
Flexible navigation with neuromodulated cognitive maps

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1

Abstract

2 Animals naturally form personalized cognitive maps to support efficient
3 navigation and goal-directed behavior. In the brain, the CA1 subregion
4 of the hippocampus plays a key role in this process, hosting spatially
5 tuned neurons that adapt based on the behavioral context and internal
6 states. Computational models of this ability include labeled graphs
7 with locally specified spatial information, which avoid global metric
8 structure, and deep neural networks trained on spatial tasks that exhibit
9 emergent spatial tuning. However, these approaches often struggle to
10 model one-shot adaptive mapping and typically rely on plasticity rules
11 that lack biological plausibility.

12 We propose a neural architecture inspired by place-cell dynamics that
13 enables rapid on-the-fly construction of cognitive maps during explo-
14 ration of novel environments. The model relies on velocity inputs and
15 grid cell modules to generate spatial representations and integrates neu-
16 romodulatory signals responsive to boundaries and rewards. Learning
17 combines synaptic plasticity, lateral inhibition, and modulatory gating
18 of place-cell activity. For reward-driven navigation, the agent uses a
19 modified Dijkstra algorithm to plan paths on the emergent cognitive
20 map, treating place cells as nodes in a locally structured graph.

21 We compare our model with standard reinforcement learning (RL)
22 agents and find that it achieves significantly higher sample efficiency,
23 solving tasks in a single episode that RL agents require thousands of
24 training steps to master. This performance advantage arises from biolog-
25 ically inspired inductive biases embedded in the model architecture. In
26 simulation, the agent adapts to dynamic reward locations and changes in
27 the environment layout. Analysis of neuromodulated place cells reveals
28 task-dependent changes in tuning field size and spatial density, aligning
29 with experimental findings from hippocampal recordings. These results
30 highlight the promise of biologically grounded computation and locally
31 structured graph representations for flexible and data-efficient cognitive
32 mapping.

33

1 Introduction

34 Survival in complex environments demands efficient navigational strategies. From desert ants to
35 humans, successful wayfinding—navigating toward goals out of sight—relies on internal spatial
36 representations, or *cognitive maps* [1, 2]. These maps enable flexible planning and decision-making
37 beyond simple stimulus-response associations.

38 Cognitive map theories propose multiple strategies for spatial navigation, ranging from simple route
39 learning to survey-based and graph-based models. Route learning stores paths as action-
40 position pairs but struggles with scalability and generalization at intersections [3, 4, 5]. Survey maps,
41 grounded in Euclidean geometry, offer greater flexibility [4, 6] but sometimes contradict neural
42 and behavioral data showing geometric distortions and topological biases [7, 8, 9, 10]. Labeled
43 graphs strike a balance—encoding landmarks and transitions in a topological network that supports
44 vector-like operations, planning, and prediction [11, 12, 13].

45 Neural substrates of spatial representations reside in the hippocampus (HP) and entorhinal cortex
46 (EC), where specialized cells—including grid, border, speed, and place cells—encode geometric
47 and contextual variables [14, 15, 16]. Place cells, particularly in CA1, anchor cognitive maps [17],
48 integrating converging inputs from grid cells, CA3, and lateral EC [18, 19, 20, 21].

49 Neuromodulation plays a critical role in shaping this circuitry. Dopamine and other modulators
50 adjust synaptic strength, tune place fields, and encode novelty and reward-prediction errors [22,
51 23, 24]. These projections reshape spatial tuning [25, 26, 27, 28], support novelty detection [23],
52 and transmit prediction errors, particularly via lateral EC inputs [29, 30]. These mechanisms echo
53 principles of reinforcement learning (RL), highlighting the role of neuromodulation in adapting
54 spatial representations to behavioral relevance [31, 24].

55 Computational models have captured individual components of this system. Early work proposed that
56 the hippocampus encodes spatial position and direction [32], while topological models based on route
57 learning highlight scalability challenges [5]. More recent approaches draw from predictive coding and
58 reinforcement learning, including successor representations and the Tolman-Eichenbaum Machine,
59 which generalize across spatial and relational tasks while mimicking biological activity patterns
60 [33, 34, 35]. Path integration models trained on motion cues give rise to grid- and place-like tunings
61 [36, 37, 38]. Others incorporate reward-driven Hebbian plasticity modulated by neuromodulators
62 [39]. Yet, few architectures unify these ingredients into a biologically grounded system that learns
63 online and adapts flexibly to novelty.

64 In this work, we introduce a biologically inspired model of cognitive map formation that integrates
65 place cell representations, neuromodulatory signals, and graph-based spatial reasoning. The model
66 constructs a topological map online, linking place cells along experienced trajectories and enriching
67 them with scalar-valued modulatory signals. These modulators form analog fields across the map
68 [40], drive local Hebbian plasticity in response to sensory prediction errors [41, 31, 42], and help
69 maintain and adapt reward-based neural representations [43, 44, 45, 46, 34].

