Functional Networks Analysis from Multi Neuronal Spike Trains on Prefrontal Cortex of Rat during Working Memory Task and Neuronal Network Simulation

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***Abstract*—Functional connectivity networks on prefrontal cortex of rat during working memory task *in vivo* are analyzed. Neural ensemble entropy coding is applied to find the time interval of working memory event occurrence. The analysis of functional connectivity networks is carried out though the method of cross-covariance. And functional networks of the occurrence working memory event and resting state are obtained. The complex network topology parameters are calculated, the two networks satisfy the small-world network property as the clustering coefficients of them are larger than their corresponding random networks and their characteristic path lengths are approximately equal to their corresponding random networks. Finally, the simulations of spiking neuronal networks of working memory event occurrence and resting state are presented. Hindmarsh-Rose neuron model is chosen as single neuron of prefrontal cortex that connected by functional network of working memory event occurrence and resting state, receptivity. The simulation results are agreed with experiment data in rat prefrontal cortex during a working memory task.**

***Index Terms*—functional connectivity, neuronal entropy coding, spike trains, working memory, small-world network, neuronal network simulation**

I. INTRODUCTION

Working memory is short-term memory, which is one of the most important research domain of cognitive science, refers to a complex cognitive tasks in the brain which can provide temporary storage and processing of the necessary information, such as learning and reasoning[1]-[2]. Physiological studies have found the neural activity of the prefrontal cortex changes in the process of new learning task, suggesting that working memory is mediated by continuous activities of prefrontal cortex neurons[3]-[8]. Therefore, understanding the information of neural activity is important to grasp the basic principle of brain function computations.

In addition, many theories such as rate coding, time coding, and nonlinear coding have laid the foundation for further studies of neural activities[9]-[10]. Entropy is a measurement of uncertainty or the amount of information, which can quantify the information and can describe the characteristics of neural activity[9]-[11]. Moreover, the nonlinear entropy can make up for the deficiency of traditional linear coding methods and show the differences between two spike trains which have the same firing rates but different temporal structures. In the present paper, entropy coding is applied to study local spatiotemporal pattern of neuronal activity in the process of working memory task and to find the period of working memory event occurrence.

The concept of brain functional connectivity first appeared in the electroencephalogram (EEG) study, which measures the statistical dependencies of the correlation and functional activities on the spatial separation of time between different brain regions. Functional network is the network obtained from deviation of statistical independence, including measuring their correlation, covariance, coherent spectrum and phase synchronization between different brain regions or neurons[12]. In the early 1990s, Friston KJ et al first proposed functional connectivity analysis on functional magnetic resonance imaging (fMRI) data[13], since then the complexity of brain networks based on functional connectivity imaging of EEG, Magnetoencephalography (MEG) or fMRI data has become an important research direction. For example, Eguiluz VM et al (2005)[14] applied the correlation coefficient method to measure functional connectivity of fMRI data, found that the human brains are small-world

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networks; Achard S and Bullmore E (2007)[15] applied correlation, partial correlation and partial coherence measurement method to study the functional connectivity networks between different brain regions, the results consistently indicate that the human brains are efficient small-world networks.

Traditional EEG, MEG, fMRI, and other macro technology, can directly measure the integrated electrical activity of neuronal population, but the measurement results cannot be acquired with high time resolution (millisecond) and spatial resolution (millimeter) at the same time. At the micro level, individual neuron is the basic functional unit of the activity in the brain, its neural information transmission and storage is very complex and highly dynamic.

Multi-channel neural discharge recording technology, developed in recent years, is the use of electrophysiology - the extracellular recording method to record the activity of neurons in the discharge. This new technology can also record the firing activity of neuronal populations of the different parts of a brain region or multiple brain regions. Therefore, the functional connectivity analysis from neuronal firing data of the multi-channel recording technology is an effective method of access to the functional activity of neurons, and to achieve high temporal resolution and spatial resolution. Yu S et al (2008)[17] studied the functional networks of visual cortex neurons; Correlation analysis method was used to calculate the functional connectivity matrix; The visual responses data were simultaneously recorded from 24 nerve cells in visual cortex of anesthetized cats; The functional networks had small-world properties. In addition, many statistical method has been used for establishing statistical associations or causality between neurons, finding spatiotemporal correlations, or studying the functional connectivity in neuronal networks[18]-[24]. The standard method of analysis functional connectivity from multi spike trains is cross-correlation method[16].

