

Effect of Long-delay Connections to Realize a Self-Organization of Firing Patterns that Vary Smoothly in Space

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Abstract. Many experimental results suggest that more precise spike timing is significant in neural information processing. We construct a self-organization model using spatiotemporal patterns, where Spike-Timing Dependent Plasticity (STDP) tunes the conduction delays between neurons. The recurrent connections with a specific conduction delays are strengthened when the input patterns are changing at a certain period. We show that, by cooperating with short delays, long-delay connections realize topological mapping where the firing clusters are changing smoothly in space.

1 Introduction

As a well-known clustering network in brain, there are column organizations in cerebral cortex, where neurons are arranged to preserve sensory topological structure [1]. Recently experimental evidence from several different preparations suggests that both the direction and magnitude of synaptic modification arising from repeated pairing of pre- and postsynaptic action potentials depend on the relative spike timing[2]. Song et al showed that an orderly topological map can arise solely through Spike-Timing Dependent Plasticity (STDP) from random initial conditions without global constraints on synaptic efficiencies, or additional forms of plasticity[3]. However, despite using the millisecond-scale model, the patterns are composed of high firing-rate Poisson inputs, and the meaning of temporal causal relationship is not clear.

On the other hand, many experiment results suggested that the more precise spike timing accomplish the key role in the brain. For example, multiunit recording studies from the frontal cortex of behaving monkey suggested that a spatiotemporal pattern of highly synchronous firing of neural populations can propagate through several tens of synaptic connections without losing high synchronicity[4]. This phenomenon is called "synfire-chain", which brings to that the neurons with long time-constant can convey the information keeping with the precise spike-time information. Diesmann et al showed that through multi-layered Feed-Forward network with Integrate & Fire neuron model, the pulse

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packet can propagate stably in the presence of background noise if the number of neurons in a pool is large enough and yet the igniting pulse packet is synchronized strong enough [5]. This propagation is due to exact timing of the excitatory inputs. Hence, it reflects temporal coding. Additionally, several studies provide that the heterogeneous structure of the network such as the Mexican-Hat-type connectivity can convey the quantitative information [6]. Similarly, Aviel et al showed that by adding inhibitory pool, synfire-chain can be embedded in a balanced network [7]. This network can also utilize the quantitative information.

In primary visual cortex (V1), responses of neurons to a stimulus presented in their receptive fields are modulated by another stimulus concurrently presented in their surrounds. Such a contextual modulation suggests an interaction between feedback connections to V1 from other areas [8].

In this paper, we show that, by using localized synfire-chain patterns, STDP can strengthen the synaptic efficiencies having specific conduction delays and then form self-organizing map whose patterns are expressed as firing clusters. Next, we consider the case that a network is composed of synaptic connections with two types of conduction delays. We show that, by cooperating with short delays, long-delay connections cause topological mapping where the firing clusters are changing smoothly in space.

2 Model

We use a simple Integrate & Fire neuron model, and the membrane potential V is determined as

$$\tau_V \dot{V} = -(V - V_S) + J_E(t)(V - V_E) + J_I(t)(V - V_I)$$

with $V_S = V_I = -70.0\text{mV}$, $V_E = 0.0\text{mV}$, and $\tau_V = 5\text{ms}$. The synaptic inputs G_E and G_I are expressed as spatiotemporal integration of synaptic efficiencies characterized by step rise time and exponential decay

$$J(t) = \sum_j W_{ij} \sum_{t_j^k} \Theta(t - t_j^k) \exp(-(t - t_j^k)/\tau). \quad (\cdot = E, I) \quad (1)$$

where $\Theta(t)$ is step function and the time-constant is chosen as $\tau_E = \tau_I = 5.0\text{ms}$. The synaptic strength W_{ij} is a transmission efficiency of the connection. All efficiencies from inhibitory neurons are assumed to have negative values (Inhibitory synapses), while all from excitatory ones are positive (Excitatory synapses). W_{ij}^I corresponding to the inhibitory ones are chosen as the constant values whose range is $[0.18, 0.22]$. On the other hand, W_{ij}^E correspond to excitatory neurons are modified via STDP whose range is $[0, 0.05]$. When the membrane potential V reaches a threshold value $V_{thr} = -54\text{mV}$, the neuron fires and the membrane potential is reset to $V_{res} = -60\text{mV}$. After firing, $G_{E,I}$ is kept zero during 3ms (absolute refractory period). On these conditions, about 20 coincident excitatory spikes elicit firing.

