Roles of Inhibitory Neurons in Rewiring-induced Synchronization in Pulse-coupled Neural Networks

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Abstract

The roles of inhibitory neurons in synchronous firing are examined in a network of excitatory and inhibitory neurons with Watts and Strogatz's rewiring. By examining the persistence of the synchronous firing that exists in the random network, it was found that there is a probability of rewiring at which a transition between the synchronous state and the asynchronous state takes place, and the dynamics of the inhibitory neurons play an important role in determining this probability.

1 Introduction

Recently, oscillations and synchronization in neural systems have attracted considerable attention. Particularly, in the visual cortex and the hippocampus, synchronized oscillations with characteristic frequencies are often observed in the averaged behavior of the neuronal ensemble. It is proposed that they are related to the binding of the information in the visual cortex and the regulation of the synaptic plasticity in the hippocampus (Gray, 1994; Buzsáki, 2006).

These phenomena are often modeled by the coupled self-oscillating neurons. Typically, the networks of excitatory neurons (Mirollo & Strogatz, 1990; Kuramoto, 1991; Abbott & van Vreeswijk, 1993; Tsodyks, Mitkov, & Sompolinsky, 1993; Hansel, Mato, & Meunier, 1995; van Vreeswijk, 1996; Sato & Shiino, 2002; DeVille & Peskin, 2008) show some degree of synchronized firing among neurons, such as perfect synchronization (Mirollo & Strogatz, 1990; Kuramoto, 1991), frequency locking (Tsodyks, Mitkov, & Sompolinsky, 1993), anti-phase synchronization (Hansel, Mato, & Meunier, 1995; Sato & Shiino, 2002), partial synchronization (van Vreeswijk, 1996), coexistence of synchrony and asynchrony (DeVille & Peskin, 2008), and so on. Moreover, it is also known that the networks of inhibitory neurons generate synchrony more easily than those of excitatory neurons (van Vreeswijk, Abbott, & Ermentrout, 1994; White et al., 1998; Lewis & Rinzel, 2003; Nomura, Fukai, & Aoyagi, 2003). In these networks, it was found that the forms of interactions play critical roles in the generation of synchrony, such as the rise and decay time of the post synaptic potential. On the other hand, in the case of the network of excitable neurons, each of which does not emit spikes without disturbance, it is known that the network composed of both excitatory and inhibitory neurons shows synchronous firing when the strength of the connections and the amount of disturbance are appropriately chosen (Brunel, 2000; Kanamaru & Sekine, 2003, 2004, 2005; Kanamaru & Aihara, 2008). The connections of the network of the above theoretical models are either random or all-to-all, and the dependence of synchrony on the topology of the network has not been examined.

Regarding the topology of networks, Watts and Strogatz (WS) proposed a network with a small average shortest path length and a large clustering coefficient whose connections are obtained by rewiring the connections of the locally connected regular network. This network is called a small-world network (Watts & Strogatz, 1998), and its properties are often observed in social networks, the Internet, gene networks, the brain, and so on (Strogatz, 2001). Roles of small-world topology on synchronization in nonlinear oscillators were examined by several authors (Barahona & Pecora, 2002; Hong, Choi, & Kim, 2002), and it was found that the effect of rewiring or adding short cuts to the network depends on the initial configuration of the network. When the number of connections of the initially local network is small, the addition of a small number of short cuts effectively enhances synchrony in the network (Barahona & Pecora, 2002).

When the connections of the initially local network is strong, the number of rewirings required for the generation of synchrony becomes small (Hong, Choi, & Kim, 2002). Both results were obtained in the diffusively connected network in which strong connections contribute to generate synchrony in the network.

In particular, the properties of the small-world network are considered to be important in the brain because they realize an efficient signal transmission even when the volume of axon wiring is limited to some ratio of the brain size (Buzsáki, 2006). The synchronization in the small-world network composed of neuronal models was examined by various authors using the leaky integrate-and-fire model (Masuda & Aihara, 2004; Netoff et al., 2004; Roxin, Riecke, & Solla, 2004) and the Hodgkin-Huxley model (Lago-Fernández et al., 2000; Buzsáki et al., 2004; Netoff et al., 2004), but the results differ depending on the models and the values of the parameters. In the research on the WS network of excitatory neurons, it is known that the optimal rewiring probability p_0 with which the degree of synchronization is maximized takes various values when regulating the rewiring probability p. It is reported that $p_0 \simeq 0.3$ (Masuda & Aihara, 2004), p_0 lies in the so-called small-world region ($0.01 \leq p \leq 0.1$) (Lago-Fernández et al., 2000), and coherent bursting emerges for $p > 0.01$ or $p > 0.2$ (Netoff et al., 2004). One of the reasons for this discrepancy is the difference in the strength of the connections; the network can have either strong connections (Lago-Fernández et al., 2000; Netoff et al., 2004; Roxin, Riecke, & Solla, 2004) or weak connections (Masuda & Aihara, 2004). Moreover, the differences between the neuron models would also affect the values of p_0 because the property of synchronization of the excitatory neurons depends on the specific neuron models used (Abbott & van Vreeswijk, 1993).

