# A neural circuit model forming semantic network with exception using spike-timing-dependent plasticity of inhibitory synapses

Kazushi Murakoshi [a,b,*], Kyoji Suganuma [a]

[a] *Department of Knowledge-based Information Engineering, Toyohashi University of Technology, 1-1 Hibarigaoka, Tenpaku-cho, Toyohashi 441-8580, Japan*

[b] *Media Science Research Center, Toyohashi University of Technology*

## Abstract

We propose a neural circuit model forming a semantic network with exceptions using the spike-timing-dependent plasticity (STDP) of inhibitory synapses. To evaluate the proposed model, we conducted nine types of computer simulation by combining the three STDP rules for inhibitory synapses and the three spike pairing rules. The simulation results obtained with the STDP rule for inhibitory synapses by Haas *et al.* [J. Neurophysiol. 96 (2006) 3305] are successful, whereas the other results are unsuccessful. The results and examinations suggested that the inhibitory connection from the concept linked with an exceptional feature to the general feature is necessary for forming a semantic network with an exception.

*Key words:*
Spike-timing-dependent plasticity; Inhibitory connection; Semantic network; Exception

## 1  Introduction

The role of memory is important for human high-order functions such as thought, motion, and recognition; high-order functions cannot be performed in the absence of memory. There are two major forms of memory, episodic

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*  Corresponding author. phone: +81-532-44-6899; fax: +81-532-44-6873.
   *Email address:* `mura@tutkie.tut.ac.jp` (Kazushi Murakoshi).

memory and semantic memory, which are both declarative (Tulving, 1972; Squire, 1987). Episodic memory is supposed to deal with individual episodes definable with respect to time and place while semantic memory contains impersonal facts undefinable in terms of time and place. The semantic network model (Collins and Quillian, 1969; Collins and Loftus, 1975) is proposed as a structure model of semantic memory. A semantic network is an oriented diagram in which nodes represent actual objects and arcs represent semantic relationships between these objects. However, the semantic network model does not have a process for constructing a semantic network.

Kobayashi and Murakoshi (2007) have proposed a neural circuit model forming a semantic network in the neocortex from direct input and episodic memory in the hippocampus using spike-timing-dependent plasticity (STDP) (Froemke and Dan, 2002), based on the hippocampus neural circuit model forming episodic memory (Ito et al., 2003). STDP is a minute time resolution version of the well-known Hebb learning rule. In the model (Kobayashi and Murakoshi, 2007), for example, after inputs such as "a canary is a bird" and "a bird can fly" are memorized, the output words "canary", "bird", and "can fly" are successively recalled by presenting the word "canary". Such results show that the model is able to form a semantic network.

However, the semantic network formed by the model proposed by Kobayashi and Murakoshi (2007) cannot represent an exception. An example of an exception is described as follows. In the case that "a canary is a bird", "a bird can fly", "an ostrich is a bird", and "an ostrich cannot fly" are presented, the exception is that "the ostrich is a bird *but* cannot fly" in contrast to the general fact that "birds can *generally* fly". We examine whether the model (Kobayashi and Murakoshi, 2007) can learn the relations with an exception: " 'canary' and 'bird' ", " 'ostrich' and 'bird' ", " 'bird' and 'can fly' ", and " 'ostrich' and 'cannot fly' ". As a result, "can fly" is additionally recalled with "cannot fly" for the input "ostrich", whereas "can fly" is only recalled for the input "canary". That is, the memory retrieval process of a semantic network with an exception is not perfectly accomplished using the model (Kobayashi and Murakoshi, 2007). For successful recall, any suppression of the output "can fly" for the input "ostrich" is necessary. In the model proposed by Kobayashi and Murakoshi (2007), only excitatory connections are used. Thus, we surmise that inhibitory connections are important for forming a semantic network with an exception in a neural circuit.

In this paper, we propose a neural circuit model forming a semantic network with exceptions using the spike-timing-dependent plasticity (STDP) of inhibitory synapses. To evaluate the proposed model, we conduct computer simulations. Because some types of STDP of inhibitory synapses are physiologically observed, we simulate each type of STDP. Additionally, since some rules for determining spike pairs are assumed, we examine each rule. It is

expected that the results of computer simulations will clarify the role of inhibitory connections in memory with an exception.

The remainder of this paper is organized as follows. In Section 2, we introduce STDP and topics related to STDP. Section 3 proposes a neural circuit model forming a semantic network with an exception. Section 4 shows the results of our computer simulation, and discusses how to form a semantic network using the STDP of inhibitory synapses. Section 5 presents our conclusions.

## 2 Spike-timing-dependent plasticity

In this section, we introduce spike-timing-dependent plasticity (STDP), which is used in the proposed model shown in Sec. 3. STDP is a special Hebbian form of synaptic plasticity where the relative timing of pre- and postsynaptic spikes determines the change in synaptic weight. STDP is considered as a neural basis of memory storage. There are two types of STDP: STDPs of excitatory and inhibitory synapses. Since the profiles of these STDPs are derived from the repetitive applications of spike pairs, some rules for determining spike pairs must be assumed in two trains of numerous spikes.

In Section 2.1, we briefly introduce the STDP of excitatory synapses. Section 2.2 describes some types of STDP of inhibitory synapses. Section 3 explains some rules for determining spike pairs.

### 2.1  STDP of excitatory synapse

The relation of synaptic plasticity for excitatory synapses with the temporal difference between presynaptic and postsynaptic activations has been electrophysiologically observed (Markram et al., 1997; Bi and Poo, 1998; Froemke and Dan, 2002). From the relation, postsynaptic potentials arriving after presynaptic potentials induce long-term potentiation, and postsynaptic potentials arriving before presynaptic potentials induce long-term depression. Froemke and Dan (2002) have derived a numerical description of the increase and decrease rates of synaptic plasticity $F(\Delta t)$ [%] from electrophysiological data as follows.

$$F(\Delta t) = \begin{cases} 102 \exp(-\frac{|\Delta t|}{15.5}) & (\Delta t > 0) \\ -52 \exp(-\frac{|\Delta t|}{33.2}) & (\Delta t < 0) \end{cases} \tag{1}$$

Here, $\Delta t$ [ms] is the temporal difference from a postsynaptic spike to a presynaptic spike.