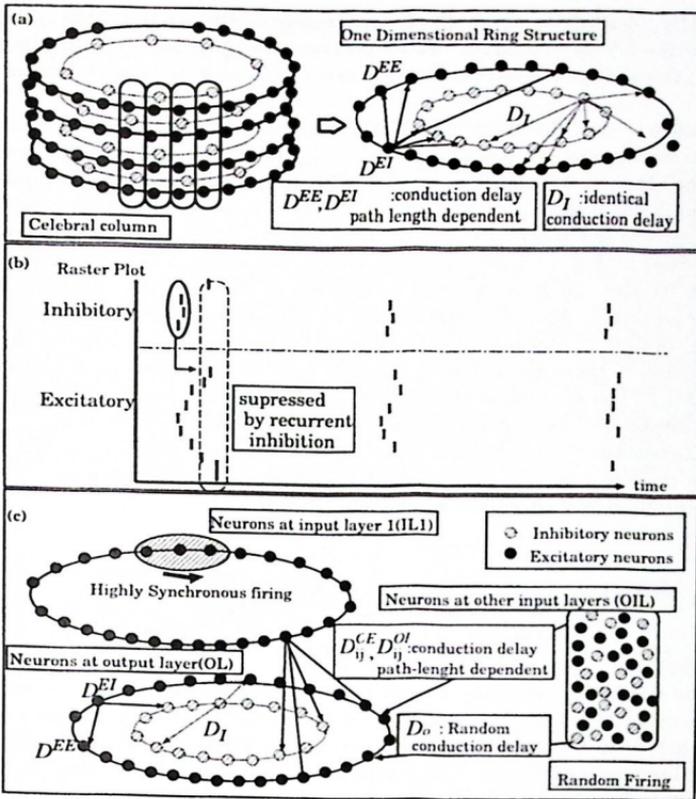


Fig. 1. (a) A network model. (b) Typical behavior of this network. (c) The whole system of this model. There are two types of inputs.

The model neural network is schematically shown in Fig. 1(a)[9]. In many brain areas, the temporal precision of spikes during stimulus-locked responses can be in the millisecond range. Reproducible temporal structure can also be found. Therefore, "delay tuning mechanism" is needed. From this viewpoint, we regard the role of STDP as a tuning of the conduction delays of the neurons. Some experiments results in cerebral cortex suggest that local inhibitory circuits contribute to improve the orientation selectivity [10]. We, therefore, determined that the inhibitory neurons receive common inputs with the excitatory ones, and consider the case that the recurrent inhibitory conduction delays D_{ij}^{IE} , D_{ij}^{II} have an identical short value $D^I = 1.0\text{ms}$. Since the excitatory and inhibitory neurons receive inputs from common layer, their firing patterns are similar to each

other. After short delay D^I , both of them receive inhibitory recurrent spikes and suppress the firings of neurons, whose postsynaptic spike latencies are large. As a result, this network detects coincident firing neurons with short latencies (Fig. 1(b)).

We assume that the input layer 1 (IL1 in Fig1(c)) has 100 excitatory neurons, of which 25 neurons fire synchronously with a small fluctuation of dispersion σ , while the other 75 neurons fire randomly (10Hz Poisson spikes). Gamma-band oscillations are widely observed in brain [11]. Therefore, we determined that input patterns are firing periodically with a 25ms interval. Each synchronized sets are represented 4 times repeatedly. Hence, the patterns are shifted at 100ms interval. At first, we chose a set of 25 neurons as the spatially continuous ones forming a pattern. After the interval, the 25 neurons are shifted. This condition yields a continuously changing pattern in which each center position of the neurons represents the stimuli. This is a simple case, while general case is discussed in Section 3. The neurons at the Output layers (OL) also receive 100 excitatory and 50 inhibitory inputs firing randomly at other input layers (OILs).

