

# **The Neural Ingredients for a Language of Thought are Available**

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## Highlights

The 'Language of thought' (LoT) hypothesis advanced by the philosopher Jerry Fodor posits that mental representations are compositional and productive. Thought is symbolic and new complex thoughts are constructed from more basic concepts.

The neurocognitive feasibility of the LoT has been challenged in light of the lack of demonstrable neural correlates.

We demonstrate that the key ingredients needed for a neural implementation of the LoT are indeed available, using the example of the parahippocampal spatial navigation system in rodents.

## Abstract

The classical notion of a 'language of thought' (LoT), advanced prominently by the philosopher Jerry Fodor, is an influential position in cognitive science whereby the mental representations underpinning thought are considered to be compositional and productive, enabling the construction of new complex thoughts from more primitive symbolic concepts. LoT theory has been challenged because a neural implementation has been deemed implausible. We disagree. Critical ingredients needed for a neural implementation of a LoT have in fact been demonstrated in the hippocampal spatial navigation system in rodents and other animals. We show that cell types found in spatial navigation – border cells, object cells, head-direction cells, etc. – provide key types of representations and computations required for the LoT, underscoring its neurobiological viability.

## A hypothesis about the nature of thought

Many of us read at some point - perhaps with a mix of surprise and bewilderment - a story about a White Rabbit with pink eyes who, as he ran by a curious and stunned girl named Alice, took a watch out of his waistcoat-pocket, looked at it, and hurried on repeating "Oh dear! Oh dear! I shall be late!"<sup>1</sup>. Whether or not captivated by the story line, no reader fails to *imagine* the described scene, despite it being highly unpredictable and outright bizarre. The experience exemplifies that our mind can combine 'old' concepts stored in memory (linked to words) in novel ways to construct an unbounded number of thoughts, from plain and commonplace to novel and wild.

In his seminal 1975 book *The Language of Thought*, the philosopher Jerry Fodor revived, developed, and sharpened ideas originally expressed in Saint Augustine's *De Trinitate*, Thomas Aquinas' *Questiones Disputatae de Veritate*, and, later and more systematically, in William of Ockham's *Summa Logicae*: that the mind's creativity is underpinned by a system that stores concepts symbolically and manipulates them in a structured way, using compositional rules<sup>2-4</sup>. Fodor named that system the Language of Thought (LoT), underscoring similarities – although crucially not identity – of the organisation of thinking with human language.<sup>1</sup> The essence of the LoT is that the mind is a computational system that operates over symbolic representations and is compositional, systematic, and productive<sup>2,3,5</sup>. Compositionality (and in a related way systematicity) refers to the principle that the meaning of a complex thought is composed of the meaning of its parts and the rules that are used to combine them. The property of productivity indicates that one is able to generate novel thoughts, because the system possesses virtually unbounded power due to its combinatorial nature over a finite set of primitives. For example, anyone who 'has' the concepts *John*, *Mary*, *run* and *pinch* can entertain all of the following thoughts: *John runs*, *Mary runs*, *John pinched Mary*, *Mary pinched John*. This outcome is expected only if thoughts are computed compositionally from primitive concepts rather than stored holistically in memory. Thoughts are expressions with a logically-deducible meaning.

In current research that seeks to link the cognitive and brain sciences, the nature of thought remains a profound problem - not to say a mystery. What neurobiological approaches have to say about concepts, the construction of thoughts, and their neural implementation is still (too) distant from the insights of the psychological and cognitive sciences, including philosophy and computer science. In particular, the computational theory of mind has, in our view, not sufficiently penetrated neuroscientific methodologies to the study of thought (but see ref.<sup>6</sup>) which we take to be a missed opportunity. The timeliness of this topic is reflected in recent publications that seek to re-examine the relevance of the LoT concept in cognition<sup>7-9</sup>.

