DIFFERENT SPATIAL SCALES IN MAPPING FROM GRID CELLS TO PLACE CELLS: A NEURAL NETWORK MODEL

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Abstract—Medial entorhinal cortex (MEC), which is known to be the hub of the brain network for navigation and spatial representation, is commonly perceived to be the major input and output structure of hippocampal formation. Grid cells, the principal cells of MEC, show multiple firing fields arranged in a triangular grid, tessellating the environment. Place cells of hippocampus have a single localized pattern of activity. The spatial scale in both MEC and hippocampus increase systematically along dorsoventral axis, which is seemingly due to a systematic variation in the gain of a movement-speed signal, generated outside the hippocampus.

In this article, an artificial neural network model has been proposed, allowing for the single confined place fields of hippocampal pyramidal cells to be emerged from the activities of grid cells. The important point is that this model considers a movement-speed signal which determines the activation of a portion of grid cells with specific spatial scales. This might establish the scale of space representation in place cells. Place fields in this model could be formed considering a modest number of grid cells (for example, 60) with diverse spatial phase and spacing which is consistent with physiological experiments.

Keywords—grid cell, entorhinal cortex, place cell, hippocampus

I. INTRODUCTION (HEADING 1)

Hippocampus as a part of a brain network for navigation and spatial representation comprises neurons with spatially localized activities. These "place cells", first discovered by O’keefe and Drostevsky in 1971, fired whenever the rat was within a certain location in the environment, called place field [1,2,3].

One synapse upstream of the hippocampus, 'grid cells' which are the principal cells of medial entorhinal cortex (MEC) also signal the animal's location in the environment [2,3,4]. These cells have special characteristics, suggesting that MEC plays a key role in navigation and spatial representation [4]. Each grid cell shows activation in multiple regions in the environment; that is, these cells have multiple place fields. The firing fields of each cell constitute a repetitive triangular grid which tessellates the environment explored by the rat [1,5].

The firing pattern of each grid cell is characterized by three parameters: spacing (the distance between vertices of the grid), orientation (tilt to an external reference axis), and spatial phase (offset relative to a reference point). These characteristics are illustrated in Fig.1. Neighboring cells in MEC share common spacing and orientation, yet their spatial phases are distributed. The spacing increases from less than 30 cm in dorsal parts to more than several meters in ventral parts of MEC. The spacing of the rat's grid cells in dorsal-most 25% of MEC varied between 39cm and 73cm in a 1x1 square environment [1,4,5].

Assuming that single localized firing patterns of place cells are constructed from positional information in MEC, it is a problem for the place cells to extract the unique position of the rat from the repetitive firing pattern of grid cells. The spatial scale increases systematically along dorsoventral axis in hippocampus place cells and MEC grid cells, apparently because of a systematic variation in the gain of a movement-speed signal [4,6]. In open environments, a place field can be approximated by a Gaussian function with a diameter increasing from 20 cm in dorsal part of hippocampus to 50 cm in intermediate region and several meters in the most ventral part [3]. The scale of hippocampal place fields might be determined by a movement-speed signal that is generated outside the hippocampus through a summation of components related to ambulation, vestibular activation, and optic flow [6].

There have been some simulation studies trying to address the intriguing problem of mapping from grids to places since the discovery of grid cells in 2005. A mathematical model was illustrated in [3], and in [7] authors proposed mechanisms using competitive learning for this mapping. Some other researches have implemented attractor dynamics for this issue [8]. ICA was proposed in [9] as a sparsification method to simulate place cell activity. Reference [10] used a Bayesian position reconstruction method to model this mapping.

In this paper it is proposed that firing patterns of entorhinal grid cells can be mapped into activities of place cells using a Radial Basis Function Network (RBFN). It is assumed that there is a movement-speed signal generated outside the hippocampus, the gain of which determines the scale of representation in MEC. Therefore, another RBFN is implemented to generate an activation signal based on the gain of the movement-speed signal. The activation signal defines which class of grid cells to be active.

In part II, the neural network structure is described first. Next, the model architecture and the inputs and the outputs of the networks, based on neurophysiological researches, are stated. Results are illustrated in part III. There is a discussion in part IV; and to sum up, we drew a conclusion in part V.
II. METHODOLOGY

A. The Neural Network

Artificial neural networks might be one of the best methods to be used in modeling complex processes in brain, in that they are models based on biological neural networks. Inasmuch as RBFNs have nonlinear approximation properties, they might be a good candidate to model complex mappings. RBFNs typically have three layers: an input layer, a hidden layer with a non-linear RBF activation function, and a linear output layer (Fig.2). The RBF chosen here is a Gaussian. In order to use these types of networks, we need to specify the hidden unit activation function, the number of processing units, and a training algorithm for finding the parameters of the network. Finding the RBF weights is called training.