We determine the conduction delay D_{ij}^{OE} , from input neuron i at IL1 to excitatory neuron j at OL, proportional to distance in such a manner that the periodical boundary condition is satisfied. That is

$$D_{ij}^{OE} \propto |i - j| \bmod N \quad (2)$$

where i and j are neuron indices, and we define

$$|i - j| \bmod N \equiv \min(|i - j|, N - |i - j|) \quad (3)$$

Since the number of inhibitory output neurons is half of the input-neurons number, the delay D_{ij}^{OI} from input neuron i at IL1 to the inhibitory neuron j at OL is determined to be proportion to $|i - 2j| \bmod N$, which should also satisfy periodical boundary condition. The maximum conduction delay is 3ms, while the minimum is 0ms. The probability that an input neuron is connected to output neuron is 0.8, and the initial values of the synaptic strength are chosen about the

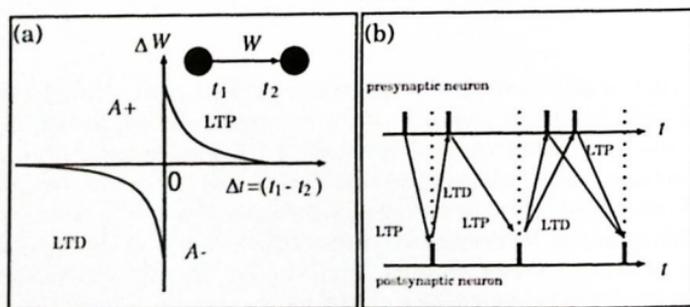


Fig. 2. (a) Window function of STDP. (b) Time Diagram showing that only spike pairs connected by arrows contribute to plasticity (near-neighbor interaction).

half of the maximum. STDP was implemented only for the excitatory synapses of the output layer's neurons,

$$\Delta W = \begin{cases} A_+ \exp(-\Delta t/\tau_+) & \Delta t > 0 \\ A_- \exp(-\Delta t/\tau_-) & \text{otherwise} \end{cases} \quad (4)$$

where A_+ and A_- are the sizes of the synaptic modification by a single STDP event. We chose $A_+ = 0.02$, $A_- = 0.025$, and $\tau_+ = \tau_- = 20\text{ms}$. LTD is implemented only after the latest firing and LTP is implemented after the last firing (near-neighbor interaction). When one firing pattern is presented, the input spikes elicit a postsynaptic response, triggering the STDP rule. Synapses carrying input spikes just preceding the postsynaptic ones are potentiated, later ones are depressed. This modification causes a decrease of the postsynaptic spike latency, firing threshold will be reached sooner. Consequently, some synapses it had previously potentiated are depressed and different synapses are reinforced which carry even earlier spikes than the preceding time. By iteration, the postsynaptic spike latency will tend to stabilize at a minimal value while the first synapses become fully potentiated and later ones fully depressed[12].

