
Flexible navigation with neuromodulated cognitive maps

Anonymous Author(s)

Affiliation

Address

email

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Abstract

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

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

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We tested the model on different environments, achieving high sample efficiency and solving tasks in a single episode, for which usual RL agents require thousands of training steps. This performance advantage arises from biologically inspired inductive biases embedded in the model architecture. In simulation, the agent adapts to dynamic reward locations and changes in the environment layout. Ablation experiments and analysis of neuromodulated place cells reveals task-dependent changes in tuning field size and spatial density, aligning with experimental findings from hippocampal recordings. These results highlight the promise of biologically grounded computation and locally structured graph representations for flexible and data-efficient cognitive mapping.

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1 Introduction

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Survival in complex environments requires efficient navigational strategies. From desert ants to humans, successful wayfinding—navigating toward goals that are not directly visible depends on emergent internal spatial representations, known as cognitive maps [1, 2]. Understanding how these maps are constructed from ongoing experiences, and how they can be exploited for flexible goal-directed navigation remains an active area of research in both neuroscience and reinforcement learning (RL).

39 The hippocampus (HP) and entorhinal cortex (EC) serve as the primary neural substrates for spatial
40 representation in the brain. They containing specialized neurons that encode spatial and contextual
41 information—including grid, border, speed, and place cells [3, 4, 5]. Place cells in the CA1 region
42 have attracted particular interest due to their convergence of inputs from periodically tuned grid
43 cells, the CA3 region, and the lateral EC [6, 7, 8, 9]. This strategic integration of diverse spatial and
44 contextual signals suggest CA1 place cells may play a critical role in the formation and maintenance
45 of cognitive maps [10].

46 Another important component are neuromodulators. Their actions include modulation of neuronal
47 dynamics, for instance adjusting the synaptic strength, tuning place fields [11, 12, 13]. Further,
48 neuromodulators such as dopamine transmit reward signals reshaping place cell tuning [14, 15, 16, 17],
49 support novelty detection [12], and encode prediction errors [18, 13], particularly via LEC inputs
50 [19, 20]—mechanisms closely related to reinforcement learning principles.

51 Traditional cognitive map theories propose multiple strategies for spatial navigation based on map-like
52 representations. Route learning encodes paths as sequences of action–position pairs, but it limited
53 in scalability and generalization, especially at route intersections [21, 22, 23]. In contrast, survey
54 maps, which rely on Euclidean geometry, offer greater flexibility [22, 24]; however, their strong
55 geometric assumptions often conflict with neural and behavioral evidence pointing to geometric
56 distortions and topological biases in spatial neural representations [25, 26, 27, 28]. As a middle
57 ground, labeled graphs encode landmarks and transitions within a topological network, enabling
58 vector-like operations, planning, and prediction [29, 30, 31].

59 Computational models have captured some of these aspects individually, showing new ways the
60 brain might use for addressing spatial navigation tasks. Early work proposed that the hippocampus
61 encodes spatial position and direction [32], while topological models based on route learning highlight
62 scalability challenges [23]. More recent approaches draw inspiration from predictive coding and
63 reinforcement learning, including successor representations and the Tolman-Eichenbaum Machine,
64 which generalize across spatial and relational tasks while mimicking biological neural activity patterns
65 [33, 34, 35]. Path integration models trained on velocity inputs give rise to spatial-like receptive fields
66 [36, 37, 38]. Others incorporate reward-driven Hebbian plasticity modulated by neuromodulators
67 [39]. Yet, none of these architectures unify these ingredients into a biologically grounded system that
68 at the same time learns a map of the environment online without relying on an external coordinate
69 system, and flexibility perform goal-directed navigation.

70 In this work, we present a biologically inspired model of cognitive map formation that integrates place
71 cell representations, neuromodulatory signals, and graph-based spatial computations. Our aim is to
72 demonstrate an architecture capable of building a content-rich topological map of the environment on
73 the fly, and leveraging it for efficient, goal-directed navigation—without requiring offline training.

74 Critically, neuromodulators play a central role, as they form analog fields over the map [40], drive
75 local Hebbian plasticity in response to sensory updates [41, 18, 42], and support the formation and
76 adaptation of reward-modulated neural representations used for planning [43, 44, 45, 46, 34]. We
77 show how this system dynamically adapts to environmental changes and how neuromodulation shapes
78 place field allocation and remapping [47, 48], linking cognitive flexibility to underlying physiological
79 mechanisms.