70 This architecture supports efficient goal-directed navigation without extensive offline training, lever-
71 aging spatial priors, online plasticity, and modulatory feedback. We demonstrate how this system
72 adapts to environmental changes and how neuromodulation influences place field allocation and
73 remapping [47, 48], linking cognitive flexibility to underlying physiological mechanisms.

74 The remainder of the paper is organized as follows: Section 2 details the model and experimental
75 setup; Section 3 presents results; Section 4 discusses broader implications and future directions.

76 2 Methods

77 Our model focuses on cognitive map formation through an agent’s experiences within a closed
78 environment, as illustrated in Figure 1a..

79 The architecture operates with minimal external information—just binary reward and collision signals.
80 Instead, spatial representation emerges primarily from idiothetic information: the agent’s perception
81 of self-motion [49]. Specifically, we use the factual velocity vector (the agent’s actual environmental
82 displacement) as the primary navigational cue, which in biological systems emerges from integrated
83 inertial and relative motion signals [50, 51].

84 **Place Cell Formation** Spatial representation begins with a stack of grid cell modules, each encoding
85 a periodic tiling of space over a 2D torus T^2 (Fig.1b,c). Grid cell activity vectors \mathbf{u}^{GC} project to two
86 place cell layers with initially zeroed weights. When no place cells activate for the current input,
87 a silent neuron is randomly selected and imprinted with the current activity. To ensure selectivity,
88 imprinting is aborted if the new weight vector overlaps too strongly (via cosine similarity) with
89 existing ones.

90 Each place cell's activation is given by a bounded activation function based on cosine similarity.
 91 Details of lateral inhibition and recurrent connectivity are given in Appendix A.1.

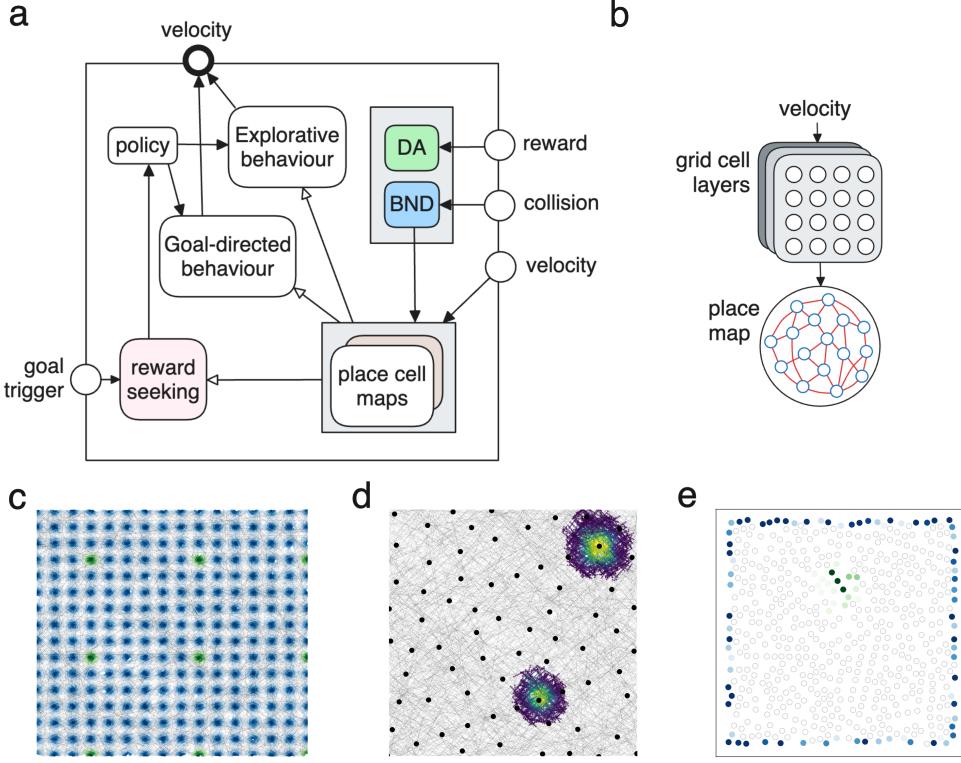


Figure 1: Model layout and spatial representations - a: the full architecture of the model, consisting of three main sensory input, targeting the two modulators and the cognitive map module, and the executive components, represented by a policy module, two behavioral programs and a reward receiver. **b:** the cognitive map component, organized with a stack of grid cell modules receiving the velocity input and projecting to the layer of place cells. **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.

92 **Neuromodulation** Neuromodulators encode environmental salience. Two scalar modulators, one
 93 for reward (DA) and one for boundary collisions (BND), are driven by binary inputs I and accumulate
 94 over time via exponential decay.

