Neuronal Ensemble Coding of Spike Trains in the Hippocampus CA3 via Small-world Network

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Abstract—**The Hindmarsh-Rose (HR) model could describe different discharge property of an excitatory or inhibitory neuron by changing the parameter r. In this paper, HR model is used to be the dynamical equations of the spiking model neurons, and different neurons in one neuronal population are connected with WS small-world network. A neurons spiking model in the hippocampus CA3 based on small-world network is established on the Matlab platform. Spike trains of the neurons spiking model are simulated when no stimulus and a pulse current acted on the model. Then rate coding and synchrony coding are used to analyze the simulated spiking trains. Experiment results indicate when no stimulus acts on the neurons spiking model, the spike firing of hippocampus CA3 is sparse. When a stimulus acts on the neurons spiking model, the mean population firing rate increased obviously. The increasing of neurons firing rate could present the ensemble activities, which highly correlate with memory.**

Index Terms—**Hindmarsh-Rose (HR) model, small-world network, spike trains, hippocampus CA3, neuronal ensemble coding**

I. Introduction

Cognitive science is one of the most challenging fields that attract the world's most attention in the 21st century. Cognitive science is a multidisciplinary study of mind and behavior, including neuroscience, philosophy, psychology, artificial intelligence and linguistics [1]. Cognitive science studies human mental activity, such as memory, perception, learning, thinking, consciousness etc. Memory is one of the most important cognitive functions, and the studies on memory encoding are regarded as a key breakthrough to understand the mechanism of information transmission and processing in complex brain [2].

In 1949, Donald Hebb proposed the famous "cell-assembly" hypothesis [3], which indicated that neural information encoding process was not conducted by a single neuron but neuronal ensemble. The brain basis of mental representation (images, ideas) was groups or assemblies of neurons that tended to be active at the same time because of Hebbian learning. The firing of neurons in a cell-assembly can persist after the triggering event and this persistence is a form of memory. Therefore, the study of neural ensemble coding of memory mechanism is very important and significant in the cognitive science.

The hippocampus is a structure within the brain that plays a key role in memory, attention, perceptual awareness and consciousness [4]. The hippocampus CA3 includes a population of billions of neurons, each making thousands of synaptic contacts with its neighbors. How the vast neurons connect with each other and process neural information has become the center problem of cognitive science in recent years [5].

Because neuronal population activities of many brain areas (hippocampus, cerebral cortex et al.) are difficult to be observed and recorded in animal experiment accurately, simulation data of neural network models is an effective way to validate the neural ensemble coding theories and methods. Various neural network models have been developed to describe neuronal population spiking of hippocampus. For example, the pulse-coupled neural networks (PCNN) model was used to simulate neuronal population firing of hippocampus CA3 neurons [6]. Based on the neural nucleus of hippocampus information connection, a hippocampus neural nucleus model was built by Meeter [7]. The model was comprised of CA1, CA3, dentate gyrus and entorhinal cortex nucleus. A neural network computational model has been undertaken to investigate how the hippocampus, neocortex, and basal ganglia work together to support cognitive and behavioral function in the mammalian brain [8].

The models mentioned above can reproduce neuronal population activity of the hippocampus CA3, but the synchronization of neuronal population spikes can not be exhibited perfectly. With the fast development of the neuroinformatics and computational neuroscience, researchers found that many biological neural systems can be cast into the form of complex networks, among which small-world networks have attracted much attention in recent years [9].

The hippocampus CA3 is a complex network on

Manuscript received January 31, 2009; revised February 18, 2009.
The work was supported by NSFC (30770545) and Foundation of Natural Science of Tianjin (07JCYBJC17100).
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doi:10.4304/jcp.5.3.448-455

multiple spatial and time scales. Studies of functional connectivity patterns among cortical regions have demonstrated that functional brain networks exhibit small-world properties, possibly reflecting the underlying structural organization of anatomical connections [10]. The small-world network could provide a powerful and versatile approach to understand the structure and function of human brain systems [11]. In addition, the spikes of neurons within small-world network could exhibit synchronization well.