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

82 **2 Methods**

83 We propose a model of cognitive map formation driven by an agent’s experience within a closed
84 environment.

85 The architecture operates with minimal external inputs—limited to binary reward and collision
86 signals—as illustrated in Figure 1a. Instead of relying on exteroceptive cues, spatial representations
87 emerge from idiothetic information, i.e., the agent’s internal perception of self-motion [49], consistent
88 with prior path integration frameworks. Concretely, we use the agent’s ground-truth velocity vector
89 (its actual displacement within the environment) as the primary navigational signal, reflecting the
90 integration of inertial and proprioceptive cues observed in biological systems [50, 51]. Since no
91 visual information is used, the agent is effectively navigating in the dark.

92 **Place Cell Formation** The primary spatial representation is formed by a set of grid cell modules,
 93 each encoding a periodic tiling of 2D space, which directly maps to a toroidal manifold \mathbb{T}^2 (Fig.
 94 1c,d). Departing from traditional grid cell modeling approaches [52, 53], we generate population
 95 activity directly via Gaussian tuning over the torus, continuously updated using the agent's velocity
 96 vector—an approach validated in prior work [8].

97 The grid cell population vector \mathbf{u}^{GC} is forwarded to a place cell network with initially zeroed synaptic
 98 weights (Fig. 1b). When no place cell is sufficiently active for a given input, a silent unit is randomly
 99 selected and imprinted with the current activity pattern. To enforce representational sparsity and
 100 tuning specificity, lateral inhibition is implemented by comparing the cosine similarity between the
 101 new weight vector and any existing one and a threshold θ_{inh}^{PC} .

102 Each place cell's activation is computed via a bounded cosine similarity function, determining its
 103 corresponding place field (Fig. 1e). Further implementation details, including lateral inhibition and
 104 recurrent connectivity, are provided in the Appendix.

105 **a:** a module of grid cells defined in a bounded square space of length 1, and an activity representation
 106 of their receptive field over a torus

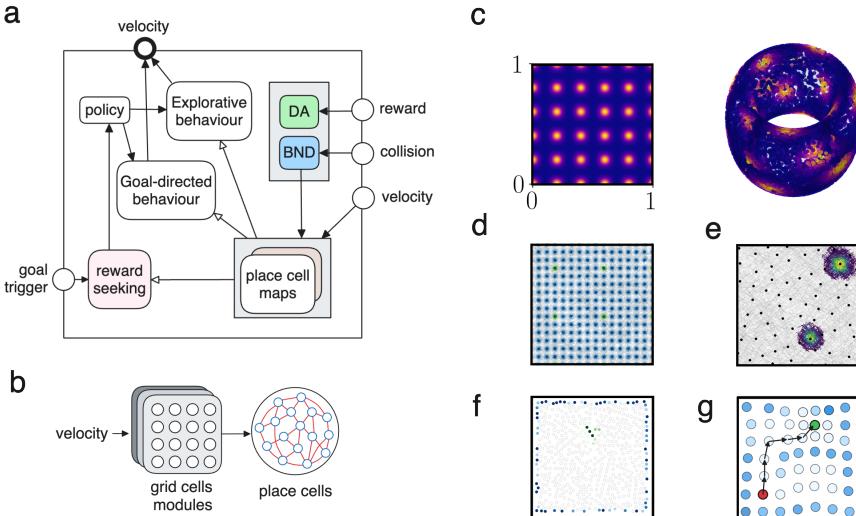


Figure 1: **Model layout and spatial representations** - **a:** the full architecture of the model, consisting of three main sensory input, targeting the two modulators and the cognitive map module, and the executive components, represented by a policy module, two behavioral programs and a reward receiver. **b:** a module of grid cells defined in a bounded square space of length 1, and an activity representation of their receptive field over a torus. **c:** the cognitive map component, organized with a stack of grid cell modules receiving the velocity input and projecting to the layer of place cells. **d:** 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. **e:** the distribution in space of the place cells centers, together with the activity of two cells showing the size of their place field. **f:** 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. **g:** the place cells layer can be regarded as a graph with values assigned to each node according to the modulation strength; a path-finding algorithm can then be used to connect any two nodes taking into account the node values.

