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An Analysis of Synchrony Conditions for Integrate-and-Fire Neurons

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Abstract. Many researchers have studied integrate-and-fire neurons and it has been shown that inhibitory connections among neurons can generate synchronized activations, if transmission delays are introduced. Transmission delays and coupling strength influence synchronization significantly. In this paper, it is shown that initial phase differences among neurons are also important factors to trigger synchronization. As a result, synchrony conditions for integrate-and-fire neurons can be determined by the relationship between the initial phase and transmission delays as well as between the coupling strength and the phase lag.

1 Introduction

Local lateral inhibition plays an important role on synchronization [7]. Especially transmission delays greatly influence the synchronization. The excitatory connections without transmission delays and without refractory period were investigated [6, 1, 3]. Mirollo and Strogatz emphasized that the convex monotonous function of membrane potentials is critically important for synchronization. They showed the analysis for dynamic systems of phase difference, but did not consider transmission delays and refractory delays for spiking neuron models. In fact, the desynchronizing effect of excitatory connections, when they are involved with transmission delays, was reported [7, 5].

It has been shown that transmission delays greatly influence synchronization for excitatory and inhibitory connections [2, 7, 4, 9]. Nischwitz and Glünder showed that some level of transmission delays can cause desynchronization and also the synchrony performance is periodic with respect to transmission delays in simulation.

Transmission delays have been so far considered as one of main important factors for synchronization, but initial phases between oscillators have been neglected. In this paper, it is proposed that synchronization is influenced by

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initial phase differences among spike neurons as well as transmission delays and coupling strength. A formulation for their relationship is studied in this paper.

2 Model

In a integrate-and-fire neuron model, an oscillator integrates its membrane potential and fires a spike, once it reaches its threshold, and then resets its potential to zero. In this paper a simple model of temporal integration for membrane potentials will be considered. It is a leaky integrate and fire neuron with constant input.

$$\frac{1}{\tau}\dot{x}_i = -x_i + c \cdot I + \sum_{k=1,k\neq i}^{N} \epsilon_{ki} s(x_k)$$

where s is the spike function to generate an impulse, N is the number of neighbouring neurons, x_i is the membrane potential, ϵ_{ki} is a connection weight from neuron k to i, and I is the input. When oscillator i reaches its threshold, it will generate a spike and then its value will be reset to zero. This potential function is periodic and its phase function is as follows:

$$\begin{aligned} f(\phi) &= c(1-e^{-\tau\phi}) \text{ if } 0 \leq \phi \leq T \\ g(x) &= \frac{1}{\tau}\log\frac{c}{c-x} \end{aligned}$$

where T is the period for oscillators, g is the inverse function of f and $g(f(\phi)) = \phi$. If $x < 0$, then $g(x) = 0$, and if $x > T$, then $g(x) = 1$.

3 Analysis

We use the same analysis method shown by Mirollo and Strogatz [6]. Let ϕ_α, ϕ_β denote initial phases for oscillators α, β, respectively, where $\phi_\alpha < \phi_\beta$. Then the initial phase difference $\hat{\phi}$ is defined as $\phi_\beta - \phi_\alpha$. Especially inhibitory connections will be focused and we will first start inhibition with no conductance delay and then discuss delayed inhibition.

3.1 Inhibition without transmission delay

Let ϵ be the coupling strength between two oscillators. We define a function w as $w(\phi, \epsilon) = g(f(\phi) - \epsilon)$. It represents a new phase caused by an inhibitory action from an oscillator.

Two oscillators interact each other with inhibition weights. We assume that two oscillators have the same period T and the same coupling strength ϵ. Oscillator β first reaches its threshold and emits a spike. The instantaneous inhibition from oscillator β makes oscillator α drop its potential level by ϵ. Then oscillator α has the phase $w(T - \phi, \epsilon)$. After integration, oscillator α

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reaches its threshold and emits a spike. At this time it will cause oscillator β to have its phase $w(T - w(T - \phi, \epsilon), \epsilon)$. Again oscillator β will integrate its potential and fire, and the above process will be repeated.

