Neurocomputing 73 (2009) 381–388

Contents lists available at ScienceDirect

Neurocomputing

journal homepage: www.elsevier.com/locate/neucom

# Synchronization enhances synaptic efficacy through spike timing-dependent plasticity in the olfactory system

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ARTICLE INFO

*Article history:*
Received 2 May 2008
Received in revised form
26 June 2009
Accepted 2 August 2009
Communicated by T. Heskes
Available online 19 August 2009

*Keywords:*
Synchronization
STDP
Learning
Synaptic efficacy
Olfaction

ABSTRACT

Synaptic modifications are measured in biological experiments with respect to spike timings. Spike timing-dependent plasticity is the latest development in refinements of Hebbian learning. We have applied additive and multiplicative STDP synaptic learning rules to a biologically inspired olfactory network. The olfactory system recognizes odorant patterns by synchronization of mitral cells. Synchronization enhances synaptic connections between mitral cells and cortical cells. Both STDP rules exhibit unimodal weight distributions which is biologically realistic. As a result, cortical cells respond with a wider range of variability and higher firing frequency. This property has potential for the improvement of artificial odor recognition through ongoing selection of mitral cells.



## 1. Introduction

The brain is the center of intelligence, necessary for learning new concepts and dealing with uncertainty. Plasticity among neuronal connections in neural networks is believed to be the major mechanism that underlies intelligence [1]. Information in neural networks is encoded in the form of spike trains. Spike trains spread from one neuron to another through synapses and finally activate specific neurons in the cortex. The spatial position, spiking time and firing frequency of spike trains are studied by researchers to reveal the coding by the brain. However, it is still an open problem how information is represented in the brain using spiking trains.

We experience learning new concepts through reenforcement of practice. For instance, we remember a telephone number by repeating it several times. Hebbian learning was introduced to neural networks in this scenario by Hebb in 1949. Hebb proposed that "when one cell repeatedly assists in firing another, the axon of the first cell develops synaptic knobs (or enlarges them if they already exist) in contact with the soma of the second cell" [1]. Hebbian theory was confirmed by experimental discoveries of long-term potentiation (LTP) in the rabbit hippocampus in 1966 [2]. LTP describes long-term enhancement of a synapse between two neurons, which are stimulated at the same time. Although there is no sufficient evidence, long-term depression (LTD) is also postulated in neural networks to balance enhancement caused by LTP. A lot of correlation learning rules inspired by Hebbian theory have proved to be successful in specific neural networks [3].

In 1998, spike timing was found to be critical to synaptic modification [4]. Synaptic changes depending on the timing of both pre- and postsynaptic spike trains are named spike timing-dependent plasticity (STDP). Feedback of postsynaptic neurons can reflect the synaptic weights locally with global knowledge of the network. There are some variations of STDP and details of differences are explained in Section 3.

STDP has been discovered to facilitate synchronization in the olfactory neural networks of locusts [5,6]. On the contrary, we have explored the features of STDP in a closed network with spontaneous synchronization [7]. Synchronization is evoked by external inputs in a recurrent network with frequency-dependent synapses [8]. For invertebrate, Finelli et al. have proposed that STDP regulates and selects specific output of projection neurons to form sparsely firing of Kenyon cells in the mushroom body [6].

In the biological olfactory system, odorants are bound to their specific receptors residing in the capillary network around sensory neurons. One neuron can only expresses one kind of receptor and neurons with the same receptors are classified as the same type of sensory neurons. These sensory neurons play an important role in the transition from chemical detection to electrical signals, which initiates olfactory perceptions.

The same type of sensory neurons are assembled at the same location in the olfactory bulb, named glomerulus. The number of

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doi:10.1016/j.neucom.2009.08.003

glomeruli is close to the types of receptors. Activity patterns of firing rates are repeatable by odorant exposures. These patterns are believed to be the representations of odors in the olfactory bulb.

The olfactory bulb connects to the cortex via mitral/tufted cells. The processing in the cortex is complicated and recent research has to focuses on a specific small region of the cortex (mushroom body for invertebrates) [9]. For simplicity, a cortical cell is used to represent the activity of one odor in the cortex in our model. Further details of the olfactory system can be found in our early work [10].

In this paper, we study how synchronization affects STDP in a feed-forward network and the potential function of STDP for synchronization in an olfactory system we have built [10]. Features of two types of STDPs, weight-dependent and weight-independent STDP, respectively, are compared to validate the advantages and disadvantages of both models. After the comparison, we apply two kinds of STDP to a previous model of the olfactory neural network and examine the effects of both STDP within the olfactory system. In the olfactory model, selective mitral cells tend to fire synchronously with each other when the target odor presents. This synchronization will therefore modify the connection strength between mitral cells and cortical cells. Synchronization is found to increase the response variability of cortical neurons and thus makes the model more realistic to neurons in the waking brain [11]. In the simulation, both STDPs potentiate connection strengths when synchronization appears and encourages more firing in the cortical cells. While non-synchronized mitral cells depress synaptic weights or even eliminate the connections, the weight becomes zero. This selection can affect the olfactory system in the evolution of mitral cell selection [12–14].