There are many methods for neuronal ensemble coding, such as rate coding, temporal coding [12], spatio-temporal coding [13], correlation coding [14], nonlinear entropy coding [15] et al. In this article, two methods are presented to describe the neurons spiking activity. They are ensemble rate coding and ensemble synchrony coding respectively.

In this paper, a neurons spiking model is built according to the physiology feature of hippocampus CA3. The model is composed of 120 neurons, in which 100 neurons are excitatory and 20 are inhibitory. We choose Hindmarsh-Rose (HR) neuron model to describe the different spiking patterns of a neuron and simulate the connection of different neurons by WS small-world network. Finally, we implement the simulation model on Matlab 7.1 platform, and analyze the simulation results by neural ensemble rate coding and synchrony coding.

II. METHODS

Hindmarsh-Rose (HR) neuron model is chosen to describe the spiking patterns of single neuron. WS small-world network structure is used to characterize the connection of different neurons. The neuronal ensemble rate coding and synchrony coding are adopted to analyze the neuronal ensemble activity of hippocampus CA3.

A. Hindmarsh-Rose model

The Hindmarsh-Rose (HR) model was proposed in 1984[16]. It describes the dynamics discharge characteristic of the neurons. The HR model is a simplified Hodgkin-Huxley (HH) neuron, which used four linked first-order differential equations to model the membrane potential of a giant squid axon. The HH model has served as a basis of most work in recent decades but its complexity imposes considerable computational costs in modeling large scale neural networks. Unlike even simpler models such as the leaky integrate-and-fire model, in HR model neurons action potentials are explicitly modeled.

The dynamic equations of HR model are shown in formula (1), (2) and (3). Where X stands for the membrane potential, Y is the fast recovery currents, Z denotes slow adaptive currents, Isim is an exogenous stimulus input current, a, b, c, d, r, g are constant parameters. In our simulations, the parameter values are set as followed [17]:

a=1.0, b=3.0, c=1.0, d=5.0, g=5.1.

$$\frac{dX}{dt} = Y - aX^3 + bX^2 - Z + I_{sim} \tag{1}$$

$$\frac{dY}{dt} = c - dX^2 - Y \tag{2}$$

$$\frac{dZ}{dt} = r(X - \frac{1}{4}(Z - g)) \tag{3}$$

B. Small-world Network Theory

The theory and method of small-world networks were proposed by Duncan Watts and Steven Strogatz in 1998 [18].

Small-world networks are characterized by two indices. One is Clustering Coefficient (CC) shown in formula (4), and the other is Characteristic Path Length (CPL) shown in formula (5).

The CC is defined as the average fraction of pairs of neighbors of a vertex that are also neighbors of each other. So CC index is a measure of the connection density of the local neighborhoods of a vertex. If a vertex i has k_i neighbors, at most $k_i(k_i-1)/2$ connections are allowed to exist between these neighbors. The CC_i is the fraction of these allowable edges that actually exist around a vertex. The CC of the small-world network is the average of all CC_i for each vertex.

$$CC = \sum_{i=1}^{N} \frac{2e_i}{k_i(k_i - 1)} \tag{4}$$

where e_i is the number of edges that actually exist among these k_i vertices.

The CPL is defined to be the mean shortest distance between vertex pairs in a network.

$$CPL = \frac{2}{n(n+1)} \sum_{i=1}^{N} d_{ij} \tag{5}$$

Where d_{ij} is the number of edges along the shortest path connecting vertex i and vertex j. if i = j then d_{ij}=0.

Changing p parameter value in such a way, the transition between order (p=0) and randomness (p=1) can be closely observed in figure 1.