95 Each modulator k updates synaptic weights to place cells through Hebbian plasticity:

$$\Delta \mathbf{W}^k = \eta^k v^k \mathbf{u}^{PC}$$

96 Weight vectors are constrained to remain non-negative. Reward modulation tags cells near rewarded
 97 locations, while boundary modulation builds a representation of environmental edges. These scalar
 98 fields form the core of the cognitive map (Fig. 1e). See Appendix A.2 for full learning rules and
 99 parameter settings.

100 **Online Adaptation** To remain resilient to environmental changes (e.g., moving rewards), the
 101 model uses a predictive mechanism to correct outdated internal representations. Before executing a
 102 movement toward position \mathbf{x}_{t+1} , the system predicts the expected value \hat{v}^k of neuromodulator k at

103 that location. Then, a prediction error is computed and used to adjust the weights:

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

104 The prediction learning rate $\hat{\eta}^k < 1$ ensures that small errors are corrected gradually, while repeated
105 mismatches lead to weight depression. This mechanism implements a simple form of predictive cod-
106 ing and is inspired by temporal-difference learning [52], aligning with evidence that neuromodulatory
107 systems signal prediction errors and update beliefs [53, 34, 54].

108 **Modulation of Place Fields** We further tested whether neuromodulators could directly alter spatial
109 tuning. Place fields were dynamically shifted and resized based on recent salience signals.

110 Following a salient event (reward or collision), place field centers were displaced in grid cell space,
111 with magnitude scaled by the neuromodulator v^k and proximity to the event:

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

112 Here, φ_σ is a Gaussian function, and c^k a scaling factor. This rule is inspired by BTSP plasticity
113 [27, 47], which shifts CA1 place fields following salient experiences. Lateral inhibition prevents field
114 overlap during remapping.

115 In addition to dislocation, field size was modulated by scaling the gain of recently active neurons.
116 The gain β_i of each cell was adjusted via a trace variable m_i . This provides a mechanism for
117 neuromodulators to transiently enhance or suppress spatial sensitivity.

118 **Policy and Behavior** To evaluate the model’s utility in navigation, we implemented a simple policy
119 toggling between exploration and goal-seeking behavior, depending on an external goal flag and the
120 internal map.

121 Exploration consisted of a stochastic walk with persistence, plus periodic plans to visit random known
122 locations to avoid stagnation. Goal-directed navigation was triggered when a reward representation
123 was present and executed via shortest-path planning on the place cell graph.

124 The graph was defined by place cells as nodes and synaptic links as edges. The agent selected targets
125 either randomly or based on cells with high dopaminergic weight, echoing hippocampal replay and
126 value-based navigation [55, 56, 57]. Planning was achieved via Dijkstra’s algorithm with a cost
127 function that penalized proximity to boundaries.

Table 1: Comparison of neural network models for spatial navigation and representation

Model	Architecture	Training method	Ext. C.
Banino et al. [36]	LSTM + linear layers + CNN	BPTT and deep RL, supervised	Yes
Cueva et al. [38]	RNN + linear layers	Hessian-free algorithm with regularization	Yes
Sorcher et al. [58]	RNN + linear layers	Backpropagation with regularization	Yes
Whittington et al. [35]	Attractor network and deep networks	Backpropagation and Hebbian learning	No
de-Cothi et al. [34]	Successor representation	TD-learning + eligibility traces	Yes
Brozsko et al. [59]	Spike Response Model	Online modulated Hebbian plasticity	Yes
Ours	Rate layers	Online neuromodulated plasticity	No

Model	Task	Input	Output
Banino et al.	Path integration, goal navigation	Velocity, visual input, reward	PC, HDC
Cueva et al.	Path integration	Velocity	Position
Sorcher et al.	Path integration	Velocity	PC
Whittington et al.	Relational graph knowledge	Observation and action	Observation
de-Cothi et al.	Planned navigation	Observation	–
Brozsko et al.	Goal navigation	Position, reward	Action
Ours	Goal navigation	Velocity, reward, collision	Action

Note: PC = Place Cells, HDC = Head Direction Cells, Ext. C. = External Spatial Coordinates

128 **Comparison with previous architectures** Several previous computational models show structural
 129 and conceptual similarities with the present work. A prominent category among them employs deep
 130 neural networks—often with recurrent components—and relies on gradient-based learning strategies
 131 such as backpropagation through time. These models typically require multiple training episodes or
 132 large datasets for convergence. In contrast, our model adopts biologically inspired, synaptically local
 133 plasticity rules, and requires only a single training episode for adaptation.

