



FORCED SYNCHRONIZATION IN MORRIS–LECAR NEURONS

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We investigate forced synchronization between electrically coupled Morris–Lecar neurons with class I and class II excitability through numerical bifurcation analysis. We find that class II neurons have wider parameter regions of forced synchronization. However, the bifurcation structure and patterns of spikes for class II are complicated; there exist period-doubling bifurcations, interesting two-periodic oscillations and irregular bursting spikes with high values of the coefficient of variation of the interspike interval.

Keywords: Class I and Class II neurons; synchronization; coupled neurons; bifurcation.

1. Introduction

A neuron, or the elementary processing units in the central nervous system, generates various temporal patterns of spikes. Among such firing patterns, synchronous firing of neurons in connection with neural signal processing has attracted much interest (see [Fujii *et al.*, 1996] and references therein). Many studies confirm that oscillatory dynamics of neural activity and its synchronization play an important role in the models of information processing in the brain [Pikovsky *et al.*, 2001]. The oscillation mechanisms of neuron models are classified into two by their bifurcations: class I (saddle-node bifurcation) and class II (Hopf bifurcation). The oscillation of the former and the latter has almost zero frequency and a finite frequency at the bifurcation point, respectively.

We study forced synchronization in electrically cyclic-coupled Morris–Lecar (ML) neurons with both class I and class II excitability. The reasons

of using ML neurons are as follow:

- Recently, Tsumoto *et al.* showed that these excitabilities are switched by only one parameter value in the ML model [Tsumoto *et al.*, 2006].
- Patel proposed the analogue VLSI ML neuron model and showed the advantage of using the ML neuron model for considering large-scale systems of coupled neural oscillators [Patel & DeWeerth, 1997].

The aim of this paper is to compare forced synchronization of a class I neuron with that of a class II neuron. For mutual synchronization of two neurons, it is clarified by using the phase resetting curve (PRC) that class II neurons are easy to achieve synchronization [Ermentrout, 1996; Rinzel & Ermentrout, 1998; Ermentrout *et al.*, 2001]. Also for large number of neurons with random connections, class II neurons present a good level of synchronization regardless of the connection topology

[Lago-Fernández *et al.*, 2001]. However, Tsuji *et al.* showed that class I neurons have wider parameter regions of synchronous firing than those of class II neurons by the detailed bifurcation analysis [Tsuji *et al.*, 2004]. For forced synchronization, the study of comparison between class I and class II neurons is not reported as far as we know.

In this paper we study the dependence of class I and class II neurons on forced synchronization using bifurcation theory. In a system of N coupled neurons as a ring by negative conductances (unforced system) spikes are synchronized at anti-phase for nearest neurons and N -phase, for even N and odd N , respectively; similar results as in the coupled two neurons' case [Varona *et al.*, 2001]. When common external forces are injected to such synchronized neurons, we find that in-phase spikes appear through a pitchfork bifurcation as the amplitude of the external forces is increased. Moreover, we obtain that class II neurons have wider parameter regions of forced synchronization. However, the bifurcation structure and patterns of spikes for class II are complicated; there exist period-doubling bifurcations, interesting two-periodic oscillations and irregular bursting spikes with high values of the coefficient of variation of the interspike interval.

2. System Equation

The ML neuron model [Ermentrout, 1996; Rinzel & Ermentrout, 1998; Tsumoto *et al.*, 2006], proposed as a model for describing a variety of oscillatory voltage patterns of Barnacle muscle fibers, is described by

$$C_M \frac{dV}{dt} = -g_l(V - V_l) - g_{ca}M_\infty(V - V_{ca}) - g_k N(V - V_k) + I_{\text{ext}} \quad (1)$$

$$\frac{dN}{dt} = \frac{N_\infty - N}{\tau_N}$$

where V is the membrane potential, $N \in [0, 1]$ is the activation variable for K^+ , I_{ext} is the external current and t denotes the time measured in milliseconds. The system parameters V_{ca} , V_k and V_l represent equilibrium potentials of Ca^{2+} , K^+ and leakage currents, respectively, and g_{ca} , g_k and g_l denote the maximum conductance of corresponding ionic currents. The V -dependent functions, M_∞ , N_∞ and τ_N are given by

