Asymmetry in pulse-coupled oscillators with delay

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Abstract

We studied the dynamics of synchronization in asymmetrically coupled neural oscillators with time delay. Stability analysis revealed that symmetric excitatory coupling results in synchrony at multiple phase relations. Asymmetry yields two saddle-node bifurcations of the stable states when coupling is asymmetric. By contrast, with inhibitory coupling only in- or antiphase are stable as long as coupling is symmetric. Otherwise these stable states shift or even vanish. The reduced bi-stability range suggests the beneficial role of asymmetric coupling for reliable neural information transfer.

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Entrainment of weakly coupled, nonlinear oscillators is well-known for many years [1, 2]. More recently, the synchronization dynamics in realistic settings received considerable interest, e.g. in nanomechanical oscillators [3], dynamic gene expression [4, 5], and in neuronal networks [6–8], to mention a few. Interestingly, entrainment is believed to support information transfer in biological networks [9–12]. In this study we discuss the emergence of and changes in synchronization between realistic neuronal systems described by nonlinear, pulse-coupled oscillators [13, 14]. Interaction between neurons is realized via changes in the membrane potential of a neuron due to the arrival of action potentials from another neuron at corresponding synapses. In several studies neural systems were investigated in the case of symmetric coupling. Mirollo and Strogatz [14] provided a rigorous discussion of two pulse-coupled oscillators with symmetric excitatory connections and showed that they synchronize at zero phase difference. Ernst and coworkers [15, 16] extended this study by introducing a time delay in the coupling due to finite conduction velocities of action potentials. The analytically derived return map of their model revealed that neurons with symmetric excitatory coupling synchronize at a phase lag equal to the delay, whereas in agreement with [17] inhibitory coupling results in stable in-phase synchronization, irrespective of the delay.

For two mutually connected neurons, the coupling strength from neuron 1 to neuron 2 can differ significantly from that from 2 to 1. Symmetrical coupling between neurons is indeed the exception rather than the rule. A previous study [18] has shown that a network of excitatory all-to-all pulse-coupled oscillators without delay but with slightly different coupling strengths always synchronizes, similar to the fully symmetric case in [14]. If time delays are introduced in a population of excitatory neurons with symmetric coupling, the network reveals emerging and decaying synchronized clusters [15]. For inhibitory coupling with time delays the activity reveals synchronization in multi-stable clusters of common phases. A network with mainly inhibitory pulse-coupled oscillators with time delays and sparse coupling, which synchronizes for symmetric coupling strengths, desynchronizes when coupling strengths become asymmetric [19]. For increasing variation in the coupling strengths the network state changes to an asynchronous, aperiodic state. In the present study we will investigate the stable states and the bifurcation diagram for two asymmetrically pulse-coupled oscillators with time delays for a large range of asymmetry in the coupling, both for excitatory and inhibitory coupling. To anticipate, the analytically derived bifurcation diagrams reveal distinct patterns of mono- and bi-stable states for
asymmetric coupling and, more importantly, novel bifurcation routes: for excitation one of
the states looses its stability and disappears; for inhibition the asymmetry shifts the in-
and antiphase solutions to stable ‘out-of-phase’ states.

Like Mirollo and Strogatz [14] we consider two oscillators with identical cycle period $T$
and describe them by their phases $\phi_i$ with $d\phi_i/dt = 1/T$. Without loss of generality we
normalize the period to $T = 1$. At $\phi_i = 0$ oscillator $i$ is at its lowest state and at $\phi_i = 1$, i.e.
at the end of the cycle, the oscillator reaches threshold, emits a pulse, and resets its phase to
zero. To cover a broad class of neuron models like the leaky-integrate-and-fire neuron with
fast synaptic responses or conductance-based threshold neurons [20], we describe the state
of an oscillator by a smooth, monotonically increasing, concave function $f : [0,1] \rightarrow [0,1]$ as
in [14, 15]:

$$ f(\phi) = b^{-1} \ln \left[ 1 + \left( e^b - 1 \right) \phi \right]. \quad (1) $$

