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Transitional function of DG to CA3 in the hippocampus*

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Abstract Using single cell channel model, the transmission features of CA3-DG network in the hippocampus are investigated. The influence of the stimulation on discharge pattern of pyramidal neurons is analyzed, which shows that it starts with period spiking discharges, followed by period-doubling bifurcation to chaos, and period 3 discharge evolving into chaos, and ultimately a period of bursting discharges. By the synaptic model, the CA3-DG network model is constructed, which analyzes the summation of postsynaptic currents in the network, the influence of postsynaptic current on discharge rhythm as well as the mechanism of bursting discharges. The strong capacity of spatiotemporal encoding in the network indicates the features of CA3 network during the information transmission process in the hippocampus. The modeling result with time delay of the synaptic transmission is in accordance with the experimental phenomena of action potential in the hippocampus.

Keywords: hippocampus, CA3-DG, period-doubling bifurcation, chaos.

The hippocampus is a part of the limbic system under neopallium, and belongs to the paleopallium. In addition to pallium, the hippocampus includes the dentate gyrus (DG) and subiculum, and is usually divided into CA1, CA2, CA3 and CA4 parts. Due to the importance of CA1 and CA3 in the memory[1-5], great efforts have been devoted to the research on their structures and functions[6-8]. Pyramidal cell is the cardinal component of CA3, each of which is connected with the others through interneurons. The excitatory postsynaptic potentials (EPSPs) are caused by spontaneous activity of the pyramidal cells in CA3. Hippocampal function and characteristics are a key in learning and memory research. The research on the memory hypothesis has also attracted great attention, such as the stochastic resonance memory hypothesis[9-11].

The experiment shows that the main input signal of the hippocampus comes from entorhinal cortex (EC) to dentate gyrus (DG) by perforant path (PP), and then arrives at CA3 through mossy fiber (MF). CA3 is connected with CA1 by schaffer collaterals (SC) synapse. Finally, it returns back to EC through subiculum[12]. All the synapses of PP, MF and SC in the circuit of hippocampus are excitory. In this process, the main input signal is from EC, and the cardinal output is CA1. Because of the complicated analysis of the whole hippocampal model, generally most of the research is concerned with the CA3-CA1 system. In this paper, the functions and properties of CA3-DG system as the information transmission intermediate are the cardinal research. Due to the limitation of the techniques and equipments in physiological experiments, the whole property of the hippocampal structure cannot be observed. Therefore, the mathematical model based on physiological structure and computer simulation becomes an effective method to assist experiment and to verify the results.

Traub founded a simplification model with 19 pyramidal cells to describe the structure of CA3 in 1982[9]. The result of this model shows that the bursting discharge of a pyramidal cell is very complicated, and that the number of the cells considered is too small. Afterwards, Traub and Jeffyerses made an improvement over the original model, building up a CA3 network with 100 pyramidal cells[10]. The excitory synapse among pyramidal cells is random, which indicates that the strong synaptic connection is a necessary condition of the synchronous bursting discharges. In 1998, Tateno et al. further amplified cells scale to 256 pyramidal cells and 25 interneurons in a CA3 network[11], in which the influence of synaptic strength on action potential had been investigated thoroughly in this model. In various models,

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CA3 was studied alone, or was investigated just with CA1; however, the influence of MF synapse of DG upon CA3 was often neglected. This paper concerns about perfecting the structure of system, adding DG network and EC's effects to the system and analyzing the influence from DG upon CA3.

1 The hippocampal neuron model

There are two kinds of cells in CA3-DG: excitory neurons (mainly granulosa cells in DG and pyramidal cells in CA3) and inhibitory neurons (mainly interneurons in CA3 and DG). Generally, the following model is employed to describe excitory neurons:

$$\begin{cases} C\dfrac{\mathrm{d}V}{\mathrm{d}t} = g_{\mathrm{Na}} m^3 h(V_{\mathrm{Na}} - V) \\ \quad + g_{\mathrm{Ca}} s^2 r(V_{\mathrm{Ca}} - V) \\ \quad + g_{\mathrm{Ca(low)}} s_{\mathrm{low}}^2 r_{\mathrm{low}}(V_{\mathrm{Ca}} - V) \\ \quad + g_{\mathrm{K(DR)}} n(V_{\mathrm{K}} - V) \\ \quad + g_{\mathrm{K(A)}} ab(V_{\mathrm{K}} - V) \\ \quad + g_{\mathrm{K(AHP)}} q(V_{\mathrm{K}} - V) \\ \quad + g_{\mathrm{K(C)}} c\min(1, \chi/250)(V_{\mathrm{K}} - V) \\ \quad + g_{\mathrm{L}}(V_{\mathrm{K}} - V) + g_{\mathrm{af}}(V_{\mathrm{syn(e)}} - V) \\ \quad + I_{\mathrm{syn}} + I_{\mathrm{stim}} \qquad (1) \\ \dfrac{\mathrm{d}z}{\mathrm{d}t} = \alpha_z(1 - z) - \beta_z z, \\ \quad z \text{ stands for } m, h, s, r, s_{\mathrm{low}}, r_{\mathrm{low}}, \\ \quad n, a, b, q, c \qquad (2) \\ \dfrac{\mathrm{d}\chi}{\mathrm{d}t} = -\phi I_{\mathrm{Ca}} - \beta_\chi \chi \qquad (3) \end{cases}$$