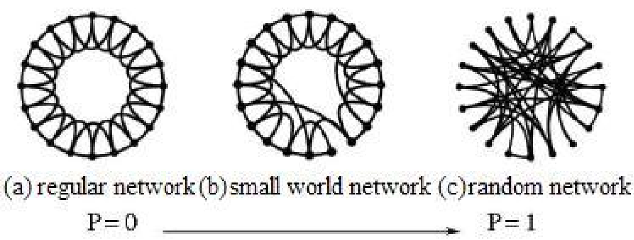

Figure 1. For p = 0, the original network is unchanged, for p = 1, all edges are rewired randomly and for 0 < p < 1, graphs are combining elements of regular and randomness. Small-world graph occurs at approx. p = 0.02. Randomness increases left to right above.

The three graphs in Fig. 1 are regular network, small-world network and random network respectively. Small-world networks are characterized by a high CC in combination with a low CPL, whereas both CC and CPL are high in regular network structures and low in random ones [19].

In our neurons spiking model, the number of neurons is N=120. The k value is 2 and the rewiring probability is p=0.02.

C. Neuronal Ensemble Rate Coding

There are many methods for neuronal ensemble coding, such as rate coding, temporal coding, spatio-temporal coding, correlation coding, nonlinear entropy coding et al.

The rate coding phenomenon was originally shown by ED Adrian and Y Zotterman in 1926. Rate coding has been one of the dominant tools for measuring neurons activity over the past 80 years of neurological study.

For many physiologists, rate coding constitutes the simplest and clearest notion of how neurons encode information. In a "rate code" the only variable of interest is the total number of spikes fired by neurons in a relatively long time period of several hundred millisecond or even seconds. In other words, one neuron would receive information from another by "counting" the number of spikes from that neuron over some extended period of time and determining the mean time between firings. Specifically, a shorter time period implies a higher activation. The rate coding model of neuronal firing communication states that as the intensity of a stimulus increases the rate of spike firing increases.

Rate coding is believed that neuron communicated information in their mean firing rate [20]. In this study, rate coding is used to represent the neural ensemble activity of hippocampus CA3 neurons under external stimulation.

Although spikes can have different amplitudes, durations or shapes they are typically treated as discrete events. By discrete events, we mean that in order to describe a spike train, one only needs to know the succession of emission times:

$$H_i = \{\ldots, t_i^n, \ldots\} \text{ with } t_i^1 < t_i^2 < \ldots < t_i^n < \ldots \quad (6)$$

Where t_i^n corresponds to the nth spike of the neuron of index i.

Let us consider a spiking neuron i. The spike train H_i associated to this neuron is defined in (6). The windowed firing rate $\gamma_i(\cdot)$ by

$$\gamma_i(t, \Delta t) = \frac{\eta_i(t-\Delta t, t)}{\Delta t}, \quad (7)$$

where $\eta_i(\cdot)$ counts the number of spikes emitted by neuron i inside the sliding time window $(t-\Delta t, t)$.

D. Neuronal Ensemble Synchrony Coding

To obtain a time-resolved measure of the firing rate of the spike train $\{t_i^x\}$, in a first step the value of the current interspike interval is assigned to each time instance.

$$x_{isi}(t) = \min(t_i^x \mid t_i^x > t) - \max(t_i^x \mid t_i^x < t) \quad (8)$$

$t_1^x < t < t_M^x$, And accordingly for the second spike train $\{t_j^y\}$. The ratio between x_{isi} and y_{isi} is taken, and the final measure is thereby obtained after introducing a suitable normalization,

$$I(t) = \begin{cases} \dfrac{x_{isi}(t)}{y_{isi}(t)} - 1 & \text{if } x_{isi}(t) \le y_{isi}(t) \\ -\left(\dfrac{y_{isi}(t)}{x_{isi}(t)} - 1\right) & \text{else} \end{cases} \quad (9)$$

The measure becomes zero in case of iso-frequent behavior, and approaches -1 and 1, respectively if the firing rate of the first (or second) train is infinitely high and the other infinitely low [21].

