A Computational Model of the Interaction between External and Internal Cues for the Control of Hippocampal Place Cells

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Abstract

Place cell activity in the hippocampus depends in a complex way on the information from two major sensory sources: External (e.g., visual) cues and internal cues (self-motion, vestibular cues). Dissociation of the two inputs in the presence of the animal modifies the place fields in ways that depend on the magnitude of the difference: If the mismatch is small, place fields typically follow the external cues, but if the mismatch is large, their activity is determined mainly by the internal cues. The dynamics underlying the interaction between the external and internal cues in the hippocampus is not completely known, but is an important issue in understanding the hippocampus' role in spatial learning and navigation. In this paper, we propose an attractor model of the hippocampus which captures the interaction between external and internal sensory inputs to the hippocampus. The proposed mechanism accounts for the difference seen in the experimental results in the case of a small versus a large discrepancy between the visual and idiothetic information.

Keywords: remapping, idiothetic cues, visual cues, path integration, continuous attractor model.

1   Introduction

Place cells in the rodent hippocampus [12, 13] are thought to encode spatial cognitive maps, with their activity providing a distributed representation of the animal's position in the environment [13]. Place cell activity depends on multiple factors such as sensory, behavioral, contextual and motivational cues [5, 11, 15, 8, 4, 18, 7, 10, 2]. Although the significance of single cue dependencies has mostly been explained through experiments and computational models, the mechanisms of interaction between cues and multiple sensory modalities for the control of the place cells are not well understood. In this paper we propose a computational model of the rodent hippocampus to study the effect of the interaction between external (i.e. visual, olfactory, tactile) and internal (i.e. self-motion, vestibular and idiothetic) sensory cues on the activity of place cells. The main aim is to account for the experimental results that show a dependence of the behavior of place cells on the magnitude of mismatch between the external and internal cues when the mismatch takes place in the presence of the animal [18, 7, 6].

2   Review of Experimental Results

Many experimenters have investigated which of the two sensory inputs — external or internal — controls the firing of place cells when the information received by the animal from the two streams is not consistent [20, 4, 18, 1, 7, 6]. In a stable and familiar environment, the external and internal sensory inputs are concordant, with small errors in the idiothetic system corrected by the visual input [4, 19, 16]. A mismatch between the two sources can appear in three situations: (1) the animal's internal cues are updated based on self motion or vestibular cues, without a change in the visual input [18, 7], (2) the visual input changes (e.g., by rotation of walls) without activation of the animal's internal sense [6], or (3) both inputs change by different amounts [6].

If the mismatch occurs in the absence of the animal and the environment has previously been perceived as stable, the visual cues always orient the place cells. Type (1) mismatch was tested in the presence of the animal [18, 7] by rotating either the only available cue [18], or the whole environment [7]. In both cases, a dependence of the control of place cells on the magnitude of the mismatch was observed [18, 7]. When

the discordance was *small*, place cells followed the visual input, and the place fields rotated with respect to the fixed reference frame [18, 7]. After a *large* discordance, the visual input was no longer dominant and the place fields either remained in the same position with respect to the fixed reference frame – complete idiothetic control [18]– or remapped [7]. The model proposed here explicitly addresses the type (1) mismatch while being consistent with the results of the other types of discordances.
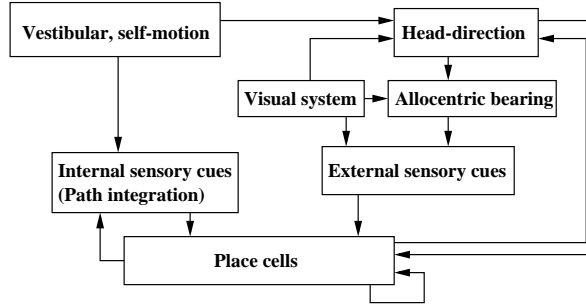
2.1 Theoretical Model

Figure 1: The architecture of the hippocampal model

Our model, shown in Figure 1, has three types of inputs to place cells: (a) The *external sensory input* which encodes distances to perceived landmarks [14] and allocentric bearings to them [9, 22], (b) The *internal sensory* input from the path integration module, which, based on vestibular and self-motion cues, biases the place cells according to the animal's location in idiothetic coordinates [22, 16], and (c) The *recurrent input* which embeds in the place cell layer a set of continuous attractors with centers uniformly distributed on the environment, where the connection strength decreases exponentially with the distance between place cell centers [23, 19, 17]. Such a pattern of connectivity can arise through Hebbian learning in the synapses between co-active place cells [17, 3].