134 Other models utilize spiking neurons [59] or explicit neural representations [34], and incorporate
 135 online learning rules more closely aligned with ours. These models also focus more directly on
 136 goal-directed navigation, in contrast to purely path integration tasks. However, both of these rely on
 137 external spatial coordinates to represent current position. Our model instead constructs an internal
 138 coordinate system by integrating its own velocity output, enabling endogenous spatial tracking.

139 **Naturalistic task** The model was evaluated on a biologically inspired navigation benchmark
 140 involving exploration and goal-seeking behavior in closed environments. Performance was measured
 141 as the total number of rewards collected over multiple trials.

142 Optimization of the model parameters was carried out using the evolutionary Covariance-Matrix
 143 Adaptation strategy (CMA-ES) [60] with a population of 128 individuals for 100 generations.

144 3 Results

145 **Performance in wayfinding** Our primary aim was to evaluate the formation of the cognitive map
 146 through neuromodulation in terms of the performance of the goal navigation in different environments.

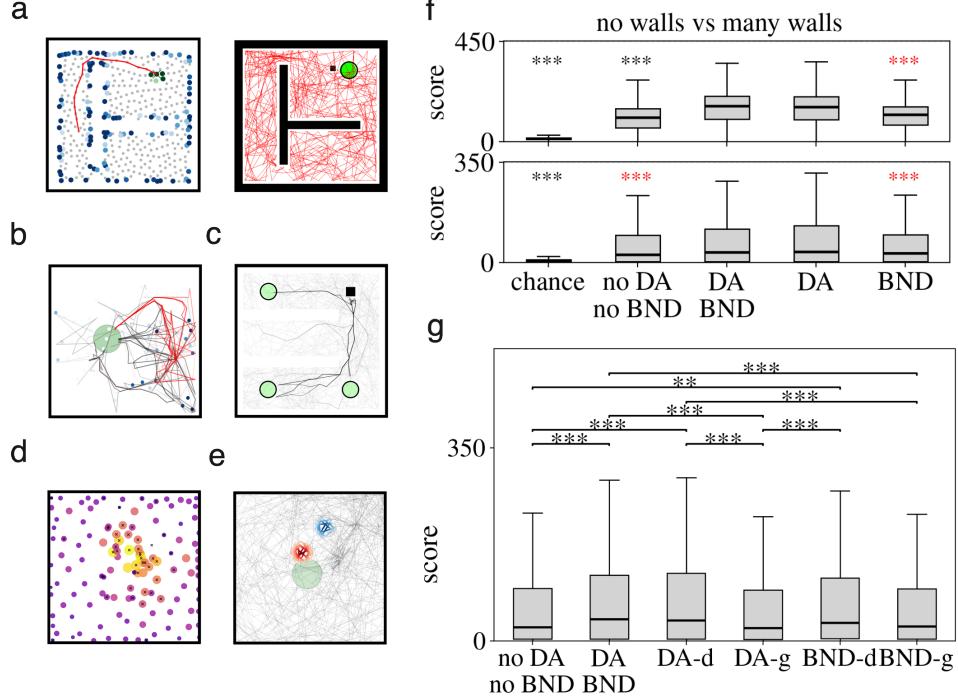


Figure 2: Cognitive maps and performance results - a: the plot on the left represent a cognitive map over a space, together with the plan (grey line) to reach a target location from a starting position. The plot on the right is a view of the same environment but with highlighted walls (black thick lines) the reward (green circle), trajectory (red line), agent position (black square). - **b:** plot of trajectories before (black) and after (red) the insertion of a wall between the starting and goal positions, the wall can be spotted from the boundary cells in blue - **c:** trajectories for multiple trials with the agent starting at the same position (black square) but with the reward location (green circles) periodically moving - **d:** place cells centers with size and color proportional to its node degree (number of neighbors); further, it notable is the correlation with the distance from the reward (in the center) - **e:** place fields of the same cell before and after several relocation of its center following reward events - **f:** 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. - **g:** ablation performance comparison similar to c, and over the same environment for model variants with different active modulatory mechanisms: no DA and BND place field modulation, full DA and BND, DA-d for PC density, DA-g activation gain, BND-d for PC density, BND-g for activation gain.

147 The best model resulting from evolution reached solid navigation and adaptation skills. The agent
 148 was able to visit a significant portion of the environment during exploration and use neuromodulation
 149 to produce useful spatial representations.

150 The left panel of plot 2a displays place cells associated with collisions and reward events, signaling
 151 boundaries (in blue) and reward (in green) locations. The overlap of these two representations and
 152 the place cells (in pink) is what we refer to as a cognitive map, since these are the main sources of
 153 spatial and contextual information used during planned navigation, whose path is depicted as a gray
 154 line. The right panel instead portrays the actual environment with walls (black), reward location
 155 (green), and multiple trajectories (red). During exploration, the main areas were visited until the
 156 reward position was located and the goal-directed navigation dominated, as highlighted by the density
 157 of the path lines. Considering the position of the walls and corners, the layout of this environment
 158 does not always make the target locations visible, as it is a non-convex area and therefore can be
 159 classified as wayfinding [61]. The challenge of not being able to use straight lines is overcome by the
 160 graph approach using local data and the consideration of boundary place cells, allowing the agent to

161 plan accordingly. In addition, by construction the path also minimized the length of the path, within
162 the part of the space covered by the cognitive map.

