

# Flexible navigation with neuromodulated cognitive maps

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## Abstract

During navigation, animals dynamically create rich representations of the environment, forming personalized cognitive maps used for exploration and goal planning. The hippocampal area CA1 features spatial cells that adapt based on behavior and internal states. A possible modeling approach is a labeled graphs that, with the intent of avoiding a map with metric structure, relies on nodes enriched with spatial information only specified locally. Another popular direction if training of deep neural networks on spatial tasks, from which record network dynamics from emerging spatially tuned neurons.

In this study, we introduce a place-cells based architecture for developing cognitive maps in one-shot while exploring novel environments. We used a simulated agent for reward-driven navigation tasks, which operates online and forms spatial representations of its surroundings. Further, by means of neuromodulators it incorporates behaviorally relevant information, such as boundaries and reward location. Learning was involved the combination of a rapid Hebbian plasticity, lateral competition, and modulation of the place cells,

The agent proved successful in exploring, retrieving and reaching goal locations in a variety of environments, and displayed adaptability when the reward was moved. Further, the analysis of the neuromodulated place cells showed the importance of dynamically changing neuronal density and tuning field size following relevant events. These results align with experimental evidence of reward effects on hippocampal spatial cells, and provides additional computational support to the labeled graph approach.

# 1 Introduction

Survival in complex environments requires adequate agency abilities, namely the capacity to explore, learn, and navigate toward goals. This becomes especially challenging when destinations are out of sight, a scenario known as *wayfinding*, where effective behavior relies on an internal model of the world [1, 2].

To support such behavior, the mammalian brain has evolved powerful spatial representations of the environment, refined through repeated experiences. These internal representations—commonly known as *cognitive maps*—were first proposed by Tolman, who observed that rats could navigate mazes in a goal-driven fashion, even when typical cues were removed [3].

Several strategies have been proposed to explain how agents reach known targets using cognitive maps. A basic method is *route learning*, where paths are stored as action-position pairs. Though effective in small-scale settings, it struggles with scalability due to ambiguities at path intersections [4, 5, 6]. A more flexible alternative is *survey knowledge*, involving metric representations that support vector operations in Euclidean space [5, 7]. However, empirical evidence suggests real brain maps often violate strict geometric constraints [8, 9, 10, 11]. A compelling compromise is the *labeled graph* model: a topological network where spatial relations are encoded locally through experience-based labels [12, 5, 13, 14]. This structure tolerates global inconsistencies while supporting local vector-like operations, aligning with both behavioral studies [15, 9, 16] and *path integration* mechanisms observed across species [17, 18, 19].

The neural substrates behind cognitive maps have been predominantly traces to the hippocampus and its surroundings, where various neuronal types have been linked to allocentric and egocentric spatial features. Border cells signal environmental boundaries; speed cells encode locomotion velocity; head-direction cells track angular orientation; place cells respond to specific locations; and grid cells exhibit hexagonal spatial tuning [20, 21, 22]. These cells are primarily found in the entorhinal cortex (especially medial EC) and hippocampal formation, including areas CA1, CA3, and the subiculum. Place cells in CA1, in particular, are often viewed as key components of cognitive maps [23]. The origin of their spatial tuning remains debated, with hypotheses focusing on input from entorhinal grid cells via the temporo-ammonic pathway or recurrent projections from CA3 through the Schaffer collaterals [24, 25, 26, 27].

Place cells in CA1 integrate spatial input from the medial EC and CA3, along with sensory and contextual signals from the lateral EC [28]. These inputs are modulated by neuromodulators which dynamically gate information and influence plasticity. In this regard, a primary role is covered by the dopaminergic projections from the VTA and LC target hippocampal subregions, including CA1, where they modulate excitatory input, regulate long-term potentiation

(LTP) via D1-like receptors, and influence memory consolidation [29, 30, 31, 32, 33]. Dopamine conveys reward-related signals that reshape place cell tuning [34, 35, 36, 37], supports novelty detection [38], and encodes reward prediction errors [39, 40], especially in relation to LEC inputs [41, 42].

Computational models of cognitive maps have evolved from early proposals—where the hippocampus encodes position and direction, and the parietal cortex supplies metric information [43]—to route-based topological graphs [6]. Recent models leverage predictive coding, such as the successor representation and Tolman-Eichenbaum Machine, which generalize across spatial and relational tasks while mimicking biological activity [44, 45, 46]. Path integration models trained on motion cues also generate grid- and place-like tunings [47, 48, 49], and some incorporate neuromodulation-driven Hebbian plasticity for reward-based learning [50].

Although many of these frameworks feature bio-realistic tuning, predictive learning, or neuromodulation, none integrates all elements simultaneously, and most depend on biologically implausible training like backpropagation.

In this study, we present a model that builds an online spatial representation of place cells, enriched with behaviorally relevant sensory information through neuromodulators.

The cognitive map is represented as a topological graph, where neighboring place cells are linked across experienced trajectories, going beyond traditional route learning [6]. Goal-directed navigation is then achieved through a path-finding algorithm that operates on this graph-level spatial data, aligning with the *labeled graph* framework [51].

