circuits, when retrieved from memory is affected by neglect. However, the fact that the patients could remember the whole piazza by simply changing their point of view suggests that an allocentric representation is stored (arguably in the hippocampal formation) and it is not affected by the parietal lesion that caused the neglect. (F) (Left panel) Allocentric organization of social conceptual space where the position of an individual in a social network is represented depending on the position of other people. (Right panel) Egocentric organization of social conceptual space where the position of an individual in a social network is represented depending on the position of an observer. Abbreviation: ERH, entorhinal cortex.

lower spatial positions, respectively [60]; experiencing high relative to low verticality [61] or far relative to close distance [62] leads one to think more abstractly, and objects presented in the upper or right side of space are judged more positively (compared with down- or left-located objects; [63]).

Many of these spatial schemas for nonspatial conceptual domains are viewpoint-dependent and seem to be modeled on sensorimotor interaction with the physical world [52,64]. For instance, the

direction of the mental timeline changes according to the direction of native language orthography (Figure 1D, left panel): people who write and read in a leftward direction (e.g., in Hebrew) associate the past with the right and the future with the left [53,65]. The mental number line is modulated by finger-counting habits, such that numbers unfold rightward or leftward in the mind depending on whether people habitually count starting with the left or the right hand, respectively [66,67]. In the representation of valence, positive and negative valences are associated with the right and left side of space, respectively (equivalent objects presented on the right are judged to be 'better' than those on the left), but only in right-handed people [63]. Left-handers show the opposite bias (i.e., 'left is good') (Figure 1D, right panel), and manipulating the fluency of the interaction with the left or right peripersonal space induces implicit changes of the space–valence association [68], showing how this spatial schema is based on egocentric spatial representations.

In sum, these experiments suggest that the representation of several conceptual domains, including time, number, valence, and social and emotional ties, is based on the recruitment of low-dimensional egocentric schemas derived from sensorimotor experience. Although the precise neural bases of these spatial schemas for abstract cognition are largely unknown, the few attempts to find their neural correlates point to the IPL as a crucial brain region [49–51,69] (Box 1 and [56,70] for a possible complementary role of the superior parietal lobe).

The idea of body-centered, sensorimotor-**grounded**, and attention-mediated schemas that structure high-level cognition is not entirely new in cognitive (neuro)science, and several names have been proposed for it, such as image schema [11,71], attention schema [72], and mental metaphors [52,73], that emphasize different aspects of this phenomenon – sensorimotor activity, the role of attention, and the correlation and mapping across experiential domains, respectively. Gibbs' definition of image schemas particularly resonates with the current account because it indicates experiential gestalts [...] that emerge during sensorimotor activity as we manipulate objects, seek orientation spatially and temporally, and direct our perceptual focus for various purposes. [Image schemas] are more abstract than ordinary visual mental images and consist

Box 1. An (Egocentric) Perspective on Past Memories

Neuroimaging experiments have shown consistent recruitment of the posterior parietal cortex, especially the angular gyrus, during episodic memory retrieval [115], suggesting that this region plays a pivotal role in memory function. However, this conclusion seems to be at odds with neuropsychological data from patients with parietal cortex lesions who show no impairment in memory performance (a classic symptom, instead, of hippocampal damage [116]). A solution to this conundrum has recently been proposed in which the parietal cortex is proposed to play a specific role in memory, namely its centrality for autobiographical memories re-experienced from the first-person perspective [117]. Indeed, parietal patients do sometimes show impairment in episodic memory retrieval, but specifically for the generation of self-related events [118]. Consistently, theta-burst stimulation (TBS) of the posterior IPL in healthy participants results in a selective reduction of free recall of autobiographical memories (whereas word-pair memories were unaffected [117]). Furthermore, fewer autobiographical episodes experienced from a first-person perspective are retrieved following angular gyrus TBS [117].

Interestingly, angular gyrus lesions (or transient disruption) affect the retrieval of egocentric autobiographical memories only during free recall, but not when those memories are cued [117,118]. This result is in keeping with a prominent model of attention [48] proposing that a ventral parietal path (that includes AG and TPJ) controls salience-based bottom-up attentional allocation, whereas a dorsal parietal path (SPL/IPS) controls top-down attentional allocation. A similar division of labor may characterize image spaces for high-level and abstract cognition [70,114]. For instance, the ventral stream (TPJ/IPL) may be particularly modulated by the salience of internally generated (e.g., memory-based) representations [70], which can correlate with psychological (e.g., spatial, temporal, social) distance from the self [62,114]. On the other hand, the superior parietal lobule may support the flexible and voluntary allocation of attention in the internal mindspace that would be useful, for instance, for manipulating information in working memory. In support of this hypothesis it has been shown, in the SPL, that machine-learning algorithms trained to distinguish between voluntary leftward and rightward shifts of attention in external space are able to predict, without further training, subtraction versus addition arithmetic operations along the mental number line [119]. However, further evidence will be necessary to support such division of labor between the ventral and the dorsal parietal lobe in abstract image spaces.

of dynamic spatial patterns that underlie the spatial relations and movement found in actual concrete images' ([71] p. 1992). However, in cognitive linguistics the term image schema (or schemata) also indicates several sensorial experiences that are encoded in language (from force dynamics, to object textures; e.g., [11]). To avoid confusion here we introduce the term 'image spaces' to refer to low-dimensional, self-centered, and flexible spatial configurations of information that are maintained to organize knowledge and guide behavior. In the next sections we suggest that image spaces may serve a complementary role with respect to cognitive maps during conceptual retrieval and manipulation. We also suggest that, compared with cognitive maps, image spaces are grounded on sensorimotor experience (as egocentric spatial representations usually are [74]) and appear to be mostly unidimensional [52,75].

Navigating Knowledge Across Different Reference Frames

Cognitive maps and image spaces may be two sides of the same coin: they may be specific manifestations of a more general propensity of the human brain to organize knowledge in low-dimensional spaces. We suggest here that this system could be akin to the two-system model of spatial navigation and memory, based both on allocentric and egocentric representations, which has been extensively studied [47,76–79] and modeled [79,80] in recent decades (*cf* [81] for a perspective based only on egocentric representations).