3

Some relations of synaptic plasticity for inhibitory synapses with temporal difference between presynaptic and postsynaptic activations have been electrophysiologically observed (Holmgren and Zilberter, 2001; Woodin et al., 2003; Haas et al., 2006). Since these observations are quite different, each profile of the STDP of inhibitory synapses is described as follows.

Holmgren and Zilberter (2001) have observed the changes in the efficacy of inhibitory postsynaptic potential depending on the temporal difference between pre- and postsynaptic potentials by experiments using cortical slices of rats. In their experiments, a conditioning train of 10 backpropagating dendritic action potentials (APs) was initiated by 5-ms current injections in the soma of a pyramidal neuron as a postsynaptic neuron at 50 Hz. In a presynaptic neuron, an AP was initiated at different times relative to the beginning of the conditioning train in the postsynaptic neuron. The pattern of sequential post- and presynaptic stimulations was repeated every 5–7 sec 25–40 times. As a result, the mean IPSP amplitudes was $160 \pm 16\%$ at a relative time of 400 ms, $142 \pm 6\%$ at a relative time of 510 ms, $75 \pm 6\%$ at a relative time of 10 ms, $69 \pm 0.05\%$ at a relative time of 205 ms, and $58 \pm 0.06\%$ at a relative time of 250 ms. In short, a longer relative time resulted in the LTP of IPSPs, whereas a shorter relative time resulted in the LTD of IPSPs.

Woodin et al. (2003) have examined the dependency of inhibitory synaptic modification on the relative timing of pre- and postsynaptic spikings in hippocampal slices of rats. In their experiments, current pulses were injected into a postsynaptic neuron with presynaptic stimulation (5 Hz, 30 s), with the peak of postsynaptic spiking relative to presynaptic activation varied from 0 to $\pm 90$ ms. They found a clear increase in the amplitude of inhibitory postsynaptic current (IPSC) when the relative time was within $\pm 20$ ms, and found a small but significant reduction in IPSC amplitude at a relative time of more than $+50$ ms or less than $-50$ ms. This observation indicates a symmetrical window for the modification of inhibitory synapses.

Haas et al. (2006) have reported experimental results of STDP at inhibitory synapses in the entorhinal cortex of rats. They paired presynaptic stimulations with single induced postsynaptic spikes, and varied the interval between those stimuli between $-25$ and $+25$ ms at a rate of 2 Hz for 5 min. For the positive relative timing, inhibitory responses potentiated, peaking at a delay of 10 ms. For the negative relative timing, inhibitory responses depressed, again with a maximal effect near 10 ms of delay. Namely, they found an asymmetrical timing rule for the plasticity of inhibitory synapses.

The profiles of most STDPs are derived from the repetitive applications of spike pairs to obtain consistent synaptic modifications. In actual biological neural networks, the spikes of pre- and postsynaptic neurons are induced by numerous neurons. Thus, the critical question of whether each presynaptic spike interacts with every postsynaptic spike is raised. As a possible answer to the question, many rules for determining spike pairs have been assumed in two trains of many spikes. Among them, all-to-all and nearest-neighbor pairing rules have been widely used (Bi, 2002; Zhu et al., 2006).

In the all-to-all interaction rule, it is assumed that each presynaptic spike interacts with each postsynaptic spike. On the other hand, in the nearest-neighbor interaction rule (van Rossum et al., 2000; Bi, 2002; Sjöström et al., 2001), the first presynaptic (postsynaptic) spike after a given postsynaptic (presynaptic) spike can produce plasticity. Alternatively, Zhu et al. (2006) have proposed a latest-neighbor interaction, in which at any time instant only the latest-neighbor pairs of pre- and postsynaptic spikes contribute to plasticity. Their theoretical and numerical studies reveal that STDP with the latest-neighbor pairing rule can generate stable and more realistic distributions of synaptic conductance. Thus, we investigate the above three spike pairing rules. For simplicity, it is assumed that the pairing rules are independent between the effects of different spike pairings.

## 3  Proposed model

We propose a neural circuit model forming a semantic network with exceptions using the spike-timing-dependent plasticity of inhibitory synapses, based on the neural circuit model forming a semantic network proposed by Kobayashi and Murakoshi (2007). The proposed model is shown in Fig. 1, and its outline is described below. This model has been provided two association cortex 2 layers: the association cortex 2a layer maintains episodic memory, whereas the association cortex 2b layer maintains semantic memory. Each state of the model neuron in each layer is synchronously renewed. The circle indicates a layer including some model neurons. The solid arrow means all-to-all connections, whereas the dashed arrow means one-to-one connections. The thick arrow connections are changed by the STDP learning rule while the thin arrow connections are constant. The thick dotted arrow are appended in this paper as recurrent inhibitory connections learned through the STDP learning rules of inhibitory synapses. This thick dotted arrow represents all-to-all connections. Using recurrent inhibitory connections, we expect to depress general memory in forming a semantic network with an exception in a neural circuit.

The reason only recurrent inhibitory connections in the 2b layer are appended is as follows. Most inhibitory connections in the real brain are localized. Additionally, we focus on a semantic network in this paper. For simplicity, inhibitory connections are recurrent although in the real brain such connections are via inhibitory interneurons.

The association cortex 2b layer receives inputs from association cortex 1 ($x_i^{\text{cx1}}$), hippocampal CA1 ($x_i^{\text{ca1}}$), subiculum, ($x_i^{\text{sub}}$), association cortex 2b (recurrent excitation $x_i^{\text{2b}}$), and the association cortex 2b (recurrent inhibitory $x_i^{\text{2b}}$), whose propagation delays are $\Delta t^{\text{cx2b·cx1}}$, $\Delta t^{\text{cx2b·ca1}}$, $\Delta t^{\text{cx2b·sub}}$, $\Delta t^{\text{cx2b·cx2b}}$, and $\Delta t^{\text{cx2b·cx2b,inh}}$, respectively. The state $x_i^{\text{cx2b}}$ of the $i$-th neuron in association cortex 2b is modified to

$$
\begin{aligned}
x_i^{\text{cx2b}}(t) = f\bigg( & \sum_j^N w_{ij}^{\text{cx2b·cx1}} x_j^{\text{cx1}}(t - \Delta t^{\text{cx2b·cx1}}) \\
& + x_i^{\text{ca1}}(t - \Delta t^{\text{cx2b·ca1}}) \\
& + x_i^{\text{sub}}(t - \Delta t^{\text{cx2b·sub}}) \\
& + \sum_k^N w_{ik}^{\text{cx2b·cx2b}} x_k^{\text{cx2b}}(t - \Delta t^{\text{cx2b·cx2b}}) \\
& + \sum_k^N w_{ik}^{\text{cx2b·cx2b,inh}} x_k^{\text{cx2b}}(t - \Delta t^{\text{cx2b·cx2b,inh}}) \\
& - \theta^{\text{cx2b}} \bigg),
\end{aligned}
\tag{2}
$$