For each firing, we can obtain phase difference functions as follows:

$$u_1(\phi) = T - w(T - \phi, \epsilon), \qquad u_2(\phi) = w(u_1(\phi), \epsilon)$$

where $u_1(\phi)$ is the phase difference after the first firing of oscillator β, and $u_2(\phi)$ is the phase difference after the firing of oscillator α. For the next firings of two oscillators, ϕ will be replaced by $u_2(\phi)$ which is the result of two consecutive firings. We assume that synchronization has no phase difference.

We are interested in the fixed point of the iteration process, if it is available. An iteration process changes ϕ into $u_2(\phi)$. Define the iteration function D as $D^{n+1}(\phi) = D(D^n(\phi))$, where $D(\phi) = u_2(\phi)$. For the fixed point, $D(\phi) = \phi$. The derivative for D can be calculated as $\frac{D(\phi)}{d\phi} = w'(u_1(\phi), \epsilon) \cdot u_1'(\phi)$, $\frac{u_1(\phi)}{d\phi} = w'(T - \phi, \epsilon)$. From the definition of w, $w'(\phi) = g'(f(\phi) - \epsilon) \cdot f'(\phi) = \frac{g'(f(\phi)-\epsilon)}{g'(f(\phi))}$. Since $0 \leq w'(\phi) < 1$ for every ϕ and $\epsilon > 0$, the derivative is $0 < D'(\phi) < 1$. For nonlinear dynamic systems, the analytical criterion for stability is $|D'| < 1$ [8]. Hence, the iteration function D has a fixed point. We can observe that u_2 function for D has a fixed point around the middle of phase space for small ϵ, rather than at $\phi = 0$. We can assert that the inhibitory connections without any transmission delay will cause desynchronization. The fixed point will change depending on the coupling strength ϵ. If we choose ϵ such that $u_1(\phi) = w(T - \phi, \epsilon) < T - \phi$ for the first inhibitory action, synchronization will occur. Otherwise, two oscillators will have desynchrony with constant phase lag. This desynchrony result is already reported in some papers [7, 6].

3.2 Inhibition with transmission delays

Now we add transmission delays to inhibitory connections. We can classify the conditions of delayed spike emission into several cases. The similar analysis shown above will be applied. Let δ be transmission delay and $\hat{\phi}$ be the initial phase lag. The period T of integrate-and-fire neurons is scaled down to 1 for convenience and the threshold for firing neuron is fixed to 1. For each case, we obtain a series of phase difference functions as follows:

case 1. $\delta \leq \frac{T}{2}, \quad \hat{\phi} \leq \delta$

$$u_1(\phi) = \delta - w(\delta - \phi, \epsilon) \quad u_2(\phi) = u_1(\phi) - \phi - \delta + w(\delta + \phi, \epsilon)$$

case 2. $\delta < \frac{T}{2}, \quad \hat{\phi} > \delta$

$$u_1(\phi) = \delta - w(T + \delta - \phi, \epsilon) \quad u_2(\phi) = w(\delta + T + u_1(\phi), \epsilon) - \delta$$

case 3. $\delta > \frac{T}{2}, \quad \hat{\phi} \leq T - \delta$

$$u_1(\phi) = \delta - w(\delta - \phi, \epsilon) \quad u_2(\phi) = u_1(\phi) - \phi - \delta + w(\delta + \phi, \epsilon)$$

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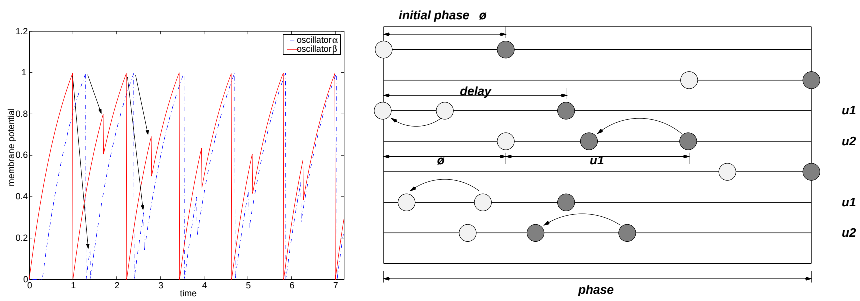

