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LOW-DIMENSIONAL STRUCTURES: SPARSE CODING FOR NEURONAL ACTIVITY

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Neuronal ensemble activity codes working memory. In this work, we developed a neuronal ensemble sparse coding method, which can effectively reduce the dimension of the neuronal activity and express neural coding. Multichannel spike trains were recorded in rat prefrontal cortex during a work memory task in Y-maze. As discrete signals, spikes were transferred into continuous signals by estimating entropy. Then the normalized continuous signals were decomposed via non-negative sparse method. The non-negative components were extracted to reconstruct a low-dimensional ensemble, while none of the feature components were missed. The results showed that, for well-trained rats, neuronal ensemble activities in the prefrontal cortex changed dynamically during the working memory task. And the neuronal ensemble is more explicit via using non-negative sparse coding. Our results indicate that the neuronal ensemble sparse coding method can effectively reduce the dimension of neuronal activity and it is a useful tool to express neural coding.

Keywords: Low-dimensional structures; sparse coding; neuronal ensemble activity; working memory; rat.

1. Introduction

Working memory refers to a brain system that provides temporary storage and manipulation of the information which is necessary for complex cognitive tasks.[1] Many studies have demonstrated that neuronal ensemble is the fundamental structure in the brain through which we represent concepts, store and recall information, and form associations between concepts. Neuronal ensemble activity codes the working memory.[2,3] Physiological studies have found that the neuronal activity in the prefrontal cortex (PFC) changes during new task learning, which suggest that working memory is mediated by continuous neuronal ensemble activities of PFC neurons.[4–9] Understanding the neural coding in the working memory is important for grasping the fundamental computations underlying brain function and interpreting signals.

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In the study of neural coding, researchers have faced huge challenges in the aspect of data analysis. Due to the rapid development of the multi-channel synchronous recording technique, vast data of neuronal population activity from various electrophysiological experiments can be obtained. Since high-dimensional data are frequently obtained, it is difficult to extract useful information from huge data at a reasonable computational expense. It brings us to a critical problem — dimension reduction. Therefore, we have to convert the high-dimensional input dataset into low-dimensional data. Here, we introduce a concept of sparse coding.

The important property of neural coding is that a relatively small number of neurons out of a large population are strongly active at any time. This refers to "sparse coding".[10–12] Sparse coding is a favorable compromise between dense coding and local coding. Several studies have applied the sparse coding algorithm to analyze physiological signals and yielded many promising results.[11,13,14] Sparse coding overcomes the limitation of independent component coding and principal components analysis, allowing the mixing matrix to be overcompleted.[15] Sparse coding can reduce the dimension of neuronal population activity and make the description of neuronal ensemble coding more effective with low dimension.

In addition, many theories, such as rate coding, time coding, and nonlinear coding[16] have laid a foundation for the further studies on neuronal activities. Entropy is a measurement of uncertainty and the amount of information,[17,18] which can quantify information as well as describe the characteristics of neuronal activity. Moreover, the nonlinear entropy can avoid the shortcomings of the traditional linear coding methods and show the differences between two spike trains which have the same firing rates but different temporal structures.

Therefore, in this work, we developed a neuronal ensemble sparse coding method, in which continuous process for neuronal firing was performed by the estimation of the neuronal firing entropy. The neuronal ensemble sparse coding method can effectively reduce the dimension of neuronal activity and it is a useful tool to express neural coding.

2. Materials and Methods

2.1. *Experiments*

Five male Sprague-Dawley rats weighting 300−350 g participated in the experiment. After habituatation and two-day food restriction, the rats received training sessions in a Y-maze task until the rats' performances reached a steady correct rate of 80%. The Y-maze working memory task included a free choice and a delayed alternation. Then a synchronous 16-channel microelectrode array was implanted in rat PFC. Multichannel spike trains were recorded while the rats were performing the working memory task. The behavioral events were marked via an infrared sensor in the Y-maze.