107 **Neuromodulation** Neuromodulators deliver event signals: rewards, denoted DA (for dopamine),
 108 and boundary collisions, denoted BND. They are driven by binary inputs and are defined through a
 109 leaky variable with exponential decay.

110 To remain resilient to environmental changes (e.g., moving rewards), the model uses a predictive
 111 mechanism to correct keep internal representations updated. Each modulator k updates synaptic
 112 weights to place cells through Hebbian plasticity:

$$\Delta \mathbf{W}^k = \eta^k \mathbf{u}^{\text{PC}} \left(\mathbf{v}^k - \mathbf{W}^k \right) \quad (1)$$

113 The term in brackets can be regarded as an error, implementing a simple form of predictive coding
 114 and is inspired by temporal-difference learning [54], aligning with evidence that neuromodulatory
 115 systems signal prediction errors and update beliefs [55, 34, 56].

116 Weight vectors are constrained to remain non-negative. Reward modulation tags cells near rewarded
 117 locations, while boundary modulation builds a representation of environmental edges. These scalar
 118 fields form the core of the cognitive map (Fig. 1f). See Appendix for full learning rules and parameter
 119 settings.

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

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

$$\Delta \mathbf{W}_i^{\text{GC,PC}} = c^k v^k \varphi_{\sigma^k} (\mathbf{u}^{\text{GC}} - \mathbf{W}_i^{\text{GC,PC}}) \quad (2)$$

124 Here, φ_{σ} is a Gaussian function, and c^k a scaling factor. This rule is inspired by BTSP plasticity
 125 [16, 47], which shifts CA1 place fields following salient experiences. Lateral inhibition prevents field
 126 overlap during remapping.

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

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

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

136 The graph was defined by place cells as nodes and synaptic links as edges. The agent selected targets
 137 either randomly or based on cells with high dopaminergic weight, echoing hippocampal replay and
 138 value-based navigation [57, 58, 59]. Planning was achieved via Dijkstra’s algorithm with a cost
 139 function that penalized proximity to boundaries, as illustrated in plot 1g.

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. [60]	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. [61]	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

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

146 Other models utilize spiking neurons [61] or explicit neural representations [34], and incorporate
 147 online learning rules more closely aligned with ours. These models also focus more directly on
 148 goal-directed navigation, in contrast to purely path integration tasks. However, both of these rely on
 149 external spatial coordinates to represent current position. Our model instead constructs an internal
 150 coordinate system by integrating its own velocity output, enabling endogenous spatial tracking.

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

154 Optimization of the model parameters was carried out using the evolutionary Covariance-Matrix
 155 Adaptation strategy (CMA-ES) [62] with a population of 128 individuals for 100 generations.

