Unsupervised Learning of Sub-Millisecond Temporal Coded Sequence by a Network of "Coincidence Detector" Neurons.

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Abstract

In this paper, we examine unsupervised learning for sequence of sub-millisecond temporal coded information in a network of neurons, which are assumed to have high temporal resolution. The learning scheme is based on a spatially and temporally local one, i.e., unsupervised Hebbian learning. The input sequence is temporal information that needs an accuracy on the order of sub-milliseconds. Through the learning, segregation of the synaptic connections occurs to form systematic structures in the network. Namely, the network develops in a self-organizing manner. The trained network works like an "associative memory" of the learned sequence, namely, the network responds when a newly input sequence is similar to the learned sequence. Consequently, the assembly of neurons is able to learn and distinguish an input sequence that carries information on the order of sub-milliseconds, although the spike emission intervals of the neurons are on the order of milliseconds.

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1   Introduction

Recently, a temporal structure of neuronal activities has been considered to play an important role in defining the function of neuronal assemblies. It has also been considered that the behavior of a single neuron is highly dependent on the timing of its input spikes (Singer and Gray, 1995; Vaadia et al., 1995; Hopfield, 1995; Fujii et al., 1996). These are called "temporal coding" hypotheses.

According to Softky and Koch, highly irregular inter-spike intervals suggest that a cortical neuron behaves more like a coincident detector than an integrator of the input spikes (Softky and Koch, 1993; Softky, 1995). If this is so, the irregular inter-spike intervals themselves may carry information. This hypothesis obviously differs from the conventional one, in which the inter-spike intervals cannot provide information representation but the temporally collective behaviors of the spikes can. The hypothesis by Softky and Koch offers a new possibility to clarify the computation mechanism of cortical neurons. However, their model had some problems in physiological plausibility (Shadlen and Newsome, 1994; Softky, 1995), i.e., a single neuron doesn't seem to have the capability to resolve spikes in such a precise timing.

Unsupervised Hebbian learning has also been much studied in the literatures. It is originally a temporally and spatially local change of the synaptic efficacy based on the correlation between pre-synaptic activities and post-synaptic activities. Synaptic changes, i.e., long-term potentiations (LTPs) and long-term depressions (LTDs), are physiologically assumed to correlate to the timing of input spikes to the synapses (Stanton and Sejnowski, 1989; Markram et al., 1997). Unsupervised Hebbian learning may play an important role in the primary development of the neural circuits. There are spontaneously generated rhythmic activities in the retina, which induce synaptic segregation in the lateral geniculate nucleus (Meister et al., 1991; Shatz, 1990). This implies that an autonomously produced sequence contributes to the development and segregation of the visual pathway. Similar wavy activities are considered to be related to the construction of "columnar" structures in the visual cortex (Toyama et al., 1996).

On the other hand, Gerstner et al. (1996) devised a time-dependent learning rule for a leaky integrate-and-fire neuron model and proposed a solution to the longtime problem of how barn owls detect the location of a sound. A barn owl detects a sound's location by using the time difference between the sound signal input to the left ear and that to the right ear. This time difference is on the order of sub-milliseconds. Interestingly, their model is able to distinguish the input on the order of sub-milliseconds, which is much smaller than the spike emission intervals of neurons. Since their model aimed to process a single frequency of the sound, a single neuron was sufficient.

Let us assume that the neurons, which are not necessarily in the auditory pathway, have a high temporal resolution. In the network of such neurons, then, information would be carried by the temporal sequence of spikes. Although a single neuron would be insufficient to process the sequence, a neuronal assembly is able to process it. Under this assumption, in this paper we intend to extend the single neuron model proposed by Gerstner et al. (1996) to an assembly of the neurons, i.e., a network.

In our study, a network of leaky integrate-and-fire neurons is trained by repeatedly providing an input sequence, i.e, by "reverberation" (Hebb, 1949). The learning scheme is based on a spatially and temporally local one, i.e., unsupervised Hebbian learning. The input sequence is a temporal information that needs an accuracy on the order of sub-milliseconds. Through

the learning, the segregation of the synaptic connections occurs to form systematic structures in the network. These structures cooperatively become distributed representation of the input sequence. Consequently, the network is able to learn and preserve the sub-millisecond input sequence, although the spike emission intervals of the neurons are on the order of milliseconds. In addition, the trained network works like an "associative memory" of the learned sequence. Namely, the trained network responds when a newly input sequence is similar to the learned sequence.

In the learning process, although each neuron independently and locally learns to select appropriate connections from the other neurons so as to preserve their own periodical spikes, the whole network preserves and distinguishes the input sequence, i.e., global information. Namely, the network develops in a self-organizing manner.

This paper is organized as follows. Section 2 describes our examined model. The model is a network version of a single neuron model proposed by Gerstner et al. (1993; 1996). Section 3 describes the unsupervised learning employed in our model. The learning scheme is a spatially and temporally local one, and it is equivalent to the time-window method devised by Gerstner et al. (1996). Section 4 shows the simulation results of our model, which are our main contributions. In section 5, we will present several discussions on our examined model. Section 6 summarizes the paper.

2 Simulation Model

This simulation model consists of a processing layer and an input layer. The processing layer is composed of 16 processing neurons. The input layer is composed of 16 input units. There are 10 additional white-noise input units.

2.1 Input layer

In this paper, we consider a situation where the input layer produces a regular spike sequence as shown in Figure 1. The same sequence is repeatedly produced. The sequence is composed of four spike timings. The intervals between the first timing and the second timing, between the second timing and the third timing, and between the third timing and the fourth timing are $9T$, $7T$, and $8T$, respectively, where $T = 0.25$[ms]. After $6T$ from the fourth timing, the first timing comes in its turn again. At every spike timing, four units among 16 input units simultaneously emit spikes. Therefore, the 16 input units are separated into four groups with respect to their spike timings, and each of the 16 input units emits a single spike during the single sequence whose time period is $30T = 7.5$[ms].

Each processing neuron is connected to each input unit. The m-th spike emitted by the j-th input unit arrives at the i-th processing neuron, according to the probability density:

$$P(t|i, j, m) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left[-\frac{(t - T_m^j - \Delta_{ij}^{\text{inp}})^2}{2\sigma^2} \right].$$ (1)

Δ_{ij}^{inp} denotes the transmission delay from the j-th input unit to the i-th processing neuron

and is assumed to obey a Gaussian distribution $N(1.00, 0.01)$.[1] T_m^j is the m-th spike emission time of the j-th input unit. σ is the input jitter, which is set at 0.02[ms].

Besides the spikes from the 16 input units, every processing neuron also receives white-noise spikes, which are produced by 10 additional input units. They fire at the rate of one spike per millisecond, which is more frequent than the rate of the regular spikes. Since these spikes obey a uniform distribution, the distribution of their arrival time also becomes uniform.

