Flexible navigation with neuromodulated cognitive maps

Krubeal Danieli

1 Introduction

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

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

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

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

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

1.1   Neuromodulation of cognitive maps

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

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

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

1.2   Computational models

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

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

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

In this study, we introduced a model architecture capable of generating online a spatial representation made of two place cells layers, which can be endowed with additional behaviourally-relevan sensory inputs by means of neuromodulators. Our primary goal was to investigate the role of neuromodulation in the formation of a cognitive map, and its impact on the agent's behaviour. The model is constructed with a pre-defined stack of grid cells layers of different scales, from which the place cells were generated through competition [56, 57], and a graph-like map is obtained by connecting place cells over one or more trajectories [8]. Previous work has applied neuromodulation in spiking neurons for controlling explorative-exploitative behaviour, inspired by the role of dopamine and acetilcholine [58, 59]. While others used it during training of deep artificial networks [60]. Here, neuromodulators are best described by nodes working as preditive analog sensors of external events. Their role is to form synaptic connections with the place cells, effectively determing a scalar field over their representation. Additionally, they have a way to correct their synaptic weights with subsequent observations, similarly to predictive coding [43, 61, 42, 51]. The result is our operationalization of a cognitive map, a neural structure built online

through experience and supporting the necessary information for behaviour. We endowed an artificial agent with this model and simple heuristics for toggling between exploration and exploitation, and tested it in a goal-directed navigation task in environments with different layout.

A secondary goal was to enquire about the effect of neuromodulation on the density of place cells, and in particular the reshaping of their place fields following meaningful events, as supported by previous studies [37, 62, 63]. Our working hypothesis was that a non-uniform distribution of place cells would be beneficial for the agent's performance, especially in terms of more stable representations of special locations.

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

2   Methods

The model is constructed around the concept of a cognitive map, which an agent builds by freely navigating a closed environment and reaching a discovered goal location. The full schema of its components its illustrated in plot 1-**a** below. The architecture relies on the core assumption that the agent has receives minimal external information, consisting solely of a reward and collision input as two binary values. These two signals are used to enrich the cognitive map with experience-dependent data, which is then used to guide the agent's behavior.
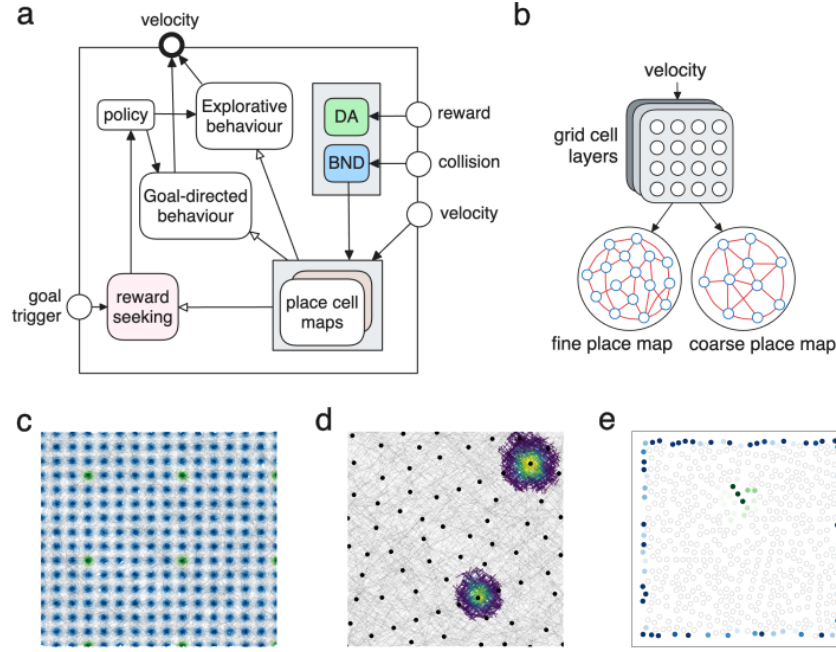
Figure 1: MODEL LAYOUT AND SPATIAL REPRESENTATIONS - **a**: *the full architecture of the model, consisting of three main sensory input, targeting the two modulators and the cognitive map module, and the executive components, represented by a policy module, two behavioural programs and a reward receiver.* **b**: *the cognitive map component, organized with a stack of grid cell modules receiving the velocity input and projecting to two layer of place cells with different place field granularity.* **c**: *the neural activity of a grid cell module from a random trajectory; in blue the repeating activity of all cell, while in green the activity of only one, highlighting the periodicity in space.* **d**: *the distribution in space of the place cells centers, together with the activity of two cells showing the size of their place field.* **e**: *neuromodulation activity over the place cells map, with in blue the cells tagged by the collision modulation, and in green the ones targeted by reward modulation.*

The formation of the spatial representation is instead based on idiothetic information, which is the agent's perception of self-motion [64]. In particular, here we assume this cue to be the factual velocity vector, namely the actual displacement of the agent in the environment. In the brain, this signal is thought to result from the integration of inertial and relative motion cues [65, 66].