2.2. *Linear mixture model for neuronal signals*

It is assumed that neuronal signals are linear mixture of source components such as brain sources, artifacts, etc. Then we have the following linear model:

$$X = AS, \tag{1}$$

where $X = [x(1), \ldots, x(n)]$ is a known neuronal activity matrix; n is the number of windows; $A = [a_1, \ldots, a_r]$ is an $n \times r$ unknown mixing constant matrix; and $S = [s(1), \ldots, s(n)]$ is an unknown source components matrix in which the rows represent brain sources. We can assume that the number of components is larger than the number of neurons.

As is well-documented, the ICA approach is often used to determine the mixing matrix and source components; however, the ICA algorithms are based on the assumption that all of the source components are mutually independent. In fact, it is not reasonable to assume that all of the brain sources are mutually independent. Therefore, the ICA approach is not ideal in determining the mixing matrix and brain sources.[13] In this paper, a sparse factorization approach is used for the determination of the mixing matrix and source components.

2.3. *Neuronal ensemble sparse coding*

2.3.1. *Continuous process for neuronal firing*

Since the neuronal activity is discrete, the method to convert neuronal activity into continuous input data is one of the key points for sparse coding. In this paper, point potential is quantified based on neuronal firing entropy in selected windows.[17] Entropy estimation of spike train for one neuron is described as the follows:

(1) Measure the neuronal firing ISI sequence and estimate ISI histogram;

(2) According to the characteristics of the neuronal firing sequence, set an appropriate bin and separate the ISI histogram using defined bin length, and then count the number of spikes z_i in each bin $i(i = 1, 2, \ldots, n)$;
(3) Compute the firing probability p_i of ith bin based on Eq. (2):

$$p_i = z_i \Big/ \sum_{i=1}^{n} z_i. \tag{2}$$

(4) From Eq. (3) calculate the entropy X of the firing sequence.

$$X = -\sum_{i=1}^{n} p_i \log p_i. \tag{3}$$

In this paper, the base of logarithm is 2 and the unit of entropy X is bit.

The entropy estimation method can be used to describe the nonlinearity of the neuronal population activity. The steps are summarized as follows:

(1) Select a window (window width = 200 ms; moving step = 50 ms) and calculate entropy for every neuron k ($k = 1, 2, \ldots, m$) in each window;
(2) Normalize neuronal firing entropy values during the whole session.
(3) The normalized entropy values matrix is used as the input data of NNSC.

2.3.2. *NNSC of neuronal population firing entropy matrix*

The source matrix S and mixing matrix A are unknown. The system takes the entropy matrix X as an input. The estimation of sources and mixing matrix is based on minimization of cost function, which minimizes the reconstruction error while preserves the sparseness and linear mixture assumptions. The cost function is given by:

$$C(A, S) = \frac{1}{2}\|X - AS\|^2 + \lambda \sum_{ij} S_{ij}. \tag{4}$$

It is assumed that the sources are inactive most of the time. In the model, this means that the elements of S have a high probability of being zero. The tradeoff between the sparsity of the decomposition and accurate reconstruction is controlled by the parameter λ. The objective is to find A and S which minimize the cost function of Eq. (4), with the following restrictions:

$$\forall\, ij : X_{ij} \geq 0, \quad S_{ij} \geq 0, \quad A_{ij} \geq 0,$$
$$\forall\, i : \|a_i\| = 1, \quad \lambda \geq 0,$$

where a_i denotes the ith column vector of A.

In optimization, a combination of multiplicative step and projected gradient descent is deemed to be the most efficient. The algorithm is the same to the one proposed by Hoyer.[19]

2.3.3. *Low-dimensional reconstruction via feature sparse components*

The sparse components were estimated from the matrix S and the feature components were extracted to reconstruct neuronal activity mapping with low dimension. The components, of which the coefficients increase suddenly during the time according to the firing rate histogram and sparse coding, are extracted as feature components or meaningful sources. The neuronal population firing dynamic spatio-temporal mapping is obtained by an inverse of sparsifying transform of sparse feature components.

2.4. *Important issues in neuronal ensemble sparse coding*

The number of desired sources r has to be set manually. So far, there is no ideal way for the reliable estimation of the number of sources. Assuming that the number of the sources is greater than the number of the neurons, if there is one zero component in source component matrix, the number of sources is named threshold. With the number of the source being greater than the threshold, there would be more zero components.