(a) (b)

Figure 1: Two oscillators with transmission delays ($\hat{\phi} = 0.3, \quad \delta = 0.4$) (a) integrate-and-fire process (b) phase diagram for phase lag between oscillators

case 4. $\delta > \frac{T}{2}, \quad \hat{\phi} > T - \delta$

$$u_1(\phi) = \delta - w(\delta - \phi, \epsilon) \qquad u_2(\phi) = u_1(\phi) - \phi - \delta + T + w(\delta + \phi - T, \epsilon)$$

$$u_3(\phi) = u_2(\phi) - u_1(\phi) + \delta - w(\delta - u_1(\phi), \epsilon)$$

$$u_4(\phi) = u_3(\phi) - u_2(\phi) - \delta + T + w(\delta + u_2(\phi) - T, \epsilon)$$

The functions u_1, u_2 are phase differences after each oscillator fires, respectively. The function u_2 will be iterated for the next series of firings. An example of integrate-and-fire process and its phase diagram are shown in Figure 1.

For the case 1, the derivative with respect to ϕ is as follows:

$$u_1'(\phi) = w'(\delta - \phi, \epsilon) \quad u_2'(\phi) = u_1'(\phi) - 1 + w'(\delta + \phi, \epsilon)$$

It will lead to the condition $-1 < u_2'(\phi) < 1$. If $u_2(\phi)$ is used as an iteration function D, it has a fixed point. If ϵ is given such that $w(\delta + \phi, \epsilon) \geq \phi$, then the equation for $u_2(\phi)$ holds. Otherwise, one phase-advanced oscillator will become phase-lagged and the other oscillator will be phase-advanced by $\phi - w(\delta + \phi, \epsilon)$. For the next firings, the phases of two oscillators are reversed and then applied to the above equations (if u_2 is negative, ϕ can be replaced by $-u_2(\phi)$ for the next iteration instead of $u_2(\phi)$). If there exists ϕ on interval $(0, T)$ for a given ϵ such that $u_2(\phi) > 0$, then two oscillators have a unique fixed point at $\phi = 0$. In other words, if u_2 is monotonically decreasing on ϕ, the fixed point does not settle down at $\phi = 0$. There are many fixed points for ϕ such that $-u_2(\phi) = \phi$, and their values depend upon ϵ. From this property, we can estimate the desynchrony condition[1] of ϵ. The condition $u_2(\phi) \leq 0$ for every ϕ should be satisfied for the monotonic function, which can determine the range of ϵ such that $\epsilon > \epsilon_{s_1}$ causes desynchrony. This desynchrony occurs when $u_1(\phi) = \delta$ and $u_2(\phi) \leq 0$. By the desynchrony conditions of $u_2(0) \leq 0$ and $u_2' < 0$, we can obtain $\epsilon_{s_1} = f(\delta)$. Thus, $\epsilon \in (0, \epsilon_{s_1}] = (0, f(\delta)]$ is a synchrony condition for

[1] We assume that the synchrony condition for phase lag is $\phi = 0$ or $\phi = T$.

