Function of attention in learning process in the olfactory bulb

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Abstract It has been suggested that in the olfactory bulb, odor information is processed through parallel channels and learning depends on the cognitive environment. The synapse's spike effective time is defined as the effective time for a spike from pre-synapse to post-synapse, which varies with the type of synapse. A learning model of the olfactory bulb was constructed for synapses with varying spike effective times. The simulation results showed that such a model can realize the multi-channel processing of information in the bulb. Furthermore, the effect of the cognitive environment on the learning process was also studied. Different feedback frequencies were used to express different attention states. Considering the information's multi-channel processing requirement for learning, a learning rule considering both spike timing and average spike frequency is proposed. Simulation results showed that habituation and anti-habituation of an odor in the olfactory bulb might be the result of learning guided by a common local learning rule but at different attention states.

Keywords: **olfactory bulb, spike effective time, learning rule, feedback, attention.**

Biological experiments[1—8] have shown that in the olfactory bulb, odor information is encoded into spatio-temporal patterns and processed in multi-channels. In the bulb, the information is divided into basic information and fine information, which are encoded into average spiking frequency (long-term pattern) and synchronization of spikes[1—8] respectively. Compared with other structures in which information is encoded into spatio-temporal patterns, the olfactory bulb's structure is rather simple. Experiments have also shown that coding of an odor in the olfactory bulb was plastic and adjusted by the attention mechanism[9,10]. Due to its simple structure and typical learning and coding, the olfactory bulb model is suitable for the study of learning and memory.

How is multi-channel information processing in the olfactory bulb carried out? Information in the neural system is accomplished by the spikes of neurons. The effect of a spike from a pre-synapse to its post-synapse includes two attributes: intensity and duration. When the criterions of coding and spike effective time are comparable, the spike effective time must be considered. This paper proposes a concept of spike effective time, defined as the effective time of a pre-synaptic

spike to the post-synaptic neuron's potential. Odor information is divided into molecular informa-tion (basic information) and the ratio information of the molecules (fine information). If these two kinds of information are processed by synapses with quite different spike effective time, it will build multiple channels for information processing.

Multi-channel coding requires that the learning rule must consider both the spike timing and the average spike frequency. This paper purposes an antisymmetric learning rule for models based on spike neurons: the modification of synapses relies on pre- and post- synaptic spike timing. In detail, the synapse is modified only when the pre- and post- synapse spikes are within a learning window (5—20 ms), the modification's direction depends on the sequence of a pair of spikes, and the modification's size depends on the interval between the pre- and post- synaptic spikes. This learning rule has the following characteristics: 1. locality: a synapse's modification only depends on its pre- and post- neuron spikes; 2. timing sensitivity: the timing of pre- and post- synaptic spikes decides the size and direction of the modification; 3. interactivity: the synapse's modific a-tion is the result of interactivity between the pre- and post- neurons, i.e. only if both pre- and post-neurons spike can the synapse be modified. In this study, with a computer model of olfactory bulb, analysis proved that such a local learning rule can induce different global learning results at dif-ferent attention states. In other words, the habituation and anti-habituation of an odor are based on the meaning of the odor to the creature. Here, the attention state reflects the effect of a cognitive environment on the learning process. The attention state is brought about by feedback from the higher cortex area, implying that the attention state might be carried out by the frequency of the feedback spikes. Data from some related biological experiments[11,12] suggested that the frequency in the cognitive process at the attention state is higher than that in the cognitive process at the no attention state.

This paper presents studies of the function of the synapse's spike effective time in coding and learning, as well as the role of attention in global learning.

1   Model

Based on anatomical data, we constructed a simplified model of the olfactory bulb, which was composed of 16 periglomerular cells, 16 mitral cells and 160 granule cells (fig. 1). The mitral cells were arranged as a one-dimensional circle. Each mitral cell interacted with 10 surrounding granule cells, and four mitral cells composed an olfactory glomerulus. The mitral cells within a glomerulus interacted with each other through inhibitory synapses, and the mitral cells from dif-ferent glomeruli interacted with each other through granule cells. The sensory neurons projected into mitral cells and periglomerular cells, and those projecting into a glomerulus had at least one common odor receptor. The feedback from the higher cortex projected into the granule cells, which affected the bulb's output by adjusting the granule cells' output.

