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Effects of Spike Frequency Adaptation on Synchronization Transitions in Electrically Coupled Neuronal Networks with Scale-Free Connectivity

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Effects of spike frequency adaptation (SFA) on the synchronous behavior of population neurons are investigated in electrically coupled networks with a scale-free property. By a computational approach, we corroborate that pairwise correlations between neurons would decrease if neurons exhibit the feature of SFA, which is similar to previous experimental observations. However, unlike the case of pairwise correlations, population activities of neurons show a rather complex variation mode: compared with those of non-adapted neurons, neurons in the networks having weak-degrees of SFA will impair population synchronizations; while neurons exhibiting strong-degrees of SFA will enhance population synchronizations. Moreover, a variation of coupling strength between neurons will not alter this phenomenon significantly, unless the coupling strength is too weak. Our results suggest that synchronous activity of electrically coupled population neurons is adaptation-dependent, and this adaptive feature may imply some coding strategies of neuronal populations.

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In biological neuronal systems, the transmission and processing of neural information have long been considered to be realized by the population activity of neuronal ensembles, rather than the activities of single neurons. During the past few decades, synchronous activities of neurons have been subjected to intensive research owing to their significant effects in some functions of the brain.\(^1\)\(^-\)\(^3\) To investigate how intrinsic and extrinsic factors would affect the population rhythms of neurons, a great number of computational network models have been constructed, and the size of the networks ranges from minimal circuits of two neurons\(^4\)\(^-\)\(^8\) to large networks each including tens to thousands of neurons\(^9\)\(^-\)\(^13\).

Scale-free properties in networks have been found in a wide variety of systems, e.g., the world wide web,\(^14\) the metabolism,\(^15\) and gene regulation.\(^16\) As revealed by functional magnetic resonance imaging (fMRI), several experimental studies have indicated that neuronal activities in some brain areas generally demonstrate the scale-free properties.\(^17\)\(^,\)\(^18\) In scale-free networks, the number of connections \(k\) per vertex satisfies a power-law probability distribution, \(P(k) \sim k^{-\gamma}\) \((\gamma\) is a positive number), especially, new vertices that add to the networks preferentially connect with the vertices that are already well connected.\(^19\) This peculiar structure of neuronal connections exhibited by scale-free networks has attracted much attention, and plenty of interesting and meaningful phenomena have been reported.\(^20\)\(^-\)\(^23\)

Previous studies have suggested that the feature of spike frequency adaptation (SFA) in neurons exerts significant influence on modulating population neuron behaviors.\(^24\)\(^,\)\(^25\) However, these studies were mostly concentrated on chemically coupled neurons, how the apply to the case for electrically coupled neurons is not completely clear yet. A recent experimental study demonstrated that for electrically coupled neurons, SFA could dramatically reduce the pairwise correlation strengths between neurons.\(^26\) In this Letter, we further analyze whether SFA exhibited by single neurons would influence the synchronous behavior of population neurons. Model results indicate that population activities of neurons are adaptation-dependent, and this variation trend is robust to coupling strength, unless the coupling strength is too weak.

The Izhikevich model was employed in this study to depict the feature of SFA in neurons. Although it is a simplified model, it can successfully reproduce many different types of neuronal firing patterns as observed in electrophysiological experiments, such as tonic spiking, tonic bursting, subthreshold oscillations, rebound firings, and SFA.\(^27\) Mathematical descriptions of the model consist of two ordinary equations, which are expressed as

\[
\frac{dv_i(t)}{dt} = 0.04v_i(t)^2 + 5v_i(t) + 140 - u_i(t) + I_i + G \sum_j c_{ij}[v_j(t) - v_i(t)], \quad (1)
\]

\[
\frac{du_i(t)}{dt} = a(bv_i(t) - u_i(t)), \quad (2)
\]

with the ancillary after-spike resetting.

If \(v_i(t) \geq 30\) mV, then \(v_i(t) \leftarrow c\)
and \(u_i(t) \leftarrow u_i(t) + d, \quad (3)\)

where \(v_i\) is the membrane potential of the \(i\)th neuron, \(u_i\) is the membrane potential of the \(j\)th neuron, \(u_i\)
represents a membrane recovery variable which provides negative feedback to \( v_i \); \( c \) represents the resting membrane potential of the neuron, and the parameters \( a, b \) and \( d \) are dimensionless. When the potential value \( v_i \) reaches its vertex (30 mV), \( v_i \) and \( u_i \) would be reset according to Eq. (3). Here \( I_i = I_0 + R \) denotes the stimulus current applied to the \( i \)th neuron, which includes two parts: a constant input \( I_0 \), and a stochastic term \( R \). The term \( R \) is a random number between 0–0.5. For different neurons, the value of \( R \) is different.