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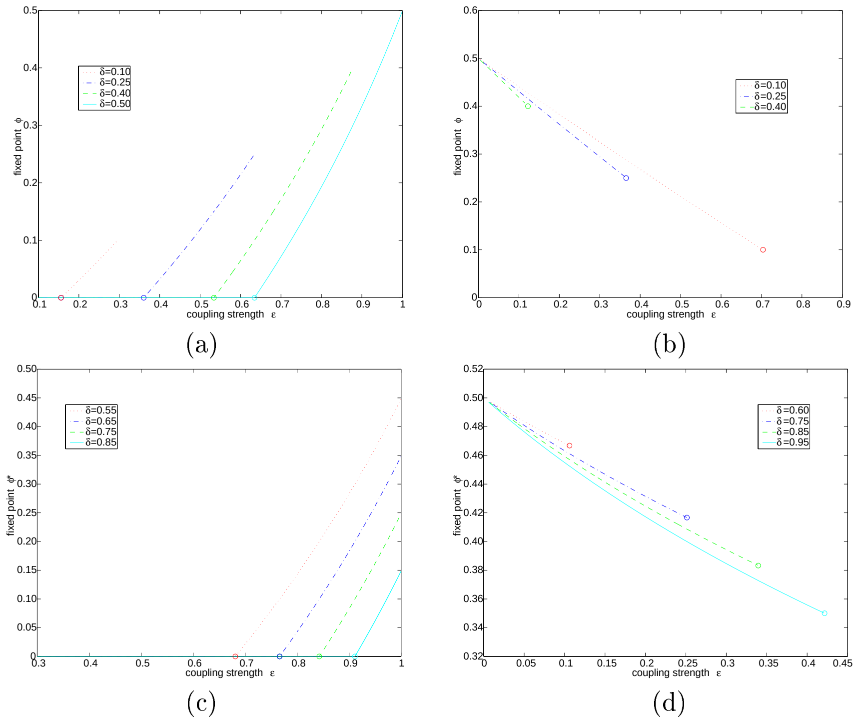

Figure 2: Fixed points on the coupling strength ϵ (a) case 1 (circle: ϵ_{s_1}) (b) case 2 (circle: ϵ_{s_2}) (c) case 3 (circle: ϵ_{s_3}) (d) case 4 (circle: $\epsilon_{s'_4}$)

the case 1. For a given $\epsilon > f(\delta)$, $\phi^* = g(\epsilon) - \delta$ becomes a fixed[2] point for the iteration map D as shown in Figure 2(a).

All the cases (case 1-4) have a fixed point by $|D' = u'_2| < 1$, but they have different attractor positions. If the attractor is located at $\phi = 0$ or $\phi = T$, it can generate synchrony of oscillator neurons. Otherwise, it has desynchrony. In case 2, $u_2(\phi)$ also has a fixed point by its dynamic property $|u'_2(\phi)| < 1$. Especially for $T - \delta \leq \hat{\phi} < T$, the phase difference after the first firing of an oscillator becomes smaller than its transmission delay and thus the problem reduces to case 1. If the initial phase has $\delta < \hat{\phi} < T - \delta$, oscillators tend to be desynchronized by moving phase lags to around half the period. The phase lag has its limit cycle and its fixed point is positioned around half the period, but the fixed point depends on the coupling strength ϵ. Large coupling strength can help synchronization for two oscillators when the phase lag is close to $T - \delta$. If the first firing of a phase-advanced oscillator makes the phase lag smaller than its transmission delay with the help of large coupling strength, this problem can also reduce to the case 1 and thus it has a potential of synchronization. We define the minimal coupling strength ϵ_{s_2} such that

[2]This will hold for $\phi^* \leq \phi < \delta$ and for $0 < \phi < \phi^*$, ϕ itself is a fixed point.

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$|u_1(\phi) = \delta - w(T + \delta - \phi, \epsilon_{s_2})| \leq \delta$. It implies $w(T + \delta - \phi, \epsilon_{s_2}) < 2\delta$. Thus, ϵ_{s_2} can be estimated as $1 - f(2\delta)$. If $\epsilon \in (\epsilon_{s_2}, \epsilon_{s_1}]$ where ϵ_{s_1} is determined in the case 1, then two oscillators will synchronize. For example, for a given delay $\delta = 0.40$, $\epsilon_{s_2} = 1 - f(2\delta) = 0.1222$ and $\epsilon_{s_1} = f(\delta) = 0.5339$. With coupling strength $\epsilon \in (0.1222, 0.5339]$, two oscillators will synchronize regardless of initial phase. Also there may exist some initial phase ϕ to synchronize oscillators with $\epsilon < 1 - f(2\delta)$, if $|u_1(\phi) = \delta - w(T + \delta - \phi, \epsilon)| < \delta$.