2.2 Processing layer

The processing layer is a one-dimensional network of 16 neurons with a periodical boundary condition. Neurons are indexed by their spatial location. Neuron i is bi-directionally connected to its ten neighboring neurons $i-5, ..., i-1, i+1, ..., i+5$. Each pair of connected neurons has four synaptic connections which are indexed by q. A spike from the i-th pre-synaptic neuron is transmitted through the axon to the j-th post-synaptic neuron with an axonal delay time of $\Delta_{ji}^{ax} = 0.25 \cdot |i - j|$[ms]. The spike provokes the synapses to release neurotransmitters, which evoke excitatory post-synaptic potentials (EPSPs) on the post-synaptic neurons. The time delay of the evoked EPSP via the qth synapse of the connection, $\Delta_{ji}^{syn\ q}$, obeys $N(0.9, 0.18)$. Then, the transmission delay from the i-th pre-synaptic neuron to the j-th post-synaptic neuron via the q-th synapse becomes $\Delta_{ji}^q = \Delta_{ji}^{ax} + \Delta_{ji}^{syn\ q}$.

It should be noted that the actual transmission delay is mainly due to the synaptic delay. Although the actual axonal delays are small enough to be ignored in comparison with the synaptic delay, we set them to be relatively large in order to discriminate the neuronal connections and to easily see the simulation result, shown in Section 4. We have investigated the case for $\Delta_{i\,i+1}^{ax} = 0.01$ and $\Delta_{ji}^{syn\ q} \sim N(1.88, 0.57)$. These conditions are physiologically more plausible than those described above. The experimental results with these conditions are, however, almost similar to those shown in Section 4.

2.3 Neuron model

We adopt a leaky-integrate-and-fire model in order to describe the membrane property of the processing neuron. The leak in this model is strong, so neurons can detect spike's incident in a short period of time. We also define refractoriness after each spike emission.

2.3.1 Membrane potential

The membrane potential of the i-th neuron is defined as $v_i = h_i + h_i^{ref}$, where h_i and h_i^{ref} represent an integration of EPSPs and a refractory potential, respectively. h_i is given by (Gerstner et al., 1996)

$$\frac{dh_i(t)}{dt} = -\frac{h_i(t)}{\tau_m} + \frac{1}{\tau_s} \sum_{j,f,q} J_{ij}^q \exp\left[-\frac{t - t_{jq}^f}{\tau_s}\right]. \tag{2}$$

The summation is taken for $t_{jq}^f < t$. t_{jq}^f is the evoked time of the f-th EPSP in the i-th post-synaptic neuron by the j-th pre-synaptic neuron through the q-th synapse, and J_{ij}^q is the

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[1] In this article, $N(a, b)$ denotes the Gaussian distribution whose mean and standard deviation are a[ms] and b[ms], respectively.

transmission efficacy of the synapse. If the j-th pre-synaptic neuron fires at t'_j, $t^f_{jq} = t'_j + \Delta^q_{ij}$.[2] The membrane time constant, τ_m, and the synaptic time constant of EPSP, τ_s, are set at 0.1[ms]. The membrane time constant value is small compared with the known physiological data (Shadlen and Newsome, 1994). According to Softly and Koch, however, cortical neurons should have a small time constant of $\tau_m \leq 0.2$[ms] in order to observe plausible inter-spike intervals (Softky and Koch, 1993). This time constant value is smaller than the actual value. In this case, each neuron behaves more like a coincidence detector than an integrator.

When the membrane potential v_i exceeds the threshold $\theta(= 3.3[\text{i.u.}]^3)$, an action potential is provoked, and v_i is reset to the resting potential. The generated action potential transmits through the axon. Since it is spatially and temporally localized and obeys an "all-or-nothing" rule, it is called a spike.

2.3.2 Refractoriness

In an actual nervous system, action potentials are generated when sodium and potassium ion channels open in turn and the membrane potential forms a sharp shape. A certain time is needed for a membrane to return to the resting state from the hyper-polarized state. Therefore, after a spike, neurons cannot fire for a while, which is called the absolutely refractory period. After the spike emission, hyper-polarizing ion current (I_{AHP}) occurs, which is slow and long lasting. This results in a relative refractory period.

Accordingly, we define the refractoriness in our model as (Gerstner et al., 1993)

$$h^{\text{ref}}_i(t) = \sum_{n=1}^{N} \int_0^t d\tau \, \eta(\tau) \, \delta(t - \tau - t^n_i), \tag{3}$$

where t^n_i is the n-th spike emission time of the i-th neuron. Refractory function $\eta(\tau)$ is defined by

$$\eta(\tau) = \begin{cases} -\infty & (\text{for } 0 < \tau \leq \tau_{\text{ref}}) \\ -\frac{\eta_0}{\tau - \tau_{\text{ref}}} & (\text{for } \tau_{\text{ref}} < \tau \,). \end{cases} \tag{4}$$

The upper and lower definitions correspond to the absolute and relative refractoriness, respectively. This refractoriness plays an important role in our model: a neuron is prohibited from producing spikes in a short interval.

2.3.3 Dendritic back-propagation of action potential

An action potential not only propagates down to the axon, but also propagates backward to the dendrite (Markram et al., 1997). After the i-th neuron fires at time t'_i, the n-th "back-propagated" potential arrives at the synapse q, which is connected to the i-th neuron, at time $t^n_{iq} = t'_i + \Delta^{dend\,q}_i$. $\Delta^{dend\,q}_i$ obeys $N(0.05, 0.025)$.

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[2]We ignore the forward transmission delay in a dendrite. Even if the delay is considered, a similar discussion to that as follows can be made, though it becomes a little confusing.

[3]i.u. = input units.

3 Time-dependent Learning Rule

At actual synapses, long-term potentiations (LTPs) are considered to be dependent on the voltage of the post-synaptic neuron (Artola and Singer, 1993). It is assumed that LTP occurs when a voltage nearly as high as the spike threshold of the post-synaptic neuron and a pre-synaptic input simultaneously occur. Therefore, it seems that LTP at a synapse tries to grasp the temporal correlation between spike timings of the pre-synaptic neuron and the post-synaptic neuron.

The time-dependent learning rule was first introduced by Gerstner et al. (1996). This rule is described only by the incident timing of action potentials. Not only the inputs from pre-synaptic neuron but also the back-propagated action potentials enter the synapse (Markram et al., 1997). The time difference between the input spike from the pre-synaptic neuron and the back-propagation of the post-synaptic neuron determines the change in synaptic efficacy.

Let t_{jq}^f and t_{iq}^n denote the arrival time of the f-th pre-input spike and that of the n-th back-propagated action potential, respectively, at the q-th synapse transmitting the spikes from neuron j to neuron i. The time-dependent learning rule, introduced by Gerstner et al. (1996) is given by

$$J_{ij}^q = J_0 + \sum_{f=1}^{F}[\gamma + \sum_{n=1}^{N} W(t_{jq}^f - t_{iq}^n)]. \tag{5}$$

J_0 is the initial value of the efficacy. F and N are the numbers of spikes produced by the j-th and i-th neurons, respectively. Each efficacy value, J_{ij}^q, is additionally controlled so that it is not larger than its upper bound ($=3.0$[i.u.]). $W(t)$ is a learning window defined by

$$W(t) = \begin{cases} 0.3\exp\left[\frac{t}{0.5}\right] & (t \leq 0) \\ 0.5\exp\left[-\frac{t}{0.5}\right] - 0.2\exp\left[-\frac{t}{5}\right] & (t > 0) . \end{cases} \tag{6}$$

Namely, the synaptic plasticity depends on the difference between the pre-input time t_{jq}^f and the post-back-propagation time t_{iq}^n.