On the other hand, it is known in networks of inhibitory neurons that the degree of synchronization increases by increasing the number of neurons with long-range connections. It is suggested that the inhibitory neurons play an important role in the generation of rhythm of the brain (Buzsáki et al., 2004). This finding coincides with the report that the inhibitory neurons are easy to synchronize (van Vreeswijk, Abbott, & Ermentrout, 1994).

Even if the inhibitory neurons are important for the generation of rhythm in the brain, it is thought that the excitatory neurons also contribute to its mechanism because the number of inhibitory neurons with long-range connections is small, and inhibitory neurons with both long-range and short-range connections have yet to be found (Buzsáki et al., 2004). Kitano & Fukai (2007) examined the dynamics of networks composed of excitatory and inhibitory neurons, whose structures are obtained by rewiring the connections of a local network with the rewiring probability p. The values of the parameters of their network were chosen so that the neurons do not show synchronous oscillations at $p = 1$. The present paper investigates the dynamics of a similar network and examines the dependence of the synchronization on the network structure, but we set the parameters of the network to show synchronous oscillations at $p = 1$ because we wish to clarify whether the synchronous oscillations persist even for small p.

In section 2, a pulse-coupled neural network composed of excitatory and inhibitory neurons is defined. Both types of neurons have connections through chemical synapses, and the inhibitory neurons also have electrical synapses with gap junctions. Watts-Strogatz's rewiring is introduced to the connections by the chemical synapses. In section 3, the dependence of the synchronization on the rewiring probability is examined. The final section provides discussion and conclusions.

2 Network of excitatory and inhibitory neurons

In the following, a pulse-coupled neural network composed of excitatory and inhibitory neurons arranged in a two-dimensional array is considered. An excitatory neuron and an inhibitory neuron are placed at the point (i, j) $(1 \leq i \leq N_x,\ 1 \leq j \leq N_y)$ in the array, and the number of neurons in the excitatory ensemble and the inhibitory ensemble is $N_x N_y$. The dynamics of the internal states $\theta_E^{(i,j)}$ of the excitatory neuron and $\theta_I^{(i,j)}$ of the inhibitory neuron at (i, j), are written as

$$\begin{aligned}
\tau_X \dot{\theta_X^{(i,j)}} &= (1 - \cos\theta_X^{(i,j)}) + (1 + \cos\theta_X^{(i,j)}) \\
&\quad \times (r_X + \xi_X^{(i,j)}(t) + g_{XE} I_{XE}^{(i,j)}(t) \\
&\quad - g_{XI} I_{XI}^{(i,j)}(t) + g_{gap}\delta_{XI} I_{gap}^{(i,j)}(t)), \quad (2.1) \\
I_{XY}^{(i,j)}(t) &= \frac{1}{2\#A_{cXY}^{(i,j)}} \sum_{(m,n)\in A_{cXY}^{(i,j)}} \\
&\quad \sum_l \frac{1}{\kappa_Y} \exp\left(-\frac{t - t_l^{(m,n)}}{\kappa_Y}\right), \quad (2.2) \\
I_{gap}^{(i,j)}(t) &= \frac{1}{\#A_g^{(i,j)}} \sum_{(m,n)\in A_g^{(i,j)}} \\
&\quad \sin\left(\theta_I^{(m,n)}(t) - \theta_I^{(i,j)}(t)\right), \quad (2.3) \\
\langle \xi_X^{(i,j)}(t) \xi_Y^{(m,n)}(t') \rangle &= D\delta_{XY}\delta_{im}\delta_{jn}\delta(t - t'), \quad (2.4)
\end{aligned}$$

where $X = E$ or I, and δ_{ij} is Kronecker's delta (Ermentrout, 1996; Izhikevich, 1999; Kanamaru & Aihara, 2008). Although the number of excitatory neurons in the cortex is much larger than that of inhibitory neurons, we set both numbers identical for simplicity. Moreover, as shown in equations 2.2 and 2.3, the synaptic strengths are divided by the number of connected neurons; therefore, the dynamics of the network do not depend on the number of neurons if there is a sufficiently large number of neurons. The connections through chemical synapses

are modeled by the postsynaptic potential with an exponential function, and electrical synapses with gap junctions based on the physiological observations (Galarreta & Hestrin, 2001) are introduced to the connections between the inhibitory neurons. The electrical synapse corresponds to the diffusive coupling in the physical system; therefore, it can induce the synchronization in the neural system (Ermentrout, 2006). $I_{XY}^{(i,j)}$ denotes the inputs by the chemical synapses from the ensemble Y to the neuron at (i,j) in the ensemble X. $A_{cXY}^{(i,j)}$ denotes a set of indices at which there is a neuron in the ensemble Y, which connects to the neuron at (i,j) in the ensemble X. $\#A_{cXY}^{(i,j)}$ is the number of elements of this set. $t_l^{(m,n)}$ denotes the lth firing time of the neuron at (m,n) in the ensemble Y, and it is defined by the time at which $\theta_Y^{(m,n)}$ exceeds π. $I_{gap}^{(i,j)}(t)$ is the input by the electrical synapses. $A_g^{(i,j)}$ denotes the set of indices at which there is a neuron that connects to the target neuron through electrical synapses. r_X denotes the parameters of the neurons in ensemble X, and it can also be regarded as a constant input to the neuron which starts to fire with $r_X = 0$ as shown below. Without Gaussian white noise $\xi_X^{(i,j)}(t)$ and input $I_{XY}^{(i,j)}$, a single neuron shows self-oscillation when $r_X > 0$. When $r_X < 0$, this neuron becomes an excitable system with the following stable equilibrium:

