

Self-Organization of Clusters Having Locally Distributed Patterns for Highly Synchronized Inputs

Toshio Akimitsu, Yoichi Okabe, and Akira Hirose

Abstract—Many experimental results suggest that more precise spike timing is significant in neural information processing. We construct a self-organization model using the spatiotemporal patterns, where Spike-Timing Dependent Plasticity (STDP) tunes the conduction delays between neurons. We show that, for highly synchronized inputs, the fluctuation of conduction delays causes globally continuous and locally distributed firing patterns through the self-organization.

Keywords—self-organization, synfire-chain, Spike-Timing Dependent Plasticity, distributed information representation

I. INTRODUCTION

MULTIUNIT recordings from the frontal cortex of behaving monkey suggest that a spatiotemporal pattern of highly synchronous firing of neural population can propagate through several tens of synaptic connections without losing high synchronicity[1]. This phenomenon is called "synfire-chain", which implies that exact spike timing is utilized in information processing.

Modeling studies showed that the pulse packet can propagate stably in the presence of background noise if a fully large number of neurons in a pool are firing and the synchronization is strong enough [4], [5]. This propagation implies that the neurons with long time-constant can convey information, with the precise spike timing preserved.

Additionally, several studies suggest that the dynamical changes in synchronized cell assemblies are equivalent to the coding of information in external stimuli. Hamaguchi et al. showed that in a feed-forward network, synchronized population can convey the quantitative information when the neurons have Mexican-Hat-type connections between layers [7]. Similarly, Aviel et al. showed that by adding inhibitory pool to a homogeneous feed-forward network, synfire-chain can be embedded in the balanced network[3]. This network can also utilize the quantitative information.

In a primary visual cortex, neurons are arranged to preserve sensory topological structure. The input patterns near to each other are mapped into spatially similar firing clusters.

On the other hand, in an inferotemporal cortex (IT), which is the last primary visual area along the ventral visual pathway, it is considered that distributed firing patterns represent information. IT neurons respond to complex object features such as a particular shape or a combination of shape. Experimental results suggest that IT neurons located near to one another often respond to the stimuli that are similar to each

other[12]. However, other results suggest that the selectivity of the neurons is quite different from that of their adjacent neurons[9].

In this paper, we show that self-organization is realized using locally synchronized input patterns. If the localized patterns are highly synchronized, the fluctuation of conduction delays causes the distributed information representation. These results suggest that STDP forms highly synchronous cell assemblies changing through external stimuli. This strategy can be crucial to solve binding problems.

II. SELF-ORGANIZATION USING LOCALLY SYNCHRONIZED INPUT PATTERNS

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

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

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

$$G_{E,I}(t) = \sum_j W_{ij}^{E,I} \sum_{s_k} \Theta(t - s_k) \exp(-(t - s_k)/\tau_{E,I}) \quad (1)$$

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). The strength 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, the strength W_{ij}^E corresponding to excitatory neurons are modified via STDP whose range is $[0, 0.05]$. When the membrane potential V reaches a threshold value $V_{\text{thr}} = -54\text{mV}$, the neuron fires and the membrane potential is reset to $V_{\text{res}} = -60\text{mV}$. After firing, $G_{E,I}$ is kept zero during 3ms (absolute refractory period). On these conditions, about 20 coincident excitatory spikes elicit firing.

The model neural network is schematically shown in Fig. 1(a). Based on column structures of cortical neurons, the model network is composed of one-dimensional N columns having m neurons, which satisfies the periodical boundary condition. In this paper, we define $m = 1$. The network consists of excitatory and inhibitory rings connected to each other. We chose that the excitatory ring has 100 neurons and the inhibitory one has 50 neurons.