In the NNSC framework, the proposed non-negative constraints are important for learning parts-based representations from non-negative data. In addition, the constraints make source estimation more efficient. Therefore, it is expected that NNSC may find local structures of neuronal firing activity.

3. Results

In NNSC, the parameter λ was set to 0.2, which ensures the balance of the sparseness of the decomposition with the accuracy of the data reconstruction.[19]

(1) The neuronal population spike trains in rat PFC during working memory task is shown in Fig. 1(a). The spatio-temporal mapping of neuronal firing entropy is shown in Fig. 1(b). The neuronal firing entropy matrix is obtained from sliding window of 200 ms with 50 ms overlapping.
(2) The neuronal population firing entropy matrix is decomposed into a mixing matrix and 34 sparse components by NNSC. In Fig. 1(b), we can see that each row contains many zero entries in the firing entropy matrix. Since most neurons do not fire continuously in every 200-ms window during the entire training set, the neuronal data are sparse. This implies that source components should also be much sparser than the inputs. Over the entire 7 s, the nonzero components (active components) are, on an average, exactly zero in most (90%) of the time. Histograms of some individual components are shown in Fig. 2. Most of the histograms are somewhat bimodal, suggesting an underlying binary process, namely, the presence or absence of a neuron.
(3) The feature sparse components are selected according to the histogram of neuronal firing rate in Fig. 3(a) and neuronal ensemble sparse coding in Fig. 3(b). We can see that the entropy values before time stamp are obviously higher than those after the time stamp. In addition, several neurons formed a neuronal ensemble before time stamp. Here, six components, whose coefficients increased dramatically before time stamp, were selected as feature components (Fig. 4).

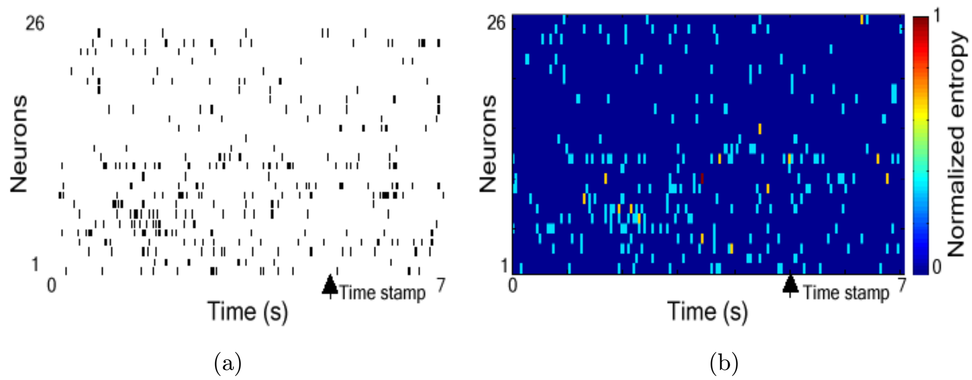


Fig. 1. Neuronal population activity: (a) Spatio-temporal spike trains. (b) Mapping of the neuronal population firing entropy. The tripping time by infrared in Y-maze is indicated by an arrow.