Alternatively, we employ the following learning rule. Here, we assume that the learning process in a synapse is localized spatially and temporally and is defined by the timings of the pre-input spikes and the post-back-propagated action potentials (Gertner et al., 1996; Markram et al., 1997). Here, the locality of the learning process is emphasized. Each synaptic efficacy changes depending on the current synaptic state and also on whether there is a pre-input or post-back-propagated spike at the present time. First, for a synapse q between two neurons j and i, we define three internal state variables α_1^{ijq}, α_2^{ijq}, and β^{ijq}, which exponentially decay by themselves with time.

$$\begin{aligned} \alpha_1^{ijq}(t + \Delta t) &= \alpha_1^{ijq}(t) \cdot \exp\left[-\frac{\Delta t}{\tau_{\alpha_1}}\right] \\ \alpha_2^{ijq}(t + \Delta t) &= \alpha_2^{ijq}(t) \cdot \exp\left[-\frac{\Delta t}{\tau_{\alpha_2}}\right] \\ \beta^{ijq}(t + \Delta t) &= \beta^{ijq}(t) \cdot \exp\left[-\frac{\Delta t}{\tau_\beta}\right] . \end{aligned} \tag{7}$$

When a spike from the j-th pre-neuron evokes an EPSP at the i-th post-neuron via synapse q, the following updating takes place.

$$\Delta\beta^{ijq} = \epsilon_\beta, \quad \Delta J_{ij}^q = \gamma + \alpha_1^{ijq}(t) - \alpha_2^{ijq}(t). \tag{8}$$

When an action potential from the i-th post-neuron back-propagates to the synapse q, which is connected to the j-th pre-neuron, the following updating takes place.

$$\Delta\alpha_1^{ijq} = \epsilon_{\alpha_1}, \quad \Delta\alpha_2^{ijq} = \epsilon_{\alpha_2}, \quad \Delta J_{ij}^q = \beta^{ijq}(t). \tag{9}$$

In the experiments, we set $\tau_{\alpha_1} = 0.5$, $\tau_{\alpha_2} = 5.0$, $\tau_\beta = 0.5$, $\epsilon_{\alpha_1} = 0.5$, $\epsilon_{\alpha_2} = 0.2$, and $\epsilon_\beta = 0.3$. With these constant values, it can be proved that the learning rules (7), (8), and (9) are equivalent to (5) and (6). The proof is described in the Appendix. Although the learning rules (5) and (6) do not explicitly satisfy the time locality, our reduced learning rules satisfy the time locality.

4 Simulation Results

The network is trained by repeatedly providing the sequence shown in Figure 1. The sequence lasts $30T = 7.5$[ms] and is represented by 16 input units. Since the 16 input units are separated into four groups by the spike emission timing, there are four spike timings in the provided sequence.

4.1 Sequence preservation

Figures 2(a) and 2(b) show the time-series of a neuron's EPSPs at the early learning stage (before learning), i.e., at $T = 4,000$[ms], and at the later learning stage (after learning), i.e., at $T = 196,000$[ms], respectively. In Figure 2(a), three spike emissions are observed where spike intervals are more than ten milliseconds. In this case, it is hard to discriminate sub-millisecond information. In Figure 2(b), on the other hand, spikes are generated almost precisely at a certain timing.

Figure 3 is a spike raster diagram after learning, i.e., $T = 196,000$[ms]. The neuron index -1 on the ordinate indicates the spikes received from the input units. The time intervals between 'A' and 'B', 'B' and 'C', 'C' and 'D', and 'D' and 'A' are $7T(= 1.75$[ms]$)$, $8T(= 2.00$[ms]$)$, $6T(= 1.50$[ms]$)$, and $9T(= 2.25$[ms]$)$, respectively. The spike timings of the 16 processing neurons were nearly regular and highly correlated with one of the four input timings from the input units. Although each processing neuron produces a spike once in about ten milliseconds, the network is able to precisely preserve the input sequence, which needs an accuracy on the order of sub-milliseconds.

This accuracy is attained by forming local structures in the network. Figures 4(a) and 4(b) are spike transmission diagrams before learning and after learning, respectively. In these figures, each line connects the firing time of a pre-neuron to the EPSP evoked time on a post-neuron. In Figure 4(a), spikes are generated almost at random, and they are transmitted to all of the ten neighboring neurons. In Figure 4(b), on the other hand, spikes are generated regularly, and they are transmitted to certain parts of the neighboring neurons. Namely, several connections have survived among neighboring connections, and they form local systematic structures of the

neurons. These systematic structures not only help the post-synaptic neurons produce spikes at precise timings, but also preserve the order of the components in the learned sequence. Thus, the structures cooperatively preserve the sub-millisecond learned sequence and enable the network to regularly produce spike trains. Consequently, the self-organized network structure becomes a distributed representation of the input sequence conveying sub-millisecond information.

4.2   Network properties

We investigated properties of the trained network by providing newly input sequences and examining the network responses.

The trained network is able to "associate" the learned sequence from a newly input sequence that is similar to the learned sequence. The new input sequences are variously prepared on the condition that each input unit emits one spike in $30T(= 7.5[\text{ms}])$. Figure 5 shows the response of the trained network for the new sequences. The abscissa and the ordinate denote the correlation between the learned sequence and the new input sequence and the number of spikes produced by the neurons of the network, respectively. We can see that the network responds to the input sequences having a large correlation value with the learned sequence. When the network responds to an input sequence, the output sequence produced by the network is similar to the learned sequence.[4] When the new input sequence has a small correlation value (< 0.5) with the learned sequence, on the other hand, the network becomes quiet. These results indicate that the self-organized network structure is able to discriminate the learned sequence from adverse input sequences, and it works like an "associative" memory. It should be noted that the difference between the learned sequence and the new input sequences is on the order of sub-milliseconds.

In order to further examine the association property of the trained network, we prepared test sequences, each of which had shifted spike timings from the learned sequence. The production algorithm of these test sequences is described in Figure 6. A test sequence is composed of 16 input units. The spike timings of the input units are shifted from those of the learned sequence one-by-one. The shift index x counts the amount of the shift. When the shift index x becomes 160, the spike timings for all of the input units are shifted by 10, and the input sequence becomes equivalent to the learned sequence; the only difference is the phase. In this case, the association becomes perfect, as can be seen in Figure. 7. When the shift index x of the test sequence deviates from 0 and 160, the spike timings in the test sequence are distant from those in the learned sequence. In such a case, the network does not respond satisfactorily (Fig. 7), implying that the network detects the timings of the input spike trains.

Figure 8 denotes the response of the trained network for various values of the input jitter σ. The test sequence is equal to the learned sequence except for the jitter value. This figure shows that even if inputs are a little noisy, the trained network is able to associate the learned sequence and respond with a precise timing. Namely, the trained network is able to conduct a robust association against the noisy input.

When the new input sequence is relatively distant from the learned sequence, the network no longer responds to the input. Figure 9 shows a sample spike raster diagram when a highly noisy input sequence, e.g., $\sigma = 0.45[\text{ms}]$, is provided to the learned network. We can observe

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[4]Note that the output sequence is a distributed representation among the 16 processing neurons, as can be seen in Figure 3.

some quiescent periods. Figure 10 shows the length of the longest quiescent periods against the difference between the test sequence and the learned sequence. The abscissa denotes the shift index of test sequence described above. We can see that the quiescent periods are short when the test sequence has similar spike timings to the learned sequence and the association is properly done.