Since the neural oscillator is confined to $f(\phi)$, an input pulse yields a state change that is
tantamount to a phase shift by a fixed amount depending on coupling type and strength.
Two distinct shifts, $\pm \varepsilon_{21}$ and $\pm \varepsilon_{12}$, have to be considered which reflect the coupling
$1 \rightarrow 2$ and $2 \rightarrow 1$, respectively; the type of coupling, i.e. excitation or inhibition, determines whether
the phase will be advanced (‘+’) or delayed (‘−’), respectively. More formally we use the
updating rule for oscillator $i$ [15, 16]:

$$ \phi_{i,new}^{(\pm)} = \begin{cases} 
1 \rightarrow 0 & \text{for } 1 < f(\phi_i) + \varepsilon_{ij} \\
 f^{-1} [f(\phi_i) \pm \varepsilon_{ij}] & \text{for } 0 < f(\phi_i) \pm \varepsilon_{ij} \leq 1 \\
0 & \text{for } f(\phi_i) - \varepsilon_{ij} \leq 0
\end{cases} \quad (2) $$

If the oscillator receives a pulse at state $f(\phi_i) > 1 - \varepsilon_{ij}$ the phase shift immediately causes
a pulse and a reset to phase zero ($\phi_{i,new}^+ = 1 \rightarrow 0$). Each input changes the phase of the
oscillator and thereby the time of the next firing of the oscillator. The change in the time
of the next action potential for input at various phases in the cycle of the oscillator relative
to the period of the oscillator defines the phase response curve [21] of the MS-oscillator
$$ \text{PRC}^{(\pm)} [\phi_i] = \frac{T_{\text{new}} - T}{T} = \phi_{i,new}^{(\pm)} - \phi_i. $$

Positive (negative) values of this function correspond to phase advances (delays) in the sense that they advance (delay) the time of the next spike.

We assess stability of the system via the phase difference at times $t_k$ at which oscillator
$i$ generates the $k^{th}$ pulse, i.e. $\Phi_k = \phi_2(t_k) - \phi_1(t_k)$. Because oscillator $1$ fires and resets
immediately, $\phi_1(t_k) \to 0$ holds, and we can simplify $\Phi_k = \phi_2(t_k)$. This stroboscopic view yields the system’s return map $R[\Phi]$ with fixed points $R[\Phi^*] = \Phi^*$. To illustrate the subsequent stability classification \cite{22}, we briefly sketch the synchronization characteristics in the case of two excitatory couplings \cite{14}; the inhibitory case can be treated equivalently.

For instantaneous couplings, i.e. without finite conduction delays, three different regimes can be distinguished depending on the firing moments $t_k$ and the PRC\(^{(+)}\). We note that here the latter is readily parameterized via the coupling strength $\varepsilon_{ij}$ since we fixed $b$. In regime I oscillator 1 receives a pulse from oscillator 2 late in its cycle and fires immediately, i.e. both are synchronized in phase. In regime II, 1 receives a pulse and returns it with a finite lag and so does 2, i.e. the system is synchronized out of phase. Finally, in regime III oscillator 1 reacts with a certain lag but 2 does reply immediately yielding again in-phase synchronization. The corresponding return maps reveal that the synchronized states are stable in I&III but not in II. That is, the oscillators always synchronize with zero phase lag (in-phase). Further, we incorporate a delay because the emitted pulse may arrive at the other oscillator after a finite time $\tau$. With delay an excitatory coupling results not in three but 14 different regimes. The corresponding return maps contain in total six fixed points, from which one half is asymptotically stable and the other half is unstable. The latter separate the attraction domains of the stable fixed points. Unlike the excitatory coupling, inhibition with delay results in marginally stable fixed points next to the asymptotically stable ones.