In order to derive a measure of spike train distance, the spike-weighted method is characterized.

$$D_I = \sum_{i=1}^{M} |I(t_i)| \quad (10)$$

E. Neurons spiking model of Hippocampus CA3

The hippocampus is perhaps the most studied structure in the brain. It forms the central axis of the Limbic System. It is critical to spatial learning and awareness, navigation, memory and associational recollection. The regions CA1 and CA3 contain pyramidal cells as their principal neurons (CA stands for Cornu Ammonis - so called because the whole structure looks like rams horns).

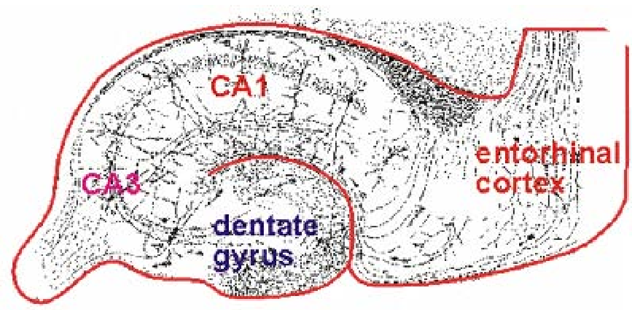

Figure 2. The hippocampus CA3 anatomy position

The hippocampus is a part of the forebrain, located in the medial temporal lobe. It belongs to the limbic system and plays major roles in short term memory and spatial navigation. Fig. 2 shows that the hippocampus CA3 area anatomy position. The hippocampus CA3 is involved in memory formation [22].

The neurons of the hippocampus CA3 are mainly composed of pyramidal cells and inhibitory interneuron. The majority of pyramidal cells are prone to excitatory neurons. The anatomical sampling of the neurons in the hippocampus CA3 has shown that about 84% of the neurons are excitatory and the rest 16% are inhibitory [23]. The ratio of excitatory neurons to inhibitory neurons is about 5 to 1 in the hippocampus CA3.

In our neural population spiking model, we use HR model as the dynamical equations for the nodes, and all nodes are connected by small-world networks. The model is described by the following equations:

$$\frac{dX_i}{dt} = Y_i - aX_i^3 + bX_i^2 - Z_i + I_{sim} + \frac{e}{N}\sum_{j=1}^{N} A_{ij}X_j \tag{11}$$

$$\frac{dY_i}{dt} = c - dX_i^2 - Y_i \tag{12}$$

$$\frac{dZ_i}{dt} = r(X_i - \frac{1}{4}(Z_i - g)) \tag{13}$$

Where the subscript i denotes the neuron number and N represents the total number of neurons. For simplicity we use N=120 throughout simulation because the number of neurons N=120 can be used to describe small-world property. $\frac{e}{N}\sum_{j=1}^{N} A_{ij}X_j$ is the coupling term of the neural population spiking model, where e is the coupling strength. A_{ij} represents the coupling matrix of the neurons and when a connection exists between neurons i and j, A_{ij}=1, otherwise, A_{ij}=0, and $A_{ii} = -\sum_{j=1}^{N} A_{ij}(j \neq i)$.

In our neurons spiking model equations, the parameter values are set as followed:

a=1.0, b=3.0, c=1.0, d=5.0, e=0.5, g=5.1.

III. RESULTS

A. Hippocampus CA3 small-world network topology connection

According to the anatomical characteristics, our simulation model is composed of 120 neurons, in which 100 neurons are excitatory and 20 are inhibitory. WS small-world network generation algorithm is adopted. Three network topologies are constructed by changing rewiring probability p. The network is a regular network when p=0, and a random network when p=1. In our simulation experiment, the 120 neurons are connected with small-world network structure when rewiring probability is p=0.02. The connections among the neuronal population are shown in Fig. 3.