4.3 Self-organization

The properties shown above are realized by self-organizing network learning, which is achieved by selecting appropriate neuronal connections. After the learning, most of the neuronal connections, i.e., synapses, can be categorized into two groups. 23% of the originally prepared synapses "survive" and acquire large synaptic efficacy values. These values are likely to be close to their upper bound value (= 3.0). 67% of the prepared synapses acquire nearly zero efficacy value; in other words, they can be regarded as "removed". Figure 11 shows the synaptic efficacy values as a matrix between the pre-synaptic and the post-synaptic neurons after learning.

Figure 12 shows the efficacy change of the synapses on a single neuron (the 8-th neuron) in the course of the learning process. There are 66 synapses on the neuron. Some of the synapses are enhanced, i.e., the efficacy J_{8j}^q increases, while others are suppressed, i.e., the efficacy J_{8j}^q decreases. Note that there are three kinds of connections. Initially, the synaptic efficacy values from the input units and from the white-noise input units are set at 1.0, and those from the processing neurons are set at 0.5.

At the early learning stage, i.e., until 10,000[ms], the connections from the white-noise input units are potentiated to have the largest efficacy values among the three kinds of connections. This occurs because the firing rate of the white-noise input units is larger than that of the regular input units, and the spike emission of the processing neurons is almost at random in this stage. Since the white-noise inputs do not have any information in spike timing, they only work to lower the effective membrane threshold of the processing neurons, so that the processing neurons are encouraged to tune to the regular spikes provided by the input layer. Then, at the following learning stage, i.e., between 10,000[ms] and 80,000[ms], the synapses from the regular input units are gradually potentiated.

Here, let us consider a situation where two processing neurons i and j are tuned to the two different input timings of the input layer. In this situation, the spikes from the processing neuron i will help the processing neuron j emit a spike when the transmission delay time from the i-th processing neuron and the j-th processing neuron is close to the difference between the two input timings. Therefore, the connection whose transmission delay is nearly as same as the input interval tends to be potentiated. The other connections will be depressed. These are competition between synapses based on their transmission delay time. At the later learning stage, i.e., between 80,000[ms] and 160,000[ms], appropriate connections from the processing neurons and from the input units are selected by the competition, and they are potentiated to the upper limit. Since each processing neuron produces its spikes by tuning to the regular inputs and some of the other processing neurons, the white-noise inputs are no longer important. Therefore, the connections from the white-noise input units are depressed to zero, i.e., "removed".

Accordingly, the contributing synapses to the neuron change in time, and the selection

depends on temporal correlation between input spikes and spikes produced by processing neurons. Note that these selections are achieved by temporally and spatially local learning at the synapses. Figures 13(a) and 13(b) show the synaptic efficacy values before learning and after learning, respectively.

Figures 14(a) and 14(b) show the schematic figures of the effective connections realized in the network before learning and after learning, respectively. Before learning, the neighboring neurons are connected to each other. After learning, some of the prepared connections have survived. These remaining connections are appropriate for the post-synaptic neurons to regularly produce their own spike trains.

5   Discussion

There have been many studies that aim to clarify the neuronal information representation and the computation in the brain by considering temporal structures of the spikes produced in the network. From this point of view, i.e., the so-called "temporal coding" viewpoint, the high irregularity of the cortical spikes implies that each neuron would have a precise time-resolution of the spikes (Softky and Koch, 1993).

In this paper, we adopted the leaky integrate-and-fire neuron that posseses the precise time-resolution, and investigated the unsupervised learning of their network. The model examined in this paper is based on the previous study by Gerstner et al. (1996) on the auditory pathway of barn owls. In this model, a single neuron is able to resolve its stational input with sub-millisecond accuracy, and thus "learn" an auditory frequency conveyed by the stational input. In our study, we extended the stational input to an input sequence whose components convey temporal information on the order of sub-milliseconds. In order to deal with the input sequence, the learning of a single neuron is insufficient. The sequence should be preserved in the local structures of the network. Then, the network becomes a distributed representation of the learned sequence.

The most important problem in our model is the very high time resolution of the neuron, i.e., the too small value for the membrane time constant, τ_m. Its value, 0.2[ms], seems quite small in comparison with the known physiological value of $7 \sim 20$[ms] for the typical neurons in the cortex. The lowest possible value is considered to be about 2[ms], which is observed in the auditory pathway (Reyes et al., 1994; 1996). Although the small membrane time constant was suggested by Softky and Koch in order to explain the high spike irregularity of the cortical neurons, this irregularity could be due to the effect of the inhibitory post-synaptic potentials (IPSPs) (Shadlen and Newsome, 1994; Softky, 1995). If we consider the effect of IPSPs in our examined model, the small membrane time constant could be improved. This consideration is our future work.

In our model, the synaptic efficacy values are uniform before learning. However, some of the synapses are enhanced, and others are "removed" after learning. This structual formation in the network is achieved by repeatedly providing the input sequence. It might be related to the synaptic segregation that is observed in the development of neural circuits.

In our model, the network becomes a memory of the input temporal sequence, by repeatedly providing the sequence, i.e., reverberation. Reverberation circuits were suggested by Hebb (1949), and a similar structure is observed in the entorhinal cortex, which holds the input

sequence for a certain period of time and provides information to the hippocampus (Iijima et al., 1996).

6 Conclusion

In our study, based on the assumption that a neuron can respond with precise timing, we considered the computational capacity of a neural network. A network of leaky integrate-and-fire neurons was trained by repeatedly providing an input sequence, i.e, by reverberation. The learning scheme was based on a spatially and temporally local one, i.e., unsupervised Hebbian learning. The input sequence was temporal information that needs an accuracy on the order of sub-milliseconds. Through the learning, the segregation of the synaptic connections occurs to form systematic structures in the network. Namely, the network develops in a self-organizing manner. In addition, the trained network works like an "associate memory" of the learned sequence. Consequently, the assembly of neurons is able to learn and distinguish an input sequence that carries information on the order of sub-milliseconds, although the spike emission intervals of the neurons are on the order of milliseconds.