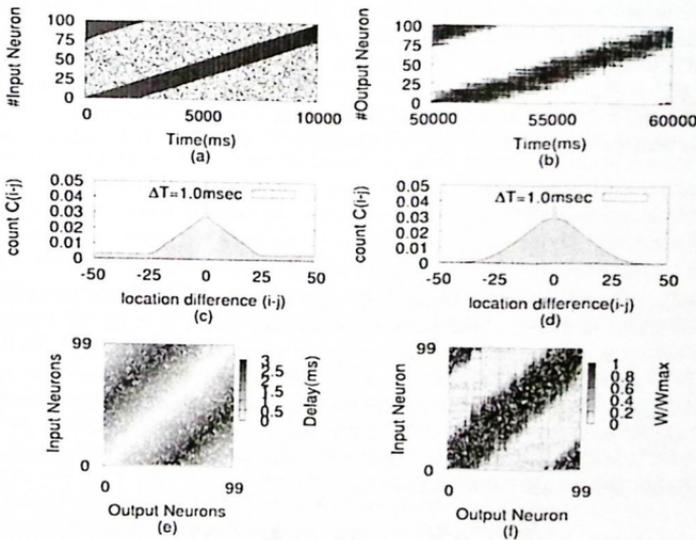


Fig. 3. (a) Spike raster showing the activity of the neurons at Input Layer 1. (b) Raster plot of excitatory neurons at Output Layer. (c)(d) Coincident clustered histogram of (a),(b). (e) Conduction delays map. (f) Weight distribution.

In this network, inhibitory neurons receive similar inputs to excitatory neurons and excitatory synapses of inhibitory ones are modified. Therefore, the changes of the postsynaptic spike latencies of inhibitory neurons are almost in keeping with excitatory ones. Therefore, this network can work as a coincidence detector, even if the synaptic efficiency has changed during learning.

To investigate a degree of spatiotemporal clustering, we calculated "coincident clustering histogram". If a difference of firing time of two neurons is within a time bin ΔT , we considered that these two neurons are coincident, and computed spatial difference histogram $\sum_k c_k(i-j)$,

$$c_k(i-j) = \begin{cases} 1 & |t_i^k - t_j^k| < \Delta T \\ 0 & \text{otherwise} \end{cases} \quad (5)$$

where t_i^k denotes the firing time of neuron i for input pattern k . The simulation result is shown in Fig. 3. The synapses only with shortest conduction delays survive and others were pruned. It also reduces noise firing. As a result, STDP refines the patterns.

3 Topological Map

Next, we consider the more general input patterns to relate this model with the topological map. In the topological map, the input patterns near to each other are mapped into spatially similar firing clusters. Here, we denote the firing patterns, $\xi^k = \{\xi_1^k, \dots, \xi_j^k, \dots, \xi_N^k\}$ where j is the neuron index at IL1 (the maximum $N = 100$) and k is the pattern index switched at a certain interval. If the neuron j fires synchronously with others, we denote $\xi_j = 1$. We assume that ξ^k satisfies

$$\sum_j \xi_j^k = R \quad (\forall k = 1, 2, \dots, N) \quad (6)$$

$$\xi^1 \cdot \xi^2 = \xi^2 \cdot \xi^3 = \dots = \xi^N \cdot \xi^1 = Rm \quad (7)$$

where m is the overlap of patterns. The high m means continuous pattern shift. In the previous sections, these parameters are kept with $R = 25$, $m = 0.96$.

In Section 2, the set of synchronous firing neurons was spatially continuous. Here, as a substitute for random conduction delays, we consider the case of shuffled input patterns. We choose a pair of neurons randomly, and exchange the indices of the neurons M times. We determined the shuffling times as $M = 400$ except the result of Fig. 4(a), $M=100$. After this shuffling, the firing pattern η^k also satisfies the condition expressed as

$$\sum_j \eta_j^k = R \quad (\forall k = 1, 2, \dots, N) \quad (8)$$

$$\eta^1 \cdot \eta^2 = \eta^2 \cdot \eta^3 = \dots = \eta^N \cdot \eta^1 = Rm \quad (9)$$

We determined the dispersion of the synchronized pattern as $\sigma = 3.0\text{ms}$. These patterns with large dispersion are considered to correspond to the Poisson input

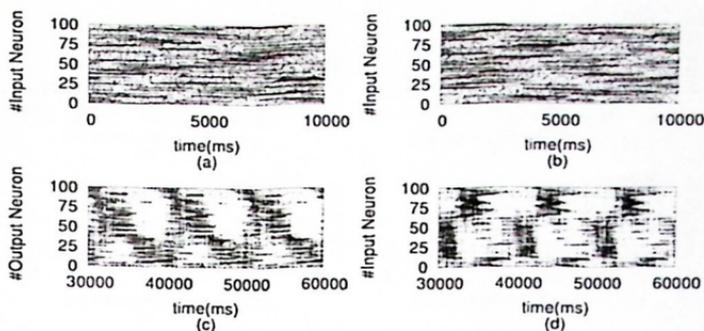


Fig. 4. Topological Mapping. Two typical output patterns are shown. (a),(b) Raster plot of the neurons at IL1. (c),(d) Raster plot of the excitatory neurons at OL.

