Synchronization transition in gap-junction-coupled leech neurons

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Abstract

Real neurons can exhibit various types of firings including tonic spiking, bursting as well as silent state, which are frequently observed in neuronal electrophysiological experiments. More interestingly, it is found that neurons can demonstrate the co-existing mode of stable tonic spiking and bursting, which depends on initial conditions. In this paper, synchronization in gap-junction-coupled neurons with co-existing attractors of spiking and bursting firings is investigated as the coupling strength gets increased. Synchronization transitions can be identified by means of the bifurcation diagram and the correlation coefficient. It is illustrated that the coupled neurons can exhibit different types of synchronization transitions between spiking and bursting when the coupling strength increases. In the course of synchronization transitions, an intermittent synchronization can be observed. These results may be instructive to understand synchronization transitions in neuronal systems.

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1. Introduction

Synchronization of a set of interacting individuals or units has been intensively studied because of its ubiquity in the natural world [1]. The synchronization of neuronal signals has been proposed as one of the mechanisms to transmit and code information in the human brain [2,3]. Mammalian nervous systems exhibit a diversity of synchronized behaviors including periodic, quasi-periodic, chaotic, noise-induced and noise-enhanced synchronous rhythms [4–8]. It was suggested that theoretical studies of such synchronized behaviors in neuronal assemblies play an

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important role in our understanding of information processing in the nervous systems. Hence, the synchronous firing of interconnected neurons has been extensively investigated by means of the theory of nonlinear dynamical systems. In Ref. [9] chaos synchronization in gap-junction-coupled neurons was studied by means of transversal and tangential Lyapunov exponents. It was shown that in strong gap junctions, the synchronous state was stable over a wide range of parameters irrespective of whether the synchronous state was chaotic or periodic. Effects of the width of an action potential on synchronization phenomena were investigated by the integrate-and-fire neuron model and the piecewise-linear version of the FitzHugh–Nagumo neuron model. It was shown that the duration of the impulse acted as a critical role in assuring synchronization [10]. By introducing weak heterogeneity to small-world networks of spiking neurons and using a semianalytical dynamical mean-field approximation, the synchronization may be slightly increased for diffusive couplings, while it is decreased for sigmoid couplings [11]. Synchronization of fast-spiking (FS) neurons interconnected by GABA-ergic and electrical synapses was investigated by Nomura and his co-workers [12]. It was observed that an FS neuron pair connected by electrical and chemical synapses could achieve both synchronous and antisynchronous firing states in a physiologically plausible range of the conductance ratio between electrical and chemical synapses. Noise-induced and noise-enhanced synchronizations including internal and external noise, have also been studied for neuronal systems [13,14]. Moreover, spatially collective motions in excitable neuronal media have been extensively studied and some novel results were shown in Ref. [15]. Synchronization in elliptic bursters was investigated and some analytic results was obtained in Ref. [16].

It is well known that neuronal oscillations can modulate cortical excitability and are critically involved in almost every cognitive task including information coding, memory formation and perception [6,17–19]. Neuronal oscillations result from the activity of individual neurons that can be roughly classified into two categories, being tonic spiking and bursting [20]. In addition, many neurons can display transitions between tonic spiking and bursting as a function of the brain state (e.g., sleep versus wakefulness); these transitions can modify the transfer mode of a neuronal population. Also, spiking and bursting modes of neuronal oscillations may co-exist under different initial conditions [21,22]. The study of synchronization on neuronal networks can also been seen in many recent references [[23,24] etc.] and the references therein.

To the best of our knowledge, there is very few reference available on synchronization dynamics of coupled multi-stable neuronal systems, thus it remains an interesting and challenging problem to be solved in the field of neuronal dynamics. In particular, dynamical mechanisms of underlying synchronization transitions of tonic spiking and bursting oscillations, as well as conditions that trigger transitions between these patterns of neuronal activity for the coupled neurons with co-existing attractors, is crucial for understanding processing of sensory information in the brain.

In the present paper, we are concerned with the synchronization process of coupled neurons that are characterized by co-existing spiking and bursting attractors as the coupling strength increases. It will be shown that the coupled neurons with co-existing attractors can exhibit different synchronization transitions between tonic spiking and bursting, which depend on the initial states of the uncoupled neurons. Even more interestingly, we will show that there exist narrow regions of the coupling strength, where an intermittent synchronization can occur when the coupled neurons transit from non-synchronization to synchronization or from spiking to bursting synchronization. Although our results are obtained for two coupled neurons, they can be generalized to multi-unit systems as well, thus shed light on the universal features of synchronization transitions in the neuronal apparatus.

The rest of this paper is organized as follows: model descriptions are introduced in Section 2. Main results of synchronization transitions in two coupled leech neurons with co-existing attractors are presented in Section 3, while a brief conclusion is given in Section 4.

