Firing pattern and synchronization property analysis in a network model of the olfactory bulb

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Abstract In the olfactory system, both the temporal spike structure and spatial distribution of neuronal activity are important for processing odor information. In this paper, a biophysically-detailed, spiking neuronal model is used to simulate the activity of olfactory bulb. It is shown that by varying some key parameters such as maximal conductances of K_s and Nap the spike train of single neuron can exhibit various firing patterns. Synchronization in coupled neurons is also investigated as the coupling strength varying in the situation of two neurons and network. It is illustrated that the coupled neurons can exhibit different types of pattern when the coupling strength varies. These results may be instructive to understand information transmission in olfactory system.

Keywords Olfactory · Spike train · Maximal conductance · Synchronization · Network

Information about the environment is generally encoded into spike sequences by neurons in animal sensory nervous

systems (Rieke et al. 1997; Du et al. 2010; Qu et al. 2011). There is a lot of evidence that (Hudspeth et al. 2000; Laurent et al. 2001; Wolf 2009), in some systems, the representation of information comes through temporal encoding. The study of the neural basis of olfactory system is important both for understanding the sense of smell and for understanding the mechanisms of neural computation. In the olfactory bulb, the temporal structure of neuronal activity appear to be very important for processing odor information (Hutcheon et al. 2000).

The temporal patterns produced by three simultaneously sampled projection neurons (PNs) in the locust antennal lobe indicate that each odor evokes a specific temporal activity pattern (Bazhenov 2001). Some experiments suggest that the time course of dendrodendritic inhibition is dependent on the network connectivity as well as on the intrinsic parameters on the synapses (Schoppa et al. 1998). In response to simulated odor stimulation, strongly activated mitral cells tend to suppress neighboring cells, the mitral cells readily synchronize their firing, and increasing the stimulus intensity increases the degree of synchronization. Preliminary experiments also suggest that slow temporal changes in the degree of synchronization are more useful in distinguishing between very similar odorants than the spatial distribution of mean firing rate.

To build a reasonable dynamical theory of such an encoding, the rules on which the neuron model is based should be understood, and advantages that such stimulus representation has for further processing are also predicted. So it is necessary to explore the effect of some key parameters such as maximal conductances of the olfactory model on temporal spike train pattern.

In this paper, a single compartment that includes voltage-dependent currents described by Hodgkin-Huxley kinetics was used to model mitral cells (Jorge 2009).

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The membrane capacitance for all cells is $1\mu\text{F}/\text{cm}^2$ and therefore not mentioned in the voltage equations. The following units are used: conductance per unit area in

$(\text{mS})/(\text{cm}^2)$, current per unit area in $(\mu\text{A})/\text{cm}^2$, voltage in (mV) and time (t) in (ms). Their membrane potentials are calculated with the equations:

Fig. 1 Spike train patterns (a) and corresponding phase plots (b) with respect to variation of the maximal conductance of K_s

Fig. 2 Spike train patterns (a) and corresponding phase plots (b) with respect to variation of the maximal conductance of Nap

$$C_m \frac{dV}{dt} = -\frac{1}{R_m}(V - E_l) - I_{Na} - I_{Kfast} - I_{Ka} - I_{Ks} - I_{Nap} - I_e, \quad (1)$$

All the intrinsic currents are described by the equation:

$$I_i = g_i m^M h^H (v - E_i), (i = Na, Kfast, Ka, Ks, Nap) \quad (2)$$

where g_i is the maximal conductance and E_i the reversal potential. The activation and inactivation variable m and h raised to the power M and H respectively follow the kinetic equation:

$$dm/dt = (m_\infty - m)/\tau_m \quad (3)$$

$$dh/dt = (h_\infty - h)/\tau_h \quad (4)$$

parameter values and further details are presented in Bhalla and Bower (1993) and (Senselab databank, <http://senselab.med.yale.cn>).

In order to reproduce the characteristic properties of mitral cell, a set of parameters is selected to reflect the different behaviors of the model. Spike train patterns of olfactory bulb are sensitive to the persistent current Nap and Ks . At first, the responses of spike train patterns at different maximal conductance of Ks are considered. Figure 1 presents the spike train patterns and corresponding phase plots when g_{Ks} changes from 0.7 to 2.7, respectively.

As shown in the Fig. 1, with the g_{Ks} increasing, the frequency of spike train firing is increasing. Then the situation of changing g_{Nap} is considered while fixing other parameters. On the contrary to the case of g_{Ks} , the frequency of spike train firing is decreasing when the g_{Nap} is increased (Fig. 2). So it is supposed to simulate the experimental phenomenon through controlling the maximal conductance of the model.

Except the contribution of a single neuron on information transmitting, it is suggested that synchronized behaviors in neuronal assemblies play an important role in our understanding of information processing in olfactory systems. Hence, synchronization of two identical coupled neurons is studied. It is shown that two coupled neurons can exhibit more complicated dynamical behaviors due to the effect of the coupling strength.

Dynamics of coupled olfactory neurons are controlled as shown by the following differential equations:

$$C_m \frac{dV_i}{dt} = -\frac{1}{R_m}(V_i - E_l) - \sum_k I_k - I_e + \sum_j g_{ij}(V_i - V_j), \quad (5)$$

where I_k is ionic current ($k = Na, Kfast, Ka, Ks, Nap$). g_{ij} is coupling strength, V_i and V_j are voltages between adjacent neuron i and j . Obviously, in the situation of two neurons, we take i and j as 1 and 2, and we take $g_{1,2}$ as g_c . All parameters are the same to the single neuron.