2.1 Place cell map

The formation of place cells is obtained from the activity of a set of grid cells organized into modules, or layers. This simple feed-forward architecture is depicted in plot 1-**b**. A grid cell module i has been defined as a set of N^{gc} neurons with gaussian tuning curve evenly distributed over the surface of a two dimensional torus $\mathbf{T}^2$. Unlike other approaches for generating grid fields [67, 68], we defined a correspondance between the global environment in which the agent moves, a two dimensional Euclidean space $\mathbf{R}^2$, and a grid module bounded local space, corresponding to the torus. Then, the global velocity $\mathbf{v} = \{x, y\}$ is then mapped to a local velocity, scaled by a speed scalar s_i^{gc} specific to the grid cell module i, which determines its periodicity in space. This approach has been used in previous works [27]. The initial position on the torus is randomly chosen at the beginning of each episode, since what matters is the sequence of displacements without any reference to a meaningful origin.

The choice of a toroidal space is motivated by consolidated experimental evidence of the neural space of grid cells, which are organized in modules of different size spanning the animal's environment. However, the shape of their firing pattern is known to be hexagonal, which corresponds to the optimal tiling of a two dimensional plane, giving rise to a neural space lying on a twisted torus. In this work, for simplicity, we consider a square tiling and thus a square torus, without much loss of generality except for the slight increase of grid cells required for a sufficiently cover. In plot 1-**c** is shown the activity of a grid cell module over a trajectory, with the periodicity underlined by the cell in green.

The activity of all grid cell modules, indicated as $\mathbf{u}^{GC}$, is then projected down to two independent layers of initially un-tuned cells, whose feed-forward weights $\mathbf{W}^{GC,PC1}$; $\mathbf{W}^{GC,PC2}$ are initialized at zero. As the agent moves and the grid cells activity changes, if no neurons within a place cell layer are active, then one is randomly chosen and its weights are set to the current (at time t) grid cells' population vector $\mathbf{W}_i^{GC,PC} \leftarrow \mathbf{u}_t^{GC}$. For the plasticity process to be completed, it is also checked the possible overlap with other cells in the same layer, effectively accounting for lateral inhibition. This mechanism is implemented by computing the cosine similarity with the weight vector of the other tuned cells and comparing it with a threshold θ_{rep}^{PC}, with the possibility of aborting the plasticity process if the similarity is too high.

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

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

where ϕ is a generalized sigmoid function $\phi(z) = [1 + \exp(-\beta(z - \alpha))]^{-1}$ with gain β and threshold α. The two layers of place cells differ in the size of their place fields. This feature is affected by the sensitivity of a cell tuning with respect to the grid cell activation, determined by the parameters of the sigmoid, and the strength of the lateral inhibition, determined by the similarity threshold. Within a layer, the connections between cells are calculated by the same cosine

similariy, but compared against a different threshold $\theta_{\text{rec}}^{\text{PC}}$. One layer is set to be more fine-grained, with an overall higher density of place cells over the space, while the other is more coarse-grained, with overall large place field sizes.

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

2.2   Neuromodulators

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

$$\dot{v}^k = -v^k/\tau^k + I \tag{2}$$

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

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

where η^k is the neuromodulator-specific learning rate.

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

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

2.3   Policy and behavior

In this work, the first interest was to test the usefulness of our simple cognitive map built from minimal assumptions for the tasks of exploration and goal-directed navigation. To this end, we defined a simple hard-coded policy that toggles between these two behaviours according to the presence of a goal signal,

externally provided, and the presence of an actual goal representation, taken care of by a special component called *reward seeking*, depicted in the pink box of plot 1-**a**. Exploration is accomplished by a random walk, with a variable number of steps in the same direction to avoid stagnation, and occasional plans to visit random positions within the known map, again for limiting stagnation. Goal-directed navigation, either for reaching a random position for exploration or the actual reward location, is achieved by calculating the shortest path between the closest place cells centers of the current and target positions. The place cells are hence treated as nodes of a graph, and their connections constitute its edges. We use a Dijkstra algorithm applied to the coarse-grained layer, which contains less and more spread out cells and it is thus cheaper to compute, to derive a coarse-grained plan. However, in the case the agent gets stuck or the distance to the target is shorter than the cells' distance, the planning switches to the other layer for devising a fine-grained plan, which it is followed until either the target or the next node in the coarse-grained are reached.

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

3 Results

3.1 Naturalistic task

The evaluation of the model ability to construct and utilize a cognitive map was defined as the total rewards collected during several rewards trials in different environments. The protocol was inspired by the behaviour of animals who are end up in a new territory in search for food in various locations.