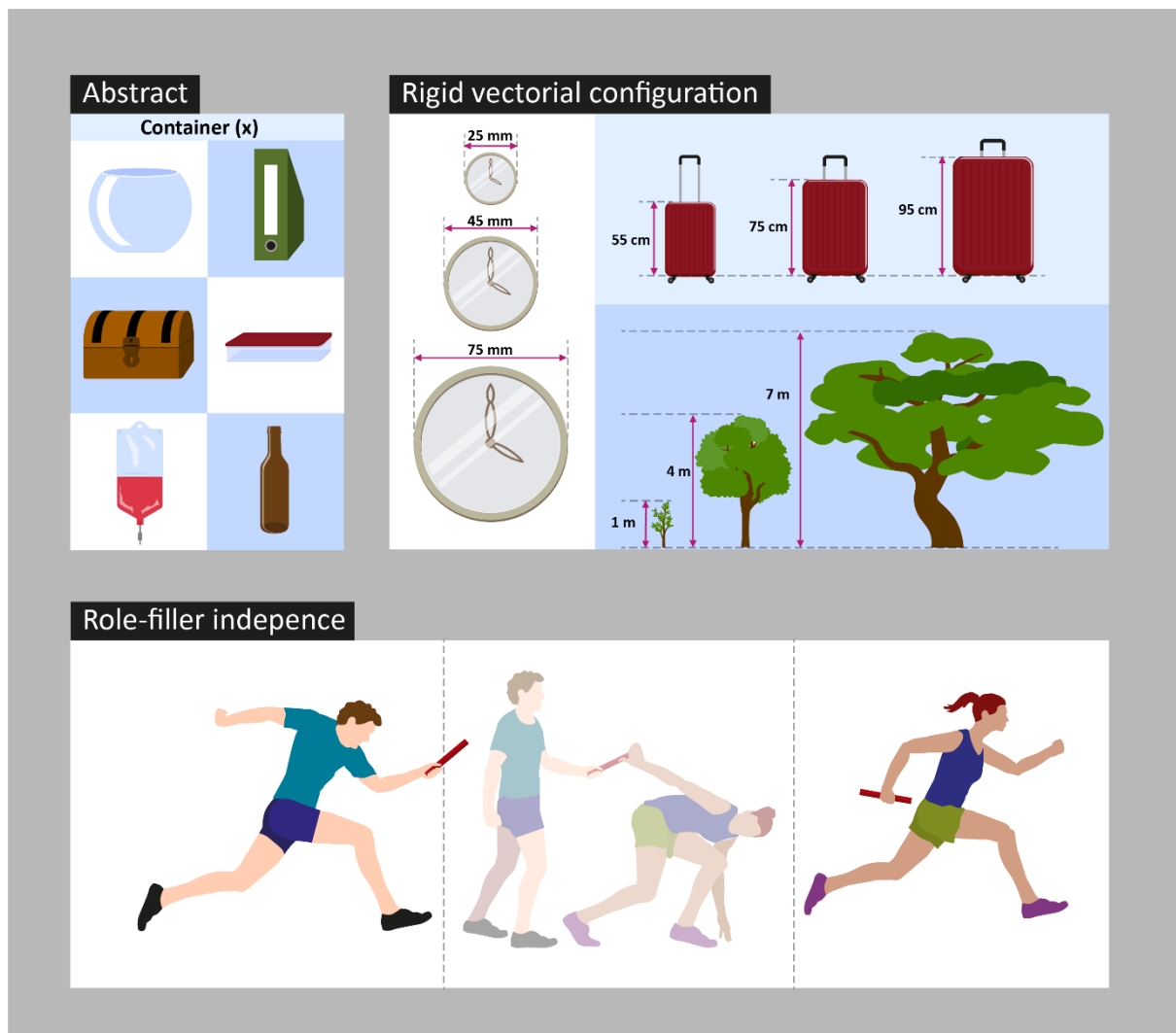
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<sup>1</sup> The locution 'language of thought' has led to some unfortunate misinterpretations due to the use of the word 'language.' A more neutral locution might be the 'formal system of thought.' Although there are notable similarities to the language system per se, the substance of the language of thought does not have to be linguistic, nor do the specific formal operations. There needs to be a mapping between the language of thought and linguistic cognition (something well beyond the scope of this paper) but it is important to acknowledge the independent properties. This independence is, for example, apparent in studying prelinguistic infants <sup>76-78</sup>.

The LoT requires that the brain supports symbolic representations that can be combined systematically and productively, enabling an infinite number of composed representations. This hypothesis, however, was set aside as neurobiologically non-viable (for discussion, see ref.<sup>10</sup>). The dominant neurobiological theories, grounded in the notion of synapses and cell assemblies as the key substrate for all knowledge<sup>11</sup>, went into different directions. As noted by Gallistel<sup>10,12</sup>, the widely accepted view whereby memory resides in synapses and synaptic weights presents problems: this notion of information storage renders memory a synaptic pattern, not a symbol; and such patterns are not the right natural kinds to support composition and computation (without relatively baroque adjustments and concessions to the underlying premises; but see refs.<sup>13–15</sup>).

Yet there in fact exists evidence from neuroscience for symbolic representations and computations over them<sup>12,16</sup>. A key piece of evidence comes from groundbreaking research on spatial navigation over the past half-century<sup>17–19</sup>: the organisation of the hippocampal formation and related structures in rodents and other animals demonstrates that at the basis of spatial navigation lies a computational system in which abstract symbolic representations enter into algebraic-like calculations.

We argue that these findings demonstrate that symbols and operations over symbols, the kind of ingredients called for by the LoT, are implemented in the brain. In examining some key findings from the spatial navigation literature, we extend Gallistel's argument that the neural machinery underpinning spatial navigation is inherently symbolic. In so doing, we demonstrate how neural cell types found in spatial navigation successfully deliver key *types* of *representations* and *computations* needed for the LoT, thereby bridging the substantial gap between cognitive and neurobiological views on knowledge representation.



