Trends in Cognitive Sciences

CellPress

Opinion

Cognitive maps as a medium for thought

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Cognitive maps are essential for navigation, but to what extent are they involved in thinking more broadly? In this opinion article, we examine whether cognitive maps constitute a genuine vehicle for thought and how they relate to the notion of a language of thought. Integrating work from philosophy, psychology, and neuroscience, we suggest that map-like representations offer a distinct, flexible medium for encoding information and exhibit compositionality in both spatial and nonspatial domains. We then consider how dynamic neural mechanisms—replay, theta sequences, and vector computation—may transform map-based representations into sequential routelike formats that interface with cortical systems supporting propositional thinking. Cognitive maps may be complementary to symbolic cognition, jointly enabling flexible human reasoning.

Highlights

Cognitive maps can represent both spatial and nonspatial knowledge, but how they might operate as a vehicle for thinking is unclear.

Cognitive maps and propositional representations (the 'language of thought') are different from each other but share some key characteristics, such as compositionality.

To be useful for thinking, cognitive maps must interface with language of thought-like representations. This may involve the same operations that are used to convert cognitive maps into routelike representations during navigation.

Dynamic neural mechanisms such as replay, theta sequences, and vector computation are possible candidates for mediating this interface.

Vehicles for thinking

What is the nature of thought? In the last 50 years, this question has generally been considered with one of two opposing possibilities in mind: mental representations are either pictorial, iconic, and continuous [1], or they are **propositional** (see Glossary), discursive, and discrete (i.e., consisting of symbols over which mental processes operate) [2,3]. A prevailing theory of thought—the '**language-of-thought hypothesis**' (**LoTH**; see Box 1) [4,15]—argues for the latter possibility. As the name implies, the LoTH holds that thoughts are structured in much the same way that language is structured. To some, this has seemed not just the 'best' description of the nature of thinking [4], but the 'only' one [15,16]. In the words of recent proponents of the LoTH: 'Contemporary cognitive science presupposes the language-of-thought' ([4], p. 1).

Meanwhile, a growing literature considers a different vehicle for thought: maps. First described by Tolman over 75 years ago [17], **cognitive maps** are believed by many to be central not only to spatial navigation but also to thought in general, as map-like structures may serve as a representational medium for nonspatial information [18–26]. In philosophy and cognitive science, maps have been discussed as a possible vehicle of thought that is distinct from a LoT [27–29]. In cognitive neuroscience, the idea that maps underlie some kinds of thinking is especially prevalent [21,22,25]: to pick a prototypical example, Gornet and Thomson [30] write that

'…the brain uses common cognitive mapping strategies for spatial and non-spatial sensory information so that common mapping algorithms might exist that can map and navigate over not only visual but also semantic information and logical rules…In such a paradigm, reasoning itself could be implemented as a form of navigation within a cognitive map of concepts, facts, and ideas' (p. 1).

Others go even further, suggesting that map-like representations and a LoT may be one and the same [12] (Box 2).

But what does it mean to say that maps support thinking? Are LoTs and cognitive maps distinct entities, or does one reduce to the other? If they are separate entities, what is the relationship between them? These are the questions we aim to address.

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Box 1. What is a language of thought?

The LoTH posits that the representations underlying thought have several languagelike properties that allow for general and flexible thinking [4,5]. One of the most important of these properties, primarily responsible for the explanatory fruitfulness of LoT, is compositionality: meaning is derived from both components and their combination. *John loves Mary* is a distinct thought from *Mary loves John*. In this way, concepts can be combined in an infinite number of ways to form new concepts, solve problems flexibly, and extrapolate, infer, and deduce. Thus, when considering the relationship between cognitive maps and 'language of thoughts' (LoT), a key question is whether mental maps are compositional, allowing them to possess similar representational advantages.

Beyond compositionality, the LoT hypothesis posits that mental representations are structured in such a way that they have discrete units that are abstract (i.e., not tied to any particular sensory input), exhibit role-filler independence (i.e., syntactic roles are independent of the items that fill these roles), exhibit predication (i.e., they are truth-evaluable), license inferential thinking (i.e., they allow for generalization beyond things that are learned explicitly, e.g., via transitivity), and can be subject to logical operations (e.g., NOT, AND, OR). In other words, as its name suggests, the LoTH proposes that (at least some) thought has all the representational and expressive properties of language itself.

The viability of LoT architectures is proven by their effectiveness in modeling behavior across a wide variety of domains. They are said to effectively describe geometric reasoning [6], rule-based learning [7], the learning of taxonomical structures [8], theory acquisition [9], analogical reasoning [10], 'common sense' reasoning [11], and much more. Given their behavioral success and supposed neural viability [12–14], LoT architectures have held their ground as accounts of mental representation, despite the impressive advances of artificial intelligence in neural network systems, which—at least at first glance—may seem to operate under different principles.