Fig. 1 shows the fixed points of the return map as a function of coupling strengths $\varepsilon_{ij}$ and delay $\tau$; in all figures we used $b = 3$. With symmetric coupling $\varepsilon_{21} = \varepsilon_{12} = \varepsilon$, two stable states coexist for small delay $\tau$ as shown in Fig. 1B (upper panel). One state is at $\Phi^* = \tau$ which implies that oscillator 2 drives 1, which in response, fires an action potential immediately after arrival of the pulse. The other one is at $\Phi^* = 1 - \tau - \text{PRC}^{(+)}(\phi_2(t_k + \tau))$. The arrival of the $\tau$-delayed pulse of oscillator 1 yields a phase shift $\text{PRC}^{(+)}(\phi_2(t_k + \tau)) > 0$, which shortens the period of oscillator 2 to $T_{\text{new}} = 1 - \text{PRC}^{(+)}(\phi_2(t_k + \tau))$ and induces a pulse delayed by $\tau$ after 1 has fired. The resulting phase shift increases for larger delays because $\text{PRC}^{(+)}(\phi_2(t_k + \tau)) = 2\tau \left[ \left( 1 / \phi_\text{crit}^{(+)} \right) - 1 \right]$; here we abbreviated $\phi_\text{crit}^{(+)} = \left( e^{k(1-\varepsilon_{12})} - 1 \right) / \left( e^b - 1 \right)$; see also APPENDIX A. The period of the coupled system hence decreases for increasing $\tau$ until it reaches $T_{\text{new}} = 2\tau$. For larger values of $\tau$, the period increases and only one stable state remains representing antiphase synchrony, i.e. $\Phi^* = 0.5 T_{\text{new}} = \tau$. At $\varepsilon =$
$1 - b^{-1} \ln \left[ 2\tau(e^b - 1) + 1 \right]$ two stable states merge via a supercritical pitchfork bifurcation into a single stable state in which the neurons oscillate in antiphase (Fig. 1B, middle and lower panels). Put differently, in the absence of time delays an excitatory coupling leads to in-phase synchronization [14], whereas a delay yields out-of-phase synchronization [16, 17]. Note that the dynamics of synaptic connections, which is typically modeled via $(t/\tau_s^2) \exp \{-t/\tau_s\}$ may add to the here-discussed delay so that larger values of $\tau_s$ may contribute the aforementioned supercritical pitchfork bifurcation from out-of-phase into antiphase synchrony [17]. The explicit form of that dynamics, however, does not alter the qualitative behavior of our system so that a pulse-like coupling appears proper for the current discussion.

As soon as the synaptic coupling strengths differ ($\varepsilon_{12} \neq \varepsilon_{21}$), the pitchfork bifurcation is no longer present and the upper stable state $\Phi^* = T_{\text{new}} - \tau$ disappears for

$$\varepsilon_{21} < 1 - b^{-1} \ln \left[ 1 + (e^b - 1) \left( 1 - 2\tau(1-\phi_{\text{crit}}^{(+)}/\phi_{\text{crit}}^{(+)}) \right) \right], \quad (3)$$

e.g. in the lower panel of 1A. That is, there is only one stable branch, $\Phi^* = \tau$, in which oscillator 2 drives oscillator 1, which, in turn, disappears for

$$\varepsilon_{21} > 1 - b^{-1} \ln \left[ 1 + \frac{e^b - 1}{1 + \frac{1-\phi_{\text{crit}}^{(+)}}{2\tau}} \right], \quad (4)$$

Stable states and corresponding attraction domains are shown in the lower panel of Fig. 1A as a function of coupling strength $\varepsilon_{21}$. At a critical value $\varepsilon_{21} < \varepsilon_{12}$ the upper stable state merges with an unstable equilibrium through a saddle-node bifurcation and vanishes for smaller $\varepsilon_{21}$. For slightly larger coupling strength $\varepsilon_{21}$ the lower stable state merges with an unstable state. Fig. 1A (middle panel) shows the corresponding stable and unstable states as a function of $\tau$ for $\varepsilon_{12} < \varepsilon_{21}$. For this asymmetry, the pitchfork bifurcation at $\varepsilon_{12} = \varepsilon_{21}$ (1B, middle panel) disappears and a saddle-node bifurcation emerges. The two excitatory coupled oscillators are precisely in antiphase if both coupling strengths $\varepsilon_{ij}$ obey

$$\varepsilon_{ij} \geq 1 - b^{-1} \ln \left[ 2\tau(e^b - 1) + 1 \right]. \quad (5)$$

From Fig. 1 and Eq. (5) we can conclude that only if $\varepsilon_{12} = \varepsilon_{21} = 1 - b^{-1} \ln \left[ 2\tau(e^b - 1) + 1 \right]$, the two stable out-of-phase states will merge (in the antiphase state). The supercritical pitchfork bifurcation, which is characteristic for excitatory, symmetrically pulse-coupled oscillators with delay, does not exist for asymmetric coupling and is replaced by two saddle-node
FIG. 1: (Color online) (Un-)stable states for two excitatory, pulse-coupled oscillators with delay. 

A: asymmetric coupling with $\varepsilon_{12} = 0.1$. B: symmetric coupling with $\varepsilon_{21} = \varepsilon_{12} = \varepsilon$. C: Asymmetric coupling with $\varepsilon_{12} = 0.2$. Top: asymptotically stable fixed points of the return map as a function of $\tau$ and $\varepsilon_{21}$. Blue lines represent the cross-sections shown in middle and bottom rows. Middle: stable (blue, solid line) and unstable (red, dashed line) fixed points and their attraction domains as a function of $\tau$ for $\varepsilon_{21} = 0.18$. Bottom: same as middle row as a function of coupling strength for $\tau = 0.3$. 
bifurcations with two stable states, at least when the difference between the two coupling strengths is sufficiently small.