Neuromodulators are modeled as analog sensor nodes that form synapses with place cells, defining scalar fields over the map [52]. Learning is conducted entirely online, mimicking animal behavior and avoiding the costly training processes typical of deep and reinforcement learning models, particularly in path integration tasks [47, 48, 49]. This is enabled by an architectural inductive bias: a predefined stack of grid cell layers with varying spatial frequencies, from which competing networks generate place cells [53, 54].

Our primary goal is to validate the emergence of a cognitive map that reflects the agent’s experiences and to assess its effectiveness in supporting goal-directed navigation. A secondary objective is to explore the map’s adaptability to environmental changes. To achieve this, we introduce a synaptic update mechanism based on prediction errors in future sensory inputs, inspired by predictive coding theories [40, 55, 56, 39]. This aligns with prior work on neuromodulation in spiking networks for exploration-exploitation dynamics [57, 58], and supports the view that modulators like dopamine are essential for maintaining and adapting neural representations tied to rewards [59, 60, 61, 62, 45].

Finally, we investigate how neuromodulation affects the density and spatial distribution of place fields, driven by experimental observations of remapping, resizing, and relocation in response to significant events [36, 63, 64].

The rest of the paper is organized as follows. In Section 2, we describe the model architecture and the task. In Section 3, we present the results of the simulations. In Section 4, we discuss the implications of the results, suggest future directions for research, and make conclusive observations.

## 2 Methods

The model is constructed around the concept of a cognitive map, which an agent constructs by freely moving in a closed environment and discovering target locations. The complete schema of its components is illustrated in the plot 1a below. The architecture relies on the core assumption that the external information is minimal, consisting solely of a reward and collision signals as two binary values.

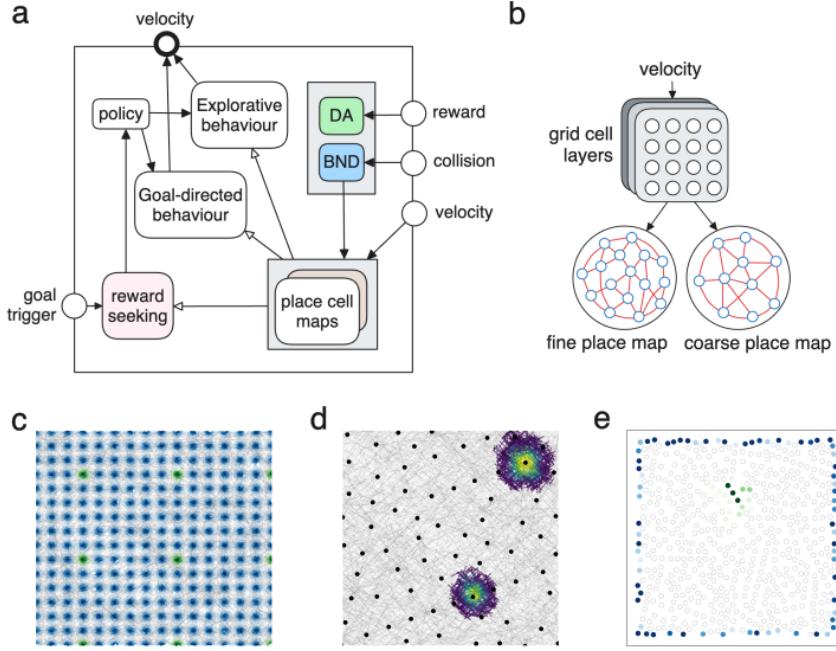


Figure 1: MODEL LAYOUT AND SPATIAL REPRESENTATIONS - **a:** the full architecture of the model, consisting of three main sensory input, targeting the two modulators and the cognitive map module, and the executive components, represented by a policy module, two behavioral programs and a reward receiver. **b:** the cognitive map component, organized with a stack of grid cell modules receiving the velocity input and projecting to two layer of place cells with different place field granularity. **c:** the neural activity of a grid cell module from a random trajectory; in blue the repeating activity of all cell, while in green the activity of only one, highlighting the periodicity in space. **d:** the distribution in space of the place cells centers, together with the activity of two cells showing the size of their place field. **e:** neuromodulation activity over the place cells map, with in blue the cells tagged by the collision modulation, and in green the ones targeted by reward modulation.

The formation of the spatial representation is instead based on idiothetic information, which is the agent's perception of self-motion [65]. In particular, here we assume this cue to be the factual velocity vector, namely the actual displacement of the agent in the environment. In the brain, this signal is believed to result from the integration of inertial and relative motion cues [66, 67].

## 2.1 Place cell map

The formation of place cells is obtained from the activity of a set of grid cells organized into modules or layers. This simple feed-forward architecture is shown in the plot 1b. A grid cell module l has been defined as a set of neurons  $N^{gc}$  with a Gaussian tuning curve evenly distributed over the surface of a two-dimensional torus  $T^2$ . In plot 1c is shown the activity of a grid cell module on a trajectory, the periodicity being underlined by the cell in green.

The activity of all modules of grid cells, indicated as  $\mathbf{u}^{GC}$ , is then projected down to two independent layers of initially silent cells, whose feedforward weights  $\mathbf{W}^{GC,PC1}, \mathbf{W}^{GC,PC2}$  are initialized at zero. As the agent moves and the activity of the grid cells changes, if no neurons within a place cell layer are active, then one is randomly chosen and its weights are set to the population vector of current grid cells (at time t)  $\mathbf{W}_i^{GC,PC} \leftarrow \mathbf{u}_t^{GC}$ . For the plasticity process to be completed, the possible overlap with other cells in the same layer is also checked, effectively accounting for lateral inhibition. This mechanism is implemented by computing the cosine similarity with the weight vector of the other tuned cells and comparing it with a threshold  $\theta_{rep}^{PC}$ , with the possibility of aborting the plasticity process if the similarity is too high.

