

Uncovering the Secrets of the Concept of Place in Cognitive Maps Aided by Artificial Intelligence

Jose A. Fernandez-Leon^{1,2} · Gerardo G. Acosta^{2,3}

Received: 15 February 2022 / Accepted: 5 October 2022 © The Author(s), under exclusive licence to Springer Science+Business Media, LLC, part of Springer Nature 2022

Abstract

Uncovering how mental representations acquire, recall, and decode spatial information about relative locations and environmental attributes (cognitive map) involves different challenges. This work is geared towards theoretical discussions on the controversial issue of cognitive scalability for understanding cognitive map emergence from place and grid cells at the intersection between neuroscience and artificial intelligence. In our view, different place maps emerge from parallel and hierarchical neural structures supporting a global cognitive map. The mechanisms sustaining these maps do not only process sensory input but also assign the input to a location. Contentious issues are presented around these concepts and provide concrete suggestions for moving the field forward. We recommend approaching the described challenges guided by AI-based theoretical aspects of encoded place instead of based chiefly on technological aspects to study the brain. SIGNIFICANCE: A formal difference exists between the concepts of spatial representations between experimental neuroscientists and computer scientists and engineers in the so-called neural-based autonomous navigation field. From a neuroscience perspective, we consider the position of an organism's body to be entirely determined by translational spatial information (e.g., visited places and velocities). An organism predicts where it is at a specific time using continuous or discrete spatial functions embedded into navigation systems. From these functions, we infer that the concept of place has emerged. However, from an engineering standpoint, we represent structured scaffolds of behavioral processes to determine movements from the organism's current position to some other spatial locations. These scaffolds are certainly affected by the system's designer. Therefore, the coding of place, in this case, is predetermined. The contrast between emergent cognitive map through inputs versus predefined spatial recognition between two fields creates an inconsistency. Clarifying this tension can inform us on how the brain encodes abstract knowledge to represent spatial positions, which hints at a universal theory of cognition.

Keywords Cognitive maps · Place cells · Grid cells · Cognition · Neuro-inspiration

Introduction

There are a growing number of international funding initiatives to understand the human brain and cognition, such as the American BRAIN Initiative $(2020)^1$ and the European Human Brain Project $(2020)^2$ These initiatives aim a common goal: to know how biological cognition emerges from interactions between neurons and across neural circuits in different brain areas to produce behavior. Success in this endeavor will eventually allow us to provide better treatments for mental disorders medically and create more intelligent machines technologically. Current artificial intelligence and machine learning technologies, including Watson (IBM, 2020³) and Siri (Apple, 2020⁴), are representative examples of cutting-edge developments that have an impact in many fields, such as computational intelligence [1]. Unfortunately, they have a limited capacity for adaptation to new experiences and act reliably as human intelligence.

[☐] Jose A. Fernandez-Leon jafphd@gmail.com; jafernandez@intia.exa.unicen.edu.ar

¹ Exact Sciences Faculty-UNCPBA, CIFICEN (UNCPBA-CICPBA-CONICET) and INTIA (UNCPBA-CICPBA), Tandil, Argentina

² National Scientific and Technical Research Council (CONICET), Buenos Aires, Argentina

³ Engineering Faculty-UNCPBA, INTELYMEC-CIFICEN (UNCPBA-CICPBA-CONICET), Olavarría, Argentina

¹ https://braininitiative.nih.gov/

² https://www.humanbrainproject.eu/en/robots

³ https://www.ibm.com/watson

⁴ https://www.apple.com/siri/

One way to proceed to address that issue is to develop a research program combining neuroscience and Artificial Intelligence (AI) fields to build robust and sophisticated algorithms for better intelligent machines (c.f., [2]). To combine those two fields, however, we need theories, models, and conceptual frameworks to be tested and refined to understand biological cognition. The current consensus in neuroscience is that there is no unique theory on how the brain works. Neural technology has been developed to address this issue such as electrophysiological neural recordings neurons with a high spatial resolution [3], image-based recordings of a relatively large number of neurons [4], and functional recordings on the dynamics of simultaneous multiple brain areas [5]. Other techniques focus on targeting specific neural features, such as optogenetic manipulation of ensembles of neurons [6], targeting precise cell types and tracing projections across neural circuits [7].

Despite the importance of these technological developments, the taken research path seems to be biased toward developing new techniques rather than formulating new hypotheses from current knowledge on the principles governing the brain. In this respect, we can speculate that it remains difficult in current systems neuroscience to have a ubiquitous theory of cognition because most studies only focus on certain region to find neural correlates and determinants of specific cognitive behaviors [8, 9]. Another significant challenge is to build biologically plausible (rather than biologically identical) models that explain the behavior of interest from neuronal data. In addition, it is convenient to find biologically relevant principles that can be coded in neural models or any other computational intelligence technique. In particular, some of the current primary efforts in neuroscience to overcome the lack of a unifying theory for neural representations are in terms of how place is encoded in the neocortex [10]. We consider in this work the concept of place as an organizing principle in neural-based systems dealing with spatial recognition. The following section presents one example of how a specific research area in systems neuroscience advanced when combined with discoveries from the AI field using that notion of encoded space.