This navigation system has two major neuroanatomical hotspots: the hippocampal formation and the parietal cortex [76,79,80]. Hippocampal regions seem to be crucial for viewpoint-independent (allocentric, or world-centered) (Figure 1D) spatial relationships [7,80,82]. On the one hand, parietal areas support egocentric [79] representations that change depending on the subject's point of view (Figure 1E); however, allocentric–hippocampal versus egocentric–parietal mapping seems to be more a bias than an actual segregation; Box 2). Egocentric spatial representations that change as the subject moves in the environment [82] are relatively precise but transient [74,79],

Box 2. Functional/Anatomical Mapping of Reference Frames within and beyond the Hippocampal–Parietal Network

The association of the hippocampal formation with allocentric representations, and the parietal cortex with egocentric representations, is probably more a bias than an actual segregation. At least, there are neurons in both hippocampal formation and parietal cortex that show conjunctive egocentric and allocentric coding [120,121], as would be expected for an integrated system that often needs to switch across frames of reference. View-specific representations are also processed in the parahippocampal cortex [122], and allocentric coding has been reported in the parietal cortex [123]. It is possible that egocentric space is represented in terms of a polar relationship in the hippocampal formation, through the integration of the two dimensions in the Cartesian axes [43], whereas in the parietal cortex the egocentric coding is more strictly unidimensional, representing movement and locations along one dimension at a time [75].

Beyond the hippocampal formation and the inferior parietal cortex, different regions in the brain may support (or strictly interact with) the low-dimensional encoding of information in cognitive maps and image spaces. Three likely candidates are the medial prefrontal cortex, the precuneus, and the retrosplenial cortex. For instance, medial prefrontal cortex is implicated in goal-directed cognition [1], in the selection of task-relevant dimensions [124], and it shows hexadirectional modulation in some tasks [21,35] and strong connectivity with the hippocampal formation [83]; the precuneus (medial parietal lobe) is involved in the retrieval of autobiographical memory [83], and in self-projection and mental simulations [125,126]; the retrosplenial cortex may be important for transformations across reference frames, and has strong anatomical connections with both medial temporal and parietal regions [78].

It might not be a coincidence that the frontal–temporal–parietal network that supports spatial navigation in the physical world [76,127], and arguably encompasses both egocentric and allocentric representations of space [47], largely overlaps [127] with the default mode network (DMN) that is active when individuals are consciously thinking about others and themselves, remembering the past, or planning the future [125], and with the general semantic system [128] that is involved in the retrieval of conceptual knowledge and multimodal simulations [99]. Our model, based on representational geometries of various dimensionality, and a dual reference frame system to govern low-dimensional cognitive maps and image spaces, will not lose its validity in such a distributed system that goes beyond a classic hippocampal/parietal functional segregation.

and are strictly related to action preparation and sensorimotor information because it is necessary to locate an object relative to one's body (or effectors) so as to act upon it [79]. On the other hand, allocentric spatial maps do not change with the subject's change of perspective, are more enduring (stored in long term memory), but are more coarsely defined [79,83,84].

According to an influential model [79,80], egocentric and allocentric spatial representations are both activated during spatial navigation. A classical and paradigmatic example suggesting that both types of representations contribute to spatial memory recollection comes from two patients with right parietal damage described by Bisiach and Luzzatti [84] (Figure 1E). When the patients were asked to describe from memory the Piazza Duomo in Milan, as if they were standing with the cathedral at their back, they could describe only the buildings to the right of the Duomo. On the other hand, if they were asked to do the same task, as if they were facing the Duomo, they could describe only the buildings on the other side of the square. This result suggests that patients preserved a world-centered representation of the Piazza (because they could retrieve all of it by changing their point of view), although their parietal damage partially impaired their egocentric access to this representation [80,84].

There is evidence that such a dual reference frame system can also mediate the retrieval of non-spatial conceptual knowledge via cognitive maps and image spaces. Conceptual processing and organization in the hippocampal formation (especially within the hippocampal-entorhinal network) presents remarkable similarities to the organization of allocentric spatial maps [2]. For instance, the hippocampus encodes the distance between points in space [85] as well as the conceptual distance (i.e., similarity) between concepts along selected dimensions [40], the map-like structure provided by grid cells during spatial navigation is also present during the exploration of abstract conceptual spaces [34–36], and both spatial (e.g., complex landscapes) and nonspatial (e.g., complex narratives) information are represented with a different level of granularity (i.e., zooming-in, zooming-out) along the hippocampal long axis [42,86]. In sum, the hippocampal formation seems to provide relational low-dimensional maps for conceptual knowledge along selected feature dimensions that are comparable with allocentric representations of low-dimensional physical landscapes (Figure 1F).

Furthermore, image spaces may be involved in conscious access and attentional manipulation of information, thus constituting an egocentric representational space for conceptual knowledge (Figure 1F). For instance, whereas the hippocampal formation represent conceptual distance in global relational terms [2,40], the IPL seems to represent conceptual distance from a deictic 'here and now' that is taken as a reference and often coincides with the position of the self in space, time, and social networks [49–51].

One of the crucial aspects of egocentric spatial representations is that they are grounded in specific, although flexible, sensorimotor experiences of the world [74,79]. Interestingly, image spaces also show egocentric flexibility and sensorimotor grounding. For instance, lateral (left to right) spatial schemas of time, number, and valence can be reoriented by transient experiences with unusual orthographic directions, finger-counting direction, and sensorimotor fluency, respectively [53,67,68].

These results suggest that, like egocentric and allocentric representations of the environment, image spaces and cognitive maps may operate at different levels of abstraction. On the one hand, the relationship between space and nonspatial knowledge in image spaces may be mostly modeled after perceptual and sensorimotor experience [67]. Bodily actions, attentional movements and their spatial correlates become the template on which knowledge can be organized

and manipulated: future events are placed 'in front' of us like future physical locations are ahead of us while we walk [87], and spatial attention can internally move from one concept to the other in working memory as it moves from one object to the other in space [59,88]. Although such egocentric and experience-based spatial schemas are necessarily limited to conceptual dimensions that can be easily mapped to the movements of spatial attention (Box 3) or that correlate with egocentric spatial experience [52,67], they provide a self-centered frame of reference in which knowledge can be consciously accessed and manipulated.

In addition, the spatial organization of knowledge in cognitive maps may allow the extraction of conceptual relationships that cannot be easily remapped on sensorimotor and attentional schemas but are necessary to form more abstract and integrated conceptual representations. For instance, food dishes can be represented in terms of how much we like them (valence) and how long it takes to cook them (time), although valence and time are not necessarily correlated in our experience (Figure 2A); taken singularly, some dimensions can be represented according to learned sensorimotor schemas (e.g., duration can be represented along a mental timeline; valence along a left–right gradient). However, the arbitrary combination of two uncorrelated dimensions of experience may require an abstraction from sensorimotor schemas and the creation of a multidimensional coordinate system. This may be one of the reasons why image spaces associated with the parietal cortex are often unidimensional ([75] and Box 3), whereas hippocampal cognitive maps seem to combine more than one dimension ([2]; also [89] for evidence of 3D representation in the medial temporal lobe).