**Figure 1. Essential properties of Language-of-Thought predicates**

**Abstractness:** meaning is not determined by a set of purely physical criteria. The objects in the picture differ in shape, size, texture, and other properties, yet all qualify as 'container'. **Role-filler independence:** the semantic content of the predicate ('role') is (at least partially) invariant with respect to its arguments ('fillers'); for example, the predicate *RUN()* has a core meaning that holds regardless of the argument (roughly, "move without all the feet on the ground at any given time"). Arguments can be temporarily bound or unbound to predicates, e.g. *RUN()* is first bound to *John*, making *RUN(John)* true while he is running his leg, then once Mary's leg starts, *RUN(John)* becomes false and *RUN(Mary)* becomes true. **Rigid vectorial configuration:** *SMALL(x)* must be more similar to *MEDIUM(x)* than to *LARGE(x)* in all contexts and for all x's, regardless of the x's size or other properties.

## Language of Thought and Predicate Calculus

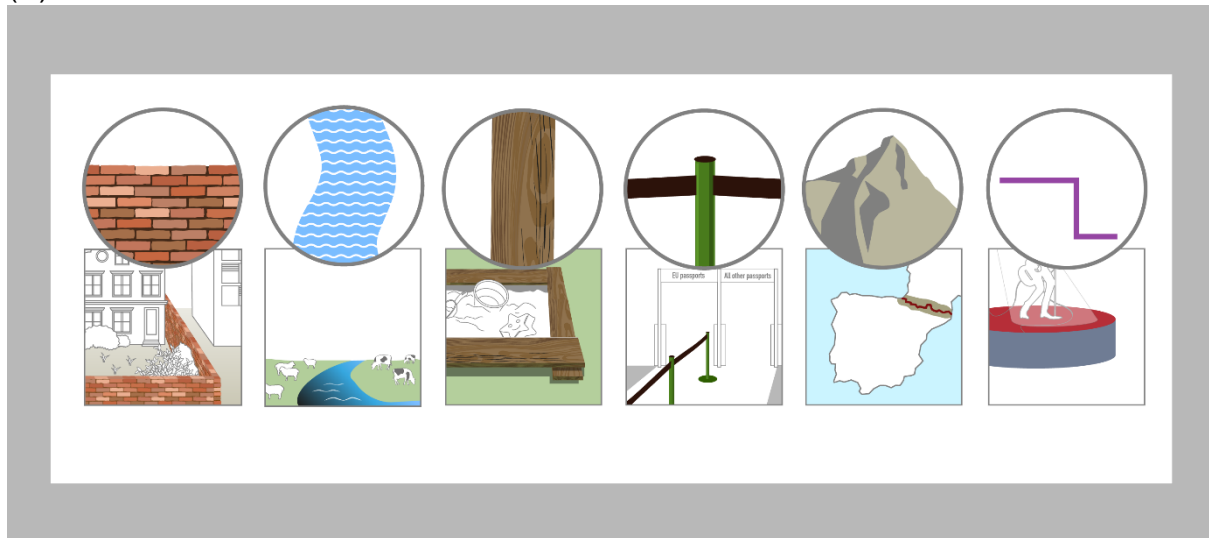
The Language of Thought, foundational in the computational theory of mind, holds that the mind is a symbolic computational system that is compositional, systematic, and productive<sup>2,3,5</sup> and can be characterized by formal logics, including Predicate Calculus (PC; **Box 1**). The key concept of PC is that of a *predicate* that takes one or more *arguments* of the type ‘individual constant’ (e.g., *Fodor*, *Hebb*, *Metropolitan Opera*) or ‘variable’ ( $x$ ,  $y$ ). LoT predicates represent a range of meanings corresponding (in language) to verbs (*RUN*, *KISS*, *LOVE*), nouns (*DOG*, *CONTAINER*, *THEORY*), adjectives (*RED*, *FRENCH*), adverbs (*QUICKLY*), prepositions (*UNDER*, *BETWEEN*), etc. A one-place predicate denotes a subset of entities that possess the quality of the predicate, e.g., of all entities in the world, *RED*( $x$ ) selects a subset of entities that are red and *DOG*( $x$ ) selects those that are dogs.

We highlight three properties of predicates (**Figure 1**) that we will subsequently link to the discourse of neurobiology. First, whereas the meaning of some predicates has a straightforward correspondence to a fixed, physically-definable criterion (e.g., *RED* is often – although not always – linked to the activity of specific cones in the retina), most predicates are abstract, in that their meaning is not determined by a set of physical criteria or surface patterns. *CONTAINER*, for instance, is an overarching category comprising physically dissimilar entities: tiny to gigantic boxes, bowls, vases or tubes; square, round or pyramid-shaped; used to hold food, clothes or furniture; made of plastic, glass or metal; with or without a lid, etc.