In constructing the scale-free networks, we used the method proposed by Barabási \textit{et al.}\textsuperscript{[19]} The preferential connection is employed through the probability \( P(k_i) = k_i / \sum_{j}^{N} k_j \), which can determine whether a new neuron will connect to neuron \( i \), where \( k_i \) is the degree of neuron \( i \) (the number of neurons that neuron \( i \) connects with). \( N \) is the total neuron number in the network, and the mean degree for each neuron in the constructed network is \( \bar{k} = \sum_{i}^{N} k_i / N \). In our networks, the mean degree is 4, and the total neuron number is 200. In Eq. (1), \( \varepsilon_{ij} = 1 \) if neuron \( i \) is coupled with neuron \( j \), otherwise \( \varepsilon_{ij} = 0 \). Here \( G \) is the coupling strength between neurons.

Initial parameters for the model neurons were \( b = 0.2, c = -65 \text{ mV}, d = 0.3, \sigma = -70 \text{ mV}, u(0) = -14, I_0 = 4.5 \). As suggested in Ref.\textsuperscript{[30]}, SFA in the Izhikevich model can be induced by adjusting the parameter \( a \). In this study, the term \( \sigma = - \log_2 a \) was used as a control parameter for simulating the feature of SFA in neurons. It is noteworthy that the role of parameter \( a \) on slow variable \( u \) is similar to the conductance of slow currents in HH-type neuron models; the SFA phenomenon can be observed in the HH-type model by changing the conductance of slow currents.\textsuperscript{[24-25]}

In describing the degree of adaptation (DA) under different values of \( e \), we used an index adopted from Ref.\textsuperscript{[28]}

\[
\text{DA} = \frac{f_{\text{init}} - f_{\text{steady}}}{f_{\text{init}}},
\]

where \( f_{\text{init}} \) is the initial value of the firing rate, and \( f_{\text{steady}} \) is the value when the neuronal firing rate reaches its steady state (corresponding to the mean of the last five instant frequencies). Larger values of DA represent stronger degrees of adaptation in the neurons.

In measuring the pairwise correlation between coupled neurons, the classical cross-correlation function was employed, whose definition is as follows:

\[
\delta_{xy}(m) = \begin{cases} 
\frac{1}{N} \sum_{i=0}^{N-|m|-1} x_i y_{i+m}, & m \geq 0, \\
\frac{1}{N} \sum_{i=0}^{N-|m|-1} x_i y_{i+m}, & m < 0,
\end{cases}
\]

\[
Z = \sqrt{\sum_{i=1}^{N} x_i^2 \sum_{i=1}^{N} y_i^2},
\]

where \( x_i \) denotes the value of sequence \( x \) at moment \( n \); \( y_{n+m} \) denotes the value of sequence \( y \) at moment \( n + m \); consequently, \( \delta_{xy}(m) \) is the cross-correlation strength between sequences \( x \) and \( y \) with a time lag of \( m \); \( Z \) is the normalized factor. Following the previous study,\textsuperscript{[26]} the peak value in the cross-correlogram is thus defined as the correlation index between spike sequences \( x \) and \( y \). For one neuron in the networks, its cross-correlation index is defined as the average strength over all connected pairs that this neuron participates in.

While in characterizing the synchronization strength of population neurons, another index was introduced,\textsuperscript{[29]}

\[
\sigma = \sqrt{\frac{1}{T} \sum_{n=1}^{T} \sigma(n)},
\]

\[
\sigma(n) = \frac{1}{N} \sum_{i=1}^{N} [x_i(n)]^2 - \left[ \frac{1}{N} \sum_{i=1}^{N} x_i(n) \right]^2,
\]

where \( x_i(n) \) is the binned spike sequence of neuron \( i \), the bin width is 10 ms, and \( T \) is the length of binned neuronal spike sequences. Hence, if neurons in the network are in the state of complete synchronization, \( \sigma = 0 \). The larger the values of \( \sigma \), the less the degree of population synchronization will be.

![Fig. 1. Spiking activity of a single neuron and the variation of DA under different values of \( e \). (a) Membrane potential, from top to bottom, the values of \( e \) are 2, 4, 4.5, 5, 8.5, and 9, respectively; (b) the degree of adaptation \( DA \) versus \( e \).](image)

The SFA property of a single neuron is demonstrated in Fig. 1. No SFA phenomenon is observed when \( e = 2 \); while a weak-degree of adaptation appears when \( e \) increases to 4; and the degree of adaptation gets relatively stronger when \( e \) reaches 8.5. Meanwhile, Fig. 1(b) provides a more intuitionistic relation-
ship between the index DA and parameter $e$, indicating that larger values of $e$ correspond to stronger degrees of SFA, until the index DA approximates to 1.