The coexistence of cognitive maps and image spaces during conceptual navigation raises questions about their interaction – is conceptual information transformed across frames of reference? And how? On the one hand, as it is the case for spatial frames of reference during physical navigation, the two systems could work in parallel but be partly independent from each other [79,90]. Such an independence might be even greater in the case of cognitive maps and image spaces compared with their 'physical' counterparts: whereas positional and geometrical

Box 3. Unidimensionality and the Parietal Cortex

An egocentric organization of knowledge, and its relationship with the attentional system, can partly explain the predominantly 1D organization of image spaces [52], compared with the 2D organization of cognitive maps [34]. Ego-related representations of objects, especially for manipulation and approach/avoidance behavior, usually restrict the focus of attention to one single object (spatial region), while ignoring others (at least momentarily). Interestingly, in the inferior parietal cortex of monkeys (region LIP), that is known for its involvement in spatial attention [129], neurons seem to encode relevant perceptual and conceptual information with similar signatures. Recent evidence suggests that LIP neurons reduce high-dimensional perceptual and conceptual information to a 1D scalar code [130–132]. For instance, when monkeys learn to distinguish between three different pairs of shapes, parietal neurons encoded different categories (pairs) by firing more for one arbitrary pair, less for a second pair, and even less for the third [132]. Instead of observing a comparable number of LIP neurons that are activated by each category (with comparable strength), neurons in inferior parietal cortex showed a linear preference for one attended category over the others. In a recent review of this line of research, Summerfield and colleagues [75] suggested, in line with our dual reference frame model, that neuronal populations in the parietal cortex may provide 1D scalar schemas that organize information. Notably, the parietal cortex is known to be involved in the representation of magnitudes across several domains (e.g., space, time, quantity, brightness) according to a unidimensional prothetic code (i.e., 'less/more than X') [133]. Although the mechanisms behind dimensionality reduction in parietal cortex need to be clarified, it is possible that the unidimensionality of some instances of image spaces is the consequence of the fluctuation of (egocentric) attention in a cognitive space where items are sampled rhythmically [80,134] and orderly organized along 1D gradients [75,130].

However, a strict mapping between dimensionality (1D–2D) and anatomical regions (parietal-hippocampal) may be too simplistic [75]. For instance, unidimensional temporal succession and duration are also encoded in the hippocampal formation [3,38,39], particularly in relation to episodic memory organization [135]. It is possible that hippocampal sequential encoding reflects the generation of allocentric relational structures [3,94], whereas parietal mental timelines encode the egocentric organization of events, from a transient deictic point, based on sensorimotor schemas [53,87].

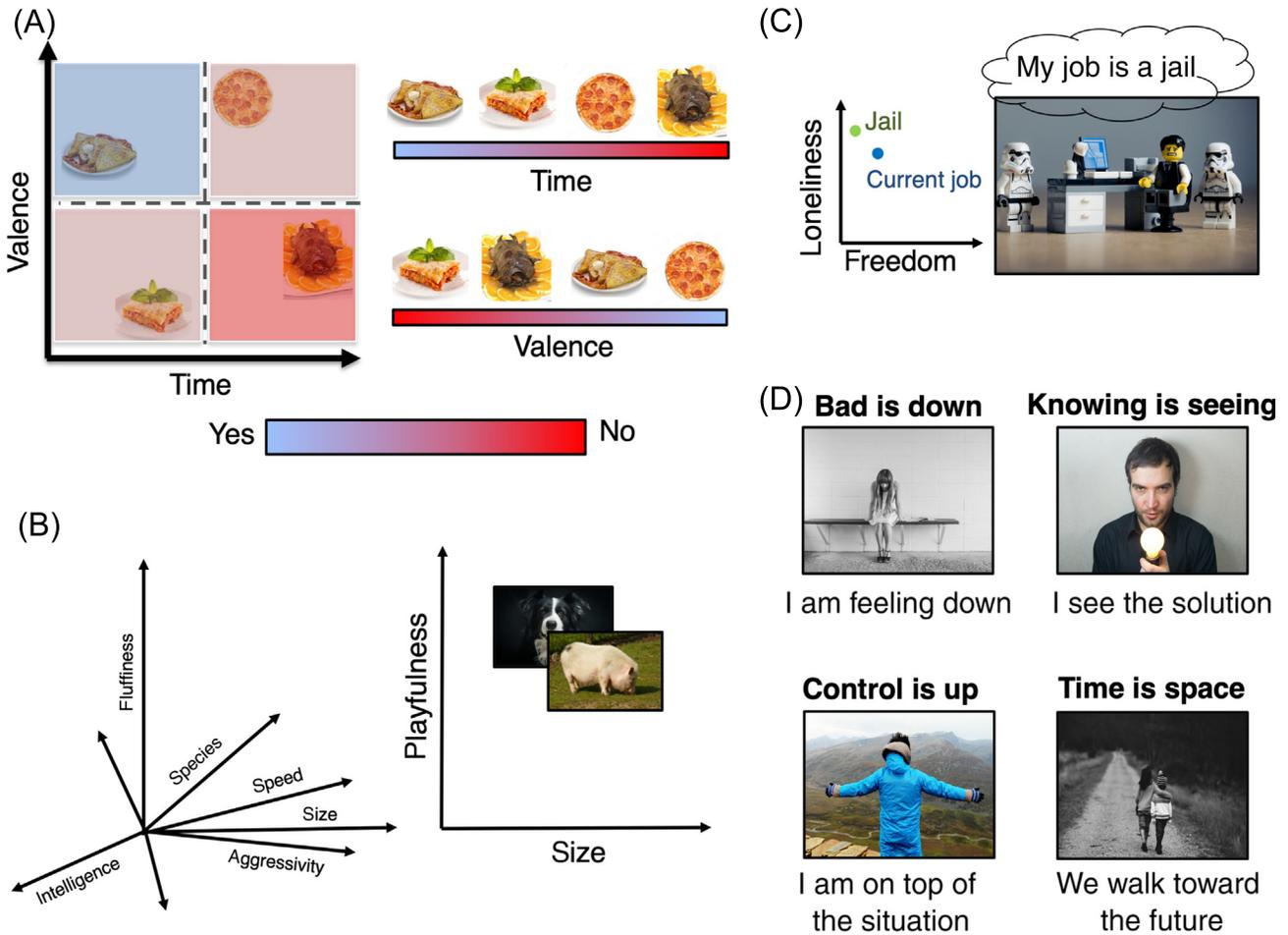


Figure 2. Low-Dimensional Geometries for Analogical and Abstract Thinking. (A) (Left panel) Multidimensional cognitive maps in which different food dishes are represented by integrating two different dimensions of experience. (Right panel) 1D representations of single dimensions according to gradients that can be grounded in sensorimotor experience (e.g., TIME: less time = left, more time = right; VALENCE: negative valence = left, positive valence = right). (B) High-dimensional conceptual space (left panel) spanning several animal features versus a low-dimensional conceptual space (right panel) spanning only two animal features that allows animal similarity to be detected along context-relevant dimensions. (C) 2D representational space according to which a job can be similar to a jail (left panel) and can lead to the creation and understanding of the metaphor 'my job is a jail' (right panel). (D) Examples of metaphorical schemas that are used to represent emotions, knowing, control, and time, reflecting primary metaphors that are based on straightforward experiential correlations.