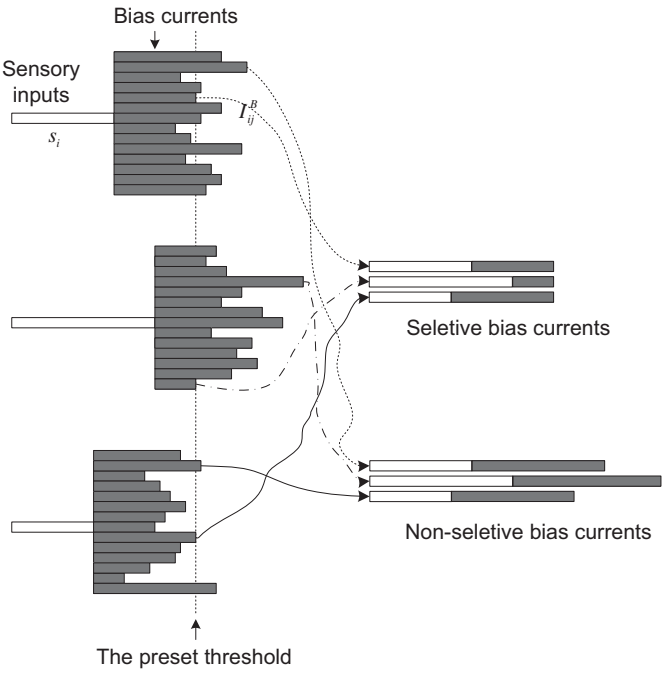


**Fig. 1.** Selection principle for bias currents and mitral cells: white bars represent sensory inputs $s_i$ and gray bars represent bias currents $I_{ij}^B$ . The sensory input $s_i$ is feeding to the $i$ th glomerulus and there are 14 bias currents within the glomerulus. Only one bias current, which makes the sum of sensory input $s_i$ and bias current $I_{ij}^B$ closest to a preset threshold, is selected for a particular odor. This sum is used as the input for the corresponding mitral cell. Bias currents and mitral cells are odor specific. As a result, selective mitral cells have similar inputs forcing them to fire synchronously.

## 2. Olfactory model

The topology of the system we constructed refers to biological olfactory systems of vertebrates like humans. The olfactory system of invertebrates like honeybees and locusts is sharing a similar structure of vertebrates. As indicated in Buck and Axel's paper, there are about 350 types of sensory receptor genes for humans and one sensory neuron can only express one species of gene [15]. All the sensory neurons expressing the same gene are dedicated to one glomerulus. The transduction between sensory neurons and mitral cells is inspired by Brody and Hopfield [16].

In our model, a 500-dimensional input is used to represent the pattern generated by sensory neurons activated by one odor. Each dimension synthesizes the signals from one kind of sensory neurons. For each odor, the 500-dimension input is distinguishable from all the others and the $i$ th element $k_{oi}$ for odor $o$ ranges from $-3$ to 3 mV. A concentration signal $c_o$ is controlling the strength of odor $o$. The $i$ th sensory input $s_i$ to the $i$ th glomerulus is summed up from the $i$ th elements of all the odors as follows:

$$s_i = \log\left(\sum_o c_o \exp(2.3k_{oi})\right), \quad i = 1,\ldots,500, \tag{1}$$

and two odors are simulated in the model, $o = 1, 2$.

There are 500 glomeruli in the olfactory model. Within the $i$ th glomerulus, 14 bias currents $I_{ij}^B$ are assigned randomly at the initial stage, where $j$ is the index for bias currents. In the meantime, 14 mitral cells are connected to one glomerulus and each mitral cell has its individual bias current. All the mitral cells and cortical cells are simulated by excitatory neurons defined by Borisyuk. The oscillatory activity of interconnected inhibitory neurons, in other words the local field potential, is simplified by a sinusoidal signal $I^P\cos(\omega t)$ [ ]. The periodical local field potential is shared by all the mitral cells among glomeruli.

When the system is constructed, two 500-dimension vectors representing two distinct odors within the sensory layer are generated. According to the odors present, mitral cells are selected for each odor. Only one mitral is chosen on each glomerulus for each odor according to the Many Are Equal (MAE) principle [17]. That mitral cell $j$ on the $i$ th glomerulus is selected for which the sum of sensory input $s_i$ and the bias current $I_{ij}^B$ is as close as possible to a preset threshold $\sigma$. The MAE principle is illustrated in Fig. 1. Additionally, it is possible that no mitral cell is chosen for some glomeruli when the odor signal $k_{oi}$ is negative. Mitral cells from those glomeruli are not counted into the subset of representative mitral cells anymore.

The sensory input $s_i$, selective bias current $I_{ij}^B$ and the local field potential $I^P\cos(\omega t)$ are summed together to form the input $I_i^M$ to the $j$ th selective mitral on glomerulus $i$, that is

$$I_i^M = s_i + I_{ij}^B + I^P\cos(\omega t). \tag{2}$$

Each odor specific subset of mitral cells converges to a cortical cell. Similarly, the cortical cells are odor specific and each of them can only recognize one odor. The representations of odors in the cortex are still mysterious, although sparseness and inhibition are revealed in biological and computational experiments [18–20]. The topology of the overall system is shown in Fig. 2.

## 3. Spike timing-dependent plasticity

Bi and Poo showed that spike timing of pre- and postsynaptic neurons is relative to the efficacy of their synapse in cultured rat hippocampus [4]. A critical window of synaptic modification was