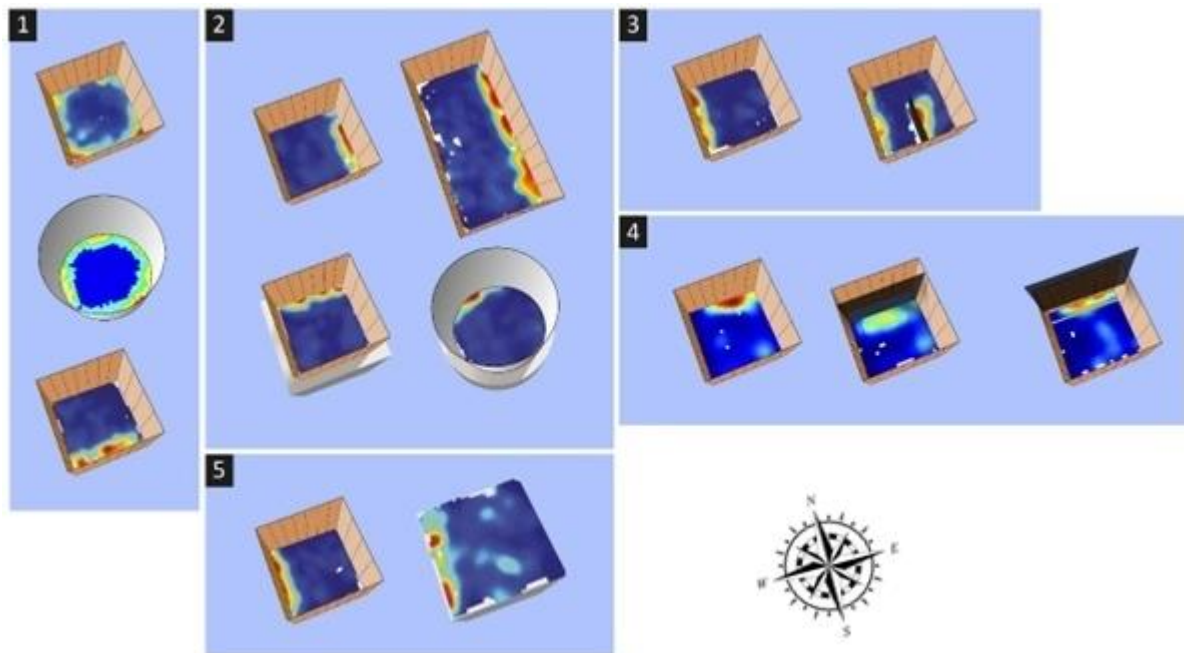
Second, predicates possess what is known as ‘role-filler independence’<sup>20,21</sup>: predicates (‘roles’) are represented independently from their arguments (‘fillers’) and thus can be dynamically bound and unbound from them. For example, in a relay situation (**Figure 1**), during his leg *John* can be temporarily bound to *RUN*() to obtain *RUN*(*John*) while Mary is bound to *PREPARE*( $\emptyset$ ). When Mary’s leg starts, *PREPARE*(*Mary*) and *RUN*(*John*) are unbound and *RUN*(*Mary*) and *WAIT*(*John*) are created. Thus, fillers can be bound to different roles at different times, contributing to the LoT’s productivity. Relatedly, the role’s semantic content is at least partially invariant with respect to its fillers. The core meaning of *RUN*() is maintained regardless of whether its argument is *John*, *Mary*, *rabbit*, etc. Consequently, one can evaluate novel, previously unencountered predicate-argument combinations such as *RUN*(*gleeb*) where *gleeb* is a newly-discovered creature.

Third, because predicates maintain their core meaning, their relative configuration in a multidimensional meaning space is constant: *DEAD*( $x$ ) remains opposite to *ALIVE*( $x$ ), *CHASE*( $x,y$ ) to *FLEE*( $x,y$ ), *ABOVE*( $x,y$ ) to *BELOW*( $x,y$ ), and *SLEEPY*( $x$ ) is more similar to *DROWSY*( $x$ ) than to *AWAKE*( $x$ ) in all contexts and for all  $x$ ’s and  $y$ ’s.

(A)



(B)



**Figure 2. LoT predicates and spatial cells**

(A) The LoT predicate *BOUNDARY()* encodes an abstract meaning 'limiter, divider'. Physically-dissimilar objects (circles) – a wall, river,... a dropped level – each make *BOUNDARY()* true, as illustrated by the corresponding scenes (squares) or their verbal descriptions (*The wall is the property boundary, The river is a boundary between fields*). (B) Border cells encode an abstract concept 'BOUNDARY'. ❶ A border cell firing at the walls of a square enclosure (top)<sup>22</sup> or of a circular enclosure (middle)<sup>23</sup>. Border cells often have a preferred direction, e.g. fire only at the south wall<sup>22</sup>. ❷ Border cells fire at boundaries of different geometries. The cell's field follows the wall geometry change when a square enclosure is stretched to a rectangle (top)<sup>22</sup> or a circle (bottom)<sup>22</sup>. ❸ Border cells respond to both peripheral and internal boundaries. A cell that fired at the north wall (left) also fired to a newly introduced north wall (black) inside the enclosure (right)<sup>22</sup>. ❹ Border cells encode the meaning 'obstruction to movement'. A cell was recorded in a square enclosure (left), when a new wall was added (middle) and subsequently lifted up (right). The cell fired at the original wall (left), and the new north wall when it obstructed the animal's movement (middle) but not when it did not (right)<sup>24</sup>. ❺ Border cells respond to diverse boundary types. A cell fires at the west wall (left) and along the west edge after the walls have been removed to produce an open surface with a 60-cm drop along the perimeter (right)<sup>22</sup>.