information about the physical environment comes necessarily through the senses before being integrated into a global reference frame [79,80], conceptual information may directly be organized into allocentric spatial schemas without egocentric mediation.

On the other hand, some interaction is also expected, by **analogy** to current models of spatial navigation and memory [80,90]. For instance, allocentric spatial maps are built over time once sufficient egocentric representations are acquired [80], whereas abstract cognitive maps can, in some cases, derive from the integration of single image spaces. For instance, a complex relational structure ($A > B > C > D > E$; where '>' indicates 'bigger than') may be constructed from the experience of single comparison pairs ($A > B$; $C > D$; $B > C$). Although there is evidence that both the hippocampal formation and the parietal cortex play a crucial role in this process [91–94], their relative functions are still not clearly understood.

Different frames of reference may emerge in the same conceptual space. By analogy with spatial navigation, the egocentric perspective in abstract feature spaces may be indexed by tracking the relative heading direction with respect to a navigational goal [47], or by the similarity between adjacent navigational paths (with a similar 'point of view' [20]), on the side of typical allocentric neural signatures (e.g., hexadirectional symmetry [34–36]). Related to this, whether and how newly learned image spaces can alter the geometry of more stable cognitive maps in long-term memory will be an interesting topic of investigation for future research. Finally, as recently suggested [95], the interaction of different frames of reference may lay the ground for the development of Theory of Mind, a fundamental process in social cognition where it is necessary to consider one's own beliefs (egocentric) in the context of other's belief systems (allocentric), and assume the points of view of different people (allocentric–egocentric combined).

The Curse of Dimensionality and the Functions of Spatial Mapping

What are the functions of cognitive maps and image spaces? We have presented low-dimensional spaces as a means to organize conceptual knowledge in the brain. However, the objects that populate the physical world are extremely diverse and differ from each other along a large number of dimensions [96–98]. Indeed, there is increasing agreement that semantic representations can be modeled as points in **high-dimensional spaces** that span both concrete and abstract dimensions (Box 4), and high-dimensional representational geometries have proved to be very effective in predicting the neural activity related to semantic representations [96,99], in some cases up to the single-item level [100,101].

However, the limits of low-dimensional spaces in representing conceptual knowledge highlight, at the same time, their advantages in organizing and manipulating it: high-dimensional representations in semantic memory will be of very limited use if some of these dimensions cannot be selected and isolated from the others. High-dimensional heterogeneous compounds, by spanning several domains of experience, provide conceptual geometries that are abstracted from every given particular experience and can be relatively unpractical. Consider, as an example, the problem of deciding which animals are more or less similar to dogs. This is easy when you only need to consider one or two dimensions (e.g., size and playfulness), but almost impossible when you must consider dozens of dimensions (including fluffiness, intelligence, docility, speed, eating habits, etc.; Figure 2B).

Box 4. High-Dimensional Geometries behind Semantic and Perceptual Knowledge

The objects that populate the physical world are extremely diverse and differ from each other along a great number of dimensions, as do concepts in our mind [96,136]. Semantic memory is likely to rely on high-dimensional geometries that can encode several perceptual, functional, and abstract features (e.g., Is it an animal? Does it fly? Lives in Africa? [97]).

Such complexity can be captured by representational geometries in high-dimensional spaces [96,97,137]. In these representational spaces each point (i.e., each concept) is a vector that contains the coordinate values for each of the dimensions that constitute that space. Feature dimensions would be different according to the level of representation and the brain region involved [136,138]. For instance, dimensions in association cortices can be features coming from modality-specific (visual, sensory) and domain-specific (faces, scene, social cognition) regions, thus providing a domain-general and high-dimensional representational space that spans different perceptual, emotional, or functional features [96,99]. On the other hand, modeling the representational space of modality- or domain-specific regions requires a more homogeneous high-dimensional space. For instance, modeling representational spaces in visual areas (e.g., V1/V2) would require dimensions representing low-level visual features such as color, orientation, texture, brightness, etc. [139,140], and in all (or many of) their possible combinations, to allow high-resolution perceptual distinctions. Similarly, in language-related areas, semantic relationships may be represented on the basis of the multidimensional spaces created by words in relationship with other words (such as in a dictionary or thesaurus), that can be captured by hundreds of co-occurrence vectors across a large corpora of text documents that reflect what we usually say and read [100]. High-dimensional cognitive spaces are a direct computational solution that support, on the one hand, fine-grained perceptual and conceptual distinctions in domain-specific regions, and, on the other hand, integrated and domain-general representations in association cortex.

In more formal terms, people refer to this problem as to 'the curse of dimensionality' [102]. Information becomes sparse and patterns get lost in high-dimensional spaces. Objects with similar properties cluster together when relatively few dimensions are concerned, but in high-dimensional spaces all objects appear to be different from the others in many ways, and the distances between all pairs of points (e.g., dog–cat, dog–coyote, dog–shark) becomes almost equal [103]. Thus, when the objective is to organize information efficiently to find patterns that are relevant for a given context, low-dimensional topological configurations such as cognitive maps and image spaces become handy. In low-dimensional spaces similarities and differences become clear and patterns appear. Conclusions such as 'A pot-bellied pig can be a good pet, pretty much like a dog', could hardly be drawn out of a high-dimensional representational space (Figure 2B).