156 3 Results

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

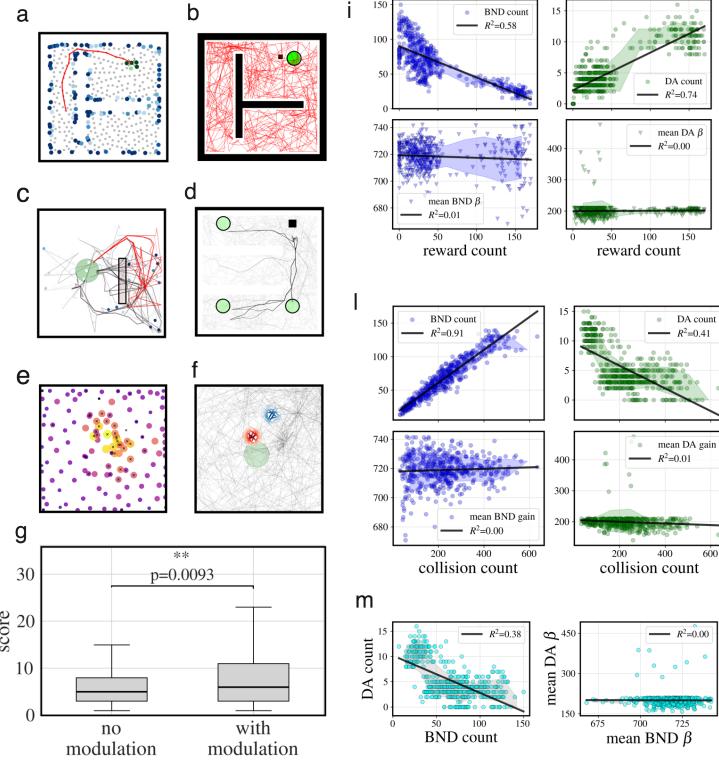


Figure 2: Cognitive maps and performance results - **a:** a cognitive map over a space, together with the plan (red line) to reach a target location from a starting position.. **b:** the same environment but with the reward (green circle), trajectory (red line), agent position (black square). - **c:** plot of trajectories before (black) and after (red) the insertion of a wall (rectangle) between the starting and goal positions, the wall can also be spotted from the boundary cells in blue - **d:** trajectories for multiple trials with the agent starting at the same position (black square) but with the reward location (green circles) periodically moving - **e:** place cells centers with size proportional to their node degree - **f:** place fields of the same cell before and after several relocation of its center following reward events - **g:** performance comparison for the same models on the same environment with and without modulation enabled. Pair-wise t-test over 128 iterations and Bonferroni correction - **i:** effect of reward count on reward and boundary modulated cells (green and blue respectively), both in count (top row) and gain modulation magnitude (bottom row). - **l:** same but with respect to collision count - **m:** relation between count of reward and boundary modulated cells, and between gain modulation magnitude

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

162 The left panel of plot 2a displays place cells associated with collisions and reward events, signaling
 163 boundaries (in blue) and reward (in green) locations. The overlap of these two representations and
 164 the place cells (in pink) is what we refer to as a cognitive map, since these are the main sources of
 165 spatial and contextual information used during planned navigation, whose path is depicted as a gray
 166 line. The right panel instead portrays the actual environment with walls (black), reward location
 167 (green), and multiple trajectories (red). During exploration, the main areas were visited until the
 168 reward position was located and the goal-directed navigation dominated, as highlighted by the density
 169 of the path lines. Considering the position of the walls and corners, the layout of this environment
 170 does not always make the target locations visible, as it is a non-convex area and therefore can be
 171 classified as wayfinding [63]. The challenge of not being able to use straight lines is overcome by the
 172 graph approach using local data and the consideration of boundary place cells, allowing the agent to
 173 plan accordingly. In addition, by construction the path also minimized the length of the path, within
 174 the part of the space covered by the cognitive map.

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

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

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

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

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

200 Our working hypothesis is that these experience-driven neuronal changes would improve the quality
201 of the cognitive map and be reflected in navigational abilities. The assessment of this claim was
202 conducted by comparing two variants of the model: with or without the modulation mechanisms,
203 namely the density and gain modulation from reward and collision events.. Both models were ran in
204 the same environment, with numerous wall, for a total of 128 simulations for each case.

205 The statistical results shown in the box plot of Figure 2g demonstrate a significant difference between
206 the two groups, supporting the important of place field modulation.

207 Plot 2e showcases the distribution of place cells with the circle size and color represent the node
208 degree, which aligns discretely with the reward position and the density. Further, in plot 2f the
209 place field of one cell is shown, before and after several reward occurences and consequent center
210 relocation.

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

213 4 Discussion

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

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

220 The contribution of the present work was to propose a rate network model, inspired by the CA1
221 hippocampal region [10]. We used grid cells together with synaptic plasticity as a mechanism to
222 develop information-rich representations based on place cells updated through experience, grouped
223 with common perspectives on cognitive maps [64]. In the spirit of minimizing the geometric
224 assumptions in the neural space, we treated the generated place network as a topological graph, with

225 sensory information added locally through the action of neuromodulators. This idea aligned with the
226 concept of a *labeled graph* [65, 26], however, it is also true that no metric violations were possible in
227 these settings.

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

233 The simulation results validated the model, showing the expected emergence of cognitive maps and
234 their encoding of information collected during the experience. The online nature of the formation
235 of the locations on the map aligns with the idea of using only idiothetic velocity input, as in path
236 integration [24, 66, 67]. Previous work followed a similar direction using recurrent networks, but
237 required extensive gradient-based training [60, 38, 51]. Another important difference is that our
238 resulting neural network was composed solely of place cells, although neuromodulated, and no other
239 types of neuron were present. This distinction is justified by the partially different task structure, which
240 did not involve supervised learning and did not receive visual information as in [36]. Furthermore,
241 our model relied on predefined grid cells layers, which constituted a strong and sufficient inductive
242 bias, and did not have to be learned from scratch.