The model comes from Traub's somatic cell model, in which a large number of ion channels are involved in spite of the simplification. In (1), the elements resulting in the variety of the neuron membrane potential include Na^+ current, Ca^{2+} current, low-threshold Ca^{2+} current, delayed rectifier K^+ current, A-type K^+ current, after-hyperpolarizing K^+ current, Ca^{2+}-activated K^+ current, the leakage current and the excitory synapse current. Therefore, it is far more complicated than other models such as Hodgkin-Huxley, Chay and FitzHugh-Nagumo models.

g_y and V_y indicate the maximum conductance and equilibrium potential for each ion channel, respectively. Especially, g_{af} and $V_{\mathrm{syn(e)}}$ are for afferent excitory synapse. If a neuron has no synaptic connection, the conductance coefficient equals zero. Eq. (2) represents the ion-gating varying. I_{Ca} indicates the summation of the calcium current and low-threshold calcium current in Eq. (3). I_{syn} is the summation of the temporal synaptic current while I_{stim} means the external stimulus corresponding to depolarization current in the experiment.

The long-term potentiation (LTP) and the long-term depression (LTD) are the important results in the hippocampal experiments. Tateno et al. observed and kept a record of the discharge patterns of the pyramidal neuron in rat CA3 hippocampus slice[11]. Pyramidal cell fires spontaneously without depolarization current outside. Fig. 1(a) is the experimental result drawn from Ref. [11]. The results of Fig. 1 (a1) to (a4) show respectively that along with the continuous decrease of depolarization current, the discharge patterns of pyramidal cells in CA3 change from the spiking discharge to chaotic discharge and then to bursting discharge. Using these models, theoretical research is made, in which the numerical simulation employs 4-order Runge-Kutta with time step 0.03 ms and the initial values are given randomly. See the Appendix for the values of other parameters.

The simulation results are shown in Fig. 1(b) and (c). In Fig. 1(c), the abscissa is stimulus and ordinate is interspike interval (ISI). The results show that along with the continuous diminishing of the stimulus, firstly the ISI is from the period 1 spiking discharges to chaos by period-doubling bifurcation, and then period 3 bursting discharges come up during internal mutation, which leads to chaos again and finally the period 2 bursting discharges. The result that period 3 leads to chaos is entirely in correspondence with that in discrete dynamics[13]. The phenomenon that there is a chaotic discharges area between two bursting discharges areas can often be seen in physiological experiments[14]. There are similar ISI graphs in many single cell models, such as Chay model[15,16] and Rose-Hindmarsh model for the thalamencephalon neuron[17]. All of them have the typical chaotic process: from period of spiking discharges to chaotic discharges by period-doubling bifurcation, and then to period of bursting discharges through converse period-doubling bifurcation. In accordance with our results, chaotic discharge exists between two periods of discharge, which indicates the universalism of this phenomenon. Under various stimuli, the diversity of the discharge patterns of pyramidal cells implies the signal encoding from EC. In other words, there are complicated encoding characteristics in the process of the hippocampus on memory object.