In many brain areas, the temporal precision of spikes during

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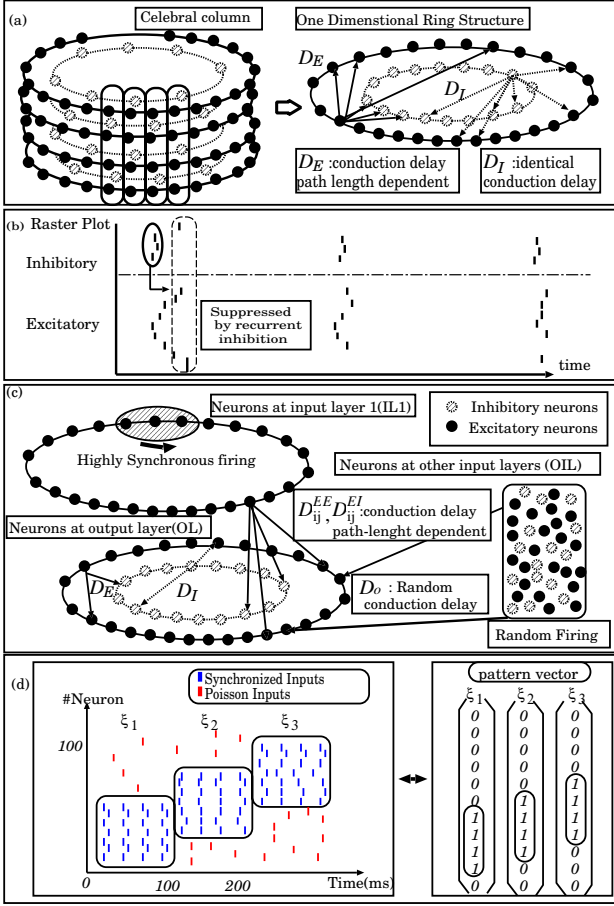


Fig. 1. (a) Network model. (b) Typical Behavior of the network, which detect synchronized firing. (c) Two types Input. (d) Schematic Illustration of input patterns.

stimulus-locked responses can be in the millisecond range. Reproducible temporal structure can also be found. Therefore, a “delay tuning mechanism” is expected. 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 [12]. 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 these inputs 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 Fig. 1(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 [8]. Therefore, we determined that input patterns are changed with a 25ms interval. We chose a set of 25 neurons as the spatially continuous ones forming a pattern. We determined that each synchronized set is represented 4 times repeatedly. After the interval, the 25 neurons are shifted. This condition yields a continuously changing pattern in which each center positions of the neurons represents the stimuli. The neurons at the Output layers (OL) also receive 100 excitatory and 50 inhibitory inputs firing randomly at other input layers (OILs). Fig. 1(d) shows schematic illustration of this inputs.

We determine the conduction delay D_{ij}^{OE} , from input

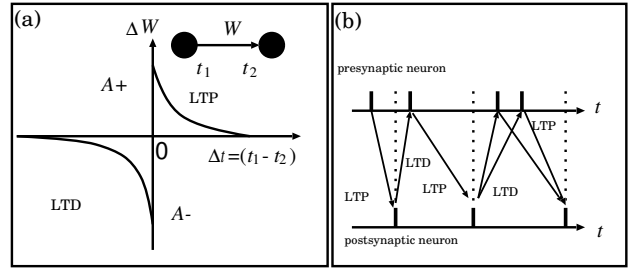


Fig. 2. (a) Window function of STDP. (b) Time Diagram shows that only spike pairs connected by arrows contribute to plasticity (near-neighbor interaction).

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 half of the maximum. In this section, we consider the case that there is no recurrent excitatory connection. STDP was implemented only for the excitatory synapses of the OL neurons. The change of the synaptic strength ΔW caused by a single STDP is expressed as

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

where A_+ and A_- are the maximum magnitude of the synaptic modification. We chose $A_+ = 0.02$, $A_- = 0.025$, and $\tau_+ = \tau_- = 20\text{ms}$. LTD occurs only after the latest firing, and LTP does after the last firing (near-neighbor interaction). When one firing pattern is presented, the input spikes elicit a postsynaptic

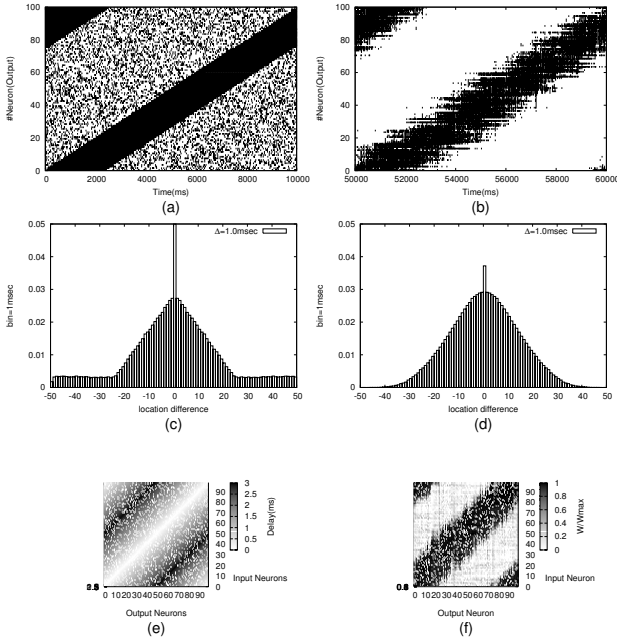


Fig. 3. Simulation results. (a) Conduct Delays map. (b) Weight distribution. (c) Raster plot.