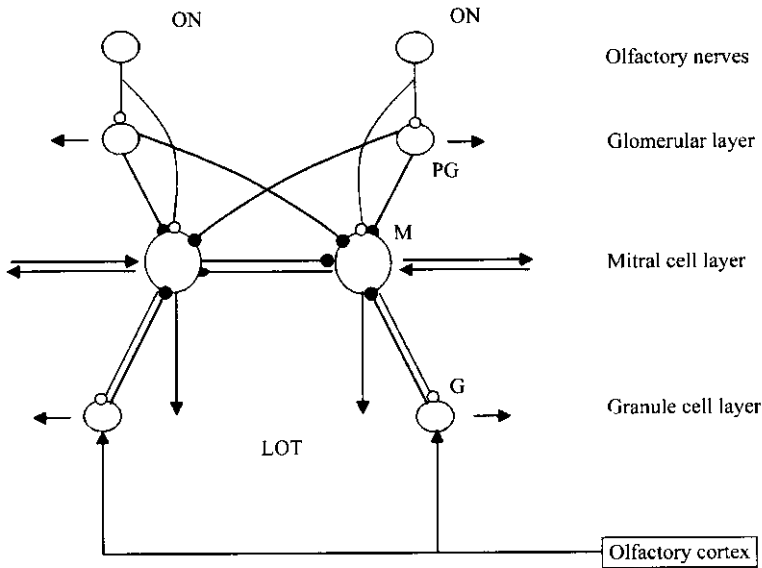A neuron spikes when its membrane potential is over certain threshold, described as

Fig. 1. Network structure of the model for the olfactory bulb. The network was composed of 3 layers: the periglomerular cell layer (PG), the mitral cell layer (M) and the granule cell layer (G). Each glomerulus was composed of 4 mitral cells, with the olfactory sensory neurons having the same odor receptor projected to mitral cells and periglomerular cells within a glomerulus, and mitral cells within a glomerulus interacting with each other. The mitral cells project to the granule cells with excitatory synapses and receive inhibitory feedback from the granule cells. The feedback from the olfactory cortex projects to the granule cells. ○, Excitatory synapse; ●, inhibitory synapse.

$$V_{x,i} = h(u_{x,i} - q_{x,i}), \quad x = m, p, g, \tag{1}$$

where $q_{x,i}$ is the x layer ith neuron's threshold for spiking, $h(x)$ is step function, if $x > 0$, it is 1, otherwise 0.

A spiking neuron's membrane potential declines quickly. The ith x neuron's potential declining speed when it is spiking is described as

$$u_{x,i}^{fire} = B_x \sum_k e^{-(t-t_k)/l}, \quad x = m, p, g, \tag{2}$$

where t is the time, t_k is the timing of the kth spike of the spike serial; B_m, B_p and B_g are the amplitudes of the declining speed during spiking; and l is the time coefficient of a membrane potential's decline induced by spiking, reflecting the refractory period, set as 2 ms. B_m, B_p and B_g were set large enough to have the neurons in the model behave as spike neurons ($B_m = B_p = B_g = 2000$ ms^{-1}), so that the spiking neuron's membrane potential declined below threshold very quickly (<1 ms).

The effect of a spike from pre-synapse to post-synapse is described as

$$F_{xy,ij}(t) = w_{xy,ij} \int_{t-d_{xy,ij}-T_{xy,ij}}^{t-d_{xy,ij}} V_{y,j}(t')dt', \quad x = m, \ g, \ y = m, \ p, \ g, \tag{3}$$

where $T_{xy, ij}$ is the synapse's spike effective time. When the two neurons connected by the synapse are within a glomerulus, it is 100 ms, otherwise 5 ms; $w_{xy, ij}$ and $d_{xy, ij}$ are the weight and delay of

the synapse from the jth y neuron to the ith x neuron.

When the spike effective times of different synapses vary greatly (e.g. different magnitudes), they will decide the role of the synapse in coding. On a long-term scale, the input caused by spikes from the short-term-effective synapses will be eclipsed by the input caused by spikes from the long-term-effective synapses. Thus the long-term output patterns mainly rely on spikes from long-term-effective synapses. On a short-term scale, because the input caused by spikes from short-term-effective synapses and long-term-effective synapses are comparable, the short-term output patterns are the result of both the spikes from long-term-effective synapses and short- term-effective synapses.

Based on the olfactory bulb's special structure, the multi-channel processing of information can be accomplished by setting the synapse's spike effective time. As mentioned before, those olfactory sensory neurons projecting into a single glomerulus have the same odor receptor. If only the interaction within a glomerulus is considered, the output patterns rely on only the odor's molecule types; if the interaction between glomeruli is considered also, the output patterns rely on the mixture ratio of the odor molecules also. In this model, only the synapses within a glomerulus are long-term-effective, so the long-term output of mitral cells encodes only the information of the odor molecule types, while the mixture ratio of the molecules can only be encoded by the short-term patterns (spike timing). Considering the element of the time scale, the model effectively represented the multi-channel processing of odor information.