$$M_\infty = 0.5 \left[1 + \frac{\tanh(V - V_a)}{V_b} \right],$$

$$N_\infty = 0.5 \left[1 + \frac{\tanh(V - V_c)}{V_d} \right],$$

$$\tau_N = \frac{1.0}{\left[\frac{\phi \cosh(V - V_c)}{2V_d} \right]},$$

where V_a and V_c are the midpoint potential at which the calcium current and the potassium current is halfactivated, V_b is a constant corresponding to the steepness of voltage dependence of activation, V_d denotes the slope factor of potassium activation and ϕ is the temperature-like time scale factor.

In this paper we consider a system of electrically cyclic-coupled (diffusively coupled) three ML neurons with common external forces. The system equation is described by

$$C_M \frac{dV_i}{dt} = -g_l(V_i - V_l) - g_{ca}M_{\infty_i}(V_i - V_{ca}) - g_k N_i(V_i - V_k) + I_{\text{ext}} - g(2V_i - V_{i-1} - V_{i+1}) \quad (2)$$

$$\frac{dN_i}{dt} = \frac{N_{\infty_i} - N_i}{\tau_{N_i}}$$

$$(i = 1, 2, 3, V_0 \equiv V_3, V_4 \equiv V_1),$$

where g is the coupling conductance fixed as 0.1 or -0.1 .

The class I and II excitability can be controlled by the value of parameter V_c ; the critical point is about $V_c = 4.6$ [Tsumoto *et al.*, 2006]. In this study we use $V_c = 12$ and 2 for class I and class II, respectively. The values of other parameters in Eq. (1) are fixed as follows:

$$C_M = 20 \left[\frac{\mu\text{F}}{\text{cm}^2} \right], \quad g_k = 8 \left[\frac{\text{mS}}{\text{cm}^2} \right], \quad g_l = 2 \left[\frac{\text{mS}}{\text{cm}^2} \right],$$

$$g_{ca} = 4 \left[\frac{\text{mS}}{\text{cm}^2} \right], \quad \phi = \frac{1}{15} [\text{s}^{-1}], \quad V_{ca} = 120 [\text{mV}],$$

$$V_k = -80 [\text{mV}], \quad V_l = -60 [\text{mV}], \quad V_a = -1.2 [\text{mV}],$$

$$V_b = 18 [\text{mV}], \quad V_d = 17.4 [\text{mV}].$$

3. Results

In this study we consider I_{ext} : $I_m \sin(\omega t) + I$ as external current in Eq. (2). The direct current I is fixed as 50 and 55 for class I and class II neurons, respectively, to have a similar oscillation frequency. Time scale is changed to ωt for fixing the period of the external force as 2π . Bifurcation sets in the

two-parameter plane (ω, I_m) are calculated using Kawakami's method [Kawakami, 1984].

We show bifurcation diagrams in Figs. 1 and 2 for systems of both class I and II neurons coupled by the positive and the negative coupling conductance. In these figures horizontal and vertical axes indicate the angular frequency (ω) and the amplitude (I_m) of the external alternative current, respectively. We note that when $I_{ext} = I$, an in-phase oscillation and a three-phase oscillation is stable in the system of

the positive and the negative coupling conductance, respectively, for both classes.

In Figs. 1(a) and 1(b) the natural frequency is 0.083 and 0.080 for the class I and II neuron, thus the regions of the fundamental harmonic oscillation touch the line of $I_m = 0$ at these values. The Arnold tongues touch the axis $I_m = 0$ which is similar to synchronization of phase-coherent chaotic oscillators [Pikovsky *et al.*, 1997], but here we have quite different bifurcations