where $N$ is the number of neurons in a layer, $f(\cdot)$ is the step function which outputs 1 when inputs are greater than 0, $\theta^{\text{cx2b}}$ is the threshold, and $x_i^{\text{cx2b}} = 1$ means firing. As for synaptic weight, for example, $w_{ij}^{\text{layerA·layerB}}$ indicates the weight from the $j$-th neuron in layer B to the $i$-th neuron in layer A. The connections $w_{ik}^{\text{cx2b·cx2b},inh}$ are learned by applying the STDP rule for inhibitory synapses, whereas the connections $w_{ij}^{\text{cx2b·cx1}}$ and $w_{ik}^{\text{cx2b·cx2b}}$ are learned by applying the STDP rule for excitatory synapses. The upper limits of their connections are set to $w_{\max}^{\text{cx2b,inh}}$ and $w_{\max}^{\text{cx2b}}$, respectively. All others except the above-mentioned structure and setting are the same as those in the model proposed by Kobayashi and Murakoshi (2007).

We examine three profiles of the STDP of inhibitory synapses, as introduced in Section 2.2. Here, the profiles of the STDP of inhibitory synapses are expressed as a numerical formula for presenting a computational model. The ratio of the change in relative synaptic weight as a function of the relative time $\Delta t$ is expressed as $\Delta w(\Delta t)$, where $n$ is the number required to induce the synaptic change per unit time.

First, the STDP rule for inhibitory synapses derived from the experiment by
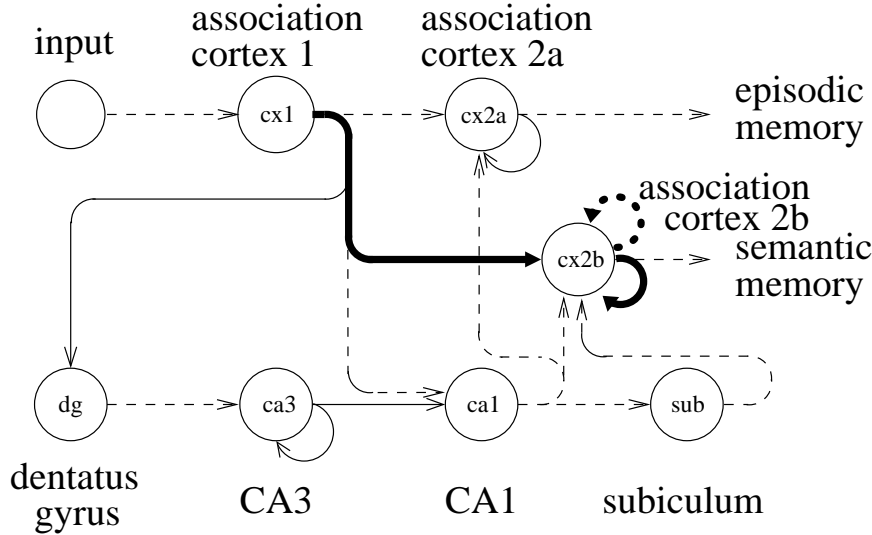
Fig. 1. Proposed model.

Holmgren and Zilberter (2001) is approximately expressed as

$$\Delta w(\Delta t) = \begin{cases} (\Delta t/400.0 * 0.6 + 0.9)/n + 1 & (-600 \leq \Delta t \leq -200) \\ (\Delta t/200.0 * -0.96 - 0.36)/n + 1 & (-200 < \Delta t < 0) \\ 1 & (\text{otherwise}) \end{cases} \quad .(3)$$

This profile at $n = 1$ is plotted in Fig. 2. For simplicity, only one postsynaptic AP without a train could cause STDP; $\Delta t$ is redefined as the temporal difference between the presynaptic AP and the ending of the AP train in the experiment (Holmgren and Zilberter, 2001). The notable features of this profile are that only a negative relative time window is available, and that the width of the relative time window is larger than those of the other profiles.

Second, the STDP rule for inhibitory synapses derived from the experiment by Woodin et al. (2003) is approximately expressed as

$$\Delta w(\Delta t) = \Big[ 1.50 * \exp(-0.004 * (\Delta t^2))$$
$$-0.50 * \exp(-0.0003 * (\Delta t)^2) \Big] /n + 1. \tag{4}$$

This profile at $n = 1$ is plotted in Fig. 3. This profile is expressed by the difference of two Gaussian functions. This profile has a symmetrical relative time window.

Third, Haas et al. (2006) expressed the STDP rule of inhibitory synapses derived from their experiment as

$$\Delta w(\Delta t) = \begin{cases} 1 + a_1 \cdot (\Delta t)^{10} \exp(a_2 \Delta t)/n & (\Delta t < 0) \\ 1 + a_3 \cdot (\Delta t)^{10} \exp(a_4 \Delta t)/n & (\Delta t > 0) \end{cases} , \tag{5}$$
$$a_1 = -2.60\text{e}{-}7 \quad a_2 = 0.94,$$
$$a_3 = 2.29\text{e}{-}6 \quad a_4 = -1.10.$$