$$\theta_0 = -\arccos\frac{1+r_X}{1-r_X}, \tag{2.5}$$

in which θ_0 approaches zero for $r_X \sim 0$. In the following, we set $r_E = r_I = -0.025$, and we consider the dynamics of networks of excitable neurons. As shown in equation 2.2, the strength of the synaptic connections is divided by the number of connected neurons which is 112 in this study as shown below; therefore many spikes are required to make the target neuron emit a spike. In contrast, other WS networks use stronger synaptic connections than ours so that a much smaller number of inputs ranging from 1 to 20 can make the target neuron emit a spike (Lago-Fernández et al., 2000; Masuda & Aihara, 2004; Netoff et al., 2004; Roxin, Riecke, & Solla, 2004). It is known that the mean EPSP amplitude is 0.55 mV in the rat visual cortex (Mason, Nicoll, & Stratford, 1991), and 1.67 mV in the rat motor cortex (Thomson, Deuchars, & West, 1993). In both cases, the amplitudes are highly variable ranging from 0.05 to 2.08 mV in the visual cortex and ranging from 0 to 9 mV in the motor cortex, and the most of the amplitudes are less than 0.5 mV (Mason, Nicoll, & Stratford, 1991). Therefore, when the difference between the threshold and the resting potential is 10 mV, the number of EPSPs to generate an action potential for one neuron would range from 1 to 200. Our assumption on the EPSP amplitude is in this range.

The sets of indices for connections $A_{cXY}^{(i,j)}$ and $A_g^{(i,j)}$ are defined as follows. First, we define a set $A^{(i,j)}(p,k)$, where p is the probability of the rewiring of connections and k scales the connection length. For $p = 0$, $A^{(i,j)}(0,k)$ is defined as a set of indices for local connections, namely,

$$A^{(i,j)}(0,k) = \left\{ (m,n) \,\middle|\, 1 \le d(i,j,m,n) \le \frac{k}{2} \right\}, \tag{2.6}$$

$$d(i,j,m,n) = |i-m| + |j-n|, \tag{2.7}$$

where the connections in both directions exist between two neurons at (i,j) and (m,n), and a periodic boundary condition is applied, namely, the point at (i',j') with arbitrary integers i' and j' is identical with the one at (i' mod N_x, j' mod N_y). In the following, we set k even, then the number of elements can be calculated as $\#A^{(i,j)}(0,k) = k(k+2)/2$. $A^{(i,j)}(p,k)$ is obtained from $A^{(i,j)}(0,k)$ by the standard method (Watts & Strogatz, 1998), namely, by rewiring each connection of $A^{(i,j)}(0,k)$ randomly with probability p. The connections through the electrical synapses are always considered to be local, namely, $A_g^{(i,j)} = A^{(i,j)}(0,k)$. The rewiring is introduced to the connections by the chemical synapses from the excitatory neurons, namely, $A_{cXE}^{(i,j)} = A^{(i,j)}(p,k)$ $(X = E, I)$. Generally, the connections from the inhibitory neurons are considered to be local, but recently, a possible role of inhibitory neurons with long-range connections is examined (Buzsáki et al., 2004). Therefore, this paper considers two networks, namely, the E-rewiring network in which the connections by the chemical synapses from the inhibitory neurons are local, that is,

$$A_{cXI}^{(i,j)} = A^{(i,j)}(0,k) \ \ (X = E, I), \tag{2.8}$$

and the E,I-rewiring network in which the rewiring is also introduced to the connections by the chemical synapses from the inhibitory neurons, that is,

$$A_{cXI}^{(i,j)} = A^{(i,j)}(p,k) \ \ (X = E, I). \tag{2.9}$$

In the following, a network with $N_x = N_y = 100$ and $k = 14$ is used. The parameters are set as $g_{EE} = g_{II} \equiv g_{int}$ and $g_{EI} = g_{IE} \equiv g_{ext}$ for simplicity. Kanamaru & Aihara (2008) analyzed the dependence of synchronization only on g_{EE}, g_{II}, g_{EI}, or g_{IE} in the global network that corresponds to our model with $p = 1$ and found that the synchronous firing exists only in some range of g_{EE}, g_{II}, g_{EI}, and g_{IE}. Moreover, the time constants of the internal dynamics and the synaptic transmission are set to $\tau_E = 1$, $\tau_I = 0.5$, $\kappa_E = 1$, and $\kappa_I = 5$. This network is sparse because the number of connections to the neuron at (i,j) is calculated to be $\#A^{(i,j)}(0,14) = 112$. As shown in Figure 1, the average shortest path length $L(p)$ and the clustering coefficient $C(p)$ in this network can be numerically calculated to be $L(p)/L(0) \sim 0.4$ and $C(p)/C(0) > 0.7$ in the range $0.01 \le p \le 0.1$; therefore, the network exhibits the small-world properties, i.e., small L and large C, in this range.