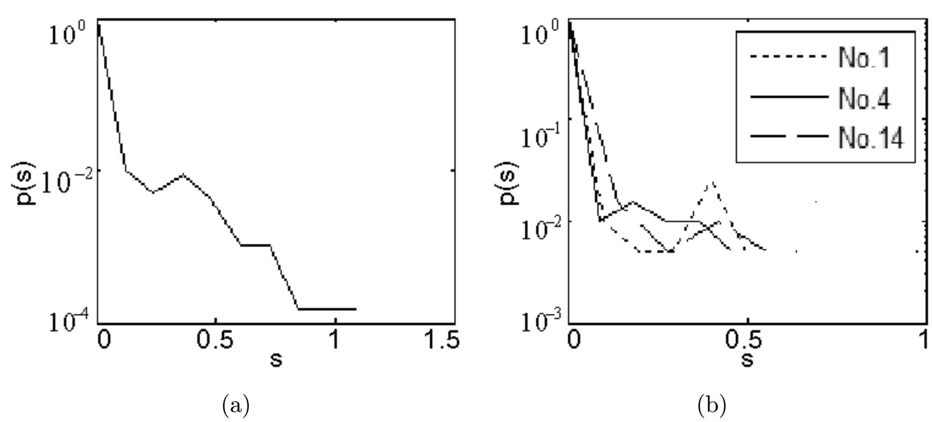
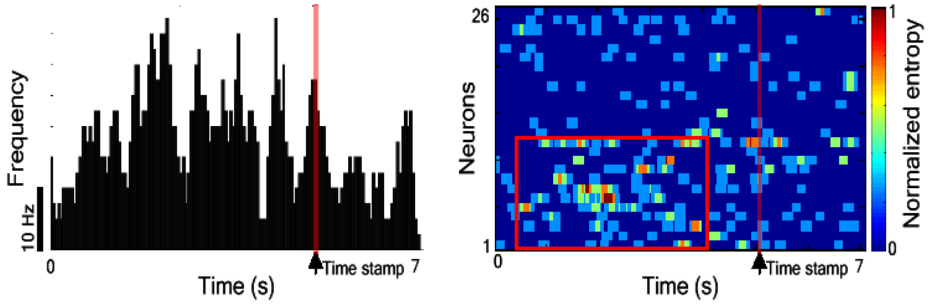


Fig. 2. A total of 34 sparse components obtained from the neuronal database, showing both high sparsity and bimodality. (a) Histogram of the activity of the source component matrix. (b) Histograms of the activities of three components.



(a) (b)

Fig. 3. Neuronal ensemble entropy coding during the working memory task. (a) Histogram of neuronal population firing. (b) Neuronal ensemble entropy coding.

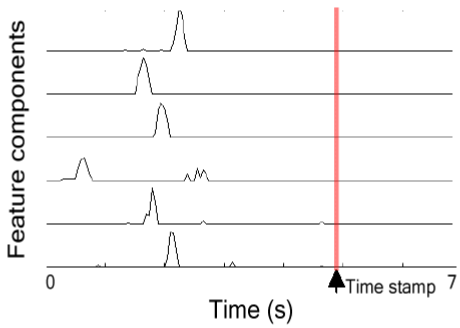
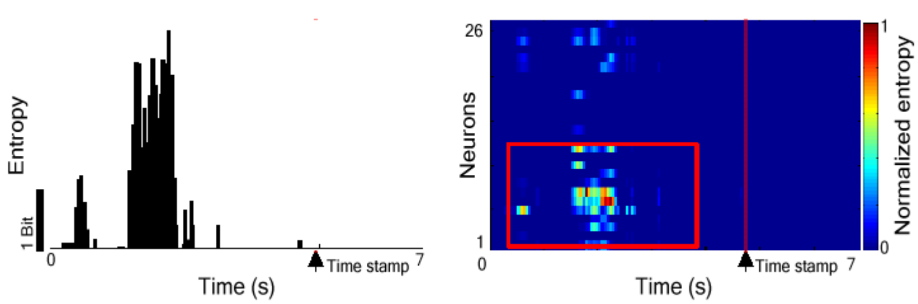


Fig. 4. Feature sparse components of the neuronal activity in rat PFC during the working memory task.

(4) The feature components were used to reconstruct the raw data by an inverse of the sparsifying transform. The histogram of reconstructed neuronal population firing entropy and the neuronal ensemble sparse coding are shown in Figs. 5(a) and 5(b), respectively. The entropy values of a few neurons change greatly around the time stamp, and these neurons forms a neuronal ensemble before the behavior response.

