Oscillatory Phenomena and Stability of Periodic Solutions in a Simple Neural Network with Delay

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A simple (two-neuron) neural network model with two delays is considered. Firstly, the linear stability of the model is studied and the bifurcation set is drawn in the appropriate parameter plane. Then a group of conditions to guarantee the global existence of periodic solutions is given. Finally, numerical simulations are performed to illustrate the analytical results found and comments are given about their possible neurobiological significance.

Key words: neural network, delay, oscillatory phenomena, stability, bifurcation

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1 Introduction

Periodic oscillations and periodic sequences of neural action potentials are of fundamental importance for a variety of brain and body functions. The questions how neural networks can sustain periodic activity for a long time lapse and what makes them fail under certain conditions are of vital importance. Local excitatory connections are, generally, synchronizing but distant ones produce phase shifts between neurons due to the finite axonal conduction time. As this delay in transmission grows larger, the synchronous mode, phase locked oscillations, looses stability and the result is phase-shift between neurons and the appearance of traveling phase waves in the network or long lasting transient oscillations and eventual amplification of stimuli. Delays of a few milliseconds, much smaller than the system time scale can destabilize otherwise apparently robust oscillations [1, 2, 3, 4].

Delays may occur due to the persistence of the postsynaptic potential, which causes the presynaptic oscillations to be felt long after a neuron has fired. Synaptic persistence can lead to synchronization e.g. for large neuron clusters with inhibitory coupling [5]. On the other hand it has also been shown that in, say, a pair of mutually coupled oscillators, a delay may result in the destabilisation of synchrony for inhibitory coupling [6]. Furthermore, in a chain of oscillators with local excitatory coupling and long-range inhibitory coupling delay can produce traveling waves if the long-range connections are strong enough to cause a destabilization of synchrony [7].

Delays have been shown to play a significant role in the dynamics of models incorporating synaptic interactions with synaptic feedback and conduction delay. Recurrent synaptic feedback is common in the vertebrate neurons system [8]. Take two neurons. Then, assume that neuron "1" fires action potentials which travel down its axon. This axon branches and one branch excites neuron "2". The synapses of the latter in turn impinge the former and either excite or inhibit it. Recurrent inhibition has been the more commonly observed. It occurs in spinal motoneurons, in pyramidal cells of the hippocampus, in the cerebellum, thalamus and neocortex, and in the retina and olfactory bulb. Recurrent excitation has been postulated as a cause of seizures in the hippocampus [9, 10, 11, 12].

Since in 1984 Hopfield [13] proposed a simplified albeit paradigmatic neural network model, in which each neuron is represented by a linear circuit consisting of a resistor and a capacitor, connected to other neurons via nonlinear sigmoidal activation functions, called transfer functions, there has been great interest in studying the dynamical properties of neural networks. The sigmoidal function is the most common form of a signal function exhibiting cooperative features e.g. like making all interactions excitatory. Based on the Hopfield neural network model it has been argued that the nonlinear sigmoidal activation functions connecting neurons may include delays due to the earlier mentioned finite propagation time or due to finite switching speed in electronic components in hardware realization [14]. These authors studied the following delayed differential equations

$$C_i \dot{u}_i(t) = -\frac{1}{R_i} u_i(t) + \sum_{j=1}^{n} T_{ij} f_j(u_j(t-\tau_j)), \quad i = 1, 2, ..., n. \tag{1}$$

The variable $u_i(t)$ represents the voltage on the input of the i-th neuron. Each neuron is characterized by an input capacitance, C_i, a delay scale, τ_i and a corresponding sigmoidal transfer function, f_j. The matrix T_{ij} defines couplings in the network. The resistance at the input of each neuron is $R_i = \left(\sum_j |T_{ij}|\right)^{-1}$. There is a critical value of the delay above which a symmetrically connected network will oscillate. In general the dynamics of the system (1) can be very sophisticated and its analytical investigation quite cumbersome and intractable. Thus it seems reasonable to start using the simplest architecture capable to sustain oscillations, i.e. a ring of neurons connected cyclically [15, 16]

$$\dot{u}_i(t) = -\frac{u_i}{T_i} + J_{ii-1} f_{i-1}(u_{i-1}(t-\tau_{i-1})), \quad i = 1, 2, ..., n, \tag{2}$$

further assuming that the time scales of decays are the same for all neurons, $T_i = T$. Then it was found that the delays tend to increase the oscillation period and to broad significantly the spectrum of possible frequencies. When the set of time scales $\{T_i\}$ has different values the quantitative analysis of Eqs. (2) becomes a formidable task.

