A feed-forward model of spatial and directional selectivity of hippocampal place cells∗

R. Chavarriaga†, D. Sheynikhovich‡, T. Strösslin‡ and W. Gerstner‡
† IDIAP Research Institute, 1920 Martigny, Switzerland
‡ Ecole Polytechnique Fédérale de Lausanne (EPFL), 1015 Lausanne, Switzerland

Introduction

In recent years a wealth of studies have focused on the role of the Hippocampus in spatial learning and navigation, triggered by the finding of place sensitive cells in this area. These cells have been interpreted as being responsible for coding a representation of space [9, 10].

Even though the term place cell suggests that location is the unique determinant of firing of hippocampal cells, there exist several other factors which influence hippocampal activity. Experimental data have shown that the firing of place cells doesn’t depend on the heading direction when the animal is foraging freely in an open environment. In contrast, on radial mazes or linear tracks the firing of these cells becomes directionally selective [8, 4]. Furthermore, place directionality also appears in open environments when the animal is constrained to follow the same path between points of special significance [7].

We have developed a model of hippocampal place cells, which reproduces both spatial and directional selectivity of these cells. In our model, place cells are intrinsically directional (responding to specific local views), and their directionality is reduced during exploration when the rat is not constrained in the direction of its movements (like in open fields or the centre of mazes). We have modelled changes in the place cell directionality as the result of experience-dependent changes (through unsupervised Hebbian learning) in feed-forward connections from a population coding for specific local views. When the animal is able to explore the same location with different head directions, it allows a single post-synaptic cell to be connected to pre-synaptic cells coding for several local views. Therefore, the directional selectivity of that cell is reduced.

Description of the Model

A location may be recognised by identifying the sensory information available at that location (i.e. local view). According to this, place-sensitive activity can be observed in cells tuned to respond to specific environmental stimuli available at each location [11]. In our model, a vision-based place representation is built by storing and comparing local views.

Similarly to [5] a spatial representation based in metric information to the walls is proposed. At each location, the local view is coded as a vector $\vec{d}$ of $N_{dir}$ dimensions. Each component $d_\phi$ corresponds to the distance to the closest wall in the allocentric head direction $\phi$. Let $\Psi$ be the visual field of the agent, and $\psi$ the current head direction, the feature vector correspond to $\vec{d} = [d_{\psi-(\Psi/2)}, \ldots, d_\psi, \ldots, d_{\psi+(\Psi/2)}]$, coding for $N_{dir}$ directions.

A population of cells encoding the encountered local views is built incrementally; at each location the agent takes a view of its environment and recruits a new cell which stores the vector $\vec{d}^i$, and the agent’s head direction $\psi^i$. This population is referred to as view cells (VC).

The activity of a given VC $i$ depends on the difference of the current local view ($\vec{d}$) and the stored features ($\vec{d}^m$). When computing this difference, local views are aligned according to the direction in

which they were perceived, and only the \( N_\Omega \leq N_{dir} \) features in the overlapping region are taken into account for the comparison. Furthermore, the difference in the gaze direction \((\psi^j - \psi)\) also modulates the response of a VC such that it will be maximally active only if the difference between the views is small, and they were taken at the same head direction. This modulation accounts for the amount of information available to compute the similarity of the two local views, i.e. the activity of a VC will be maximally only if all the features in both local views were taken into account to compute the difference. The VC activity is then computed as follows,

\[
r^\text{VC}_i = \exp \left[ - \frac{1}{2\sigma^2_{\text{VC}}} \left( \frac{1}{N_\Omega} \sum_{\phi \in \Omega} (|d^\text{obs}_\phi - d^\phi|) \right)^2 \right] \exp \left[ - \frac{(\psi^j - \psi)^2}{2\sigma^2_{\text{CANG}}} \right]
\]

where the first Gaussian depends on the difference between the features of the local views, and the second depends on the difference in the head direction. \( \psi^j \) is the heading direction at the moment when the VC \( i \) was recruited, and \( \psi \) is the current heading direction.

The VC population project downstream onto another population where information from several local views is integrated to build a vision based place representation. This population corresponds to our simulated place cells (PCs).