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Appendix

At the time $t(< t', > t_i^N, t_j^F)$, $J_{ij}(t)$ is described as

$$
\begin{aligned}
J_{ij}(t) - J_0 &= \gamma + W(t_j^1 - t_i^1) + \dots + W(t_j^1 - t_i^N) \\
&+ \dots \\
&+ \gamma + W(t_j^F - t_i^1) + \dots + W(t_j^F - t_i^N).
\end{aligned} \tag{A.1}
$$

At the time $t'(> t, t_{jq}^F, t_{iq}^N)$ the internal state variables can be described as

$$
\begin{aligned}
\alpha_1^{ij}(t') &= \sum_{n=1}^{N} \epsilon_{\alpha_1} \cdot \exp\left[-\frac{t' - t_i^n}{\tau_{\alpha_1}}\right] \\
\alpha_2^{ij}(t') &= \sum_{n=1}^{N} \epsilon_{\alpha_2} \cdot \exp\left[-\frac{t' - t_i^n}{\tau_{\alpha_2}}\right] \\
\beta^{ij}(t') &= \sum_{f=1}^{F} \epsilon_{\beta} \cdot \exp\left[-\frac{t' - t_j^f}{\tau_{\beta}}\right].
\end{aligned} \tag{A.2}
$$

If a spike from the j-th pre-neuron evokes an EPSP on the i-th post-neuron at the time $t'(> t, t_j^F, t_i^N)$, the synaptic efficacy becomes

$$
\begin{aligned}
J_{ji}(t') &= J_{ij}(t) + \gamma + \sum_{n=1}^{N} W(t' - t_i^n) \\
&= J_{ij}(t) + \gamma + \sum_{n=1}^{N} \left\{ \epsilon_{\alpha_1} \cdot \exp\left[-\frac{t' - t_i^n}{\tau_{\alpha_1}}\right] - \epsilon_{\alpha_2} \cdot \exp\left[-\frac{t' - t_i^n}{\tau_{\alpha_2}}\right] \right\} \\
&= J_{ij}(t) + \gamma + \alpha_1^{ij}(t') - \alpha_2^{ij}(t').
\end{aligned} \tag{A.3}
$$

If a spike from the j-th pre-neuron evokes an EPSP on the i-th post-neuron at the time $t'(> t, t_i^N, t_j^F)$, the synaptic efficacy becomes

$$
\begin{aligned}
J_{ji}(t') &= J_{ji}(t) + \sum_{f=0}^{F} W(t' - t_j^F) \\
&= J_{ji}(t) + \sum_{f=1}^{F} \epsilon_{\beta} \cdot \exp\left[-\frac{t' - t_j^f}{\tau_{\beta}}\right] \\
&= J_{ji}(t) + \beta^{ij}(t').
\end{aligned} \tag{A.4}
$$

Then, by using the mathematical induction, we can prove that the learning rule (7), (8), and (9) are equivalent to (5) and (6).

- **Figure 1**
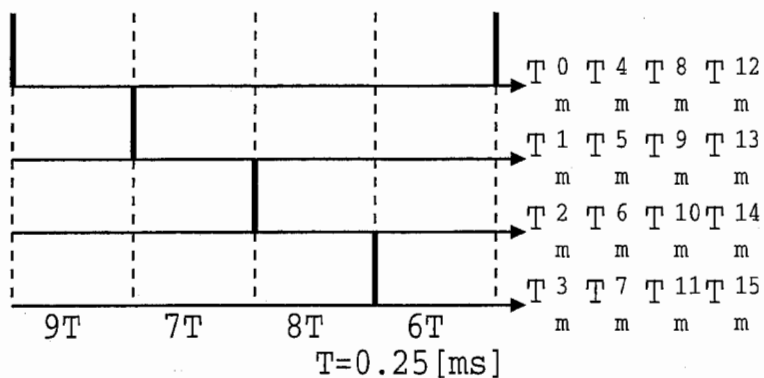
Figure 1: Training sequence is produced by 16 input units. There are four spike timings, and at each timing four input units emit spikes.
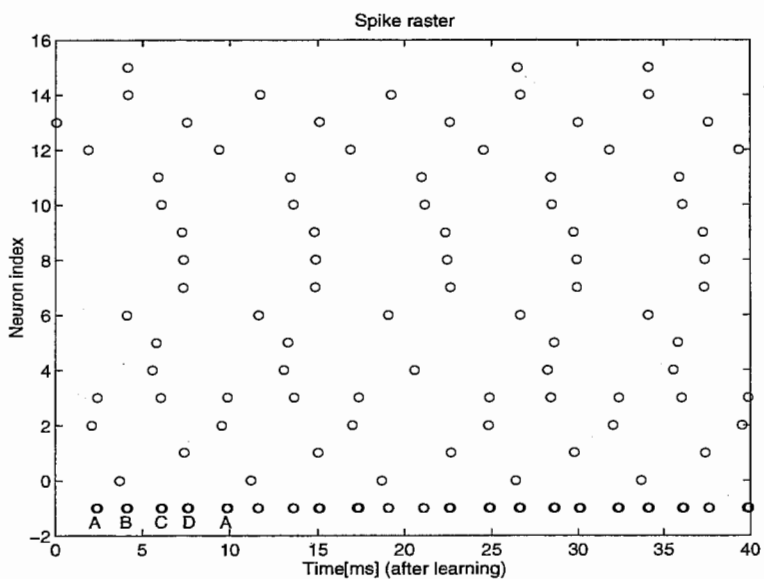
- **Figure 3**

Figure 3: Spike raster diagram after learning. Ordinate denotes Neuron index. Neuron index −1 indicates spikes received from input units. Each circle 'o' denotes a spike.
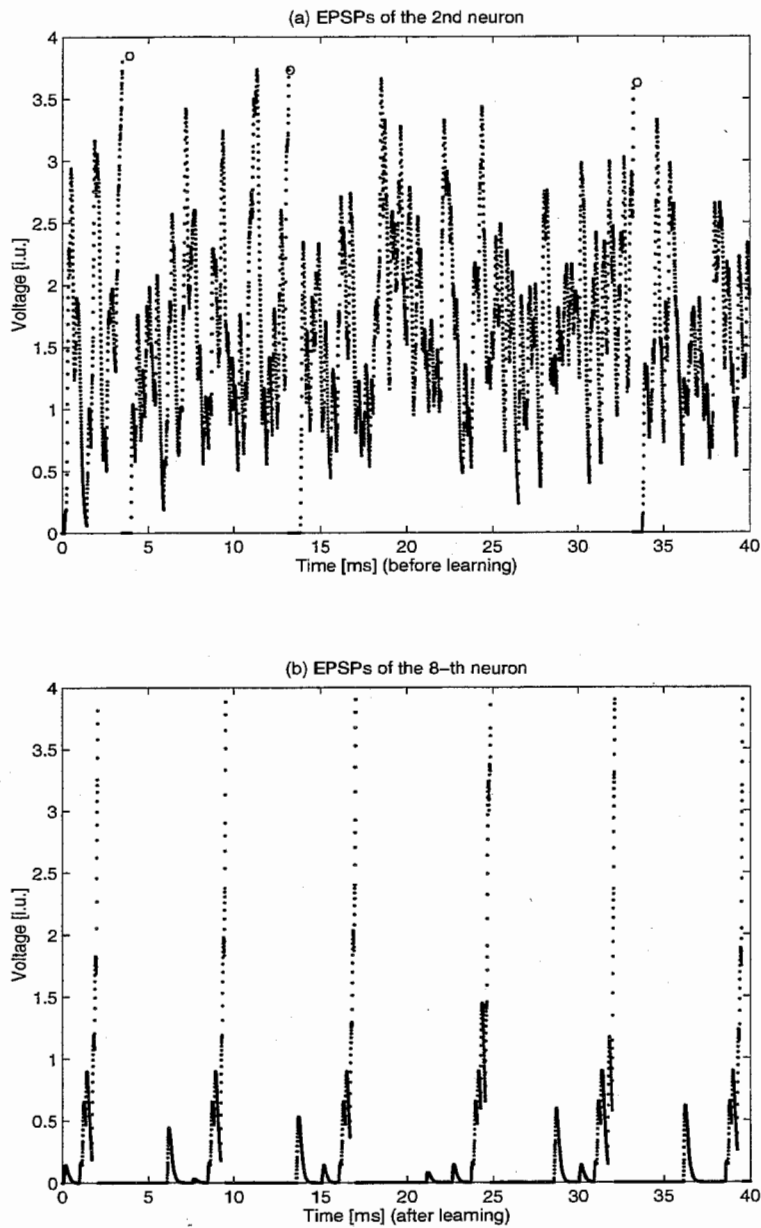
• **Figure 2**

Figure 2: EPSPs of the 2nd neuron. (a) Before learning ($T = 4,000[\text{ms}]$), circle ('o') denotes a spike emission. (b) After learning ($T = 196,000[\text{ms}]$). Note that in each figure the ordinate denotes the EPSPs value, *not* the membrane potential value.