A variety of neural network models have been proposed to simulate the spike potentials of neural population. For instance, Xiao ZG and Tian X(2010) [25] built small-world neural network model of hippocampal CA3 based on the characteristics of the hippocampal CA3 neurons, simulated the response spike trains of neuronal population under three types of stimulus, and studied the respective neural ensemble encoding of three types of stimulus. Meeter M(2003)[26] built a neural nucleus model of hippocampus, which composed by CA1, CA3, dentate gyrus, and entorhinal cortex nucleus; The model was based on the neural information connection relation of hippocampus. Atallah HE and et al (2004)[27] used a computational neural network model to investigate how the hippocampus with together neocortex and basal ganglia operate, which can sustain cognitive and behavioral function in the brain.

In the present paper, we aim to provide functional connectivity networks analysis on prefrontal cortex of rat in the process of working memory task *in vivo*, during the period of working memory event occurrence and the period of resting state. Neural ensemble entropy coding can be applied to find the period of working memory event occurrence and the period of resting state. The analysis of functional connectivity networks carried out though the method of cross-covariance. The complex network topology parameters are calculated. Finally, the simulations of spiking neuronal networks of working memory event occurrence and resting state are presented. Hindmarsh-Rose (HR) neuron model is chosen as single neuron that is connected by functional network of working memory event occurrence and resting state, receptivity.

II. METHODS

A. Experimental Data Acquired on Prefrontal Cortex of Rats during Working Memory Task in Vivo

Experimental data were conducted with the approval from Animal Care and Use Committee of Tianjin Medical University and were in conformity to the Guide for the Care and Use of Laboratory Animals. 16-channel micro-wire electrodes were planted in rat prefrontal cortex and neural activities were recorded while the rats performed a working memory task in Y-maze. Effective period of 7 seconds were selected, which is deemed to be enough to represent the entire working memory process.

B. Neural Ensemble Entropy Coding for Working Memory in Rats Prefrontal Cortex

Entropy, especially Shannon entropy in this paper, is computed from inter-spike intervals (ISIs), which are generally regarded as an important carrier of encoded information. Assume there is an N-element information source sequence$\{z_1, z_2, ..., z_n\}$; Shannon entropy is defined as the following (1) (Shannon CE, 1948)[28]:

$$E = -\sum_{i=1}^{n} p_i \log_2 p_i \ , \tag{1}$$

where p_i, (i=1, 2, ..., n), is the occurrence probability of each element of information source sequence. The algorithms of Shannon entropy for spike train from single neuron estimation are described as the followings: The Inter Spike Interval (ISI) sequence of the neural firing was measured and the ISI histogram was estimated; The ISI histogram was separated with appropriate bin base on the defined bin length and the characteristics of the spike trains; The spikes number S_i in each bin i (i=1, 2, ..., n) was counted; The firing probability p_i of bin i was calculated based on the equation of $p_i = S_i / \sum_{i=1}^{n} S_i$; From (1) the entropy E of the firing sequence was calculated.

Above entropy estimation method can be used to present nonlinearity of neural population activity. The steps of Neural ensemble entropy coding are summarized as: An appropriate window length L was selected and Shannon entropy was calculated for the individual neuron k, (k=1, 2, ... , L) in the window; The window

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along the time till the end of spike trains was slid with a moving step; The entropy values in each window were estimated; All the entropy values were normalized and the dynamical map can be represented the neural ensemble activity as a response to the event.

C. Functional Network from Neuronal Spike Train Data

The method to determine directed network is to calculate the covariance between neurons, which is used to analyze the influences between pairs of spike trains. Spike trains are binned in window of 1 millisecond, and then 10 milliseconds time-step is applied to count the number of spikes of each spike train, the corresponding vectors are obtained. To measure whether there is an influence from a reference neuron (vector y) to a target neuron (vector x), (2) is applied to calculate covariance between neurons,

$$C_{xy}(d)=\begin{cases}\sum_{n=1}^{N-|d|}\left(x_{(n+d)}-\frac{1}{N}\sum_{i=1}^{N}x_i\right)\left(y_n-\frac{1}{N}\sum_{i=1}^{N}y_i\right) & d\geq 0\\ \sum_{n=1}^{N-|d|}\left(y_{(n-d)}-\frac{1}{N}\sum_{i=1}^{N}y_i\right)\left(x_n-\frac{1}{N}\sum_{i=1}^{N}x_i\right) & d<0\end{cases}, \quad (2)$$

