

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

Agency in a large environment is a challenging task for any organism. Productive exploration and effective goal-directed navigation are essential in this regard, and become even more crucial when target locations are out of sight. In this scenario, often labelled as *wayfinding*, an adequate understanding of one's surroundings is necessary [1, 2].

For this scope, one of the tools evolved by the mammalian brain are neural spatial representations of the environment, enriched by repeated experiences. In the literature, they are often referred to as cognitive maps, which were first introduced by Tolman who noticed the reward-driven navigation ability of rats in a maze [3].

There are multiple approaches that can be used for solving the task of reaching a known target in its environment with a cognitive map, and the choice might depend on the task as well as personal traits, at least in humans [4, 5]. However, which are the ones the brain generally prefers the most is still debated. One of straightforward possibilities is *route learning*, where the gist is to memorize the previous paths as simple action-position pairs. This approach is effective in small environments, but it is impractical for constructing a proper map to exploit more generally, given the ambiguity at combining intersecting paths [6, 7, 8]. In contrast, a more general strategy is to rely on *survey knowledge*, where the subject builds an explicitly general representation of the environment by endowing it with an Euclidean metric, namely a global coordinate system based on distances and angles in which perform vector operations [7, 9]. The resulting map is highly flexible, and allows for the computation of short-cuts and arbitrary routes. However, it lacks convincing experimental evidence, with several studies in humans and mice highlighting how real brain maps often violate the strict algebraic constraints [10, 11, 12, 13]. Another possibility is a so-called *labeled graph* [7, 14, 15], which consists of a topological graph of the environment over locations in space. Importantly, it does not possess a universal metric but instead relies on local labels, built through experiences [16], for supporting information about distances and angles. The lack of a rigid operational structure leads to more tolerance for global spatial inconsistencies, while still allowing for affine vector operations, at least locally. Multiple studies have shown support for this type of representation, in which the graph-based map and its labels are generated and successfully exploited for goal-reaching tasks, despite clearly infringing Euclidean geometry [17, 11, 5]. This online formation of position nodes is also aligned with *path integration*, the process of integrating velocity vectors for tracking the trajectory leading home, supported by observations in multiple species [18, 19] and theoretical analysis [20].

Regarding the main neural substrates of the cognitive maps, a variety of neuronal types has been associated to allocentric and egocentric spatial features.

Among others, border cells have been associated to boundary detection, speed cells with the magnitude of the perceived velocity, head-direction cells with the angular position of the head as per vestibular perception, place cells with unimodal tuning for spatial positions, and grid cells with an hexagonal periodic tuning [21, 22, 23]. Parts of this neuronal ecosystem has been found in various part of the cortex, but more predominantly in the entorhinal cortex (EC), in particular the medial region (MEC), and sub-regions of the hippocampal formation, particularly the cornus ammonis area CA3 and CA1, and the subiculum (SB). Specifically, place cells in CA1 have been often considered as the component of the cognitive maps [24]. The origin of the spatial tuning of these cells is still debated. Some theories trace it back to competitive dynamics over projections from entorhinal grid cells through the temporo-ammonic pathway, while others point at the Schraffer's collaterals from CA3 [25, 26, 27, 28].

1.1 Neuromodulation of cognitive maps

The upstream afferences to these place cells populations carry a variety of inputs, ranging from spatial information from the medial EC and CA3, to sensory and contextual data from the lateral EC [29]. In addition, they are also targeted by a multiple neuromodulators, molecules gating information and affecting neuronal dynamics in a multitude of ways, the most prominent of which in this context are dopamine and acetilcholine.

There are several set of dopaminergic innervations to the hippocampus, targeting all its main sub-components. The ones more directly involved with CA1 place cells are those from the ventral tegmental area (VTA) and locus coeruleus (LC) [30, 31, 32]. Their actions have been linked to synaptic excitation, modulation of the glutamatergic projections from EC, and regulation of long term potentiation (LTP) through D1-like receptors [33, 34]. One important function of dopamine concerning spatial navigation is the delivery of reward-related information, supporting memory consolidation of salient locations [35, 36] and active reshaping of the place cells tuning [37, 38]. Another extensively documented role is novelty detection [39], especially for contextual inputs from LEC [34, 40, 41], as well as encoding prediction errors of reward events [42, 43].