The activity of a tuned place cell i is given, again, by the cosine similarity between the current grid cells' population vector and the weight vector of the cell:

$$u_i^{PC} = \phi \left( \cos \left( \mathbf{u}^{GC}, \mathbf{W}_i^{GC,PC} \right) \right) \quad (1)$$

where  $\phi$  is a generalized sigmoid function  $\phi(z) = [1 + \exp(-\beta(z - \alpha))]^{-1}$  with gain  $\beta$  and threshold  $\alpha$ . The two layers of place cells differ in the size of their place fields. This characteristic is affected by the sensitivity of a cell tuning with respect to the grid cell activation, determined by the parameters of the sigmoid, and the strength of the lateral inhibition, determined by the similarity threshold. Within a layer, connections between cells are calculated by the same cosine similarity, but compared against a different threshold  $\theta_{rec}^{PC}$ . One layer is set to be more fine-grained, with an overall higher density of place cells over the space, while the other is more coarse-grained, with overall large place field sizes. In addition, for each layer, a neural trace  $\mathbf{m}$  of activity is recorded, decaying with a fixed time constant.

In figure 1d are shown the centers of one of the fine-grained layers and the activity of two cells are shown, with their place field highlighted as a heat map.

## 2.2 Neuromodulators

The fine-grained layer of place cells constitutes the main cognitive map of the agent, since it captures the environment with greater detail. Neuromodulators are operationalized as analog sensors of meaningful environmental events, here to reward and collision, and map directly to the place cells through plastic connections  $\mathbf{W}^{k,PC}$ . For each neuromodulator k, it is defined a leaky variable  $v^k$  that accumulates the corresponding signal I over time, and decays exponentially

to zero in the absence of inputs with time constant  $\tau^k$ :

$$\dot{v}^k = -v^k / \tau^k + I \quad (2)$$

This variable is then paired with the activity of each place cell  $i$  for updating the synaptic weights in a Hebbian fashion:

$$\Delta W_i^k = \eta^k v^k u_i^{PC} \quad (3)$$

where  $\eta^k$  is the neuromodulator-specific learning rate, and the weights are kept  $\geq 0$ .

On the one hand, the reward modulation, signed as  $W^{DA}$ , is sensitive to the instantaneous presence of the reward, defined as a Boolean value. Over time, its coupling with the population vector  $u_t^{PC}$  delineates a region of the environment where the reward has been experienced. On the other hand, the collision modulation, referred to as  $W^{BND}$ , signals the occurrence of a collision with a boundary, which is again given as a boolean. After enough events, the profile of the resulting weight matrix with the place cells provides an approximation of the shape of the environment given by its boundaries. From the perspective of the agent, this intuition of the topology of its surroundings is crucial to efficiently planning routes to target locations.

At each moment during navigation, the weight matrices  $W^{DA,PC}$ ,  $W^{BND,PC}$  act as scalar fields over the neural space of the place cells, and their simultaneous contributions delineate what in this work is referred to as a cognitive map. In plot 1e the activity of the two neuromodulators is shown on the fine-grained place cells map, showcasing the limits of the environment and the reward location.

### 2.2.1 Online adaptation

For what concerns resilience with respect to environmental changes, such as reward location, the model was endowed with a prediction-base mechanism to correct for the accuracy of internal representations. During navigation, before execution of each movement towards a future location  $x_{t+1}$ , a prediction of the activity of the neuromodulator  $k$  is computed and cached:  $\hat{v}^k = \sum_i^N W_i^{DA,PC} \hat{u}_i^{PC}$ , where  $\hat{u}_i^{PC}$  is the predicted population activity at  $x_{t+1}$ . Then, a prediction error with a specific learning rate is calculated and added to the weight update:

$$\Delta W^k = \Delta W^k + \hat{\eta}^k (\hat{v}^k - v^k u_i^{PC}) \quad (4)$$

Further, since the rate  $\hat{\eta}^k$  is less than 1, it takes several erroneous prediction to effectively set connections to zero.

The rationale is to depress those synapses that no longer reliably predict the sensory experience referenced by the neuromodulator. This simple rule follows the framework of predictive coding and temporal-difference learning [68]. Previous computational models have used neuromodulatory signals to control neuronal dynamics, applied to the learning process [58, 69] or as a feedback error [70]. Furthermore, it aligns with the experimental evidence for the involvement of neuromodulation in dynamic update of internal beliefs [71, 45, 72].

### 2.2.2 Modulation of place fields

Lastly, in order to study the possibility of neuromodulatory alteration of neuronal properties, coarse-grained place cells were subjected to relocation and resizing of their place fields according to neuromodulatory input. The choice of this layer over the fine-grained one is motivated by empirically better performance results.