patterns[3]. The recurrent synapse is needed to form a smoothed map. We determine the conduction delay D_{ij}^{EE} from excitatory neuron i to excitatory neuron j in proportion to $|i - j| \bmod N$ in the range of $[0.5, 1.5]$. We also determined the delay D_{ij}^{EI} from excitatory neuron i to inhibitory neuron j in proportion to $|i - 2j| \bmod N$ in the same range. Hence, some of the neighboring connections are shorter than the identical inhibitory conduction delay $D^I = 1.0\text{ms}$. The initial synaptic efficiencies are also determined in proportion to $\frac{N}{2} - |i - j| \bmod N$ in the range of $[0.25W_{\max}, 0.75W_{\max}]$, where W_{\max} is the maximum efficiency ($W_{\max} = 0.05$). In this paper, we assumed that there is only one neuron in each column ($m = 1$). In cerebral cortex, however, there are much more neurons than those in this model. It is reasonable that not all the neurons in a column fire for each pattern. Some firings can cause the long-term potentiation of the other connections that were not considered in this network model. Taking this into consideration, the modification parameters of recurrent connections B_{\pm} are not necessarily the same values as those of external connections A_{\pm} . We, therefore, determined the sizes of the synaptic modifications for recurrent connections as $B_{+} = 0.02$, $B_{-} = 0.015$.

The result is shown in Fig. 4 and Fig. 5. Two types of results are shown. In Figs. 5(c) and (d), the gentle peak shows a synchronicity despite the asynchronous input. Figures 5 (e) and (f) show the change of the center position of the firing neurons in each pattern. Figure 5 (f) shows that the center position does not vary smoothly. This result suggests that the external stimulus is coded into the highly-synchronously and spatially-continuously clustered firing. However, such clusters do not always vary smoothly in space.

4 Interaction to different area

In this section, we investigate effects of interactions of two neurons distant from each other. We considered two types of conduction delays. For local connection,

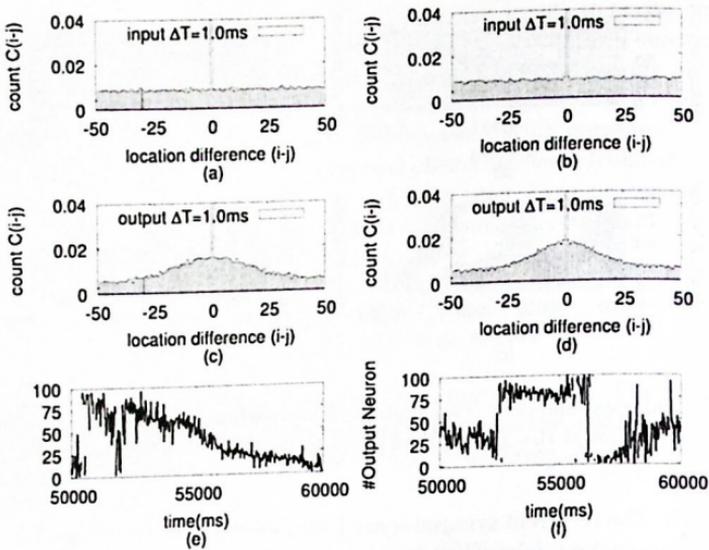


Fig. 5. (a,b) Coincident clustering histogram for input neurons. (c,d) Coincident clustering histogram for output neurons. (e,f) The center position of neurons firing in each pattern.