The structure of the model is consistent with existing experimental evidence about the activity of place cells [5, 21, 15, 4] and current models of the hippocampus [9, 22, 16, 19, 17]. The main assumptions of the model are: (a) the external sensory input encodes not only distances to perceived landmarks, but also allocentric bearings to them [9, 22], and (b) the existence of distinct external and internal pathways to place cells in the hippocampus [16].

The model explains the dependence of the place representation on the magnitude of a type (1) mismatch between external and internal sensory cues as follows. When the simulated rat is introduced in a stable and familiar environment, the external visual input aligns the place code, and through it, the idiothetic input and, implicitly, the allocentric bearing or the rat's internal sense of direction (tuning curves of head direction cells are constant across trials in a familiar environment [21]). Experiments in which rotations of the environment take place in the presence of the animal activate its idiothetic system, but do not change the egocentric position of visual cues. If the environment transformations do not disorient the rat by altering its sense of direction, the *allocentric bearings* to landmarks are updated correctly by the internal cues, but they differ from the learned bearings in the initial, stable orientation of the environment. Thus, a type (1) mismatch can affect the location encoded by the internal sensory input, and the strength of the external input - which decreases with the magnitude of the difference between the learned allocentric bearing to landmarks and the perceived ones after the environment modification. The recurrent input has an inertial role by biasing the place cells active before the environment transformation.

In the model, a mismatch between external and internal sensory inputs is resolved by a competitive mechanism for the activity of place cells, since only a small number of place cells fire at any time. A *small mismatch* decreases the strength of the external input only slightly, so that, with the inertial tendency of the recurrent input, it wins the competition over the internal input and maintains the same set of active place cells as before the change in the environment and place fields rotate in the fixed frame of reference by the same angle as the rotation of the environment. A *large mismatch*, in contrast, decreases the magnitude of the external input significantly, so that the internal input takes control over the activity of place cells and place fields do not rotate with respect to the fixed frame of reference.

Experiments also show that a large mismatch can remap the place code if the idiothetic system cannot correctly follow the displacement of the animal (e.g. in the case of a very abrupt and fast rotation [7]). The model explains this by a random reset of the location encoded by the internal sensory input, though biased by the location indicated by external cues ([7] shows that in approximately half of the large, fast rotation experiments the place representation rotates by the same amount, while in the other half it remaps). If the new coordinates of the internal system are close to the location specified by the external input, then

place fields will rotate with the magnitude of the rotation, exhibiting external control. If the internal input indicates a position far away from that of the external input, the active place cells will switch to that location. This results in a remapping of the place representation, equivalent to a translation of the cognitive map to the position of the idiothetic input. In this case, new place cells will start firing, some place cells will become silent, and others will change their place fields.

We consider this type of remapping distinct from the remapping seen in dissimilar environments where a new attractor map is selected. Based on experimental results, the overlap between the set of active place cells in distinct environments is much smaller [23] than the one seen after a large mismatch between internal and external inputs [7]. In the latter case, approximately 50% of the place cells have (different) place fields both before and after the rotation [7]. If the set of active place cells in different maps is chosen by chance, the percentage of common place cells should be lower than 50%.

2.2   Computational Model

The place cell layer has N cells with centers distributed uniformly on a circular grid representing a cylindrical environment [18, 7]. Some place cells have centers inside the cylinder and some outside. The dendritic input of a place cell is as follows:

$$h_i(t) = g_{ext}h_i^{ext}(t) + g_{int}h_i^{int}(t) + g_{rec}h_i^{rec}(t) \tag{1}$$

where $h_i^{ext}(t)$ is the external sensory input, $h_i^{int}(t)$ is the internal sensory input, $h_i^{rec}(t)$ is the recurrent input and $g_{(.)}$ are the corresponding gains. At each time step, a competitive updating rule fires the K_N neurons with the largest dendritic sums ($K_N < 0.02N$).