163 In general, this result confirms the ability of the model to focus on navigation and obstacle avoidance.
164 However, it is worth nothing that not all simulations resulted in a reward being found in the first place,
165 due to the randomness of the exploratory process; this was more pronounced in complex environment.

166 **Detour task** The planning ability and the plastic nature of the cognitive map should provide re-
167 silience against unexpected changes in the environment layout. In order to verify this we implemented
168 a detour experiment. Initially, the agent was familiarized with a square environment with the reward
169 in the middle and starting always from the same position. Then, a wall was placed in between the
170 starting position and the reward, therefore forcing new trajectory for reaching it. As expected, the
171 agent was able to form a representation of the new obstacle and calculating new paths around it,
172 succeeding the task. In plot 2b they are shown the trajectories before and after the wall placement,
173 and it is manifested the ability of detour in the new layout.

174 **Adaptive goal representation through prediction error** Then, we tested the adaptability to
175 environmental changes. In this scenario, the reward object was moved after being fetched a fixed
176 number of times. Here, the difficulty was to unlearning previous locations and discovering new ones,
177 in a protocol similar to [39]. In plot 2c is reported the set of trajectories over many trials with the
178 reward displaced in three possible locations. The agent was capable of planning behavior, as earlier,
179 but also exploring and finding the new rewards, as shown by the density of lines. Whenever a goal
180 path resulted in a failed prediction, the DA-based sensory error weakened the association between the
181 place cells and the reward signal, leading to an extinction of its representation at that location.

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

184 **Modulation of spatial resolution affects performance** Lastly, we investigated the effect of
185 modulating the density of place cells and the size of the field. The goal position was fixed, but the
186 agent was randomly relocated after fetching; performance was defined as the total number of reward
187 counts within a time window.

188 Our working hypothesis is that these experience-driven neuronal changes would improve the quality
189 of the cognitive map and be reflected in navigational abilities. The assessment of this claim was
190 conducted by comparing variants of the model, obtained by progressively ablating the reward (DA)
191 and collision (BND) modulation of density and field size, but a cognitive map was still possible as
192 their representations of goals and boundaries were preserved. We also defined a chance level by
193 instead blocking all modulation-based plasticity and allowing only place cells to form. All models
194 were run in two different environments differing by number of internal walls, in total 2048 simulations
195 were done for each case.

196 Plot 2d showcases the distribution of place cells with the circle size and color represent the node
197 degree, which aligns discretely with the reward position and the density. Further, in plot 2e the
198 place field of one cell is shown, before and after several reward occurrences and consequent center
199 relocation.

200 The statistical results are shown in plot 2f. The top reports the scores in the setting without internal
201 walls. All models performed above chance, but the main finding is the affirmation of the importance
202 of neuronal modulation, as revealed by the statistical difference between those endowed with it and
203 the one not. Furthermore, possession of DA modulation resulted in a significantly higher score than
204 BND modulation alone (red stars). In fact, in a situation with a convex region such as this, once the
205 reward has been located, the boundary information has limited utility.

206 A similar pattern emerged when more internal walls were introduced, as shown by the results at the
207 bottom. In this environment, scores were overall lower as navigation became more difficult, and
208 the difference among groups thinner, although noticeable. Here, the sole presence of the boundary
209 modulation of place cells did not result in better performance than the baseline. This outcome
210 highlights how the main improvements are brought by reward-driven neuronal modulation (DA).

211 Then, in order to enquiry which particular modulatory action was mostly relevant, we conducted a
212 similar test on the same environment but ablating not only specific neuromodulators, but also whether

213 they affected the place cells density or the activation gain parameter. In plot 2g are reported the
214 comparisons among different variants. The general trend matched the previous results 2c, in that DA
215 is the best neuromodulator in terms of correlation with performance. The additional finding was that
216 density modulation is significantly the primary action behind the behavioural improvements, and
217 alone does not perform worse than the model with all actions together.

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

220 4 Discussion

221 Exploration and planning in the known and past environment are essential behaviors of animals,
222 directly affecting their success in world understanding and goal reaching.