Each time a new VC is recruited, a new PC is selected and its activity set to maximal rate \( r^\text{PC}_i = 1 \). Connections from all active VCs \( j \) with activity \( r^\text{VC}_j > \theta_{\text{VC}} \) to PC \( i \) are updated to a value \( w_{ij} = r^\text{VC}_j r^\text{PC}_i \). In subsequent time steps, initialised connections \( w_{ij} \) are updated using a Hebbian rule \( \Delta w_{ij} = \eta_{\text{PC}} r^\text{PC}_i (r^\text{VC}_j - w_{ij}) \) this allows the integration of information from several local views into a single place cell.

Assuming that a PC receives input from \( n \) VCs coding for uniformly distributed heading directions, a subset of \((\frac{360}{n})\) pre-synaptic cells may be sufficient to activate the postsynaptic PC cell, where \( \Psi \) corresponds to the visual field. The activity of a PC \( i \) is computed as,

\[
r^\text{PC}_i = \left\lfloor \tau \frac{\sum_j w_{ij} r^\text{VC}_j}{\sum_j w_{ij}} \right\rfloor
\]

where \( \lfloor x \rfloor = x \) if \( 0 < x < 1 \), \( \lfloor x \rfloor = 1 \) for \( x > 1 \), and zero otherwise. The scale factor \( \tau = \frac{360}{\Psi} \) accounts for the limited view field.

Connectivity between VC and PC depends on the simultaneous activation of cells in both populations. Local views corresponding to the same location and taken at different orientation may converge onto a single PC, with uniformly distributed weights yielding an omnidirectional place cell firing. For this to happen, the agent should be able to explore uniformly the same location with different head directions - as is the case when an animal freely explores an environment. In contrast, if the agent only experiences local views corresponding to a small subset of orientations (as in linear tracks and directed search tasks), the PC will receive projections from VCs coding for these orientations. Therefore, the activity of this PC will be direction-dependent.

**Results**

In order to test the model, we test simulate explorations of both open environments and radial mazes (4-arm and 8-arm). Directionality of place cells was assessed using the directionality index proposed in [7],

\[
D_i = \max_\theta \frac{|r_i(\theta) - r_i(\theta + 180^\circ)|}{r_i(\theta) + r_i(\theta + 180^\circ)}
\]

Where \( r_i(\theta) \) is the activity of cell \( i \) when the animal is heading in direction \( \theta \). An index \( D_i = 0 \) corresponds to a cell which fires equally for all head directions (i.e. an omni-directional cell). In contrast, an index value \( D = 1 \) corresponds to a cell which fires maximally when the animal is heading in one direction while being silent in the opposite direction.

Figure 1 illustrates the directionality of the place cell population after random (left) and directed (centre) exploration of open environments, as well as exploration of a 8-arm maze (right). Directionality histograms (a-c) show that the model yields less directional place cells when there is no constraint in
the exploratory behaviour (average directionality $\hat{D} = 0.48$, $SD = 0.1$); whereas linear trajectories or exploration of mazes result in an increased directional selectivity ($\hat{D}_L = 0.66$, $SD_L = 0.03$, after a linear trajectory; $\hat{D}_S = 0.65$, $SD_S = 0.15$, for 8-arm mazes). This results are consistent with experimental findings reported in rats [7]. The typical place fields for each type of exploration is presented in Figure 1(d-f).

Figure 1: Directionality after Left random exploration of open environments; Centre Directed trajectories in open environments; and Right exploration of a 8-arm maze. Top. Histogram of the magnitude of directionality of place cell population. Bottom. Receptive field of place cells after exploration of (d) open environment ($D = 0.50$); (e) Linear trajectory ($D = 0.66$); (f) 8-arm maze ($D = 0.74$).

The model reproduces the directional selectivity of place cells depending on the exploratory behaviour of the animal (or agent). Reduced directionality in the model, results from the combination of several directional sub-components (sensitive to specific local views). This contrasts with previous models addressing the issue of place cells directionality [2, 6], in which this property is the product of experience dependent changes in recurrent connections among place cells. Such models have proposed the recurrent network in CA3 as the putative locus of directional changes in the hippocampal place code.

Experimental results show that CA3 → CA1 projections are not required to develop directional dependency of CA1 cells in linear tracks [1]. Moreover, mEC cells show a reduced directionality (D=0.45) in open environments after disruption of feedback projections from the hippocampus to the entorhinal cortex [3], suggesting that a functional CA3 recurrent network is not required to produce changes in the directionality of both entorhinal and CA1 cells. This supports our assumption that feed-forward projections onto the hippocampus may suffice to yield directional changes in the PC activity.

References