One of the inputs to the bulb comes from olfactory sensory neurons. Each glomerulus received the exciting input from the sensory neurons that have the same odor receptor. $I_{m,i}(t)$ and $I_{p,i}(t)$ are inputs from the olfactory sensory neurons to the ith mitral cell and pre-glomerulus cell. For the odor $X(X1, X2, X3, X4)$, the ratio of molecules are $(I(X1), \quad (X2), \quad (X3), I(X4))$. $I_{m,i}(t)$ and $I_{p,i}(t)$ are defined as

$$I_{m,i}(t) = I_{p,i}(t) = x \sum_{n=1}^{4} I(X_n) x_i(X_n), \tag{4}$$

where x is the density of the odor ($x = 10$); $_i$ is used to describe the speciality of the neurons to odor molecules. When the ith mitral cell is sensitive to the odor molecule X_n, $_i(X_n) = 1$, otherwise 0.

The feedback from the olfactory cortex projects into the granule cells, and the feedback input on the ith granule cells is

$$I_{g,i}(t) = I_g(\sin 2\eth v(t)t + 1). \tag{5}$$

Setting $w_{gm, ii}$ and I_g, we can make a granule cell spike only when the following conditions are satisfied: (i) it receives its pre-synaptic mitral cell input (the spike is effective); (ii) the feedback reaches its peak. Such a granule cell is a kind of coincident detector[13]. The frequency of feedback relies on the attention state, which is set to 200 Hz at attention state, or 50 Hz at no attention state. Noticing the synapses from mitral cells to granule cells are all within a glomerulus, the spike ef-

fective time of these synapses is 100 ms. At attention state, the interval between the granule cell spike and its pre-synaptic cell spike is in the time window of 0—5 ms; while at no attention state, the interval is mostly in the time window of 5—20 ms[14].

According to the bulb's structure, mitral cells, periglomerular cells and granule cells' state function are defined as:

$$\frac{du_{m,i}}{dt} = -A_m u_{m,i} - u_{m,i}^{fire} + \sum_x \sum_j^{j \in \boldsymbol{G}_{m\,x\,i}} F_{mx,ij}(t) + I_{m,i}(t) + E_m, \ x = m, p, g, \tag{6}$$

$$\frac{du_{p,i}}{dt} = -A_p u_{p,i} - u_{p\,i}^{fire} + I_{p\,i}(t), \tag{7}$$

$$\frac{du_{g,i}}{dt} = -A_g u_{g,i} - u_{g,i}^{fire} + F_{gm,ii}(t) + I_{g,i}(t), \tag{8}$$

where $u_{m,i}(t)$, $u_{p,i}(t)$ and $u_{g,i}(t)$ are membrane potentials, A_m, A_p and A_g are coefficients describing the decline ($A_m = A_p = A_g = 1$ ms^{-1}), E_m is the mitral cell's self-enhancing coefficient[15,16].

The model used an anti-symmetric Hebb learning rule for spike neurons[17]. The modification of the weight of the synapse between spike neurons relies on spiking timing. The size is an inverse ratio to the spikes interval and the direction of modification is decided by the sequence of the spikes, described as

$$\Delta w = \boldsymbol{e} G(\Delta t), \tag{9}$$

where $\boldsymbol{e}$ is the synapse's modification coefficient, and Δt is the difference between timing of post- and pre- synaptic cell spikes. $G(\Delta t)$ defines the relativity of the spikes:

$$G(\Delta t) = \begin{cases} \boldsymbol{h} \dfrac{1}{\Delta t} & |\Delta t| \in (5,20), \\ 0 & \text{otherwise}, \end{cases} \tag{10}$$

where   is 1 for an excitatory synapse and −1 for an inhibitory synapse.

The lower limit (5 ms) defined in the learning rule reflects the time needed for a pre-synaptic spike to induce a post-synaptic cell to respond; the upper limit reflects the scale of information relativity. If the interval between the spikes of pre- and post- synaptic cells is less than 5 ms or more than 20 ms, then the relation between these two spikes is not certain, this pair of spikes would not be able to modify the synapse.

For this paper, we used an odor composed of four kinds of molecules as input to study multi-channel encoding, the response to the same odor at the attention state (high frequency feedback) and at the no attention state (low frequency feedback), and learning.