Using a more efficient design of RBF, The proposed architecture in this paper iteratively creates a radial basis network by adding one neuron each time. Neurons are added to the hidden layer of the network until the sum-squared error falls beneath a predefined maximum error. Training is accomplished when obtaining the desired performance.

B. The Model Architecture

The model architecture illustrated in Fig.3, comprises three parts: grid cells, place cells, and a movement-speed signal which is generated somewhere outside the hippocampus. In the following sections each part will be explained separately.

1) The movement-speed signal: As it was mentioned, the increase in the spatial scale in MEC and hippocampus is seemingly because of systematic variation in the gain of a movement-speed signal which is generated outside the hippocampus [6]. Thus, in the proposed model, it is assumed that a speed signal has been generated based on the rat's movement. The gain of the speed signal was considered to be in six different levels between 0 and 1; each level comprised of 10 different gains. Within which level the gain of this signal lied, defined which classes of grid cells to be active. Each class of grid cells had a specific scale for space representation, i.e. spacing and field size. A RBFN was used to generate an activation signal based on the gain of the speed signal. The activation signal made three classes of grid cells active and made the others silent. The inputs of this network were the gain of the movement-speed signal which was assumed to be between 0 and 1. The output layer, which had 8 neurons, generated an activation signal for grid cells. In other words, the activation signal was an eight-bit signal for grid cells. In order to define the desired output of the network, the time three neighboring bits of the signal were set to one based on the gain of movement-speed signal.

2) Grid cells: As mentioned in part I, grid cells are activated at the nodes of a triangular grid which tessellates the environment. Such a grid in a square environment is depicted in Fig.4 in which d is the grid spacing. The activity of each simulated grid cell was defined as Gaussian functions with centers located at the nodes of its grid. The square environment was discretized into 50x50 bins over 1m². The activity of each grid cell, AGC, is a function of the virtual rat's position in the environment, (x,y), as:

\[ AGC(x,y) = \sum_{i=1,2,...,N} \left[ \exp\left(-\frac{(x-a_i)^2}{s^2}\right) \cdot \exp\left(-\frac{(y-b_i)^2}{s^2}\right) \right] \] (1)

Where N is the number of nodes of the triangular grid for a specific spacing, \((a_i, b_i)\) is the coordinates of the grid nodes. \(s\) is the subfield size and depends on the spacing of the grid vertices(d). In order to identify parameter 's', the activity was considered to decrease to 20% of its maximum value within a distance less than d. The spacing of the rat's grid cells varied between 39cm and 73cm in a 1x1 square environment [5]. To be consistent with the physiological data, eight classes of grid cells with different spacing were considered along dorsoventral axis in the proposed model depicted in Fig.3. The spacing was selected systematically between 28cm and 73cm. Each class, i.e. GCi(i=1,2,...,8), comprised of 20 grid cells with the same spacing and orientation, but different spatial phases. According to the speed at which the rat was traversing, and the activation signal, each time three classes of grid cells(GCi, GCi+1, GCi+2) were active and the rest were silent. Therefore, for each amount of movement speed 60 grid cells contributed to representing the space. In order to have the input for the network, the activity of each grid cell in all 2500 points of the environment was measured based on \(\text{“}(1)\text{”}\). Fig.5 shows the activities of eight grid cells of eight different classes in the square environment.

3) Place cells: In the proposed model six classes of place cells were considered. Each class, PCi(i=1,2,...,6), comprised 100 place cells, each of which increased its firing rate in a specific location in the square environment. In order for all locations of the environment to be represented in terms of firing rates of place cells, The square environment was discretized into 10x10 bins over 1m².

In open environments place fields can be approximated by a Gaussian function [3]. To be consistent with the physiological data, the diameter of place fields was assumed to be between 20 cm and 40 cm along dorsoventral axis in hippocampus. That is, each of six classes of place cells comprised 100 cells with place fields, diameters of which were chosen systematically in this range. Place cell activity was defined as:

\[ APC(x,y) = \exp\left(-\frac{(x-a_0)^2}{t^2}\right) \cdot \exp\left(-\frac{(y-b_0)^2}{t^2}\right) \] (2)

Where (x,y) is the virtual rat's location in the environment and \((a_0, b_0)\), the center of the Gaussian function, is the specific place cell's preferred location. The subfield size, \(t\), was estimated related to the diameter of the place fields. In order to estimate the diameter of the place fields, they were assumed to be where the activity is upper than 10% of its maximum value. As mentioned in [1], firing fields of neighboring cells overlap.