## Cells underpinning spatial navigation encode symbols and perform computations of the type required by the LoT

The linking hypothesis developed here is that the neurobiological mechanisms found in the rodents' spatial navigation system are ontologically sufficient to represent symbols and operations required by the LoT. In light of the central role of *predicates* in the LoT, the position we advocate most critically calls for a rigorous demonstration of how such predicates – abstract, maintaining role-filler independence, and providing configurational stability - can be implemented using the neural architecture observed in spatial navigation. Of equal importance is to demonstrate that individual predicates can be combined into more complex expressions dynamically and productively.

Our linking hypothesis is stateable and viable due to trailblazing research on spatial navigation over the past half-century, pioneered by O'Keefe and Dostrovsky<sup>17</sup> and provided with deep theoretical foundations by O'Keefe and Nadel<sup>25</sup>. Various cell types have been discovered, mostly in the hippocampal formation and related structures: place, grid, head-direction, border, landmark, object cells, etc. (see Glossary and **Box 2**). These cells enable the animal to build a cognitive map of the environment that holds information about “places in the organism's environment, their spatial relations, and the existence of specific objects in specific places”<sup>25</sup>. We take the spatial navigation system to be a well-motivated model for the LoT: despite being restricted to space, navigation possesses *basic solutions needed for a neurobiological implementation* of the LoT.

Most foundationally, the spatial navigation system features a ‘*lexicon*’ or ‘*inventory*’ of different spatial predicates encoded by single neurons: distinct cell types such as border, object, or landmark cells essentially implement a specific spatial predicate, *BOUNDARY(X)*, *SMALL-OBJECT(X)* or *LANDMARK(X)*. Take **border cells** (also referred to as ‘boundary cells’) that fire when the animal is immediately adjacent to an obstacle that blocks its path<sup>22,26,27</sup>. That is, of all possible locations within the animal's navigational space, the border cell fires only in the subset of locations where there is an environmental boundary within the reach of the animal's whiskers (**Figure 2B**). This is nothing other than the brain's implementation of the predicate *BOUNDARY(X)* in the spatial domain that returns True if the cell's receptive field *X* contains a boundary and False otherwise. [Here *X* is a variable that uniquely encodes position in 2d space, e.g., via two coordinates on the horizontal and vertical axis in the Cartesian system.]

Importantly, the predicate *BOUNDARY(X)* implemented by border cells is *abstract* (**Figure 2B**). Border cells (and the closely related boundary-vector cells) fire at barriers of different textures and colours; at protruding barriers or drops in the surface level; at barriers that form the periphery of the animal's environment or are internal to it<sup>22,28,29</sup>. That boundary-vector cells' firing reflects abstraction is underscored even in the first report<sup>28</sup> of such cells: “[A] boundary is an abstract concept that may reflect sensory properties of environment features such as the sight or feel of a wall or an extended edge, as well as impediments to movement”. The border/boundary cell's firing pattern parallels the abstractness and open-texture of human concept ‘boundary’ that can be represented by many forms (**Figure 2A**). This demonstrates that abstract, open-textured concepts are represented by the brain.



Another compelling example of a predicate implemented in neural tissue comes from **object cells** that fire when the animal is located next to an object<sup>23,30,31</sup>. As with border cells, the representation computed by the object cell is abstract. The cell fires in the vicinity of *any* small object, notwithstanding its shape, texture or familiarity; it fires even in the dark, when no visual information about the object is available<sup>23</sup>. An object cell continues to fire when an object is replaced with a different object, but stops when the object is removed completely<sup>23</sup>. These cells therefore reflect the predicate *SMALL-OBJECT(X)* that returns True iff the cell's receptive field X contains a (small) object.

Border cells, object cells, and their vectorial counterparts (see **Glossary**) satisfy *role-filler independence*. These cells fire for *any* boundary or small object within their receptive field, indicating that object *identity* (filler) is coded by a separate neuronal population (hypothesized to be in the perirhinal cortex<sup>32,33</sup>) than the predicate expressed by the cell (role). Each cell type encodes a specialised core meaning, '(location of) a boundary' for border cells or '(location of) a small object' for object cells. This also enables generalization: novel, previously unseen objects can be categorised as boundaries, small objects, etc. Indeed, border cells immediately fire along novel, previously-unencountered boundaries<sup>22,26</sup> (**Figure 2B**), underscoring that – just like in the LoT – the membership in the category 'boundary' can be extended to novel instances that represent an impediment to the animal. Similarly, object cells fire immediately if a new familiar or unfamiliar object is introduced into the arena<sup>23</sup>. The content of the cell's receptive field is productively evaluated against particular criteria and translates into the cell's firing.

Border, head-direction and object-vector cells maintain their relative vectorial configuration. They fire coherently across environments. For example, two border cells that fire along the same/opposite walls in one environment will also fire along the same/opposite walls in another environment<sup>22</sup>. This also holds across cell types: the angular difference from environment A to environment B is constant for different head direction cells, and also matches that for an object vector cell<sup>24,34</sup>. Thus, the cells' *relative* configuration is maintained - akin to how the relationship between predicates is maintained in the LoT.