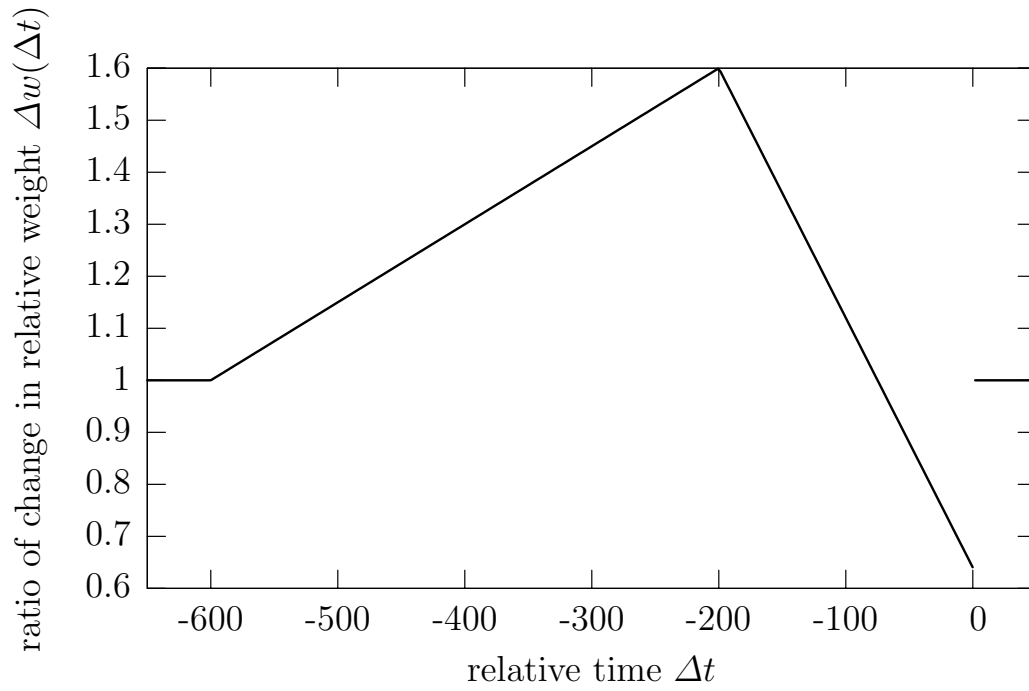This profile at $n = 1$ is plotted in Fig. 4. This profile has an asymmetrical

Fig. 2. Profile of STDP of inhibitory synapses by Holmgren and Zilberter (2001).
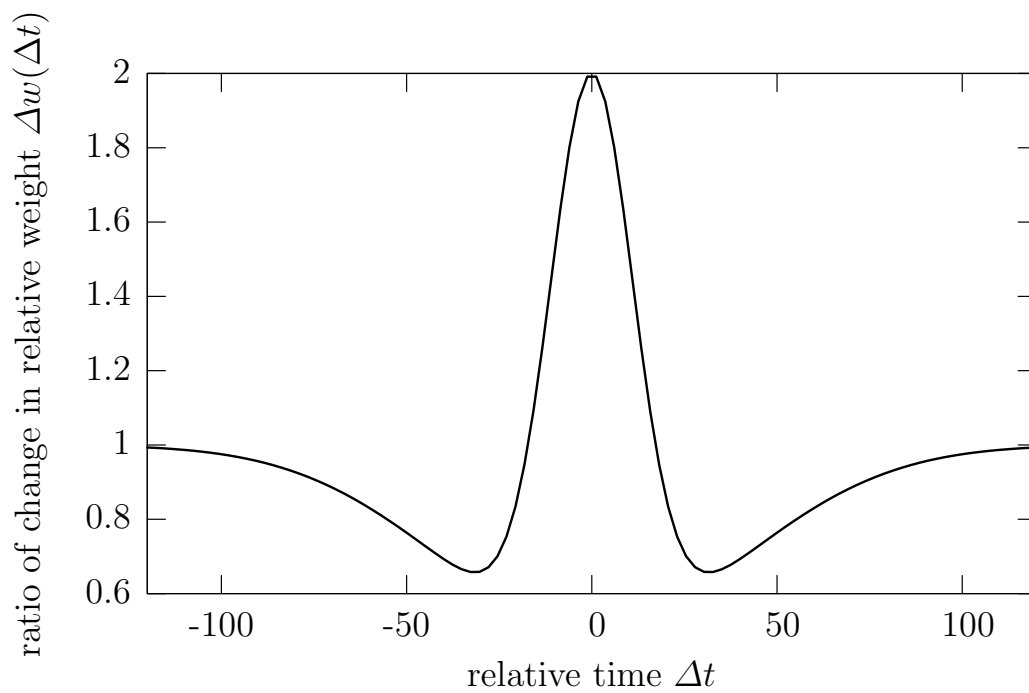


Fig. 3. Profile of STDP of inhibitory synapses by Woodin et al. (2003).
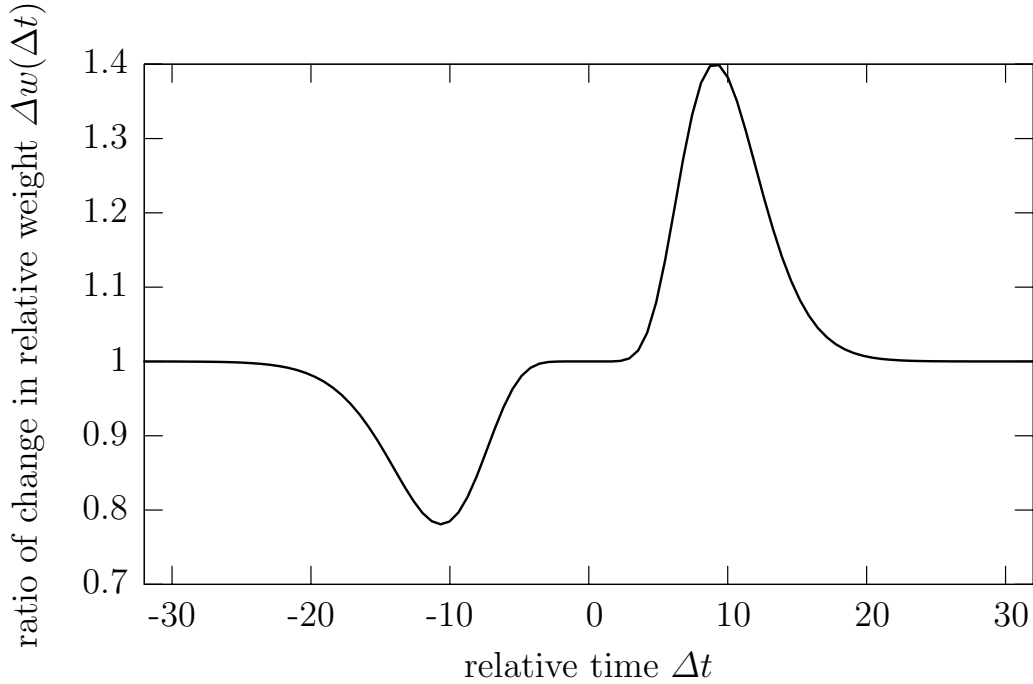
relative time window.

Fig. 4. Profile of STDP of inhibitory synapses by Haas et al. (2006).