![Fig. 2. Raster plot of the 200 model neurons under different degrees of adaptation when $G = 0.08$. From top to bottom, the values of $e$ are 2, 4 and 8.5, respectively.](image1)

![Fig. 3. Cross-correlation indices of the 200 model neurons in the presence and absence of SFA when $G = 0.08$. (a) Three examples of cross-correlograms under different degrees of adaptation, $e = 2$ (the first row), $e = 4$ (the second row), and $e = 8.5$ (the third row). (b) Scatter plot presenting the cross-correlation indices of neurons, black points denote weak adaptation ($e = 4$), while hollow circles represent strong adaptation ($e = 8.5$).](image2)

As demonstrated in the first row of Fig. 2, the 200 neurons activate in a state of nearly complete synchronization, when neurons in the network exhibit no SFA. However, when the model neurons have a weak-degree of SFA, the population activity enters into a relative tanglesome state. The result in the second row of Fig. 2 shows that population activity of the neuronal ensembles seems rather asynchronous compared with that in the first row of Fig. 2. Nevertheless, when neurons possess a strong degree of SFA, the population activity turns back into a more synchronous state again (the bottom row in Fig. 2). Although stronger adaptation of neurons could lead the population activity back into a synchronous state, the pattern is very different. In the case of no SFA, the population synchronization pattern manifests as spiking synchronization, while in the case of high-degree SFA, the pattern of population synchronization behaves as bursting synchronization.

Next, the cross-correlation indices for the 200 neurons in the presence and absence of SFA were calculated. Figure 3(a) presents three examples of cross-correlogram between connected neurons when the value of $e$ is 2 (no adaptation), 4 (weak adaptation), and 8.5 (strong adaptation), respectively. It is apparent that the peak value of the cross-correlogram is higher when neurons exhibit no SFA compared with neurons exhibiting SFA. A more palpable comparison is demonstrated in Fig. 3(b), in which the distribution of cross-correlation indices is around 0.9 when neurons have no SFA. However, when neurons show the feature of SFA (in despite of weak or strong), cross-correlation indices decrease significantly, distributing around 0.2-0.45. From this group of results, we conclude that SFA acts as a vital factor in decreasing the cross-correlation strength between neuron pairs, which is consistent with previous experimental observations.

![Fig. 4. Synchronization transitions of neuronal populations induced by SFA when $G = 0.08$, repeating 10 times. (a) Scatter plot presenting the effects of SFA on the population synchronous activities of the networks, black points denote weak adaptation ($e = 4$), hollow circles denote strong adaptation ($e = 8.5$). (b) Diagram showing the variation of the population synchronization index with the change of SFA. Error bar denotes the std.](image3)
activity is fairly low. However, when neurons are in a state of strong-degree adaptation, the population synchronization indices decrease dramatically, closing to the dividing line. Figure 4(b) shows how the synchronization indices of neuronal populations vary with the linearly increased parameter $e$. These results show that synchronous activity of population neurons is also adaptation-dependent, specifically weak-degree adaptation would impair the synchronization, while strong-degree adaptation would further stabilize the synchronization.

In the former analysis, the value of coupling strength $G$ is fixed at 0.08, but how about the variation trend of population synchronous activity induced by neuronal adaptation if the value of $G$ varies? To answer this question, we calculated the population synchronization indices of neurons under different coupling strengths $G$. The results in Fig. 5 show that except for the case when $G$ is too small ($G = 0.02$), the adaptation-induced synchronization transition trends under different values of $G$ are almost the same. Since a too small coupling strength would make the networks rather loose, signals transmit among neurons slowly and inefficiently, eventually, neurons in the networks hardly synchronize with each other. In addition, we also observe that the larger the value of $G$ is, the more rapidly the neurons turn into asynchronous states. It should be pointed out that although the change of $G$ would not influence the variation trends of population synchronization significantly, the effect of $G$ on the population synchronization indices is obvious, especially under no adaptation and weak adaptation. When no adaptation is present, a larger value of $G$ would induce a more synchronized state of the population neurons, while if weak adaptation is present, a larger value of $G$ would lead to a less synchronized state of the population neurons. This is a very interesting and novel phenomenon, and the underlying mechanisms related to this phenomenon need to be clarified in future studies.

In summary, we have performed a computational investigation on the influence of SFA in modulating the population activities of neurons. Our model results suggest that SFA, which has been proven to have a negative effect on regulating the correlated firing behavior between neuron pairs, displays a rather different role in modulating population synchronization of neuron ensembles. Compared with the case when neurons exhibit no SFA property, the population synchronous behavior of neurons with a weak-degree of SFA decreases, while the synchronization of population activity increases when a strong degree of SFA is endowed to the model neurons. In addition, an alteration of coupling strength between neurons will not change the variation trend of population synchronization, except when the coupling strength is too weak.

It is noteworthy that the connection type in the networks investigated here is the electrical synapse, thus our model results may have some limitations in extending to other networks in the brain, especially for networks predominantly coupled by chemical synapses. Hence, for further investigations, networks with connection types similar to realistic neuronal networks can be considered, and we believe that some more meaningful results might be obtained. Moreover, a similar variation trend of population synchronous activity induced by SFA has been observed in electrically coupled square-lattice networks (data not shown), which may indicate that the adaptation-induced synchronization transition of population neurons in electrically coupled networks is general; however, sufficient explorations on other kinds of networks are needed to confirm this inference.

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