The movement of the place centers occurred after a reward or collision event and affected all nearby cells. More in details, each cell center was displaced, within the grid cells space, by a vector in the direction of the current position  $\mathbf{u}^{GC}$ , and with magnitude proportional to the value  $v^k$  of the neuromodulator  $k$  and its distance:

$$\Delta \mathbf{W}_i^{GC,PC} = c^k \cdot v^k \cdot \varphi_{\sigma^k} (\mathbf{u}^{GC} - \mathbf{W}_i^{GC,PC}) \quad (5)$$

where  $c^k$  is a strength scale and  $\varphi$  is a Gaussian distance with width  $\sigma^k$ . In addition, lateral inhibition was still taken into account, to avoid overlaps. This approach has been inspired by the BTSP rule [63, 36, 73], which has been responsible for the dislocation of the CA1 place cells after reward events (or an external step current), changing their associated spatial position.

Concerning the field resizing, it again occurs when its reference event occurs. The neuromodulatory action was determined by scaling the baseline neural activation gain  $\bar{\beta}$  of the most recently active neurons, identified by their neural trace  $m_i$ , according to a constant  $\gamma^k$ :

$$\beta_i = \gamma^k \cdot \bar{\beta} \cdot m_i + \bar{\beta} \cdot (1 - m_i) \quad (6)$$

The rationale is to modulate the surface over which neurons are sensitive, with  $\gamma < 1$  having a shrinking effect while  $\gamma > 1$  an enlarging one.

## 2.3 Policy and behavior

In this work, the first interest was to test the usefulness of our simple cognitive map built from minimal assumptions for exploration tasks and goal-directed navigation. To this end, we defined a simple hard coded policy that toggles between these two behaviors according to the presence of a goal signal, externally provided, and the presence of a real goal representation, cared for by a special component called *reward seeking*, depicted in the pink box of plot 1a. Exploration is accomplished by a random walk, with a variable number of steps in the same direction to avoid stagnation, and occasional plans to visit random positions within the known map, again for limiting stagnation. Goal-directed navigation, namely exploitation, serves the dual purpose of going to a random position within the map to improve exploration and reach the actual reward location. In practice, goal navigation is achieved by calculating the shortest path between the current position, identified by the cells with the most active place, and a target position, picked randomly or considering the cells with the

strongest dopaminergic weights, inspired by hippocampal replay and experimental observations [74, 75, 76]. The place cells are thus treated as nodes of a graph, and their connections constitute its edges. We use a Dijkstra algorithm applied to the coarse-grained layer, which contains less and more spread out cells, and it is thus cheaper to compute to derive a coarse-grained plan. However, in the case where the agent gets stuck or the distance to the target is shorter than the cells' distance, the planning switches to the other layer for devising a fine-grained plan, which it is followed until either the target or the next node in the coarse-grained are reached.

The advantage of this dual-layer planning lies in its flexibility, as it lightens the computational load of planning by exploding the sparser and lighter map and only invokes the detailed one when necessary. In the process of behavior, learning does not occur explicitly, but is instead accounted for in the online formation of the cognitive map.

## 2.4 Naturalistic task

The evaluation of the model to construct and use a cognitive map was defined as the total count of rewards collected during several trials. All environments used were closed boxes with different layouts, determined by the location and number of internal walls.

The testing protocol was inspired by the behavior of animals that venture into new territories in search of food. First, there was an exploration phase, in which the agent was placed in a random location and walked a pseudo-random route for 5000 time steps. Then an exploitation phase began, in which a circle of 5% of the total was designated to provide a binary reward  $R \sim \mathcal{B}(p_r)$  drawn from a Bernoulli with probability  $p_r$ .

Optimization of the model parameters was carried out using the evolutionary Covariance-Matrix Adaptation strategy (CMA-ES) [77] with a population of 256 individuals for 100 generations.

# 3 Results

## 3.1 Performance in wayfinding

Our primary aim was to evaluate the formation of the cognitive map through neuromodulation in terms of performance of goal-navigation in different environments. The best model resulting from evolution reached solid navigation and adaptation skills. The agent was able to visit a significant portion of the environment during exploration, and use neuromodulation to produce useful spatial representations.

In figure 2, three emerging cognitive maps are shown different environments. The left panel of plot 2-a displays fine-grained place cells associated with collisions and reward events, signaling boundaries (in blue) and reward (in green)

locations. The overlapping of these two representations and the coarse-grained place cells (in pink) is what we refer to as a cognitive map, since these are the main source of spatial and contextual information used during planned navigation, whose path is depicted as a grey line. The right panel instead portraits the actual environment with walls (black), reward location (green), and multiple trajectories (red). During exploration, the main areas were visited, until the reward position was located, and goal-directed navigation dominated, as highlighted by the density of path lines. Considering the position of the walls and corners, the layout of this environment does not make target locations always visible, as it is a non-convex area, and can be thus be classified as wayfinding [78]. The challenge of not being able to use straight lines is overcome by the graph approach using local data and the switching between the differently grained place cells layers, allowing the agent to successfully going around obstructions and avoiding being stuck. Further, the plans were also minimizing path length by construction, within the part of the space covered by the cognitive map.

Overall, this result confirm the model ability to goal-directed navigation and obstacle avoidance. However, it is worth nothing that not all simulations resulted in reward being found in the first place, due to the randomness of the exploratory process; this was more pronounced in complex environment.