## 4 Simulation

To examine the formation of a semantic network with an exception by the proposed method, we conduct many computer simulations. The parameters used in these simulations are shown in Table 1. The other parameters are the same as those used by Kobayashi and Murakoshi (2007). Total simulation time, the input frequency of sequential patterns, and the number for making synaptic change per unit time are varied. The initial inhibitory weight is the same as the excitatory weight. The upper limit set by the STDP of inhibitory synapses is the same as that set by the STDP of excitatory synapses. The inhibitory recurrent propagation delay is twice the excitatory propagation delay, because we consider that the inhibitory recurrent connection is assumed to pass from an excitatory neuron to an excitatory neuron via an inhibitory neuron.

The input patterns are of 10 types (A–J), where each pattern consists of five non-overlapping elements. In these simulations, it is assumed that A, B, C, D, and E mean "canary", "bird", "can fly", "ostrich", and "cannot fly", respectively. The description (ABC) denotes a time sequence pattern, and A, B, and C are sequentially input; (ABC) means "a canary is a bird, and can fly". The symbol '?' of the description (AB?) denotes an arbitrary pattern except A and B, for examples, the description (AB?) means (ABC), (ABD), · · ·; (AB?) means "a canary is a bird" with an arbitrary attribute.

9

In the above-mentioned simulations, the exception focused on in this research is simply expressed as follows. The exceptional inputs are (DE?) and (DB?) as the exception "the ostrich is a bird *but* cannot fly", whereas the regular inputs are (BC?), (AB?), and (AC?) as the episode including the general fact "birds can *generally* fly". Thus, the five sequential patterns (AB?), (AC?), (BC?), (DB?) and (DE?) are input to the proposed model for learning.

We conduct nine types of computer simulations by combining the three STDP rules of inhibitory synapses and three spike pairing rules. After each learning, the patterns A, B, C, D, and E are input to confirm the formations of memories as results. The results are shown in the following Figs. 5–10. In the figures, the horizontal axis indicates time while the vertical axis indicates the output of each neuron composing the patterns. The figures show the outputs of association cortex 1 (input layer) and 2b (output; semantic memory layer) from the top to the bottom. The squares in the figures indicate firings of neurons. The results obtained with the all-to-all spike pairing rule are omitted, because the results with all STDP rules of inhibitory are unsuccessful in a forming semantic network with an exception.

Figures 5 and 6 indicate the results obtained with the STDP rule by Holmgren and Zilberter (2001). From the results in both figures, when the patterns A, B, C are input, the output patterns are successfully recalled: A, B, and C for input A, all for input B, and A, B, and C for input C. However, when the patterns D and E are input, the output patterns are unsuccessfully recalled: both C and E for input D or E, that is, "can fly" and "cannot fly" for the input "ostrich" or "cannot fly".

Figures 7 and 8 indicate the results obtained with the STDP rule by Woodin et al. (2003). These results are quite similar to those obtained with the STDP rule by Holmgren and Zilberter (2001); the output patterns are unsuccessfully recalled for the input D or E.

Figures 9 and 10 indicate the results obtained with the STDP rule by Haas et al. (2006). The results are different from the above results; the output patterns are successfully recalled even for the input D or E. This means that "can fly" is suppressed for the input "ostrich" or "cannot fly".

ch:param

We examine the inhibitory connections obtained in the above simulations in order to investigate how to form a semantic network with an exception. The inhibitory connections are shown in the following Figs 11–14. In the figures, an arrow indicates inhibitory connection whose weight is more than 0.02. The figures of inhibitory connections obtained with the STDP rule by Holmgren and Zilberter (2001) are omitted, because there are no connections whose weight is more than 0.02. Figures 11 and 12 indicate the inhibitory connec-

Table 1

List of parameters.

| parameter | value |
|---|---|
| total simulation time $T$ | variable |
| input frequency of sequence patterns | variable |
| number for making synaptic change per unit time $n$ | variable |
| propagation delay from CA1 to CX2b | |
|    direct $\Delta t^{\mathrm{cx2b\cdot ca1}}$ | 15[ms] |
|    via subiculum $\Delta t^{\mathrm{sub\cdot ca1}} + \Delta t^{\mathrm{cx2b\cdot sub}}$ | 21[ms] |
| initial inhibitory weight from CX2b to CX2b | 0.002 |
| upper limit of CX2b by STDP of inhibitory synapses $w_{\max}^{\mathrm{cx2b,inh}}$ | 0.2 |
| inhibitory recurrent propagation delay in CX2b $\Delta t^{\mathrm{cx2b\cdot cx2b,inh}}$ | 10[ms] |
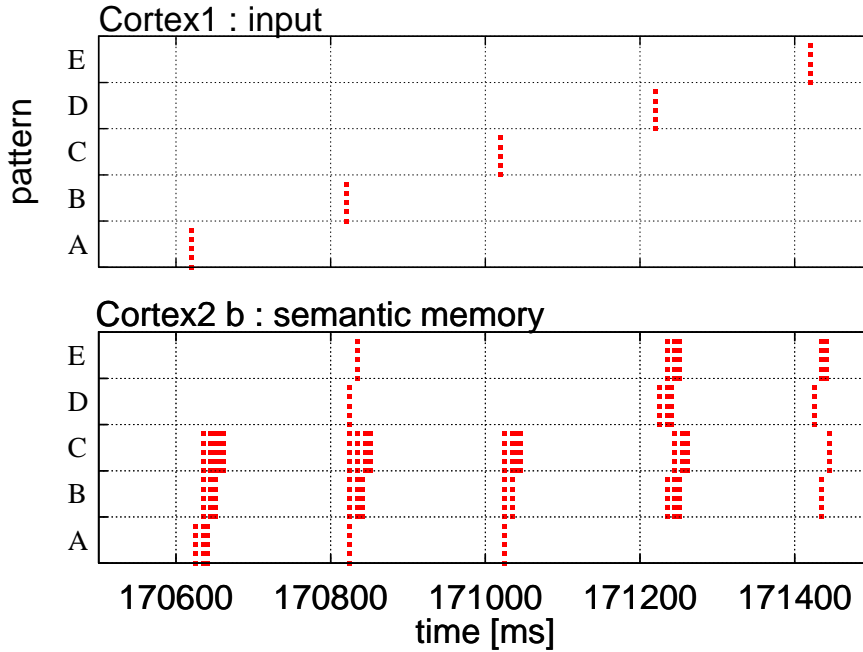