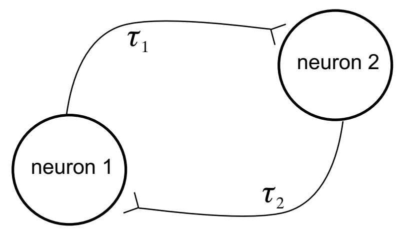

FIG. 1. Sketch of the simplest neural network with different input characteristics and delays in signal propagation. Couplings may be excitatory or inhibitory, that corresponds to positive/negative signs of parameters a and b in Eqs. (3).

In the simplest case of two non-identical neurons, $n = 2$, we can write (Fig. 1)

$$\begin{aligned} \dot{u}_1(t) &= -\mu_1 u_1(t) + aF(u_2(t-\tau_2)), \\ \dot{u}_2(t) &= -\mu_2 u_2(t) + bG(u_1(t-\tau_1)), \end{aligned} \tag{3}$$

where the parameters a, and b account for the coupling strength between neurons. Their values may be different and their signs account for excitatory or inhibitory type of synapses, i.e., according to whether the coupling increases or decreases the potential of the postsynaptic neuron as a response to an activation of the presynaptic neuron. For the system (3) with identical delays in signal propagation, $\tau_1 = \tau_2$, it has been shown that under certain conditions the delay induces a Hopf bifurcation and hence a new genuine, specific oscillatory state [17]. The asymptotic stability of the bifurcated periodic solution has also been studied. A Hopf bifurcation occurs when the sum of the two delays is allowed to vary and passes through a sequence of critical values. Wei and Ruan [18] applied the normal form theory and the center manifold theorem to determine the stability and direction of the Hopf bifurcation. By using the S^1- equivariant degree theory [19] it was assessed the *global* existence of periodic solutions [20]. The study was limited to the case $\tau_1 = m\tau_2$ (or $\tau_2 = m\tau_1$), where m is an integer. Recently, considering $\tau = \tau_1 + \tau_2$ as a bifurcation parameter and using the theory of cyclic systems [21, 22] slowly oscillating periodic solutions in Eqs. (3) have been found [23].

Here we further extend the study of the dynamics of Eqs. (3), assuming that both constants μ_1 and μ_2 are positive, the time delays τ_1 and τ_2 are both non-negative, the restriction $\tau_1 = m\tau_2$ (or $\tau_2 = m\tau_1$) is not imposed, and F and G are bounded $\mathbb{C}^2$-functions. We shall apply the S^1–equivariant degree theory [19] to study the *global* existence of periodic solutions, using the composite coupling parameter

$$\nu = -abF'(0)\, G'(0) \tag{4}$$

as a bifurcation parameter. A positive sign of ν corresponds to excitatory-inhibitory coupling when one neuron excites the other and the latter in turn sends inhibitory feedback to the former. A negative sign of ν describes couplings of the same type, hence either excitatory-excitatory or inhibitory-inhibitory. In Section 2, we transform Eqs. (3) into a form that has a single delay parameter. We show that the origin is a fixed point, which we call base state. Then we study the stability of this base state and we consider the existence of bifurcations when the delay changes value. Besides, we give the bifurcation diagram in the $(\mu_1\mu_2, \nu)$ plane, to show the stability properties of the fixed point. Section 3 is devoted to the investigation of the *global* existence of periodic solutions. In Section 4, we provide a numerical simulation to illustrate the analytical results found. In Section 5 we summarize the general results obtained and point out their possible neurobiological significance.

2 Local stability analysis

For convenience, let us introduce new variables $x(t) = u_1(t - \tau_1)$, $y(t) = u_2(t)$ and the global delay in the neuron circuit $\tau = \tau_1 + \tau_2$ (Fig. 1). The variable $x(t)$ can be considered as the delayed input to the first neuron. Then Eqs. (3) can be rewritten in the form

$$\begin{aligned} \dot{x}(t) &= -\mu_1 x(t) + aF(y(t-\tau)), \\ \dot{y}(t) &= -\mu_2 y(t) + bG(x(t)), \end{aligned} \tag{5}$$

hence reducing the problem to a single delay parameter. Further we shall consider Eqs. (5) together with the following assumptions:

(H_1) $F, G \in \mathbb{C}^2$ and $xF(x) > 0$, $xG(x) > 0$ for $x \neq 0$.