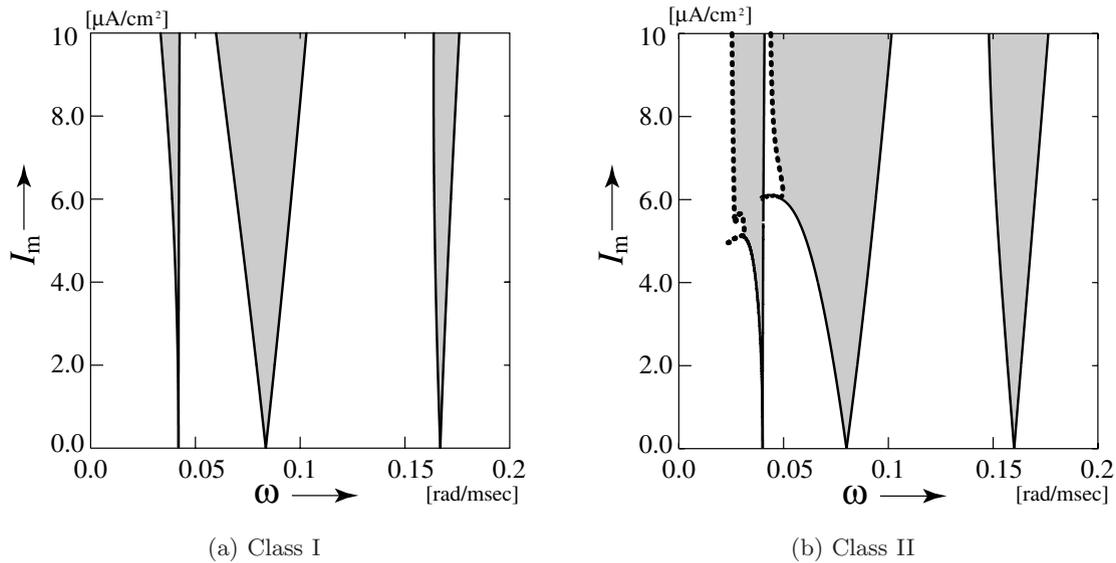


Fig. 1. Bifurcation diagram in Eq. (1) for $g = 0.1$. Solid and dashed curves indicate the saddle-node and the period-doubling bifurcation, respectively. We observe stable in-phase synchronized states in the shaded regions; in each figure from right to left higher harmonic oscillation of order two, fundamental harmonic oscillation and subharmonic oscillation of order two.

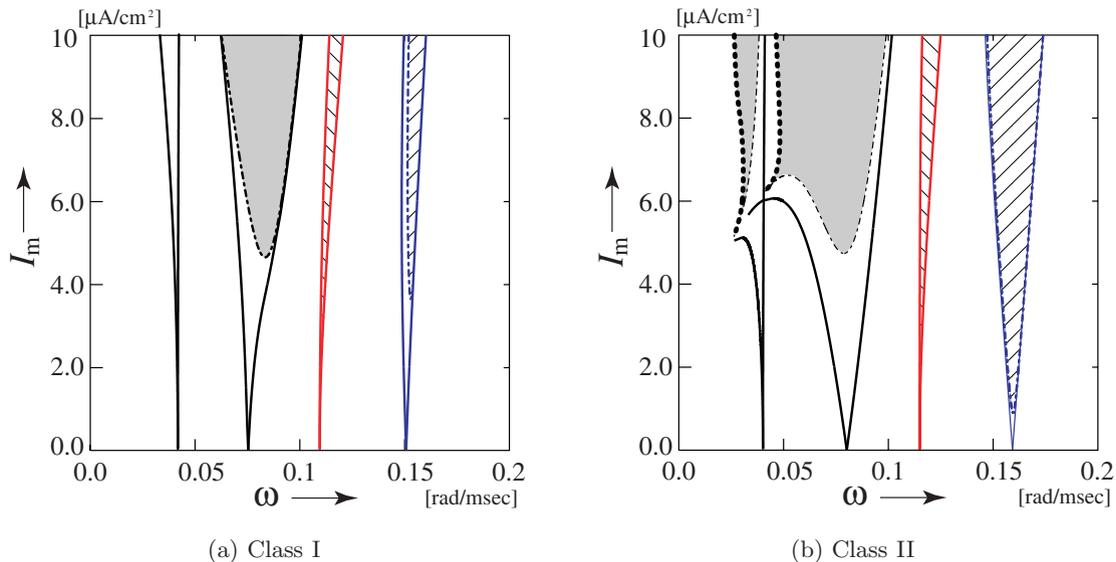


Fig. 2. Bifurcation diagram for $g = -0.1$. Types of curves are the same as in Fig. 1 except for the thin dashed curves for the pitchfork bifurcation. Red and blue curves indicate bifurcations of three-phase and a pair of in-phase oscillations, respectively.