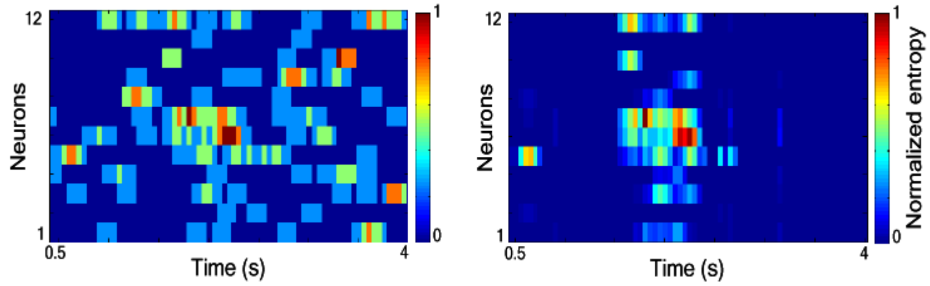
(5) From the results of the neuronal ensemble sparse coding, we can see that neuronal population firing pattern had a great change during the working memory. Besides, both the methods express the neuronal ensemble coding of working memory. Sparse coding made the neuronal ensemble more explicit by picking out feature components and reducing the redundancy. For the convenience of comparison, we enlarge the mapping in red rectangles in Figs. 3(b) and 5(b), shown in Fig. 6. Using entropy coding, the neuronal ensemble composed of the 1st, 3rd, 5th, 6th, 7th, 8th, 9th, 10th and 12th neurons. The ensemble lasts 3.5 s from 0.5 s to 4 s. In the result of sparse coding, the 5th, 6th and 7th neurons form a neuronal ensemble, which lasts 1 s from 1.5 s to 2.5 s.

In order to show the efficiency of neuronal ensemble sparse coding more clearly, 10 trials with chronic



(a) (b)

Fig. 5. Neuronal ensemble sparse coding during the working memory task. (a) Histogram of sparse reconstructed neuronal population firing entropy. (b) Neuronal ensemble sparse coding.



(a)

(b)

Fig. 6. Neuronal ensemble entropy coding and sparse coding during the working memory task. (a) Entropy coding. (b) Sparse coding.

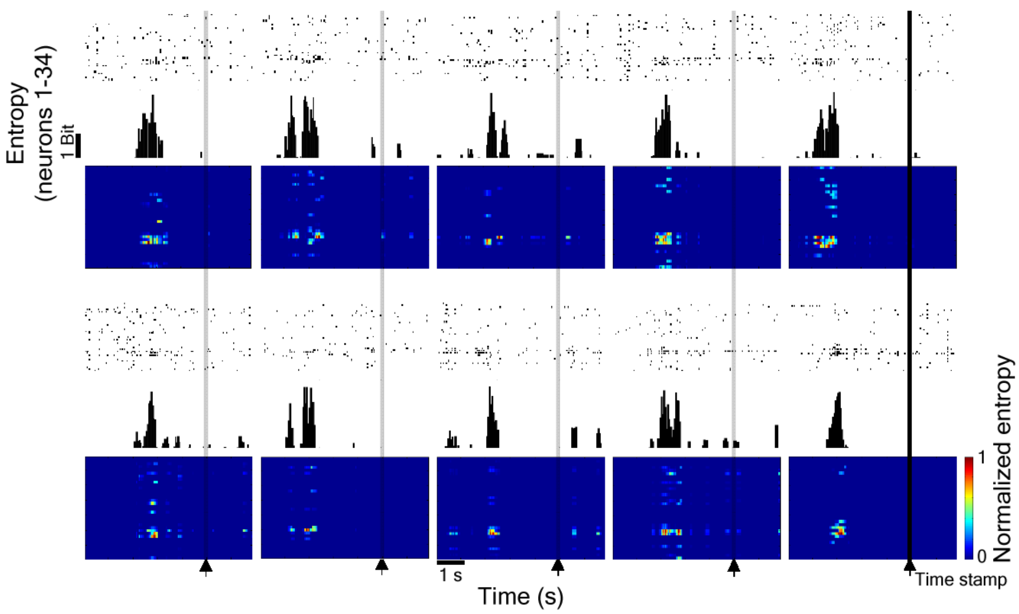


Fig. 7. Neuronal ensemble sparse coding during working memory task. The tripping time by infrared in Y-maze is indicated by an arrow. The rasters indicate the timestamps of spikes. Histogram of sparse reconstructed neuronal population firing entropy. Dynamic mappings present results of neuronal ensemble sparse coding. Ten trials have been shown and each column represents one trial.

recording were analyzed. The results of neuronal ensemble sparse coding and entropy coding in rat PFC during the working memory task are shown in Figs. 7 and 8, respectively. As can be seen in Fig. 7, three neurons in the population changed their firing patterns greatly during the working memory task and formed a relatively stable neuronal ensemble. The neuronal ensemble was composed of the 9th, 10th and 11th neurons. In time terms, the neuronal ensemble defined via sparse coding lasted shorter ($0.8478 \pm 0.2896\,\mathrm{s}$) than that of entropy coding ($2.9780 \pm 1.0031\,\mathrm{s}$), and t-tests showed remarkably difference ($p < 0.01$).