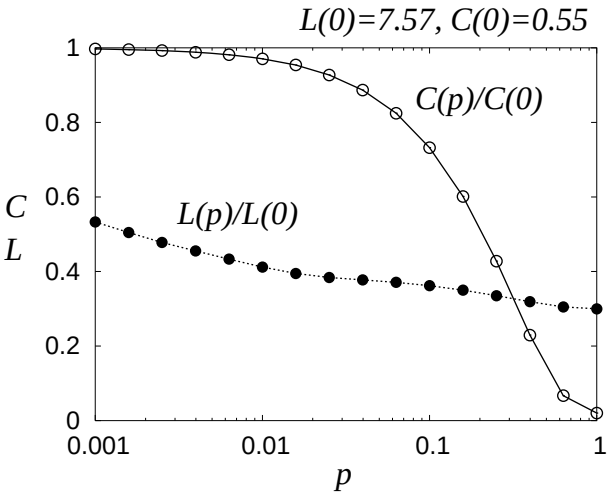

Figure 1: The average shortest path length $L(p)$ and the clustering coefficient $C(p)$ in our two dimensional network. It is observed that $L(p)/L(0) \sim 0.4$ and $C(p)/C(0) > 0.7$ in the range $0.01 \leq p \leq 0.1$; therefore, the network exhibits the small-world properties, i.e., small L and large C, in this range.

3 Effect of rewiring on synchronization

In the following, the parameters are set to $g_{gap} = 0.10$, $g_{int} = 5$, $g_{ext} = 3.2$, and $D = 0.004$ so that this network shows synchronous firing for $p = 1$ (Kanamaru & Aihara, 2008) because we wish to clarify whether the synchronous firing persists even for small p. In Figures 2 and 3, the firing of neurons in the E-rewiring network with $p = 0.6$ and $p = 0.8$ is shown, respectively. Figures 2A, 2C, 3A, and 3C show the firing rates J_E and J_I of the excitatory and inhibitory ensemble, which are defined as an average instantaneous firing rate of a neuron, namely,

$$J_X(t) \equiv \frac{1}{N_x N_y w} \sum_{(i,j)} \sum_{l} \Theta(t - t_l^{(i,j)}), \quad (3.1)$$

$$\Theta(t) = \begin{cases} 1 & \text{for } 0 \leq t < w \\ 0 & \text{otherwise} \end{cases}, \quad (3.2)$$

where $w = 1$. The small fluctuations in J_E and J_I for $p = 0.6$ indicate that the firing of neurons is asynchronous. On the other hand, the temporal changes of J_E and J_I for $p = 0.8$ indicate that there is synchronization of neuronal firing within each class and correlation between the firing of inhibitory and excitatory neurons; we refer to such firing as globally synchronous firing. The raster plots of the firing of neurons in Figures 3B and 3D for $p = 0.8$ show almost uniform synchronous firing. It is also shown that the degree of synchronization in the inhibitory ensemble is stronger than that in the excitatory ensemble. The trajectory of J_E and J_I for $p = 0.8$ forms a noisy limit cycle in the (J_E, J_I) plane as shown

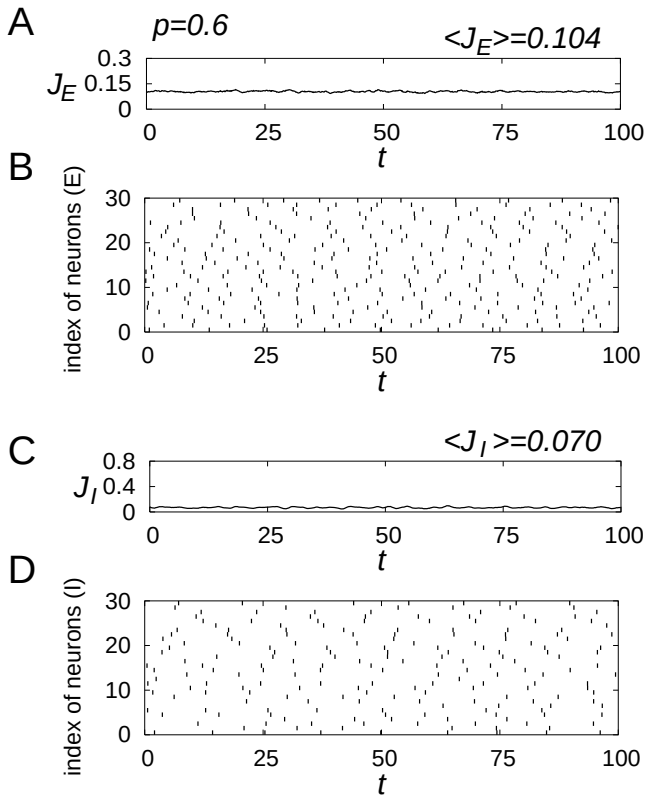

Figure 2: The firing of neurons in the E-rewiring network with $p = 0.6$, $N_x = N_y = 100$, $k = 14$, $g_{gap} = 0.10$, $g_{int} = 5$, $g_{ext} = 3.2$, and $D = 0.004$. (A), (C) Temporal changes of the firing rates J_E and J_I of the excitatory and inhibitory ensemble. (B), (D) The corresponding raster plots of the firing of neurons. The firing of 30 neurons among 10000 neurons in each ensemble is shown. The index of the neuron at (i, j) is calculated as $jN_x + i$.

in Figure 4B. In contrast, that of J_E and J_I for $p = 0.6$ fluctuates around an equilibrium because there is little correlation among the firing spikes of neurons for $p = 0.6$ (see Figure 4A).