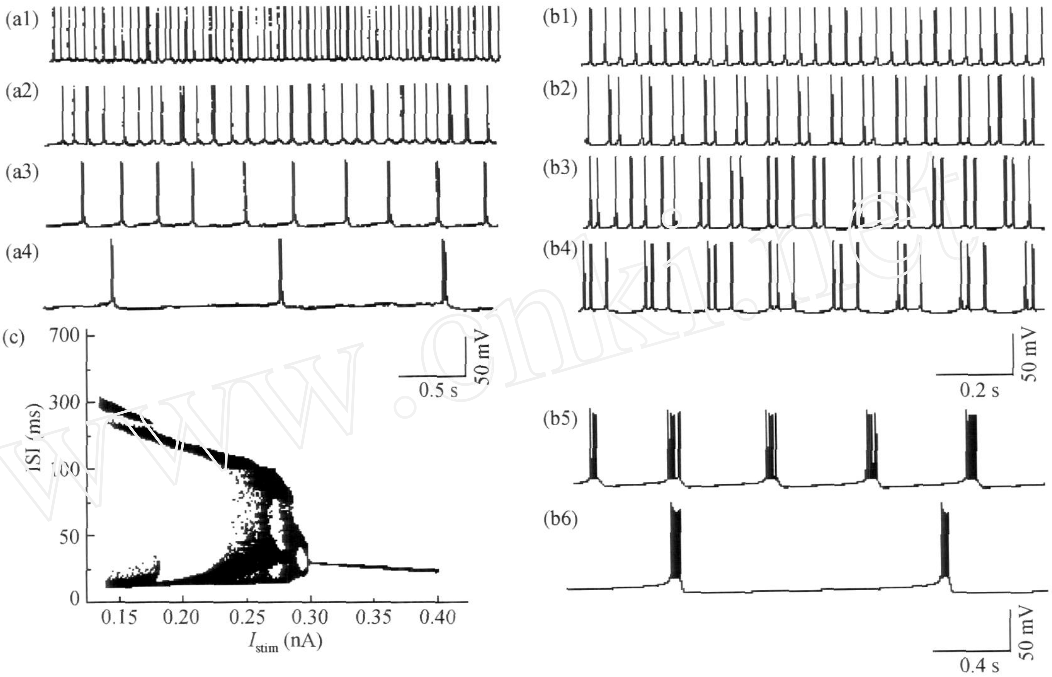

Fig. 1. (a) Discharge patterns of the rat CA3 hippocampal pyramidal cell (from Ref. [11]). (a1) Spiking discharges. Depolarizing current is 0.3 nA. (a2) Chaotic discharges. Depolarizing current is 0.2 nA. (a3) Bursting discharges with 2—4 spikes per burst. Depolarizing current is 0.1 nA. (a4) Spontaneous bursting discharges. Depolarizing current is 0 nA. (b) Discharge patterns of CA3 hippocampal pyramidal cell from model simulation. (b1) Period 1 spiking discharges. Stimulation is 0.35 nA. (b2) Period 2 spiking discharges. Stimulation is 0.29 nA. (b3) Chaotic discharges. Stimulation is 0.28 nA. (b4) Period 3 bursting discharges. Stimulation is 0.27 nA. (b5) Bursting discharges with 4 spikes per burst. Stimulation is 0.15 nA. (b6) Spontaneous bursting discharges. Stimulation is 0 nA. (c) Bifurcation diagram. The abscissa is the stimulation.

Corresponding to ISI, various action potential graphs in Fig. 1(b1—b6) further verify the diversity and complexity of the discharge patterns in the experiment, and also show the bifurcation process of ISI[11]. Along with the decrease of the stimuli, the processes take the following turns: period 1 spiking discharges first, followed by period-doubling bifurcation to period 2 bursting discharges, and chaos to period 3 bursting discharges, and period 4 bursting discharges to period 6 bursting discharges. The ISI graph also verifies the changing process of the discharge patterns in the experiment. Basically, the discharge patterns of model simulation are in accordance with the experimental results; especially, when the stimulation is 0 in Fig. 1(b6), that is, the depolarization current is 0, the spontaneous bursting discharges fit in with the experimental results. The modeling results not only reproduce various discharge patterns in the experiment, but also imply a further conclusion of the discharge patterns through ISI, from period 3 to chaos and period-doubling bifurcation to chaos also. Therefore, the model here can well explain the discharge phenomenon of the pyramidal cell in the hippocampus.

In addition to a large number of excitory neurons, there are a few interneurons in CA3 and DG. Despite its small proportion, interneurons play an important role in maintaining the equilibrium between excitation and inhibition in the hippocampus. The interneuron also has Ca^{2+}-activated K^{+} channel; however, it differs from that in pyramidal cells in that Ca^{2+}-buffering in interneurons would severely inhibit the Ca^{2+} concentration increase of the cytoplasm[18]. Therefore, it is seen that the influence of the Ca^{2+}-activated K^{+} channel on the potential between inner and outer of the cell can be ignored and that Eqs. (4) (5) include only Na^{+}, delayed K^{+} and leakage current. The interneuron model can be described in the following way:

$$\begin{cases} C\dfrac{\mathrm{d}V}{\mathrm{d}t} = g_{\mathrm{Na}} m^3 h(V_{\mathrm{Na}} - V) \\ \quad + g_{\mathrm{K(DR)}} n^4 (V_{\mathrm{K}} - V) \\ \quad + g_{\mathrm{L}}(V_{\mathrm{L}} - V) + I_{\mathrm{syn}} & (4) \\ \dfrac{\mathrm{d}z}{\mathrm{d}t} = \alpha_z(1 - z) - \beta_z z, \\ \quad z \text{ stands for } m, h, n & (5) \end{cases}$$

(4) and (5) can be adopted to describe the interneurons in the hippocampus. While neurons are connected by synaptic models, these models can analyze the system of the hippocampus.

2 The system model of CA3-DG

2.1 The introduction of network

In order to analyze the system of CA3-DG, firstly a network structure should be constructed, which is the key in this paper. Since there are a large number of excitory pyramidal cells in CA3, from the consideration of calculation complexities, 256 pyramidal cells are placed on 16 × 16 lattice points. As is shown in the experiment that the number of inhibitory interneurons in the hippocampus is about 10 percent of that of pyramidal cells[19], each of the 25 interneurons is placed in an individual area occupied by 4 × 4 pyramidal cells. By synapses, each pyramidal cell excites the pyramidal cells and interneurons around which in turn inhibit this pyramidal cell. For the sake of convenience, each pyramidal cell excites 8 pyramidal cells around in the network, and each interneuron inhibits 16 pyramidal cells around, which is subjected to the excitation from these 16 pyramidal cells. Hence, two adjacent interneurons together inhibit four common pyramidal cells (the shadows in Fig. 2 (a)).