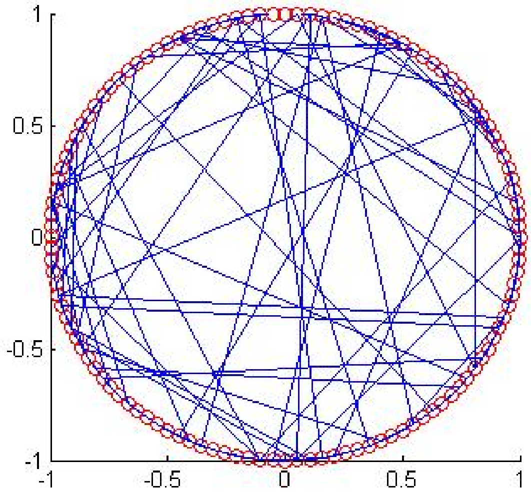

Figure 3. Small-world network topology graph (120 neurons)

To compare characteristics of different network, we calculate the CC and CPL indexes according to formula (4) and (5). The results are shown in table 1.

TABLE I.
CC AND CPL INDEXES OF THREE NETWORKS

Networks	CC	CPL
Regular network	0.60	8.76
Small-world network	0.48	3.09
Random network	0.06	2.75

As shown in table 1, the CC of the small-world network (120 neurons) is 0.48 and the CPL is 3.09. The two indexes satisfy the small-world network property.

B. RS and FS neurons spiking pattern

The HR model exhibits realistic neuronal response properties, including a range of periodic, chaotic, and irregular bursting behavior depending on a single input parameter r.

There are mainly two physiological types of hippocampus CA3 neurons. They are excitatory regular spiking (RS) neurons and inhibitory fast spiking (FS) neurons. The RS neurons are identified as spiny and pyramidal neurons and exhibit evident and rapid firing frequency adaptation responding to a continuous depolarizing current injection. The hippocampus CA3 excitatory neurons spiking pattern is shown in Fig. 4.

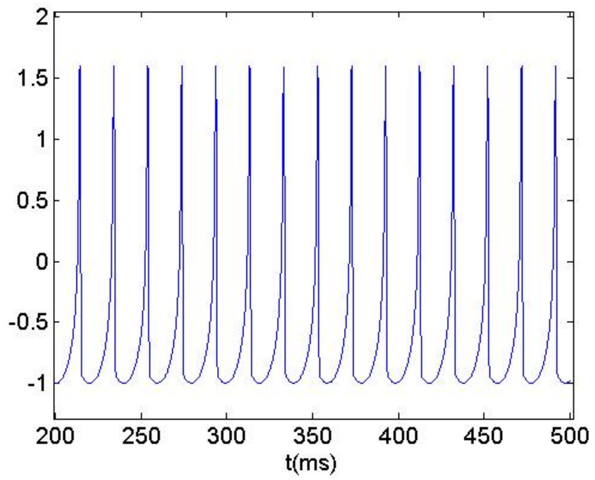

Figure 4. The hippocampus CA3 excitatory neurons spiking pattern (RS)

The FS neurons are identified as non-spiny and non-pyramidal neurons and respond to long depolarizing current stimulus with higher rate of firing and less prominent spike frequency adaptation than the RS neurons. The parameter r_{RS}=0.16 and r_{FS}=0.006 describe the excitatory and inhibitory spiking properties in the HR neuron models. The hippocampus CA3 inhibitory neurons spiking pattern is shown in Fig. 5.

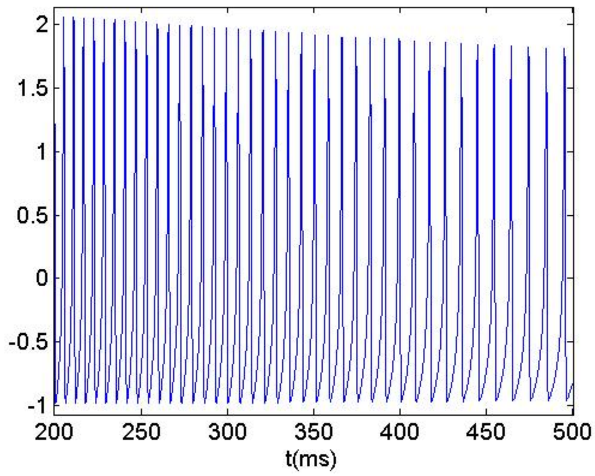

Figure5. The hippocampus CA3 inhibitory neurons spiking pattern (FS)

C. Spike Trains

In our experiment, the simulation time is set to be 1000ms. In order to achieve the stable results, we choose the neurons spiking trains from 200 to1000ms.