2. Model descriptions

It is unknown what happens when one bistable neuron is coupled with another identical bistable neuron. The answer to this question manifests inherent difficulties. In what follows, it is demonstrated that dynamics of coupled bistable neurons are actually much richer and complicated, including different types of transitions between spiking and bursting synchronization, as well as intermittency.

To illustrate the above final statement, one may employ a minimal dynamical system, consisting of two leech neurons [22] that are coupled via a gap-junctional flux, and study their synchronization properties. The resultant dynamics of the coupled neurons are described by the following differential equations:
The values of parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Membrane capacitance (C)</td>
<td>0.5 (nF)</td>
</tr>
<tr>
<td>Conductance constants (nS)</td>
<td>(\bar{g}<em>{Na} = 200), (\bar{g}</em>{K2} = 30), (g_1 = 8)</td>
</tr>
<tr>
<td>Time constants (s)</td>
<td>(\tau_{K2} = 0.9), (\tau_{Na} = 0.0405)</td>
</tr>
<tr>
<td>Reversal potentials (V)</td>
<td>(E_K = -0.07), (E_{Na} = 0.045), (E_I = -0.046)</td>
</tr>
</tbody>
</table>

\[
\begin{align*}
\frac{dV^1}{dt} &= -\frac{1}{C} (\bar{g}_{K2}(m_{K2}^1)^2 V^1 - E_K) + g_i (V^1 - E_I) \\
&\quad + \bar{g}_{Na} f(-150, 0.0305, V^1)^3 h_{Na}(V^1 - E_{Na})) + g_{syn}(V^2 - V^1), \\
\frac{d m_{K2}^1}{dt} &= \frac{f(-83, 0.018 + V_{K2}^{shift}, V^1) - m_{K2}^1}{\tau_{K2}}, \\
\frac{d h_{Na}^1}{dt} &= \frac{f(500, 0.03391, V^1) - h_{Na}^1}{\tau_{Na}}, \\
\frac{dV^2}{dt} &= -\frac{1}{C} (\bar{g}_{K2}(m_{K2}^2)^2 V^2 - E_K) + g_i (V^2 - E_I) \\
&\quad + \bar{g}_{Na} f(-150, 0.0305, V^2)^3 h_{Na}(V^2 - E_{Na})) + g_{syn}(V^1 - V^2), \\
\frac{d m_{K2}^2}{dt} &= \frac{f(-83, 0.018 + V_{K2}^{shift}, V^2) - m_{K2}^2}{\tau_{K2}}, \\
\frac{d h_{Na}^2}{dt} &= \frac{f(500, 0.03391, V^2) - h_{Na}^2}{\tau_{Na}},
\end{align*}
\]

where variables \(V^i\), \(m_{K2}^i\), and \(h_{Na}^i\) \((i = 1, 2)\) represent the membrane potential, activation of \(I_{K2}\), and inactivation of \(I_{Na}\), respectively, and superscript 1 (or 2) is used to indicate the first (or second) neuron. The parameter \(C\) denotes the membrane capacitance, \(\bar{g}_{K2}\) denotes the maximum conductance of \(I_{K2}\), and \(E_K\) and \(E_{Na}\) are the reversal potentials of \(K^+\) and \(Na^+\), respectively. \(\bar{g}_{Na}\) represents the maximal conductance of \(I_{Na}\), \(g_1\) and \(E_1\) are the conductance and reversal potential of the leak current, respectively. \(\tau_{K2}\) and \(\tau_{Na}\) are the time constants of activation of \(I_{K2}\) and inactivation of \(I_{Na}\), respectively. \(V_{K2}^{shift}\) is the shift of the membrane potential of half-inactivation of \(I_{K2}\) from its canonical value. \(f\) is a Boltzmann function: \(f(x, y, z) = 1/(1 + \exp(x (y + z)))\) and \(g_{syn}\) is the coupling strength between neuron 1 and 2.

For the above model (1), values of all parameters that we use in our discussions are listed in Table 1.

For a single leech neuron, the detailed bifurcation analysis has been conducted by means of the Lukyanov–Shilnikov bifurcation theory of a saddle–node periodic orbit with noncentral homoclinics [22]. To study the synchronization behavior of the coupled leech neurons with the co-existing attractors, we may fix the parameter \(V_{K2}^{shift} = -0.02598\) such that each neuron can fire spiking or bursting depending on different initial conditions as shown in Fig. 1.

3. Synchronization transition of coupled leech neurons

In this section, synchronization transitions will be investigated in two coupled leech neurons with various initial states (which determine different dynamics of the uncoupled neurons) as the coupling strength \(g_{syn}\) increases. It is shown that the coupled leech neurons with various initial states can exhibit different transitions of spiking and bursting synchronization.