- **Figure 4**
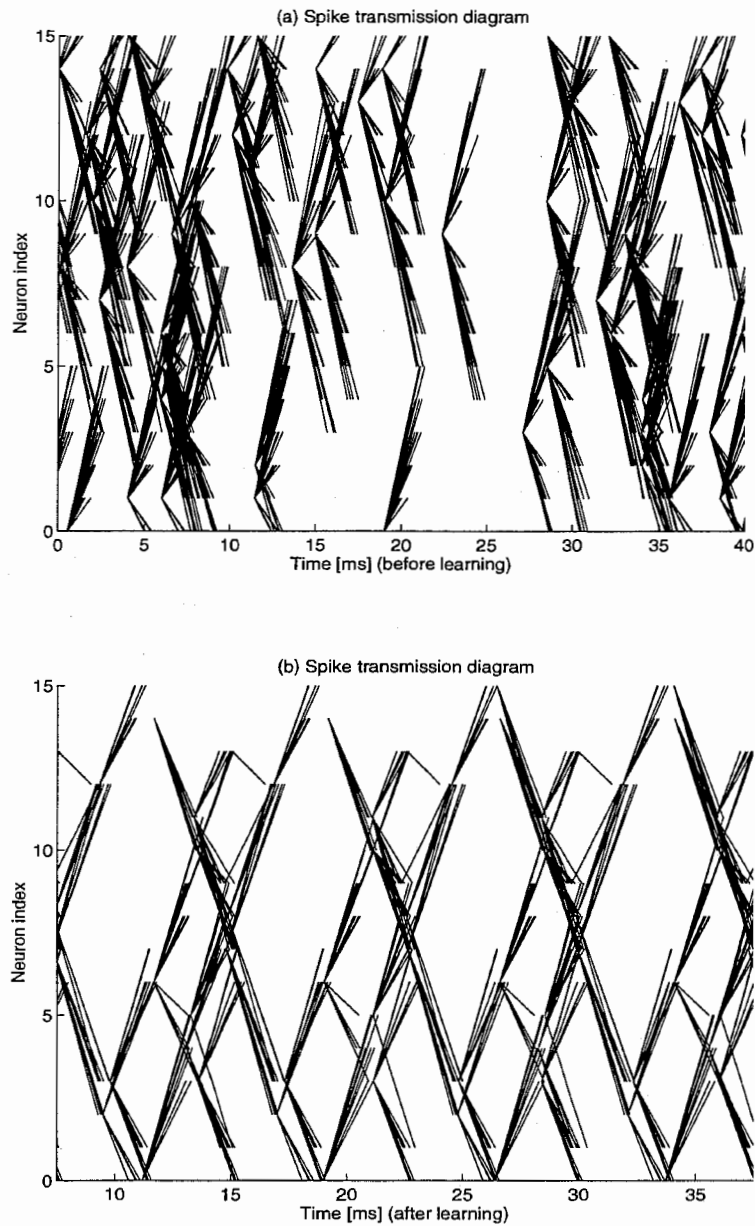
Figure 4: Spike transmission diagrams. Abscissa denotes time, ordinate denotes neuron index. Each line connects firing time of presynaptic neuron with EPSP "evoked" time of post-synaptic neuron. For observational simplicity, connections across the network boundary, as with those between 0-th pre-neuron and 15-th post-neuron, are omitted. (a) Before learning ($T = 4,000$[ms]). (b) After learning ($T = 196,000$[ms]). Weak spike transmissions are also omitted.

- **Figure 5**
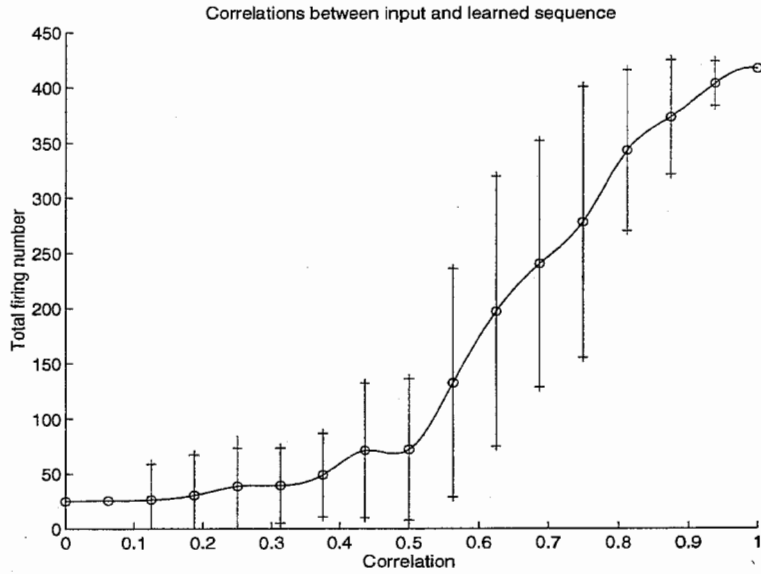
Figure 5: Network can associate learned sequence. Abscissa denotes the correlation between learned sequence and newly input sequence. We investigated many sequence patterns for each correlation value. Mark 'o' and error bar denote mean and standard deviation for patterns.

- **Figure 6**

```
for(i=0~15)
  for(j=0~9)
   {Shift the firing time of
       the i-th input unit to Ti+T*j;
    Simulate the network response;
    Print x=10*i+j,
          y=number of spikes,(Fig.7)
          y=the longest blank;(Fig.10)}
```

Figure 6: Algorithm for preparing input sequences in Fig. 7 and Fig. 10.