where $C_{xy}(d)$ is covariance between reference neuron (vector y) and target neuron (vector x), d is time lag between reference neuron (vector y) and target neuron (vector x), x and y are length N vectors obtained from corresponding spike trains of neuron. The $C_{xy}(d)$ will show a peak if there is some consistent pattern between vector y and vector x with a time lag d. When a peak occurs at a time lag $d \geq 0$ in lag window of 50 milliseconds, there is an effect from reference neuron (vector y) to target neuron (vector x) with target neuron delay d, the influence strength is the value of peak. If the peak exceeded a threshold, we can obtain a connection from reference neuron to target neuron with connectivity weigh of peak value. Each neuron is considered with no connectivity to itself, in other words, the main diagonal elements of functional connectivity matrix are zero.

D. Complex Network Topology Parameters

Small-world networks theory is presented by Watts DJ and Strogatz SH(1998)[29]. Usually two parameters are used to characterize the complex network characteristics. One is clustering coefficient (CC), and another is characteristic path length (CPL). Suppose there are k edges connected to one node; there are at most $k(k-1)/2$ probable exist edges among k neighbor nodes which are connected to k edges. The CC of one node is the number of actual exist edges divide by the number of at most probable exist edges. The CC of the network is defined as the average value of all nodes, as the followings (3).

$$CC=\sum_{i=1}^{N}\frac{2e_i}{k_i(k_i-1)}, \quad (3)$$

where N is the nodes number of the network, e_i is the number of actual exist edges among k_i nodes. Arbitrarily select two nodes in a complex network, connecting these two nodes with the minimum number of edges, which is defined as the shortest path length of these two nodes. The CPL of the network is defined as the average value of all shortest path length between node pairs, as the followings (4),

$$CPL=\frac{2}{n(n+1)}\sum_{i=1}^{N}d_{ij}. \quad (4)$$

where d_{ij} is the shortest path length between the two nodes i and j in the complex network, N is the nodes number of the network.

Characteristics of small-world network are high CC and shorter CPL. Meanwhile the two parameters are high in regular networks and low in corresponding random networks[30].

E. Spiking Neuronal Network Simulation of Prefrontal Cortex

Single spiking neuron model is the basis computational model of the neural physiological activity study. The Hindmarsh-Rose (HR) model was proposed by Hindmarsh J and Rose RM (1984)[32]. Used HR neuron model, the action potential can be simulated. HR model can be used to study single neuron spiking characteristics as well as the basic unit of the large-scale network. HR neuron model is used as network nodes in our neural population model. The equations of HR neuron model are shown in (5), (6) and (7),

$$\frac{\mathrm{d}X}{\mathrm{d}t}=Y-aX^3+bX^2-Z+I_{\text{stim}}, \quad (5)$$

$$\frac{\mathrm{d}Y}{\mathrm{d}t}=c-\mathrm{d}X^2-Y, \quad (6)$$

$$\frac{\mathrm{d}Z}{\mathrm{d}t}=r(X-\frac{1}{4}(Z\text{-}g)), \quad (7)$$

where X is the membrane potential of neuron, Y represents the fast recovery currents, Z represents slow adaptive currents, I_{stim} is an external stimulus input currents, a, b, c, d, r and g are constant parameters. The values of these parameters are set according to [33]. In HR neuron model, the parameter r is related to the concentration of calcium ions. By adjusting the value of the parameter r, the neuron can be shown a different discharge mode.

The prefrontal cortex neurons are mainly divided into two categories: excitatory neurons and inhibitory neurons; The anatomical sampling of the neurons in the prefrontal cortex has shown that about 80% of the neurons are excitatory neurons and the rest 20% are inhibitory

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neurons[31]. Excitatory neurons are pyramidal cells in morphology. The firing characteristics of excitatory neurons are regular spiking (RS) neurons, which present rapid and evident firing frequency adaptation responding to a continuous depolarizing current injection. Inhibitory neurons are interneuron cells. The firing characteristics of excitatory neurons are fast spiking (FS) neurons, which respond to long depolarizing current stimulus with higher firing rate and less prominent spike frequency adaptation than RS neurons.

