Modified integrate-and-fire models with excitatory or inhibitory synaptic couplings and synchronization phenomena

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Abstract

In this paper, we propose a new type of neuronal firing model and study synchronization phenomena in the two coupled models. By analytically constructing the return map of solution to the model, we systematically investigate conditions for the occurrence of in-phase as well as anti-phase synchronized oscillation, in terms of parameters representing the synaptic strength and the decaying relaxation rate of synaptic couplings.

1. Introduction

Previous physiological and computer simulation experiments[1, 2] have demonstrated that neuronal ensembles become asynchronized and synchronized by mutual excitatory and mutual inhibition respectively. A theoretical study[3] based on the two integrate-and-fire (IF) oscillator models and on two phase oscillator models with synaptic couplings, has given an explanation of how the synaptic time constant governs the stability of phase-locked solutions. It was confirmed that inhibitory synchrony and excitatory asynchrony occur when the synaptic time constant is small. That is, the key reason for the occurrence of excitatory or inhibitory synchronization in the two neuron models is that synaptic response is longer than the width of action potential, namely slow synaptic response. In their work, systematic exploration of the parameter space of the synaptic and model dynamics, however, has been lacking.

On the other hand, in the other previous works[4, 5, 6, 7, 8], studies based on simulations of networks of either two or more synaptically interconnected neurons with time-delay couplings have extensively been conducted to systematically explore the collective behavior such as synchronization phenomena. Although these studies haven't analyzed the behavior, it enables us to consider that the study of two coupled neurons can still yield a useful insight into the synchronization phenomena found in larger neural networks.

In this paper, we propose a new type of neuronal firing model and study the behavior of the so-called double integrate-and-fire (DIF) models with excitatory or inhibitory interaction. Solving the equations, we analytically construct the return map of the solutions to examine conditions for the occurrence of synchronized oscillations of the in-phase ($\frac{T'}{T} = 0$ or 1) as well as the anti-phase ($\frac{T'}{T} = 0.5$), in terms of the parameters representing the strength and the decaying time constant of the synaptic couplings. As a result, we show that the results agree with the previous ones[3]. Then, we summarize the result by drawing a phase diagram of the parameter space of the synaptic couplings and compare this result with numerical simulations. The simulations are conducted using the fourth-order Runge-Kutta method for the DIF model.

2. Proposition of a new model and the solutions

We begin by proposing a new type of neuronal firing model. The so-called double integrate-and-fire (DIF) model modifies the original IF model by adding the equation that demonstrates the duration of firing, namely $-\gamma x$. Then, we describe two interconnected neuronal oscillators of the DIF type with synaptic couplings:

$$\frac{dx_i}{dt} = F(x_i) + I_{syn}^{(i)} \qquad (i = 1, 2) \quad (1)$$

$$F(x) = \begin{cases} -\gamma x & [\theta_2, X_1] \\ X_0 - x & [0, \theta_1] \end{cases} \quad (2)$$

where θ_1 and θ_2 are the thresholds for the starting and finishing of a neuronal firing. γ is the decaying relaxation rate for the dynamics of a firing. x is an activation variable like membrane potential. Here we call $[\theta_2, X_1]$ and $[0, \theta_1]$ the firing and non-firing phases respectively. In the original IF model, when an activation variable arrives at the threshold ($x = \theta_1$) it is reset to 0. However, when we consider the DIF model, even if x arrives at the threshold, it is not reset to 0 and jumps up to $x = X_1$

to start firing. Its trajectory follows as an exponential decaying path over time until $x = \theta_2$. Then, it is reset to 0.

The DIF model is a more general one because, taking the limit of $\gamma \to \infty$, the aforementioned equations become the same as those in the original IF model. In spite of retaining the physiological neuron's impulse, this model shows simplified dynamics of the firing. It also allows us to analytically understand synchronization phenomena in the two coupled neurons and to systematically explain them by the characteristic of synaptic response.

For synaptic coupling $I^{(i)}_{syn}$, we incorporate first order kinetics

$$I^{(i)}_{syn} \quad = \quad G_{syn} s_{\bar{i}} \tag{3}$$

where $\bar{i}$ represents the counterpart of neuron i and G_{syn} the synaptic strength. It represents excitatory couplings when $0 < G_{syn}$, and inhibitory ones when $G_{syn} < 0$. We consider s_j to obey the following equation:

$$\frac{ds_j}{dt} \quad = \quad \begin{cases} 0 \longrightarrow s_j = 1 & (x_j > \theta_1) \\ -\beta s_j & (x_j < \theta_1). \end{cases} \quad (j = 1, 2) \tag{4}$$

where β represents the synaptic decaying relaxation rate. The equation demonstrates instantaneously rising and slow decaying synaptic response.