the synaptic delays are chosen in proportion to the location indices. With a probability p , the synapse is determined to connect to neurons to a distant area. We chose the conduction delays,

$$D_{ij}^{EE} = \begin{cases} N(1, 15) & \text{Probability } p \\ |i - j| \bmod N + 0.5 & \text{otherwise} \end{cases} \quad (10)$$

where N means a Gaussian and the conduction delays from distant area are determined to have a value in the range of $[1, 30]$. The center position of the neurons firing for the certain patterns is considered to code a kind of information such as location. We calculate a regression line of the center positions of the neurons for all patterns. Since the patterns are changing in a certain period, a trend of the recurrence is assumed to have a constant value. Therefore, we calculate a y -intercept value to give a minimum value of mean squared error as an index showing a smooth changing of the clusters.

$$\begin{aligned} E_+(b)^2 &\equiv \min_b \sum_k (y_i - 0.01(x_k - b))^2 \\ E_-(b)^2 &\equiv \min_b \sum_k (y_k + 0.01(x_k - b))^2 \\ E(b) &\equiv \min_b (E_+(b), E_-(b)) \end{aligned} \quad (11)$$

Figure 6 shows the result. With a small probability ($p \sim 0.1$), the clusters are

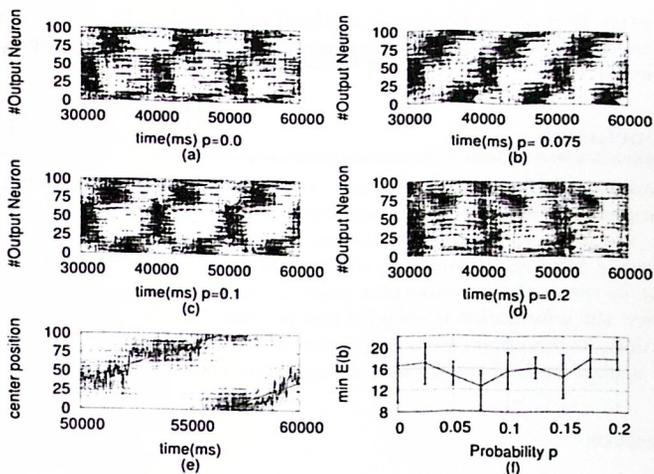


Fig. 6. (a),(b),(c),(d) Examples of raster plot of output neurons for various initial conditions. (e) A regression line for center position of the neurons. (f) Average Error for different probability values p .

changing smoothly.

5 Discussion

The neurons in a primary visual area show different behavior depending on the stimuli concurrently presented in their receptive-field surrounds. Such modulations are considered to be caused by interactions from different area. We investigate the effects of long-delay connections when the input patterns are changing in a certain period. Recurrent connections are needed to form the firing clusters. However, such clusters are not always varying smoothly in space. The long-delay connections help to interpolate clusters that might be changing discontinuously. When the neurons receive discontinuously changing patterns, the firing clusters can vary smoothly in space. Through STDP, synaptic efficiencies are modified depending only on the pre- and post-spike timing of each firing. Respective changing in efficiency can not utilize information of the whole patterns. A highly adaptable initial condition is needed to organize itself suitably to environment. We showed that an appropriate existence of long-delay connections interpolates firing clusters, which leads to the organization of firing clusters varying smoothly in space.

In pattern recognition, the network learns patterns by using only small set of samples. It is important ability for a network to retrieve patterns similar to learned ones without being affected by small perturbations. On the other hand,

the receptive field of the neurons is confined only locally. Therefore, a mechanism to modify randomly changing patterns into smoothly changing ones is also needed in the brain.

6 Conclusion

We demonstrated that self-organization with locally synchronized patterns can be performed by tuning the conduction delays between neurons. Through STDP, spatially and temporally random patterns are bunching. The long-delay connection causes a topological mapping where such bunching clusters are changing smoothly in space. As an important point in neural research, there is a question of how the information is encoded and processed in the brain. These results suggest that, as temporal rate is translated into the firing frequency, the neural network utilizes both of temporal and population codes.

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