In our Spiking neuronal network simulation of prefrontal cortex, all HR neurons are coupled by functional connectivity. The equations of network model are shown as (8), (9), and (10):

$$\frac{\mathrm{d}X_i}{\mathrm{d}t} = Y_i - aX_i^3 + bX_i^2 - Z_i + I_{\mathrm{stim}} + w\sum_{j=1}^{N} A_{ij}X_j, \quad (8)$$

$$\frac{\mathrm{d}Y_i}{\mathrm{d}t} = c - \mathrm{d}X_i^2 - Y_i, \quad (9)$$

$$\frac{\mathrm{d}Z_i}{\mathrm{d}t} = r(X_i - \frac{1}{4}(Z_i - g)), \quad (10)$$

where the subscript i represents the neuron number, N is the number of neurons. In our simulation we use N equals to the neuron number in working memory experiment in rat prefrontal cortex. $w\sum_{j=1}^{N} A_{ij}X_j$ is the coupling term of the neural network model, where w is the coupling strength of connectivity from neuron j to neuron i. A_{ij} is an $N \times N$ martix, which represents the coupling matrix of the neurons when a connection exists between neurons i and j.

III. Results

A. Neural Ensemble Coding from Experimental Data

After using software of spike sorting (off-line sorter, Plexon, TX, USA) to separate single neuron data from 16-channel data, we obtain 34 neurons and corresponding spike trains. Neuronal population spatiotemporal activities in rat prefrontal cortex during the performance of working memory task *in vivo* are shown in Fig. 1.

In Fig. 1, effective period of 7 seconds is selected to represent the whole working memory process. The dynamic entropy coding method was applied to characterize activity of neural population response to the working memory event. We calculated the entropy values of population firing during working memory task. The neural firing entropy matrix is obtained in sliding window of 200 milliseconds with 50 milliseconds overlapping, representing the local entropy for each neuron. And neural ensemble entropy coding is shown in Fig. 2.

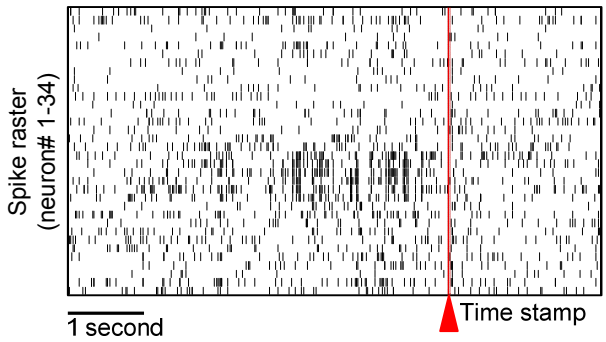

Figure 1. Neuronal population spatiotemporal activities in rat prefrontal cortex during a working memory task in vivo. The triangle "▲" indicates the time stamp.

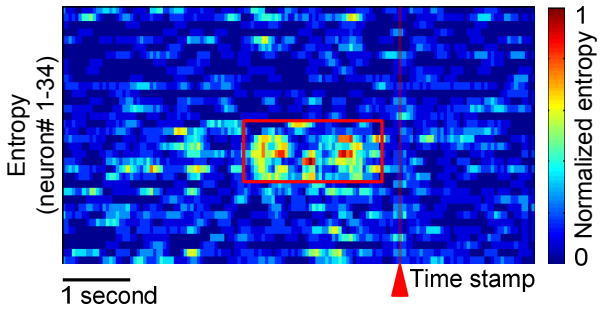

Figure 2. Neural ensemble entropy coding in rat prefrontal cortex during a working memory task in vivo. The triangle "▲" indicates the time stamp.

In Fig. 2, Normalization is achieved by dividing spike trains by the maximum entropy values over the time period. Simultaneous increase of firing rate and entropy demonstrate the occurrence of working memory event. Neuron 12, 13, 14, 15, 16, 17, 18 and 19 form a neural ensemble during the occurrence of working memory event. The triangle "▲" indicates the time stamp.

B. Functional Connectivity Network

The analyses of functional connectivity networks were carried out during the occurrence of working memory event (time interval [2.818s, 4.818s], before time stamp) and the period of resting state (time interval [5.000s, 7.000s], i.e. the period of 2s after time stamp). The method of cross-covariance between pairs of neurons has been used to determine directed connectivity edges. For 34 neurons, $N(N-1)/2$, or 561 pairs of neuron have been calculated. And at most there are 1122 cross-covariance peaks greater than zero. To determine the threshold of the connectivity, the peaks sorted by their values are shown in Fig. 3. If the threshold is too low, the result network is a fully connected graph. However, if the threshold is too high, the graph has several edges. Here, threshold was determined with the value when the mean degree $K \approx \ln(N)$ [34].