The external sensory input is modeled as a vector encoding the distances and allocentric bearings to perceived landmarks [9, 22, 16]. A cell's external receptive field is formed by a product of Gaussian functions, each representing the response to a landmark:

$$h_i^{ext}(t) = exp[-\sum_{k=1}^{n_i} w_k (\frac{[d(r_{ext}(t), l_k) - d(c_i, l_k)]^2}{2\sigma_{ext}^2(c_i)} + \frac{[\alpha_{rk}(t) - \alpha_k]^2}{2\sigma_{dir}^2(c_i)})] \tag{2}$$

where n_i is the number of landmarks the cell responds to and w_k is the significance of the landmark. The

distance between the rat's position ($r_{ext}(t)$) and landmark position (l_k) is denoted by $d(r_{ext}(t), l_k)$ (in the environment reference frame). The distance between the cell center (c_i) and landmark l_k is $d(c_i, l_k)$. The perceived allocentric bearing to landmark l_k is $\alpha_{rk}(t)$, and α_k is the learned one. These angles are expressed with respect to an arbitrarily chosen reference direction. All positions are expressed in Cartesian coordinates.

The internal sensory input encodes the position of the rat in path-integrator coordinates:

$$h_i^{int}(t) = exp(-\frac{d(r_{int}(t), c_i)^2}{2\sigma_{int}^2})$$ (3)

where $d(r_{int}(t), c_i)$ is the distance between the simulated rat's position in path-integrator coordinates and the place cell center. It is assumed that, initially, external and idiothetic reference frames are superimposed and identical with the position of the rat in absolute coordinates: $r_{ext}(t) = r_{int}(t) = r_{abs}(t)$.

The third input is formed by the feedback connections onto place cells. Their strength is set through associative learning, such that it decays exponentially with the distance between connecting place cell centers. This establishes a set of continuous attractors spread uniformly on a familiar environment [19, 17]. The relation of the recurrent input is:

$$h_i^{rec}(t) = \sum_{j=1, j \neq i}^{N} w_{ij} x_i(t-1)$$ (4)

with $w_{ij} = \beta_{ij} exp[-d(c_i, c_j)^2/(2\sigma_w^2)]$, the recurrent weights and $x_i(t) \in \{0, 1\}$ the state of the neuron i at time t. The value of β_{ij} expresses the strength of the recurrent connection.

3   Simulation results

We have used simulations to replicate the experimental results obtained by (Rotenberg and Muller, 1997) and (Knierim et al., 1998). The environment was simulated as a circular surface of radius R_{cyl}. In the model there are N=2912 place cells with centers spread uniformly on a $2R_{cyl}$ circular surface. Initially, the cue card is oriented to the east, symmetrically across the horizontal axis, and specified by three points representing the landmarks: two at each end of the cue card and one in the middle.

The rotation phase was simulated for the Rotenberg and Muller, 1997, experiment — denoted RM97 — by

slowly rotating counterclockwise the position of the cue card along the wall (increments of 5°) while the simulated rat followed the margin of the cue [18] such that the relative position of the rat with respect to the card remained constant during the rotation (as in the RM97 experiment).
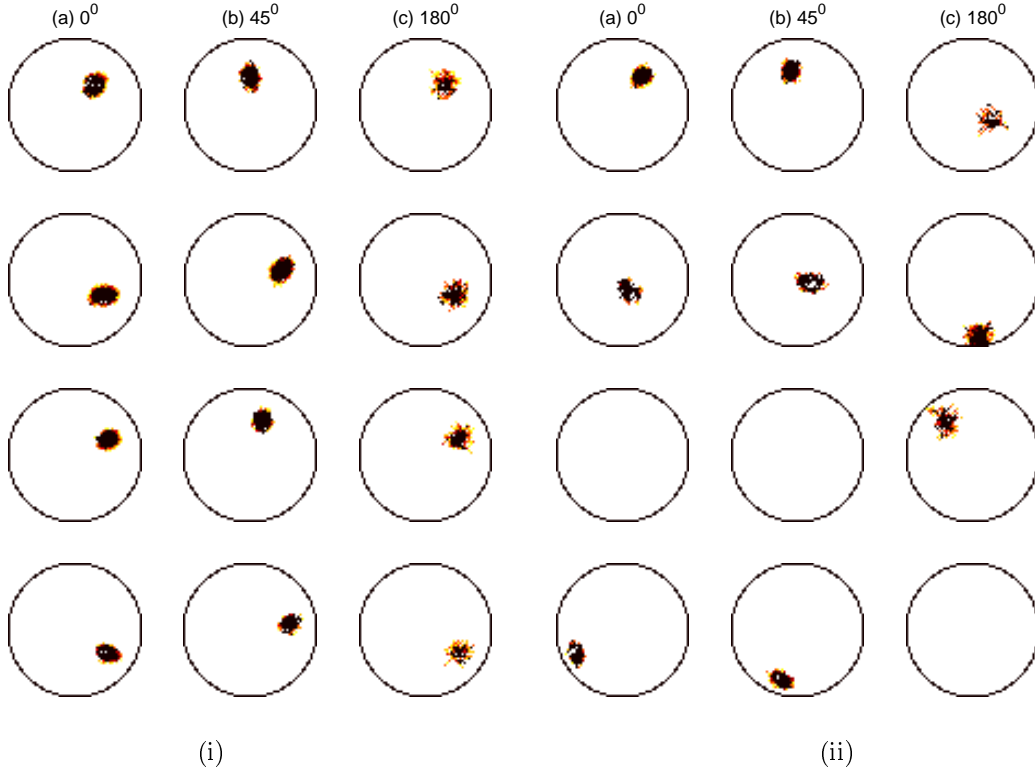