Scalability and Cognitive Spatial Maps

We step back in this section to look at the literature and offer a potential explanation of how cognitive maps integrate multiple sources of information to create the concept of place in neural networks. Cognitive maps refer to a neuronal representation in a biological or an artificial organism (e.g., a cognitive robot), and they take role in spatial memories of an experienced environment by combining current senses and stored memories [11, 12]; see also [13] and [14] for a related non-spatial understanding of this concept. This section aims to outline first that there is a significant difference between representation of a place in biological and engineered networks. We focus on how cognitive place maps can be scalable from brain areas to cortical columns at the intersection between neuroscience and artificial intelligence. This scalability is discussed less in the literature. Initially, we highlight what information is needed at the highest level of abstraction and show the corresponding elements in the brain to drill down into the details. Our assumption in this discussion is that many of the neurons absorb information from various sources. This assumption aims to address the issue of information needed for cognitive spatial maps and support that view from findings in neuroscience.

The discovery of hippocampal 'place cells' (i.e., neurons that show an increased activity at specific locations in space; Fig. 1) by O'Keefe and Dostrovsky [11] opened discussions on how the mammalian nervous system processes sensorimotor information for navigation. In [15], it is discussed that place fields (i.e., spatial areas where place cells becoming active when an animal enters in that area) (Fig. 1) of place cells in CA1 region of the hippocampus emerge rapidly. Rapid place field formation in CA1 could mediate the ability of the hippocampus to rapidly represent episodes generating unique environmental representations, and continuously updated by exploratory experience to predict the near future (e.g., where to go). In parallel, place cells in CA3 region of the Hippocampus are more stable and gradually form representations with robust trial-to-trial dynamics, thus encoding location in the present moment (e.g., where I am). The difference in dynamics of place cells shed light on the neural mechanisms involved in task orientation in unfamiliar environments.

O'Keefe's work influenced research of May-Brit and Edvard Moser, who discovered 'grid cells', i.e., entorhinal cells that fire at regular intervals as the animal navigates an area [16] (Fig. 1). These cells are believed to code the animal's position in space because grid cells respond to location and distance to objects [16–19]. Grid cells are thought to provide a multi-scale periodic representation of the space that functions as a metric [20], which is critical to integrate self-movement (path integration) [21] and to plan direct trajectories to targets (vector-based navigation; Fig. 2) [22]. Both place and grid cell types were found during experiments with rats, but the grid cells' topology was predicted theoretically and recently reported experimentally. In [23], a toroidal topology of grid cells based on attractor dynamics has been described from neural recordings.

There has also been indication for two simultaneous cognitive maps represented in the hippocampus which is the core of the Parallel Map Theory [24]. The first map can be understood as a 'bearing map' facing direction at a relative angle from the current position. This map represents the environment through self-movement and gradient cues, where these

Fig. 1 Grid and place cells work together to determine the animal's position. Schematics of hippocampal place cells and entorhinal grid cells during spatial navigation of a rat in a squared arena. Representations of the positioning of the hippocampal formation, including different hippocampal subfields (CA1 and CA3) and the entorhinal cortex. On the right side, the cells' firing fields with color indicating the place in the arena where the neurons emitted action potentials through high density (red) to no spikes (blue) scale



vector-based cues create a loose environmental representation. The second map can be seen as a 'sketch map', as an outline drawn from observation rather than from exact survey measurements, and only shows the environment's main features. In this later map, positional cues are internally represented by coding specific objects or landmarks and their

Fig. 2 Schematic of vectorbased navigation using grid place code. Emergent representations of place cells through their place fields provide anchoring spatial information for grid cells. Goal-directed navigation in novel environments can be based on comparing grid cell codes at different environmental positions. Entorhinal grid cells function to support a Euclidean spatial metric for goal-directed vectors. The direct dynamical relationship between place and grid cells during navigation is usually omitted in computational modeling despite experimental evidence showing their anatomical connections and disruption effects. Every squared activity map represents the cells' firing fields with color indicating the place in the arena where the neurons emitted action potentials through high density (yellow) to no spikes (blue) scale



Fig. 3 The brain's navigation system based on place and grid cell integration. Specialized place cells in the hippocampus encode specific locations, while entorhinal grid cells provide a long-range coordinate system to determine position. The mapping of one location represented by a place cell occurs when the animal is situated at the current position. A grid cell that fires at that location also fires at the other positions in a hexagonal array. The mapping path involves the animal's movement in which the activity of several grid cells records the locations the animal visited through the overlapping hexagonal coordinate system (based on [88])



relative locations. Evidence showed that the sketch map had been found in neurobiological processes and explanations, but the bearing map has unclear supporting evidence [25]. The overall cognitive map predicted by the theory is thus obtained by combining these two separate maps [24].

The Parallel Map Theory also suggests that at least two maps could emerge in parallel by integrating different sources of information. However, we can also think that maps could form hierarchies and control structures that enable the 'activation' of certain behaviors when needed. This view of hierarchies is rooted on evidence suggesting that an integrated map is difficult to be divided into the bearing (directional) and sketch (positional) maps to test the Parallel Map Theory. By restricting a navigational task to one class of environmental cues (directional or positional), it is not always possible to observe the induced changes in an animal's behavior or patterns of neural activity. A parallel map can be partially observed by specifically impairing the channel for the other map through brain lesions [24]. Despite many publications on the physiology and function of the hippocampus (see reviews in [12, 26]), however, few studies have provided these types of tests in enough detail to test the theory. This lack of studies is because either the lesions are not specific (or the task's environment contains both types of cues), or the assay of spatial learning is not precise enough to detect the presence and nature of residual spatial learning [24]. These difficulties suggest that, in addition to the existence of parallel maps, those maps integrate at neuronal level and hierarchical organization.