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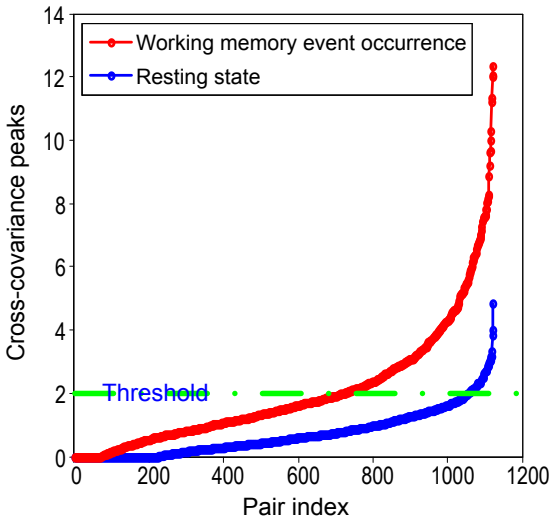

Figure 3. Cross-covariance peaks between neuronal pairs

In Fig. 3, the threshold=2.0 at the point where the increment of the curve changes notably. If the peak exceeds the threshold, a directed edge of functional connectivity network could be obtained from the reference neuron to the target neuron with the connectivity weight of peak value. Via the analysis of two time intervals (the occurrence of working memory event in the time interval before time stamp; period of resting state in the time interval after time stamp), two corresponding functional connectivity networks were obtained and their connectivity matrix are shown in Fig. 4 and Fig. 5, respectively.

In Fig. 4 and Fig. 5, each column of the matrix indicates whether there is a direct connection from the reference neuron to the target neurons, where the neuron number corresponds to the column number is a reference neuron. The nonzero elements of the matrix indicate that there is a functional connection from the reference to the target neuron and the color shows the strength of the connection. Comparing the Functional connectivity matrix of working memory event occurrence network (Fig. 4) with resting state network (Fig. 5), the number of edges of working memory event occurrence network is more than the number of the latter network. And the mean connectivity strength shows the same, as shown in Table 1.

TABLE 1
CONNECTION NUMBER AND MEAN CONNECTIVITY STRENGTH OF TWO NETWORKS

	Connection number	Mean connectivity strength
Working memory event occurrence network	402	3.93 ± 1.93
Resting state network	67	2.55 ± 0.51

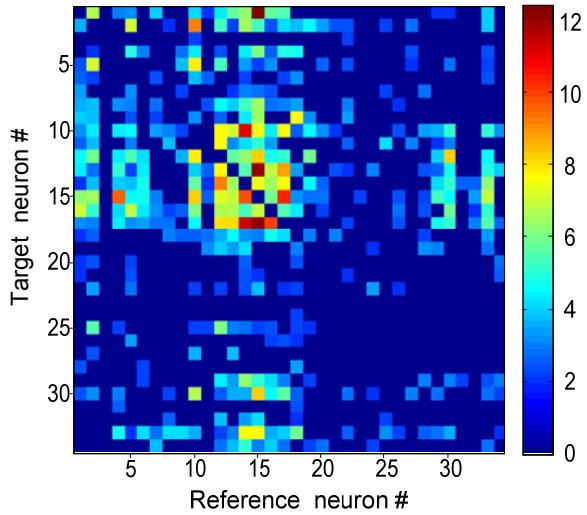

Figure 4. Functional connectivity matrix of neurons during the occurrence of working memory event in vivo (time interval [2.818s, 4.818s], before time stamp)

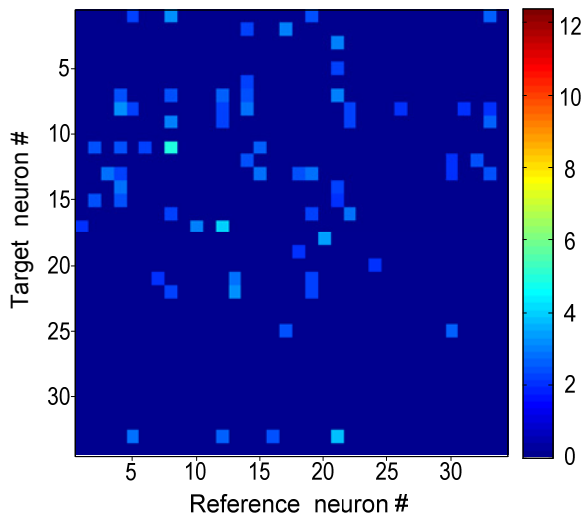

Figure 5. Functional connectivity matrix of neurons during the period of resting state in vivo (time interval [5.000s, 7.000s], i.e. the period of 2s after time stamp).