Characteristics of cognitive maps

Tolman's [17] original conception of cognitive maps was metaphorical. Maps were like 'a central control room' in which information from multiple sources could come together. In subsequent decades, psychology and neuroscience came to define cognitive maps more concretely, focusing primarily on Euclidean descriptions of space, analogous to canonical, modern maps [32–34]. The essential part of the cognitive map was taken to be the coordinate system—the mental 'sheet of paper' on which a physical map might be drawn. For example, O'Keefe and Nadel [32] discuss

Box 2. Are cognitive maps and the language(s) of thought one and the same?

In a recent paper, Kazanina and Poeppel [12] argue that 'neural cell types found in spatial navigation successfully deliver key types of representation and computation needed for the LoT' (p. 997). In other words, the hippocampal cognitive map is, at least potentially, a neural substrate of the LoT (albeit a reduced version that is restricted to the specific domain of space, at least in rodents). This contrasts with our view that cognitive maps are a fundamentally different kind of representation from the LoT.

Kazanina and Poeppel focus on specific characteristics of spatial cells. First, they note that the responses of these cells exhibit a high level of abstraction. Second, they note that some of these spatial cells respond to combinations of spatial quantities, for example, boundary cells that respond only when facing a specific direction. They interpret the first characteristic as evidence for role-filler independence: a boundary vector cell implements the predicate BOUNDARY(X), where X reflects the contents of the receptive field, and the firing of the cell indicates a true/false response as to whether a boundary is present at the receptive field location. They interpret the second characteristic as evidence for compositionality: a conjunctive border × head direction cell might be thought of as combining the ideas 'facing north' and 'boundary to the east', insofar as it only fires when both of these conditions are satisfied.

A recent commentary [31] pointed out several limitations to these ideas, most notably that we currently have no theory of how the hippocampal system might implement symbolic fillers and bind roles and fillers together. Without such a theory, any cell with a receptive field (e.g., a classical Hubel–Wiesel simple cell in primary visual cortex) might be interpreted as exhibiting role-filler independence. Moreover, as Kazanina and Poeppel themselves acknowledge, conjunctive coding is, on its own, a poor form of compositionality. To get 'true' compositionality, one needs to be able to combine two arbitrary predicates 'on the fly' using a dynamic mechanism (ideally using a mechanism that is sensitive to the order of the predicates). They point to context-sensitive conjunctive cells as evidence that the hippocampal system does flexibly combine elements; in this opinion article, we discuss several mechanisms for dynamically combining spatial (and nonspatial) elements. Overall, we agree with Kazanina and Poeppel's basic observation that the hippocampal system exhibits several LoT-like features, though we think that cognitive maps and any putative LoT are likely to be supported by distinct neural mechanisms.

Glossary

Cognitive graph: a representation of space in terms of nodes (locations) connected by links (path segments). A cognitive graph can be topological (representing only whether locations are connected to each other or not) or labeled (representing local metric information, such as the distances or angles between nodes).
Cognitive map: an internal model of the structure of a space (physical or abstract) that enables flexible navigation, planning, and inference. The exact format of cognitive maps is a topic of ongoing debate.
Compositionality: the principle that complex structures or meanings can be constructed from simpler, reusable elements, with specific rules governing their combination.
Concept cell: a cell in the human hippocampus that shows a high degree of selectivity for a specific concept, such as a person or a building. Concept cells have been shown to be active during perception, mental imagery, and memory recall, and may be the nonspatial equivalent of hippocampal place cells.
Default mode network (DMN): a set of functionally interconnected brain regions that were originally identified because they showed less activity during active cognitive tasks than during a resting baseline, suggesting that they support a 'default' mental state. More recent work implicates the DMN in episodic memory, semantic memory, prospective thinking, and social cognition.
Language-of-thought hypothesis (LoTH): the theory that thinking is the product of an internal symbolic system—a 'mental language' with combinatorial syntax and semantics—that enables structured, productive thought.
Propositionality: the property of mental representations being structured in a way that links objects, properties, and relations, thus allowing for cognitive operations over symbolic constituents. For instance, the thought 'The cat is on the mat' may have the following propositional structure: ON(cat, mat).
Replay: the spontaneous activation of neuronal ensembles in a sequence that recapitulates (or reverses) the order observed in a prior experience or anticipates the order in an upcoming experience, often at a faster rate. It is

the idea that our minds might represent space as 'a framework or container within which material objects can be located but which is conceived as existing independently of particular objects or objects in general' (p. 7). Langille and Gallistel [35] define maps as 'set[s] of vectors in a 2- or 3-dimensional vector space, on which navigation-relevant vector functions are defined' (p. 8). This conception of cognitive maps drew strength from neural recordings that identified cells in the hippocampal formation that encode elements of absolute space; these include place cells representing locations [32], grid cells representing a spatial metric [36], and head direction cells representing angular headings [37].

Some psychological work has explored the idea that cognitive maps might take alternative forms, less analogous to a cartographic map [38–43]. This work differentiates between Euclidean maps and **cognitive graphs**, with the latter including 'topological graphs' (encoding nodes and edges) and 'labeled graphs' (encoding nodes, edges, and local spatial information such as the angles between edges at each node) [41]. However, irrespective of the specific form of the cognitive map, its essential hallmark is its flexibility [22,25,32]. A cognitive map of an environment allows for the retrieval of spatial relationships between any represented points and for those relations to be systematically recombined, thus exhibiting a degree of **compositionality** (i.e., the ability to form complex representations out of simpler components through systematic procedures).

