

Episodic Memory and Cognitive Map in a Rate Model Network of the Rat Hippocampus

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Abstract. The hippocampus of rodents seems to play a central role in navigation: place cells are prone to serve as elements of a cognitive map. The hippocampus of primates is apparently involved in episodic memory processes. Here we show how the hippocampi of different species (with their anatomy and physiology being considerably similar) can fulfill both purposes. A network was built from simple rate neurons, synaptic weights were modified by a batch version of the coincidence-based Bienenstock–Cooper–Munro learning rule. The network was trained with temporally contiguous sensory stimuli, and then tested in two different paradigms: (1) for navigational performance, place field profiles were evaluated to allow comparison with experimental data; (2) for memory performance, associative capability was assessed. The same neuron network was found to be able to show place cell properties and function as episodic memory, even when trained with non-topographical stimuli.

1 Introduction

Only few investigators have yet addressed directly the question, how the hippocampi of different species, showing remarkable anatomical and physiological similarity, (or even the hippocampus of the same species) meet demands made by two different functions: navigation and episodic memory. Some of these investigations give only a qualitative description on how this two-fold function could be achieved [10, 12]. Computational models are ideal for making quantitative predictions, but those already dealing with this problem did not attempt to test their network explicitly on both tasks [14, 13, 2]. Quantitative measurements on place cells (firing rate profiles, time necessary to establish place fields, etc.) provide a good basis for assessing navigational performance (although intact place cells were found under conditions when navigation was heavily impaired, see [8]). Episodic memory, however, is more loosely defined [3]. From the various definitions, two criteria can be postulated on a network to function as an episodic memory buffer: it has to be able to perform pattern completion (episodes can

be recalled from their fragments) and to make cross-associations between memories (recall of an episode leads to the recall of preceding or successive episodes – sequence learning is a prominent demonstration of the latter [5, 7, 17], but is usually restricted to associating from earlier to later memory traces).

Another key problem of hippocampal models is the choice of input. Most models use topographical inputs where they presume the similarity of stimuli perceived by the animal at adjacent locations, i.e. the closer two locations are the more similar input patterns belong to them [16, 6, 4]. This approach is ideal for place cell modeling but does not seem to be realistic when addressing episodic memory: it is hard to see why input patterns belonging to consecutive episodes would be more similar than those belonging to temporally more distant events. Thus, as a “worst case” presumption, non-topographical inputs should rather be picked, i.e. the correlation of subsequent stimuli should be minimal.

Based on these considerations we built a neural network that was fed by non-topographical input during training, when a rat was running around on a circular track and thus input sequences were repeated several times. After training, the network was tested both for navigational performance (indicated by properly formed place fields), and for episodic memory performance (bidirectional cross-association between memory traces). This way we intended to directly show under strict conditions (same network, same non-topographical input, two different performance measures) how the apparently two different functions of the hippocampus can be reconciled.

2 Methods

2.1 Network dynamics

The model network of CA3 pyramidal neurons consisted of $N = 40$ units. Cells that had a similar afferentation pattern were grouped into a single unit and characterized by a single scalar, the mean firing rate in the group. Activity values of units were arranged into an activity vector \mathbf{a} . Activity dynamics was described by the following equation:

$$\mathbf{a}(t + 1) = c\mathbf{W}\mathbf{a}(t) + \mathbf{\bar{a}}(pos(t)) , \quad (1)$$

where \mathbf{W} is the weight matrix of recurrent connections, \mathbf{i} is the input vector of external stimulation and $c = 1$ is a scale factor.

Connection weight between two units was considered as the mean of individual connection strengths between neurons of the units. A linear version of the Bienenstock–Cooper–Munro learning rule [1] applied on recurrent networks was used to train connections:

$$\frac{d\mathbf{W}(t)}{dt} = (\mathbf{a}(t) - \vartheta \langle \mathbf{a} \rangle) \mathbf{a}^T(t) , \quad (2)$$

where ϑ is an unlearning factor and $\langle \mathbf{a} \rangle$ is the time average of activities. Here we used a batch version of this learning rule, meaning that connection weights

were updated after $E = 100$ long epochs of iterations without weight changes (for a derivation of this formula, see [15]):

$$\mathbf{W}(t + E) = \mathbf{W}(t) - \mu\mathbf{W}(t) + \frac{\nu}{E} \sum_{t'=t+1}^{t+E} \left(\mathbf{a}(t') - \frac{\vartheta}{E} \sum_{t''=t+1}^{t+E} \mathbf{a}(t'') \right) \mathbf{a}^T(t'), \quad (3)$$

where μ is a decay time constant, and ν is learning speed. Elements of \mathbf{W} were always kept non-negative, diagonal elements were kept at a fixed value of $f = 0.8$, and off-diagonal elements were initialized to 0.

2.2 Stimulus

External stimulus to the network depended on the position of the modeled animal. We examined a rat exploring a one-dimensional circular track in discrete time and space. The circle was divided into $P = 40$ locations. Position on the track was described by $pos(t)$. During exploration the rat moved in one direction along the track, proceeding one step forward with p probability and staying at its position with $1 - p$ probability in each time step.