(transitions to synchronization). In this figure, we only show the regions of stable in-phase synchronized states, because other types of synchronized states are all unstable regardless of increasing I_m .

On the other hand, we observe several synchronized states for the negative coupling conductance: three-phase, a pair of in-phase and in-phase in the regions ,  and  in Fig. 2, respectively. When $I_{\text{ext}} = I$, only a three-phase synchronized state is stable, however, unstable in-phase and a pair of in-phase oscillations also exist. Thus, only the three-phase synchronized states form Arnold tongues (red curves in Fig. 2) in the parameter plane (ω, I_m) . These unstable states at $I_m = 0$ pass through the pitchfork bifurcations (symmetry-recovering bifurcation in this case) by increasing the value of I_m and become stable in shaded and hatched regions; the same as coupled BVP (Bonhöffer–van der Pol) oscillators' case [Kitajima *et al.*, 1999].

One-parameter bifurcation diagrams changing the value of parameter ω on $I_m = 8.0$ in Figs. 1(a) and 1(b) are shown in Figs. 3(a) and 3(b), respectively. From these figures we can see that the class II neurons are easy to achieve forced synchronization for small values of ω .

The biggest difference of forced synchronization between class I and class II neurons is the

existence of the period-doubling bifurcation only in coupled class II neurons. We observe an interesting two-periodic oscillation due to the period-doubling bifurcation, see Fig. 4. In this figure neuron 1 produces a two-periodic oscillation (the period is 4π) while neuron 2 generates a one-periodic oscillation (the period is 2π). Common external currents (the amplitude is $10 [\mu\text{ A/cm}^2]$) are injected into these neurons, however the oscillation period of neuron 1 (also neuron 3) is double that of neuron 2. In coupled class I neurons, we never observe such interesting oscillations, because there are no period-doubling bifurcations.

To compare complexity of spikes in the regions of no locking, we calculate the coefficient of variation (C_v) of the interspike interval (ISI). When the membrane potential crosses zero from negative to positive, we assume that the neuron generates a spike. Here, C_v is a measure of spike train irregularity defined as the standard deviation divided by the mean interspike interval. For a very regular spike train, the ISI histogram will have a very narrow peak and $C_v \rightarrow 0$. In the case of a random spike train, the mean interspike interval is exponentially distributed and $C_v \rightarrow 1$ [Softky & Koch, 1993]. C_v is also used as an indicator of synchronous firing in coupled neurons [Kitajima & Kurths, 2005].

Figure 5 shows waveforms for some values of C_v . For class I neurons C_v is small and almost