The view of having hierarchies that control spatial navigation refers to the brain scale theory that is challenging when referring to scaffoldings of cognitive maps. Instead of guiding the navigation via parallel maps as predicted by the Parallel Map Theory, we see the possibility that a specific navigation system (Fig. 3) represents integrated sensory information for action selection in an intimate and bottom-up fashion [27]. A hierarchical organization can be related to grid cell models that represent different grid layers resembling the topographical organization in the dorsocaudal MEC [28]. These layers are commonly modelled through the orientation and phase of the grid by means of the spacing (minimal inter-subfields distance) and size of its subfields [29]. In terms of the relationship between place and grid cells, that link is still debated.

In contrast to Parallel Map Theory, or a hierarchical organization, theoretical studies usually assumed that error reduction for path integration (Fig. 2) occurs intrinsically in grid cell networks without a possible role of place cells. In other words, grid cells would have intrinsic features that do



Fig.4 A possible decomposition of a navigation strategy under the view of layered cognitive maps representation. The figure shows how the components interact to implement path integration and vector navigation (Fig. 2). The architecture is based on path integration provided

by simulated grid cells and location coded by place cells. Bold dashed lines represent alternative ways to understand the connections (adapted based on [38])

not need external (or even hierarchical) information from place cells, where grid cells alone represent a reference (a metric) frame of the environment. However, experimentally, the inactivation of one region affects the dynamics of the other, such as an extinguished grid pattern after hippocampus silencing [30] or a decreased place field stability after MEC inactivation [31]. Regarding brain connectivity, studies also reported that a significant portion of excitatory afferent projections of MEC originates in grid cells and project to place cells [32–34]. Large feedback projections from place cells to the deep layers of MEC were similarly reported [35] and these works suggest that certain hierarchical relationships are necessary to explain place coding [36, 37] (Fig. 3). It seems then that parallel and hierarchical organizations of neural structures sustain cognitive maps.

We can think that is possible to decompose the navigation into sub-behaviors through a hierarchy of layers, and then combine with mechanisms that integrate in neural networks as observed in grid cells. In this view, each layer implements certain behavioral competence, and higher levels can subsume lower levels to create a viable behavior. For example, because an organism must be able to 'avoid objects' to 'reach a goal' effectively, the hierarchical control navigation architecture creates a system in which the higher layers utilize the lower-level competencies. The layers, which all receive sensory information, work in parallel and generate outputs, where these outputs can be actuators' commands or signals that suppress or inhibit other layers. A possible decomposition of a navigation strategy under the view of layered cognitive maps can be found in Fig. 4. The figure shows how the components might interact to implement path integration and vector navigation using simulated grid cells and location coded by place cells [38]. Under this view, cognitive maps could emerge guided by scalability principles for spatial location based on different behavioral modules. Each module evolves sequentially or in parallel, specialized in performing a specific task (e.g., some having different populations of place cells or grid cell layers [28]). The 'layered evolution' paradigm [39] can be also considered and verified through simulations based on the subsumption architecture [40], widely influential in autonomous robotics and realtime AI.

Place Coding at Systemic Level

Using computational AI models, we can test and discuss whether map hierarchies could be helpful in our understanding of cognitive maps on every scale, ranging from simple to more abstract maps. We saw that the concept of place can emerge as integrated into parallel and hierarchical neural structures based on place and grid cells. However, we briefly discussed that overall cognitive maps emerge mostly following AI-based learning rules in engineered systems which seems in opposition to the mechanisms in the brain. The integrated view of grid cells' coding place seems guided by intrinsic activity and proposes a reference frame of the environment. In this respect, grid cell-based navigation provide means of navigation without external cues (e.g., in the absence of visual cues) but sensing of the organism's velocity internally [28]. Place cells instead provide a means of navigation through external cues where there are landmarks and other locations to provide spatial information. These coding strategies seem to complement each other in how to code the place and they are useful for situations where one strategy is more convenient than the other; e.g., navigation in cluttered environments [41], and generalization of place learning [42, 43]). The hierarchical, engineering-based approach seems only tangential to these issues but has other benefits when understanding how place is encoded.

Following an engineering bio-inspired approach, emergent cognitive maps could be evaluated over different scenarios in a given environment, ranging from a detailed simulation model to a real-world experiment. Using these simulations, we can restrict the task environment to some external cues or patterns (from sensor signals), affecting an agent or a simulated animal's behavior or impairing specific maps, not the others. This approach presents advantages compared to a biological experiment to test the Parallel Map Theory. Furthermore, the AI-based computational approach could be the first step to obtaining a layered map theory focused on explaining biological-like cognition for the emergent complex behaviors in spatial navigation or visual navigation [44]. We hypothesize that by having access to all components and variables of a cognitive map, in coupling with the environment, we could observe that these maps form part of a brain-like scale perspective in terms of creation of complex behaviors from simple ones. This approach is beneficial because the parallel and hierarchical organization of complex behaviors such as navigation and learning to move toward a goal remains an unsolved issue for biologically inspired robotics [39, 41].

