2009 International Symposium on Nonlinear Theory and its Applications
NOLTA'09, Sapporo, Japan, October 18-21, 2009

Modulation of Memory Retrieval by Spike Train Input with Temporal Pattern

Keita Tokuda† and Kazuyuki Aihara‡

†Department of Mathematical Informatics, Graduate School of Information Science and Technology, The University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-8656, Japan
‡Institute of Industrial Science, The University of Tokyo, Komaba 4-6-1 Meguro-ku, Tokyo 153-8505, Japan
Email: tokudakeita@sat.t.u-tokyo.ac.jp

Abstract—Temporally precise structure of spike trains are widely observed in the brain, such as in hippocampus, but its functional role is not fully elucidated. We demonstrate that different temporal patterns of an identical cell group can modulate differently the retrieval of memory patterns in its downstream network. The downstream network consists of leaky-integrate-and-fire neurons and retrieves memory patterns as cell-assemblies. Each pattern is assigned with a specific temporal sequence of spikes of the upstream network mimicking hippocampal activity. Each pattern is then embedded by spike timing-dependent plasticity, while receiving the spike sequence assigned with it. Retrieval phases take place after the learning phase, where the temporal pattern representing hippocampal cells and noisy input representing a bottom-up signal are given to the network. The network can use both the temporal pattern and the bottom-up input and also represent them with the memorized patterns.

1. Introduction

Temporally precise structure of spike trains are widely known in the brain, but its functional role is not clear [1]. One striking example of the temporally precise sequence of spikes is found in the hippocampus. The spike activities in the hippocampus are known to be locked to the theta rhythm - regular oscillation of the local field potential at 4-12 Hz [4]. Because a specific neuron fires at a specific phase of the theta oscillation, the spike interval of a specific pair of cells is preserved, and this phase-locking activity leads to ordered temporal sequence of the spikes of the neurons. So it is natural to ask whether this spatiotemporal pattern of spikes can be used as information and can be decoded by downstream neuronal network.

The hippocampus is one of the most important circuits in the brain for learning and memory, and thought to play an important role in contextually flexible behavior. Electrophysiological studies showed that hippocampal activity may be able to represent contextual information and change the behavioral response to the external stimuli [2,3]. Taking into account that hippocampus does not receive any direct sensory stimuli nor give direct motor outputs, it is likely that lower-order nervous systems ,which are responsible for dealing with external stimuli more directly, receive top-down signal from hippocampus and their activities are modulated. This dynamics may enable an animal to be able to interpret an external stimulus in accordance with the abstract information held in higher nervous system, which may correspond to such as behavioral context, environmental context or animal's intention. This concept leads us to the question whether the lower-order network, receiving both the bottom-up signal and temporal activity from hippocampus, can utilize both information and represent them.

In this paper we propose an abstract model for the modulatory effect of temporal pattern to downstream memory retrieval. We model the downstream network receiving both temporal spike train from the hippocampus and bottom-up signal from external stimuli. This network behaves as winner-take-all network, and represents the response to the inputs reactivating a memorized cell-assembly. Firstly, a learning phase takes place where each memory pattern is learned. Each pattern is assigned with a specific sequence of upstream spikes mimicking hippocampal activity, and learned while the network receives the assigned sequence. Spike-timing-dependent-plasticity (STDP) is employed in order to make the network able to recognize the temporal structure [5,6]. In the retrieval phase, the network receives external inputs representing the bottom-up signal, which has only ambiguous information to select one of the memorized patterns, and receives temporal pattern inputs from the hippocampal cells. The network is able to represent the response to the stimuli with a cell-assembly employing both the top-down and bottom-up signals.

2. The Model

2.1. The model outline

Figure 1 shows the schematic illustration of the model network we consider, in which leaky integrate-and-fire neurons are recurrently connected. Each integrate-and-fire neuron is connected to all other neurons. In addition, a globally uniform inhibition without modification of learning is included in an all-to-all manner. The spatiotemporal spikes of "hippocampal cells" and bottom-up currents are

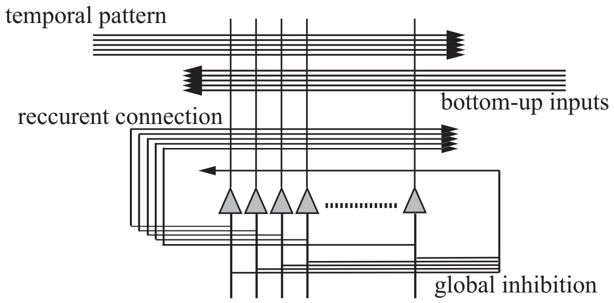


Figure 1: Schematic diagram depicting the structure of the network model

employed as controllable external dynamical inputs.