Firing fields of three of 100 place cells are illustrated in Fig.6. The firing rate of the place cell has its maximum value in the cell's preferred location. Activities of all 100 place cells provided the desired output data set for us.
Fig. 1. Characteristics of grid cell activity: a) spacing, b) phase shift (Px, Py), c) orientation. Circles are the nodes of triangular grid where the grid cell has its most firing rate.

Fig. 2. Radial basis function network architecture

Fig. 3. The model architecture. The proposed model comprises three parts: 1) A movement-speed signal which is generated outside the hippocampus, 2) grid cells of MEC which are assumed to be in eight different classes from dorsal to ventral MEC, 3) place cells of hippocampus. There are six classes of 100 place cells, from dorsal to ventral HPC. The two arrows, depicted in the figure, show a mapping through a RBFN.

III. RESULTS

Two RBFNs were implemented in the model. The first network, which generated the activation signal from speed signal, consisted of 60 neurons in the input layer and 8 neurons in the output layer. Training was done until MSE=0.013 after 15 epochs, i.e. by adding 15 neurons to the hidden layer. In order to get the desired result in testing, the elements of the output matrix which were greater than 0.5 were set to one and the others were set to zero.

Simulations of mapping from grid cells to place cells in the two-dimensional environment were accomplished by implementing the second RBFN. Each time, three classes of grid cells, i.e. 60 grid cells, and a class of place cells, i.e. 100 place cells were involved in space representation. The training consisted of moving of the virtual rat continuously through the 50x50 training locations, i.e. moving from left to right in different rows iteratively.

The MSE in this part was about 0.001. The number of neurons in the hidden layer was 75, 100, 125, 225, 325, and 500 for the six states of the movement-speed signal gain, respectively. Measuring the number of peaks in a unit's output by counting the number of distinct contiguous areas containing pixels with at least 80% of the unit's maximum activity, all of the output units showed a single spot of activity.

Fig. 5 shows the activities of three place cells in PC1 before and after training. The units do not show a confined activity pattern before training was done. After 75 epochs of training, a high precision (MSE= 0.001) was obtained. Therefore, the single localized firing pattern of place cells was generated through this RBFN.
The results illustrated in this paper show that confined place fields might be formed from a relatively low number of grid cells through RBFNs. Having nonlinear approximation properties, RBFNs are capable of modeling complex mappings, which perceive neural networks can only model by means of multiple intermediary layers.

The model comprised of three parts: grid cells, place cells, and a movement-speed signal. Eight classes of grid cells and six classes of place cells with different spatial scales along dorsoventral axis were considered, which is consistent with the observation that the spatial scale of grid cells and place cells increases systematically from dorsal to ventral regions of both hippocampus and MEC [4]. This increase is apparently due to a systematic change in the gain of a movement-speed signal which is generated outside the hippocampus [6]. Thus, this signal in the model was considered to lie within six levels between 0 and 1. A RBFN was responsible for generating an 8-bit activation signal, defining which classes of grid cells must be active, based on the speed signal.

According to physiological data, every grid cell projects to about 25% of hippocampal dorsoventral axis [4]. In the proposed model every grid cell projects to a portion of place cells (20% to 50% of place cells) from dorsal to ventral hippocampus. The spacing in grid cells was considered to vary systematically between 28 cm to 73 cm as stated in [5]. The diameter of the place fields was assumed to increase from 20 cm to 40 cm. The model predicts that place field size might be determined by activation of grid cells in specific regions along dorsoventral axis which is defined by a movement-speed signal.

It took a few minutes for the model to learn the environment in terms of firing rate of place cells which is consistent with former experiments [5]. As former experiments reveal that all locations in the environment are represented within a local ensemble of grid cells [3], in order to encode all the locations of the square environment, the proposed model needed only 60 grid cells with three different spacing and diverse spatial phases.

A similar work published recently [7], used competitive learning rule to model mapping from grids to places. This model considered 125 grid cells and 100 place cells in the two-dimensional environment. The RBF network model obviously has the advantage of needing much less number of grid cells which is more plausible due to experimental data mentioned above [3,5]. Furthermore, the RBFN model took into account different scales of space representation and the impacts of movement on it. To our knowledge, this work is the first one which considered the impact of speed of movement on the scale of space representation.

It is very important to have an acceptable performance in mapping from grid cells to place cells. In order to achieve a unique representation of the environment, every place cell must be active in a confined region, i.e. its place field. The RBFN model has a very good performance in encoding every location in the environment, as 100% of place cells showed a single spot activity. ICA was used to model the mapping from grid cells to place cells in [9]. In this model 75% of output units showed a confined activity pattern.

Overall, the proposed model seems to be capable of explaining how grids with different scales of space representation can map to place cells with different spatial scales. Considering neurophysiologically plausible assumptions, the model performed well. In conclusion, it could be proposed that a similar procedure might be implemented in brain.

REFERENCES