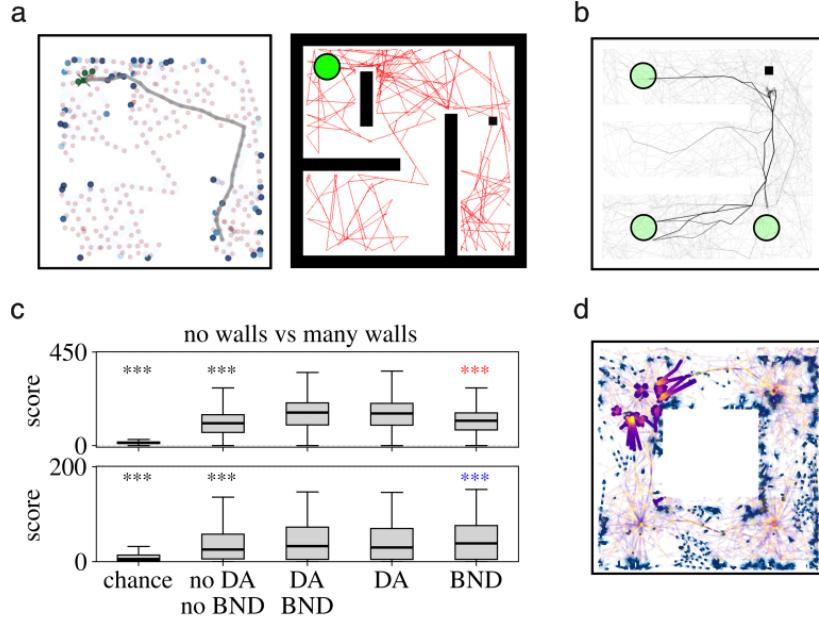


Figure 2: COGNITIVE MAPS AND PERFORMANCE RESULTS - **a:** the plot on the left represent a cognitive map over a space, together with the plan (grey line) to reach a target location from a starting position. The plot on the right is a view of the same environment but with highlighted walls (black thick lines) the reward (green circle), trajectory (red line), agent position (black square). - **b:** trajectories for multiple trials with the agent starting at the same position (black square) but with the reward location (green circles) periodically moving - **c:** performance comparison with same environmental conditions for five different models: one baseline as chance level (plasticity disabled, except for place cells generation), and four variants with different ablations of DA and BND modulations of place fields density and size. Results in terms of reward count and Bonferroni-corrected pairwise t-test, black stars stand for statistical difference with respect to all other groups, red starts only to the DA and DA+BND, and blue stars only to t DA in the case solely the upper median split is considered when testing the significance. - **d:** cognitive map but in terms of the activity of the place cells over multiple trajectories with a fixed reward location. Further, it is marked with high opacity the activity of the DA-modulated coarse-grained place cells, with their place fields enlarged near the reward.

### 3.2 Adaptive goal representation through prediction error

Then, we tested the adaptability to environmental changes. In this scenario, the reward object was moved after it was fetched a fixed amount of times. Here, the difficulty lied in the unlearning of past locations and the discovery of the new ones. In plot 2-b it is reported the set of trajectories over many trials with the

reward displaced in three possible locations. The agent was capable of planning behaviour, as earlier, but also to explore and find the new rewards, as shown by the density of lines. Whenever a goal path resulted in failed prediction, the DA-based sensory error weakened the association between the place cells and reward signal, leading to an extinction of its representation at that location.

This result validates the resilience of the model to changing sensory expectations, in this case reward position.

### 3.3 Modulation of spatial resolution affects performance

Lastly, we investigated the effect of modulating the place cells density and field size. The goal position was fixed, but the agent was randomly relocated after fetching; performance was defined as total number of reward count within a time window. Our working hypothesis is these experience-driven neuronal changes would improve the quality of the cognitive map, and be reflected in the navigation abilities. The assessment of this claim was conducted by comparing variants of the model, obtained by progressively ablating the possibility reward (DA) and collision (BND) modulation of density and field size, but a cognitive map was still possible as their representations of goals and boundaries were preserved. We also defined a chance level by instead blocking all modulation-based plasticity and allowing only place cells formation. All models were ran in two different environments differing by number of internal walls, in total 2048 simulations were done for each case.

The results are shown in plot 2-c. The top reports the scores in the setting without internal walls. All models performed above chance, but the main finding is the affirmation of the importance of neuronal modulation, as revealed by the statistical difference between those endowed with it and the one that was not. Further, the possession of DA modulation resulted in a significantly higher score with respect to BND modulation alone (red stars). Indeed, in a situation with a convex region such as this one, once the reward has been located boundary information has a limited utility.

A partially different pattern emerged when more internal walls were introduced, as shown by the results at the bottom. In this case, BND modulation became the dominant factor. Moreover, in the circumstance of considering only the upper half of the scores it also turned statistically greater than DA modulation, despite the latter still outperforming the absence of either. In this environment, scores were overall lower as navigation became more difficult, and the difference among groups thinner, although noticeable.

Lastly, in plot 2-d is showed a cognitive map for another environment, characterized by the place cells activity over several trajectories instead of the centers. In particular, the DA-modulated place fields are reported, highlighting their enlarged size and density near the reward location.

Taken together, these findings support the hypothesis of practical utility of direct modulation of place field structure for active navigation, even in these simple settings.

## 4 Discussion

Exploration and planning in known and past environment are essential behaviours of animals, directly affecting their success in world udnerstanding and goal reaching.