Low-dimensional cognitive maps and image spaces may have a key role in the remarkable human ability of making analogies (in its most general sense, the ability to think about pattern similarity across domains). After all, making analogies involves ignoring the (many) differences and focusing on the (few) similarities between entities [104]. Consider the analogy 'My job is a jail' (Figure 2C): to understand it, one must ignore the many dimensions in which jobs and jails are often different (e.g., salary, guards, barbed wire, privacy) and focus on the dimensions that can make them similar, such as lack of freedom or loneliness [105]. Similarly to dogs and pot-bellied pigs, jobs and jails will never be similar in a high-dimensional semantic space. Low-dimensional cognitive maps may be important to create analogies between objects and events that may be far in our experience, but that can be compared along a few selected dimensions [104].

Low-dimensional image spaces, nevertheless, may facilitate **primary conceptual metaphors** that scaffold several abstract domains (e.g., time, numerosity, or emotions) on the basis of grounded sensorimotor experience [11,52]. Across languages and cultures, egocentric sensorimotor experience is a productive source of metaphors (Figure 2D), both along self-centered unidimensional spatial axes: 'You have a bright future in front of you' (TIME is SPACE), 'I feel depressed' (BAD is DOWN), 'Prices are rising' (MORE is UP); as well as in general perception and action: 'I see things more clearly' (KNOWING is SEEING), 'I am carefully dismantling this theory' (THINKING is ACTION), etc. These metaphorical schemas are largely based on dimensions that are correlated with spatial experience (e.g., I move through time while I move through space [53,87]), or that carry some iconic resemblance with sensorimotor experience (both dismantling a mechanism and dismantling a theory require controlled and fine-grained movements of attention). Thus, primary metaphors (e.g., INTIMACY is CLOSENESS, MORE is UP, KNOWING is SEEING) that are based on 'straightforward experiential correlations' ([71], p. 1196) may be particularly facilitated by image spaces, whereas more abstracted metaphorical mapping such as 'LOVE is a JOURNEY' or 'OLD AGE is like WINTER', which hold a more complex and arguably multidimensional analogical structure, may rely on the additional activation of cognitive maps.

Analogical thinking and conceptual metaphors have been largely investigated in cognitive science and neuroscience [52,106]. Although the underlying neural bases of these processes remain unspecified, there is compelling evidence that the parahippocampal and inferior parietal areas play a role in the production and comprehension of novel metaphors [106–108]. The evidence of a direct hippocampal involvement in metaphorical thinking is more limited [109], although both the hippocampus and the IPL seem to play a role in relational thinking and transitive inference [94,110], which are the basis of analogical mapping [104,111,112]. In sum, the study of low-dimensional spaces in the hippocampal and parietal cortex could provide exciting neuroscientific advances on these topics (see [Outstanding Questions](#)).

Concluding Remarks

We have reviewed evidence that world-centered cognitive maps [2, 113] and self-centered image spaces [52, 75, 114] provide low-dimensional schemas that are useful for structuring conceptual knowledge. We have further suggested that cognitive maps and image spaces may be two different instantiations of the propensity of the human mind to create low-dimensional 'internal models' [95] that are useful for organizing, retrieving, and manipulating information. Spatial navigation is made possible by the combination of two different frames of reference that model both the stable location of objects in the environment, and the self-centered agent that navigates this environment interacting with the various objects [79]. Likewise, conceptual navigation may rely not only on the formation of stable multidimensional maps of knowledge across integrated selected dimensions, but also on the self-centered flexible interaction with this knowledge modeled after sensorimotor experience and orchestrated by the attentional system.

Acknowledgments

We thank Jacob Bellmund, Talia Brandman, Kyle Jasmin, Léo Dutriaux, and Yangwen Xu for comments on an earlier draft. Our research is supported by the European Research Council (ERC-StG NOAM 804422) (R.B); and by the Max Planck Society, the European Research Council (ERC-CoG GEOCOG 724836), the Kavli Foundation, the Centre of Excellence scheme of the Research Council of Norway – Centre for Neural Computation, The Egil and Pauline Braathen and Fred Kavli Centre for Cortical Microcircuits, the National Infrastructure scheme of the Research Council of Norway – NORBRAIN, and The Netherlands Organisation for Scientific Research (NWO-Gravitation 024-001-006) (C.F.D.).

References

- Behrens, T.E.J. *et al.* (2018) What is a cognitive map? Organising knowledge for flexible behaviour. *Neuron* 100, 490–509
- Bellmund, J.L.S. *et al.* (2018) Navigating cognition: spatial codes for human thinking. *Science* 362, eaat6766
- Buzsáki, G. and Tingley, D. (2018) Space and time: the hippocampus as a sequence generator. *Trends Cogn. Sci.* 22, 853–869
- Tononi, G. *et al.* (2016) Integrated information theory: from consciousness to its physical substrates. *Nat. Rev. Neurosci.* 17, 450–461
- Hassabis, D. *et al.* (2017) Neuroscience-inspired artificial intelligence. *Neuron* 95, 245–258
- Buzsáki, G. and Moser, E. (2013) Memory, navigation and theta rhythm in the hippocampal–entorhinal system. *Nat. Neurosci.* 16, 130–138
- O'Keefe, J. and Nadel, L. (1978) *The Hippocampus as a Cognitive Map*, Clarendon Press
- Tolman, E.C. (1948) Cognitive maps in rats and men. *Psychol. Rev.* 55, 189–200
- Shepard, R.N. (1987) Toward a universal law of generalization for psychological science. *Science* 237, 1317–1323
- Bergson, H. (1889) *Time and Free Will*, Martino Publishing
- Lakoff, G. and Johnson, M. (1999) *Philosophy in the Flesh*, Basic Books
- Scoville, W.B. and Milner, B. (1957) Loss of recent memory after bilateral hippocampal lesions. *J. Neuropsychiatr. Clin. Neurosci.* 20, 11–21
- Kensinger, E.A. and Giovanello, K.S. (2005) The status of semantic and episodic memory in amnesia. In *Progress in Neuropsychology Research: Brain Mapping and Language* (Chen, F.-J., ed.), pp. 1–13, Nova Science
- Eichenbaum, H. (2004) Hippocampus: cognitive processes and neural representations that underlie declarative memory. *Neuron* 44, 109–120
- O'Keefe, J. and Dostrovsky, J. (1971) The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Res.* 34, 171–175
- Hafting, T. *et al.* (2005) Microstructure of a spatial map in the entorhinal cortex. *Nature* 436, 801–806
- Moser, M. *et al.* (2015) Place cells, grid cells, and memory. *Cold Spring Harb. Perspect. Biol.* 7, a021808
- Doeller, C.F. *et al.* (2010) Evidence for grid cells in a human memory network. *Nature* 463, 657–661
- Horner, A.J. *et al.* (2016) Grid-like processing of imagined navigation. *Curr. Biol.* 26, 842–847
- Bellmund, J.L.S. *et al.* (2016) Grid-cell representations in mental simulation. *Elife* 5, e17089
- Jacobs, J. *et al.* (2013) Direct recordings of grid-like neuronal activity in human spatial navigation. *Nat. Neurosci.* 16, 1188–1190
- Ekstrom, A. *et al.* (2003) Cellular networks underlying human spatial navigation. *Nature* 425, 184–188
- Nau, M. *et al.* (2018) How the brain's navigation system shapes our visual experience. *Trends Cogn. Sci.* 22, 810–825
- Rolls, E.T. (1999) Spatial view cells and the representation of place in the primate hippocampus. *Hippocampus* 9, 467–480
- Georges-François, P. *et al.* (1999) Spatial view cells in the primate hippocampus: allocentric view not head direction or eye position or place. *Cereb. Cortex* 9, 197–212
- Killian, N.J. *et al.* (2012) A map of visual space in the primate entorhinal cortex. *Nature* 491, 761–764
- Nau, M. *et al.* (2018) Hexadirectional coding of visual space in human entorhinal cortex. *Nat. Neurosci.* 21, 188–190
- Julian, J.B. *et al.* (2018) Human entorhinal cortex represents visual space using a boundary-anchored grid. *Nat. Neurosci.* 21, 191–194
- Lee, A.C.H. *et al.* (2005) Specialization in the medial temporal lobe for processing of objects and scenes. *Hippocampus* 15, 782–797
- Lee, A.C.H. *et al.* (2005) Perceptual deficits in amnesia: challenging the medial temporal lobe 'mnemonic' view. *Neuropsychologia* 43, 1–11
- Lee, A.C.H. *et al.* (2012) The hippocampus and visual perception. *Front. Hum. Neurosci.* 6, 91
- Erez, J. *et al.* (2013) Neuropsychologia It does not look odd to me: perceptual impairments and eye movements in amnesic patients with medial temporal lobe damage. *Neuropsychologia* 51, 168–180
- Aronov, D. *et al.* (2017) Mapping of a non-spatial dimension by the hippocampal–entorhinal circuit. *Nature* 543, 719–722
- Constantinescu, A.O. *et al.* (2016) Organizing conceptual knowledge in humans with a gridlike code. *Science* 352, 1464–1468
- Bao, X. *et al.* (2019) Grid-like neural representations support olfactory navigation of a two-dimensional odor space. *Neuron* 102, 1066–1075
- Viganò, S. and Piazza, M. (2020) Distance and direction codes underlie navigation of a novel semantic space in the human brain. *J. Neurosci.* 40, 2727–2736