Complementing this empirical research, work in philosophy has been interested in understanding what maps are from a representational perspective—that is, how to understand maps with respect to theories of mental representation more broadly [27,29,44–47]. This work tends to take as a starting point the idea that cognitive maps are like physical maps and then considers the properties these maps might exhibit if this were the case. It tackles head-on questions about what maps are *in general* and what maps are *in the context of human cognition*. Do maps represent conceptual content or nonconceptual content [44]? Are they propositional [46]? How do they relate to the notion of a LoT [29,47]? The emphasis tends to be more on the elements that make up the map (the symbols on the paper) and less on the coordinate system (the paper itself).

There are several key takeaways from these philosophical treatments. First, maps are a distinct form of representation. Maps are unlike sentential representations of the sort handled by the putative LoT in several critical respects, including, for example, the fact that they are not propositional. In practice, this means that maps express information in different ways. For example, in language, the distinction between 'The store is on the corner' versus 'The store is *not* on the corner' is trivial. On a map, this is not so. Maps could, in theory, represent negation or absence (e.g., if blank spaces are taken as a positive indicator of absence) [27], but it is not clear that they always do. More importantly, even if maps can, in theory, represent absence or negation, this need not mean that *cognitive* maps in human minds do so [44].

Second, while maps may not be as rigid as sentential representations, they *are* structured. Maps are not, in other words, merely 'icons' without any constituent parts [48]. Cartographic maps have properties of structured representations, such as recurrent constituents and combinatorial semantics [27,46,49], and the structural features of graphlike representations are even more self-evident [40,41,50].

Third, and relatedly, maps are *diverse*. Canonical road maps are different from subway maps, for instance: the former have a higher degree of spatial isomorphism and constituent parts that more closely resemble the represented entities (i.e., a park on a canonical cartographic map might be represented by an extended area, whereas on a subway map it might be represented by a mere point; see Figure 1A). Additionally, 'maps' may include diagrammatic representations, such as

classically observed in hippocampal place cells during sharp-wave ripple events.

Theta sequences: the sequential activation of place cells across the phase of a theta oscillation, producing a temporally compressed sweep of spatial positions, trajectories, or cognitive states within each cycle.

Vector computation: the imputation of latent variables from other known variables. For example, one might infer a novel trajectory from A to C by virtue of knowing the trajectories from A to B and from B to C.