There are some similarities of DG to CA3, for example, a large number of excitable granulosa cells exist; some interneurons are among granulosa cells; granulosa cells excite each other; and interneurons inhibit these cells around. Here suppose that DG has the similar network to CA3, hence ○ in Fig. 2(a) indicates granulosa cells, and then a CA3-DG network is attained in Fig. 2(b). This system includes two parallel networks connected by MF synapse, each of which has the structure and synaptic connection as Fig. 2(a), DG is excited by PP signal from EC. Two special synapses exist in the system, mossy fiber (MF), and perforant path (PP) connecting EC and DG. MF is relatively sparse, but its connection strength is strong. By MF, each pyramidal cell in CA3 is excited by 20 granulosa cells which are randomly selected in DG, while by PP, each granulosa cell in DG is excited from EC. As the information transmission system in the hippocampus, CA3-DG has two levels: the information transmission between neurons in DG or CA3, and the information transmission between DG and CA3.

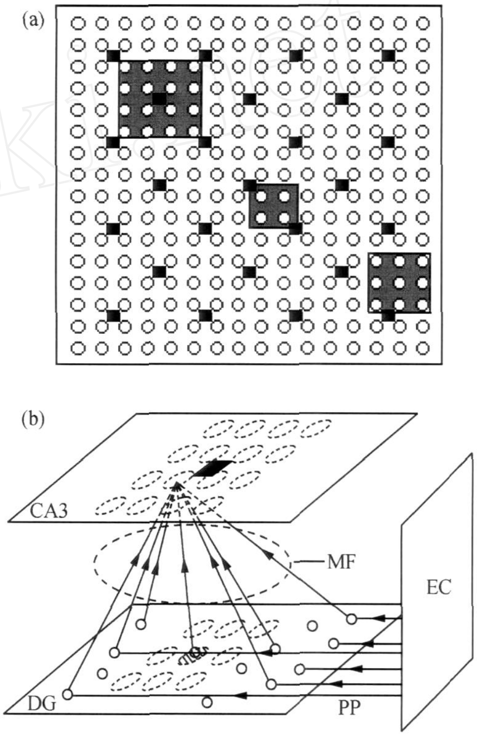

Fig. 2. (a) CA3 or DG network: 16 × 16. ○ Pyramidal cell or granulose cell, ■ interneuron. (b) CA3-DG system structure. Each pyramidal cell is excited by 20 granulose cells with MF synapse. Each granulose cell is excited by PP signal.

The cells form the network by synaptic connection which is given below. Each presynapstic action potential always causes an impulse of postsynaptic cells.

$$\begin{cases} I_{\mathrm{syn}} = g_{\mathrm{syn}}(V_{\mathrm{syn}} - V) & (6) \\ g_{\mathrm{syn}} = C_{\mathrm{syn}}(\exp(-t/\tau_1) - \exp(-t/\tau_2)) & (7) \end{cases}$$

where C_{syn} indicates the synaptic strength and V_{syn} means the synaptic equilibrium potential.

Chrobak and Buzsakis observed the Gamma oscillation (40—100 Hz) in EC of the hippocampus in 1996[2], so 50 Hz impulse within this scope is used to simulate PP signal from EC. Each postsynaptic current caused by PP signal or MF synapse can be described by (6) and (7). For the distinction from the former synaptic conncetions, these two kinds of connection strengths are represnted by W_{perp} and W_{MF} respectively. Since there is an interval during the chemical transmission of neurons by synapse, a time delay exists in postsynaptic current. We adopt 1 ms for the analysis.

According to network structure and synaptic connection, as for the granulosa cells, the pyramidal cells, and the interneurons in DG and CA3, the summation of the temporal synaptic currents in (1) can be described by the following formula:

$$\begin{cases} I_{p\_DG} = \sum_{k=1}^{8} I_{pp}(k) + \sum_{k=1}^{2} I_{ip}(k) + I_{perp}(t) & (8) \\ I_{p\_CA3} = \sum_{k=1}^{8} I_{pp}(k) + \sum_{k=1}^{2} I_{ip}(k) + \sum_{k=1}^{25} I_{MF}(k) & (9) \\ I_{i\_DG} = I_{i\_CA3} = \sum_{k=1}^{16} I_{pi}(k) & (10) \end{cases}$$

where $I_{pp}(k)$, $I_{pi}(k)$, $I_{ip}(k)$, $I_{MF}(k)$ mean the postsynaptic current caused by the kth presynatic cell through all kinds of connections. $I_{perp}(t)$ indicates the postsynaptic current caused by PP signal at t.

When the presynaptic neuron produces an action potential at t_0 (Fig. 3(a)), postsynaptic neuron is subjected to postsynaptic current by synaptic connection, resulting in excitation or inhibition. There is an interval of 1 ms for synaptic transmission, so an impulse current is caused at $t_0 + 1$, namely, the postsynaptic current. Fig. 3(b1) is an inhibitory synaptic current; (b2) is an excitatory synaptic current. The excitory current is a positive impulse, while the inhibitory current is a negative impulse. Here the initial resting potential of postsynaptic neurons is chosen as - 60 mV.