To quantify the degree of synchronization among the firing spikes of neurons, we use the standard deviation $S(J_X; p)$ of $J_X(t)$ ($X = E$ or I) over time, defined as

$$\langle J_X \rangle = \frac{1}{T} \int_0^T J_X(t) dt, \quad (3.3)$$

$$\langle J_X^2 \rangle = \frac{1}{T} \int_0^T J_X(t)^2 dt, \quad (3.4)$$

$$S(J_X; p) = \sqrt{\langle J_X^2 \rangle - \langle J_X \rangle^2}. \quad (3.5)$$

Typically, the time interval of T is chosen 1000, and larger values such as $T = 3000$ or 6000 are used when p is close to p_0. When $S(J_X; p)$ is large, the synchronous firing of neurons is observed. The dependence of $S(J_E; p)$ on the rewiring probability p and a fitted curve with $A \tanh(\beta(p - p_0)) + \delta$ are shown in Figure 4C. There is a

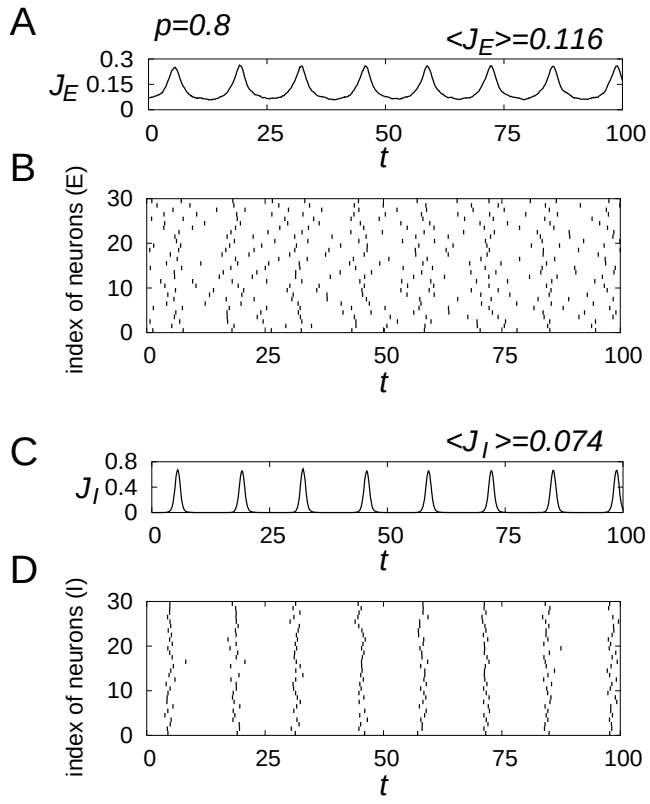

Figure 3: The firing of neurons in the E-rewiring network with $p = 0.8$, $N_x = N_y = 100$, $k = 14$, $g_{gap} = 0.10$, $g_{int} = 5$, $g_{ext} = 3.2$, and $D = 0.004$. (A), (C) Temporal changes of the firing rates J_E and J_I of the excitatory and inhibitory ensemble. (B), (D) The corresponding raster plots of the firing of neurons. The firing of 30 neurons among 10000 neurons in each ensemble is shown. The index of the neuron at (i, j) is calculated as $jN_x + i$.

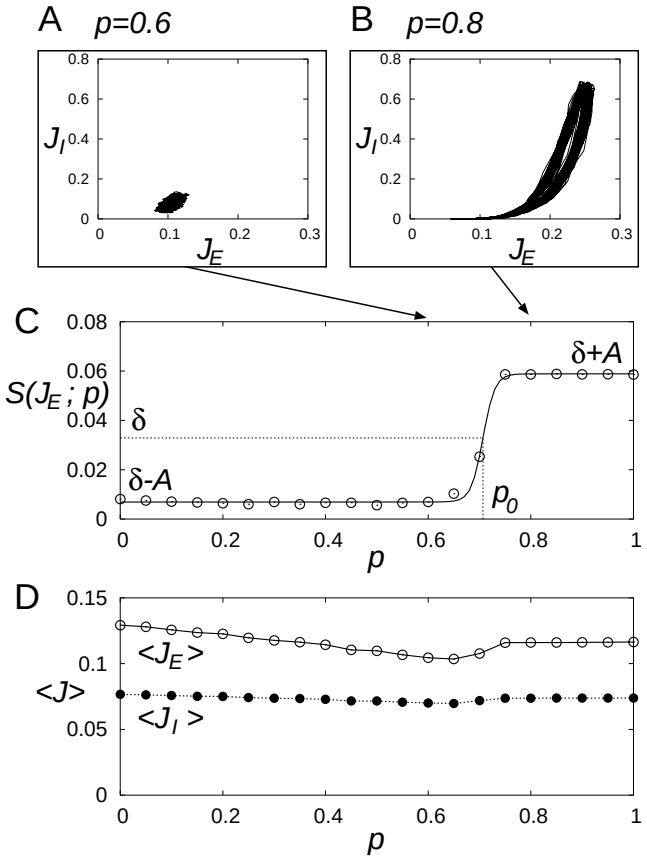

Figure 4: The trajectories of J_E and J_I in the E-rewiring network for (A) $p = 0.6$ and (B) $p = 0.8$. The values of the other parameters are identical with those of Figures 2 and 3. (C) The dependence of $S(J_E; p)$ on the rewiring probability p. A fitted curve $A\tanh(\beta(p - p_0)) + \delta$ with $A = 0.0260$, $\beta = 43.3$, $p_0 = 0.707$, and $\delta = 0.0329$ is also shown. (D) The dependence of $\langle J_E \rangle$ and $\langle J_I \rangle$ on p.