### Further attributes found in spatial navigation crucial for the LoT hypothesis

Just like LoT predicates vary in whether they reflect a more elementary or more derived meaning, so do spatial cells. Some LoT predicates may be viewed as composed of several more primitive predicates, e.g., *WOMEN(x)* can be viewed as *PERSON(x) ∧ FEMALE(x)* and *GIRL(x)* as *PERSON(x) ∧ FEMALE(x) ∧ YOUNG(x)* (see ref.<sup>2</sup> for counterarguments). Such decomposable predicates are ample, as evidenced by the linguistic lexicon, often taken as a proxy for the LoT lexicon. The spatial navigation system has a similar mix of primitive and complex cells. For example, alongside simple border and head-direction cells, ref.<sup>35</sup> reports conjunctive cells that fire when the animal encounters a border while its head is turned in a specific direction, representing complex meanings such as *BOUNDARY(X) ∧ HEAD-DIRECTION\_NORTH(A)*, where X represents the location of the cell's receptive field and A represents the animal's head-direction/location. These conjunctive cells are rigid and designate a very specific meaning, i.e. boundaries encountered when the

animal faces north. Other conjunctive cell types have been reported, e.g. place x head-direction and grid x head-direction cells<sup>36,37</sup>.

Whereas some non-elementary meanings may be encoded by conjunctive cells, the LoT asserts a further, properly compositional mechanism that enables creating new complex meanings dynamically. In the PC, production of complex meanings 'on the fly' is achieved by combining predicates using logical connectives and quantifiers (**Box 1**). For example, *PURPLE BOOK* is a conjunction of two predicates,  $PURPLE(x) \wedge BOOK(x)$ , whereas *NOT A PURPLE BOOK* calls for a further combination with negation,  $\neg(PURPLE(x) \wedge BOOK(x))$ . These computations are dynamic and productive (i.e. applicable to completely novel combinations), and hence not implementable via conjunctive cells 'hardwired' to conjoin specific, fixed inputs.

There exists, importantly, clear evidence that dynamic computation is available in neural tissue. Cacucci and colleagues<sup>38</sup> found, in addition to typical place and head-direction cells, another cell type that they named theta-modulated place-by-direction (TPD) cells. TPD cells conjunctively code both for the animal's location and head direction. (Additionally, their firing is also theta modulated, with spikes concentrated at certain phases of the locally recorded theta-rhythm.) Thus, TPD cells combine information of two types (location, head direction), with the value of one of the conjuncts (location) changing from one context to the next. Using a PC-like notation, the TPD cell encodes the meaning  $LOCATION(A, X) \wedge HEAD-DIRECTION\_SOUTH(A)$ , i.e. it fires when the cell's receptive field  $X$  coincides with the animal's current location and the animal is facing south. Crucially, whereas the locational and head-directional values of a TPD cell remain fixed across repeated exposures to the same environment, they de-couple in a new environment. For example, a TPD cell that fires when the animal is facing south and is in the north-east corner in one environment, fires at the same head-directional signal value (facing south) but in a completely different location (e.g. in the centre) in a different environment. The locational signal of TPD cells therefore remaps similarly to how place cells remap, i.e. it changes randomly from environment to environment (see below and **Glossary**). Subsequently, the value of  $LOCATION(A, X)$  and the entire conjunction must be computed dynamically in a given context. Thus, TPD cells *exemplify dynamic computation of new complex meanings needed by the LoT*. For instance, a single TPD-like cell can successfully compute a combination for a noun, e.g. *BOOK*, with different adjectives: *PURPLE BOOK*, *ORANGE BOOK*, etc.

The process of remapping observed with place cells is a further aspect of neural architecture and function that exemplifies a feature essential for the LoT. (Global) remapping refers to the observation that a place cell's receptive field changes across contexts: a place cell that fires in a particular location in one environment (e.g. north-east corner) may fire in a completely different location in another environment (e.g. the centre) or not at all<sup>39-42</sup>. As a result, a limited set of place cells can be efficiently re-used to represent location across many different environments at different times<sup>43</sup>. (Without remapping, each place cell would denote a unique location in a specific environment, which is unrealistic if the animal needs to encode many different locations and environments.) More generally, besides encoding different contexts in memory<sup>41,44,45</sup>, remapping may enable transient representation of the ever-changing

entities relevant in the current context, i.e., entities that are active in working memory and can be inputs into further computation.

## Concluding remarks

The types of ingredients for the representations and computations posited in the LoT framework can be found in the spatial navigation system. The navigation system features a lexicon of different spatial predicates encoded by different cell types. These spatial predicates are similar to LoT predicates in that they show *abstraction from physical properties*, *role-filler independence*, and *relative configurational stability*. Spatial predicates can also be dynamically bound into more complex meanings.