response, triggering the STDP. Synapses carrying input spikes just preceding the postsynaptic ones are potentiated and those with later ones are depressed. This modification causes a decrease of the postsynaptic spike latency. Hence, at the next time, when the same input pattern is presented, firing threshold will be reached sooner. Consequently, some synapses that were previously potentiated are depressed. At the same time, the input may potentiate other synapses concerning proceeding spikes. By iteration, the postsynaptic spike latency will tend to be stabilized at a minimal value. That is, the first-spike synapses become fully potentiated, while later firings are fully depressed [6].

In this network, inhibitory neurons receive inputs similar to those that excitatory neurons receive, and excitatory synapses to inhibitory neurons are modified. The changes of the post-synaptic spike latencies of inhibitory neurons are almost in keeping with excitatory ones. Therefore, this network can detect coincident firings, 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

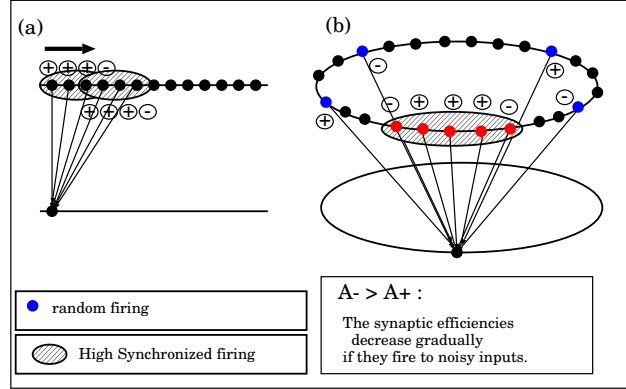


Fig. 4. Schematic illustration of self-organization. (a) The case that there is no inhibitory feedback inputs. (b) This model.

pruned. It also reduces noise firing. As a result, STDP refines the patterns.

We consider a mechanism of this self-organization. If there is no feedback from the inhibitory neurons at OL and all the neurons at IL1 synchronize, only synapses with the shortest conduction delays are strengthened. However, in the case that only a part of input neurons fire synchronously, if the number of the synchronized neurons are enough small, all neurons at OL fire after receiving the input spike arriving. Then, all synaptic connections are strengthened (Fig. 4(a)).

On the other hand, in the case that inhibitory feedback inputs suppress the firings, only neurons having short conduction delays fire, and modify their synaptic connections. Moreover, in this situation, other input neurons fire randomly. Such firings of input neurons contribute to LTP and LTD in the almost same probability. Since a modification value A_- is larger than A_+ , the connections for the neurons are depressed gradually. Therefore, the mechanism of the synchronous firing detection by the inhibitory neurons brings the effect of leaky integration in synaptic modification (Fig. 4(b)).

Thus, the inhibitory recurrent connection causes coincident detection, and the network having short conduction delays is organized through STDP.

III. MOTIVATION

In Section II, we showed that self-organization can be realized using locally synchronized input patterns. We previously showed that in this model an orderly topological map is formed using locally synchronized input patterns[2]. In higher brain area, since neurons receive inputs from many area, it is considered that the locally various firing patterns are needed to represent the various information with a limited number of neurons. We consider that an output layer consists of N neurons, out of which K neurons fire for each pattern. Then there are $\binom{N}{K}$ types of firing patterns. However, if firing neurons exist locally continuous, there exist only N kinds of firing patterns. In order to express the difference in each pattern, locally discontinuous firing patterns are required.

In animal brain, neural selectivity in IT is more complex

than that in a primary visual cortex [12]. An experimental result of optical imaging showed that there are spots specifically activated by a certain shape, and the position of activating spot changes gradually along the cortical surface as the stimulus is rotated in depth[11]. On the other hand, the selectivity of the neurons is quite different from that of their adjacent neurons[9].

Wada et al. proposed a self-organization map model trained with inputs randomly generated from two rings embedded in a three dimensional unit sphere[10]. In their model, the network has local and random intra-layer connections. They showed that the large distance of two rings causes the globally continuous and locally distributed firing patterns, while the small distance causes locally continuous firing patterns. They concluded that the difference between the information representation of V1 and IT cortices is caused by a difference in the input space structures.