The external stimulus event is a pulse current. The duration of the stimulus is set to be 100ms. When no stimulus current acts on the neurons spiking model, that is Istim=0. At the time 300ms, the stimulus current acts on the neurons spiking model. The intensity is set to be 2mA, that is Istim=2.0.

Simulation of the spike trains before and after the external stimulus acting on the neurons spiking model is shown in Fig. 6.

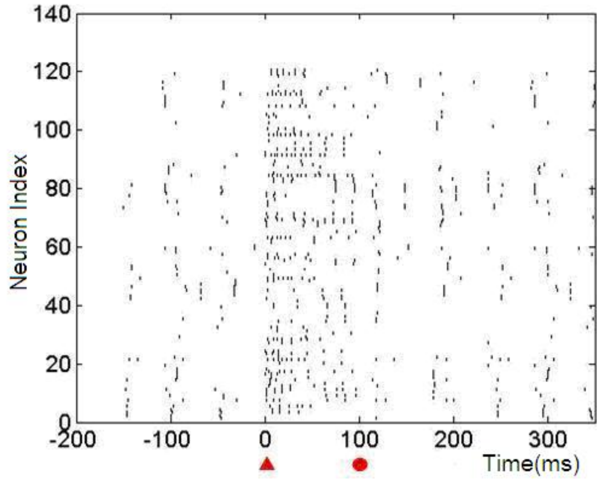

Figure 6. Spike trains of the neurons spiking model. The start of the stimulus is indicated by the red triangle, and the end of the stimulus is indicated by the red circle.

In Fig. 6, the X axes represent the spiking time (unit is ms), and the Y axes is the index of neurons. A dot represents the time of a neuronal spike train.

D. Neuronal ensemble rate coding

The average spike firing in unit time is defined as mean population firing rate [24]. In this experiment, when no stimulus acts on the model, that is before the zero time in Fig. 6. The mean population firing rate is 7.8% in accordance with the sparse spike firing characteristic of hippocampus CA3.

When stimulus current acts on the neurons spiking model, the start of the stimulus is indicated by the red triangle and the end of the stimulus is indicated by the red circle. The duration of the stimulus is 100ms. During the stimulus time, the mean population firing rate is increased to 28%. When the stimulus event is removed, the mean population firing rate is decreased gradually.

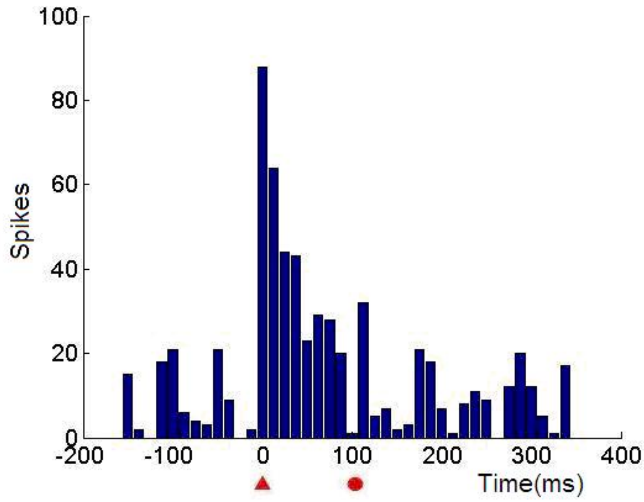

Figure 7. The neuron spike histogram before and after the stimulus acting on the neurons spiking model. The start of the stimulus is indicated by the red triangle and the end of the stimulus is indicated by the red circle.