If one neuron in the neuronal population shows different activity in six or more trials, the neuron is considered to be a member of the neuronal ensemble which encodes the working memory. The numbers of ensemble neurons in the 10 trials are shown in Table 1. It is clear that the neuronal ensemble is composed of the 9th, 10th and 11th neurons. However, the number of the neural ensemble is not stable in 10 trials via neuronal ensemble entropy coding.

For well-trained rats, neuronal ensemble activities in the PFC changes dynamically during the working memory task. The neuronal ensemble is

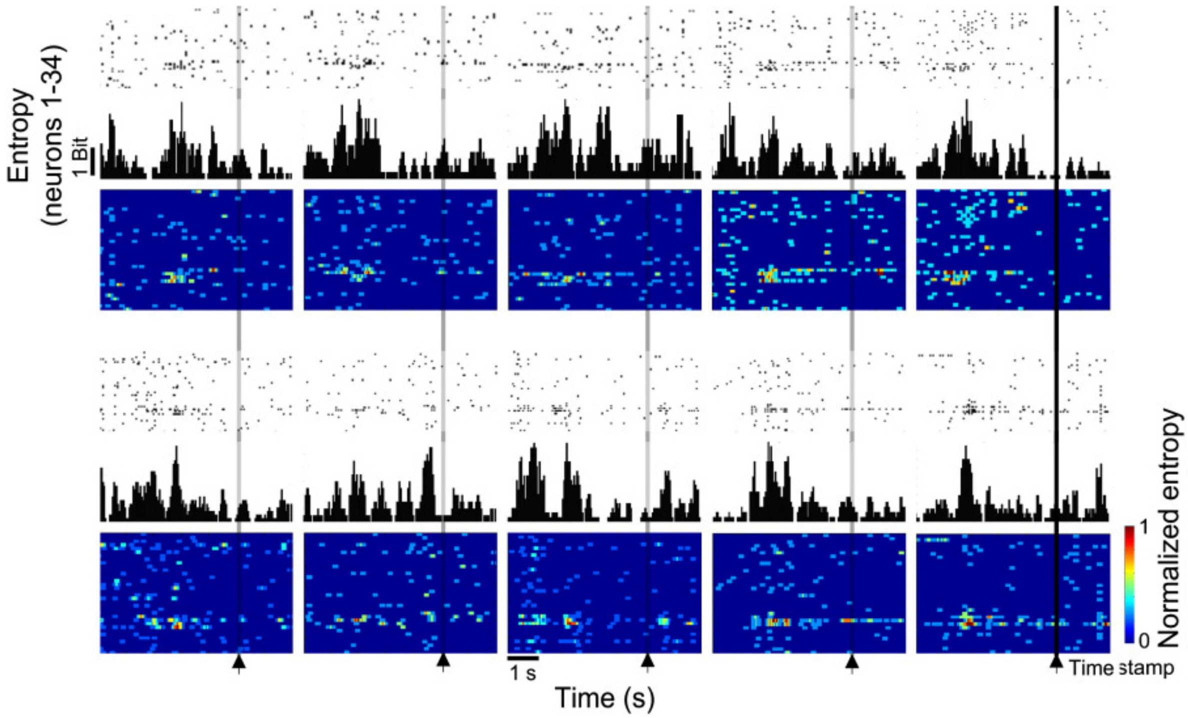


Fig. 8. Neural ensemble entropy coding during the working memory task. The tripping time by infrared in Y-maze is indicated by an arrow. The rasters indicate the time stamps of spikes. The histograms show firing entropy for neurons recorded simultaneously during the working memory task. Dynamic mappings present results of neural ensemble entropy coding. Ten trials have been shown and each column represents one trial.