In their model, patterns are coded based on the mean firing rate. However, recently there exists many experimental results that suggest more precise spike timing plays a key role in the brain. In this paper, we treat the problem of the self-organization of clusters having locally distributed patterns using synchronized input patterns.

IV. MODEL

Next, we consider the model having fluctuated conduction delays. Fig. 5 shows a schematic image of this model.

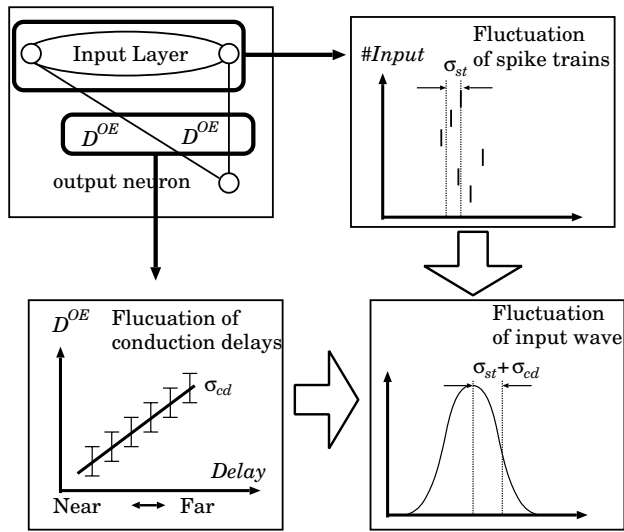


Fig. 5. Two types of fluctuation of input waves.

We denote a firing time of neuron i at IL1 as $t_i^I(k)$. If a mean firing time of pattern k as $T(k)$, the firing time $t_i^I(k)$ of neuron i is expressed as $T(k) + t_i^{st}(k)$, where $t_i^{st}(k)$ is the variance of firing time which depend on $N(0, \sigma_{st}^2)$. We denote a time of this spike arrival for neuron j as $t_j^O(k)$. Then the time $t_j^O(k)$ is expressed as

$$t_j^O(k) = T(k) + t_i^{st}(k) + D_{ij}^{OE} \quad (6)$$

We denote the mean and the variance of the conduction delays from IL1 to OL as D_{ave}^O and σ_{cd}^2 . Eqn.6 is expressed as

$$t_j^O(k) = T(k) + D_{ave}^O + t_i^{st}(k) + d_{ij}^O \quad (7)$$

where $t_i^{st}(k) + d_{ij}^O$ is depend on $N(0, \sigma_{st}^2 + \sigma_{cd}^2)$. We consider the influence on these fluctuations for the self-organization.

We simulated for two different sets of fluctuation of dispersion (σ_{st}, σ_{cd}). We determined that input patterns are changed with a 25ms interval. At first, we chose a set of 30 neurons as the spatially continuous ones forming a pattern. Each synchronized set is represented 4 times repeatedly. Hence, the patterns are shifted at 100ms interval. After the interval, the 30 neurons are shifted.

After learning, we use 10 input patterns each of which is represented 40 times. Each pattern is shifted at 1000ms interval. Fig. 6 shows the raster plot of the input patterns.

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 $B_+ = 0.02$, $B_- = 0.015$.

Each neuron at OL connects to their neighboring 20 excitatory neurons. We determined that the recurrent excitatory conduction delays D_{ij}^{EE} , D_{ij}^{IE} have an identical short value $D^E = 0.5$ ms. If the neurons receive large recurrent excitatory inputs, the neurons can continue firing without inputs from IL1. To avoid this bursting, the strength W_{ij}^I corresponding to the recurrent inhibitory synapses are chosen as the constant values whose range is [0.18, 0.22]. On the other hand, the strength W_{ij}^E corresponding to recurrent excitatory synapses are modified via STDP whose range is [0, 0.025]. Additionally, we determined that the maximum conduction delay from neurons at IL1 to those at OL is 5ms, while the minimum is 0ms.