Aiming to synthetize such cognitive map from an engineering perspective, the robot should take advantage of a computer simulation model of the entorhinal grid cells for a discretization map considering the spatial dimensions of the scenario. We should also include into this bioinspired computer model a neural network representing the hippocampus place cells to allow the robot to self-locate in the previously discretized map from grid cells. The granularity of the grid would also give idea of which cues or patterns are necessary to consider. If the trajectory planner must outcome a path in a big city, it is useless to consider little stones aside the roads as references. Instead, it should consider buildings, squares and so forth to turn into a corner or keep a straight direction. If the scenario now is a sleeping room, the grid cells-based map should be adjusted to detail in smaller objects, even when the robot maintains the same size. The coexistence of these two maps resembles also hierarchical levels of control. Even with the same sensors and actuators, supervisory controllers would tune low-level controllers to reach the targets without major inconveniences. We can think of a lower layer with sets of control loops regulating positioning and errors to targets considering as input certain cues and other upper layer scaling the robot mission scenario. Also, the control must be completed considering the world model and hence adjusting the gains of the lower layer control loops from the perceived granularity of the map, in a typical supervisory control architecture. The interaction of both systems, one living in the grid cells and the other in the place cells, would assure a stable behavior for the whole cognitive map.

The feasibility of having such a stable sophisticated cognitive maps obtained from the coordination of simple behavioral modules allows several engineering applications. For instance, mobile robot navigation in unknown environments needs online replanning of trajectories and tasks to face unforeseen situations [45]. It is vital in these systems to have a mechanism to self-adapt and organize tasks by activating selectively different components of a cognitive map. Under the idea of scalability of cognitive maps, the place cells can be activated for a topological strategy, while grid cell modules (e.g., layers [29, 46]) support metric vector navigation providing the direction toward a goal. In this, the selection of the most appropriate strategy under certain navigation conditions can be supported by integrating a grid cell-based vector navigation mechanism with local obstacle avoidance mediated by place cells forming a topological graph of the environment.

Although this work does not present a formal theoretical demonstration of systemic stability and phenotypic (online) adaptation, our previous work with neuro controllers [39] represents a step in this direction. That work denotes a successful case study of mission fulfillment in the presence of obstacles and while targets and topologies change. We can distinguish having a layered behavioral control: (a) there is an emphasis on iterative development and its relationship to biological-like strategies; (b) emphasis on identifying the connections between limited, task-specific perception directly to the expressed actions that require it; (c) the emphasis on distributive and parallel control, thereby integrating the perception, control, and action systems in a manner like animals. However, the main disadvantage is the difficulty of designing versatile action selection through



Fig. 5 The canonical cortical column and its connections represent the basic building block for a reference frame in the Thousand Brains Theory of Intelligence [50]. **A** Representation of cortical columns based on nonhuman primate cortex (\sim 200 µm in size and six layers). Layers 2/3 provide outputs to near cortical columns (green arrows) and other cortical areas (blue arrow from layer 2/3). Layer 4 receives inputs from for example visual areas. Layers 5/6 provide outputs to subcortical targets represented as blue arrows, e.g., LGN: lateral geniculate nucleus; SC: superior colliculus). All six layers share infor-

a highly distributed system of inhibition and suppression understood as biologically friendly [27]. It would be very interesting to implement this trajectory planning and navigation system based on the grid cells plus place cells cognitive map, perhaps with the Numenta technology of Thousand Brains [10], to experimentally test how the grid cells map interacts with the place cells and vice versa, at least in a synthetic way over an autonomous robot. In any case, further investigations should be made to determine if the effects of using layered coordination can be widespread as a new engineering paradigm for scaling up within cognitive robotics.

Place Coding at Cortical Level

It has been hypothesized that cortical columns (Fig. 5) not only capture a sensation (e.g., orientation selectivity) but also "the relative location of that sensation" in space, referring to a theory proposing that knowing is inseparable from

mation via interlaminar connections (yellow arrows). Figure based on [89] and interpretations on grid cell-like processing based on [50]. **B** Schematics of the perspective introduced by the Thousand Brains Theory of Intelligence based on cortical columns. Columns seem to create reference frames for every object based on similar processes observed for grid cells like a map. Yellow arrows represent local horizontal connections between columns. Red arrows represent inputs to specific cortical layers. Figure based on (50)

doing [47]. This theory rests on internally generated models of cognitive maps referring to a location where the local and anatomical network of cortical columns embodies inputs selectivity. These columns represent a group of neurons in the brain's cortex that have nearly identical receptive fields and are organized hierarchically across six cortical layers (laminar structure) and subdivisions [48]. The receptive field or sensory space, like in place cells' place fields, indicates a delimited medium where some physiological stimuli can evoke a sensory neuronal response in specific organisms [49].

The Thousand Brains Theory [10] proposed that the concept of place is also embedded into the cortical columns in a similar way that grid cells are defined. We believe that there is one missing piece in understanding how grid-like place coding emerges in the cortex. No clear indication of physiological findings of how place cell-like activities emerge within cortical columns. This understanding is crucial if the theory wants to be based on the concept of grid cell-like activities we previously showed. Let us touch on this issue in more detail as follows.