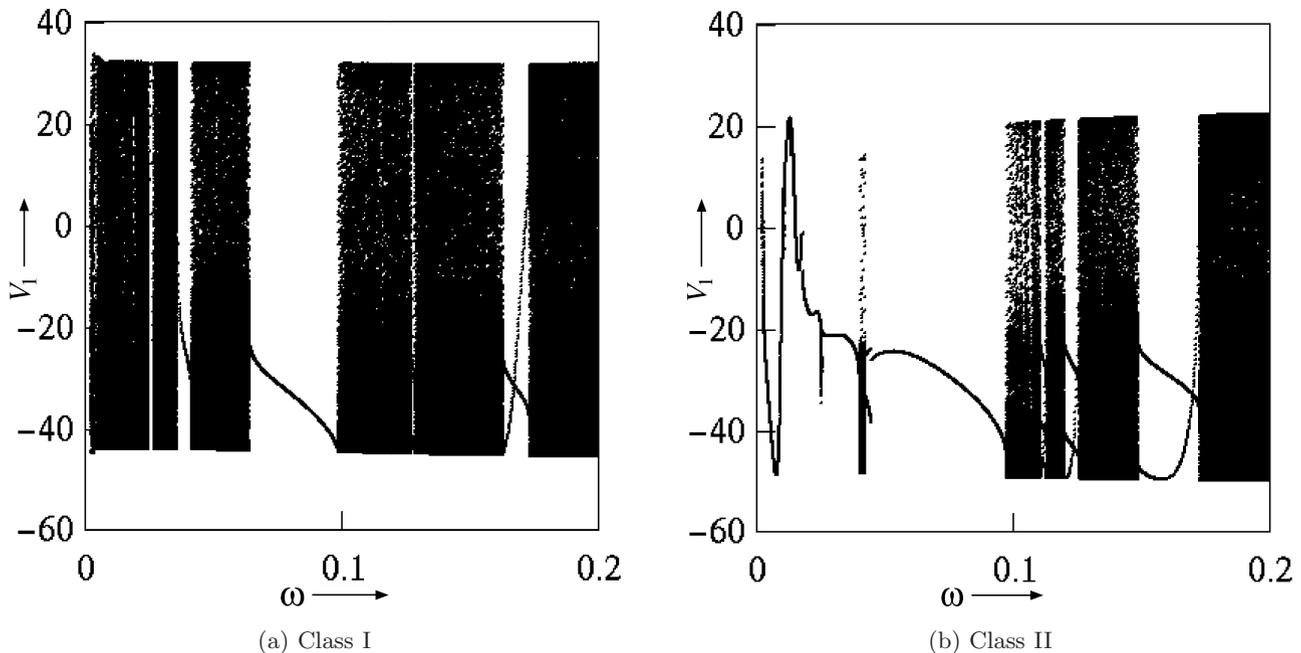


Fig. 3. One-parameter bifurcation diagram on the line at $I_m = 8.0$ in Figs. 1(a) and 1(b). The points are from the Poincaré mapping at each time $t = 2\pi j$ ($j = 1, 2, \dots, 1000$) for the membrane potential of neuron 1.

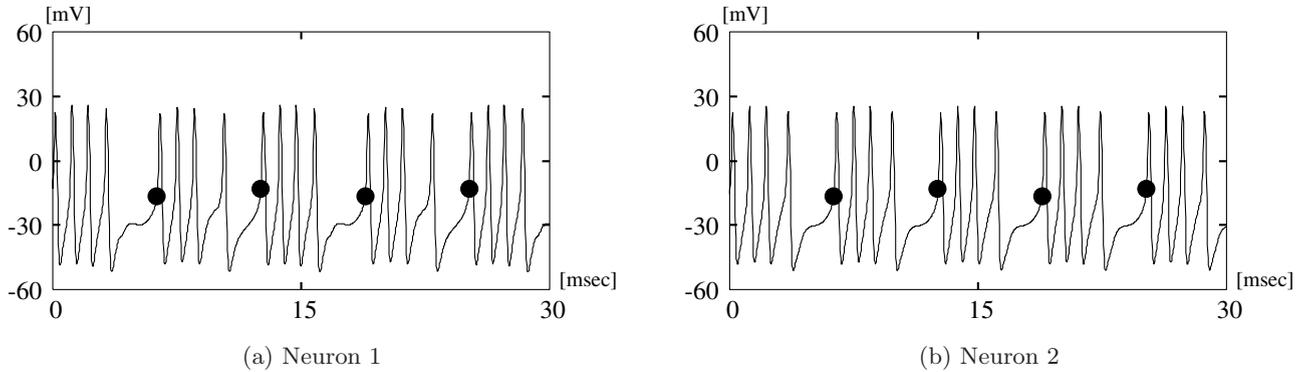


Fig. 4. Waveform of interesting oscillation observed in coupled class II neurons. The closed points are from the Poincaré mapping. $g = -0.1$, $\omega = 0.016$ and $I_m = 10.0$.