2 Simulation results

In order to contrast with the biological experiments, we provided 4 groups of simulation results: (i) responses induced by 2 similar odors in the bulb; (ii) responses induced by an odor before

and after blocking interaction from granule cells to mitral cells; (iii) responses induced by an odor at high frequency feedback and low frequency feedback; and (iv) responses induced by an odor before and after learning process.

The simulation results coincided well with the biological experiment results[2,3,5,9,10], and proved: (i) in the bulb, synapses having different spike effective times can build multiple channels for odor information processing; (ii) the different responses induced by the same odor in the bulb might be caused by the attention state; (iii) with a local learning rule, the bulb can use the attention state to produce different global learning results. In detail, first, the similar odors induce similar long-term patterns, but short-term patterns (spike timing synchronization) are quite different. Second, the response induced by an odor at high frequency feedback is stronger than that at low frequency feedback. Third, the learning process at high frequency feedback strengthens the response, while the learning process at low frequency feedback weakens the response. Finally, after a learning process under high frequency feedback, synchronization is enhanced, while after a learning process under low frequency feedback, there is no obvious difference.

At the scale of 100 ms, interactions through short-term (5 ms) spike effective synapses are eclipsed by interactions through long-term (100 ms) spike effective synapses (fig. 2). Because the olfactory sensory neurons projecting to the same glomerulus have the same odor receptor, and only the synapses within a glomerulus are long-term spike effective, patterns induced by similar odors at this time scale (100 ms) are similar too, while the synapses from granule cells and mitral cells affect only the short-term pattern.

Attention state affects the response's strength in the bulb. The responses induced by an odor at the attention state (high frequency feedback, 200 Hz) and at the no attention state (low frequency feedback, 50 Hz) are shown in fig. 3. Both strength and range of responses at the attention state are stronger than at the no attention state. Meanwhile, the attention state responses include all the responses found in the no attention state, as shown in fig. 3. This was effectively simulated, and the simulation results coincided well with biological experiment results.

The biological experiments suggested that odor learning is adjusted by the attention state[9,10]. The model was used to study how this was carried out in the bulb. The learning results were checked at the attention state after the odor was learned at different attention states for 2 s.

Considering computations, the attention state can affect learning results only by adjusting the synapses from granule cells to mitral cells (fig. 4). The biological studies showed that a mitral cell's input came from olfactory sensory neurons, other mitral cells and granule cells. The modification of these synapses from these three kinds of cells determined the output patterns after learning. Because of the relativity of spikes, the synapses from olfactory sensory neurons to mitral cells would be enhanced in any case. Because of the symmetry of connections and anti-symmetry of learning rule, the learning of synapses between mitral cells adjusted the distribution of spikes but had nothing to do with the global strength of response. In fact, only the learning process of synapses between granule cells and mitral cells relied on the attention state directly. At the attention