There are two successive phases in the model: (1) learning phase and (2) retrieval phase. In the learning phase, the model neurons are divided into four groups: A, B, C, D. Each of the them is referred as a memory pattern. Theare are two kinds of spike sequence patterns of hippocampal cells. The memory patterns A and C are assigned to one of them, and the other two, B and D, are assigned with temporally reversed sequence. When synaptic modification takes place, each pattern is activated one by one with noisy membrane currents, while the whole network receives the temporal spike pattern from the hippocampal cells, which is assigned with that memory pattern. In the retrieval phase, the network receives both external currents representing the bottom-up signal and the spatiotemporal pattern from the "hippocampal cells", which is same as the spike trains given to the network in the learning phase. There are two kinds of bottom-up signals. One of them has biased currents into two of the memory patterns: A and B. The other one has biased currents into C and D. We examine whether the memory pattern associated with both the top-down signal and the bottom-up signal is retrieved in the retrieval phase.

2.2. Dynamics of the model

We adopt integrate-and-fire neurons for the network. The subthreshold membrane potential of the ith neuron $V_i(t)$ obeys the following equation:

$$\frac{dV_i(t)}{dt} = -\frac{1}{\tau_m}(V_i(t) - V_{rest}) + I_i^{TOP}(t) + I_i^{REC}(t) + I_i^{I}(t) + I_i^{BOT}(t), \quad (1)$$

where $V_i(t)$ is the membrane potential of the ith neuron, and τ_m is the time constant of neuronal membrane decay, and V_{rest} is the resting potential, and $I_i^{TOP}(t)$, $I_i^{REC}(t)$, $I_i^{I}(t)$, $I_i^{BOT}(t)$ are the input currents from top-down, recurrent connection, global inhibition, bottom-up, respectively. When $V_i(t)$ reaches the threshold voltage, V_{th}, a spike of the ith neuron is generated, and $V_i(t)$ is instantaneously reset to the resting potential, V_{rest}. The synaptic currents are given by the following equations:

$$I_i^{TOP}(t) = \sum_{l}^{M}\sum_{k} w_{il}^{TOP}\exp((\mathrm{t} - \mathrm{t}_\mathrm{l}^\mathrm{k} - \mathrm{d}_\mathrm{il})/\tau_\alpha), \quad (2)$$

$$I_i^{REC}(t) = \sum_{j}^{N}\sum_{k} w_{ij}^{REC}\exp((\mathrm{t} - \mathrm{t}_\mathrm{j}^\mathrm{k} - \mathrm{d}_\mathrm{ij})/\tau_\alpha), \quad (3)$$

$$I_i^{I}(t) = \sum_{j}^{N}\sum_{k} w^{I}\exp((\mathrm{t} - \mathrm{t}_\mathrm{j}^\mathrm{k} - 1)/\tau_\alpha), \quad (4)$$

$$I_i^{BOT}(t) = I_i^0 + D\xi, \quad (5)$$

where w_{il}^{TOP} denotes the strength of the synaptic connections from the jth hippocampal cell to the ith neuron, w_{ij}^{REC} denotes the strength of the recurrent synaptic connection from the jth neuron to the ith neuron, w^I is the strength of the global inhibitory synapses, t_l^k is the time of the kth spike of the lth presynaptic neuron in the hippocampus, t_j^k is the time of the kth spike of the jth presynaptic neuron in the network, d_{ij} denotes the axonal delay from the jth neuron to the ith neuron, I_i^0 is tonic external current and $D\xi$ is Gaussian white noise with zero mean and standard deviation of D. N and M are the number of neurons in the model network and hippocampus, respectively.

2.3. Structure of the spatiotemporal patterns of modulation network

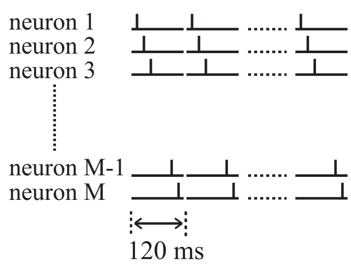


Figure 2: Spatiotemporal pattern of the "hippocampal cells" used as the top-down input.