The cholinergic innervation to the hippocampus is mainly provided by the medial septum (MS). Through the action of different muscarinic receptors, it modulates the afferences to CA1 from MEC and CA3, and promotes both long-term synaptic potentiation and depression [44, 45, 46]. Its role in spatial navigation includes the support of explorative behaviour, contributions to novelty detection, and attentional regulation by increasing the input signal-to-noise ratio [47, 48, 44].

1.2 Computational models

There have been several efforts for devising computational models capturing the construction and functionality of cognitive maps. In relation to purely spatial navigation, a notable modelling framework is the one proposed by [49], in which

the hippocampus was envisioned to encode positions with directional information, while metric properties were brought by the pariental cortex. Later work has extended it into a route-based formalism [8], centered on the idea of a route graph formed by concatenation of episodic routes. Further, these graphs could have different granularity, organized hierachially in layers. Another direction has seen the use of the successor representation (SR) algorithm, based on predictive modeling, for learning navigation tasks in spatial and semantic spaces, with good performance [50], also in comparison to humans and rats [51]. A similar approach for generating task-dependent is the Tolman-Eichenbaum Machine (TEM), based on artificial neural networks [52], which has been applied to navigation and relational reasoning. Interestingly, some of these artificial neurons resembled the firing pattern of actual hippocampal and entorhinal cells. Such bio-realistic neuronal tunings have also been consistently obtained in recurrent neural networks trained to solve *path integration* problems, using only idiothetic information such as the agent’s velocity vector [53, 54, 55]. This line of normative research has been particularly successful in generating a rich ecosystem of spatial cells, such as grid cells and place cells, and reasoning through their functional importance for navigation.

However, what these models have in common is the reliance on backpropagation for training, which is not biologically plausible, and the lack of a proper real-time learning dynamics. Although they rely solely on locally available information during inference, the type of cognitive map they can support is limited to purely spatial data. For more diffult behaviours such as goal-directed navigation, a richer representation of the environment should be more advantageous. Furthermore, the role of neuromodulation in the formation of cognitive maps has been largely overlooked, despite its relevance in actively regulating neuronal dynamics and gating important information.

In this study, we introduced a model architecture capable of generating online a spatial representation made of two place cells layers, which can be endowed with additional behaviourally-relevan sensory inputs by means of neuromodulators. Our primary goal was to successfully construct a bio-realistic cognitive map and the effectivess of neuromodulation in enriching it with sensorial information, and evaluating their impact on the agent’s performance in goal-directed navigation. One important modeling assumption was to solely rely on the spatial information available within the local graph, namely without invoking a global coordinate system, justified by the controversial evidence for a proper metric space in brain cognitive maps. This is thus more aligned with the *labellel graph* approach, although metric data is not explicitly attached to the nodes but rather inferred on-the-fly with an implicit and weak embedding into an affine space, similarly to other proposals [56]. Another assumption was that learning occurs entirely online, as animals do, avoiding a costly network training, which is instead popular in standard deep and reinforcement learning as well as in most models applied to *path integration* [53, 54, 55]. This feature is achieved by introducing a structural inductive bias in the form of a pre-defined stack of grid

cells layers with different spatial frequencies, from which multiple layers of place cells are generated through network competition [57, 58]. A map is then obtained by connecting neighboring place cells obtained over several trajectories, thus going beyond route learning [8] and constructing a topological graph. For what concerns neuromodulators, in this work they are best described by nodes working as analog sensors of external events. Their role is to form synaptic connections with the place cells, effectively determining a scalar field over their representation [59].

A secondary goal was to investigate the possibility of updating the cognitive map to environmental changes, accounting for the adaptation and flexibility in animals behaviour. For this scope, the model was endowed with a way to correct the synaptic weights between neuromodulators and place cells, based on prediction error of future sensory observations. This mechanism is aligned with principles of neural predictive coding [43, 60, 61, 42], according to which prediction-based learning is a relevant part of brain activity. We took inspiration from previous work which has applied neuromodulation in spiking neurons for controlling explorative-exploitative behaviour [62, 63]. Further, it is well established the role of modulators such as dopamine in actively maintaining and updating the state of neural representations, particularly those associated with reward features [64, 65, 66, 67, 51].