An important element behind these abilities is the formation of a map of their surroundings as they make new experiences, known as a cognitive map. Numerous speculations have been made about the shape and neural foundations of such object, varying in the type of modeling assumptions and experimental support.

The contribution of the present work was to proposal a rate network model, inspired by the CA1 hippocampal region [23]. We used grid cells together with synaptic plasticity as a mechanism for developing place cells-based information rich representations updated through experience, lined up with common perspectives on cognitive maps [79]. In the spirit of minimizing the geometric assumptions on the neural space, we treated the generated place network as a topological graph, with information added locally through the action of neuromodulators. This idea aligned with the concept of a *labeled graph* [14, 9] as it ignores premises of global spatial properties, however it is also true that no metric violations were actually possible in these settings.

The tasks we applied the agent consisted in an exploratory and exilotatitve phase, in which it was prompted to plan and reach reward positions. For simplicity, the first stage relied on a random walk process, as it was outside the scope of this work. This choice had the side effect that the reward was not always discovered, leading to the formation of incomplete maps and thus impairing performance. Nonetheless, this issue was limited in frequency.

The simulation results validated the model, showing the expected emergence of cognitive maps and their encoding of information collected during experience. The online nature of the formation of the map places aligns with the idea of using only idiothetic velocity input as in path integration [7, 18, 80]. Previous work followed a similar direction using recurrent networks, but required an extensive gradient-based training [81, 49, 67]. Another important difference that our resulting neural network was composed by construction solely of place cells, although neuromodulated, and no other neuron types were present. This distinction is justified by the partially different task structure, which did not involved supervised learning, and it did not receive visual information as in [47]. Further, our model relied on pre-defined grid cells layers, which constituted a strong andsufficient inductive bias, and did not have to be learned from scratch.

An additional relevant aspect is also the consideration of the place cells layer as an explicit graph data structure, on which the path-planning and decision-making algorithm was applied. The adoption of this level of description lead to robustness and flexibility, enabling effective navigation in all tested environments, which varying in layout complexity. Nonetheless, this approach did act as another clear inductive bias, which lifted the necessity of learning an approximation of it through network dynamics and even more differently tuned neurons.

Adaptability was tested by occasionally moving the rewarding position, leading to the generation of an internal prediction error that was used to update its representation on the map. The agent proved capable of unlearning previous associations, returning to exploration, and memorizing new reward locations. This behavioural protocol is similar to previous work [58], where dopaminergic and cholinergic activity was utilized within an Hebbian plasticity rule for strengthening or weakening reward-associated spatial representations. However, alternatively to exploiting neuromodulators with opposite valence, we followed a predictive coding framework, a direction linked to hippocampal representations [45, 82] and explored in various computational approaches [83, 84, 85]. This choice departed from our focus of using operations over the cognitive map itself, by simulating future sensory experiences and learning from feedbacks. In fact, neuromodulation has been long associated with such functionality as well [52], especially dopamine [34, 59, 62, 39].

Lastly, the hypothesis of relevance of the active modulation of neuronal properties of place cells was corroborated by simulating ablation experiments. These tests reported a significant impact of resizing place fields and density on the total count of collected rewards. Further, boundary modulation showed to be more impactful in environments with more internal walls, reasonably because it enhanced their representation in neural space leading to better planning. Overall, these results aligns with the experimental observations of alteration of place cells upon reward events [36, 86], in particular in terms of increased cells clustering [87, 88], reminiscent of firing rate changes following contextual shifts [89, 90].

Concerning the modulation of place fields, there is significant experimental evidence of their alternation during reward events [91, 92, 93], some reporting shrinking near rewarding objects [94], and boundaries [95]. The coupling with higher local density might be explained by a better optimization of cell distribution for goal representation and planning [70]. In our settings, however, the fields became enlarged, especially in the direction of target. A possible explanation can be the simplicity of our reward, which was solely defined as an area of space. The lack of rich non-spatial features thus did not required the place cells to code for smaller spatial variation. Therefore, the enlargement might have improved the stability of the representation, marking the nodes associated with rewards more solidly, given the stochasticity of its delivery. Further, the graph-path algorithm utilized the strength of the DA-modulated connections for determining the goal representation, stronger fields inherently developed stronger weights, making planning more reliable planning. Although these finding are confined within the limit our simulation protocol, there have been experimental observations of elongation of place fields along trajectories over meaningful experiences [96, 97].

In conclusion, this work showed a possible architecture for coupling emergent spatial representations with neuromodulated plasticity for achieving an experience-driven cognitive map. The reliance of few spatial and algorithmic inductive biases, grid cells and planning algorithm, supports the idea of label graph for goal navigation. Future work can investigate the application to other

spatial domains, such as motor control and three-dimensional navigation. Additionally, richer input feature can be added, such as visual information [98], as well as new neuromodulators encoding for different sensory dimensions or internally-generated signals.

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The authors declare no competing interests.

The code is publicly available and can be found at <https://github.com/iKiru-hub/PCNN>.

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## 5 Appendix

### 5.1 Spatial representations

### 5.2 Grid cell module

Unlike other approaches to generate grid fields [99, 100], we defined a correspondence between the global environment in which the agent moves, a two-dimensional Euclidean space  $\mathbf{R}^2$ , and a bounded local space of a grid module, corresponding to the torus.