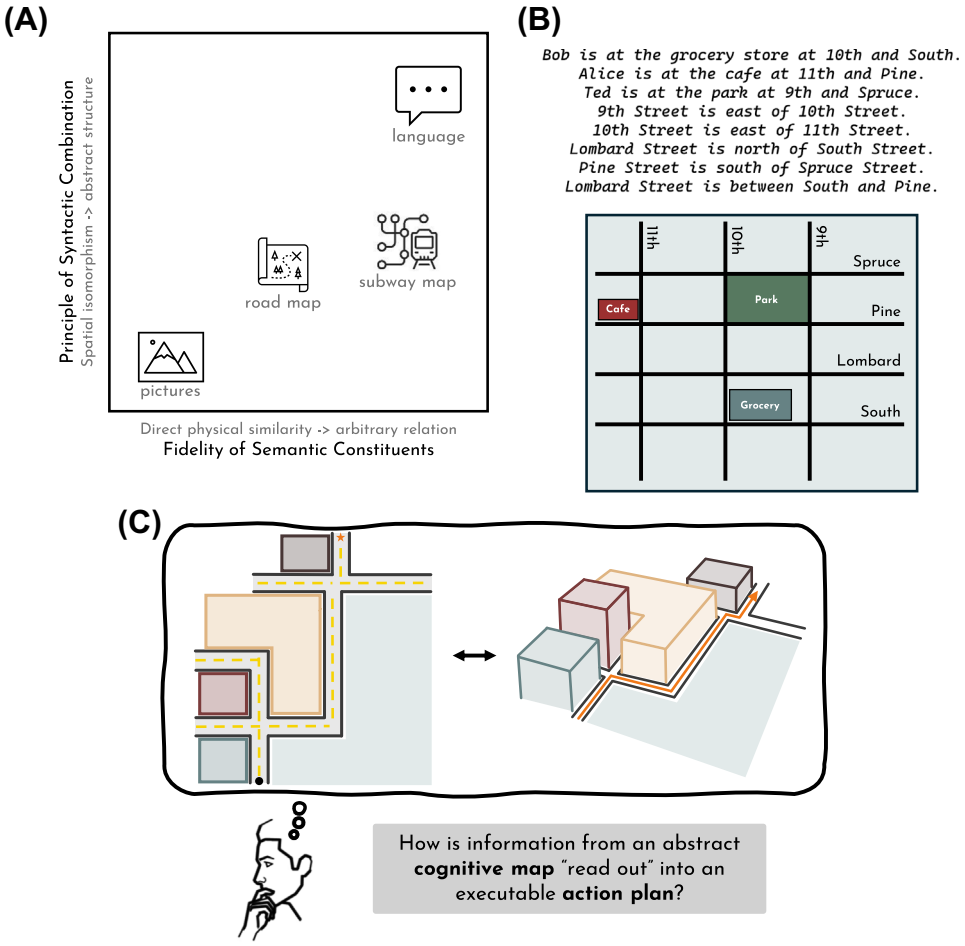

Figure 1. Thinking with maps. (A) Different types of representations are plotted with respect to the fidelity of their semantic constituents (i.e., faithful to the physical world vs. arbitrary) and how those constituents syntactically combine (i.e., spatial isomorphism vs. abstract structure). (B) A series of propositions describing the spatial layout of an area of Philadelphia (top) is compared with a representation of the same area in the form of a map (bottom). The spatial relationships among the elements are difficult to determine from the propositions but are readily apparent from the map. (C) A depiction of a translation from an abstract map to a specific planned route is shown. The map represents the allocentric relationships between all the elements in the environment; the route represents the sequence of elements that one encounters and the spatial choices (e.g., turns) that one must make to reach a specific destination. Subpanels A and B are adapted from [27].

seating charts or Venn diagrams [27]. This is not to say that the mind instantiates each of these representational forms exactly, but that it encodes various semistructured representations that are analogous to them.

Fourth, maps are not a substitute for other systems of thought. Even proponents of maps as a medium for thought acknowledge that maps are one format among several. Per Camp [27], 'Ultimately, any plausible cognitive system, including especially our own, is likely to [represent information] in cartographic, diagrammatic, and sentential formats' (p. 175). Thus, any account of maps as a medium of thought must explain how map-based thought interfaces with other forms.

In sum, psychology, neuroscience, and philosophy have converged on the idea that maps exist somewhere in between maximally unstructured, continuous representations (e.g., pictures) and maximally structured, discrete ones (e.g., sentential and languagelike representations). And in this way, maps may fill a critical cognitive niche, possessing some of the qualities of both pictorial and propositional representations.

Thinking with maps

What is this niche? Why does the mind have map-like representations at all? Maps do something that propositional representations egregiously fail to do: they capture large amounts of multi-dimensional information in a condensed form. Imagine describing the spatial environment of a city via a series of propositions (Figure 1B,C; adapted from [27]). Not only is it hard to *intuit* the structure of this space, but it is also hard to *recreate it*, even upon reflection. On its surface, this series of propositions reads like a puzzle. As a map, however, the structure is readily apparent.

This is a powerful demonstration of the value of map-like representations. They are vital not only to everyday navigation but also to all sorts of ordinary decision processes. Suppose you are tasked with selecting an automobile to compete in a racing competition (an example from [21]). You may have extensive knowledge about vehicles, which psychological research suggests is represented as a high-dimensional conceptual 'space' [18,51–53]. To make an optimal decision, you must reduce this high-dimensional space to a lower-dimensional manifold spanning the relevant dimensions (e.g., weight and power) while ignoring irrelevant dimensions (e.g., color). You must then evaluate the relevant dimensions simultaneously to select the vehicle with the highest possible speed (high power and low weight). It seems implausible that this decision is made by evaluating a series of pairwise propositions. As the number of cars increases, the computational tractability of solving the problem propositionally rapidly diminishes. With a map-like representation of the relevant car features, however, the number of cars under consideration hardly influences the difficulty of the decision. You simply select an item that is in the high-power, + low-weight region of the map. Critically, multidimensional problems such as this are commonplace. When cooking, a chef takes care to balance saltiness, savoriness, sweetness, and acidity to achieve an optimal flavor. When making hiring decisions, employers balance dimensions such as work ethic, prior experience, and communication skills. Decisions such as these are substantially easier if all items can be considered together in a common, continuous, low-dimensional space. Behavioral and neuroimaging studies suggest that we do indeed create such 'maps' for abstract, conceptual, and social information [19,23,24,26].

Indeed, cognitive maps may be part of a larger suite of spatial reasoning mechanisms that play a similar role in facilitating thinking about complex material [54,55]. Consider, for instance, the classic case of the *mental number line*: numbers are organized in the mind in a spatial way, such that, among individuals who read from left-to-right, lower numbers are represented on the left side of space and higher numbers are represented on the right side of space [56,57]. In this way, spatial position is tantamount to magnitude. To think about the magnitude 5, one needs only to consider the position of 5 on the mental number line. To assess whether 5 is greater than 3, one can simply ask whether 5 is farther to the right. Indeed, classic works interpret numerical thinking as a product of traversal through an imagined space [58,59].

Bottini and Doeller [55] suggest that 1-dimensional spatial reasoning mechanisms, such as the number line, which are often grounded in sensorimotor experience and have an implicit egocentric coordinate system, may play a complementary role alongside cognitive maps, which are more abstract and have an implicit allocentric coordinate system. Both kinds of

representations might serve to reduce the high-dimensional space of semantic knowledge to a smaller set of relevant dimensions. Critically, these are not esoteric cases of 'thinking'; basic geometric principles might support many varieties of thought via abstract and conceptual spaces [18]. Thus, we take it that 'thinking with maps' (or, at least, via spatial representations) is a regular occurrence in everyday life.