Outstanding Questions

Can we track simultaneously both egocentric and allocentric representations of the same conceptual space?

What are the mechanisms that allow the transformation between allocentric and egocentric representations of conceptual knowledge?

Is there a relationship between the dimensionality (1D, 2D) and the preferred frame of reference (self-centered, world-centered) of image spaces and cognitive maps?

How do high-dimensional semantic information and low-dimensional geometries interact? How is a lower number of dimensions selected, in a given context, among the possible dimensions?

Do image spaces extend beyond supporting unidimensional linear mapping (e.g., of time, number, valence) to encompass multidimensional egocentric representations, for example, in relation to acting and manipulating objects in 3D space?

How do image spaces and maps support analogical thinking and conceptual metaphors? Can we track changes in analogical thinking within low-dimensional spaces supported by hippocampal and parietal neurons?

Do patients with hippocampal and parietal damage show a greater impairment of cognitive maps and image spaces, respectively?

What is the developmental trajectory of cognitive maps and image spaces? Does one precede the other during ontogenetic development? Is their development synchronized with the emergence of allocentric and egocentric representations of the physical space?

37. Garvert, M.M. *et al.* (2017) A map of abstract relational knowledge in the human hippocampal-entorhinal cortex. *Elife* 6, e17086
38. Eichenbaum, H. (2014) Time cells in the hippocampus: a new dimension for mapping memories. *Nat. Rev. Neurosci.* 15, 732–744
39. Bellmund, J.L. *et al.* (2019) Mapping sequence structure in the human lateral entorhinal cortex. *Elife* e45333, 8
40. Theves, S. *et al.* (2019) The hippocampus encodes distances in multidimensional feature space. *Curr. Biol.* 29, 1226–1231
41. Solomon, E.A. *et al.* (2019) Hippocampal theta codes for distances in semantic and temporal spaces. *Proc. Natl. Acad. Sci.* 116, 24343–24352
42. Collin, S.H.P. *et al.* (2015) Memory hierarchies map onto the hippocampal long axis in humans. *Nat. Neurosci.* 18, 1562–1564
43. Tavares, R.M. *et al.* (2015) A map for social navigation in the human brain. *Neuron* 87, 231–243
44. Amorapanth, P. *et al.* (2010) The neural basis for spatial relations. *J. Cogn. Neurosci.* 22, 1739–1753
45. Colby, C.L. and Goldberg, M.E. (1999) Space and attention in parietal cortex. *Annu. Rev. Neurosci.* 22, 319–349
46. Schindler, A. and Bartels, A. (2013) Parietal cortex codes for egocentric space beyond the field of view. *Curr. Biol.* 23, 177–182
47. Spiers, H.J. and Maguire, E.A. (2007) A navigational guidance system in the human brain. *Hippocampus* 17, 618–626
48. Corbetta, M. *et al.* (2008) The reorienting system of the human brain: from environment to theory of mind. *Neuron* 58, 306–324
49. Peer, M. *et al.* (2015) Brain system for mental orientation in space, time, and person. *Proc. Natl. Acad. Sci.* 112, 11072–11077
50. Parkinson, C. *et al.* (2014) A common cortical metric for spatial, temporal, and social distance. *J. Neurosci.* 34, 1979–1987
51. Gauthier, B. and van Wassenhove, V. (2016) Time is not space: core computations and domain-specific networks for mental travels. *J. Neurosci.* 36, 11891–11903
52. Casasanto, D. and Bottini, R. (2014) Spatial language and abstract concepts. *Wiley Interdiscip. Rev. Cogn. Sci.* 5, 139–149
53. Casasanto, D. and Bottini, R. (2014) Mirror reading can reverse the flow of time. *J. Exp. Psychol. Gen.* 143, 473–479
54. Casasanto, D. and Jasmin, K. (2012) The hands of time: temporal gestures in English speakers. *Cogn. Linguist.* 23, 643–674
55. Saj, A. *et al.* (2013) Patients with left spatial neglect also neglect the 'left side' of time. *Psychol. Sci.* 25, 207–214
56. Hubbard, E.M. *et al.* (2005) Interactions between number and space in parietal cortex. *Nat. Rev. Neurosci.* 6, 435–448
57. Loetscher, T. *et al.* (2010) Eye position predicts what number you have in mind. *Curr. Biol.* 20, 264–265
58. Previtani, P. *et al.* (2010) Placing order in space: the SNARC effect in serial learning. *Exp. Brain Res.* 201, 599–605
59. van Dijk, J.-P. and Fias, W. (2011) A working memory account for spatial-numerical associations. *Cognition* 119, 114–119
60. Dolscheid, S. *et al.* (2013) The thickness of musical pitch: psychophysical evidence for linguistic relativity. *Psychol. Sci.* 24, 613–621
61. Slepian, M.L. *et al.* (2015) Cognition from on high and down low: verticality and construal level. *J. Pers. Soc. Psychol.* 108, 1–17
62. Liberman, N. and Trope, Y. (2008) The psychology of transcending the here and now. *Science* 322, 1201–1205