A correlation coefficient is introduced to measure the synchronization degree of the coupled neurons, and it is defined as follows:
Fig. 1. Co-existence of tonic spiking and bursting firings in the leech neuron model (1) in the plane \((m_{k2}, V)\) projection at \(V_{k2}^\text{shift} = -0.02598\). Initial conditions leading to tonic spiking and bursting are \((V, m_{k2}, h_{Na}) = (0.0, 0.13, 0.08)\) and \((V, m_{k2}, h_{Na}) = (0.0, 0.16, 0.08)\), respectively.

\[
C = \frac{\sum_{i=1}^{n} (V_i^1 - \langle V_i^1 \rangle)(V_i^2 - \langle V_i^2 \rangle)}{\sqrt{\sum_{i=1}^{n} (V_i^1 - \langle V_i^1 \rangle)^2 \sum_{i=1}^{n} (V_i^2 - \langle V_i^2 \rangle)^2}},
\]

where \(V_i^1\) (or \(V_i^2\)) represents the samplings of the membrane potential \(V^1(t)\) (or \(V^2(t)\)). \(\langle \cdot \rangle\) denotes the average over the number of the sampling. It is easy to see that the more synchronous the coupled neurons are, the larger the correlation coefficient \(C\) is, and the complete synchronization state of the coupled neurons is achieved when \(C\) is equal to 1.

In the following discussions, synchronization transitions of the coupled leech neurons are treated for three cases:

Case I. we set initial conditions of two uncoupled neurons as \((V^1, m_{k2}^1, h_{Na}^1) = (0.0, 0.13, 0.08)\) and \((V^2, m_{k2}^2, h_{Na}^2) = (0.0, 0.16, 0.08)\), which indicate that the two uncoupled neurons fire the tonic spiking and bursting, respectively. Bifurcation diagram of inter spike intervals (ISIs) with respect to the coupling strength \(g_{syn}\) is shown in Fig. 2(a). The correlation coefficient \(C\) is calculated as illustrated in Fig. 2(b). It is shown that the coupled neurons can fire from spiking to bursting, and eventually spiking accompanied by two courses of irregular firings. At the same time, it can be seen from Fig. 2(b) that synchronization transition looks complex, which exhibits a route of transition as: non-synchronization \(\rightarrow\) nearly synchronization \(\rightarrow\) spiking synchronization \(\rightarrow\) nearly synchronization \(\rightarrow\) bursting synchronization \(\rightarrow\) spiking synchronization. In what follows, it is demonstrated that the nearly synchronization is an intermittent synchronization.

For more details, complete synchronization cannot occur when \(g_{syn}\) is less than 1.66. When \(g_{syn} \in (1.82, 3.12)\) or \((3.32, +\infty)\), complete synchronization can be observed as shown in Fig. 2(b), in which \(C\) is equal to 1. It can be observed from Fig. 2(a) and (b) that bursting synchronization occurs for \(g_{syn} \in (3.32, 4.42)\), where a long ISI accompanied by some short ISIs appears (This is a characteristic of neuronal bursting). Non-synchronization will appear for two narrow intervals: \(g_{syn} \in (1.66, 1.82)\) or \((3.12, 3.32)\). These non-synchronizations imply two transition processes: one is associated with the change from non-synchronization to spiking synchronization, and the other is associated with the change from spiking to bursting synchronization. Furthermore, it is shown that the coupled neurons show an intermittent synchronization in transition regions as illustrated in Fig. 3 (a) and (b). The intermittent synchronization here implies intermittent switches between a synchronous and an asynchronous state. More interestingly, it is shown that bursting synchronization transits to spiking synchronization through a sudden jump at \(g_{syn} = 4.42\). It is noted that synchronization transition is closely related to the bifurcation behavior of neurons.

Case II. Synchronization of two coupled bursting neurons is investigated. To do this, we set initial conditions of two neurons as \((V^1, m_{k2}^1, h_{Na}^1) = (0.0, 0.16, 0.08)\) and \((V^2, m_{k2}^2, h_{Na}^2) = (0.0, 0.165, 0.08)\), which denote that neurons can fire bursting simultaneously. Bifurcation diagram of ISIs and correlation coefficient are shown in Fig. 4(a) and (b) when the coupling strength \(g_{syn}\) varies. For smaller coupling, the coupled neurons can fire spiking instead of bursting, and synchronization degree increases as \(g_{syn}\) is increased. When \(g_{syn} \in (1.84, 3.16)\) and \((3.52, +\infty)\),
Case III. Finally, we will investigate synchronization transition of two coupled spiking neurons. We take initial conditions of two coupled neurons as $(V^1, m_{k_2}^1, h_{Na}^1) = (0.0, 0.13, 0.08)$ and $(V^2, m_{k_2}^2, h_{Na}^2) = (0.0, 0.14, 0.08)$, respectively. Under these initial conditions, neurons can fire in spiking modes. The bifurcation diagram of ISIs and variation of correlation coefficient with respect to the coupling strength $g_{syn}$ are presented in Fig. 5(a) and (b). It is observed that there is only one narrow region, where the coupled neurons fire irregularly. This is a transition set from non-synchronization to spiking synchronization. It is easy to see that synchronization transition of the coupled spiking neurons is completely different from that of Case I and Case II. There does not exist bursting synchronization in the coupled spiking neurons. Hence, synchronization transition of spiking and bursting cannot occur in Case III.