Figure 2: Example of place fields for the RM97 simulation (i) and for the K98 simulation (ii). Each row shows a different place cell. (a) Place fields when the cue card is in the familiar position, (b) After the 45° rotation, (c) After the 180° rotation.

Place fields were reconstructed from the activity of a subset of the simulated place cells as follows: With the card in the initial position, after a 45° counter-clockwise manipulation, and after a 180° counter-clockwise manipulation. Figure 2(i) shows the place fields of four place cells in the three situations corresponding to the simulation of the RM97 experiment. The place fields after the 45° rotation (column (b)), rotate by the same amount, while those after 180° rotation remain unchanged (column (c)).

For the simulation of the experiment by Knierim et al., 1998 – denoted K98 – the rotation of the environment is modeled by a sudden jump in the path-integrator coordinates. The external input remains in the same

relative position as before the rotation, but its strength is modulated by the change in the sense of direction perceived by the animal. Depending on the initial coordinates of the internal sensory input after the rotation, the place representation can either appear rotated by 180°, or remapped. Figure 2(ii) shows place fields obtained after a small and a large rotation, where a remapping of the place representation occurs in the latter one. After the 45° rotation (column (b)), the place fields rotate by the same angle. After the 180° rotation (column (c)) there are place cells which change their place field, new place cells start firing, and place cells that lose their place field. The simulation initializes the internal sensory input at a large distance relative to the absolute position of the simulated rat immediately before the rotation and a perceived rotation angle of 90°.

In the simulation, the proportion of place cells that stop firing (26%), change their place fields (46%) and start firing (26%) is very similar to results of remapping given in [7].

4   Conclusions

We have presented an attractor model of the hippocampus that accounts for the interaction between the external and internal sensory cues for the control of place cells when the two inputs become discordant. In particular, the model accounts for the difference in the experimental results with the magnitude of the discordance between external and internal cues in the presence of the animal. The model also provides a simple explanation for the kind of remapping seen in these situations. This remapping is considered different from that seen between two distinct environments.

The following predictions can be made based on the model:

- After a remapping following a large mismatch between internal and external inputs, the model predicts that the position of the modified place fields can be obtained by the same linear translation from the original position. The model simulates remapping by a translation of the path integrator coordinates such that the resulting attractor map does not overlap entirely with the original one. By this transformation place cells acquire new place fields, some cells stop firing and some cells start firing. What this

implies is that the position of the modified place fields can be obtained by a linear translation from the initial location. Of course, in reality there are cumulative errors in the path integration, and the initial distance and angle of the translation could be different for each place cell. Whether the modified place fields can be reconstructed from the original ones by means of the same transformation could be easily checked by analyzing data coming from simultaneous recordings of place cells.

- The locus of the competition – hippocampus or HD cells – following similar environmental manipulations might be determined by inactivating the hippocampus during and after the rotation and recording from HD cells. If the HD cells still show similar responses as with the hippocampus active [7] (i.e. predominant idiothetic control to large rotations of the environment), then the HD system is capable of resolving the mismatch between the internal and external sensory cues.

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