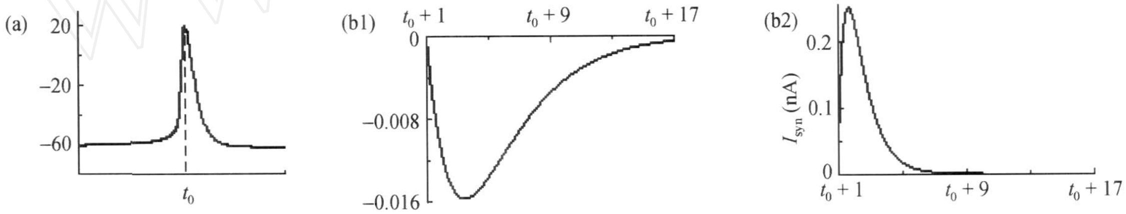

Fig. 3. (a) The action potential of presynaptic neuron. (b) The postsynaptic current caused by this action potential. (b1) Inhibitory, (b2) exitory.

2.2 The simulation results of CA3-DG system

CA3 and DG both produce bursting discharges under the synergism of the PP signal, which is in accordance with the discharge patterns in the experiment[11]. Fig. 4(a3) and (a4) indicate the potential of interneuron and that of granulosa cell inhibited by this interneuron in DG, respectively; (b3) and (b4) represent the potential of interneuron and that of pyramidal cell inhibited by this interneuron in CA3, respectively. The excitation or inhibition relationship between them causes the almost synchronous bursting discharges. The slight difference in time and spike number is due to the diversity of neurons, the perturbation by other postsynaptic currents around and the time delay in synaptic transmissions. Interneuron is resting neuron, which will fire to transmit signal only when it is excited; however, it does not fire when it is isolated or no postsynaptic currents. When the pyramidal cell or granulosa cell is to fire, the interneurons by the excitory synaptic connection with this cell will be excited by postsynaptic current so as to cause an action potential if the summation of temporary postsynaptic current exceeds the threshold. Hence they turn over to inhibit the same pyramidal cell or granulosa cell, which will be excited by the same kind of surrounding neurons for a following spiking discharge. In the same way, the second action potential of interneurons follows; repeatedly, a series of tight spikes become bursting discharges; finally, cells with the mutual excitation or inhibition between each other are caused to fire synchronously. Only when the summation of temporary postsynaptic current from the other cells is too small this neuron can go rest.

Now let us investigate the influence of the important synapse MF from DG to CA3 on the pyramidal cell firing. Fig. 4(b6) is the summation of the postsynaptic current caused by 20 DG granulosa cells which link to the pyramidal cell in Fig. 4(b4). It turns out to be a great influence of this kind of synapse upon firing. Each concentrated bursting discharge corresponds to the period with a larger fluctuation of the current summation, in that the postsynaptic current during the period with a relatively large fluctuation disturbs the stable and resting state of neurons, and stires up an intensive firing of neurons. For a more direct observation of the influence of MF postsynaptic current upon the bursting discharges of pyramidal cell, let us define the binary encoding:

$$\text{Binary} = \begin{cases} 1, & I_{\mathrm{MF}} < -0.05 \text{ or } I_{\mathrm{MF}} > 0.35 \\ 0, & -0.05 \le I_{\mathrm{MF}} \le 0.35 \end{cases} \tag{11}$$

By this method, a binary encoding of MF postsynaptic current is obtained in Fig. 4 (b5). In comparison with Fig. 4(b4), it is found that MF postsynaptic current causes the severe oscillation of the pyramidal cell potential, and has the synchronization with the firing of that pyramidal cell, the synchronous firing making signals among cells on the transmission. This outcome is in accordance with that from Traub and Jeffyers[10]. After a further frequency analysis of the summation of MF postsynaptic current, a probability distribution of current is given (Fig. 4(b7)). It is detected that the distribution is at a relatively concentrated interval. Numerical integration from 0 to 0.35 shows that the probability for the postsynaptic current within this interval is 94%.