Interactions between cognitive maps and the LoT

If cognitive maps do indeed underlie a distinct form of thinking, the question arises as to how they interface with symbolic, sentential representations—or whether, instead, they possess sufficient representational expressivity to operate independently. This remains a mystery [44]. We will not fully answer this question, but we will offer some suggestions.

We will start by positing that some kind of interface between cognitive maps and LoT is useful, and perhaps even necessary. To see why, consider that, for the information in a map to be employed, it must somehow be translated into a complex action plan (Figure 1C). Imagine that you are trying to use a map of campus to get from the bookstore to the café. On the map, the icon for the café is 2 cm to the upper right of the icon for the bookstore. The implication of this fact is that the café is 200 m to the northeast of the bookstore, but this fact about the world is only obtainable via some sort of interpretive mechanism. First, the mind must attend to the bookstore and café icons. Second, it must assess the spatial relationship between these icons within the spatial framework of the map. Finally, it must convert this into a representation of the spatial relationship between the elements of the world by using one's understanding of things such as 'Top on the map equals North' and '1 cm on the map scales to 100 m in the world'. For a cognitive map, some aspects of the internal procedure would be different—for example, physical maps are always experienced from a particular viewing position, while cognitive maps are usually postulated to be inherently allocentric. But the crucial point remains: the map, on its own, is not in a format that can directly guide action—it must be converted into a representation that is more like a vector or a path [47,60]. It must be converted into a representation that is not a map.

The same reasoning applies to a cognitive map in a nonspatial domain. Consider the earlier example of using a cognitive map of automotive features to decide which car would be the fastest. Immanent in the map are many different specific relationships between cars: for example, the fact that Porsches are more powerful than Volkswagens. But to access these specific relationships, they must be made explicit—they must be converted into something that resembles propositional representations (see [44] on 'S-representations').

Indeed, the process of reading out a cognitive map is, in many ways, just the converse of the process by which the map is created. Our experience of the spatial world is through unique navigational episodes in which we travel along specific paths. Cognitive maps are condensations of the knowledge obtained from these episodes into a coherent knowledge structure [61], which can then be used to flexibly think about new paths, including ones that we have not directly experienced. The translation between route and map (or episode and knowledge) must occur both at the learning state and at the read-out state. This gives us plenty of reason to believe that the architecture for this translation must exist.

In sum, cognitive maps are not propositional, but to be used, they must be convertible into a format akin to propositions. (A similar requirement might apply to visual representations; see Box 3). This suggests that we should look to the conversion process to understand the mechanisms by which cognitive maps are used in thinking.

Box 3. Visual representations and LoT

One of the main aims of this opinion article is to understand the interface between *cognitive maps* and a more symbolic, sentential representation system, such as the *LoT.* A similar interface may be required to mediate between LoT and pictorial visual representations [125]. As Quilty-Dunn and colleagues [4] put it: 'If cognition is largely LoT-like, and perception feeds into cognition, then we should expect at least some elements of perception to be LoT-like, because the two systems need to interface' (p. 6). For example, even pictorial representations may capture certain relational structures via a 'scene grammar' [126,127] that possesses several of the representational hallmarks of LoT. Other work has explored the 'algebraic rules' governing compositionality in visual representations [128].

Lande [129], taking inspiration from models in computer vision, argues for 'image grammars' that can be construed as 'literal grammars for images' that have a 'rich syntactic structure, though of a markedly different form than sentences in a language' (p. 518). On this view, scenes are composed of objects that are composed of defined spatial regions that are finally composed of individual line segments and edges that combine in structured ways. Thus, even pictorial representations are built up from smaller representations that are systematically combined.

Despite discussions of an interface between vision and a LoT, little is known about the neural mechanisms underlying this interface. One possibility is that the dorsal visual stream represents the visual world using a compositional code in which objects, parts, and relationships are represented explicitly, whereas the ventral visual stream mediates more imagistic representations [130]. Alternatively, representations throughout the visual system might have a hybrid imagistic-grammatical structure [129]. A key question is whether the vision–LoT interface utilizes the same mechanisms or principles as the map–LoT interface.

Neural mechanisms in the hippocampal system and the cortex

To specify these mechanisms, we now turn to the neural underpinnings. The hippocampal system underlying cognitive maps has been shown to be involved in route-based planning [62–64] and also in prospective thinking in terms of imagined episodes [65,66]. Previous work has identified several dynamic mechanisms within the hippocampal formation that allow map-like representations to become cognitively active and may subserve these functions by converting cognitive maps into routelike or episodelike representations [67]. In this section, we discuss three candidate mechanisms: **replay**, **theta sequences**, and **vector computation** (Figure 2). We focus, in particular, on the ability of these mechanisms to construct compositional structures that could undergird the formation of LoT-like representations.