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

227 The contribution of the present work was to propose a rate network model, inspired by the CA1
228 hippocampal region [17]. We used grid cells together with synaptic plasticity as a mechanism to
229 develop information-rich representations based on place cells updated through experience, grouped
230 with common perspectives on cognitive maps [62]. In the spirit of minimizing the geometric
231 assumptions in the neural space, we treated the generated place network as a topological graph, with
232 sensory information added locally through the action of neuromodulators. This idea aligned with the
233 concept of a *labeled graph* [63, 8], however, it is also true that no metric violations were possible in
234 these settings.

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

240 The simulation results validated the model, showing the expected emergence of cognitive maps and
241 their encoding of information collected during the experience. The online nature of the formation
242 of the locations on the map aligns with the idea of using only idiothetic velocity input, as in path
243 integration [6, 64, 65]. Previous work followed a similar direction using recurrent networks, but
244 required extensive gradient-based training [58, 38, 51]. Another important difference is that our
245 resulting neural network was composed solely of place cells, although neuromodulated, and no other
246 types of neuron were present. This distinction is justified by the partially different task structure, which
247 did not involve supervised learning and did not receive visual information as in [36]. Furthermore,
248 our model relied on predefined grid cells layers, which constituted a strong and sufficient inductive
249 bias, and did not have to be learned from scratch.

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

256 Adaptability was tested by occasionally moving the reward position, leading to the generation of
257 an internal prediction error that was used to update its representation on the map. The agent was
258 proved capable of unlearning previous associations, returning to exploration, and memorizing new
259 reward locations. This behavioral protocol is similar to previous work [59], in which dopaminergic
260 and cholinergic activity was utilized within a Hebbian plasticity rule to strengthen or weaken reward-
261 associated spatial representations. However, alternatively to exploiting neuromodulators with opposite
262 valence, we followed a predictive coding framework, a direction linked to hippocampal representations
263 [34, 66] and explored various computational approaches [67, 68, 69]. This choice departed from our
264 focus on using operations on the cognitive map itself by simulating future sensory experiences and

265 learning from feedback. In fact, neuromodulation has been long associated with this functionality
266 [40], especially dopamine [25, 43, 46, 31].

267 Lastly, the hypothesis of the relevance of the active modulation of the neuronal properties of place
268 cells was corroborated by simulating ablation experiments. These tests reported a significant impact
269 of altering the place cells density on the total count of collected rewards. In general, these results are
270 consistent with the experimental observations of alteration of place cells following reward events
271 [27, 70], in particular in terms of increased clustering of cells [71, 72], reminiscent of changes in
272 firing rate after contextual changes [73, 74].

273 Concerning the modulation of place fields, there is significant experimental evidence of their alter-
274 nation during reward events [75, 76, 77], some reporting shrinkage near reward objects [78], and
275 boundaries [?]. The coupling with higher local density could be explained by better optimization of
276 the cell distribution for goal representation and planning [79]. However, in our settings, the fields
277 become enlarged, especially in the direction of the target, although the performance improvements
278 were not tested significantly. A possible explanation can be the simplicity of our reward, which was
279 solely defined as an area of space. The lack of rich non-spatial features thus did not require the place
280 cells to code for smaller spatial variation. Therefore, enlargement might have improved the stability
281 of the representation, marking the nodes associated with rewards more solidly, given the stochas-
282 ticity of its delivery. Further, the graph-path algorithm utilized the strength of the DA-modulated
283 connections for determining the goal representation; stronger fields inherently developed stronger
284 weights, making planning more reliable. Although these findings are limited within the limits of our
285 simulation protocol, there have been experimental observations of elongation of place fields along
286 trajectories over meaningful experiences [80, 81].

287 In conclusion, this work showed a possible architecture for coupling emergent spatial representations
288 with neuromodulated plasticity to achieve an experience-driven cognitive map. The reliance on a few
289 spatial and algorithmic inductive biases, grid cells, and a planning algorithm supports the idea of a
290 label graph for goal navigation. Future work can investigate the application to other spatial domains,
291 such as motor control and three-dimensional navigation. In addition, a richer input feature can be
292 added, such as visual information [82], as well as new neuromodulators that encode different sensory
293 dimensions or internally generated signals.

294
295

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528 5 Appendix

529 5.1 Grid cell module

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

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

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

542 A grid cell module l of size N^{gc} is identified by a set of positions defined over a square centered
 543 on 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
 544 space has boundary conditions for each dimension, such that, for instance, when $x_t + s_l^{gc} \cdot v_x > 2$
 545 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
 546 velocity in the local space of the module l with respect to the real global agent velocity $\mathbf{v} = \{v_x, v_y\}$.
 547 When the module is initialized, the starting positions of its cells are uniformly distributed over the
 548 square forming a lattice. When the agent is reset in a new position at the beginning of new trial, a
 549 displacement vector is applied to the last cells positions such that the mapping between the module
 550 local space and the global environment is preserved.