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

249 Adaptability was tested by occasionally moving the reward position, leading to the generation of
250 an internal prediction error that was used to update its representation on the map. The agent was
251 proved capable of unlearning previous associations, returning to exploration, and memorizing new
252 reward locations. This behavioral protocol is similar to previous work [61], in which dopaminergic
253 and cholinergic activity was utilized within a Hebbian plasticity rule to strengthen or weaken reward-
254 associated spatial representations. However, alternatively to exploiting neuromodulators with opposite
255 valence, we followed a predictive coding framework, a direction linked to hippocampal representations
256 [34, 68] and explored various computational approaches [69, 70, 71]. This choice departed from our
257 focus on using operations on the cognitive map itself by simulating future sensory experiences and
258 learning from feedback. In fact, neuromodulation has been long associated with this functionality
259 [40], especially dopamine [14, 43, 46, 18].

260 Lastly, the hypothesis of the relevance of the active modulation of the neuronal properties of place
261 cells was corroborated by simulating ablation experiments. These tests reported a significant impact
262 of altering the place cells density on the total count of collected rewards. In general, these results are
263 consistent with the experimental observations of alteration of place cells following reward events
264 [16, 72], in particular in terms of increased clustering of cells [73, 74], reminiscent of changes in
265 firing rate after contextual changes [75, 76].

266 Concerning the modulation of place fields, there is significant experimental evidence of their alter-
267 nation during reward events [77, 78, 79], some reporting shrinkage near reward objects [80], and
268 boundaries [81]. The coupling with higher local density could be explained by better optimization of
269 the cell distribution for goal representation and planning [82]. However, in our settings, the fields
270 become enlarged, especially in the direction of the target, although the performance improvements
271 were not tested significantly. A possible explanation can be the simplicity of our reward, which was
272 solely defined as an area of space. The lack of rich non-spatial features thus did not require the place
273 cells to code for smaller spatial variation. Therefore, enlargement might have improved the stability
274 of the representation, marking the nodes associated with rewards more solidly, given the stochas-
275 ticity of its delivery. Further, the graph-path algorithm utilized the strength of the DA-modulated
276 connections for determining the goal representation; stronger fields inherently developed stronger
277 weights, making planning more reliable. Although these findings are limited within the limits of our
278 simulation protocol, there have been experimental observations of elongation of place fields along
279 trajectories over meaningful experiences [83, 84].

280 In conclusion, this work showed a possible architecture for coupling emergent spatial representations
281 with neuromodulated plasticity to achieve an experience-driven cognitive map. The reliance on a few
282 spatial and algorithmic inductive biases, grid cells, and a planning algorithm supports the idea of a
283 label graph for goal navigation. Future work can investigate the application to other spatial domains,
284 such as motor control and three-dimensional navigation. In addition, a richer input feature can be
285 added, such as visual information [85], as well as new neuromodulators that encode different sensory
286 dimensions or internally generated signals.

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529 5 Appendix

530 5.1 Grid cell module

531 It is defined a correspondence between the global environment in which the agent moves, a two-
 532 dimensional Euclidean space \mathbf{R}^2 , and a bounded local space of a grid module, corresponding to a
 533 torus.

534 The global velocity $\mathbf{v} = \{x, y\}$ is then mapped to a local velocity, scaled by a speed scalar s_l^{gc} specific
 535 to the grid cell module l , which determines its periodicity in space.

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

$$553 r_i = \exp\left(-\frac{x_i^2+y_i^2}{\sigma_l^{gc}}\right), \text{ where } \sigma_l^{gc} \text{ is the width of the tuning curve for module } l. \text{ An illustration of the}\\
 554 \text{receptive field over a 2D environment and a toroidal space is reported in Figure 3a-b.}$$

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

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

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^{GC} , 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, lateral inhibition is implemented. More specifically, the
 565 tuning process is aborted in case the cosine similarity of the new pattern and the old ones is greater
 566 than a threshold θ_{inh}^{PC} .