In working memory event occurrence network, the high strength and dense connection concentrates on several neurons (especially on neuron 12, 13, 14, 15, 16, 17, 18 and 19). And this phenomenon was not found in the latter network. It agrees with neural ensemble coding form experimental data that neuron 12, 13, 14, 15, 16, 17, 18 and 19 form a neural ensemble during the period of working memory event occurrence.

Fig. 6 and Fig. 7 show the topological graphs of working memory event occurrence network and resting state network, respectively. The color of the edges reflects the connection strength from the reference neurons to the target neurons, with magenta being largest and blue being smallest.

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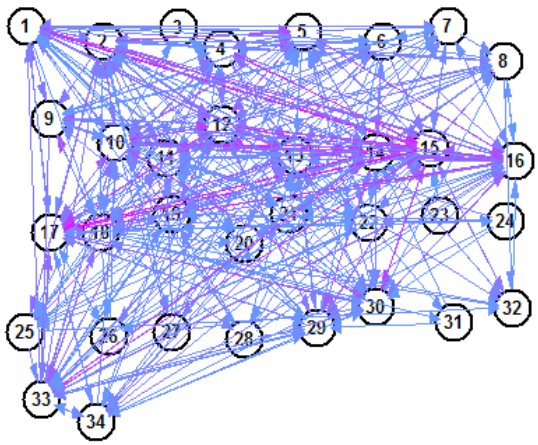

Figure 6. Connectivity graph of working memory event occurrence network in vivo (during time interval [2.818s, 4.818s], before time stamp)

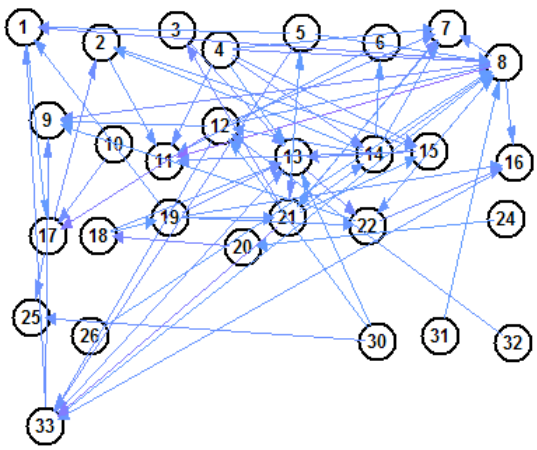

Figure 7. Connectivity graph of resting state network in vivo (during time interval [5.000s, 7.000s], i.e. the period of 2s after time stamp)

To compare characteristics of different networks, the *CC* and *CPL* were calculated. The *CPL* of the working memory event occurrence network is 1.678, and its equivalent random network is 1.657; the *CC* of the working memory event occurrence network is 0.604, and its equivalent random network is 0.356. The *CPL* of the resting state network is 3.045, and its equivalent random network is 3.683; the *CC* of the working memory event occurrence network is 0.098, and its equivalent random network is 0.066. The two networks satisfy the small-world network property as the clustering coefficients of them are larger than their corresponding random networks and their characteristic path lengths are approximately equal to their corresponding random networks.

C. *Results of Simulation*

The neuronal spiking networks of working memory event occurrence and resting state were simulated. Our simulation model is composed of 34 neurons, of which the simulation time is 2000 milliseconds, respectively. In our Spiking neuronal network simulation of prefrontal cortex, all HR neurons are coupled by two functional connectivity networks as showing in Fig. 4 and Fig. 5. The Spike raster of neuronal network model simulation of working memory event occurrence and resting state are shown in Fig. 8 (a)(b), respectively. And we calculate neural ensemble entropy coding of the two simulation results as shown in Fig. 9 (a) (b), respectively. In Fig. 9 (a)(b), normalization is achieved by dividing by the maximum entropy values from spike trains over the time period.

In Fig. 8(a) and Fig. 9(a), Several neurons increases simultaneously in firing rate and increases in Entropy, and Neuron 10, 12, 13, 14, 15, 16 and 17 form a neural ensemble during the simulation of working memory event occurrence. In Fig. 8(b) and Fig. 9(b), there is no neural ensemble formed. The simulation results are agreed with experiment data in rat prefrontal cortex during a working memory task *in vivo*.