Table 1. Ensemble neurons identified by sparse coding and entropy coding.

Trails	Sparse coding	Entropy coding
1	9, 10, 11	8, 9, 10, 12, 34
2	9, 10, 11	9, 10, 11, 12
3	9, 10, 11	9, 10, 11
4	9, 10, 11, 12	9, 10, 11, 12
5	8, 9, 11	8, 9, 11, 18, 29, 31
6	8, 9, 10	8, 9, 11
7	10, 11	9, 10, 11
8	9, 10	9, 10
9	9, 10	9, 10
10	9, 10, 11	9, 10, 11

more explicit both in time and space via using non-negative sparse coding.

4. Discussions

Sparse coding is a novel and relatively new tool for analyzing the non-negative data structure. The results presented in this paper indicate that the neuronal ensemble sparse coding can reconstruct neuronal activity mapping with low dimension and make the description of neural coding more effective with low dimension, both in temporal and spatial terms.

Sparse coding is a useful tool for analyzing neuronal data to reveal the neuronal activity patterns. However, there is still an issue when using NNSC for neuronal data analysis. The methodology detects patterns of activity, but the feature components have to be selected by hand. The results obtained in our investigation suggest that some issues have to be studied further, including the automatic selection of the feature components and application of sparse coding in different areas of neuronal activity analysis.

4.1. *Parameters*

Sparse coding allows the mixing matrix to be overcompleted, meaning that a greater number of the sources than the dimension are in the input signal. But there is no straightforward way for the

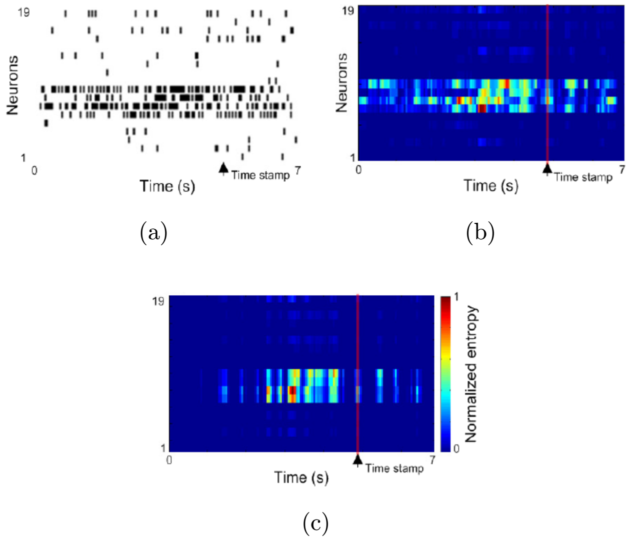


Fig. 9. Neuronal ensemble sparse coding when using different λ. (a) Spike trains. (b) Neuronal ensemble sparse coding. $\lambda = 0.2$. (c) Neuronal ensemble sparse coding. $\lambda = 0.5$.

estimation of the number of sources now. So the number of the sources has to be set by hand. Here, the threshold was obtained for a neuronal dataset and then the maximum of the thresholds for 10 neuronal datasets for one rat was obtained. The number was set as the dimension of the sources. Much work needs to be done in order to obtain the number. This will be further studied in the future work.

The choice of the parameter λ needs to be investigated. We found that, for a 20-element dictionary, the performance decreases if $\lambda > 0.3$. In this paper, λ was set to 0.2. Here, we took one trial as an example. Keeping the same number of sources, the results of neuronal ensemble sparse coding were shown when λ was 0.2 and 0.5, respectively. In Fig. 9(c), larger λ values generated bad reconstruction of all sparse components. The result in Fig. 9(c) lost much information, which may be crucial for working memory.

4.2. *Initializing the mixing matrix*

The mixing matrix needs to be initialized before sparse coding. Here, the non-negative mixing matrix is selected randomly and each column is normalized. In fact, initializing the mixing matrix influences the results of sparse coding to a certain extent. Therefore, it is essential to choose proper basis that is able to express the neuronal firing characteristic. But now we have not found the proper basis as columns of the mixing matrix.

Acknowledgments

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