● **Figure 7**
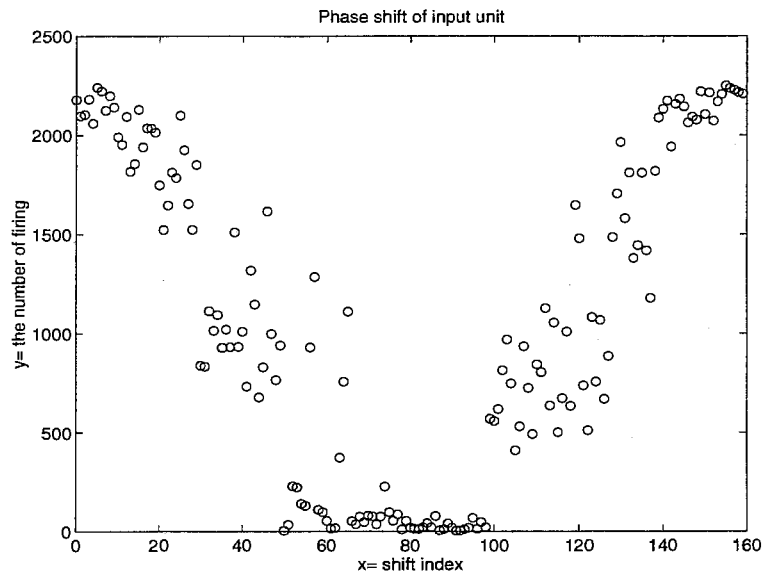
Figure 7: Network can associate learned sequence when spike timings of test sequence are similar to those of learned sequence. Abscissa denotes shift index of test sequence described by algorithm in Fig. 6. Ordinate denotes number of spikes produced by neurons in network.

● **Figure 8**
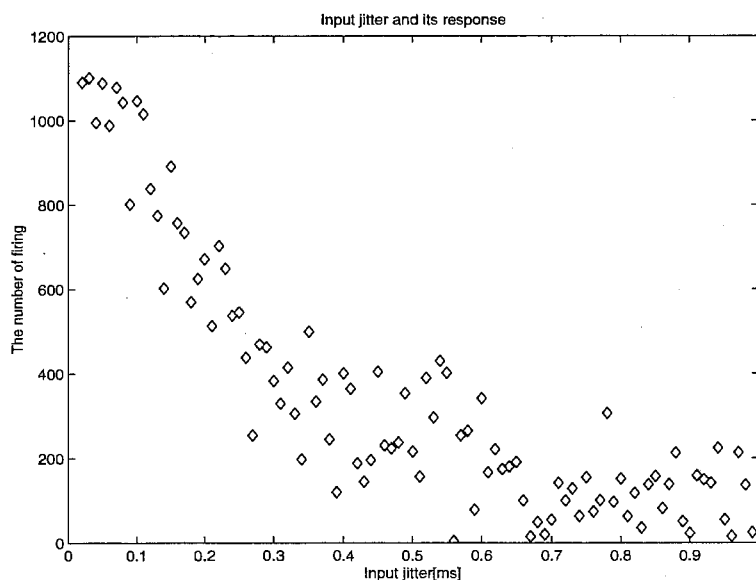
Figure 8: Network response against input noise. Abscissa denotes input jitter of test sequence. Ordinate denotes number of spikes produced in trained network.
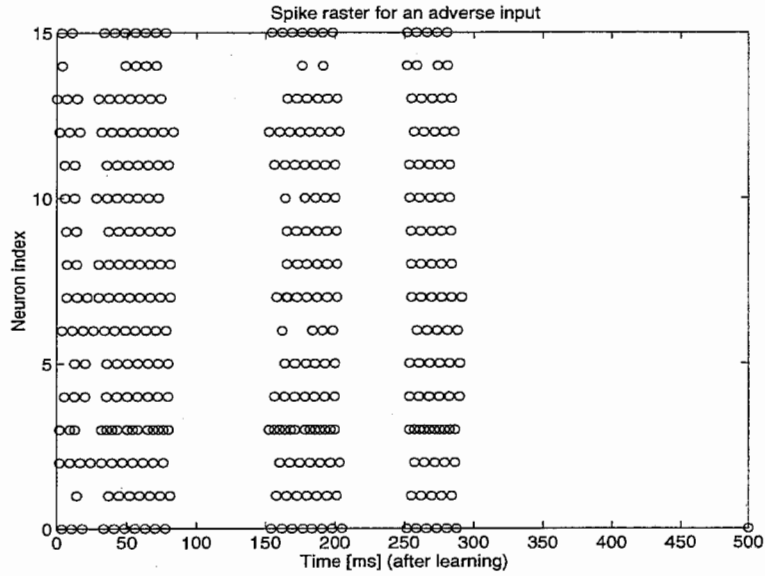
• **Figure 9**

Figure 9: Sample spike raster diagram when highly noisy input sequence is provided to trained network.

• **Figure 10**
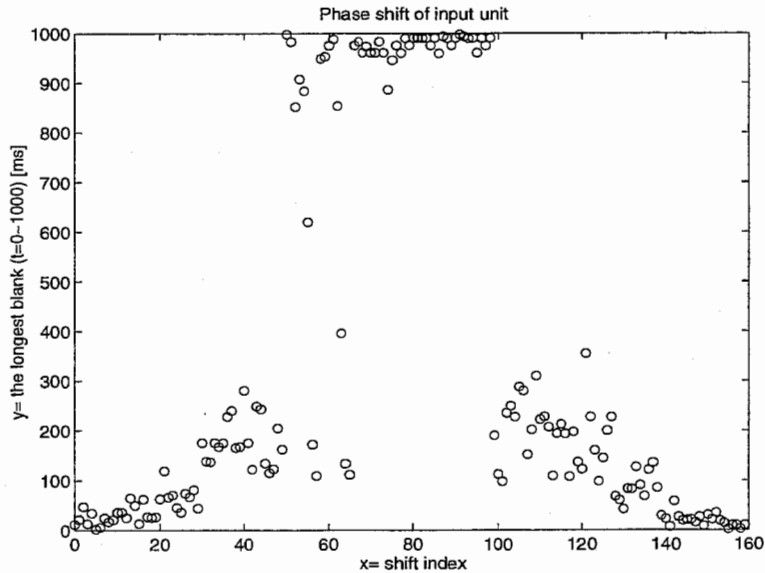
Figure 10: Abscissa denotes shift index of test sequence, which is described by algorithm in Fig. 6. Ordinate denotes length of longest quiescent period produced by network.
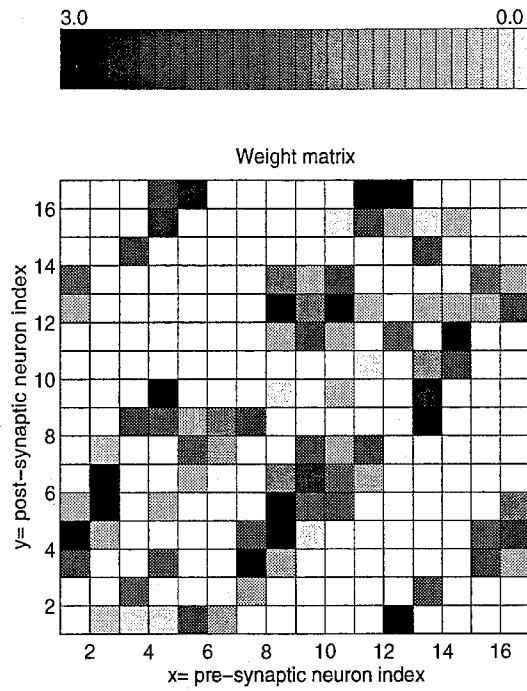
- **Figure 11**