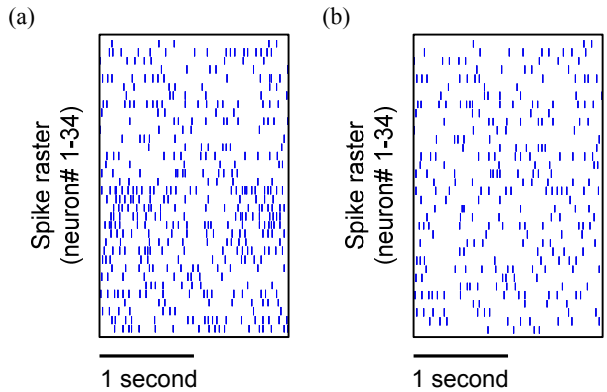

Figure 8. Spike raster of neuronal network model simulation. (a) Neuronal network model of neurons spiking of working memory event occurrence. (b) Neuronal network model of neurons spiking of resting state.

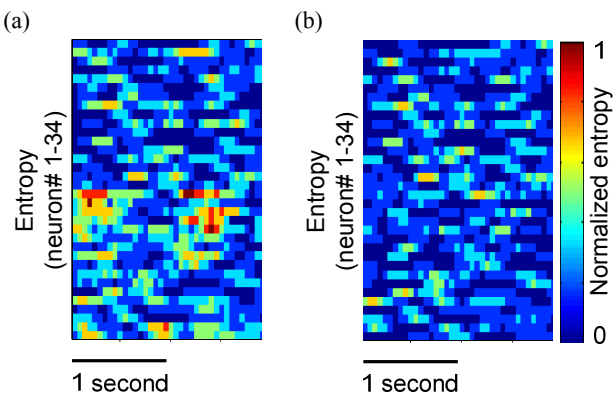

Figure 9. Neural ensemble entropy coding of neuronal network model simulation. (a) Neural ensemble entropy coding of neurons spiking of working memory event occurrence simulation. (b) Neural ensemble entropy coding of resting state simulation.

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IV. CONCLUSIONS

In the present paper, functional connectivity networks on prefrontal cortex of rat during working memory task *in vivo* are analyzed. Neural ensemble entropy coding is applied to find the time interval of working memory event occurrence. The neural firing entropy matrix is obtained in sliding window of 200 milliseconds with 50 milliseconds overlapping, representing the local entropy for each neuron. Simultaneous increase of firing rate and entropy demonstrate the occurrence of working memory event (time interval [2.818s, 4.818s]). Neuron 12, 13, 14, 15, 16, 17, 18 and 19 form a neural ensemble during the occurrence of working memory event. The analysis of functional connectivity networks carried out though the method of cross-covariance The analyses of functional connectivity networks were carried out during the occurrence of working memory event (time interval [2.818s, 4.818s], before time stamp) and the period of resting state (time interval [5.000s, 7.000s], i.e. the period of 2s after time stamp). The complex network topology parameters are calculated. The number of edges of working memory event occurrence network is more than the number of the latter network. And the mean connectivity strength shows the same. In working memory event occurrence network, the high strength and dense connection concentrates on several neurons (especially on neuron 12, 13, 14, 15, 16, 17, 18 and 19). And this phenomenon was not found in the latter network. It agrees with neural ensemble coding form experimental data that neuron 12, 13, 14, 15, 16, 17, 18 and 19 form a neural ensemble during the period of working memory event occurrence. The two networks satisfy the small-world network property as the clustering coefficients of them are larger than their corresponding random networks and their characteristic path lengths are approximately equal to their corresponding random networks. Finally, the simulations of spiking neuronal network of working memory event occurrence and resting state are presented. Hindmarsh-Rose (HR) neuron model is chosen as single neuron that connected by functional network of working memory event occurrence and resting state, receptivity. The two simulation models are composed of 34 neurons, of which the simulation time is 2000 milliseconds, respectively. Several neurons increases simultaneously in firing rate and increases in Entropy, and Neuron 10, 12, 13, 14, 15, 16 and 17 form a neural ensemble during the simulation of working memory event occurrence. There is no neural ensemble formed during the simulation of resting state. The simulation results are agreed with experiment data in rat prefrontal cortex during a working memory task.

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