To systematically analyze and understand the behavior of the dynamics of the two interconnected DIF type of oscillators, we first need to solve the model and then consider the following three fundamental cases according to whether two neurons are firing or not.

- CASE 1: Both neurons are firing.
- CASE 2: One neuron is firing while the other is not.
- CASE 3: Neither neuron is firing.

3. Temporal firing pattern diagram and return map

To systematically understand the behavior of the dynamics of the two coupled neurons, we consider, as an initial condition, the state of the two neurons that occurs immediately after one of them has fired. We then analytically construct the return map corresponding to the time evolution of the system with use of the three fundamental types of solutions. To this end, it is necessary to denote some temporal firing pattern diagrams (TFPDs), which represent how each neuron switches between the firing and non-firing phases. According to the feature of the TFPD, we obtain two- or three-dimensional maps. They enable us to gain some solutions from the synchronization phenomena in the model.

There can be several TFPDs leading to in- and anti-phase synchronizations of the two interconnected neurons. The simplest and most important case can be shown in Tables I and II. TABLE I shows that, supposing both neurons are firing, one expects the neuron that stops firing earlier can start firing and become active after the other neuron stops firing. TABLE II shows that, supposing both neurons are firing, one expects the neuron that stops firing earlier can start firing before the other neuron stops firing.

We construct the return map by focusing on the state of the two neurons that exists immediately after the second neuron has fired. Let $x_1^{(n)}$, $x_2^{(n)}$, $s_1^{(n)}$ and $s_2^{(n)}$ denote the values of x_i and s_i for the occurrence of such states. The return map can be defined as a map from $(x_2^{(n)}, s_1^{(n)}, s_2^{(n)})$ to $(x_2^{(n+1)}, s_1^{(n+1)}, s_2^{(n+1)})$. We then support $x_1^{-+}(0) = x_1^{++}(0) \equiv x_1^{(n)}$, $x_2^{+-}(0) = x_2^{++}(0) \equiv x_2^{(n)}$, $s_1^{-}(0) = s_1^{+}(0) \equiv s_1^{(n)}$ and $s_2^{+}(0) \equiv s_2^{(n)}$. Here time 0 is set to one when neuron 1 starts firing and hence the initial state of neuron is $x_1^{(n)} = X_1$. In line with Tables I and II, we then write build the return maps of the solution to eqs.(1) $\sim$ (4) for studying the Tables, that is, $F^{(i)}(x_2^{(n)}, s_1^{(n)}, s_2^{(n)}) = (x_2^{(n+1)}, s_1^{(n+1)}, s_2^{(n+1)}) = (x_2^{++}(\Delta_1 + \Delta_1'), s_1^{+}(\Delta_1 + \Delta_1'), s_2^{+}(\Delta_1 + \Delta_1'))$ where $i = \mathrm{I}, \mathrm{II}$.

Moreover, from the TFPD analysis of the solutions of the map, we obtain the time lag rates between the firings of the two neurons at the solutions and define the rate as $\frac{T'}{T}$. T is neuron 1's spike interval. T' is the time that it takes for neuron 2 to start firing after neuron 1 has fired. We denote the rate as following:

- $\frac{T'}{T} = 1.0$ and 0.0 : the in-phase synchronized solution
- $0.75 \leq \frac{T'}{T} < 1.0$ and $0.0 < \frac{T'}{T} \leq 0.25$: the quasi-in-phase synchronized solution
- $0.5 < \frac{T'}{T} < 0.75$ and $0.25 < \frac{T'}{T} < 0.5$: the quasi-anti-phase synchronized solution
- $\frac{T'}{T} = 0.5$: the anti-phase synchronized solution.

4. Simulation and linear stability analysis

Now we set $X_0 = X_1 = 2$, $\gamma = 1$ and $\theta_1 = \theta_2 = 1$ to gain more easily some synchronized solutions. We then show the results of the synchronization phenomena of our system obtained theoretically and by numerical simulations.