The conditions (H_1) ensure that the origin $0 = (0, 0)$ is a fixed point of Eqs. (5), called here the base state.

2.1 Role of the global delay τ

Figure 2 illustrates the results of the following theorem

Theorem 2.1 *(i) If $\nu < -\mu_1\mu_2$ the base state (0,0) of Eqs. (5) is unstable for all $\tau \geqslant 0$. (ii) If $-\mu_1\mu_2 < \nu \leqslant \mu_1\mu_2$ the base state (0,0) is absolutely stable, hence stability is ensured whatever the value of the delay τ. (iii) If $\nu > \mu_1\mu_2$, there exists a value of $\tau = \hat{\tau}_0 > 0$, such that the base state (0,0) is asymptotically stable when $\tau \in [0, \hat{\tau}_0)$, and unstable for $\tau > \hat{\tau}_0$. Moreover, there exists an infinite sequence of values of the time delay parameter, $\hat{\tau}_0 < \hat{\tau}_1 < ... < \hat{\tau}_j < ...$, such that the system (5) undergoes a Hopf bifurcation at the origin (0,0) when $\tau = \hat{\tau}_j, j = 0, 1, 2, ...$, i.e. at every value of the above given sequence of time delay values.*

The linearization of Eqs. (5) around (0,0) yields

$$\begin{aligned} \dot{x}(t) &= -\mu_1 x(t) + aF'(0)\, y(t-\tau), \\ \dot{y}(t) &= -\mu_2 y(t) + bG'(0)\, x(t), \end{aligned} \tag{6}$$

whose characteristic equation is

$$\lambda^2 + (\mu_1 + \mu_2)\lambda + \mu_1\mu_2 + \nu\, e^{-\lambda\tau} = 0. \tag{7}$$

Lemma 2.1 *In the absence of delay, $\tau = 0$, all solutions of Eq. (7) have negative real parts when $\nu > -\mu_1\mu_2$, and Eq. (7) has a positive solution when $\nu < -\mu_1\mu_2$.*