From [17], we can summarize entorhinal grid cells as representing a reference frame for environments. These cells represent the location of the organism's body and movements and are needed for mapping environments. The proposed hypothesis is that grid-cell-like processing exists in every cortical column to create reference frames for objects, represent the location of columns' input in that reference frame, and are used for learning the structure of objects and moving limbs [10, 50]. This idea is also rooted in the intrinsic connectivity between the cortical layers. Based on the mouse brain [51], it was reported that layer 5 (L5) projection neurons account for intracortical outputs (e.g., motor outputs). L2/3, L4, and L6 neurons contact a subset of the L5 cortical targets. Most patterns are consistent with hierarchical position between cortical areas (feedforward, feedback). L2/3 and L4 neurons are primarily associated with feedforward projection patterns and L6 with feedback. L5 has feedforward and feedback projection patterns (see also [10, 50] for an account of other cortical column projections as a complete sensory-motor modeling system). Based on that evidence, there is no clear understanding of how to conceive grid cell-like activities in cortical columns or how these columns encode place as place cells do. The possible argument in favor of the theory is that the embedded mechanism that uses the cortical column for coding place is not the same as those for grid and place cells, as discussed in this work.

Thus, we should ask whether neocortical-based principles will be essential for AI, because sensory-motor learning and inference in AI and robotics should not be separate. The Thousand Brains Theory proposes some guiding principles in the brain regarding a hierarchy of cortical regions [52]. These regions encode memory sequences of spatiotemporal patterns to understand how that hierarchy works and predictions. At the same time, some few other neurons are highly active between and within regions. Each layer of cells in a region is a memory sequence based on sparse distributed representations, columns representing feedforward data. Overall, these observations suggest that not only parallel but also hierarchical groups of neurons organize physiologically in the cortex. Uncovering how these groups encode space and enable certain aspects of the emergence of cognitive maps could be crucial. This observation is essential if we want to understand how the brain understands the world and what it means to be intelligent (see also [10]).

Contentious Issues

We discuss next some contentious issues and concrete suggestions for merging neuroscience and AI through the layered maps view of place coding.

Cognitive Map Scalability and Other Theories

One central goal in theoretical neuroscience is to predict the response properties of sensory and non-sensory neurons from the first principles. Some examples of 'grand' theories in neural coding include sparse coding [53, 54], and information maximization principles [55, 56], among others. We think that the discussions of these theories on how they address the scalability issue of the acquired information can be linked to explanations on cognitive maps emergence.

Let us briefly discuss this view for each of these theories. Efficient coding posits that sensory neurons (note first that place and grid cells are not such neurons) encode maximal information about their inputs. Many variants of efficient coding such as redundancy reduction, different formulations of predictive coding for continuous on-line learning, robust coding, among others, differ in their regimes of applicability and the relevance of signals to be encoded given constraints [57]. It is unclear then how these types of efficient coding relate to or what is expected when diverse coding features are combined to form a more complex representation at non-sensory representations such as place and grid cells. Seeing cognitive maps as scalable might shed some light on understanding the process of information maximization, from initial to full exploration of a new environment. This explanation seems possible from neural processes observed in the hippocampus and entorhinal cortex, and could indicate how that information is maximized across time associated with episodic memories; i.e., encoded experiences that contain information on where and when it happened [58].

In addition, it has recently been suggested that sparse coding may be one of the underlying organizing principles for the brain's navigational system [36] and that 'emergent elasticity' in the neural code for space is crucial [59]. Sparse representations seem to relate to robust systems in that they reduce the complexity of the represented information. Other works have reported specific properties of place cells such as remapping (i.e., change in the place field characteristics) when an animal experiences a new environment or the same environment in a new context [60, 61]. By considering strategies that are biologically plausible on how the coding of place evolves when more information is acquired, we believe that the introduced approach has the potential to explain how the integration of multiple maps is made in the brain.

Replay and Scalability

The role of forward and backward replay of hippocampal sequences has been argued to solve AI's significant credit assignment problem (CAP), which refers to determining the actions that lead to a particular outcome [62]. Different works from neuroscience showed that there is a differentiation in terms of conveyed information in sensory signals coming to place cells and the information replayed after sensing, while the decision to determine the actions seems to form part of a different system. Examples of this understanding can be found based on actor-critic models and grid cell emergence [63], and object avoidance in undesirable situations (i.e., the agent gets stuck) where place cells replay events to set closer subgoals for vector navigation [41]. Furthermore, other examples can be considered on when sensing specific landmarks and the activation of different types of space-coding neurons is possible [44, 64], where many are partly controlled by environmental visual landmarks [65, 66]. It is then important to discuss a little bit more how visual inputs triggers the replay of information.

Recently, a neuronal type in the medial entorhinal cortex has been reported signaling the animal's distance and direction to discrete objects in the environment, the so-called object-vector (OV) cells [67]. It has been argued that this cell type is part of a vast network of neurons coding spatial features, including allocentric tuned neurons situated in the hippocampal-parahippocampal regions (i.e., place cells [11], boundary vector cells [44, 68, 69] landmark-controlled cells [61, 70, 71], and egocentric tunned neurons coordinating the relative position to the animal's body [72-75]. Interestingly, the OV cells responded to landmark objects with various features. Still, the firing of these neurons increased gradually as the object's contrast increased [64]. Additionally, other cell types signaling the dynamics of the animal's movement were previously discovered, such as coding the animal's position [18, 76], head direction [77, 78], speed [79], and c.f. [80]) and proximity to borders [81]. In the rodent hippocampus, the firing of place cells has been discussed as having visual modulation [66] and conveying distance information [82]. Most of these significant discoveries in the neural navigation system have been reported considering the visualization of specific objects, and some were based on computational modeling [83, 84]. Less work has been done on extracting landmark information from real-world scenes during movements [64], which leaves the question of how visual information is maintained by place cells as highly dynamic along with animal's movements yet sensitive to landmark position [65].