state, the granule cells spiked immediately after a pre-synaptic mitral cell spike (<5 ms), so the strength of the synapses did not change (eq. (9)). Therefore, learning at the attention state strengthened the response induced by the odor. At the no attention state, most of the spikes of a
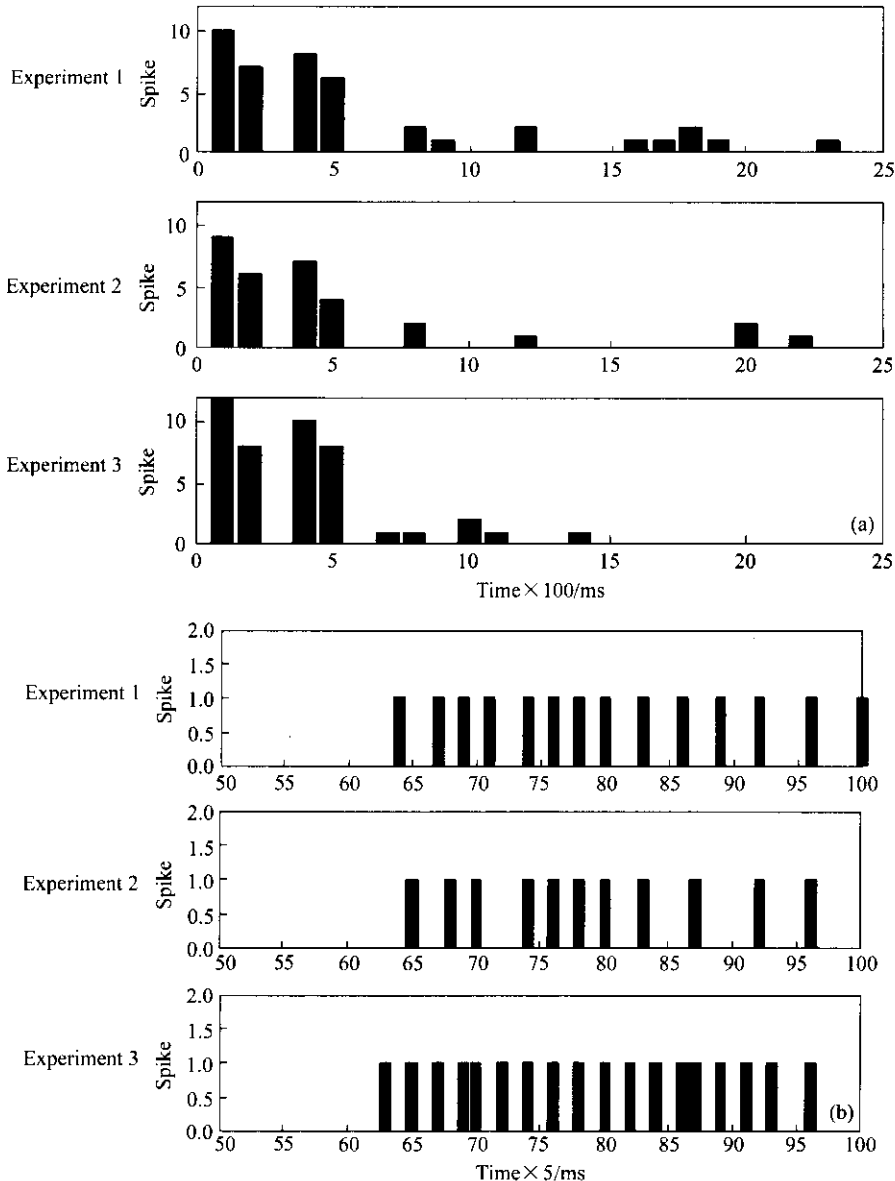