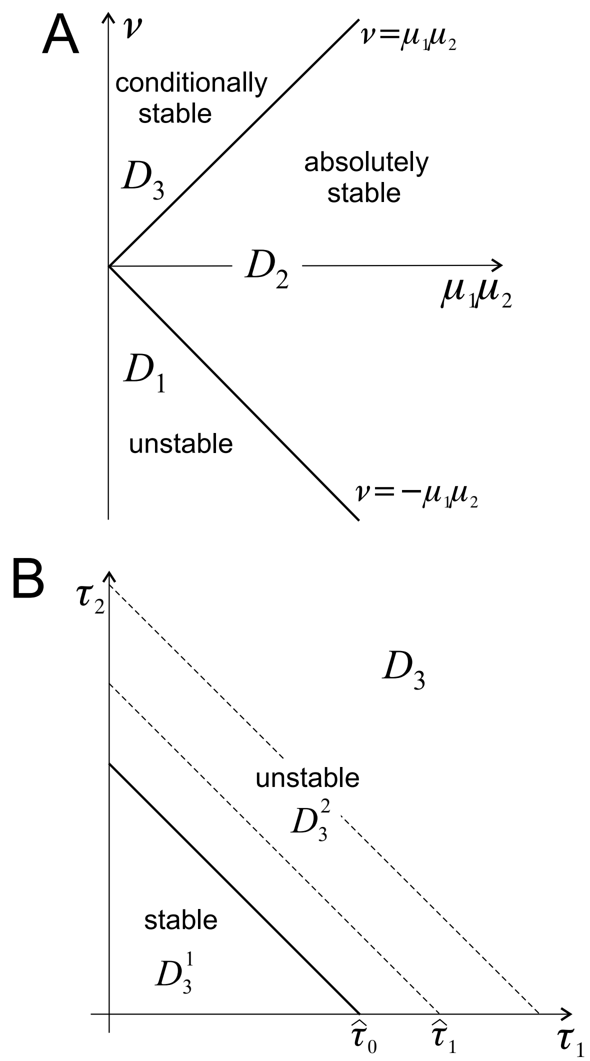

FIG. 2. Bifurcation diagram for the system (5). A). The solid straight lines $\nu = \pm\mu_1\mu_2$ divide the right half plane $(\mu_1\mu_2, \nu)$ in three regions, D_1, D_2, and D_3 with qualitatively different behavior of trajectories in a vicinity of the base state $(0, 0)$ of the system. B). In the region D_3 the local stability of the fixed point depends on the value of the total delay. The value of the delay $\hat{\tau}_0 > 0$ is such that the straight line $\tau_1 + \tau_2 = \hat{\tau}_0$ divides the first quadrant of (τ_1, τ_2)-plane in two regions, D_3^1 and D_3^2. The origin $(0, 0)$ is asymptotically stable in D_3^1, and unstable in D_3^2. For points (τ_1, τ_2) close to the line $\tau_1 + \tau_2 = \hat{\tau}_j$ Eq. (3) has a periodic solution.

Indeed, for $\tau = 0$ the roots of Eq. (7) are

$$\lambda_{1,2} = -\frac{(\mu_1 + \mu_2)}{2} \pm \sqrt{\frac{(\mu_1 + \mu_2)^2}{4} - (\mu_1\mu_2 + \nu)},$$

and Lemma 2.1 follows. ■

Let us now assume that $i\omega$ $(\omega > 0)$ is a root of Eq. (7) with nonzero delay, $\tau \neq 0$, then we have

$$\begin{aligned} \omega^2 - \mu_1\mu_2 &= \nu\cos\omega\tau, \\ (\mu_1 + \mu_2)\,\omega &= \nu\sin\omega\tau, \end{aligned} \tag{8}$$

which implies

$$\omega^4 + \left(\mu_1^2 + \mu_2^2\right)\,\omega^2 + \mu_1^2\mu_2^2 - \nu^2 = 0. \tag{9}$$

Solving Eq. (9) we obtain

$$\omega_\pm^2 = \frac{-\mu_1^2 - \mu_2^2 \pm \sqrt{\left(\mu_1^2 - \mu_2^2\right)^2 + 4\nu^2}}{2}.$$

Accordingly, ω_+^2 is real and non-vanishing when $|\nu| > \mu_1\mu_2$. Otherwise is meaningless. Also the value ω_-^2 is meaningless. Thus we have the following results:

Lemma 2.2 *(i) If $|\nu| > \mu_1\mu_2$, then Eq. (7) has a pair of purely imaginary roots, $\pm i\omega_0$, when $\tau = \hat{\tau}_j = \frac{1}{\omega_0}[\tau_0 + 2\pi j]$, $j = 0, 1, 2, \ldots$ with*

$$\begin{aligned} \omega_0 &= \frac{1}{\sqrt{2}}\left[-\mu_1^2 - \mu_2^2 + \sqrt{\left(\mu_1^2 - \mu_2^2\right)^2 + 4\nu^2}\right]^{\frac{1}{2}} \\ \hat{\tau}_0 &= \begin{cases} \frac{1}{\omega_0}\arcsin\left(\frac{(\mu_1+\mu_2)\,\omega_0}{\nu}\right), & \text{if } \nu \geqslant M^* \\ \frac{1}{\omega_0}\left[\pi - \arcsin\left(\frac{(\mu_1+\mu_2)\,\omega_0}{\nu}\right)\right], & \text{if } |\nu| < M^* \\ \frac{1}{\omega_0}\left[2\pi + \arcsin\left(\frac{(\mu_1+\mu_2)\,\omega_0}{\nu}\right)\right], & \text{if } \nu \leqslant -M^* \end{cases} \\ M^* &= \sqrt{\mu_1\mu_2}(\mu_1 + \mu_2) \end{aligned} \tag{10}$$

(ii) If $-\mu_1\mu_2 < \nu \leqslant \mu_1\mu_2$, then for $\tau \geqslant 0$ all roots of Eq. (7) have negative real parts.