Fig. 7 shows the raster plot of the excitatory neurons during

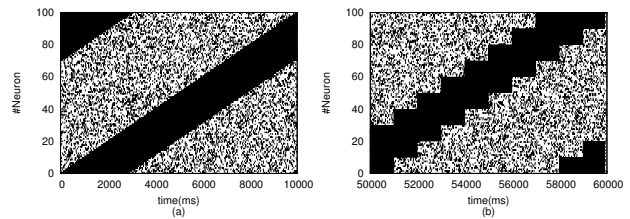


Fig. 6. (a) Input pattern sets for training. (b) Inputs pattern sets after learning.

learning. When the fluctuation of input synchronization σ_{st} is larger than the fluctuation of conduction delays σ_{cd} , in each firing cluster, neurons fire locally continuously (Fig.7(a)). While the fluctuation of conduction delays σ_{cd} is larger

than the fluctuation of input synchronization σ_{st} , there exist neurons that do not fire in firing clusters.

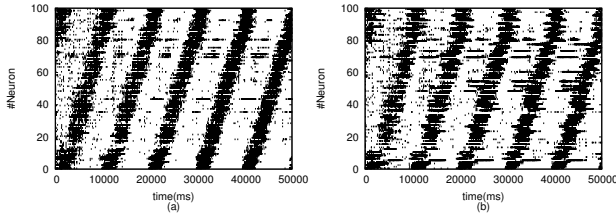


Fig. 7. (a) and (b) Raster plot for different set of fluctuation. (a) $(\sigma_{st}, \sigma_{cd}) = (3.0, 1.0)$ (b) $(\sigma_{st}, \sigma_{cd}) = (1.0, 3.0)$

When both a neuron with short conduction delay and that with long one fire simultaneously, the input spike from the neuron with short conduction delay arrives earlier and the synaptic connection is strengthened. On the other hand, the connection with long conduction delay is depressed.

When the fluctuation of conduction delay is small and the input variation is large, the order of the spike arrival changes with each input pattern. In this case, reflecting the conduction delays, the connection having shorter conduction delay is strengthened through the learning. Since the conduction delays of the neurons are similar to those of their adjacent neurons, the behavior of the neurons is similar to those of neighboring neurons. Therefore, locally continuous neurons fire for each pattern.

On the other hand, when the fluctuation of conduction delay is large, the order of the spike arrival reflects the fluctuation of the conduction delays, and synaptic connections with the short conduction delays are strengthened. The conduction delays of the neuron at OL for the neurons at IL1 are different from those of their neighboring neurons. It causes locally discontinuous firing patterns. Since the time of spike arrival is identical for each trial, the neuron with the specific connections is strengthened.

We denote the firing rate of each neuron i for each pattern k ($k = 1, 2, \dots, 10$) as $x_i(k)$. We denote the spatially smoothed firing rate as $\tilde{x}_i(k)$,

$$\tilde{x}_i(k) = \frac{1}{2n+1} \sum_{l=-n}^{l=n} x_{i+l}(k) \quad (8)$$

Fig. 8 expresses the changing of the firing rate for each pattern. We determined the smoothing parameter as $n = 5$. Fig. 8 (a) and (b) show that the each firing pattern is globally continuous and changing smoothly. On the other hand, Fig. 8 (d) shows that the firing of a discontinuous neuron has occurred spatially locally.

Fig. 9 shows the firing patterns for a specific input pattern (pattern 8). Fig. 9 (b) shows that even if the neurons are near to each other, the firing rate is different.

Fig. 10 shows the a covariance of the firing rate and the clustered histogram. Fig. 10 (d) shows that when the fluctuation of the conduction delays is large, the histogram has ripples.

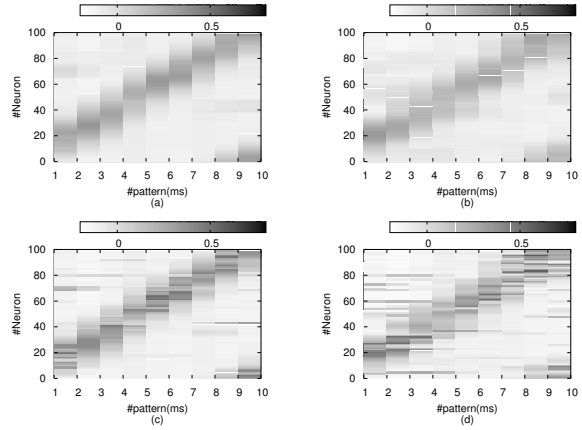


Fig. 8. Firing rate of the neurons after learning. (a) Average firing rate of the neighboring 11 neurons for $(\sigma_{st}, \sigma_{cd}) = (3.0, 1.0)$, (b) that for $(\sigma_{st}, \sigma_{cd}) = (1.0, 3.0)$, (c) firings rates of each neurons for $(\sigma_{st}, \sigma_{cd}) = (3.0, 1.0)$, and (d) that for $(\sigma_{st}, \sigma_{cd}) = (1.0, 3.0)$.