transition probability p_0 at which $S(J_E; p)$ shows a sharp transition. $S(J_I; p)$ also shows a similar transition at p_0 (data not shown). This sharp transition is a property of this network composed of excitatory and inhibitory neurons. The network composed only of inhibitory neurons shows a gradual increase (Buzsáki et al., 2004) of $S(J_I; p)$ (data not shown). The averages of J_E and J_I over time, $\langle J_E \rangle$ and $\langle J_I \rangle$, are shown in Figure 4D. As shown later, $\langle J_I \rangle$ plays an important role for the emergence of the synchronous firing, but the dependence of $\langle J_I \rangle$ on the rewiring probability p is not significant in this figure. Namely, when changing p, the average firing rate of the inhibitory neurons $\langle J_I \rangle$ maintains almost constant values, and only the correlation among the firing spikes of neurons changes. Although $\langle J_E \rangle$ slightly changes with variations in p, its dependence on p is not large.

The dependence of p_0 on the inter-ensemble connection strength g_{ext} is shown in Figure 5A. Three values of the connection strength of the electrical synapses, $g_{gap} = 0, 0.1$, and 0.3, both for the E-rewiring and the E, I-rewiring networks are investigated. Note that in the network with $g_{gap} = 0$, p_0 does not exist for $g_{ext} > 3.6$ because globally synchronous firing does not exist in this range (Kanamaru & Aihara, 2008). The number of data points for $g_{ext} < 2.5$ is small because the data were insufficient for fitting $A\tanh(\beta(p - p_0)) + \delta$ to $S(J_E; p)$ when p_0 is close to 0, and fitting becomes difficult due to the small magnitude of A. Typically, it is observed that p_0 in the E, I-rewiring network is smaller than that in the E-rewiring network because the number of the rewired connections is larger in the E, I-rewiring network, and the large number of rewirings tends to break the local synchronization in favor of the global synchronization.

To understand Figure 5A, let us divide the range of g_{ext} into two parts, namely, small g_{ext} ($g_{ext} < 3.3$) and large g_{ext} ($g_{ext} \geq 3.3$). For small g_{ext}, smooth changes of p_0 are observed, and for large g_{ext}, p_0 changes drastically. In order to examine the dynamics of the network, the dependences of $\langle J_I \rangle$ at $p = 1$ and $p = 0$ on g_{ext} are shown in Figures 5B and 5C, respectively. $\langle J_I \rangle$ at $p = 1$ reflects

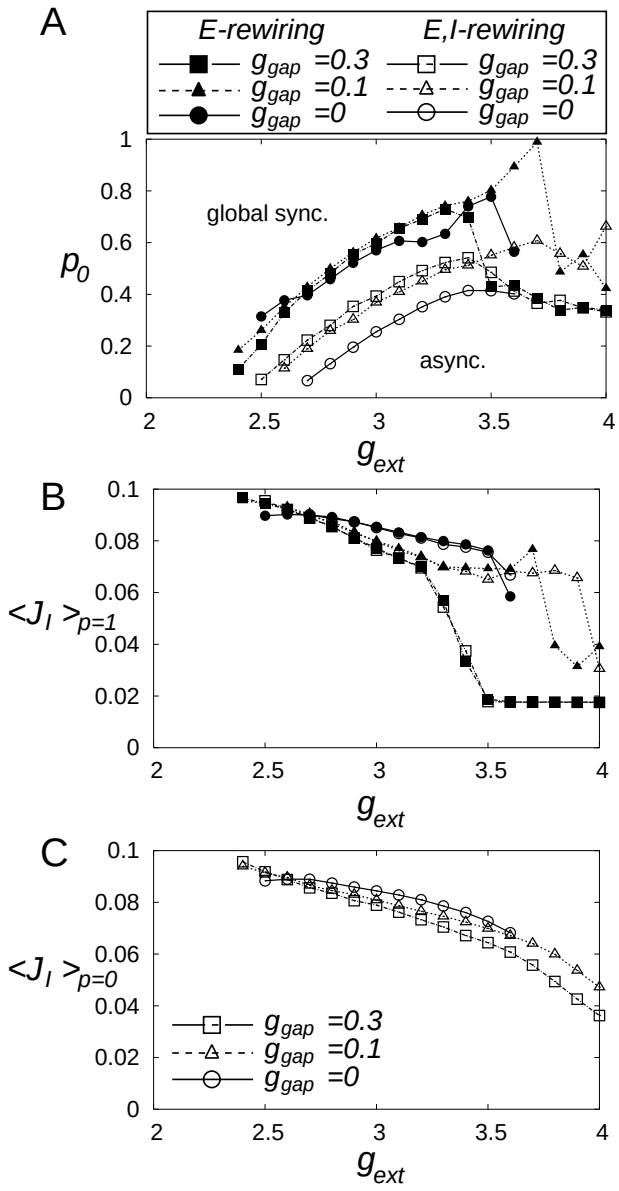

Figure 5: (A) The dependence of the transition probability p_0 on the inter-ensemble connection strength g_{ext}. The dependence of $\langle J_I \rangle$ on g_{ext} (B) at $p = 1$ and (C) at $p = 0$. $\langle J_I \rangle$ at $p = 0$ is common to both the E-rewiring network and the E, I-rewiring network because both networks have only local connections for $p = 0$.