The whole return map $F(x_2^{(n)}, s_1^{(n)}, s_2^{(n)})$ is defined as $x_2^{(n)}$ in the entire region of the firing and non-firing

Duration	CASE	neuron 1	neuron 2
$[0, t_2]$	1	$+$	$+$
$[t_2, \Delta_1]$	2	$+$	$-$
$[\Delta_1, t_2 + \Delta_2]$	3	$-$	$-$
$[t_2 + \Delta_2, \Delta_1 + \Delta_1']$	2	$-$	$+$

Table 1: Type I time evolution of neurons 1 and 2. t_2 and Δ_1 is the duration of an action potential. Δ_1' and Δ_2 represent the time durations of neurons 1 and 2 staying in the non-firing phase. There are three CASE scenarios. "$+$" and "$-$" indicate that each neuron is firing and non-firing.

Duration	CASE	neuron 1	neuron 2
$[0, t_2]$	1	$+$	$+$
$[t_2, t_2 + \Delta_2]$	2	$+$	$-$
$[t_2 + \Delta_2, \Delta_1]$	1	$+$	$+$
$[\Delta_1, \Delta_1 + \Delta_1']$	2	$-$	$+$

Table 2: Type II time evolution of neurons 1 and 2.

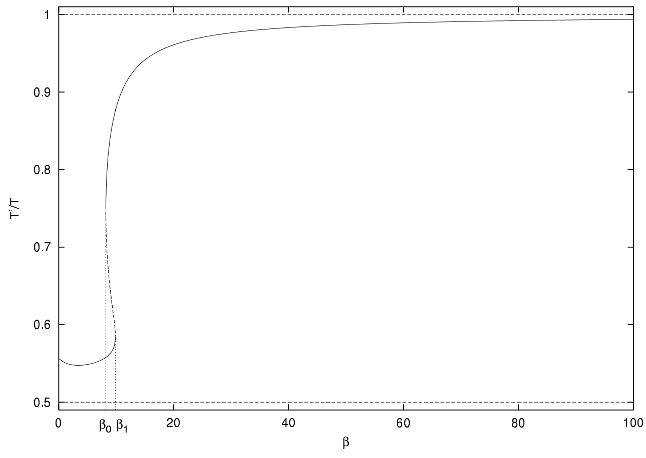

Figure 1: β-$\frac{T'}{T}$ diagram in the case of excitatory couplings.

phases. This map can be obtained by incorporating other TFPDs as well as the TFPD Types I and II shown in Tables 1 and 2. On the basis of such a return map, we deal with in-phase as well as anti-phase synchronized solutions together with the transient dynamics incorporated into them after a long period of time. As a result, we obtain some parameter spaces of synaptic dynamics, as shown in Figures.1 and 2.

Fig.1 represents the plot of $\frac{T'}{T}$ as a function of β in the case of weak excitatory synaptic couplings ($G_{syn} = 0.1$). The solid and broken lines demonstrate stable and unstable synchronized solutions respectively. In this figure, the two coupled neurons consist of only the Type I (as shown in Table 1) quasi-anti-phase synchronized solution for $\beta < \beta_0$, the co-existence of the quasi-anti-phase and quasi-in-phase ones for $\beta_0 < \beta < \beta_1$ and only the quasi-in-phase one $\beta_1 < \beta$. Here, in the case of slow rising synaptic response, there also exists the Type II quasi-anti-phase synchronized solution in the system (not as shown). Moreover, we find that the plot $\frac{T'}{T} = 1.0$ is unstable. As a result, when synaptic response decays so slowly, namely small β, the two coupled neurons become synchronized in the quasi-anti-phase. On the other hand, when β is large, the neurons become synchronized in the quasi-in-phase. The neurons cannot become synchronized in the in-phase for any β. Furthermore, the in-phase synchronized solution is also unstable for any G_{syn} (not as shown).

Next, Fig.2 shows the G_{syn}-β phase diagram when the two neurons are interconnected by mutual inhibition. In Fig.2, there occur several types of synchronous behavior after a long time according to the differing level of G_{syn} and β. For Region I, one neuron continue to fire while the other is at rest. While the two interconnected neurons demonstrate the only anti-phase synchronized solution in Region II, they show the co-existence of the anti-phase and quasi-anti-phase (or quasi-in-phase) synchronized solutions in Region III. In Region VII, the in-phase and anti-phase synchronized solutions exist. Moreover, in Region VI, the two neurons become synchronized in the in-phase, the quasi-anti-phase or the anti-phase due to their differing initial conditions. In Regions IV and V, the two neurons become synchronized in the only in-phase and only quasi-anti-phase respectively. The notable point is in Region VIII, where there occur some synchronization phenomena with an alternating firing order of two neurons. For any β and G_{syn}, alternating the firing order, the two neurons' system are attracted to the in-phase, the anti-phase synchronized solutions and synchronized solutions with a constant phase difference of the two neurons.