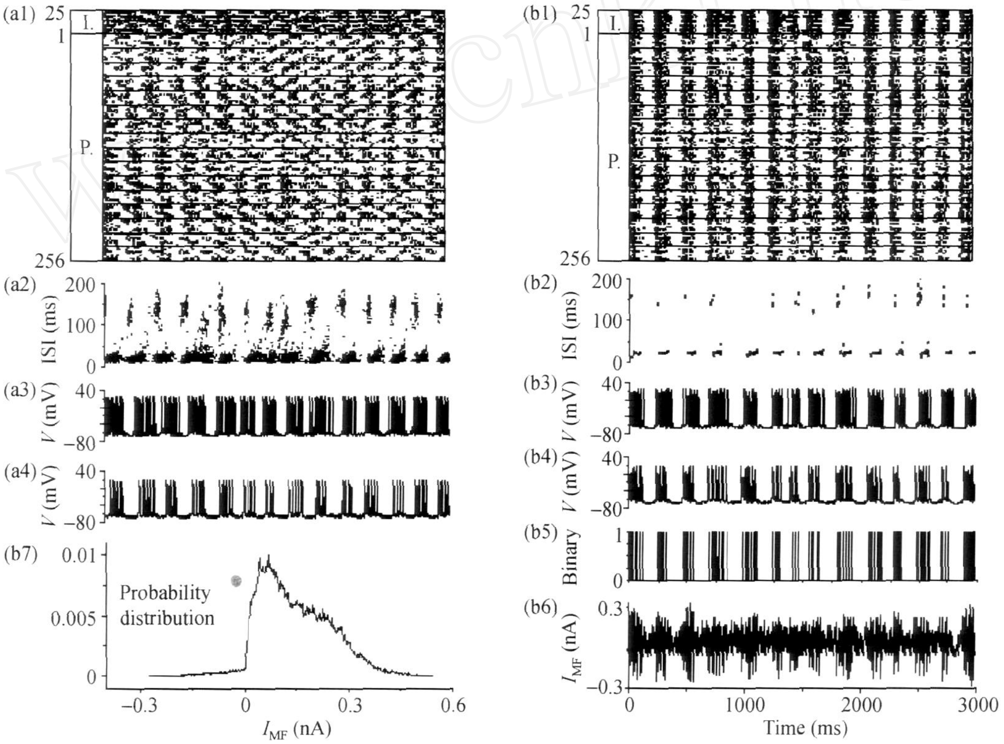

Fig. 4. (a) Result of DG. (a1) Spatiotemporal encoding. $W_{\mathrm{perp}} = 0.05$. (a2) ISI diagram with time. (a3) The discharge pattern of interneuron. (a4) The discharge pattern of granulosa cell inhibited by this interneuron. (b) Result of CA3. (b1) Spatiotemporal encoding. (b2) ISI diagram with time. (b3) The discharge pattern of interneuron. (b4) The discharge pattern of pyramidal cell inhibited by this interneuron. (b5) The binary code of MF postsynaptic current of this pyramidal cell. (b6) MF postsynaptic current. (b7) The probability distribution of MF postsynaptic current.

At present, it is generally recognized that the action potential of neurons may contain the encoding of life information. As the learning and memory tissue, the action potential of the hippocampal neurons is sure to imply the spatiotemporal encoding of the learning and memory. The first step for encoding is to record the spatiotemporal information for each action potential in the whole nervous system. Taking time as the horizontal axis, the space distribution of all neurons as the vertical axis, the basic spatiotemporal frame is constructed. The ordinate upwards means action potential encoding of 25 interneurons, while downwards represents the potential encoding of 256 pyramid or granulosa cells, with each row for 16 pyramid or granulosa cells. Each point represents an action potential, which constitutes the spatiotemporal encoding for DG and CA3 (Fig. 4(a1) (b1)). They have described the time relation of potential firing between neurons and the space rule of the information transmissions, which shows that DG firing is much more complicated. Generally, no synchronous firing happens between two neurons in long distance; however, the firing of two adjacent neurons appears synchronously, which means that the information among

DG neurons transmits through cells nearby, and that one neuron can only send its information to the others nearby via synapses. These neurons send their information in the same way. Fig. 4(a3) (a4) and (b3) (b4) further reveal the information transmission function of interneurons, which also embodies the rule of DG in the space information transmission. It is shown from CA3 that more neurons burst at the same period, even though two neurons stay a great distance away from each other. This is due to the stronger MF synapse, which verifies again the formation of the synchronous firing by the strong MF synapse. The distinction between DG and CA3 can also be shown clearly from ISI (Fig. 4(a2) (b2)). Almost at any time, DG has the firing of neurons, while CA3 seems to be sparser, that is, they always burst at almost the same time. ISIs all can be divided into two layers clearly, because they all produce bursting discharges. The bottom layer represents the interval between two spikes, and the top layer indicates the interval between two bursting discharges. Bursting discharge is the basic mode of neuron firing and the most usual phenomenon in the hippocampal experiments. The neuron encoding diversities are included in spike number and interspike interval. All these results well accord with experimental phenomenon as the basis of our further study.

The hippocampus is the tissue of accepting and dealing with the memory objection from environment. The PP signal in EC shows the stimulus to cortex from the external world, the object that CA3-DG is to transmit and deal with. The signal strength describes the different inputs outside, and input signal patterns are applied to CA3-DG system. Each signal lasts 1 s, and then Fig. 5 is obtained. It is indicated that the nervous system causes different response mode to each signal. The interspike interval, the bursting interval, and the spatiotemporal responses turn out to be of great variety, which contain the encoding modes of various signals. The abundant varieties show a very strong encoding competence of the network. The stronger the encoding competence is, the better the information storage capacity is. This is an indispensible property of CA3 as an associative memorizer.