In case 3, the iteration map has the same form as case 1. Its iteration converges to a fixed point $\phi = 0$ and thus leads to synchrony of two oscillators, unless the coupling strength is too large. If there exists some interval $(0, \phi)$ such that $D^n(\phi) = D(|D^{n-1}(\phi)|) > 0$, then it converges to $\phi = 0$. The desynchrony of oscillators occurs when $u_1(\phi) = \delta$ and $\epsilon > \epsilon_{s_3} = f(\delta)$. For example, $\epsilon = 0.8$ has a set of fixed points for $\phi \in [0, g(\epsilon_{s_3}) - \delta] = [0, 0.093]$ where $\epsilon_{s_3} = f(\delta)$.

In case 4, a series of firing continues and awaits inhibitory action for an oscillator while the other oscillator experiences phase shift. It is because two oscillators have relatively long transmission delays and phase lags. Thus, two previous firing actions should be applied to calculate the next phase shift.

$$\begin{aligned}
\phi_1 &= u_2(\phi_0) = w(\delta + \phi_0 - T, \epsilon) - w(\delta - \phi_0, \epsilon) - \phi_0 + T \\
&\dots \\
\phi_n &= w(\delta + \phi_{n-1} - T, \epsilon) - w(\delta - \phi_{n-1} - z_{n-1}, \epsilon) - \phi_{n-1} + T - z_{n-1}
\end{aligned}$$

where $z_n = u_{2n-1} - u_{2n} = \phi_{n-1} + \delta - T - w(\delta + \phi_{n-1} - T, \epsilon)$. From the above equation for $D^{(n)} = \phi_n$, we can obtain the following derivative:

$$\begin{aligned}
D' &= w'(\delta + \phi - T, \epsilon) - w'(\delta - \phi - z, \epsilon)(-1 - z') - 1 - z' \\
&= (1 + z')w'(\delta - \phi - z, \epsilon) - 2z'
\end{aligned}$$

where $z' = 1 - w'(\delta + \phi - T, \epsilon)$. If we have $0 < z' < 0.5$, then we can obtain stable fixed points by $|D'| < 1$. If w is continuous and its derivative is defined, $0 < z' < 0.5$ holds within a range of coupling strength.

If $\hat{\phi} < \delta$ for case 4, then it follows the formulation for the case 4. Otherwise, the formulation of firing sequences depends on the result of u_1, one transmission delay after the first firing of a phase-advanced oscillator; if $\hat{u_1} = |\delta - w(T + \delta - \hat{\phi}, \epsilon)| \leq T - \delta$, it follows the case 3 formulation. That is, the condition with synchrony potential is $w(T + \delta - \hat{\phi}, \epsilon) \geq 2\delta - T$, thus leading to $\epsilon < f(\delta) - f(2\delta - T)$ with $\phi > \delta$. Thus, $\epsilon \in (0, f(\delta) - f(2\delta - T))$ will guarantee synchronization for any $\phi > \delta$. Also there may exist some initial phase $\phi > \delta$ to synchronize oscillators with $f(\delta) - f(2\delta - T) < \epsilon < 1 - f(2\delta - T)$. If $\hat{u_1} > T - \delta$, then the firing sequence of two oscillators starts with a new phase lag $\hat{u_1}$ which follows the case 4 formulation.

To obtain stable fixed points ($\phi^* > 0$) in case 4, we need a phase shift z such that $w(z, \epsilon) > 0,\ \phi^* + \delta - T = z,\ 2z + \phi^* \leq \delta$, where ϕ^* is a fixed point. From this relationship, we can find the maximal coupling strength $\epsilon_{s'_4} = f(\frac{2\delta - T}{3})$ so that $\epsilon < \epsilon_{s'_4}$ can imply local stability of iteration map. Figure 2(d) shows fixed points depending on the coupling strength.