Fig. 2. The long-term (100 ms) and short-term (5 ms) responses induced by two similar odors before and after the synapses from granule cells to mitral cells were blocked. Experiment 1 and experiment 2 are the responses of odor A and odor B before the synapses were blocked. Odor A and odor B are composed of the same odor molecules, but the ratios were different. Experiment 3 is the response induced by odor A after the synapses were blocked. (a) Long-term patterns (100 ms); (b) short-term patterns (5 ms). The odor input began at 0 ms and ended at 1000 ms. The plots show that the long-term patterns are similar but the short-term patterns are quite different. This implies that the information of the ratio of the odor molecules and the synapses from granule cells to mitral cells affected only the short-term patterns of mitral cells' output, but was unrelated to long-term patterns.
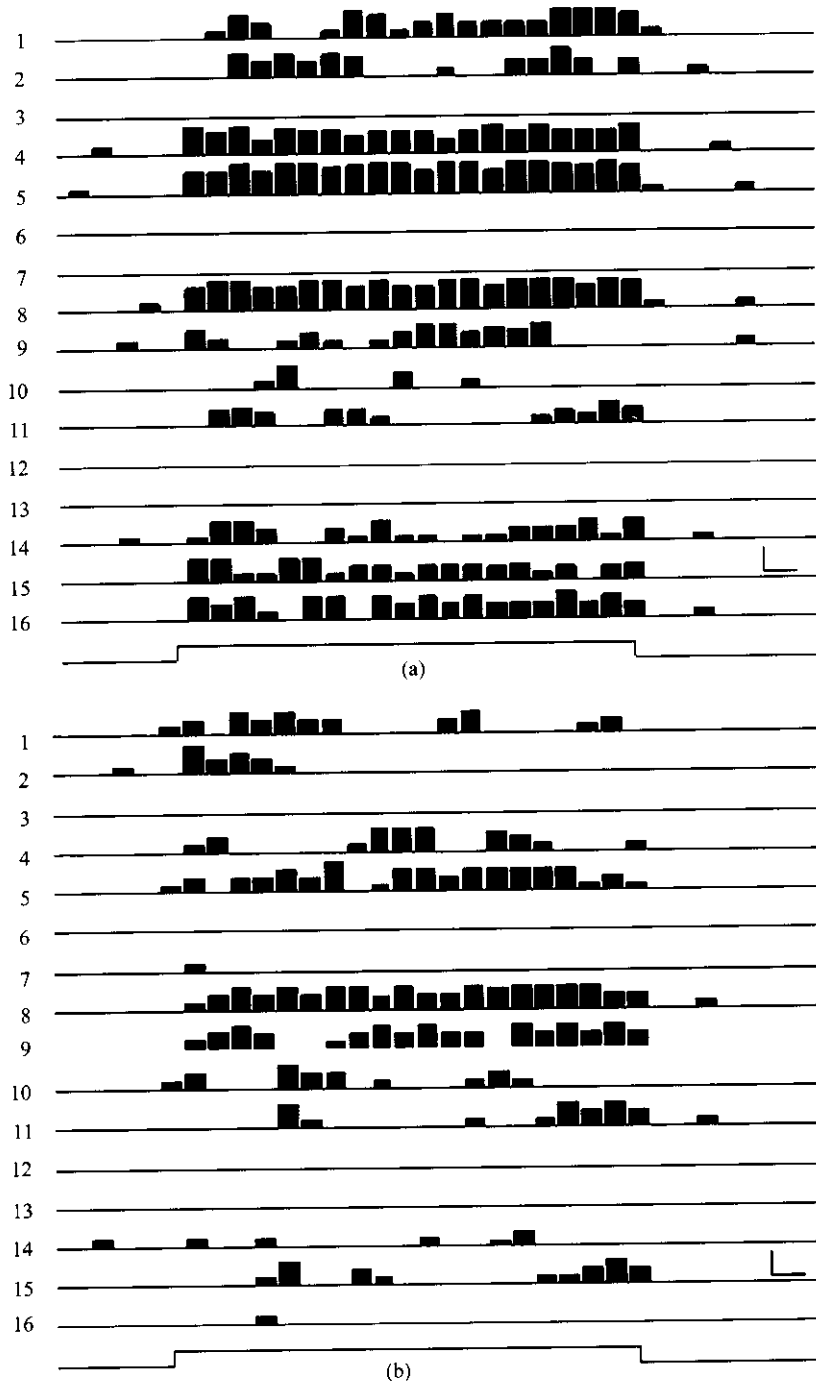
Fig. 3. The response of mitral cells induced by the same odor at the attention state and at no attention respectively. (a) and (b) are the responses at the attention state and the no attention state respectively. 1——16 represent the identity numbers of mitral cells. Criterion: horizontal, 100 ms; vertical, 100 Hz. The frequency of the feedback spike serial was 200 Hz at the attention state and 50 Hz at the no attention state (subsequent figures correspond to this). As shown in the plot, the response at the attention state is stronger than that at no attention state.
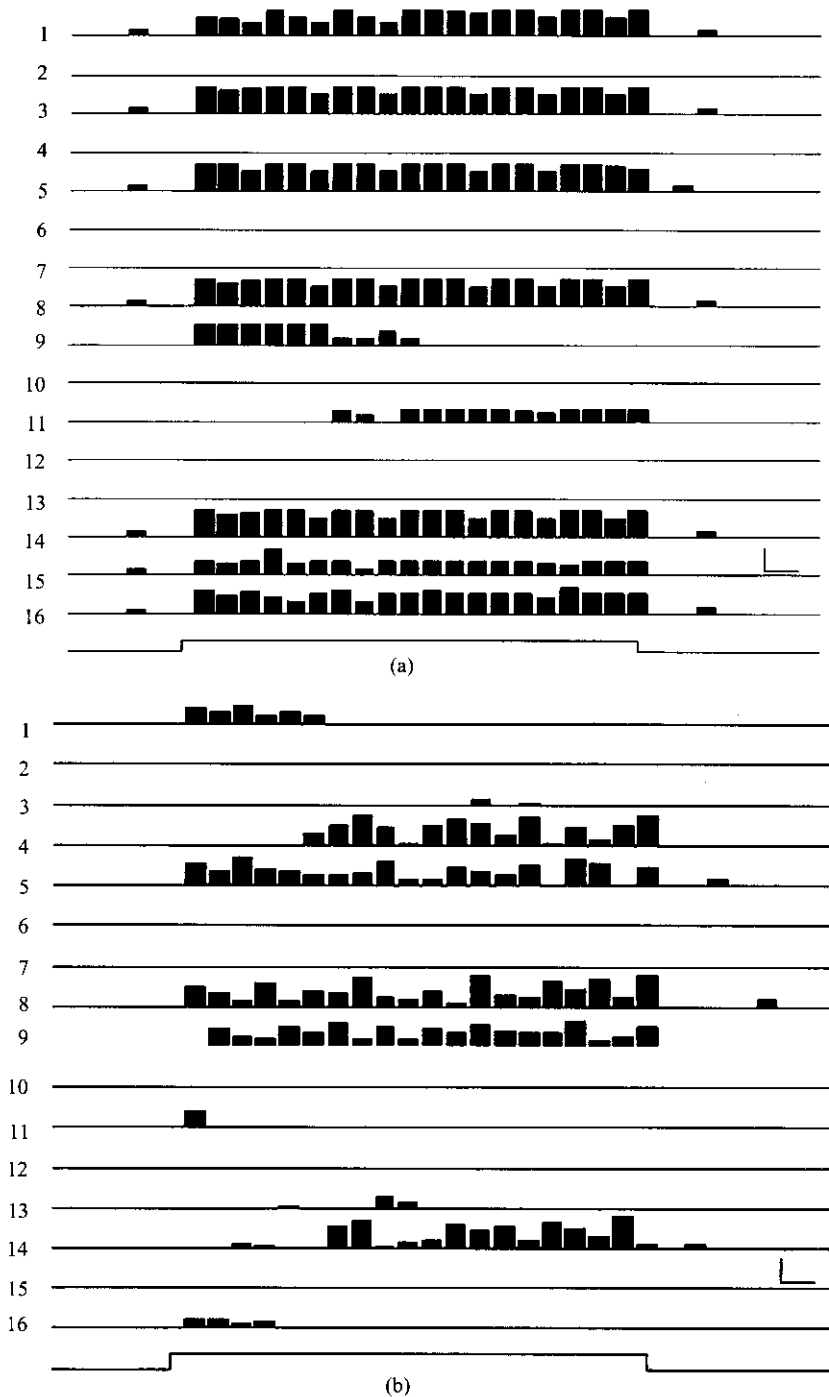
Fig. 4. Odor learning in the bulb is adjusted by feedback. These plots show the effect of feedback on the long-term response induced by odor A. After 2 s of learning, output patterns of the 1—16 mitral cells at attention state were checked. (a) Response after attention-state learning; (b) response after no-attention-state learning. Criterion: horizontal, 100 ms; vertical, 100 Hz. The plots show that the response after learning at high frequency feedback (attention state) was strengthened and the response after learning at low frequency feedback (no attention state) was weakened.