The arguments in this paper are based on the spatial navigation literature in rodents. However, spatially modulated cell types have also been found in the hippocampus and para-hippocampal regions in bats<sup>46,47</sup>, non-human primates<sup>48,49</sup> and humans<sup>50–52</sup>, indicating that the spatial navigation system is conserved in evolution. Interestingly, compared to rodents, these structures in primates contain a much larger proportion of cells that respond to objects<sup>48,49</sup>. Notably, the human hippocampus contains cells that fire to unique concrete entities, such as a well-known person or landmark<sup>53,54</sup>. These cells encode an abstract concept and respond to highly varied physical signals that activate the concept, e.g., a ‘Halle Berry’ cell responds to different photographs of the actress, line drawings of her face, her photographs as Catwoman, the spelled words ‘Halle Berry’ - but not to other women’s photographs or drawings. These so-called ‘concept cells’ correspond, roughly, to individual constants in the LoT. Similarly, cells corresponding to categories ‘animal’ or ‘rodent’ were found in the amygdala<sup>55</sup> and can be considered as neural counterparts for the eponymous LoT predicates.

Our perspective is inspired by innovative research in human cognitive neuroscience that is rooted in Tolman’s seminal work<sup>56</sup> and has brought neural mechanisms found in animal spatial navigation to the problem of general knowledge organisation and reasoning in humans<sup>57–62</sup>. Behrens and colleagues<sup>59</sup> highlight the need to separate structure from objects; such a factorisation forms the basis for filler-role independence. Frankland and Greene<sup>58</sup> provide a thorough perspective on LoT-relevant computations in the brain and argue that a fronto-parietal control network is responsible for compositional operations over abstract variables in the LoT. However, few details are provided as to the neurobiological mechanisms. Relatedly, some authors propose that spatial map-like representations can be used to encode abstract relations and concepts<sup>63–65</sup>. However, these lines of argumentation have largely set aside the strictly productive, compositional aspect of computation that is central to the LoT.

The approach we take emphasizes the rich representational and computational capacity of single neurons. Typically, this capacity is considered to be a function of the cell’s position within a neural assembly and its synaptic connectivity<sup>66</sup>; however, there are provocative recent proposals on how this can be achieved using within-neuron RNA-based computation<sup>67</sup>. While it is beyond the scope of this paper to argue for one or the other position, we note that an essential dimension for evaluating each approach from the LoT perspective is whether it enables dynamic

compositional computation over symbols. We also note that while most animal research concerns parahippocampal neurons, LoT representations and computations in humans need not be restricted to the hippocampal formation. In fact, even in rodents similar cell types have been recorded in the cortex<sup>68</sup>, demonstrating that such representations are supported widely across the brain.

We discussed the most essential components of the LoT, namely one-place predicates and compositional dynamic binding via conjunction. A fuller argument will need to provide details on two+ place predicates, negation, tense, etc (see **Outstanding Questions**). The outstanding questions notwithstanding, we suggest that an influential position in cognitive science can be mechanistically linked to neurobiology, and that a long-standing rift between cognitive symbolic theories of reasoning (and language) and neurobiological theories of memory and computation can be productively bridged.

### **Outstanding Questions**

- What is the neural substrate for memory, given that the prevailing synaptic view is unlikely to be complete?
- How are objects and variables represented?
- How are elementary functions like conjunction represented?
- Which conjunctive cells have fixed conjunct values and which have dynamic ones?
- How are two-place predicates represented?
- How are quantifiers (*any*, *there is*) represented?
- What is the physical basis of the type vs. token distinction? What is a neural mechanism for representing an individual novel token that is computed from a type?

## Box 1: Formalisation of Language of Thought via Predicate Calculus

Which formalism is suited to represent the LoT? Logical formalisms used to analyse natural language semantics are good candidates. The predicate calculus (PC, also known as first-order logic or predicate logic<sup>69,70</sup>) is an often-used approach that can underpin a large part of compositional productivity and systematicity. (See ref.<sup>71</sup> for discussion of limitations of PC.)

The lexicon of PC consists of individual constants (*Hebb*, *Fodor*), individual variables ( $x$ ,  $y$ ), predicates (*SING*, *RED*, *NEUROSCIENTIST*), logical connectives ( $\wedge$  'AND',  $\vee$  'OR',  $\neg$  'not',  $\rightarrow$  'entails'), and quantifiers ( $\exists$  'there exists',  $\forall$  'for all/any'). These items can be combined to produce complex expressions using rules determining which combinations of lexical items constitute well-formed expressions in PC. For example, *NEUROSCIENTIST(Hebb)* is a well-formed PC formula in which the predicate *NEUROSCIENTIST* takes an individual constant *Hebb* as argument; it corresponds to the thought *Hebb is a neuroscientist*. Predicates can also take a variable as input, as in *SING(x)* which is a PC formula equivalent to the LoT idea *x sings*.

PC also has semantic rules that assign a meaning to individual constants, variables, and predicates. Individual constants denote entities in the outside world, e.g., the individual constant *HEBB* denotes the person Hebb who happens to be a famous neuroscientist. A one-place PC predicate such as *HUMAN* or *SING* denotes a (sub)set of entities: of all entities in the outside world, the predicate returns a subset of entities that possess the property designated by the predicate, i.e., entities that are human or that sing, respectively.