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

$$553 r_i = \exp\left(-\frac{x_i^2 + y_i^2}{\sigma_i^{gc}}\right), \text{ where } \sigma_i^{gc} \text{ is the width of the tuning curve for module } i.$$

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

556
 557 In our model, each grid cell had a tuning width of 0.04. They were defined as 8 modules of size 36,
 558 and the relative speed scales were
 559 $\{1., 0.8, 0.7, 0.5, 0.4, 0.3, 0.2, 0.1, 0.07\}$.

560 5.2 Place cells

561 **Tuning formation** The tuning of a new place cell is simply defined as the current GC population
 562 vector \mathbf{u}_i^{PC} , and its index is that of the first silent cell, which is added to the forward weight matrix
 563 $\mathbf{W}_i^{GCToPC} \leftarrow \mathbf{u}^{GC}$.

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

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

572 **Activity** The current firing rate of the PC population is determined by the cosine similarity between
 573 the GC input and the forward weight matrix, then passed through a generalized sigmoid $\phi(z) =$
 574 $[1 + \exp(-\beta(z - \alpha))]^{-1}$. The parameter α represents the activation threshold, or horizontal offset,
 575 while β the gain, or steepness.

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

576 It is also defined as an activity trace, which has an upper value of 1 and decays exponentially:

$$m_i = -m_i/\tau^{PC} + u_i$$

577 It is used as a proxy for a memory trace.

578
 579 In the model, a PC population is defined by its average place field size, determining the granularity of
 580 the representation of the place.

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

	β	α	θ_{rep}^{PC}	θ_{rec}^{PC}	τ^{PC}
pc	33.0	1.0	0.86	43	140

Table 2: PC layer parameters

582 5.3 Modulation

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

$$\begin{aligned} v_k &= -v_k/\tau_k + x_k \\ v_k &= \max(v_k, 0) \end{aligned} \tag{1}$$

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

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

592 The full connection update then becomes:

$$\Delta \mathbf{W}_i^k = \eta^k v_i^k \mathbf{u}_i^{\text{PC}} - \eta_{\text{pred}}^k (\hat{v}_i^k - v_i^k) \mathbf{u}^{\text{PC}}$$

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

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

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

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

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

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

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

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

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

609 5.4 Decision making

610 Behaviour selection logic

611 The possible behaviours are *exploration* and *exploitation*, and an action is defined as a 2D velocity
 612 vector. For exploration, an action can be generated either as random navigation, using a polar vector
 613 of fixed magnitude (the speed) and angle sampled from a uniform distribution, or as a step within
 614 a goal-directed navigation plan to reach a random destination, which corresponds to a randomly
 615 sampled existing place cells. In the goal-directed navigation the magnitude of the velocity vector
 616 is less or equal than a fixed speed value, depending on the distance from the next target position in
 617 the plan. Instead, for the exploitation behaviour, the action is a step within a goal-directed navigation
 618 towards the reward location. The behaviour selection process depends on the experience of collision,
 619 the presence of a plan, and the success in the navigation planning. A diagram of this logic is reported
 620 in Figure 3.