The activity patterns of the "hippocampal cells" are employed as controllable external inputs. The spike activities are generated and are input to the model network with synaptic connection, w_{il}^{TOP}, from the hippocampal cells to the retrieval network. Figure 2 depicts the construction of the patterns. Each pattern is a repetition of an identical 120 ms long specific cycle. Each hippocampal neuron fires once a cycle at a specific phase. The phase of a neuron is chosen randomly from uniform distribution between 0 and 120 ms. There are two hippocampal patterns employed. One is generated according to the rule mentioned above, and the other is temporally reversed pattern of it for simplicity and comparison. One is assigned with the memory pattern A and C, and the other is assigned with B and D.

2.4. The learning phase

In the learning phase, STDP learning is employed so that the network can recognize the temporal orders of the spikes. The top-down synaptic weights and the recurrent synaptic weights evolve according to the STDP rule illustrated in Figure 3. The magnitude of change of synaptic weight between a pre- and a postsynaptic neuron depends on the timing of spikes: if the presynaptic spike arrives at the postsynaptic neuron before the postsynaptic neuron fires, the synapse is potentiated, and the reverse order results in a decrease of the synaptic weight.

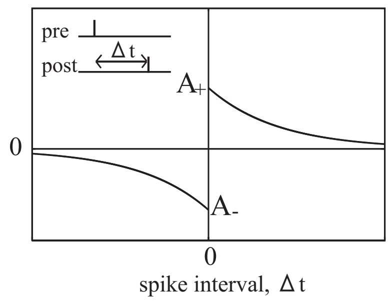


Figure 3: STDP rule.

For each pair of pre- and postsynaptic spikes, the corresponding synaptic weight is modified by $g \rightarrow g + F(t_{post} - t_{pre})$. The STDP function $F(\Delta t)$ is given by the following equation:

$$F(\Delta t) = \begin{cases} A_{+}exp(\frac{-\Delta t}{\tau_{+}}) & \text{if } \Delta t \geq 0 \\ A_{-}exp(\frac{\Delta t}{\tau_{-}}) & \text{if } \Delta t \leq 0 \end{cases} \quad (6)$$

where t_{post}, t_{pre} are the time of spike emission of postsynaptic neuron and the time of spike arrival from presynaptic neuron.

Each memory pattern is activated one by one for 2000 ms by giving incoherent Gaussian noise inputs with tonic mean and deviation to the cells contained in the pattern.

2.5. The retrieval phase

In the retrieval phase, we employ two kinds of bottom-up inputs: I^{BOT_AB} and I^{BOT_CD}. I^{BOT_AB} gives biased membrane currents to neurons contained in patterns A or B, and I^{BOT_CD} gives biased currents to patterns C and D. The tonic value of mean of external current, I_i^0, depends on which bottom-up signal is used: $I_i^0 = 2$ if the ith neuron is contained in the biased patterns, and otherwise $I_i^0 = 0$. The bottom-up input gives currents to two of the memory patterns, so that there is not enough information in a bottom-up signal to select one memory pattern.

The dynamics of the network is examined under four conditions, which means all the combinations of two hippocampal inputs and two bottom-up inputs. A simulation of 5000 ms is conducted and the spike rate for each memory pattern is calculated.

2.6. Simulation results

The number of the neurons, N, is 400, which means there are 100 neurons in each memory pattern. The number of hippocampal cells, M, is 20. We set the model parameters as follows: $V_{rest} = -65$, $V_{th} = -50$, $\tau_{\alpha} = 4ms$, $w^{I} = 1$, $A_{+} = A_{-} = 3$, $\tau_{+} = \tau_{-} = 20$. Each value d_{ij} was selected from uniform distribution over [1 20]. In learning phase, each memory pattern is activated by Gaussian noise with mean of 1 and standard deviation of 2 mV. The initial values of w^{TOP} and w^{REC} are set at 0.5.

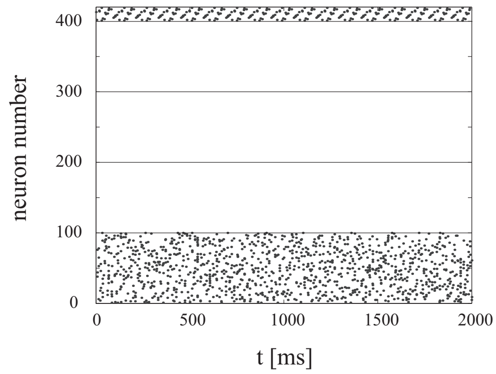


Figure 4: Activated memory pattern "A" in the learning phase.