Similar results can be obtained as the above for combinations of other initial conditions in the coupled leech neurons. In summary, the coupled leech neurons with co-existing attractors can exhibit different transitions of spiking and bursting synchronization when two neurons are located at different initial states. In fact, synchronization transition results from fractal boundaries of basins of attraction of the co-existing attractors and a fact that multi-stable systems

complete spiking and bursting synchronization can be achieved. It is observed that there are two narrow regions, in which transitions appear to change from non-synchronization to spiking synchronization and from spiking to bursting synchronization, respectively. In these two narrow regions, the intermittent synchronization can also be observed. Comparison between Fig. 4 with Fig. 2 shows that there are similar synchronization transition processes. However, it is illustrated in Fig. 4 that the coupled neurons eventually synchronize in bursting firings. This is different from the case of Fig. 2, where the coupled neurons eventually synchronize in spiking firings.

Fig. 2. (a) Bifurcation diagram of ISIs of the first neuron in two coupled leech neurons with respect to $g_{syn}$. (b) Variation of the correlation coefficient $C$ of the membrane potentials $V^1$ and $V^2$ with respect to $g_{syn}$. Their initial conditions are $(V^1, m_{k_2}^1, h_{Na}^1) = (0.0, 0.13, 0.08)$ and $(V^2, m_{k_2}^2, h_{Na}^2) = (0.0, 0.16, 0.08)$, respectively.

Fig. 3. (a) Intermittent synchronization of the coupled leech neurons in transition regions. (a) $g_{syn} = 1.75$ and (b) $g_{syn} = 3.13$ with initial conditions: $(V^1, m_{k_2}^1, h_{Na}^1) = (0.0, 0.13, 0.08)$ and $(V^2, m_{k_2}^2, h_{Na}^2) = (0.0, 0.16, 0.08)$, respectively.
are extremely sensitive to perturbations due to their complexly interwoven basins of attraction. Hence, for the case I, when the coupling strength is increasing, the coupled neurons initially synchronize to spiking firings through an intermittent synchronization since the coupling pulls two neurons to slide into the attraction basin of the spiking. As the coupling is further increased, bursting synchronization appears with spiking synchronization being ceased by an intermittent synchronization since the stronger coupling can kick two neurons into bursting region. As the coupling becomes strong enough, the coupled neurons go back to spiking synchronization again. On the other hand, it is understandable that an intermittent synchronization occurs when the coupled neurons stay on fractal boundaries of basins of attraction of the co-existing attractors through the effect of a suitable coupling. For case II, the mechanism of transition to bursting synchronization is similar to the case I. Thus, the coupled neurons eventually synchronize in bursting instead of spiking. It is in agreement with the well-accepted case, in which, the coupled identical systems can synchronize to the manifold of uncoupled system when the coupling gets sufficiently large. For case III, it is a simple transition from non-synchronization to spiking synchronization accompanied by an intermittency. This is understandable that the behavior of the coupled neurons appears the same as that of the uncoupled one when the coupling becomes sufficiently large.
4. Conclusion

In this paper, synchronization transitions were investigated numerically for the coupled leech neurons with co-existing attractors. It was shown that the transition of neuronal spiking and bursting synchronization is closely related and sensitive to initial conditions of the coupled neurons. Synchronization transitions can be identified by means of the bifurcation diagram of ISIs and the correlation coefficient. It was shown that synchronization transition of the coupled leech neurons with co-existing attractors can exhibit the different process, which depends on initial conditions of two neurons. Three transition modes were found in two coupled leech neurons: (1) the route of transition is, spiking synchronization with lower degree $\rightarrow$ intermittent synchronization $\rightarrow$ spiking synchronization $\rightarrow$ intermittent synchronization; (2) spiking synchronization with lower degree $\rightarrow$ intermittent synchronization $\rightarrow$ spiking synchronization $\rightarrow$ intermittent synchronization; and (3) spiking synchronization with lower degree $\rightarrow$ intermittent synchronization $\rightarrow$ bursting synchronization. Other models exhibiting co-existence of spiking and bursting attractors may show similar transitions to synchronization, as for example by intracellular calcium oscillations [25].

References