Fig. 7 shows that the neuron spike histogram before and after the stimulus effects on the neurons spiking model. In Fig. 7, the X axes represent the spiking time (unit is ms), and the Y axes is the neurons population spikes number. The red triangle represents the onset time of stimulus and the red circle represents the finish time of stimulus in the figure.

The neuron mean spikes number is about 7 before the stimulus act on the neurons spiking model can be seen from Fig.7.

When the stimulus act on the neurons spiking model via small-world network connection, the neuron mean spikes number is increased to 28. The increasing of neurons firing rate presents the ensemble activities, which highly correlate with memory. When the stimulus event is finished, the neuron mean spikes number is decreased.

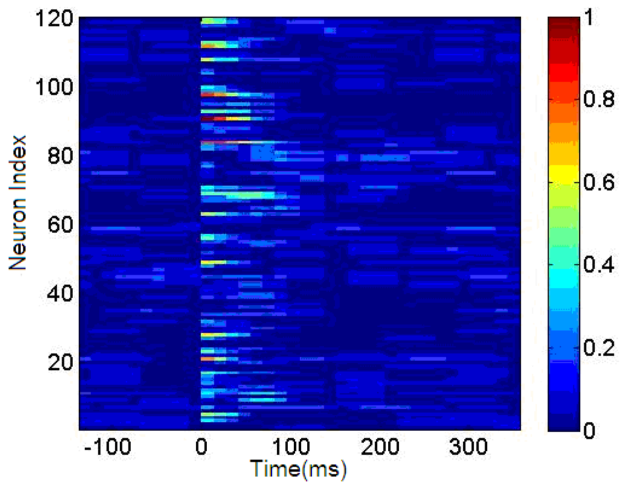

Figure 8. Dynamic neuronal ensemble rate coding

The dynamic rate coding of neuronal firing around the stimulus point is shown in Fig.8. The X axes represent the spiking time (unit is ms) before and after the stimulus acting on the neurons spiking model, and the Y axes is the index of neurons. The firing rate values (after normalization) are described via color. The results show that the firing rate is lower when no stimulus act on the network model with no ensemble activity. When the stimulus event is appeared, the firing rates are higher, where presented obvious ensemble activity.

E. Neuronal ensemble synchrony coding

The number 63 neuron is marked in blue and the number 56 neuron is marked in red. For this pair of spike trains an ISI-distance D_I=0.054 is obtained. In Fig.9 the ISI-distance is applied to two spike trains of 800ms duration.

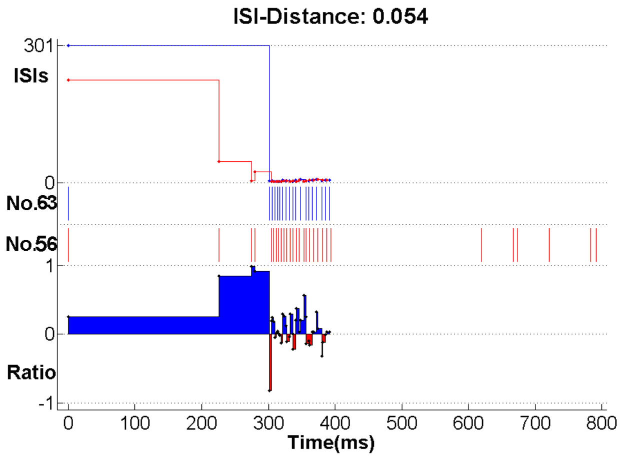

Figure 9. Synchrony measure based on ISI-distance between neuron 63 and neuron 56.