A correlation coefficient is introduced to measure the synchronization degree of the coupled neurons, and it is defined as follows:

$$C = \frac{\sum_{i=1}^n |(V_i^1 - \langle V_i^1 \rangle) \parallel (V_i^2 - \langle V_i^2 \rangle)|}{\sqrt{\sum_{i=1}^n (V_i^1 - \langle V_i^1 \rangle)^2 (V_i^2 - \langle V_i^2 \rangle)^2}} \quad (6)$$

where V_i^1 (or V_i^2) represents the samplings of the membrane potential $V^1(t)$ (or $V^2(t)$). $\langle \cdot \rangle$ denotes the average over the number of the sampling. It is easy to see that the more

Fig. 3 Variation of the correlation coefficient C of the membrane potential V^1 and V^2 with respect to g_c

Fig. 4 The spike trains of two coupled neurons when g_c is taken as 0.0002

Fig. 5 **a** Phase plot in $(V1, V2)$ plane, **b** membrane potential error $(V1 - V2)$ when $g_c = 0.0002$

Fig. 6 **a** The spike trains of two coupled neurons when g_c is taken as 0.12. **b** Enlarged figure of dotted square area of **a**, **c** Phase plot in $(V1, V2)$ plane and **d** membrane potential error $(V1 - V2)$

synchronous the coupled neurons are, the larger the correlation coefficient C is, and the complete synchronization state of the coupled neurons is achieved when C is equal to 1.

The correlation coefficient C is calculated as illustrated in Fig. 3. It is shown that synchronization exhibits a rout of process as: non-synchronization $\rightarrow$ nearly synchronization

Fig. 7 **a** The spike trains of two coupled neurons when g_c is taken as 0.2. **b** Enlarged figure of *dotted square* area of **a**, **c** Phase plot in $(V1, V2)$ plane and **d** membrane potential error $(V1 - V2)$

→ spiking synchronization. Complete synchronization cannot occur when g_c is less than 0.14, while complete synchronization can be observed as shown in Fig. 6, in which C is equal to 1.

For more detail, spike train patterns of two coupled neurons at different constant g_c are considered. At first, $g_c = 0.0002$ is taken. It is observed that $V1$ (red dotted line) and $V2$ (blue line) are absolutely inconsistent shown as Fig. 4. C is calculated as 0.3251 at this case.

In Fig. 5, phase plot of $V2$ versus $V1$ (Fig. 5a) and error of $V1$ and $V2$ (Fig. 5b) are used to characterize the synchronization of the coupled neurons. As illustrated in the Fig. 5, they have the corresponding same results as shown in the Fig. 4.

When taking the $g_c = 0.12$, the value of C is 0.9158. It is a nearly synchronized situation, which can be seen in Fig. 6a: $V1$ (red dotted line) and $V2$ (blue line) are almost coincident. However, if the figure is enlarged (Fig. 6b), it is

observed that there is still difference, which also be illustrated in Fig. 6c, d.

At last, the case of $g_c = 0.2$ is considered. Like illustrated in Fig. 3, the value of C is 1 at this situation. It is known that the two coupled neurons are completely synchronized shown as Fig. 7a, b. Phase plot in $(V1, V2)$ plane becomes a line at the angle of 45 (Fig. 7c), and membrane potential error $(V1 - V2)$ is lasting as zero (Fig. 7d).

Then we use this olfactory model to simulate a sparse network of 800 spiking cortical neurons with 800×799 synaptic connections. Spatiotemporal patterns of all neurons with synaptic coupling in the complex networks are displayed in Fig. 8.

Figure 8a simulates a network of globally connected 800 neurons in real time, whose coupling strengths are chosen as random values. We find the coupled neurons locate in chaotic states in this situation and neurons show

Fig. 8 Simulation of a network of 800 coupled spiking neurons. **a** Raster plot showing the spiking activity of the globally connected 800 neurons. **b** The spike train pattern of network neurons when G is taken as 0.2. **c** The situation of $G = 0.4$. **d** Completely synchronization when G is taken as 0.8, *right corner* is enlarged situation

rather irregular. The synaptic connection weights between the neurons are given by the matrix $G = (g_{ij})$, so that firing of the j th neuron instantaneously changes variable v_i by g_{ij} .

In the Fig. 8b–d, neurons at different synaptic coupling weights $G = (g_{ij})$ are considered. At first, $G = 0.2$ is taken, that is, all g_{ij} are taken the same as 0.2. Compared to the Fig. 8a, it is shown that the neurons organize into assemblies and exhibit collective rhythmic behavior. With the coupling weights increasing, we find the width of the assemblies is becoming larger (Fig. 8c), the coupled neurons could achieve local synchronization inside the assemblies as showed in the enlarged picture of Fig. 8c. When the coupling weights is added to $G = 0.8$, the coupled neurons eventually achieve synchronization as shown in Fig. 8d. It is evident that the synaptic coupling weight is increased and the synchronous action between neurons is strengthened.

The conclusion: the maximal conductances of the olfactory model have obviously effects on the spike train pattern: the frequency of spike train firing is increasing

with the g_{Ks} increasing, while the frequency of spike train firing is decreasing when the g_{Ks} is increased. It was also shown that the coupled neurons could achieve synchronization with the variation of coupling strength. The same results can also be observed in the network situation. In the olfactory system, these analysis maybe helpful to understand the integration of the many factors influencing the construction and transformation of odor representations.

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