The testing environments varied in layout, determined by the position and number of walls.

First there was the exploration phase, in which the agent was placed in a random location and let roam through a pseudo-random walk for 5000 steps. Depending on environment layout, the formed map was more or less matching the the actual topology. Then the exploitation phase began, in which a circle the 5% of the total are was designated to provide a binary reward $R \sim \mathcal{B}(p_r)$ drawn from a Bernoully with probability p_r. When the reward was successfully fetched, the agent was teleported to a random location in the environment. Further, in order to mimic the depletion of a food source the reward area was modeled with as leaky variable $\dot{v}_r = (E_r - v_r)/\tau_r + R$, and its location moved whenever its level went below a threshold $v_r < \theta_r$.

The optimization of the parameters of the model was carried out using the Covariance-Matrix Adaptation evolutionary strategy (CMA-ES) [69] with a population of 256 individuals for 100 generations.

3.2 Performance over different environments

Our primary aim was to test the reward performance in different environments. The best model resulting from evolution reached solid navigation and adaptation skills. Within the limits imposed by the rudimentary exploration policy based on random walks, the agent was able to visit a significant portion of the environment during exploration, and tune its modulatory system to craft cognitive maps useful during exploitation.

In figure 2 we can see the cognitive maps formed by the agent in three different environments. In plot 2-**a** it is reported a linear track with wide margins, represented in terms of four layers: the nodes of the fine-grained place cells (top), the graph of the coarse-grained place cells (center-top), the boundary-tagged place cells (center-bottom), and the reward-tagged place cells (bottom). The overlap of these last three representations is what we refer to as the cognitive map, since these are the layers providing the main information used during goal planning. In plot 2-**b** and 2-**c** we can see the cognitive maps formed in a square environment without and with internal walls, respectively.

In red is indicated the trajectory of the agent, and notable it is the greater number of lines crossing into the rewarding zone, in green. The agent's planned path is shown in grey, highlighting how it dodges the walls and go straight to the goal.

3.3 Modulation of spatial resolution affects performance

Our second aim was to investigate the possibility of online alteration of the place cells density, in terms of its potential performance improvement. This action is motivated by the consolidated phenomenon of hippocampal rate remapping, for which the place cells change their firing pattern according to contextual shifts [70, 63]. Additionally, there is growing experimental evidence that place fields can be moved in space following behaviourally relevant events, such as the occurrence of reward, according to a plasticity rule known as behavioural time-scale plasticity (BTSP) [37, 71].

In our model, we associated this process to both collision and reward signals, whose location is set to be the center towards which the cells within a certain radius r_{BND}, r_{DA} are pulled. The centers of the cells involved are shifted with a force proportional to the Gaussian distance from the center of the signal, and the strength is weighted by a parameter λ_{BND}, λ_{DA}.

Our working hypothesis is that the online re-configuration of the cognitive map can lead to a representation of the environment more tailored with the agent experience. This changes introduced by this mechanism should then be reflected in the adaptability and navigation abilities.
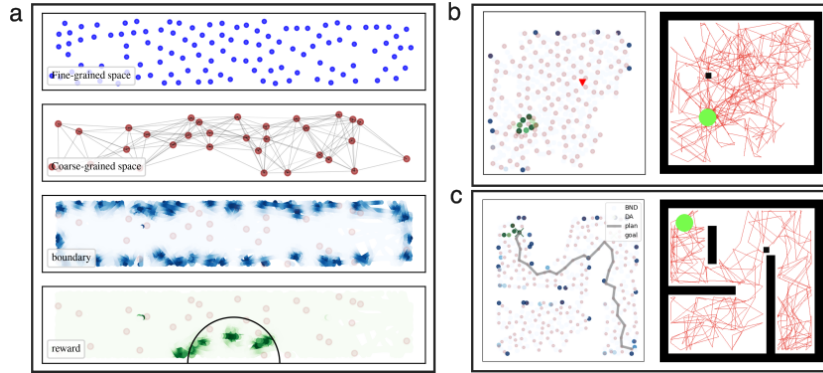
Figure 2: Cognitive maps and agent behaviour - **a**: *place cells (PCs) over a rectangular environment, where the top plot report the node centers of the fine grained PCs, the top-center plot the node centers of coarse grained PCs together with their edges, the bottom-center instead shows the activity of the PCs tagged with the boundary neuromodulator over the coarse grained PCs, while the bottom plot shows the same but with the PCs tagged by the reward neuromodulator; the semicircle corresponds to the reward area - **b**: square environment, the right plot is the agent's trajectory (red) and reward area (green), the left plot si the cognitive map, defined as overlay of the coarse-grain PCs, boundary and reward-sensitive PCs. - **c**: square environment with internal walls, the right and left plot as before, but with the addition of the path planned by the agent to reach the target (grey)*

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