If coupling is inhibitory, the spectrum of solutions and bifurcations changes entirely. Fig. 2B shows the results for inhibitory symmetrically pulse-coupled oscillators with delay. The in-phase synchronization $\Phi^* = 0$ is a stable state for all coupling strengths and delays and a stable antiphase state exists for

$$\varepsilon \leq -b^{-1} \ln \left[ \frac{2\tau - 1}{1 + \frac{1}{e^b - 1}} + 1 \right];$$

see upper surface in Fig. 2B, upper panel, and the cross-section at fixed $\tau$ in the lower panel. Since unstable states are absent, the attraction domain of the antiphase solution is an open manifold: if the phase difference $\Phi$ lies on one of the two separatrices, here at

$$\Phi = 1 - \tau \text{ and } \Phi = (2e^b - 1)\tau + \phi_{\text{crit}};$$

it converges to the stable in-phase state or to the region of marginal stability ($\varepsilon \geq b^{-1} \ln \left[ \tau (e^b - 1)^2 + 1 \right]$). The cross-section for fixed $\tau$ (Fig. 2B, lower panel) shows that in-phase and antiphase states coexist for small $\varepsilon$ and marginally stable states exist for large $\varepsilon$, which agrees with previous studies [e.g. 15]. In the middle and lower panels of Fig. 2B we find that one stable fixed point and two separatrices merge and vanish. This novel bifurcation occurs at

$$\varepsilon = -b^{-1} \ln \left[ \frac{2\tau - 1}{1 + \frac{1}{e^b - 1}} + 1 \right].$$

If asymmetry is introduced to the inhibitory coupling, the in-phase and antiphase do not remain stable (upper panels of Figs. 2A and C). The stable state $\Phi^* = 0$ changes to a stable phase difference near zero (middle and lower panels of Figs. 2A and C). Similarly, a stable near antiphase state exists for a range of values for $\tau$ and $\varepsilon$ being smaller than for the antiphase oscillation in the symmetrically coupled system. For $\varepsilon_{12} < \varepsilon_{21}$ this state merges with the lower separatrix for

$$\varepsilon_{21} = b^{-1} \ln \left[ 1 - \frac{e^{-b\varepsilon_{12}} - 1}{e^{-b} + 2\tau (1 - e^{-b})} \right];$$

see also right-hand side of the stable state range in the middle panel of Figs. 2A and the lower panels of Figs. 2A, C. Similarly, for $\varepsilon_{12} > \varepsilon_{21}$ the near antiphase state merges with the upper separatrix at

$$\varepsilon_{21} = -b^{-1} \ln \left[ 1 + (1 - e^b) \left( 2\tau (1 - e^{-b}) + e^{-b}) \right) \right];$$
FIG. 2: (Color online) (Un-)stable states for two inhibitory pulse-coupled oscillators with delay. 
A: asymmetric case with $\varepsilon_{12} = 0.2$. B: symmetric case: $\varepsilon_{21} = \varepsilon_{12} = \varepsilon$. C: asymmetric coupling with $\varepsilon_{12} = 0.4$. Asymptotically stable fixed points $\Phi^*$ of the return map as a function of $\tau$ and $\varepsilon_{21}$; cf. Fig. 1 now with $\varepsilon_{21} = 0.3$ (middle row) and $\tau = 0.1$ (bottom row).

see left-hand side of the stable state range in the lower panels of Figs. 2A,C and right side of the stable state range in the middle panel of Fig. 2C. At $\Phi^* = 0$ a degeneration to multiple stable states occurs if the minimum value of the actual coupling strengths equals
\[ b^{-1} \ln \left[ \tau \left( e^b - 1 \right) + 1 \right]; \]

see middle panels of Figs. 2A,C and lower panel of Fig. 2C. Notice that the dynamics of synapses, i.e. \( (t/\tau_s^2) \exp \left\{ -t/\tau_s \right\} \) in the inhibitory case with delay makes the marginally stable states disappear and causes the co-existence of stable in-phase and antiphase states for all delays and coupling strengths as long as coupling is symmetric. For asymmetric coupling two stable states co-exist, which are not precisely in-phase or antiphase.