granule cell and its pre-synaptic mitral cell fell into a learning window (5—20 ms), and the inhibitory interaction from granule cells to mitral cells increased noticeably. When this inhibitory interaction increased faster than the excitatory interaction from the olfactory sensory neurons, the learning process caused a response decline. The simulation results showed that learning at the attention state enhanced the response globally, while learning at the no attention state reduced the response strength and distribution. This coincided well with the previous biological experiments[9,10]. In other words, the simulation results proved that the odor's habituation and inhabituation might be determined by feedback frequency.

In the bulb, the synchronization of spikes plays an important role in information coding. The figures show synchronization patterns after learning at different attention states. As shown in fig. 5, the learning process at the attention state noticeably strengthened the spike synchronization, and it showed some periodicity also. In contrast, the learning process at the no attention state made no
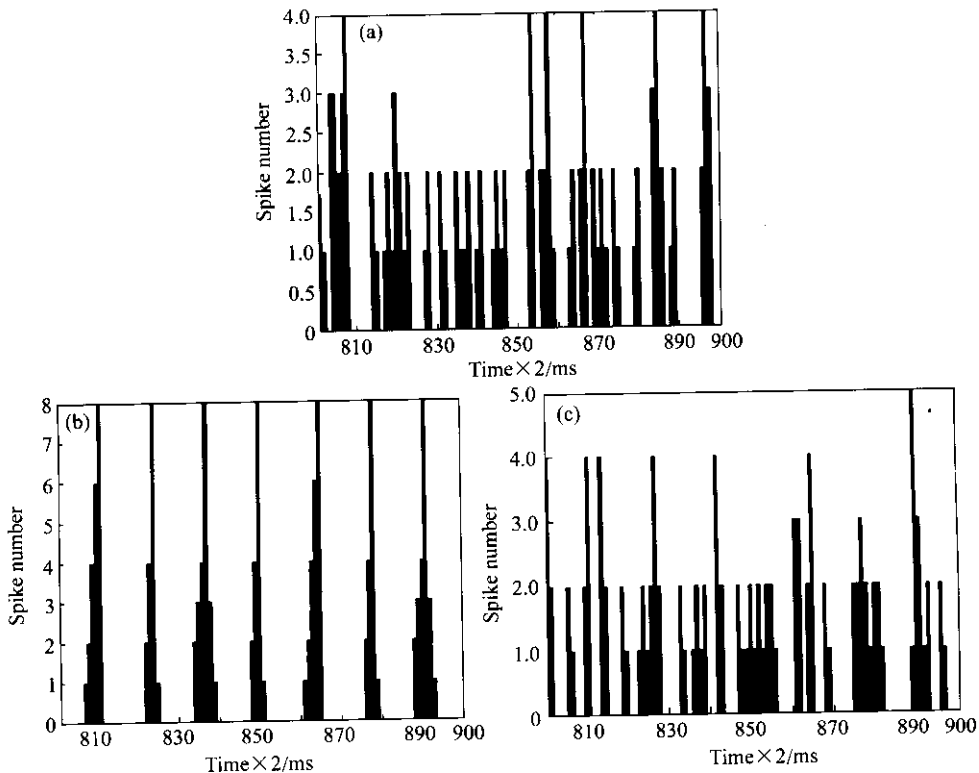