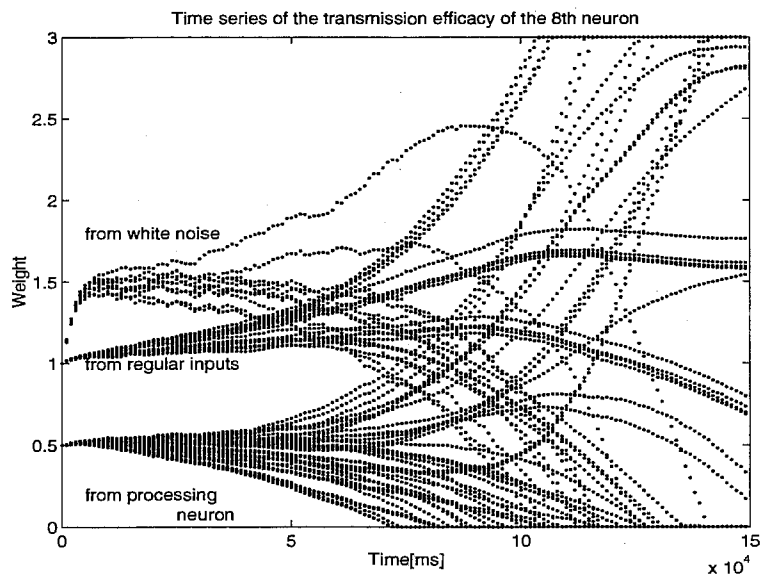Figure 11: Synaptic efficacy matrix. Transmission efficacy values are illustrated by gray scale.

- **Figure 12**

Figure 12: Time-series of transmission efficacy $J_{8,x}$.
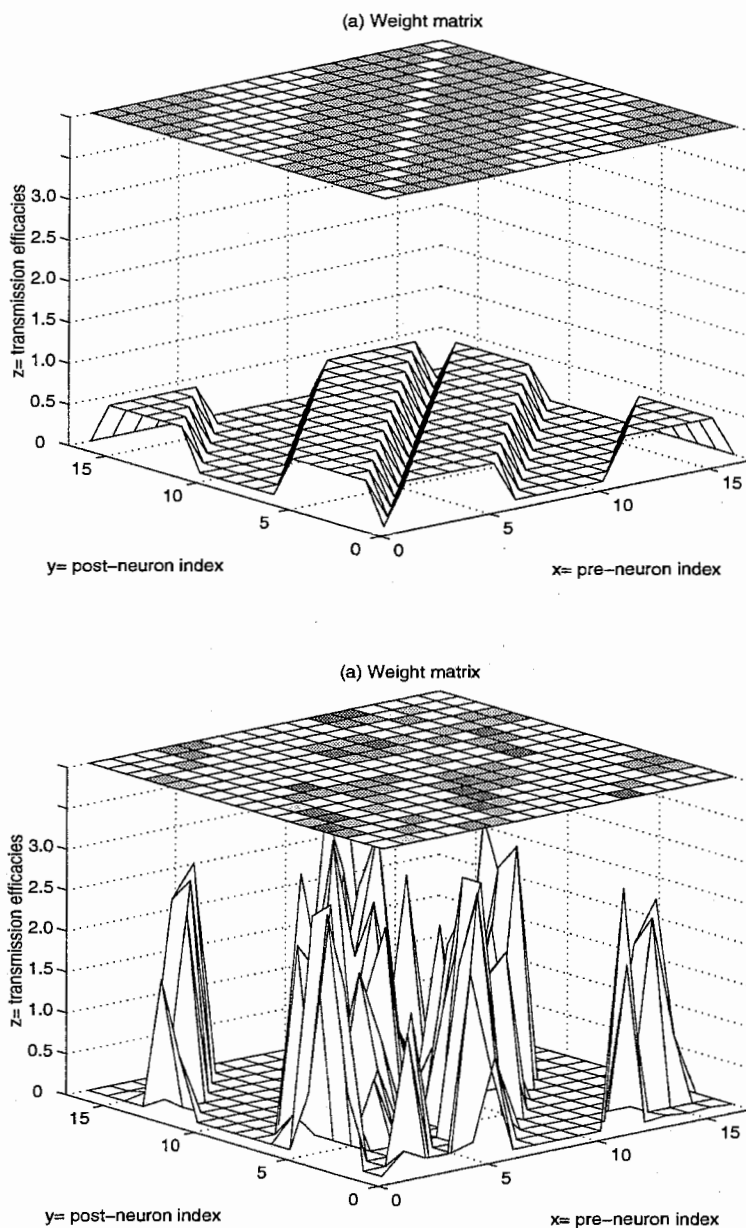
● **Figure 13**

(a) Weight matrix

(a) Weight matrix

Figure 13: Transmission efficacy values (weights) between pre-synaptic and post-synaptic neurons. z-axis denotes $\sum_q^4 J_{ij}^q/4$, i.e., average synaptic efficacy value between pre-synaptic neuron i and post-synaptic neuron j. (a) Before learning. Neighboring connections keep their initial efficacy values. (b) After learning. Many connections are depressed to zero, and some connections are potentiated to have large value.
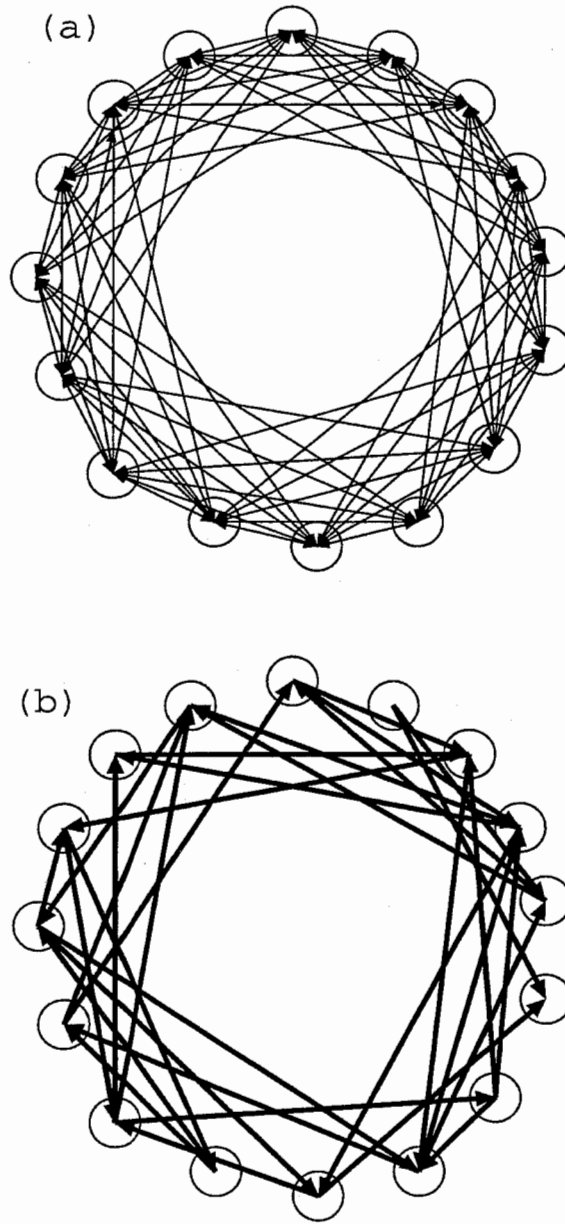
- **Figure 14**

Figure 14: Effective connections (a) before and (b) after learning. Some originally prepared connections survived.