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

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

$$u_i^{PC} = \phi \left(\cos \left(u^{GC}, W_i^{GC,PC} \right) \right) \quad (3)$$

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

$$m_i = -m_i/\tau^{PC} + u_i \quad (4)$$

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

579
 580 In the model, a PC population is defined by its average place field size, determining the granularity
 581 of the representation of the place. In plot 3b it is illustrated an example of place cells layer tuning
 582 obtained from a continuous trajectory over a square environment.

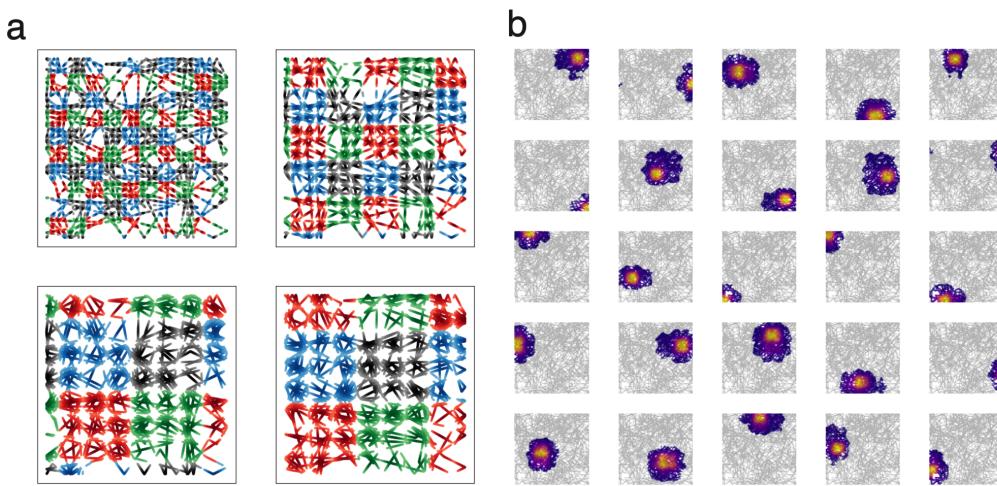


Figure 3: **Place fields obtained from grid cells activity** - **a:** grid cell modules with different granularity represented over a continuous trajectory in an open space. For visualization purposes, each module is represented as composed of four sub-modules of 9 grid cells each, whose periodic tuning generates activity that repeats in space. **b:** place cells whose spatial tuning has been obtained from the concatenation of the grid cells population vector.

583 **5.3 Modulation**

584 Neuromodulation is implemented as a reward-sensitive signal, represented as DA (mimicking the
 585 function of dopamine), and a collision-sensitive signal, represented as BND (for boundary). Its
 586 dynamics are defined in terms of a leaky variable v whose state is perturbed by an external input x ,
 587 whose qualitative meaning differs for each neuromodulator k .

$$\begin{aligned} v_k &= -v_k/\tau_k + x_k \\ v_k &= \max(v_k, 0) \end{aligned} \quad (5)$$

588 **Learning rule** The connection weights \mathbf{W}^k are updated according to a plasticity rule composed of
 589 an Hebbian term, involving the leaky variable, the place cells that are above a certain threshold θ^k ,
 590 and the current connection weights value:

$$\Delta \mathbf{W}^k = \eta^k \mathbf{u}^{\text{PC}} \left(v^k - \mathbf{W}^k \right) \quad (6)$$

591 where η^k is the learning rate, the weight contribution of the Hebbian update. Additionally, connections
 592 values are kept non-negative.

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

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

$$\beta_i = c_a^k m_i \bar{\beta} + (1 - m_i) \bar{\beta} \quad (7)$$

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

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

$$q_i = c_b^k v^k \exp \left(-\frac{\|\mathbf{x}_i - \mathbf{x}_j\|}{\sigma^k} \right) \quad (8)$$

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

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

605 **5.4 Decision making**

606 **Behaviour selection logic**

607 The possible behaviours are *exploration* and *exploitation*, and an action is defined as a 2D velocity
 608 vector. For exploration, an action can be generated either as random navigation, using a polar vector
 609 of fixed magnitude (the speed) and angle sampled from a uniform distribution, or as a step within
 610 a goal-directed navigation plan to reach a random destination, which corresponds to a randomly
 611 sampled existing place cells. In the goal-directed navigation the magnitude of the velocity vector
 612 is less or equal than a fixed speed value, depending on the distance from the next target position in
 613 the plan. Instead, for the exploitation behaviour, the action is a step within a goal-directed navigation
 614 towards the reward location. The behaviour selection process depends on the experience of collision,
 615 the presence of a plan, and the success in the navigation planning. A diagram of this logic is reported
 616 in Figure 4.