Neural Activities and Scalability

A contentious issue is how many place and grid cell activities, and their properties are necessary to be included in a model within the layered cognitive map approach. Place cells have several properties such as phase precession, directionality, remapping, etc. Other properties can involve sensory input because the information received by place cells is a compilation, a functional derivative of different stimuli such as visuospatial, olfactory, vestibular, and movement inputs [85]. Another property is plasticity in general and spike-timing-dependent plasticity [86] in particular. It is unclear however the necessity of including how many of these properties in the layered approach, or whether AIbased learning rules. In this respect, our experiments with layered evolution of complex behaviors indicated that plastic neurocontrollers do not necessarily convey better performance during spatial navigation [39]. Based on hierarchical generative models for learning high-level representations from visual invariances [87], place field emergence can be studied using neural plasticity. Therefore, there is no indication on whether plasticity is compulsory required in each case study.

Overall, using artificial and computational intelligence models, it is possible to show that the synergetic properties of neurons can help our understanding of the principles behind spatial coding, which could clarify how the concept of place emerges in the brain. Models with these features must be seen as a computational tool to explore the most spartan possible conditions for obtaining a feature of interest, in our case the emergence of place coding in neural networks. In this way, models of spatial cognition in AI could allow us to refute or defend our working hypotheses by demonstrating an existence proof for spatial cognition given conditions we have supposed are necessary. In this way, there is an attempt to introduce as few assumptions as possible about the nature of spatial cognitive integration at the neural network level.

Conclusions

Previous sections in this opinion paper examined the importance of theory-driven research to understand place coding by means of hippocampal place-like and entorhinal grid-like cells. We showed that the elusive principles governing cognitive maps had not been fully revealed yet. It is highly desirable to develop a holistic approach to cognitive map coding and its spatial information processing, in which AI modeling could be beneficial for this endeavor. This work briefly discussed that experimental and theoretical evidence had proposed either integrated or distributed strategies for cognitive maps definition. We discussed that not only parallel maps could emerge, but also hierarchical scaffolds of these maps must be considered.

The discovery of neural principles that guide these hierarchies and maps around the concept of place coding could be used to develop theories for cognitive maps emergence. Rather than proposing a shift in the approach taken in neuroscience research, we recommend approaching the described challenges in an integrative manner guided by theoretical aspects of encoded place rather than focusing on new technologies to record brain activity. This cross-disciplinary strategy may be nurtured from different standpoints and offer significant discoveries in overlapping research areas.

Acknowledgements We thank Ahmet Kerim Uysal for comments on the final manuscript.

Author Contribution JAF-L: Conceptualization, Investigation, Methodology, Writing—original and final draft, Writing—review and editing; GGA: Writing—final draft, Writing—review and editing.

Funding JAF is supported by The National Scientific and Technical Research Council (CONICET), Argentina, through the Scientific and Technological Researcher Career program (DI-2019–2516-APN-GRH-CONICET).

Data Availability No data recording or analysis were made for this manuscript.

Declarations

Ethics Approval None declared. This is a theoretical/computational study. No ethical approval is required.

References

- Engelbrecht AP. Computational Intelligence: An Introduction: Second Edition. Computational Intelligence: An Introduction: Second Edition. 2007.
- Macpherson T, Churchland A, Sejnowski T, DiCarlo J, Kamitani Y, Takahashi H, et al. Natural and Artificial Intelligence: A brief introduction to the interplay between AI and neuroscience research. Neural Networks. 2021.
- 3. Hong G, Lieber CM. Novel electrode technologies for neural recordings. Nat Rev Neurosci. 2019.
- Weisenburger S, Vaziri A. A guide to emerging technologies for large-scale and whole-brain optical imaging of neuronal activity. Ann Rev Neurosci. 2018.
- Friston KJ. Modalities, modes, and models in functional neuroimaging. Science. 2009.
- Josselyn SA, Tonegawa S. Memory engrams: Recalling the past and imagining the future. Science. 2020.
- Lerner TN, Ye L, Deisseroth K. Communication in Neural Circuits: Tools, Opportunities, and Challenges. Cell. 2016.
- Buzsáki G. Large-scale recording of neuronal ensembles. Nat Neurosci. 2004.
- Urai AE, Doiron B, Leifer AM, Churchland AK. Large-scale neural recordings call for new insights to link brain and behavior. Nat Neurosci. 2022.
- Hawkins J, Lewis M, Klukas M, Purdy S, Ahmad S. A framework for intelligence and cortical function based on grid cells in the neocortex. Front Neural Circuits. 2019.
- O'Keefe J, Dostrovsky J. The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. Brain Res. 1971.
- 12. O'Keefe J, Nadel L. Hippocampus as cognitive map. Behav Brain Sci. 1979.
- Wu X, Zheng Z, Weng J. On Machine Thinking. In: Proceedings of the International Joint Conference on Neural Networks. 2021.
- O'Keefe J, Krupic J. Do hippocampal pyramidal cells respond to nonspatial stimuli? Physiol Rev. 2021.
- Dong C, Madar AD, Sheffield MEJ. Distinct place cell dynamics in CA1 and CA3 encode experience in new environments. Nat Commun. 2021.