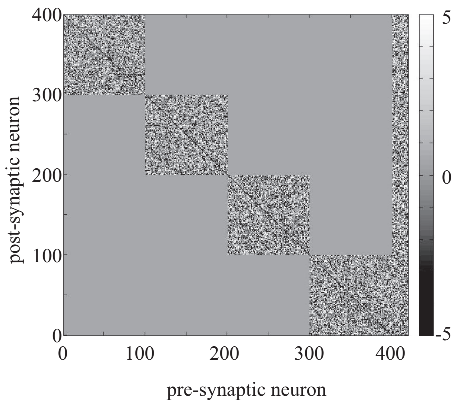


Figure 5: Plot of the strengths synapses after the learning

Figure 4 illustrates a typical activated pattern in learning phase. In this figure, the pattern A is activated by noisy membrane currents. The repetitive hippocampal spike activity employed as controllable top-down inputs is plotted at the top.

Figure 5 illustrate a typical example of the strengths of recurrent synapses and top-down synapses after the STDP learning. The presynaptic hippocampal cells are numbered 401 to 420, and illustrated with the network neurons. The synaptic connections within each group have been modified in the learning phase. This synaptic modification leads to the characteristics of winner-take-all network.

Figure 6 shows an example of the network dynamics in the retrieval phase. In this case, $I_i^{BOT\_AB}$ is given to the network as a bottom-up input, and the temporal sequence of the hippocampal cells is same as which is paired with pattern A and pattern C in the learning phase. The firing frequency of the pattern A ,which is associated with both the hippocampal inputs and bottom-up signal, is high.

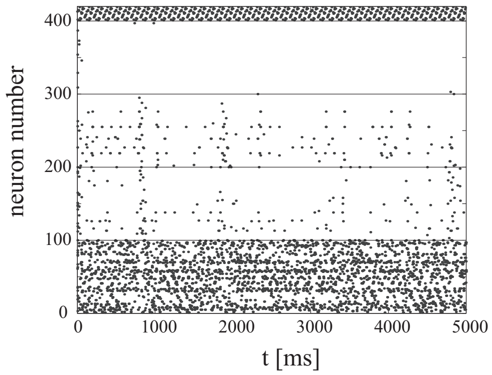


Figure 6: Typical retreival dynamics with I^{BOT_AB} and temporal input assigned with A, C.

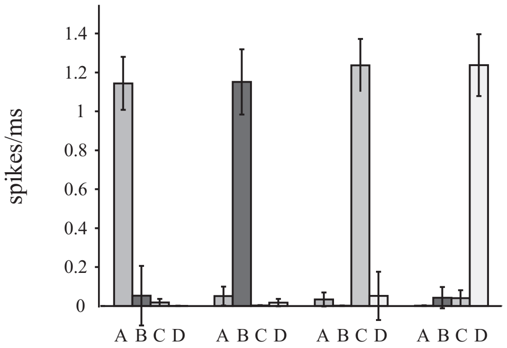
Figure 7 compares the spike rates of the patterns under all four conditions in retrieval phase. A set of a learning phase and a retrieval phase is simulated for 100 times, and the numbers of spikes rate in each of the memory patterns in the retrieval phase is averaged. In all four cases, the spike rate in one pattern is high, and the pattern is the one which receives biased bottom-up signal and has been paired with the given top-down signal. Note that each hippocampal cell project to all of the neurons in the network, and the synaptic weights are fixed in the retrieval phase for all of the four conditions.

2.7. Discussion

We proposed a model, in which a network utilizes both the information of noisy bottom-up input and the temporal spike sequence from another cell group, and represent them by reactivating the embedded cell assembly. To make the network able to recognize the temporal pattern of the spikes, spike-timing-dependent plasticity is employed to determine the synaptic connections. Although the cell group giving the temporal spike trains is referred as hippocampus, we assume that the same dynamics can be used to decode temporal codes and to represent them as spatial assemblies in a number of different brain areas.

Acknowledgments

This research is partially supported by Grant-in-Aid for Scientific Research on Priority Areas - Higher-Order Brain Functions-(17022012) from MEXT of Japan.



Top-down	A, C	B, D	A, C	B, D
Bottom-up	A, B	A, B	C, D	C, D

Figure 7: Spike rate of each pattern under four conditions. The nunmer of spikes in each group per a millisecond is calculated. Each bar indicates the spike rate average of each memory pattern for the condition indicated below: conbination of the top-down and the bottom-up signals.

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