A last interest of ours regarded the effect of neuromodulation on the density of place cells, and in particular the reshaping of their place field, with respect to task performance. The motivation stems in the experimental observations of modulation of place cells representation following meaningful events, in terms of remapping, fields resizing and dislocation on the map [37, 68, 69].

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 builds by freely navigating a closed environment and reaching a discovered goal location. The full schema of its components its illustrated in plot 1-a below. The architecture relies on the core assumption that the agent has receives minimal external information, consisting solely of a reward and collision input as two binary values. These two signals are used to enrich the cognitive map with experience-dependent data, which is then used to guide the agent’s behavior.

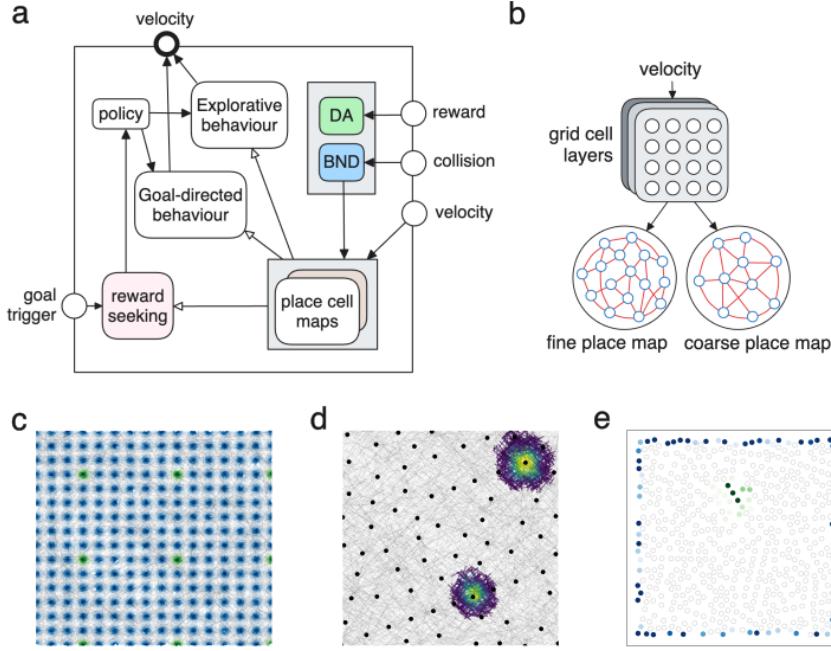


Figure 1: MODEL LAYOUT AND SPATIAL REPRESENTATIONS - **a:** the full architecture of the model, consisting of three main sensory input, targeting the two modulators and the cognitive map module, and the executive components, represented by a policy module, two behavioural programs and a reward receiver. **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 [70]. 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 thought to result from the integration of inertial and relative motion cues [71, 72].

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 displayed in plot 1-**b**. A grid cell module l has been defined as a set of N^{gc} neurons with gaussian tuning curve evenly distributed over the surface of a two dimensional torus \mathbf{T}^2 . Unlike other approaches for generating grid fields [73, 74], we defined a correspondance between the global environment in which the agent moves, a two dimensional Euclidean space \mathbf{R}^2 , and a grid module bounded local space, 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 [27]. The starting position on the torus is randomly chosen when the model is initialized, since what matters is the sequence of displacements without any reference to a meaningful origin.

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 size 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. In plot 1-**c** is shown the activity of a grid cell module over a trajectory, with the periodicity underlined by the cell in green.

The activity of all grid cell modules, indicated as \mathbf{u}^{GC} , is then projected down to two independent layers of initially un-tuned cells, whose feed-forward weights $\mathbf{W}^{GC,PC1}, \mathbf{W}^{GC,PC2}$ are initialized at zero. As the agent moves and the grid cells activity changes, if no neurons within a place cell layer are active, then one is randomly chosen and its weights are set to the current (at time t) grid cells' population vector $\mathbf{W}_i^{GC,PC} \leftarrow \mathbf{u}_t^{GC}$. For the plasticity process to be completed, it is also checked the possible overlap with other cells in the same layer, 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 θ_{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 ϕ is a generalized sigmoid function $\phi(z) = [1 + \exp(-\beta(z - \alpha))]^{-1}$ with gain β and threshold α . The two layers of place cells differ in the size of their place fields. This feature 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, the connections between cells are calculated by the same cosine

similariy, but compared against a different threshold $\theta_{\text{rec}}^{\text{PC}}$. 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. Further, for each layer it is recorded a neural trace \mathbf{m} of the activity, decaying with a fixed time constant.