the shape of the noisy limit cycle (Figure 4B), and $\langle J_I \rangle$ at $p = 0$ shows the properties of the asynchronous state (Figure 4A). As shown in Figures 5B and 5C, $\langle J_I \rangle$ at $p = 1$ and $p = 0$ have similar values for small g_{ext}, but they largely differ for large g_{ext}, suggesting that the properties of the dynamics differ in two ranges of g_{ext}. Actually, in this network, the properties of synchronous firing depend both on the rewiring probability p and on the parameters of the network such as g_{ext}, g_{int}, and D, and for large g_{ext}, it is known that complex dynamics such as chaotic synchronization and weakly synchronous firing exist at $p = 1$ (Kanamaru & Aihara, 2008). Therefore, we must examine the behavior of the network in the two ranges of g_{ext} separately. In the following, we focus mainly on the analysis of the network with small g_{ext} ($g_{ext} < 3.3$).

In the E, I-rewiring network with small g_{ext}, it is observed in Figure 5A that a larger g_{gap} makes the transition probability p_0 larger, which is necessary to break the local synchronization created by the electrical synapses. Moreover, in both networks, p_0 tends to decrease as g_{ext} decreases for $g_{ext} < 3.3$. In other words, globally synchronous firing emerges with a small number of rewirings when g_{ext} is small. By decreasing g_{ext} further (e.g., $g_{ext} < 2.3$), globally synchronous firing is observed even when $p = 0$. This phenomenon can be explained as follows. When g_{ext} is decreased, the average firing rate $\langle J_E \rangle$ increases similarly to $\langle J_I \rangle$ shown in Figure 5C. When $\langle J_E \rangle$ is large, the inhibitory neurons become self-oscillating, and it is known that the network of self-oscillating inhibitory neurons are easy to synchronize (van Vreeswijk, Abbott, & Ermentrout, 1994); therefore, inhibitory neurons with large $\langle J_I \rangle$ in our network show synchronous firing without rewiring, and globally synchronous firing appears. Based on the above discussion, it can be inferred that the average firing rate $\langle J_I \rangle$ of the inhibitory ensemble might play an important role in the generation of globally synchronous firing. Therefore, in Figure 6, p_0 is plotted as a function of $\langle J_I \rangle$ at $p = 0$. In both networks, it is observed that p_0 approaches 0 at $\langle J_I \rangle \simeq 0.09$, and for $\langle J_I \rangle > 0.09$, globally synchronous firing is observed in the network without rewiring. In particular, the graphs for three values of g_{gap} overlap each other around $\langle J_I \rangle = 0.09$ in the E, I-rewiring network. We plotted p_0 as a function of other variables, e.g., $\langle J_E \rangle$ or $\langle J_E \rangle + \langle J_I \rangle$, but such an overlap of three graphs was not observed. These observations mean that p_0 is determined only by $\langle J_I \rangle$ in the E, I-rewiring network, and its dependence on g_{gap} is weak in this range. This is because the rewiring of the connections by the chemical synapses among inhibitory neurons dominates the effect of the electrical synapses. In the E-rewiring network, the graphs for three values of g_{gap} are not completely coincident because the connections through the chemical synapses among the inhibitory neurons are local, therefore, the effect of the electrical synapses is relatively large.

Next, let us consider the dynamics of the network for large g_{ext}. As shown in Figure 5A, changes in g_{gap} largely affect the dynamics of networks with large values of g_{ext}, and this behavior is also observed for small $\langle J_I \rangle$ in Figure 6. This is because the electrical synapses can transmit information even when there is no firing, and their effect is strengthened relatively when the firing rate of neurons is small. Moreover, it is known that complex dynamics such as chaotic synchronization and weakly synchronous firing exist for large g_{ext} at $p = 1$ (Kanamaru & Aihara, 2008). When the emerged synchronous firing is chaotic, this transition would be caused by bifurcations to chaos such as successive period doubling