Replay

In replay, hippocampal place cells fire in a rapid sequence that resembles, in a time-compressed format, the sequences observed during navigation [68,69]. Replay is observed during navigational pauses (and also during sleep) and often involves the firing of cells that represent 'remote' locations (i.e., locations that are not currently occupied by the animal). Some replay sequences recapitulate paths recently traversed, but others anticipate paths that the animal will subsequently take [70]. The latter phenomenon is evocative because it seems to suggest that replay may be a mechanism for thinking about the future [71,72], a function that has been linked to the hippocampus [66,73].

The question of whether replay subserves navigational planning, memory consolidation, or some other function is a topic of ongoing debate [74,75]. The strongest evidence for a navigational planning role comes from the fact that these sequences are predictive of future paths [71] and that they flexibly reroute around barriers when the structure of the environment changes [76]. The strength of the trial-by-trial relationship between replay sequences and immediately following behavior, however, remains to be established. In any case, the phenomenon is relevant to the current discussion because it is a mechanism by which the multitude of potential spatial trajectories immanent in the hippocampal cognitive map can be converted into representations of specific spatial paths.

Notably, replay sequences in rodents show evidence of compositional structure [77,78]. During sleep, these sequences can be divided into shorter two to four 'tuplets' that are recapitulated

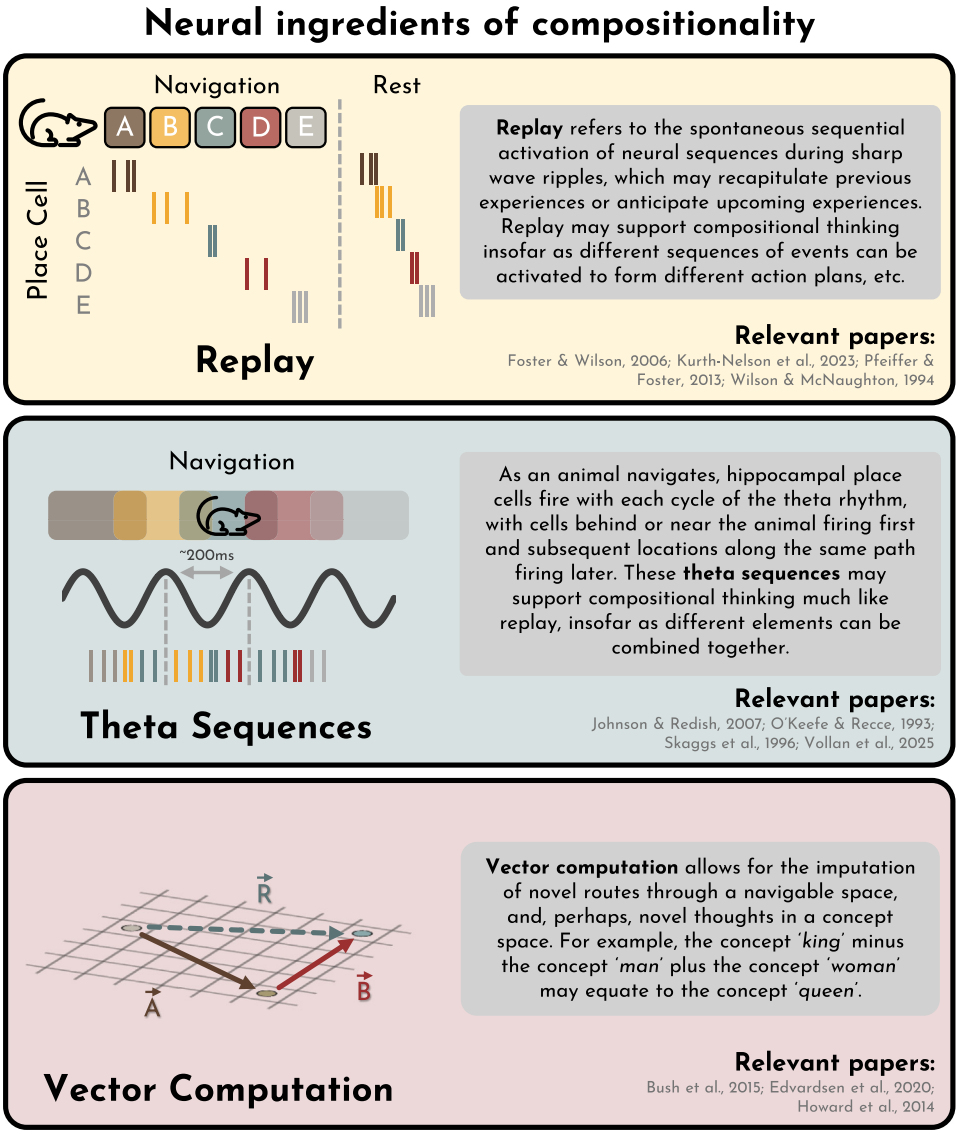

Figure 2. Neural ingredients of compositionality in the hippocampal formation. Replay, theta sequences, and vector computation are mechanisms for cognitive map readout in the spatial domain. Each mechanism exhibits some evidence for compositionality, suggesting that they are all candidates for supporting compositional thinking (in collaboration with cortical mechanisms). However, it remains to be seen whether any of them are necessary or sufficient for compositional thought. Referenced articles: [13,64,68,69,71,84–87,103,105].

in subsequent awake navigational sessions [79]. This suggests that replay sequences may be generatively constructed by recombining simpler, pre-existing elements, in the same way that DNA sequences are constructed from codons or sentences are constructed from words [80]. Compositional organization is also observed *among* replay sequences. In mazes consisting of multiple arms, replay sequences extending across arms are composed of arm-specific subsequences, which can occur in separate sharp-wave ripple events, thus demonstrating a compositional structure related to the topological organization of the environment [81].