617 The positions of the agent and of the target location for planning are identified by the place cells
 618 population vector. In particular, the reward position (x_r, y_r) is determined by the weighted average of

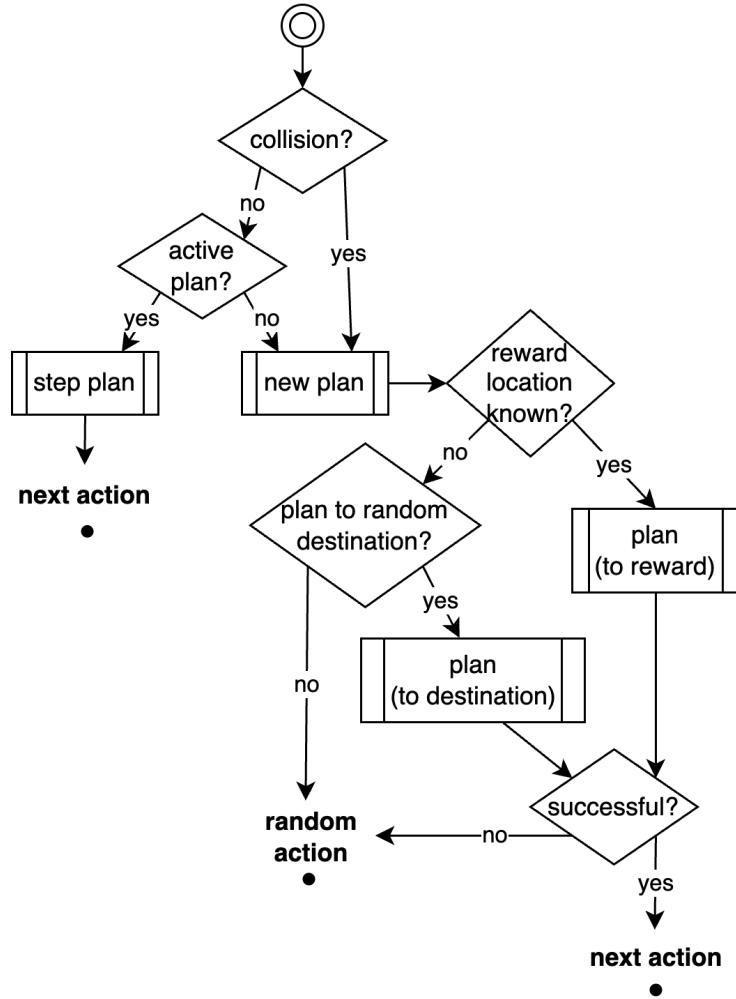


Figure 4: Diagram of the behaviour selection process

619 the centers x_i, y_i of the place cells with respect to their DA-modulated connections weights. Further,
 620 only the top 5 place cells are considered.

$$x_r = \sum_i^5 \mathbf{W}_i^{DA} x_i \quad (9)$$

$$y_r = \sum_i^5 \mathbf{W}_i^{DA} y_i$$

621 **Path-planning algorithm**

622

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.