The global velocity  $\mathbf{v} = \{x, y\}$  is then mapped to a local velocity, scaled by a speed scalar  $s_l^{gc}$  specific to the grid cell module  $l$ , which determines its periodicity in space. This approach has been used in previous works [26].

The choice of a toroidal space is motivated by consolidated experimental evidence of the neural space of grid cells, which are organized in modules of different sizes spanning the animal's environment. However, the shape of their firing pattern is known to be hexagonal, which corresponds to the optimal tiling of a two-dimensional plane, giving rise to a neural space lying on a twisted torus. In this work, for simplicity, we consider a square tiling and thus a square torus, without much loss of generality except for the slight increase of grid cells required for a sufficiently cover.

A grid cell module  $l$  of size  $N^{gc}$  is identified by a set of positions defined over a square centered at the origin and size of 2, such that  $\{(x_i, y_i) \mid i \in N^{gc} \wedge x_i, y_i \in (-1, 1)\}$ . This local square space has boundary conditions for each dimensions, such that for instance when  $x_t + s_l^{gc} \cdot v_x > 2$  then the position update is taken to the other side  $x_{t+1} = x_t + s_l^{gc} \cdot v_x - 2$ , where  $s_l^{gc}$  is the scale of the velocity in the local space of module  $l$  with respect to the real global agent velocity  $\mathbf{v} = \{v_x, v_y\}$ . When the module is initialized, the starting positions of its cells are uniformly distributed over the square forming a lattice. When the agent is reset in a new position at the beginning of new trial, a displacement vector is applied to the last cells positions, such that the mapping between the module local space and the global environment is preserved.

The firing rate vector of each cell is determined with respect to a 2D Gaussian tuning curve centered at the origin at  $(0, 0)$ , and it is calculated as

$$r_i = \exp\left(-\frac{x_i^2 + y_i^2}{\sigma_l^{gc}}\right), \text{ where } \sigma_l^{gc} \text{ is the width of the tuning curve for module } l.$$

The final population vector of the grid cell network GC is the concatenated and flattened firing rate vector of all modules  $\mathbf{u}^{GC}$ .

In our model, each grid cell had a tuning width of 0.04. They were defined 8

modules of size 36, and the relative speed scale were  $\{1., 0.8, 0.7, 0.5, 0.4, 0.3, 0.2, 0.1, 0.07\}$ .

### 5.3 Place cells

**Tuning formation** A new place cell's tuning is simply defined as the current GC population vector  $\mathbf{u}_t^{\text{GC}}$ , and its index is that of the first silent cell, which gets added to the forward weight matrix  $\mathbf{W}_i^{\text{GCtoPC}} \rightarrow \mathbf{u}^{\text{GC}}$ .

In order to avoid overlapping of place fields, the tuning process is aborted in case the cosine similarity of the new pattern and the old ones is greater than a threshold  $\theta_{\text{rep}}^{\text{PC}}$ .

Each cell represents a position in the GC activity space, which can be considered a node within a graph of place cells (PC). Although it is totally possible to only use the  $N^{\text{GC}}$ -dimensional tuning patterns and be agnostic about the dimensionality of the space in which the agent lives, to simplify the calculations we mapped each pattern to a 2D positions in a vector space. Then, the PC recurrent connectivity matrix is calculated with a nearest neighbors algorithm, which instead of a fixed number  $K$  of neighbors it uses a distance threshold  $\theta_{\text{rec}}^{\text{PC}}$ .

**Activity** The current firing rate of the PC population is determined by the cosine similarity between the GC input and the forward weight matrix, then passed through a generalized sigmoid  $\phi(z) = [1 + \exp(-\beta(z - \alpha))]^{-1}$ . The parameter  $\alpha$  represents the activation threshold, or horizontal offset, while  $\beta$  the gain, or steepness. It is also defined an activity trace, which has an upper value of 1 and decay exponentially:

$$m_i = -m_i/\tau^{\text{PC}} + u_i \quad (7)$$

it is used as a proxy for a memory trace.

In the model, two PC populations are defined, which are named *fine-grained* and *coarse-grained* as their main difference were their average place field size, determining the granularity of the place representation.

Below it is reported a table of the parameters specific to the two PC populations.

	$\beta$	$\alpha$	$\theta_{\text{rep}}^{\text{PC}}$	$\theta_{\text{rec}}^{\text{PC}}$	$\tau^{\text{PC}}$
Fine	33.0	1.0	0.86	43	140
Coarse	16.6	1.0	0.76	41	24

Table 1: COMPARISON OF FINE AND COARSE PARAMETERS

## 5.4 Modulation

Neuromodulation is defined in terms of a leaky variable  $v$  whose state is perturbed by an external input  $x$ , whose qualitative meaning differs for each neuromodulator  $k$ .

$$\begin{aligned} v_k &= -v_k/\tau_k + x_k \\ v_k &= \max(v_k, 0) \end{aligned} \quad (8)$$

**Learning rule** The connection weights  $\mathbf{W}^k$  are updated according to a plasticity rule composed of an Hebbian term, involving the leaky variable and the place cells above a certain threshold  $\theta^k$ , and a prediction error.