There is some evidence that the compositional structure of replay sequences could be used to encode compositional meanings. Insofar as replay involves a set of discrete neural events that form a sequence in time, the events themselves could provide a 'role' that might be 'filled' by the cells that fire during the event [13]. Different thoughts might then be composed based on the contents of the fillers and their ordering within the sequence. Evidence for this idea comes from an magnetoencephalography (MEG) study in which participants learned two temporal sequences of four objects each [82]. In rest periods after learning, sharp-wave ripples in MEG power were observed, during which representations of the objects and the sequence positions were replayed. The representation of each sequence position was grouped temporally with the representation of the corresponding object, with the position representations preceding the object representations by 50 ms. This suggests that the position representation encoded a 'role' that was 'filled' by the closely following object representation. A similar role-filler binding could, in theory, encode other kinds of relationships, such as verb-actor, although at present there is no direct evidence for this idea [13]. **Concept cells** in the human hippocampus have been shown to represent people, places, and things [83], but—thus far—not actions.

Theta sequences

A second mechanism for cognitive map readout is the sequential firing of hippocampal place cells during cycles of the theta rhythm. In contrast to replay sequences, which occur when the animal is resting before or after movement, theta sequences occur when the animal is engaged in active navigation. At any moment as it travels, the animal occupies multiple place fields, which may have slightly different centroids. The firing of these hippocampal place cells is ordered in time by the theta oscillation cycle, such that place fields centered behind the animal fire earlier in the cycle and place fields centered in front of the animal fire later, a phenomenon known as theta-phase precession [84]. Thus, the firing of place cells recapitulates, in compressed form, the past and future trajectory of the animal [85]. Moreover, when the animal is paused at a decision point with more than one possible path before it, nonlocal firing is observed within theta cycles, proceeding forward along one path and then another in alternating cycles of the theta rhythm [86]. A similar phenomenon is observed in open spaces, where the firing fields sample paths that alternate on the left and right sides of the animal [87].

Theta sequences have been linked to cognition through the behavioral phenomenon of vicarious-trial-and-error (VTE): when the animal pauses at a navigational decision point, it will point its head down one path, then the other, as if it were actively considering the consequences of the two alternatives [88,89]. While this is happening, theta sequences will 'sweep' forward to trace out the path to the goal, with longer sweeps when the goal is farther away [90]. Because theta sequences are observed when the animal is actively navigating rather than being at rest, alternate between possible paths, and co-occur with the choice-related behavior of VTE, they seem, on the surface, to be even more likely than replay to be related to deliberation and, hence, to thought. Notably, two recent studies have demonstrated a tight link between theta sequences and navigational planning by showing that theta sequences represent vectors toward remembered goal locations [91] and upcoming navigational trajectories [92].

As with replay, theta sequences are compositional insofar as they organize discrete elements within a temporal series. Higher-frequency gamma oscillations are often coupled to theta oscillations, providing a mechanism for organizing different 'slots' within a temporal framework [93,94]—an organization that has been analogized to 'words within a sentence' [95,96]. Theta sequences and theta-gamma coupling have been observed to organize memories of sequentially experienced items [97,98], and they are observed during the encoding and retrieval of naturalistic movie clips, where they are predictive of memory success [99]. However, we currently lack

evidence that these mechanisms are involved in organizing mental contents that might correspond to actual words and sentences, or to precursor elements that a person might generate during self-initiated thought.

If such evidence were found, the compositionality of such 'thoughts' may be limited to contents that are representable within individual theta sequences. Theta appears to divide experience into discrete segments, which can be observed during both real and imagined navigation [100]. However, the navigational paths traced out by theta sequences tend to extend only to the next goal or landmark [101]. This contrasts with replay sequences, which can extend over multiple segments [102] and thus may have a larger compositional scope.

Vector computation

Replay and theta sequences are readouts of cognitive maps that take the form of sequential paths of overlapping locations. Another way to read out a cognitive map is to calculate vectors that express the spatial relationship between points, even if the points are not adjacent [103]. Such vectors would be the equivalent of simple statements, which could capture spatial relationships ('the café is north of the bank') or conceptual relationships ('the Buick is more expensive than the Chevy'). Notably, computational work shows that vector computation offers a plausible framework for understanding some kinds of thought composition [104]. For example, in continuous language spaces, concepts can be approximated as the sum of related concepts (e.g., 'queen' is 'king' *minus* 'man' *plus* 'woman'; see Figure 2).