- Moser EI, Kropff E, Moser MB. Place cells, grid cells, and the brain's spatial representation system. Ann Rev Neurosci. 2008.
- 17. Hafting T, Fyhn M, Molden S, Moser MB, Moser EI. Microstructure of a spatial map in the entorhinal cortex. Nature. 2005.
- 18. Fyhn M, Molden S, Witter MP, Moser EI, Moser MB. Spatial representation in the entorhinal cortex. Science. (80);2004.
- Sorscher B, Mel GC, Ganguli S, Ocko SA. A unified theory for the origin of grid cells through the lens of pattern formation. In: Advances in Neural Information Processing Systems. 2019.
- Bush D, Barry C, Manson D, Burgess N. Using Grid Cells for Navigation. Neuron. 2015.
- McNaughton BL, Battaglia FP, Jensen O, Moser EI, Moser MB. Path integration and the neural basis of the "cognitive map." Nat Rev Neurosci. 2006.
- Erdem UM, Hasselmo M. A goal-directed spatial navigation model using forward trajectory planning based on grid cells. Eur J Neurosci. 2012.
- 23. Gardner RJ, Hermansen E, Pachitariu M, Burak Y, Baas NA, Dunn BA, et al. Toroidal topology of population activity in grid cells. Nature. 2022.
- Jacobs LF, Schenk F. Unpacking the Cognitive Map: The Parallel Map Theory of Hippocampal Function. Psychological Review. 2003.
- 25. Jacobs LF. The evolution of the cognitive map. In: Brain, Behavior and Evolution. 2003.
- Redish a. D. Beyond the cognitive map: from place cells to episodic memory. Cambridge, MA MIT Press. 1999.
- 27. Arkin RC. Behaviour-Based Robotics. Robotics. 1998.
- 28. Guanella A, Kiper D, Verschure P. A model of grid cells based on a twisted torus topology. In: Int J Neural Sys. 2007.
- 29. Santos-Pata D, Zucca R, Low SC, Verschure PFMJ. Size matters: How scaling affects the interaction between grid and border cells. Front Comput Neurosci. 2017.
- Bonnevie T, Dunn B, Fyhn M, Hafting T, Derdikman D, Kubie JL, et al. Grid cells require excitatory drive from the hippocampus. Nat Neurosci. 2013.
- Zhao R, Grunke SD, Keralapurath MM, Yetman MJ, Lam A, Lee TC, et al. Impaired Recall of Positional Memory following Chemogenetic Disruption of Place Field Stability. Cell Rep. 2016.
- Henriksen EJ, Colgin LL, Barnes CA, Witter MP, Moser MB, Moser EI. Spatial representation along the proximodistal axis of CA1. Neuron. 2010.
- Zhang SJ, Ye J, Miao C, Tsao A, Cerniauskas I, Ledergerber D, et al. Optogenetic dissection of entorhinal-hippocampal functional connectivity. Science. (80);2013.
- Lu L, Leutgeb JK, Tsao A, Henriksen EJ, Leutgeb S, Barnes CA, et al. Impaired hippocampal rate coding after lesions of the lateral entorhinal cortex. Nat Neurosci. 2013.
- 35. Deadwyler SA, West JR, Cotman CW, Lynch G. Physiological studies of the reciprocal connections between the hippocampus and entorhinal cortex. Exp Neurol. 1975.
- 36. Lian Y, Burkitt AN. Learning an efficient hippocampal place map from entorhinal inputs using non-negative sparse coding. eNeuro. 2021.
- Dordek Y, Soudry D, Meir R, Derdikman D. Extracting grid cell characteristics from place cell inputs using non-negative principal component analysis. Elife. 2016.
- Edvardsen V. Goal-directed navigation based on path integration and decoding of grid cells in an artificial neural network. Nat Comput. 2019.
- Fernandez-Leon JA, Acosta GG, Mayosky MA. Behavioral control through evolutionary neurocontrollers for autonomous mobile robot navigation. Rob Auton Syst. 2009.
- Brooks RA. A Robust Layered Control System For A Mobile Robot. IEEE J Robot Autom. 1986.
- 41. Edvardsen V, Bicanski A, Burgess N. Navigating with grid and place cells in cluttered environments. Hippocampus. 2020.