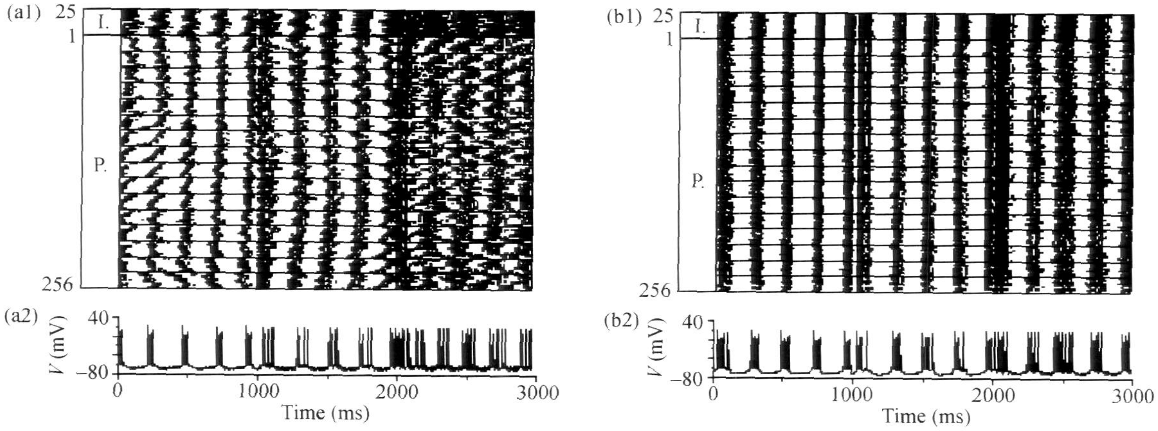

Fig. 5. (a1) Spatiotemporal encoding of DG under signal pattern $W_{\text{perp}} = \{0.02, 0.04, 0.06\}$. (a2) The discharge pattern of granulosa cell. (b1) Spatiotemporal encoding of CA3. (b2) The discharge pattern of pyramidal cell.

CA3-DG is an important structure in the hippocampus, a mid-transmission structure that links the outside information source EC and the output area CA1 in the hippocampus, which performs a significant function in the information transmission of the learning and memory in the hippocampus. The PP signal after DG processing is passed to CA3 through MF synapse by the granulosa cells, and immediately the CA3 pyramidal cells transfer the information to CA1 through SC synapse. The spatiotemporal encoding is used to describe the internal transmission property of this structure.

3 Discussion

This paper reproduces the discharge rhythm in the experiment through the numerical simulation of single hippocampal pyramidal cell, the process from the period-doubling bifurcation to chaos and the process from period 3 to chaos due to the outside input variety. Based on the model above, the numerical simulation is done to build a CA3-DG nervous system model built by the synaptic connection with a time delay 1 ms among cells. The basic property of the network transmission is analyzed in this nervous system. The synchronous firing between two adjacent cells indicates the information transmission methods among cells. The strong synapse MF causes the overall synchronization of CA3, while the strong spatiotemporal encoding competence of the nervous system well explains the fundamental property of CA3 as an associative memorizer. All the results manifest the functions of the hippocampal CA3-DG structure in the information transmission process, which indicates the complicated transmission property of the CA3-DG network structure.

Much research is made on the firing of a single neuron. The experiment manifests that the neuron discharge rhythm experiences a complicated bifurcation process from period of bursting discharges to period of spiking discharge. In this paper, the same result appears along with the variety of the stimulus outside. It also includes the process from period-doubling bifurcation to the chaotic bursting discharges and the process from the chaotic bursting discharges to the period 3 spiking discharges by sudden change, then immediately to the chaotic bursting discharges. The calculation results[20] from Chay model under the excitory cells indicate that if the Ca^{2+} equilibrium potential is considered as the parameter, some processes are obtained, such as the gradual bifurcation of ISI, the process from period 1 and 2 bursting discharges through period-doubling bifurcation to chaos, and the process from period 3 through period-doubling bifurcation to chaos, which is similar to the results of Chay model and which also well shows the firing diversity of the neuron potential. Taking the stimulus strength as the parameter, the ISI turns out to the same bifurcation phenomenon.

For the firing and dynamics property of the general neurons in network, almost no corresponding references can be found; however, much attention has already been aroused to research on network dynamics property. This paper gives a deep depiction of some transmission properties of the CA3-DG network structure. The model points out the synchronous phenomenon caused by the network, and shows that network has a stronger encoding competence by various inputing, which directly explains part of the experimental phenomena of CA3 in the hippocampus. The study of the whole functions of the hippocampus is far from adequacy. Many questions are left for further research, such as to further perfect the nervous system in the hippocampus, and to think more about the special role of CA1 region in hippocampus for the ultimate study of the functions of hippocampus on the learning and memory.

Appendix parameter values:

Parameter values of CA3 pyramidal cells and DG granulosa cells:

$$\alpha_m = \frac{-0.32(51.9+V)}{\exp(-(51.9+V)/4)-1}$$

$$\beta_m = \frac{0.28(24.9+V)}{\exp((24.9+V)/5)-1}$$

$$\alpha_h = 0.128\exp\left(\frac{-48-V}{18}\right)$$

$$\beta_h = \frac{4}{\exp(-(25+V)/5)+1}$$

$$\alpha_s = \frac{0.2}{\exp(-0.072V)+1}$$

$$\beta_s = \frac{0.0025(13.9+V)}{\exp((13.9+V)/5)-1}$$

$$\alpha_r = \begin{cases} \dfrac{\exp(-(65+V)/20)}{1600} & (V > -65) \\ 0.000625 & (V \leq -65) \end{cases}$$