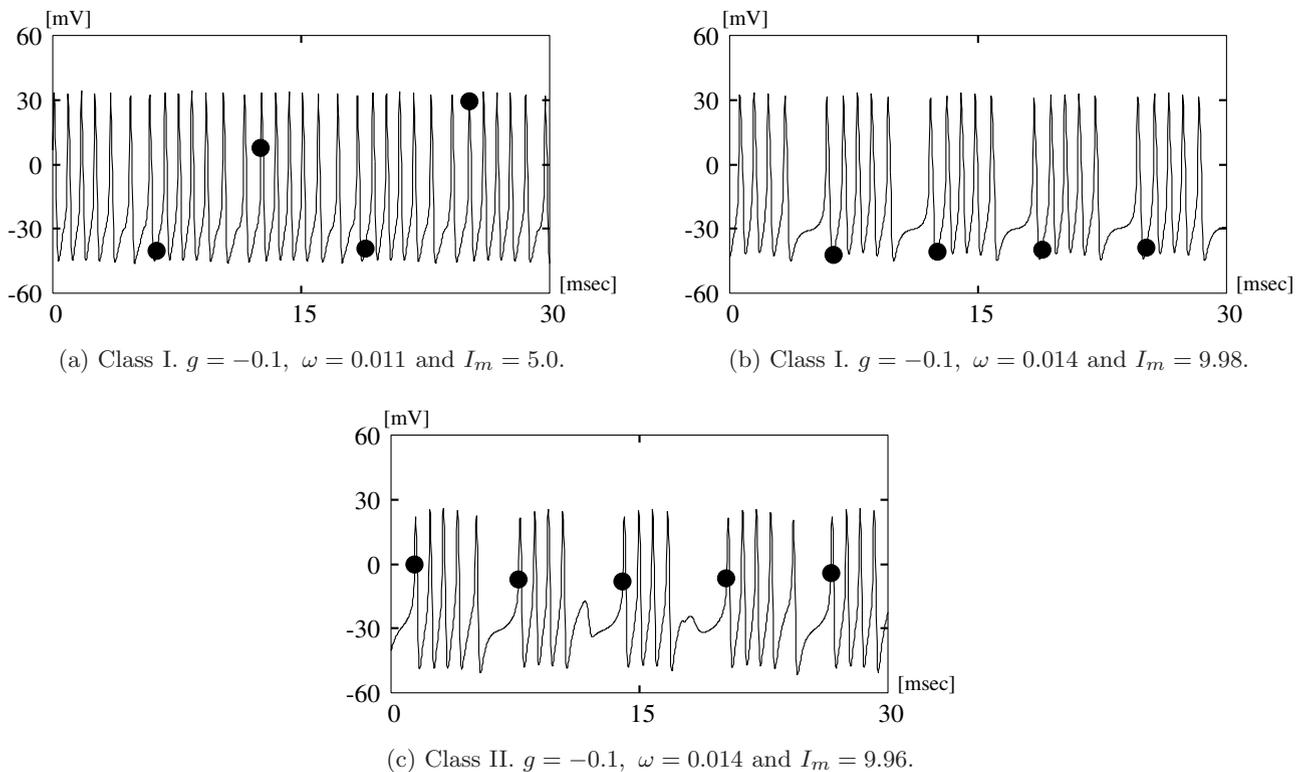


Fig. 5. Waveform of (a) $C_v = 0.16$, (b) $C_v = 0.49$ and (c) $C_v = 0.70$. The closed points are from the Poincaré mapping.

regular spikes are generated [Figs. 5(a) and 5(b)]. On the other hand, C_v is high for some parameter values for class II neurons and irregular burst spikes are produced.

4. Conclusion

We have investigated forced synchronization of class I and class II neurons. As similar to the results of mutual synchronization, class II neurons have wider parameter regions of forced synchronization. However, we found that the bifurcation structure and

patterns of spikes of class II are complicated; there exist period-doubling bifurcations, interesting two-periodic oscillations and bursting spikes with high values of the coefficient of variation of the interspike interval. It is an open problem to study universality of these phenomena.

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