A prediction  $p$  is calculated before each time-step and signifies the expected neuromodulation activation for a given place cell  $p_i = \mathbf{W}_i^k \hat{u}_{PC}$ , where  $\hat{u}_{PC}$  is the PC population vector obtained by simulating the planned action. A prediction error is computed as the difference between the prediction and the current modulated place activation.

The full connection update then becomes:

$$\Delta \mathbf{W}_i^k = \eta^k v^k u_i^{PC} - \eta_{pred}^k (p_i - v^k u^{PC}) \quad (9)$$

where  $\eta^k$ ,  $\eta_{pred}^k$  are the learning rates, interpretable as the weight contribution of the Hebbian coupling and prediction accuracy respectively. Additionally, connections values are kept non-negative and, in order to speed up the extinction of past place-reward associations, if a non-zero prediction error is below a 0.5 then it is set to 0.5.

**Active neuronal modulation** Neuromodulation acts on the neuronal profile of the place cells by affecting the value of the activation gain and relocate the center of their tuning.

Gain modulation is implemented using the activity traces and a constant reference gain value  $\bar{\beta}$ :

$$\beta_i = c_a^k \bar{\beta} m_i + (1 - m_i) \bar{\beta} \quad (10)$$

where  $c_a^k$  is a scaling gain parameter, and if it is 1 then no modulation takes place.

Concerning center relocation, it is applied to recently active neurons with non-zero trace  $m_i$ . For a place cell  $i$  with position  $\mathbf{x}_i$  (in the vector space), it is calculated a displacement vector  $q_i$  with respect to the current position  $\mathbf{x}_j$ , identified as the most active place cell  $j$ .

$$q_i = c_b^k v^k \exp\left(-\frac{\|\mathbf{x}_i - \mathbf{x}_j\|}{\sigma^k}\right) \quad (11)$$

where  $c_b^k$  is a scaling relocation parameter, while  $\sigma^k$  the width of the Gaussian distance. This displacement is used to move in GC activity space and get the new GC population vector to use as tuning pattern.

Also in this case, it is ensured that the new place field center is at a minimum distance  $\theta_{\min}^{\text{PC}}$  from the others; here Euclidean distance is used.

## 5.5 Decision making

### 5.5.1 Path-planning algorithm

The planning of a new route is implemented as a modified Dijkstra algorithm over the coarse-grained place cell graph, provided as connectivity matrix C. Its particularity is the use of a weighting  $\widetilde{\mathbf{W}}$  of the nodes according to the neuromodulation map.

## 5.6 Evolutionary optimization

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**Algorithm 1** Modified Dijkstra algorithm

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**Require:** Connectivity matrix  $\mathbf{C} \in \{0,1\}^{N^{PC} \times N^{PC}}$ , Node coordinates  $\mathbf{x} \in \mathbb{R}^{N^{PC} \times 2}$ , Node weights  $\widetilde{\mathbf{W}} \in \mathbb{R}^{N^{PC}}$ , Start node s, End node t

**Ensure:** Shortest path from  $t_0$  to T

```
1: distances  $\leftarrow [\infty, \infty, \dots, \infty]$                                  $\triangleright$  Initialize distances
2: distances[ $t_0$ ]  $\leftarrow 0$ 
3: parent  $\leftarrow [-1, -1, \dots, -1]$                                           $\triangleright$  Parent pointers
4: finalized  $\leftarrow [\text{false}, \text{false}, \dots, \text{false}]$                        $\triangleright$  Set of finalized nodes
5: PQ  $\leftarrow \emptyset$                                                         $\triangleright$  Priority queue
6: PQ.push((0,  $t_0$ ))                                                  $\triangleright$  Insert start node with priority 0
7: while PQ  $\neq \emptyset$  do
8:   (dist, j)  $\leftarrow$  PQ.extractMin()
9:   if finalized[j] or dist > distances[j] then
10:    continue
11:   end if
12:   finalized[j]  $\leftarrow$  true
13:   if j = T then
14:     break                                                                $\triangleright$  Destination reached
15:   end if
16:   for each node i where  $\mathbf{C}_{i,j} = 1$  and not finalized[i] do
17:     if  $\widetilde{\mathbf{W}}[i] < -1000$  then
18:       continue                                          $\triangleright$  Skip nodes with high negative weights
19:     end if
20:      $\Delta x \leftarrow \mathbf{x}_{j,0} - \mathbf{x}_{i,0}$ 
21:      $\Delta y \leftarrow \mathbf{x}_{j,1} - \mathbf{x}_{i,1}$ 
22:     edge_dist  $\leftarrow \sqrt{\Delta x^2 + \Delta y^2}$                           $\triangleright$  Euclidean distance
23:     new_dist  $\leftarrow d[j] + \text{edge\_dist}$ 
24:     if new_dist < d[i] then
25:       d[i]  $\leftarrow$  new_dist
26:       parent[i]  $\leftarrow$  u
27:       PQ.push((new_dist, i))
28:     end if
29:   end for
30: end while
31: path  $\leftarrow []$ 
32: if d[T] =  $\infty$  then
33:   return  $\emptyset$                                                $\triangleright$  No path exists
34: end if
35: curr  $\leftarrow t$ 
36: while curr  $\neq -1$  do
37:   path.append(curr)
38:   curr  $\leftarrow$  parent[curr]
39: end while
40: path.reverse()
41: if path is empty or path[0]  $\neq s$  then
42:   return  $\emptyset$ 
43: end if
return path
```