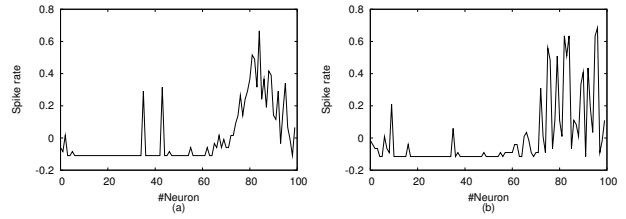


Fig. 9. An example of the firing rate for a pattern. (a) $(\sigma_{st}, \sigma_{cd}) = (3.0, 1.0)$ (b) $(\sigma_{st}, \sigma_{cd}) = (1.0, 3.0)$

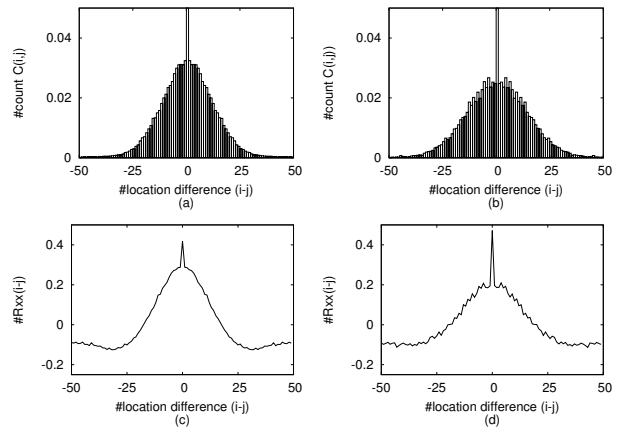


Fig. 10. (a) Covariance of firing rate for $(\sigma_{st}, \sigma_{cd}) = (3.0, 1.0)$, and (b) that for $(\sigma_{st}, \sigma_{cd}) = (1.0, 3.0)$. (c) Clustered histogram for $(\sigma_{st}, \sigma_{cd}) = (3.0, 1.0)$, and (d) that for $(\sigma_{st}, \sigma_{cd}) = (1.0, 3.0)$

V. DISCUSSION

When the degree of synchronization of input patterns is low, a network consisting of locally continuous cluster is organized. On the other hand, when the input patterns are highly synchronized, the fluctuation of conduction delays brings the locally distributed firing patterns through this self-organization.

In this case, there exists neurons that do not fire even if their adjacent neurons fire. It is probable that other input patterns, which are not used in this self-organization, cause the firings of these neurons. This means that the self-organized network can express more information using the various combination of neurons. It is known that IT neurons show more complicated firing patterns[9].

In a primary visual area, the receptive field of neurons is relatively narrow. Therefore, the fluctuation of the conduction delays is small, and the fluctuation of the synchronicity is predominant. Consequently, it is considered that firing patterns of the neurons become locally continuous.

On the other hand, IT neurons receive inputs from many visual areas. Therefore, the fluctuation of the conduction delays becomes large. Then, the degree of synchronicity of inputs becomes high during the processing, and it is possible that locally discontinuous firing pattern arises.

If firing patterns are locally discontinuous, there are many considerable combinations. IT is the last primary visual area and IT neurons must treat huge information at the retina stage. Therefore, the locally distributed firings are effective for treating various information.

Thus, it is possible that the high synchronicity of inputs plays a key role to organize the various changing of local combination of the neurons.

VI. CONCLUSION

Within brain, sensory information such as visual information is decomposed and processed in parallel. Therefore, when many stimuli are received, it is considered that the mean firing rate of many neurons corresponding to the composition element rises up simultaneously. In this case, there exist many alternatives to recombine the combination of each element. In order to organize appropriate neural assemblies suited for the sensory information, additional information other than a mean firing rate is required.

We consider that the synchronicity of neurons yields the appropriate combination of cell assembly. We showed that the network can self-organize using locally synchronized input patterns. In this network, synchronized firing clusters are changing the combination of neurons dynamically according to the changing of the input patterns. This strategy can be crucial to solve binding problems.

It is known that the orientation selectivity of IT neurons is more complex than that of V1. In this paper, we showed that, through self-organization, the highly synchronous firing and the fluctuation of the conduction delays cause globally continuous and locally distributed firing patterns that are consistent with the behavior of IT neurons.

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