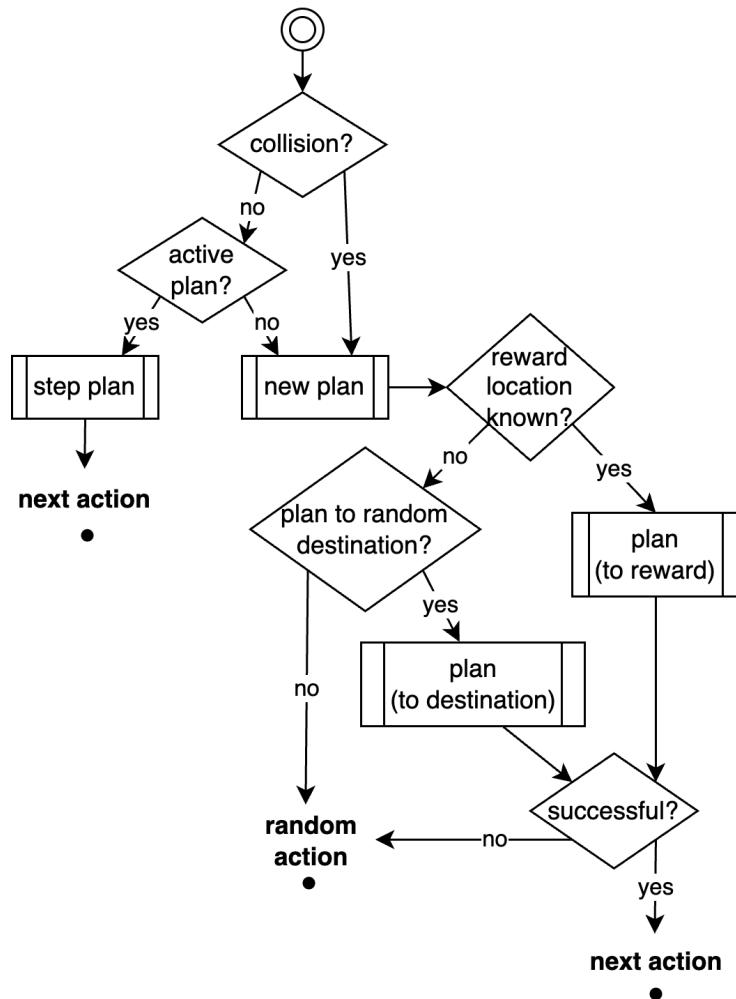


Figure 3: Diagram of the behaviour selection process

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 $\tilde{\mathbf{W}} \in \mathbb{R}^{N^{PC}}$, 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  $\tilde{\mathbf{W}}[i] < -1000$  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                                                  $\triangleright$  No path exists
33:   return  $\emptyset$ 
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

```

623 The planning of a new route is implemented as a modified Dijkstra algorithm over the place cell
 624 graph, provided as connectivity matrix C. Its particularity is the use of a weighting $\tilde{\mathbf{W}}$ of the nodes
 625 according to the neuromodulation map. A description is reported in algorithm 5.4.

626 **5.5 Environments**

627 The game in which test the model has been developed with the python library Pygame, used under
 628 license GNU LGPL version 2.1 and available at <https://github.com/pygame/pygame>. The
 629 environment layout consisting in a customizable arrangement of vertical and horizontal hard walls
 630 with variable length and fixed width. Below in Figure 4 some samples are shown.

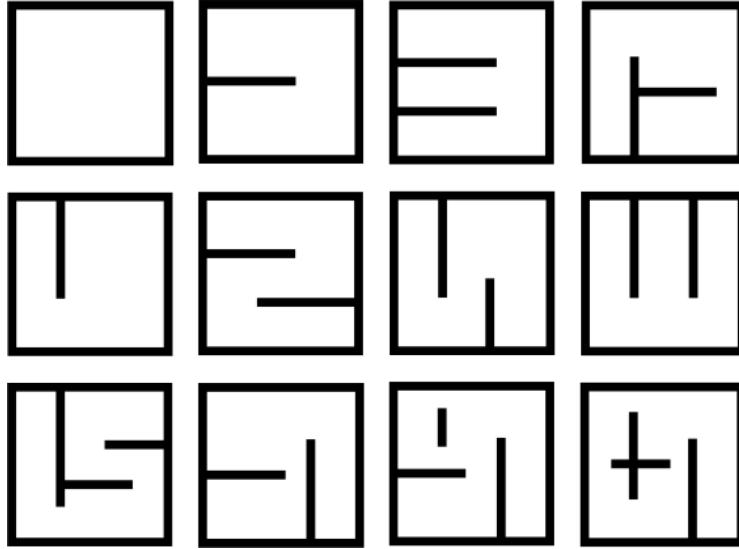


Figure 4: Sample of generated environments

631 The reward object is defined as a circle with size the 5% of the total environment area. When the
 632 agent position is within its boundary, it is provided a binary signal $R \sim \mathcal{B}(p_r)$ drawn from a Bernoulli
 633 with probability $p_r = 0.6$. The duration of the reward fetching is set to 2 time steps.

634 The agent object is defined as a square with size the 3.3% of the total environment area.

635 The testing protocol was inspired by the behavior of animals that venture into new territories in search
 636 of food. It was divided into two parts:

- 637 • **exploration phase:** the agent was placed in a random location within the environment for
 638 10'000 time steps. In this phase the reward is not present. Further, in order to force greater
 639 exploration of the environment, every 3'000 steps it was teleported to another random
 640 location. This external intervention was meant to mitigate the randomness in the exploratory
 641 behavioural strategy of the agent.
- 642 • **reward phase:** a reward is insert in a random location, and it is available to be discovered.
 643 When it is encountered, the agent is teleported to a random location within the environement,
 644 and after a fixed about 100 time step it is enabled its reward-seeking behaviour, in the form
 645 of goal-directed navigation. The total duration of this phase is set to 20'000 time steps.

646 An episode is defined as a continuous trajectory during the reward phase, namely a set of time steps
 647 starting from when the agent is place in a position until either it finds the reward or the simulation
 648 ends.

649 **Detour experiment** The protocol is modified such that after a fixed number of episodes the layout
 650 of the environment is changed, *e.g.* a wall is inserted. This experiment is meant to test the ability
 651 to reach the reward location by using the same cognitive map, and possibly update it with the new
 652 sensory information, such as the detection of the new boundaries.

653 **Changing reward experiment** During the reward phase, the reward location is changed after a
 654 fixed number of fetches.

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