In figure 1-d are shown the centers of one of the fine-grained layer and the activity of two cells, with their place field highlighted as an heatmap.

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. The neuromodulators are operationalized as analog sensors of meaningful environmental events, here reward and collision, and map directly to the place cells through plastic connections $\mathbf{W}^{k,\text{PC}}$. 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 τ^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:

$$\Delta \mathbf{W}_i^k = \eta^k v^k \mathbf{u}_i^{\text{PC}} \quad (3)$$

where η^k is the neuromodulator-specific learning rate, and weights are kept ≥ 0 .

On the one hand, the reward modulation, signed as \mathbf{W}^{DA} , is sensitive to the instantaneous presence of reward, defined as a boolean value. Over time, its coupling with the population vector \mathbf{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 \mathbf{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 for effectively planning routes to target locations.

At each moment during navigation, the weight matrices $\mathbf{W}^{\text{DA},\text{PC}}$, $\mathbf{W}^{\text{BND},\text{PC}}$ 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 1-e is shown the activity of the two neuromodulators over the fine-grained place cells map, showcasing the bounds of the environment and the reward location.

2.2.1 Online adaptation

For what concerns the resilience with respect to environmental changes, such as reward location, the model was endowed with a prediction-base mechanism

for correcting the accuracy of the internal representations. During navigation, before the execution of each movement towards a future location \mathbf{x}_{t+1} , it is computed and cached a prediction of the activity of neuromodulator k : $\hat{v}^k = \sum_i^N \mathbf{W}_i^{DA,PC} \cdot \hat{u}_i^{PC}$, where \hat{u}_i^{PC} is the predicted population activity at \mathbf{x}_{t+1} . Then, a prediction error with a specific learning rate is calculated and added to the weight update:

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

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 no longer reliably predicting the sensory experience referenced by the neuromodulator. This simple rule following the framework of predictive coding and temporal-difference learning [75]. Previous computational models have used neuromodulatory signals for controlling neuronal dynamics, applied to the learning process [63, 76] or as a feedback error [77]. Additionally, it alignes experimental evidence of the involvement of neuromodulation in the dynamic update of internal beliefs [78, 51, 79].

2.2.2 Modulation of place fields

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

The movement of the place centers occurred following a reward or collision event, and involved 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 φ is a Gaussian distance with width σ^k . Additionally, lateral inhibition was still accounted for, such to keep avoiding overlappings. This approach has been inspired by the BTSP rule [68, 37, 80], through which has been accounted the dislocation of of CA1 place cells following reward events (or an external step current), changing their associated spatial position.

Concerning the field resizing, it again takes place when its reference event occurred. 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 γ^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 the 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 the tasks of exploration and goal-directed navigation. To this end, we defined a simple hard-coded policy that toggles between these two behaviours according to the presence of a goal signal, externally provided, and the presence of an actual goal representation, taken care of by a special component called *reward seeking*, depicted in the pink box of plot 1-a. 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 random position within the map for improving exploration, and reaching the actual reward location. In practice, goal navigation is achieved by calculating the shortest path between the current position, identified by the most active place cells, and a target position, picked randomly or by considering the cells with the strongest dopaminergic weights, inspired by hippocampal replay and experimental observations [81, 82, 83]. The place cells are hence 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 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 exploiting the sparser and lighter map and only invokes the detailed one when necessary. In the process of behaviour, learning does not occur explicitly, but it is instead accounted for in the online formation of the cognitive map.

2.4 Naturalistic task

The evaluation of the model ability to construct and utilize 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 behaviour of animals who venture in new territories in the search of food. First there was an exploration phase, in which the agent was placed in a random location and let roam through a pseudo-random walk for 5000 time-steps. Then an exploitation phase began, in which a circle the 5% of the total area was designated to provide a binary reward $R \sim \mathcal{B}(p_r)$ drawn from a Bernoulli with probability p_r .