To describe preprocessed information about the environment we assigned an arbitrary input vector to each position: $\mathbf{i}(pos(t))$. Input vectors were uncorrelated, that was achieved by stimulating only one unit per position and by that each unit was only stimulated in one position (the “driving” position of the unit, note that units were just defined on the basis of common input, see previous section), and for the sake of clarity units were ordered based on their driving positions:

$$i_k(pos(t)) = \begin{cases} 1 & \text{if } k = pos(t), \\ 0 & \text{otherwise,} \end{cases} \quad k = 1, 2, \dots, N \quad (4)$$

where $i_k(pos(t))$ is the k^{th} element of $\mathbf{i}(pos(t))$.

2.3 Evaluation of performance

During training the rat explored the track for $T_{\text{training}} = 1000$ time step. After training, connections were no longer modified and performance of the network was assessed on two different tests. For measuring navigational performance, the rat moved around the track for an other $T_{\text{test1}} = 8000$ time steps, and activity profiles of units were calculated corresponding to experimental characterization of place cell firing profiles [11]. To test memory performance, the network was presented the same input vector for $T_{\text{test2}} = 1000$ simulation steps and activities of cells at the end of this period were recorded. This procedure was repeated for every input vector that was encountered by the network during the training session.

A four dimensional parameter exploration was performed on parameters ν , μ , p and ϑ . At $\nu = 0.3$, $\mu = 0.5$, $p = 0.1$ and $\vartheta = 3.2$ parameter values \mathbf{W} was found to be convergent, and the network sufficiently reproduced the experimental place field data [11] and its memory performance was also satisfactory. This parameter set was used in further simulations.

3 Results

When memory performance of the initial network was examined, each unit responded only to one input vector and was not affected by other inputs (Fig. 1A). Navigational performance was similarly poor, but due to high self excitation and unidirectional movement of the rat, each unit had a small tail of activation on positions following its driving position (Fig. 1B).

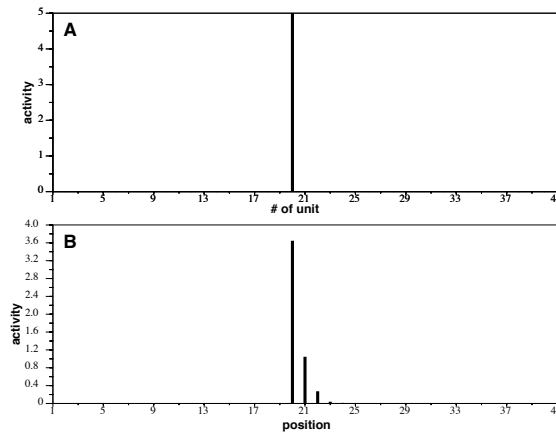


Fig. 1. Performance of the network before training. A: Memory performance. Developing unit activities after the input pattern belonging to position 20 was presented: only unit no. 20 showed activity. (Similar results were obtained with all inputs.) B: Position dependent activity (place field) of unit no. 20. (Similar results were obtained for all units.)

During exploration, spreading of activities could be observed (data not shown): activity of units began gradually earlier and lasted longer at later phases of exploration than at the beginning. This was caused by potentiation of recurrent connections between units, as units began to receive excitation through their intra-network connections well before and after they received external stimulation at their driving position, and in turn, due to the coincidence-based learning rule, this spreading led to further potentiation of recurrent synapses.

Memory and navigational performance of the trained network was different from the initial network. Stimulating the network with an input vector, not only directly driven units showed activity but also units that were driven by stimuli experienced consequently either earlier or later during exploration (Fig. 2A). Similarly, when navigation performance was tested, unit activity did not only occur in the driving position but also at adjacent locations (Fig. 2B), most importantly at locations ahead of the driving position, thus producing realistic firing profiles [11], and reproducing the experience-dependent expansion and

backward-shifting of place fields [9]. Note, that the effects of self-excitations (seen on Fig. 1B) added to the activity at successive positions.

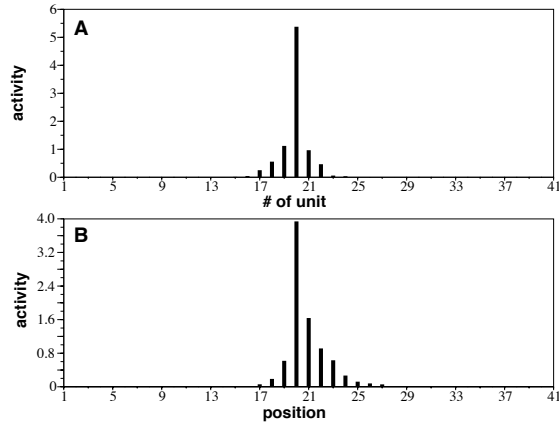


Fig. 2. Performance of the network after training. A: Memory performance. Developing unit activities after the input pattern belonging to position 20 was presented: units driven by preceding and successive inputs were also activated (Similar results were obtained with all inputs.) B: Position dependent activity (place field) of unit no. 20. Note, that its place field expanded asymmetrically backwards compared to its initial size and position of center of mass. (Similar results were obtained for all cells.)

4 Conclusions

We have shown that consistent recurrence of sensory input patterns may convey enough information to establish place sensitive firing patterns. We found a good match between our model results and experimental place field data. Using non-topographical input vectors we did not assume similarity of consecutive stimuli, thus examining episodic memory properties became available in the same network. Presenting an input vector belonging to an episode to the network resulted in partial recall of earlier and later episodes. With this results the same network was shown to have place cell properties and function as episodic memory. This might allow an interpretation that the hippocampus is a more general memory system and is not confined to solve only spatial problems.

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