63. Casasanto, D. (2009) Embodiment of abstract concepts: good and bad in right- and left-handers. *J. Exp. Psychol. Gen.* 138, 351–367
64. Casasanto, D. (2011) Different bodies, different minds: the body specificity of language and thought. *Curr. Dir. Psychol. Sci.* 20, 378–383
65. Fuhrman, O. and Boroditsky, L. (2010) Cross-cultural differences in mental representations of time: evidence from an implicit non-linguistic task. *Cogn. Sci.* 34, 1430–1451
66. Fischer, M.H. (2008) Finger counting habits modulate spatial-numerical associations. *Cortex* 44, 386–392
67. Pitt, B. and Casasanto, D. (2020) The correlations in experience principle: how culture shapes concepts of time and number. *J. Exp. Psychol. Gen.* 149, 1048
68. Casasanto, D. and Chryssikou, E.G. (2011) When left is 'right'. Motor fluency shapes abstract concepts. *Psychol. Sci.* 22, 419–422
69. Cutini, S. *et al.* (2014) Number-space interactions in the human parietal cortex: enlightening the SNARC effect with functional near-infrared spectroscopy. *Cereb. Cortex* 24, 444–451
70. Cabeza, R. *et al.* (2012) Cognitive contributions of the ventral parietal cortex: an integrative theoretical account. *Trends Cogn. Sci.* 16, 338–352
71. Gibbs, R.W. *et al.* (2004) Metaphor is grounded in embodied experience. *J. Pragmat.* 36, 1189–1210
72. Graziano, M.S. and Kastner, S. (2011) Human consciousness and its relationship to social neuroscience: a novel hypothesis. *Cogn. Neurosci.* 2, 98–113
73. Casasanto, D. (2010) Space for thinking. In *Language, Cognition and Space: State of the Art and New Directions* (Evans, V. and Chilton, P., eds), pp. 453–478, Equinox Publishing
74. Waller, D. and Hodgson, E. (2006) Transient and enduring spatial representations under disorientation and self-rotation. *J. Exp. Psychol. Learn. Mem.* 32, 867–882
75. Summerfield, C. *et al.* (2020) Structure learning and the posterior parietal cortex. *Prog. Neurobiol.* 184, 101717
76. Maguire, E.A. *et al.* (1998) Knowing where and getting there: a human navigation network. *Science* 280, 921–924
77. Burgess, N. *et al.* (2001) A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events. *Neuroimage* 14, 439–453
78. Vann, S.D. *et al.* (2009) What does the retrosplenial cortex do? *Nat. Rev. Neurosci.* 10, 792–802
79. Burgess, N. (2006) Spatial memory: how egocentric and allocentric combine. *Trends Cogn. Sci.* 10, 551–557
80. Bicanski, A. and Burgess, N. (2018) A neural-level model of spatial memory and imagery. *Elife* 7, e33752
81. Wang, R.F. (2012) Theories of spatial representations and reference frames: what can configuration errors tell us? *Psychon. Bull. Rev.* 19, 575–587
82. Burgess, N. *et al.* (2002) The human hippocampus and spatial and episodic memory. *Neuron* 35, 625–641
83. Moscovitch, M. *et al.* (2016) Episodic memory and beyond: the hippocampus and neocortex in transformation. *Annu. Rev. Psychol.* 67, 105–134
84. Bisiach, E. and Luzzatti, C. (1978) Unilateral neglect of representational space. *Cortex* 14, 129–133
85. Morgan, L.K. *et al.* (2011) Distances between real-world locations are represented in the human hippocampus. *J. Neurosci.* 31, 1238–1245
86. Strange, B.A. *et al.* (2014) Functional organization of the hippocampal longitudinal axis. *Nat. Rev. Neurosci.* 15, 655–669
87. Clark, H.H. (1973) Space, time, semantics, and the child. In *Cognitive Development and the Acquisition of Language* (Moore, T., ed.), pp. 27–63, Academic Press
88. Bottini, R. *et al.* (2016) Early blindness alters the spatial organization of verbal working memory. *Cortex* 83, 271–279
89. Grieves, R.M. *et al.* (2020) The place-cell representation of volumetric space in rats. *Nat. Commun.* 11, 789
90. Meilinger, T. and Vosgerau, G. (2010) Putting egocentric and allocentric into perspective. *Lect. Notes Comput. Sci* 6222, 207–221
91. Van Opstal, F. *et al.* (2008) A hippocampal-parietal network for learning an ordered sequence. *Neuroimage* 40, 333–341
92. Liu, Y. *et al.* (2019) Human replay spontaneously reorganizes experience. *Cell* 178, 640–652
93. Alfred, K.L. *et al.* (2020) Mental models use common neural spatial structure for spatial and abstract content. *Commun. Biol.* 3, 17
94. Dusek, J.A. and Eichenbaum, H. (1997) The hippocampus and memory for orderly stimulus relations. *Proc. Natl. Acad. Sci. U. S. A.* 94, 7109–7114
95. Arzy, S. and Schacter, D.L. (2019) Self-agency and self-ownership in cognitive mapping. *Trends Cogn. Sci.* 23, 476–487
96. Binder, J.R. *et al.* (2016) Toward a brain-based componential semantic representation. *Cogn. Neuropsychol.* 33, 130–174
97. Borghesani, V. and Piazza, M. (2017) The neuro-cognitive representations of symbols: the case of concrete words. *Neuropsychologia* 105, 4–17
98. Collins, A.M. and Loftus, E.F. (1975) A spreading-activation theory of semantic processing. *Psychol. Rev.* 82, 407–428