The optimization of the parameters of the model was carried out using the Covariance-Matrix Adaptation evolutionary strategy (CMA-ES) [84] 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 [85]. 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.

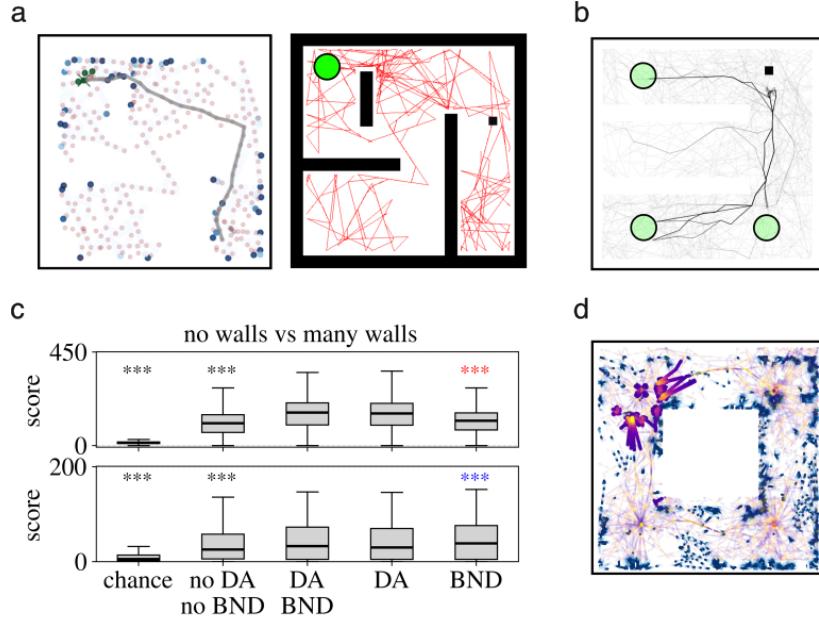


Figure 2: COGNITIVE MAPS AND PERFORMANCE RESULTS - **a:** the plot on the left represent a cognitive map over a space, together with the plan (grey line) to reach a target location from a starting position. The plot on the right is a view of the same environment but with highlighted walls (black thick 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 [24]. 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 [86]. 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* [16, 11] 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 [9, 19, 87]. Previous work followed a similar direction using recurrent networks, but required an extensive gradient-based training [88, 55, 72]. 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 [53]. 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 [63], 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 [51, 89] and explored in various computational approaches [90, 91, 92]. 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 [59], especially dopamine [35, 64, 67, 42].

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 [37, 93], in particular in terms of increased cells clustering [94, 95], reminiscent of firing rate changes following contextual shifts [96, 97].

Concerning the modulation of place fields, there is significant experimental evidence of their alternation during reward events [98, 99, 100], some reporting shrinking near rewarding objects [101], and boundaries [102]. The coupling with higher local density might be explained by a better optimization of cell distribution for goal representation and planning [77]. 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 [103, 104].

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 [105], as well as new neuromodulators encoding for different sensory dimensions or internally-generated signals.

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The authors declare no competing interests.

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5 Appendix

5.1 Spatial representations

5.2 Grid cell module

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 $v = \{v_x, v_y\}$. 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

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

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^{GC} , and its index is that of the first silent cell, which gets added to the forward weight matrix $\mathbf{W}_i^{GCtoPC} \rightarrow \mathbf{u}^{GC}$.

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 θ_{rep}^{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^{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 θ_{rec}^{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 α represents the activation threshold, or horizontal offset, while β the gain, or steepness. It is also defined an activity trace, which has an upper value of 1 and decay exponentially:

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

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.

	β	α	$\theta_{\text{rep}}^{\text{PC}}$	$\theta_{\text{rec}}^{\text{PC}}$	τ^{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 θ^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 $p_i = \mathbf{W}_i^k \hat{u}^{\text{PC}}$, 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:

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

where η^k , η_{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 σ^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 θ_{\min}^{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{W} of the nodes according to the neuromodulation map.

5.6 Evolutionary optimization

Algorithm 1 Modified Dijkstra algorithm

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
```