Fig. 5. Simulation result obtained with STDP rule by Holmgren and Zilberter (2001) and latest-neighbor rule.

tions obtained with the STDP rule by Woodin et al. (2003), which is for an unsuccessful case. On the other hand, Figures 13 and 14 indicate the inhibitory connections obtained with the STDP rule by Haas et al. (2006), which is for a successful case. By comparing these connections to each other, the following fact is proved. The inhibitory connection from the pattern D ("ostrich") to the pattern C ("can fly") is necessary to suppress the output pattern C. The connection is only available in Figs. 13 and 14 as successful cases, and not in Figs. 11 and 12 as unsuccessful cases. The connections from B to E and from E to C that are available only in Fig. 14 are not essential, because they are not available in Fig. 13 as a successful case.
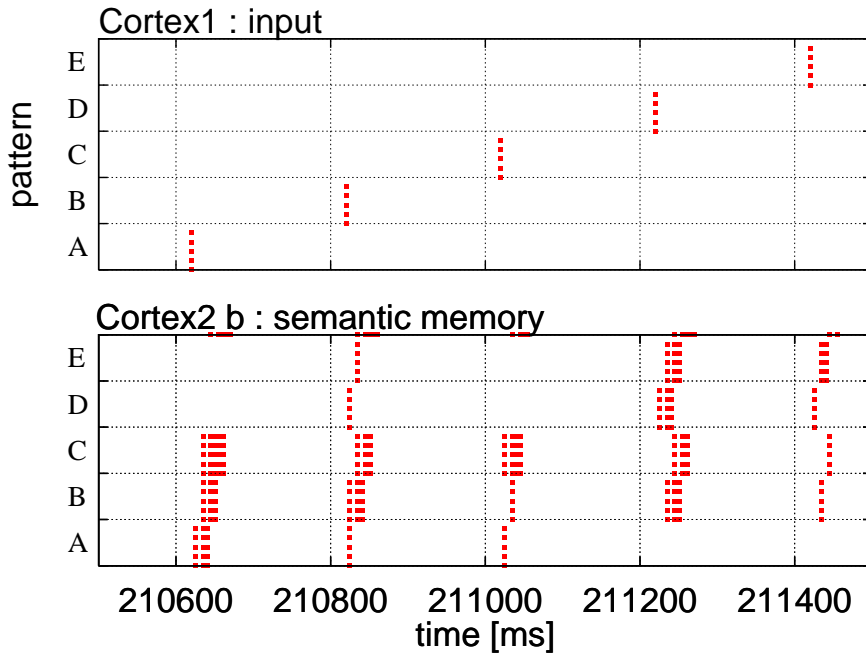
Fig. 6. Simulation result obtained with STDP rule by Holmgren and Zilberter (2001) and nearest-neighbor rule.

In summary, the above results and examinations suggest that inhibitory connections are essential for forming a semantic network with an exception. Moreover, inhibitory connections are suggested to be connections from the concept linked with an exceptional feature to the general feature.

## 5 Conclusions

We proposed a neural circuit model forming a semantic network with exceptions using the spike-timing-dependent plasticity (STDP) of inhibitory synapses. To evaluate the proposed model, we conducted nine types of computer simulation by combining the three STDP rules for inhibitory synapses and the three spike pairing rules. The simulation results obtained with the STDP rule for inhibitory synapses by Haas et al. (2006) are successful, whereas the other results are unsuccessful. The results and examinations suggested that the inhibitory connection from the concept linked with an exceptional feature to the general feature is necessary for forming a semantic network with an exception.

Here, we discuss the profiles of three STDP rules of inhibitory synapses (Holmgren and Zilberter, 2001; Woodin et al., 2003; Haas et al., 2006). We think
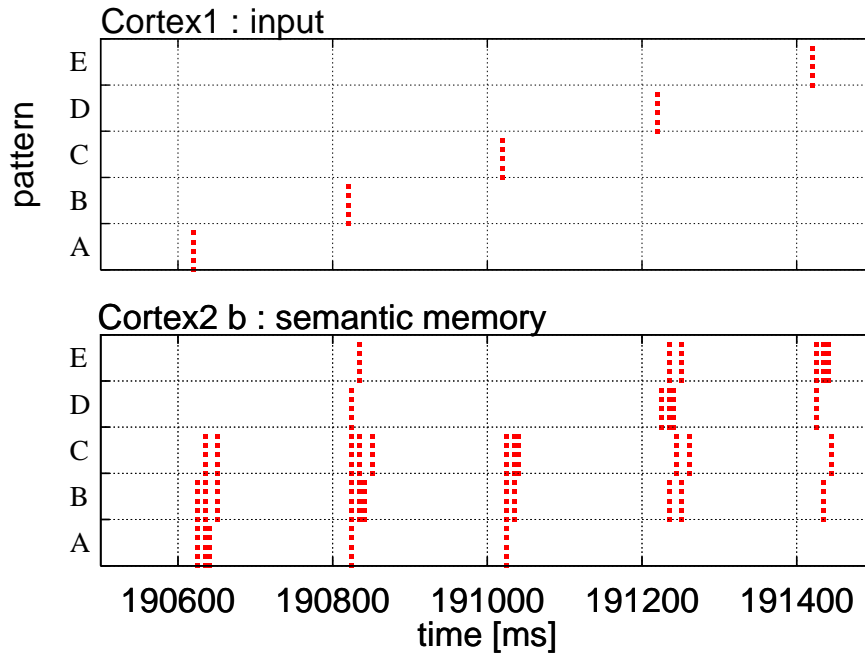
12

Fig. 7. Simulation result obtained with STDP rule by Woodin et al. (2003) and latest-neighbor rule.

that the reasons the results obtained with the STDP rule by Holmgren and Zilberter (2001) are unsuccessful are: only the negative relative time window is available, and the width of the relative time window is larger than those of the other profiles. In the case with the STDP rule by Woodin et al. (2003), we think that the reason is symmetrical profile. In contrast, the profile by Haas et al. (2006) is asymmetrical, and the width of the relative time window is appropriate.

We think that the two STDP rules for inhibitory synapses by Holmgren and Zilberter (2001) and Woodin et al. (2003) are utilized for other functions except for forming a semantic network with an exception. The investigation of such functions is reserved for future work. Finally, we hope to verify the function of inhibitory synapses suggested in this study through actual biological experiments.