To analyze the existence of alternating firing order of two neurons, or the instability of $G_{syn} > 0$, we define the phase difference at n-th iterate between two neurons, as $x_n \equiv x_2^{(n)} - \theta_2 (x_n \geq 0)$. To this end, in line with the Type I TFPD, it is necessary to construct a one-dimensional return map for the phase difference at $(n+1)$-th iterate, namely $f(x_n) = f_1(x_n - \theta_2) - \theta_2$. Here $f_1(x)$ is the value of x_2 that occurs immediately after neuron 1 has fired again. Therefore, the linear stability of the map enables us to gain some boundary line of stable and unstable in-phase solutions, or alternating and non-alternating firing orders.

We finally investigate the map $x_{n+1} = f(x_n)$. Note that $x = 0$ is a fixed point solution of $x_{n+1} = f(x_n)$ and gives rise to the in-phase synchronization of two neurons. Stability of this solution is examined by the linear

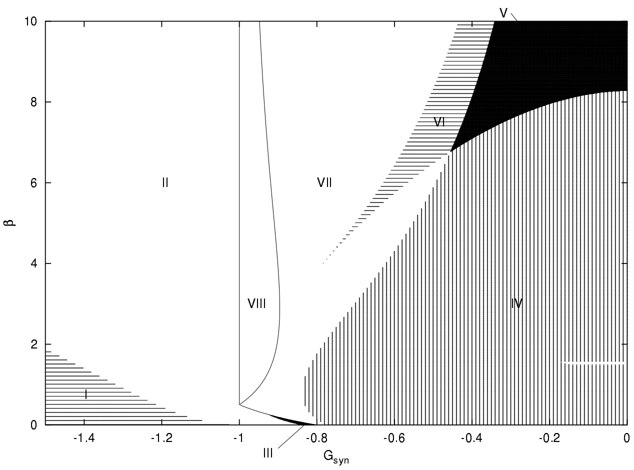

Figure 2: G_{syn}-β phase diagram for $G_{syn} < 0$.

stability analysis:

$$\left.\frac{df}{dx}\right|_{x=0} = \frac{(-\gamma X_1 + G_{syn}e^{-\beta T_2})(Ae^{-T_2} + \beta B(e^{-\beta T_2} - e^{-T_2}))}{(\theta_1 - A)(\gamma X_1 - G_{syn})} \quad (5)$$

where $A = X_0 + G_{syn}$, $B = \frac{G_{syn}}{1-\beta}$ and T_2 is satisfied with $X_0(1 - e^{-T_2}) + B(e^{-\beta T_2} - e^{-T_2}) = \theta_1$.

Stability condition is given by $0 \leq \left.\frac{df}{dx}\right|_{x=0} < 1$. Accordingly, $\left.\frac{df}{dx}\right|_{x=0} = 1$ represents the boundary line which determines whether the synchronized solutions are stable or unstable. The equation show implicitly that $G_{syn} > 0$ is unstable and represents the solid boundary line between Regions II and VII in Fig.2. On the other hand, $\left.\frac{df}{dx}\right|_{x=0} = 0$ demonstrates the boundary line of alternating and non-alternating firing orders, which represents the solid curve between Regions VII and VIII as shown in Fig.2. Therefore, we show that two neurons become synchronized in the in-phase with an alternating firing order. Moreover, we understand that two neurons become synchronized in the in-phase when $G_{syn} < 0$, while they never become synchronized in the in-phase when $G_{syn} > 0$.

5. Conclusions

In this study, the proposed model makes it possible to thoroughly and systematically explain synchronizational behavior by studying the characteristics of synaptic response. As a result, from Figures 1 and 2, we find that the key feature that determines excitatory asynchrony and inhibitory synchrony is that synapse response is longer than the width of action potential, namely a slow synaptic response. This result obtained by the figures supports the conclusions drawn by a diversity of researchers[2, 3]. Moreover, a new observation is made in Regions I and VIII for $G_{syn} < 0$ in Fig.2. We then show that the analysis is consistent with numerical simulations.

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