99. Fernandino, L. *et al.* (2015) Concept representation reflects multimodal abstraction: a framework for embodied semantics. *Cereb. Cortex* 26, 2018–2034
100. Pereira, F. *et al.* (2018) Toward a universal decoder of linguistic meaning from brain activation. *Nat. Commun.* 9, 963
101. Mitchell, T.M. *et al.* (2008) Predicting human brain activity associated with the meanings of nouns. *Science* 320, 1191–1195
102. Ganguli, S. and Sompolinsky, H. (2012) Compressed sensing, sparsity and neural data. *Annu. Rev. Neurosci.* 35, 463–483
103. Radovanović, M. *et al.* (2010) Hubs in space: popular nearest neighbors in high-dimensional data. *J. Mach. Learn. Res.* 11, 2487–2531
104. Gentner, D. *et al.* (2001) Metaphor is like analogy. In *The Analogical Mind: Perspectives from Cognitive Science* (Gentner, D. *et al.*, eds), pp. 199–253, MIT Press
105. Gentner, D. (1983) Structure-mapping: a theoretical framework for analogy. *Cogn. Sci.* 7, 155–170
106. Rapp, A.M. *et al.* (2012) Where in the brain is nonliteral language? A coordinate-based meta-analysis of functional magnetic resonance imaging studies. *Neuroimage* 63, 600–610
107. Beaty, R.E. *et al.* (2017) Brain networks underlying novel metaphor production. *Brain Cogn.* 111, 163–170
108. Benedek, M. *et al.* (2014) Creating metaphors: the neural basis of figurative language production. *Neuroimage* 90, 99–106
109. Papagno, C. (2001) Comprehension of metaphors and idioms in patients with Alzheimer's disease: a longitudinal study. *Brain* 124, 1450–1460
110. Waechter, R.L. *et al.* (2013) Transitive inference reasoning is impaired by focal lesions in parietal cortex rather than rostrolateral prefrontal cortex. *Neuropsychologia* 51, 464–471
111. Holyoak, K.J. (2012) Analogy and relational reasoning. In *Oxford Handbook of Thinking and Reasoning* (Holyoak, K.J. and Morrison, R.G., eds), pp. 234–259, Oxford University Press
112. Wendelken, C. and Bunge, S.A. (2010) Transitive inference: distinct contributions of rostrolateral prefrontal cortex and the hippocampus. *J. Cogn. Neurosci.* 22, 837–847
113. Behrens, T.E.J. *et al.* (2018) What is a cognitive map? Organizing knowledge for flexible behavior. *Neuron* 100, 490–509
114. Parkinson, C. and Wheatley, T. (2015) The repurposed social brain. *Trends Cogn. Sci.* 19, 133–141
115. Wagner, A.D. *et al.* (2005) Parietal lobe contributions to episodic memory retrieval. *Trends Cogn. Sci.* 9, 445–453
116. Aggleton, J.P. and Brown, M.W. (1999) Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. *Behav. Brain Sci.* 22, 425–444
117. Bonnici, H.M. *et al.* (2018) Specifying a causal role for angular gyrus in autobiographical memory. *J. Neurosci.* 38, 10438–10443
118. Berryhill, M.E. *et al.* (2007) Parietal lobe and episodic memory: bilateral damage causes impaired free recall of autobiographical memory. *J. Neurosci.* 27, 14415–14423
119. Knops, A. *et al.* (2009) Recruitment of an area involved in eye movements during mental arithmetic. *Science* 324, 1583–1585
120. Lachance, P.A. *et al.* (2019) A sense of space in postthral cortex. *Science* 365, eaax4192
121. Wilber, A.A. *et al.* (2014) Interaction of egocentric and world-centered reference frames in the rat posterior parietal cortex. *J. Neurosci.* 34, 5431–5446
122. Epstein, R. *et al.* (2003) Viewpoint-specific scene representations in human parahippocampal cortex. *Neuron* 37, 865–876
123. Chen, X. *et al.* (2018) Flexible egocentric and allocentric representations of heading signals in parietal cortex. *Proc. Natl. Acad. Sci.* 115, 3305–3312
124. Mack, M.L. *et al.* (2020) Ventromedial prefrontal cortex compression during concept learning. *Nat. Commun.* 11, 46
125. Buckner, R.L. and Carroll, D.C. (2007) Self-projection and the brain. *Trends Cogn. Sci.* 11, 49–57
126. Xu, Y. *et al.* (2016) Intrinsic functional network architecture of human semantic processing: Modules and hubs. *Neuroimage* 132, 542–555
127. Spreng, R.N. *et al.* (2008) The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. *J. Cogn. Neurosci.* 21, 489–510
128. Binder, J.R. *et al.* (2009) Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb. Cortex* 19, 2767–2796
129. Bisley, J.W. and Goldberg, M.E. (2003) Neuronal activity in the lateral intraparietal area and spatial attention. *Science* 299, 81–87
130. Ganguli, S. *et al.* (2008) One-dimensional dynamics of attention and decision making in LIP. *Neuron* 58, 15–25
131. Chafee, M.V. (2013) A scalar neural code for categories in parietal cortex: representing cognitive variables as 'more' or 'less'. *Neuron* 77, 7–9
132. Fitzgerald, J.K. *et al.* (2013) Biased associative representations in parietal cortex. *Neuron* 77, 180–191
133. Walsh, V. (2003) A theory of magnitude: common cortical metrics of time, space and quantity. *Trends Cogn. Sci.* 7, 483–488
134. Fiebelkorn, I.C. and Kastner, S. (2019) A rhythmic theory of attention. *Trends Cogn. Sci.* 23, 87–101
135. Folkerts, S. *et al.* (2018) Human episodic memory retrieval is accompanied by a neural contiguity effect. *J. Neurosci.* 38, 4200–4211
136. Borghesani, V. and Piazza (2017) The neuro-cognitive representations of symbols: the case of concrete words. *Neuropsychologia* 105, 4–17
137. Kriegeskorte, N. and Kievit, R.A. (2013) Representational geometry: Integrating cognition, computation, and the brain. *Trends Cogn. Sci.* 17, 401–412
138. Anderson, A.J. *et al.* (2015) Reading visually embodied meaning from the brain: visually grounded computational models decode visual-object mental imagery induced by written text. *Neuroimage* 120, 309–322
139. Connolly, A.C. *et al.* (2012) The representation of biological classes in the human brain. *J. Neurosci.* 32, 2608–2618
140. Naselaris, T. *et al.* (2009) Bayesian reconstruction of natural images from human brain activity. *Neuron* 63, 902–915