In Fig.9, the X axes represent the neurons spiking time (unit is ms). In the middle traces the two neurons spike trains are shown. The neuron 63 spike time series is marked in blue, and the neuron 56 spike time series is marked in red. According to equation (8), the two neurons ISI-values are depicted on the top. At the bottom the corresponding renormalized ISI-distance is shown. Here colors mark the times where the respective spike train is slower. In the first 300ms, the two spike trains are desynchronized and this is reflected by a large ISI-distance value. When the stimulus (pulse current) acts on the neurons spiking model at the time of 300ms, the synchrony relation of the two spike trains is changed. During the stimulus time(100ms), the two spike trains are 1:1 synchronized and this is reflected by an ISI-distance $I(t)\approx 0$. When the stimulus is removed from the neurons spiking model, the two spike trains are desynchronized again.

In Fig.10, the two spike trains are neuron 63 and neuron 69 spiking time series. The synchrony measure of the two spike trains in the same way as in Fig.9. In this case the two spike trains are desynchronized during the stimulus acts on the neurons spiking model. This is reflected by a large ISI-distance value during the stimulus time (100 ms).

In this way, the synchrony measure of other neurons and neuron 63 can be undertaken. The neuronal assembly is composed of the highly synchrony neurons (neuron 63, 56, 50, 32, 20, 83, 97, 112). When the stimulus event is occurred, the neuronal ensemble is formed.

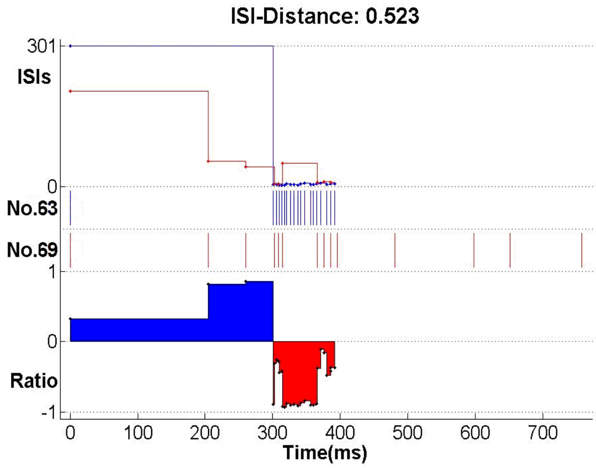

Figure 10. Synchrony measure based on ISI-distance between neuron 63 and neuron 69.

IV. CONCLUSIONS

In this paper, a neurons spiking model of hippocampus CA3 is established based on the small-world network theory and anatomical connections features.

In our experiments, the neurons spiking model is composed of 120 neurons. According to the anatomical characteristics of hippocampus CA3, the ratio of the excitatory to inhibitory neurons is about 5 to 1. Therefore, we designate 100 excitatory and 20 inhibitory neurons in our simulation model. HR model is chosen to describe the different spiking patterns of a neuron. Furthermore, the connection of different neurons is implemented by WS small-world network on Matlab 7.1 platform.

Experiment results indicate the neuronal population spiking model of hippocampus CA3 could simulate spike trains. It is evident that neuronal firings are provided with completely different coding patterns before and after the stimulus act on the neurons spiking model. Neuronal ensemble rate coding and synchrony coding are used to represent the neuronal ensemble activity of the hippocampus CA3. The synchrony measure of spike trains based on ISI-distance is an effective neuronal ensemble coding method.

When no stimulus acts on the neurons spike model, the spike firing of hippocampus CA3 is sparse (the mean population firing rate is less than 10%). This means that no ensemble activity is presented, which indicated that memory is not formed. When a stimulus acts on the neurons spike model, the mean population firing rate is increasing obviously (in our experiment is 28%). The increasing of neurons firing rate could present the ensemble activities, which showed that the memory (external stimulus event) has been built up.

ACKNOWLEDGMENT

This research is supported by Grant from the National Foundation of Natural Science of China (No. 30770545), and Foundation of Natural Science of Tianjin (No. 07JCYBJC17100).

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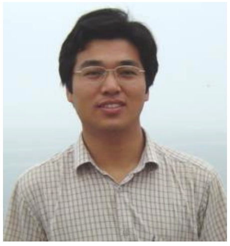

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