- 42. Tommasi L, Thinus-Blanc C. Generalization in Place Learning and Geometry Knowledge in Rats. Learn Mem. 2004.
- 43. Krupic J, Bauza M, Burton S, O'Keefe J. Framing the grid: effect of boundaries on grid cells and navigation. J Physiol. 2016.
- 44. Bicanski A, Burgess N. Neuronal vector coding in spatial cognition. Nat Rev Neurosci. 2020.
- Acosta GG, Curti HJ, Calvo OA. Autonomous underwater pipeline inspection in AUTOTRACKER Project: The navigation module. In: Oceans 2005 - Europe. 2005.
- 46. Guanella A, Verschure PFMJ. Prediction of the position of an animal based on populations of grid and place cells: A comparative simulation study. J Integr Neurosci. 2007.
- 47. Greeno JG, Moore JL. Situativity and Symbols: Response to Vera and Simon. Cogn Sci. 1993.
- Mountcastle VB. Modality and topographic properties of single neurons of cat's somatic sensory cortex. J Neurophysiol. 1957.
- 49. Hubel DH, Wiesel TN. Receptive fields of single neurones in the cat's striate cortex. J Physiol. 1959.
- Hawkins J, Ahmad S, Cui Y. A theory of how columns in the neocortex enable learning the structure of the world. Front Neural Circuits. 2017.
- Harris JA, Mihalas S, Hirokawa KE, Whitesell JD, Choi H, Bernard A, et al. Hierarchical organization of cortical and thalamic connectivity. Nature. 2019.
- 52. Felleman DJ, Van Essen DC. Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex. 1991.
- Barlow H. Sensory Mechanisms, the Reduction of Redundancy, and Intelligence. NPL Symp Mech Thought Process. 1959.
- 54. Földiák P. Forming sparse representations by local anti-Hebbian learning. Biol Cybern. 1990.
- 55. Bell AJ, Sejnowski TJ. The "independent components" of natural scenes are edge filters. Vision Res. 1997.
- Olshausen BA, Field DJ. Emergence of simple-cell receptive field properties by learning a sparse code for natural images. Nature. 1996.
- 57. Chalk M, Marre O, Tkačik G. Toward a unified theory of efficient, predictive, and sparse coding. Proc Natl Acad Sci USA. 2018.
- Clayton NS, Salwiczek LH, Dickinson A. Episodic memory. Curr Biol. 2007.
- Ocko SA, Hardcastle K, Giocomo LM, Ganguli S. Emergent elasticity in the neural code for space. Proc Natl Acad Sci USA. 2018.
- Colgin LL, Moser EI, Moser MB. Understanding memory through hippocampal remapping. Trends in Neurosci. 2008.
- Muller RU, Kubie JL. The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. J Neurosci. 1987.
- Minsky M. Steps Toward Artificial Intelligence. Proceedings of the IRE. 1961.
- 63. Banino A, Barry C, Uria B, Blundell C, Lillicrap T, Mirowski P, et al. Vector-based navigation using grid-like representations in artificial agents. Nature. 2018.
- 64. Andersson SO, Moser EI, Moser MB. Visual stimulus features that elicit activity in object-vector cells. Commun Biol. 2021.
- Fuhs MC, Redish AD, Touretzky DS. A Visually Driven Hippocampal Place Cell Model. In: Comp Neurosci. 1998.
- 66. O'keefe J, Conway DH. Experimental Brain Research Hippocampal Place Units in the Freely Moving Rat: Why They Fire Where They Fire. Brain Res. 1978.
- Høydal ØA, Skytøen ER, Andersson SO, Moser MB, Moser EI. Object-vector coding in the medial entorhinal cortex. Nature. 2019.

- Barry C, Lever C, Hayman R, Hartley T, Burton S, O'Keefe J, et al. The boundary vector cell model of place cell firing and spatial memory. Rev Neurosci. 2006.
- Lever C, Burton S, Jeewajee A, O'Keefe J, Burgess N. Boundary vector cells in the subiculum of the hippocampal formation. J Neurosci. 2009.
- 70. O'Keefe J, Recce ML. Phase relationship between hippocampal place units and the EEG theta rhythm. Hippocampus. 1993.
- 71. Burgess N, O'Keefe J. Models of place and grid cell firing and theta rhythmicity. Curr Opin Neurobiol. 2011.
- Jercog PE, Ahmadian Y, Woodruff C, Deb-Sen R, Abbott LF, Kandel ER. Heading direction with respect to a reference point modulates place-cell activity. Nat Commun. 2019.
- 73. Wang Y, Xu X, Wang R. An energy model of place cell network in three dimensional space. Front Neurosci. 2018.
- Sarel A, Finkelstein A, Las L, Ulanovsky N. Vectorial representation of spatial goals in the hippocampus of bats. Science. 2017;(80).
- 75. LaChance PA, Todd TP, Taube JS. A sense of space in postrhinal cortex. Science. 2019;(80).
- Boccara CN, Sargolini F, Thoresen VH, Solstad T, Witter MP, Moser EI, et al. Grid cells in pre-and parasubiculum. Nat Neurosci. 2010.
- Taube JS, Muller RU, Ranck JB. Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. J Neurosci. 1990.
- Sargolini F, Fyhn M, Hafting T, McNaughton BL, Witter MP, Moser MB, et al. Conjunctive representation of position, direction, and velocity in entorhinal cortex. Science. 2006;(80).
- 79. Kropff E, Carmichael JE, Moser MB, Moser EI. Speed cells in the medial entorhinal cortex. Nature. 2015.
- Kropff E, Carmichael JE, Moser EI, Moser MB. Frequency of theta rhythm is controlled by acceleration, but not speed, in running rats. Neuron. 2021.
- Solstad T, Boccara CN, Kropff E, Moser MB, Moser EI. Representation of geometric borders in the entorhinal cortex. Science. 2008;(80).
- Moser EI, Moser MB. Hippocampus and Neural Representations. In: Encyclopedia of Neuroscience. 2009.
- 83. Touretzky DS, Redish AD. Theory of rodent navigation based on interacting representations of space. Hippocampus. 1996.
- Burgess N, Recce M, O'Keefe J. A model of hippocampal function. Neural Networks. 1994.
- Jeffery KJ, Anderson MI, Hayman R, Chakraborty S. A proposed architecture for the neural representation of spatial context. Neurosci Biobehav Rev. 2004.
- Dayan P, Abbott LF. Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems. Comp Mathematical Model Neural. 2001.
- Wiskott L, Sejnowski TJ. Slow feature analysis: Unsupervised learning of invariances. Neural Comput. 2002.
- Cepelewicz J. The brain maps out ideas and memories like spaces. Quanta. 2019.
- 89. Roe AW. Columnar connectome: Toward a mathematics of brain function. Netw Neurosci. 2019.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.