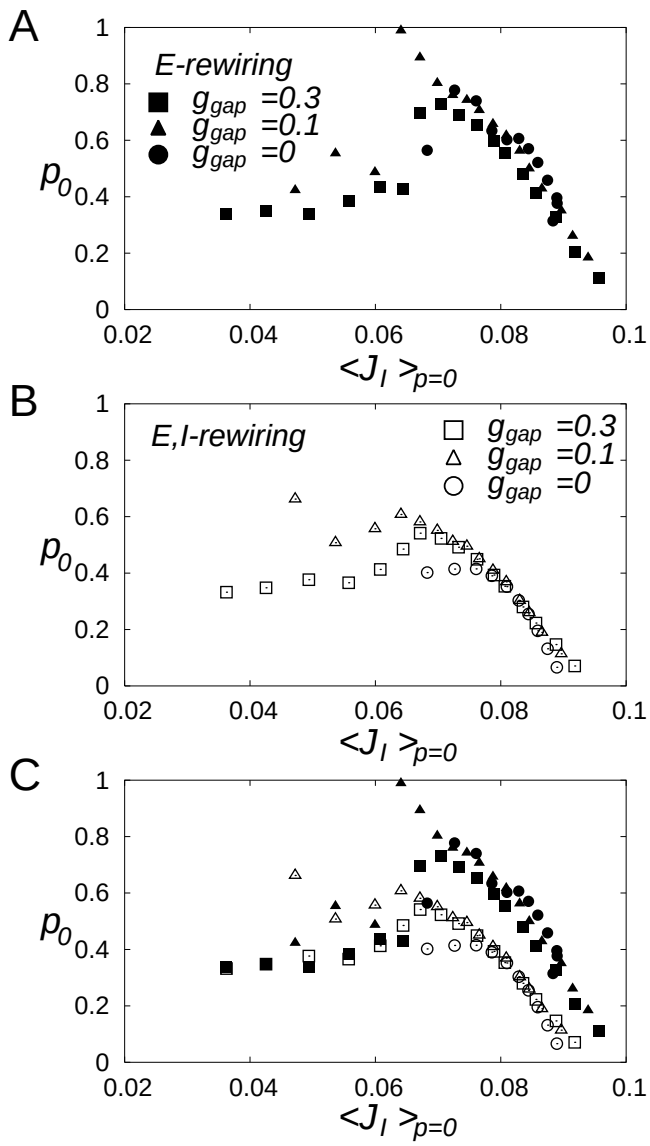

Figure 6: The dependence of p_0 on $\langle J_I \rangle$ for (A) the E-rewiring network and (B) the E, I-rewiring network. The data for both networks are shown again in (C). The values of $\langle J_I \rangle$ at $p = 0$ are used (see Figure 4D). In both networks, it is observed that p_0 approaches 0 at $\langle J_I \rangle \simeq 0.09$. Moreover, for large $\langle J_I \rangle \simeq 0.09$, it is observed that p_0 is determined only by $\langle J_I \rangle$, and its dependence on g_{gap} is weak in this range.

bifurcations. The bifurcation point that relates to chaos (i.e., p_0) does not necessarily change smoothly when the values of the parameters (i.e., g_{ext} and g_{gap}) is changed. Therefore, the dependence of p_0 on large g_{ext} (small $\langle J_I \rangle$) is different from that for small g_{ext} (large $\langle J_I \rangle$). Further analysis of such complex dynamics is the subject of our future studies.

4 Conclusion

In the E-rewiring network with rewired connections of excitatory chemical synapses and in the E, I-rewiring network with the rewired connections of excitatory and inhibitory chemical synapses, the conditions for the existence of globally synchronous firing were investigated. We used the values of the parameters with which the network shows synchronous oscillations in the random network because we wish to clarify whether the synchronous oscillations persist even for small rewiring probabilities. In both networks, when the firing rate $\langle J_I \rangle$ of the inhibitory ensemble is large, it was observed that the transition probability p_0 of the rewiring becomes small with increasing $\langle J_I \rangle$. In particular, in the E, I-rewiring network, the dependence of p_0 on the strength of the electrical synapses was weak, when $\langle J_I \rangle$ is large, and p_0 decreases with the increase of $\langle J_I \rangle$. However, when $\langle J_I \rangle$ is small, the dependence of p_0 on the strength of the electrical synapses was significant because the electrical synapses can transmit information even when there is no firing. In the neural systems, it is known that the electrical synapses are widely observed among inhibitory interneurons. Therefore, our results suggest that the inhibitory neurons play an important role in maintaining stable synchronous firing irrespective of their firing rates.

In this paper, we analyzed the dependence of the transition probability p_0 on the parameters of the system, and it was found that p_0 takes small values, including the values in the small-world region (see Figs. 1 and 5A), when the system is close to the critical point to generate the global synchrony (i.e., $g_{ext} \simeq 2.5$ in our model as shown in Fig. 5A). Similar results were obtained in some previous works (Barahona & Pecora, 2002; Hong, Choi, & Kim, 2002). All the networks treated in these works show global synchronization at $p = 1$. On the other hand, in some networks, the dependence of p_0 on the values of the parameters is not so much clear (Lago-Fernández et al., 2000; Masuda & Aihara, 2004; Netoff et al., 2004; Roxin, Riecke, & Solla, 2004; Kitano & Fukai, 2007). It is a future work to understand the relationship between the above two groups of studies.

As for the roles of the inhibitory neurons in synchronization, it has already been known that the inhibitory neurons play important roles to generate synchrony in the network both in theoretical studies (van Vreeswijk, Abbott, & Ermentrout, 1994; White et al., 1998; Lewis & Rinzel, 2003; Nomura, Fukai, & Aoyagi, 2003) and in the experimental studies (Buzsáki et al., 2006). Based on these findings, we analyzed the dynamics of networks composed of both excitatory neurons and inhibitory neurons. A similar network has already been analyzed by Kitano & Fukai (2007), but, to our knowledge, this is the first report to show that the network topology required for the generation of synchrony is determined mainly by the dynamics of the inhibitory neurons.

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