Fig. 5. Effect caused by different feedback on learning. After 2 s of learning, the short-term response was checked at the attention state. In order to clearly show the synchronization state, only 200 ms data are shown in the plots. The vertical dimension is the sum of the spikes of all 16 mitral cells, and the horizontal dimension is the time. (a) Output patterns before learning; (b) output patterns after attention-state learning; (c) output patterns after no-attention-state learning. After learning at the attention state, the synchronization of spikes strengthened measurably.

3   Discussion

Since neural systems are dynamic, information encoded might not be invariable. The learning process of coding might improve the efficiency of the neural system. Logically, learning enhances the response to meaningful information and reduces the response to meaningless information. In this paper, synapse spike effective time, as well as the olfactory bulb's special structure was used to achieve odor information multi-channel processing, and the results proved that the odor's habituation and in-habituation can be the result of learning guided by a common local rule at different attention states.

As the interaction from the higher cortex area to the lower cortex area, attention can only be carried out by feedback, and different attention states are expressed by different feedbacks. As one of the important properties, the frequency of the feedback spike serial can efficiently identify variation in feedback. In addition, biological experiments suggested that in the olfactory bulb, the frequencies of EEG induced by the odors varied with the familiarity degrees of the odor[11,12]. Therefore, it is biologically plausible to suppose that attention's variation expressed by the variation of the feedback spike serial's frequency.

One of the most important characteristics of this model is the synapse's spike effective time. For models based on the average frequency coding, the synapse's spike effective time is not related to coding because the output time scale is much larger than the synapse's spike effective time. But for models based on spike timing coding, which is comparable to the scale of coding, the synapse's spike effective time must be considered. This study examined the function of spike effective times with a model in which the synapses had different spike effective times, and proved that multiple channels for information processing can be constructed by such synapses.

A Hebb learning rule based on spike neurons was also proposed. Compared with other Hebb learning rules based on average frequency coding neuron[18—21], it stressed the function of spike timing. The window limit to learning showed the time relativity of pre- and post- synaptic spikes on coding; at the same time, because of the anti-symmetry of the learning rule, learning strengthened the excitatory synapses on the pathway of information transferring and weakened the others, and the learning of inhibitory synapses enhanced the synchronization of spikes.

The anti-symmetric learning rule of the model shows the function of the information's relativity on learning. For a creature, the aim of local learning is to increase the information transfer. The learning rule adopted in this paper achieves this aim: if the pre- and post- synaptic spikes transfer information, they will strengthen the excitatory synapses and weaken the inhibitory synapses; otherwise, they will weaken the excitatory synapses and strengthen the inhibitory synapses.

Finally, and most importantly, this work examined how global learning was accomplished by local learning. Global learning is composed of local learning, but is not the sum of local learning. Global learning enhances the efficiency of meaningful information transfer and weakens meaningless information transfer based on judgment of the information's relevance. For a certain network, the use of its output can be judged only by its higher layer. In other words, global learning is the

result of cooperation between local learning and feedback. In this paper, the attention state adjusted a granule cell's sensitivity to its pre-synaptic mitral cell spike, thereby adjusting the modification of the synapses from granule cells to mitral cells. Because the synapses from granule cells to mitral cells play an important role in odor coding in the bulb[22, 23], feedback will eventually affect the odor's coding in the bulb, and the attention state in the learning process will adjust global learning.

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