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
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
```

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 5 some samples are shown.

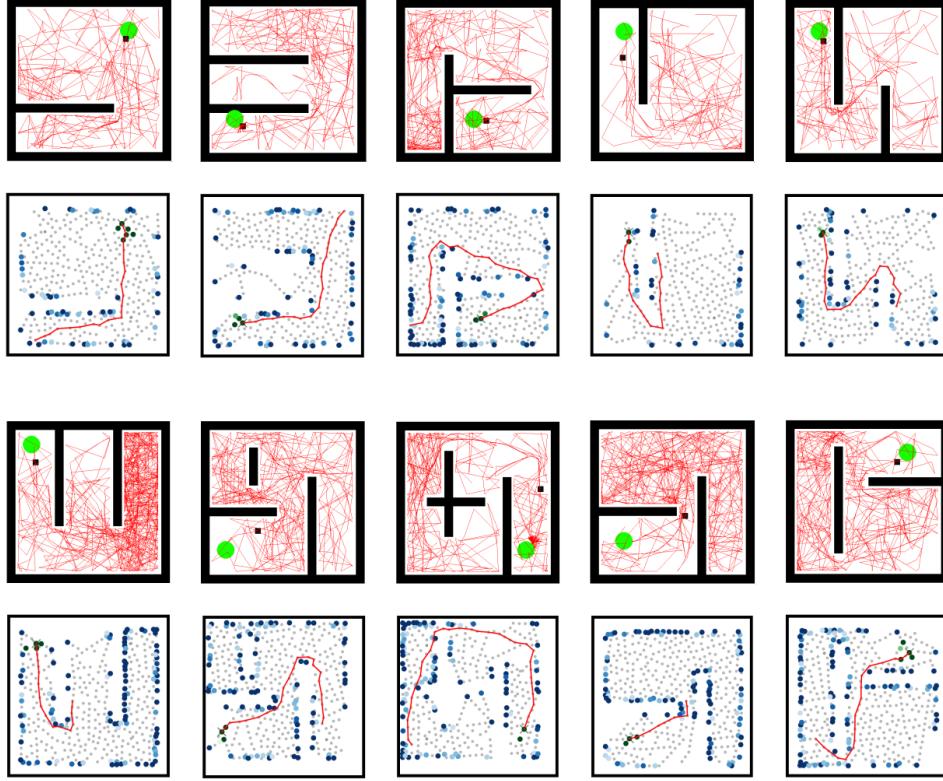


Figure 5: Sample of generated environments

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.

655 **Optimization** The model hyper-parameters such as the constants for the neural dynamics and
 656 the behaviour selection have been optimized through a evolutionary algorithm. Initially, an initial
 657 population of individuals with different random genomes (string of hyper-parameters values) is
 658 evaluated according to a fitness function, in this case a set of different environments.
 659 Next, the population of a new generation is constructed from the first by combining and mutating the
 660 genomes of the top ranked individuals from the previous generation.
 661 In particular, we used the Covariance Matrix Adaptation algorithm, in which the shape of distribution
 662 of genome values is iteratively adapted according to the recent performances.
 663 The evolved hyper-parameters are: neural gain β , lateral inhibition threshold θ_{inh}^{PC} , lateral distance
 664 threshold θ_{rec}^{PC} , activity trace time constant τ^{PC} , reward modulation scale c_b^{DA} , reward modulation
 665 spread x_b^{DA} , boundary modulation scale c_b^{BND} , boundary modulation spread c_b^{BND} , reward gain
 666 modulation c_a^{DA} , and boundary gain modulation c_a^{BND} . The distribution of the genome values is
 667 reported in Figure 6.

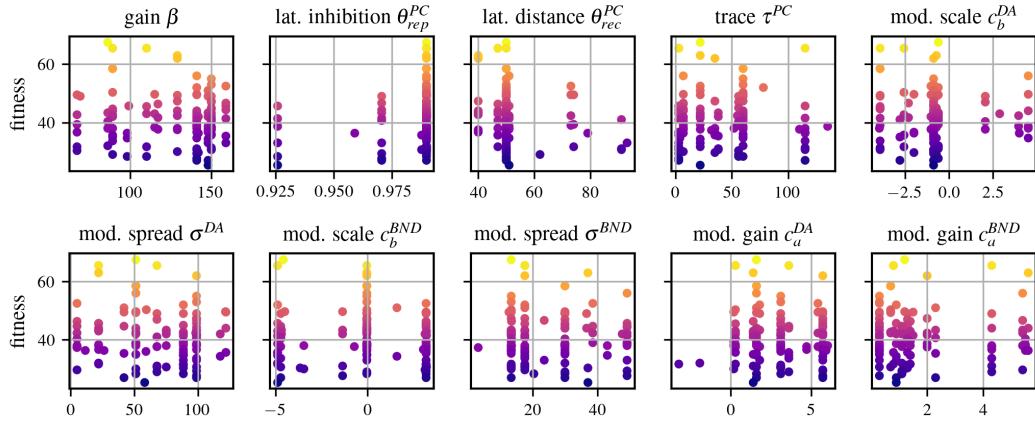


Figure 6: **Distribution of evolved parameters** - Results relative to the last generation, from a run with population size of 128 individuals.

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