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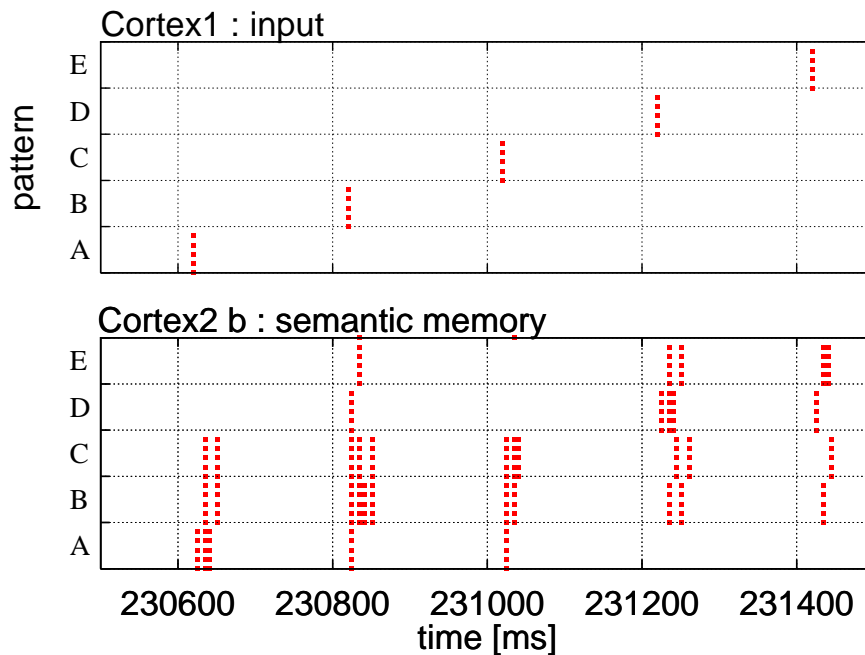Bi, G.-Q., Poo, M.-M., 1998. Synaptic modifications in cultured hippocampal

Fig. 8. Simulation result obtained with STDP rule by Woodin et al. (2003) and nearest-neighbor rule.

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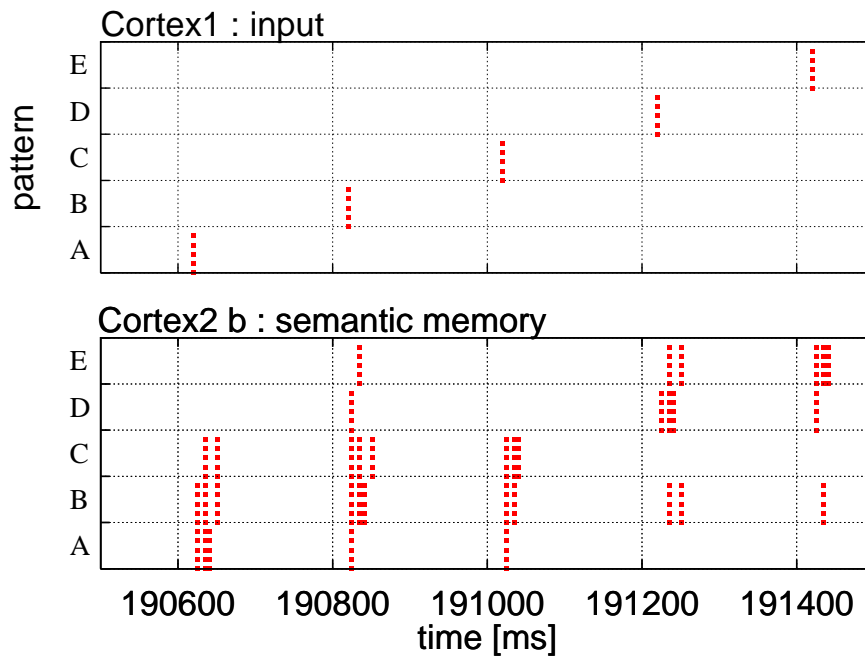
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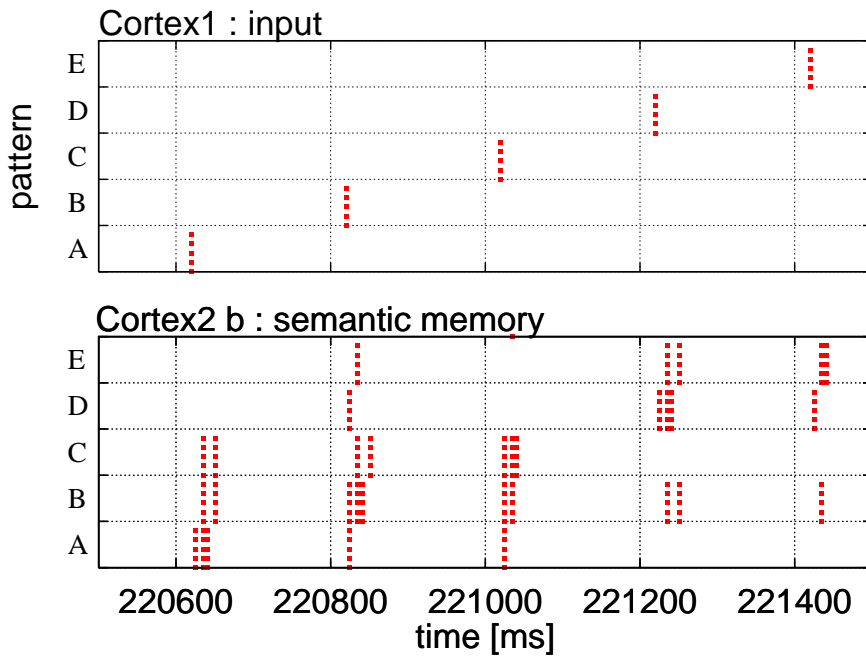
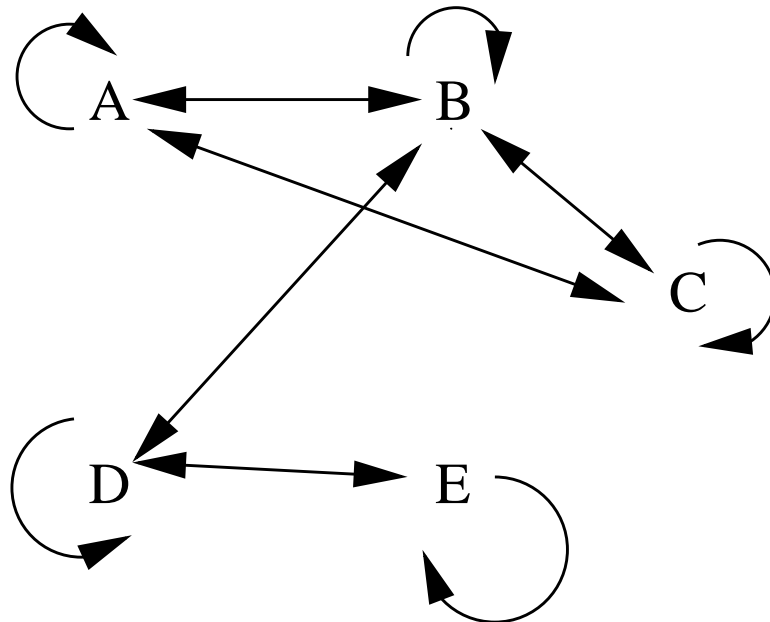Fig. 10. Simulation result obtained with STDP rule by Haas et al. (2006) and nearest-neighbor rule.