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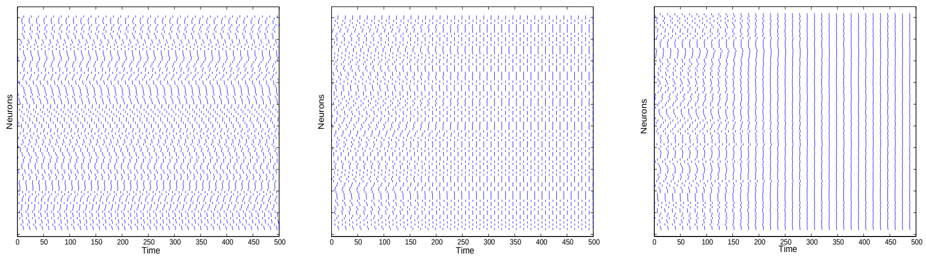

(a) (b) (c)

Figure 3: Synchronization of 100 neurons (vertical bar: neuron spike) (a) $\delta = 0$ (b) $\delta = 0.2T$ (c) $\delta = 0.5T$

If we summarise the above result, the synchrony condition for coupling strength is as follows:

case 1: $\epsilon \in (0,\ \epsilon_{s_1}] = (0,\ f(\delta)]$
case 2: $\epsilon \in (\epsilon_{s_2},\ \epsilon_{s_1})] = (1 - f(2\delta),\ f(\delta)]$ with $|u_1| \le \delta$
case 3: $\epsilon \in (0,\ \epsilon_{s_3}] = (0, f(\delta)]$
case 4: $\epsilon \in (\epsilon_{s_4},\ \epsilon_{s_3}) = (0,\ f(\delta) - f(2\delta - T))$ with $|u_1| \le T - \delta$

It is so far shown that there are many synchrony conditions for transmission delays less than period T. The integrate-and-fire neuron model has a period T and the phase difference between two oscillators are within T. It is believed that longer transmission delays have almost the same effect as transmission delays within the period, though they are slow to update a new phase information. If $\delta > T$, we can represent it as $\delta = nT + \hat{\delta}$. The synchrony condition for δ is similar to that for $\hat{\delta}$ which is smaller than T, unless δ is too large. We can apply the same rules shown above to long transmission delays. This kind of periodic phenomenon has been shown in simulation [7, 5]. Figure 3 shows synchrony of multiple neurons. We can infer from the analysis that the best transmission delay is half the period of integrate-and-fire neurons. Even multiple neurons with constant coupling strength, which is given as one over the number of neighboring neurons, show the best performance for the delay of half the period. In addition, strong coupling strength can accelerate the synchrony even if the delay is different from half the period.

Mirollo and Strogatz showed the formal analysis for excitatory connections without transmission delay and the excitatory connections can lead to synchrony [6]. When transmission delays are added to excitatory couplings, dynamic systems for iteration map have a fixed point not any more at $\phi = 0$ or $\phi = T$. Normally they have a fixed point around $\phi = \delta$ for small coupling strength. It means they have constant phase lag.

Some researchers have worked on post-synaptic models to demonstrate synchrony [2]. From the analysis, it is presumed that their model function has a convex shape with a decay function and dynamic thresholds. Their model is

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different from the simple model in this paper, but a sequence of firings will be influenced by the derivative of phase lag functions in a similar way and thus the synchrony will depend on coupling strength and initial phase lags.

4 Conclusion

The synchrony state is not always stable even for inhibitory synapses. It is shown that it depends on the coupling strength and the initial phase lag between two neurons. For the future work we can apply formal analysis to the synchrony of multiple neurons and also have an interest in the analysis of more realistic model such as noisy potential and post-synaptic neuron models. Also we have not considered refractory period in this paper. We will study how refractory period can influence synchrony conditions.

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