Fig. 3 summarizes the results for different values of \( \tau \). A system with two excitatory pulse-coupled oscillators with delay hence reveals mono- or bi-stability depending on \( \epsilon_{12} \), \( \epsilon_{21} \), and \( \tau \). At the transition from mono- to bistability a saddle-node bifurcation is found. These two saddle-node bifurcations meet at the diagonal \( \epsilon_{12} = \epsilon_{21} \) and combine into a supercritical pitchfork bifurcation.

![FIG. 3: (Color online) Number of stable states for two asymmetric pulse-coupled oscillators as function of excitatory coupling strengths \( \tau = \{0.2, 0.3, 0.4\} \); from left to right. Dark blue areas corresponds to bi-stability contrasting mono-stability outside this area. The light-blue square in the right upper corner represents the region where the two oscillators are in antiphase.](image)

Several studies have studied asymmetry in the coupling between excitatory oscillators. For small differences in mutual coupling strength the results are qualitatively similar to that for symmetrical coupling [18]. In this study we show that two stable states merge into a single stable state, when the differences in coupling strengths increase. Networks with inhibitory pulse-coupled oscillators behave qualitatively different. Denker et al. [19] showed that a population of mainly inhibitory pulse-coupled oscillators desynchronize if asymmetry in coupling strengths increases. In addition to Denker et al.[19], who started with a synchronized network which turns into a desynchronized state for asymmetric coupling, we find that both the in-phase and anti-phase state become unstable.
Symmetrically and asymmetrically coupled oscillators show qualitatively different behavior of mono-/bi-stability. Asymmetric excitatory coupling yields a novel bifurcation pattern in which two saddle-node bifurcations merge into a pitchfork bifurcation when switching to symmetry. For inhibitory coupled oscillators two stable states are present corresponding to either in- or antiphase synchronization in the symmetric case or near in- or antiphase for asymmetric coupling. In the latter case, stable states vanish by merging with a separatrix. When synaptic dynamics are incorporated, marginal stability vanishes and the symmetric inhibitory coupled system has two stable states for all coupling strengths and delays. Irrespective of the coupling type (excitatory or inhibitory, with or without synaptic dynamics) asymmetry generally leads to a smaller range of bio-stability as compared to its symmetric counterpart. A pronounced asymmetry in coupling hence supports the (directed) information exchange between neurons. Information is transmitted reliably in one direction, since the receiving excitatory neuron will instantaneously emit a pulse after arrival of the pulse from the sending neuron. The bifurcation diagrams shows that the transfer of information is robust for fluctuations in coupling strength. Transmission is readily achieved since the receiving neuron is driven by the sending neuron and the phase relation between the neurons does not change in case of small changes in coupling strengths caused by synaptic plasticity.

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APPENDIX A

The PRC of Mirollo & Strogatz shows always a phase advance if the oscillator generates a pulse, which seems improper for realistic neurons. Hence we corrected

$$\text{PRC}^{(+)} = 1 - \phi + \begin{cases} \phi / \phi_{\text{crit}}^{(+)} - 1 & \text{for } \phi \leq \phi_{\text{crit}}^{(+)} \\ 0 & \text{otherwise} \end{cases}$$

where \(\phi_{\text{crit}}^{(+)} = \left( e^{b(1-\varepsilon)} - 1 \right) / (e^b - 1)\) represents the phase at which the maximum shift is reached. When a pulse arrives at the oscillator at phase \(\phi > \phi_{\text{crit}}^{(+)}\), the oscillator emits a pulse. For biological systems the phase shift reaches its maximum when the input arrives in the second half of the cycle period (see [23]), i.e. \(\phi_{\text{crit}}^{(+)} > 0.5\) yielding \(\varepsilon \leq 0.21\). Similarly, for the inhibitory case we used

$$\text{PRC}^{(-)} = -\phi + \begin{cases} e^{-be} \left( \phi - \phi_{\text{crit}}^{(-)} \right) & \text{for } \phi > \phi_{\text{crit}}^{(-)} \\ 0 & \text{otherwise} \end{cases}$$
with $\phi_{\text{crit}} = \left( e^{b\varepsilon} - 1 \right) / \left( e^b - 1 \right)$ and $\phi \in [0, 1)$. Note that here the coupling is not bounded apart from $\varepsilon < 1$.

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[22] The map $R[\Phi] \in [0, 1]$ is defined via $R[\Phi_k] = \Phi_{k+1}$. Fixed points $R[\Phi^*] = \Phi^*$ are asymptotically
stable for $|R'| < 1$, unstable for $|R'| > 1$, and marginally stable if $|R'| = 1$ when $R'$ denotes the map's derivative with respect to $\Phi$.