Fig. 11. Inhibitory connections obtained with STDP rule by Woodin et al. (2003) and latest-neighbor rule.
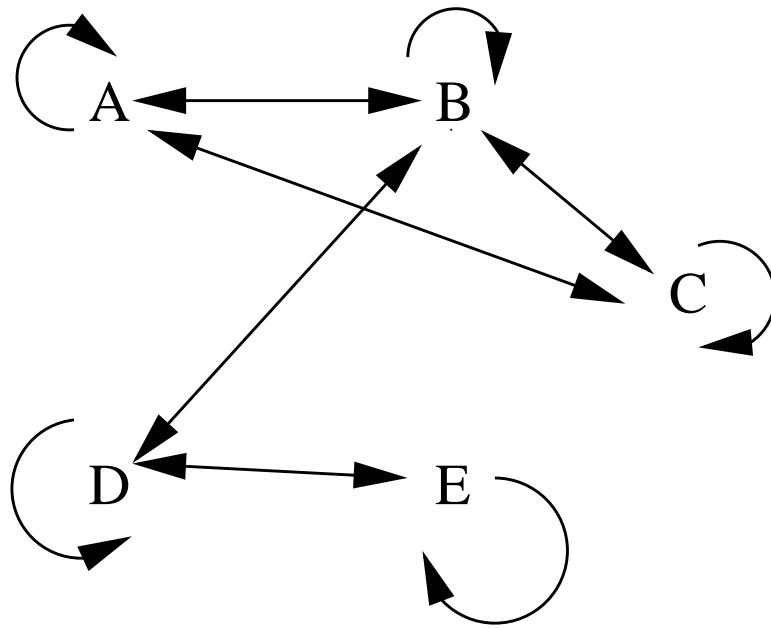
16

Fig. 12. Inhibitory connections obtained with STDP rule by Woodin et al. (2003) and nearest-neighbor rule.
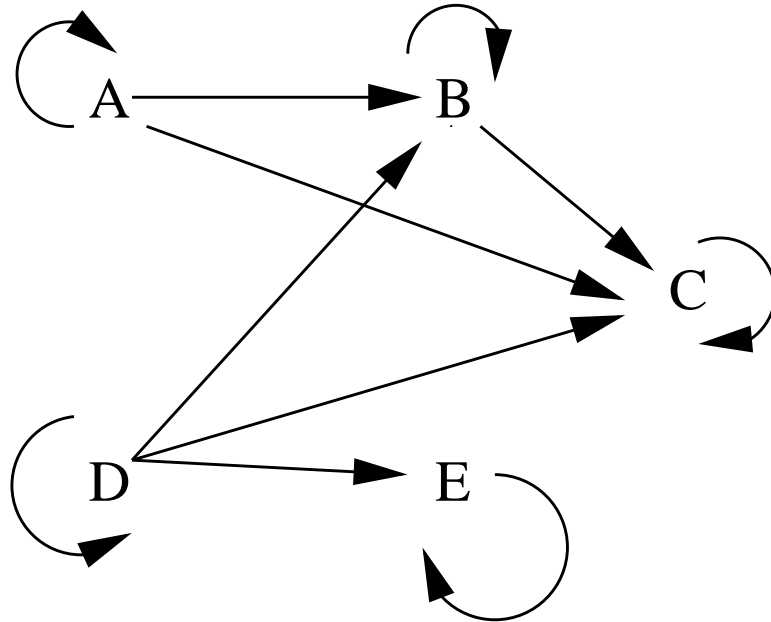


Fig. 13. Inhibitory connections obtained with STDP rule by Haas et al. (2006) and latest-neighbor rule.
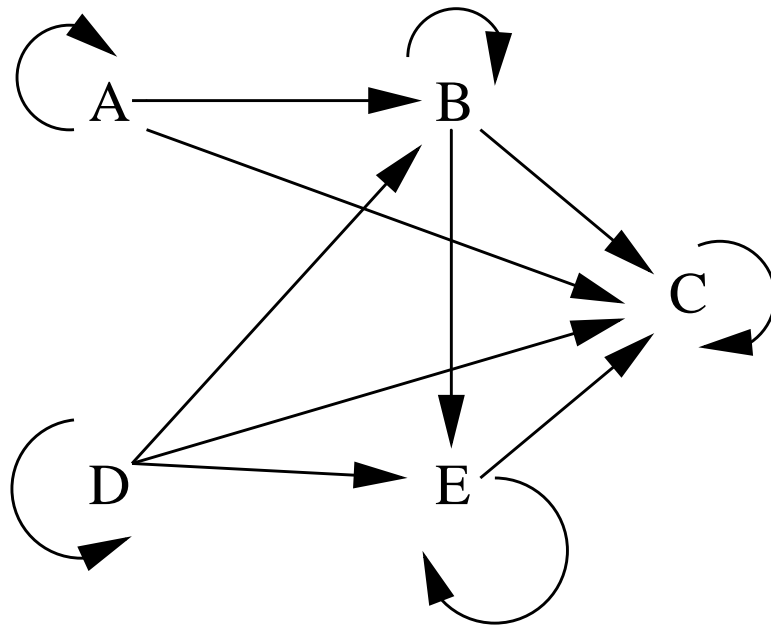
Fig. 14. Inhibitory connections obtained with STDP rule by Haas et al. (2006) and nearest-neighbor rule.