Several theories have been proposed about how these vectors might be computed [105–107]. These often posit that entorhinal grid cells play a key role, which is a reasonable assumption given that grid cells provide a metric that tiles space in a regular manner. Consistent with this idea, fMRI studies have observed activity corresponding to Euclidean distances to the goal in the entorhinal cortex (and also the anterior hippocampus), whereas activity corresponding to the path distance is observed in the posterior hippocampus [64]. Moreover, thinking about the relationship between points activates gridlike responses in the entorhinal cortex for both navigable spaces [108] and conceptual spaces [109].

Beyond the hippocampus

The hippocampal mechanisms described above may be crucial for converting map-like representations into LoT-like thoughts. Moreover, they may play a broader role in cognition insofar as damage to the hippocampus impacts not only spatial navigation [110] but also imagination and future thinking [66], transitive inference [111], and even social behavior [112]. We do not believe, however, that they are mechanisms of LoT itself (Box 2). The little neural evidence we have suggests that LoT is implemented (at least partially) elsewhere, perhaps distributed throughout cortical systems [14,113]. Moreover, the rapid instantiation of information in hippocampal sequences seems to be on a faster timescale than that of conscious thought [114]. Thus, we believe that compositionality in replay, theta sequences, and vector computation would simply allow for an interface between cognitive maps and LoT.

Key to this interface might be the putative episodic simulation function of the **default mode network (DMN)** [14,115]. The DMN is a set of functionally connected regions that includes the hippocampal formation as well as cortical regions such as the posterior cingulate, angular gyrus, and medial prefrontal cortex [116]. The DMN has been associated with episodic memory, semantic memory, prospective thinking, and social cognition [117]; moreover, DMN regions exhibit gridlike spatial codes during virtual spatial navigation [118] and 'navigation' of abstract feature spaces [26]. The DMN is functionally connected to the hippocampal formation,

and hippocampal replay events have been shown to be coincident with activity in the DMN [119,120]. We hypothesize that spatial or cognitive routes instantiated by dynamic hippocampal mechanisms might manifest as episodic simulations in the DMN, which might then be further reified as languagelike thoughts through interaction with other cortical networks (e.g., [121,122]).

Thus, we might conceptualize the interaction between cognitive maps and LoT as follows: cortical networks encode a high-dimensional representation of our long-term knowledge, albeit in latent form. To form an original thought, we activate the relevant subset of that knowledge, which takes the form of a lower-dimensional manifold or cognitive map. We then recover a specific routelike or vectorlike representation from the activated map, which is instantiated in the DMN as an imagined scene or episode in which specific entities and their relationships are highlighted. It is this representation that we believe naturally coheres with the structure of language.

Damage to different parts of the brain would impact this process at different points. For example, damage to the hippocampal formation, as in the case of Henry Molaison, would tend to make thinking repetitive and stimulus-bound, with reduced ability to employ long-term knowledge in flexible and creative ways [123]. More extensive damage to the DMN might impact the thought process more profoundly, as in the case of Clive Wearing, who stated that he was 'completely incapable of thinking' despite his ability to form and understand sentences [124].

Concluding remarks

Cognitive maps are a critical tool in our cognitive toolkits—an instrument for representing complex, multidimensional information in an efficient, interpretable manner. In this way, we believe that cognitive maps are a proper *medium for thought*, distinct from but interfacing with a putative *LoT*. A growing body of work is taking this possibility seriously, and we have attempted to provide a succinct overview of this literature here. While uncertainty remains about how maps support compositional thinking and how they interact with other media of thought, future work in cognitive science, particularly in cognitive neuroscience, may do well to examine this interface directly (see Outstanding questions).

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Declaration of interests

The authors declare no competing interests.

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Outstanding questions

To what extent is map-based, compositional thought uniquely human? Do nonhuman animals possess map-like representations that can participate in compositional operations, or does such integration require capacities—such as symbolic abstraction or recursive structure—that are exclusively human?

Do the neural mechanisms discussed here, such as replay and theta sequences, support navigational planning in an intelligent, trial-by-trial manner? Or do they merely lay the groundwork for such planning; for example, by fine-tuning the hippocampal cognitive map during memory consolidation?

Can we link dynamic mechanisms in the hippocampus not only to navigation but also to thinking in general? Hippocampal damage has been shown to reduce the complexity of imaginative constructions—can we take this further by showing that interruption of specific dynamic mechanisms impacts compositional thinking? Can we obtain direct neuronal-level evidence for replay in the human hippocampus—evidence that has remained elusive?

Can concept cells in the human hippocampus represent the full range of concepts that undergird thinking, including not only people, objects, and landmarks (i.e., nouns) but also actions (i.e., verbs)? If dynamic hippocampal mechanisms, such as replay and theta sequences, organize cognitive maps into thoughtlike representations, this would require the hippocampus to have a greater representational expressivity than has been hitherto observed.

What are the roles of the language network (believed to represent linguistic forms) or the multiple-demand network (believed to support the coordination and online combination of mental contents) in mediating the interface between cognitive maps and the LoT? We have speculated that the DMN plays a key role, but other cortical networks are very likely also involved.

Are the mechanisms that mediate the visual system–LoT interface the same as or similar to the mechanisms that mediate the cognitive map–LoT interface?

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