$$\beta_r = \begin{cases} \dfrac{0.005-8\alpha_r}{8} & (V > -65) \\ 0 & (V \leq -65) \end{cases}$$

$$\alpha_{s(\mathrm{low})} = \frac{1.6}{\exp(-0.072(40+V))+1}$$

$$\beta_{s(\mathrm{low})} = \frac{0.02(53.9+V)}{\exp((53.9+V)/5)-1}$$

$$\alpha_{r(\mathrm{low})} = \begin{cases} \dfrac{\exp(-(105+V)/20)}{200} & (V > -105) \\ 0.000625 & (V \leq -105) \end{cases}$$

$$\beta_{r(\mathrm{low})} = \begin{cases} 0.005-\alpha_{r(\mathrm{low})} & (V > -105) \\ 0 & (V \leq -105) \end{cases}$$

$$\alpha_n = \frac{-0.016(29.9+V)}{\exp(-(29.9+V)/5)-1}$$

$$\beta_n = 0.25\exp\left(\frac{-45-V}{40}\right)$$

$$\alpha_a = \frac{-0.02(51.9+V)}{\exp(-(51.9+V)/10)-1}$$

$$\beta_a = \frac{0.0175(24.9+V)}{\exp((24.9+V)/10)-1}$$

$$\alpha_b = 0.0016\exp\left(\frac{-78-V}{18}\right)$$

$$\beta_b = \frac{0.05}{\exp(-(54.9+V)/5)+1}$$

$$\alpha_q = \begin{cases} 0 & (\chi < 140) \\ 0.00002(\chi-140) & (140 \leq \chi < 640) \\ 0.01 & (\chi \geq 640) \end{cases}$$

$$\beta_q = 0.001$$

$$\alpha_c = \begin{cases} \dfrac{\exp((55+V)/11-(58.5+V)/27)}{18.975} & (V \leq -15) \\ 2\exp\left(\dfrac{-58.5-V}{27}\right) & (V > -15) \end{cases}$$

$$\beta_c = \begin{cases} 2\exp\left(\frac{-58.5 - V}{27}\right) - \alpha_c & (V \leq -15) \\ 0 & (V > -15) \end{cases}$$

$C = 0.1(\mu F)$

$g_{Na} = 1.0, \quad g_{Ca} = 0.13$

$g_{Ca(low)} = 0.03, \quad g_{K(DR)} = 0.08$

$g_{K(A)} = 0.17, \quad g_{K(AHP)} = 0.07$

$g_{K(C)} = 0.366, \quad g_L = 0.0033(\mu S)$

$g_{af} = 0.005(\mu S)$

$V_{Na} = 50, \quad V_{Ca} = 75$

$V_K = -80, \quad V_L = -65$

$V_{syn(e)} = -10(mV)$

$\phi = 50$

$\beta_\chi = 0.075(ms^{-1})$

Parameter values of interneurons:

$$\alpha_m = \frac{-0.64(51.9 + V)}{\exp(-(51.9 + V)/4) - 1}$$

$$\beta_m = \frac{0.56(24.9 + V)}{\exp((24.9 + V)/5) - 1}$$

$$\alpha_h = \frac{0.128\exp(-(48 + V)/18)}{0.65}$$

$$\beta_h = \frac{4}{0.65(\exp(-(25 + V)/5) + 1)}$$

$$\alpha_n = \frac{-0.016(48.9 + V)}{0.65\exp(-(48.9 + V)/5) - 1}$$

$$\beta_n = \frac{0.25\exp(-(64 + V)/40)}{0.65}$$

$C = 0.1(\mu F)$

$g_{Na} = 1.5, \quad g_{K(DR)} = 0.3$

$g_L = 0.02(\mu S)$

$V_{Na} = 50, \quad V_K = -80$

$V_L = -65(mV)$

Parameter values of synapse:

$C_{pp\_CA3} = C_{pp\_DG} = 0.005$

$C_{pi\_CA3} = C_{pi\_DG} = 0.02$

$C_{ip\_CA3} = C_{ip\_DG} = 0.01$

$W_{SC} = 0.0007, \quad W_{mf} = 0.005$

$W_{perp} = 0.08$

$$V_{pp\_CA3} = V_{pp\_DG} = V_{pi\_CA3} = V_{pi\_DG} = V_{SC} = V_{MF} = V_{perp} = -10$$

$V_{ip\_CA3} = V_{ip\_DG} = -70(mV)$

$$\tau_{1(pp\_CA3)} = \tau_{1(pp\_DG)} = \tau_{1(ip\_CA3)} = \tau_{1(ip\_DG)} = \tau_{1(SC)} = \tau_{1(MF)} = \tau_{1(perp)} = 3$$

$\tau_{1(pi\_CA3)} = \tau_{1(pi\_DG)} = 1$

$$\tau_{2(pp\_CA3)} = \tau_{2(pp\_DG)} = \tau_{2(ip\_CA3)} = \tau_{2(ip\_DG)} = \tau_{2(SC)} = \tau_{2(MF)} = \tau_{2(perp)} = 2$$

$\tau_{2(pi\_CA3)} = \tau_{2(pi\_DG)} = 0.5(ms)$

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