*Of all possible entities, HUMAN() is true only for a subset that are humans (yellow circles)*

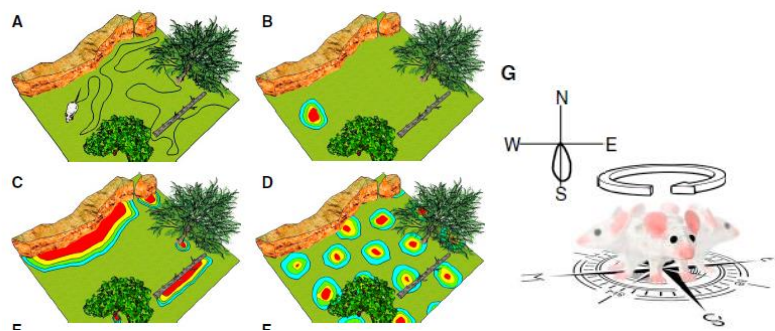
Semantic rules also make it possible to compositionally derive the meaning of any complex well-formed PC formula from its parts and to evaluate it as True or False relative to states of affairs in the world. Several examples of complex PC formula, their semantic interpretation and a corresponding LoT idea are given below:

PC formula (semantic interpretation)	Corresponding LoT idea
$\neg \text{Sing}(\text{Hebb})$ (it's not the case that Hebb sings)	<i>Hebb doesn't sing</i>
$\exists x(\text{Neuroscientist}(x) \wedge \text{Sing}(x))$ (there is $x$ , such that $x$ is a neuroscientist and $x$ sings)	<i>Some neuroscientists sing</i>
$\forall x \neg (\text{Neuroscientist}(x) \rightarrow \text{Fish}(x))$ (for every $x$ , if $x$ is a neuroscientist then $x$ is not fish)	<i>Neuroscientists are not fish</i>
$\neg \forall x(\text{Neuroscientist}(x) \rightarrow \text{Sing}(x))$ (it is not the case that for every $x$ that is a neuroscientist, it follows that $x$ sings)	<i>Not every neuroscientist sings</i>

## Box 2. Cognitive maps and the hippocampal formation

Many animal species are known to possess impressive navigational capacities. Edward Tolman's research on rats' navigation led him to formulate *cognitive map theory*, whereby the animals' navigation is underpinned by a map of the environment in the animal's brain<sup>56</sup>. Cognitive maps are constructed during exploration and are internal representations of the external space in which distances and directions between places are encoded. They enable the animal to represent the environment comprehensively, yielding more flexible navigation than can be expected based purely on past memories, e.g. dead-reckoning<sup>72</sup>.

O'Keefe and Dostrovsky's (1971) discovery of place cells in the rat's hippocampus that fire when the animal is in a specific location within an environment was a first step towards outlining the neural basis of cognitive maps<sup>25</sup>. Later, other types of cells contributing to building of cognitive maps were found in the hippocampal formation and related structures, most notably head-direction cells, boundary cells (including border cell and boundary vector cells) and grid cells (see the figure below and Glossary; see also ref.<sup>73</sup> for a review).



Schematic illustration of different types of spatially modulated cells in the hippocampal formation. Such cells are recorded, for example, when a rat forages in an enclosed two-dimensional space (A). Schematic examples of firing rate maps for a place cell (B), border cell (C), and grid cell (D). The region that yields the highest firing in the cell is indicated in red, followed by yellow, green and so on. (G) A polar plot for a head direction cell, which fires strongly when the animal faces cell's preferred direction, here southward. Source: ref.<sup>74</sup>, Figure 1.

An important point is that place cells and other cells do not reflect a simple sensory activation<sup>12,28,75</sup>. For example, the same place cell may fire in response to a visual cue such as a landmark, an olfactory cue, or idiothetic cues, e.g., when the animal moves in the dark and/or the current location is calculated using path integration. Place cell firing is independent of whether the animal is moving or stationary. This suggests that the place cell's activity is not determined by the concurrent sensory input<sup>25</sup>. Rather, location is an abstract concept defined by reference to a cognitive map stored in memory. The symbolic nature of the cognitive map is emphasized by ref.<sup>12</sup>: the map uses a coordinate system in which places can be identified using their coordinates, i.e. symbols for representing location.

## Glossary

**Place cell** – a neuron that fires when the animal is located in a narrowly defined region of space known as the 'place field'.

**Grid cell** – a neuron that fires when the animal is located at one of multiple locations corresponding to vertices of a periodic triangular array that tiles the surface. The name 'grid cell' points to its function as providing a coordinate grid/frame upon which the animal can construct their cognitive map

**Border cell** – a neuron that fires when the animal is immediately adjacent to an environmental boundary, e.g. a wall or a ridge.

**Boundary-vector cell** (a vectorial counterpart of a border cell) – a neuron that fires when the animal is located at a particular distance and direction from an environmental boundary.

**Landmark-vector cell** – a neuron that fires when the animal is located at a particular distance and direction from a (large) landmark object.

**Head-direction cell** – a neuron that fires when the animal's head is in a particular orientation in allocentric coordinates.

**Object cell** – a neuron that fires when the animal is in the vicinity of a (small) object.

**Object-vector cell** – a neuron that fires when the animal is located at a particular distance and direction from a (small) object.

**(Global or complete) remapping** – a phenomenon whereby a place cell ensemble may reorganise itself from one environment to the next in an unpredictable way. A place cell that fires in some location in one environment may fire at a completely different location or not at all in a different environment.

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