Indeed, from the discussion above follows that when $|\nu| > \mu_1\mu_2$ the only positive root of Eq. (9) is ω_0. Now let $\tau = \hat{\tau}_j$ be such that $\hat{\tau}_0\omega_0 \in (0, \pi)$ when $\nu > 0$, and $\hat{\tau}_0\omega_0 \in (\pi, 2\pi)$ when $\nu < 0$. Then $(\hat{\tau}_j, \omega_0)$ is a solution of the Eq. (8) for $j = 0, 1, \ldots$ Hence $i\omega_0$ is a root of the Eq. (7) with $\tau = \hat{\tau}_j$, $j = 0, 1, \ldots$ and the statement (i) follows.

On the other hand, Eq. (7) has no purely imaginary root when $|\nu| \leqslant \mu_1\mu_2$. Hence $\lambda = 0$ is not a root of Eq. (7) when $\nu \neq -\mu_1\mu_2$. Therefore, Eq. (7) has no roots appearing on the imaginary axis when $-\mu_1\mu_2 < \nu \leqslant \mu_1\mu_2$. By applying Corollary 2.4 from the work by Ruan and Wei [24] and the above given Lemma 2.1 the statement (ii) follows. ■

Now let us consider the behavior of the roots of Eq. (7) near the values $\hat{\tau}_j$. To do this we assume that

$$\lambda(\tau) = \alpha(\tau) + i\omega(\tau), \tag{11}$$

is a solution of Eq. (7) satisfying $\alpha(\hat{\tau}_j) = 0$ and $\omega(\hat{\tau}_j) = \omega_0$.

Lemma 2.3 *$\alpha'(\hat{\tau}_j)$ is positive. Furthermore, we have: (i) if $\nu > \mu_1\mu_2$, then all roots of Eq. (7) have negative real parts when $\tau \in [0, \hat{\tau}_0)$, and for $\tau > \hat{\tau}_0$ Eq. (7) has at least one root with positive real part. (ii) if $\nu < -\mu_1\mu_2$, for all $\tau \geqslant 0$, Eq. (7) has at least one root with positive real part.*

Indeed, substituting $\lambda(\tau)$ into Eq. (7) and taking the derivative with respect to τ, we obtain

$$\left(\frac{d\lambda(\tau)}{d\tau}\right)^{-1}\Bigg|_{\tau=\tau_j} = \frac{(\mu_1+\mu_2)+i2\omega_0}{(\mu_1+\mu_2)\omega_0^2+i\left(\omega_0^3-\mu_1\mu_2\omega_0\right)} + \frac{i}{\omega_0},$$

which implies that

$$\mathrm{Re}\left(\frac{d\lambda(\hat{\tau}_j)}{d\tau}\right)^{-1} = \frac{\omega_0^2}{\Delta}\left[\mu_1^2+\mu_2^2+2\omega_0^2\right] > 0,$$

with $\Delta = (\mu_1+\mu_2)^2\omega_0^4 + \omega_0^2\left(\omega_0^2-\mu_1\mu_2\right)^2$. Now we have

$$\mathrm{sign}\left[\frac{d\alpha(\hat{\tau}_j)}{d\tau}\right] = \mathrm{sign}\left[\frac{d\mathrm{Re}\lambda(\hat{\tau}_j)}{d\tau}\right] = \mathrm{sign}\left[\mathrm{Re}\frac{d\lambda(\hat{\tau}_j)}{d\tau}\right] = \mathrm{sign}\left[\mathrm{Re}\left(\frac{d\lambda(\hat{\tau}_j)}{d\tau}\right)^{-1}\right] > 0.$$

Applying again Corollary 2.4 from the Ref. [24], and the above given Lemma 2.1 and 2.2, the statements (i) and (ii) follow. ■

Finally, applying Lemmas 2.2 and 2.3 and the Hopf bifurcation theorem for retarded functional differential equations ([25], pp. 331-333), then Theorem 2.1 follows. ■

2.2 Role of the composite coupling parameter ν

Ruan and Wei [20] have studied Eq. (7) for $\nu \geqslant 0$, which corresponds to couplings between neurons of different types (excitatory-inhibitory). Here we shall allow $\nu < 0$ hence considering couplings of the same type (and recall τ_1 need not be equal to $m\tau_2$). Then the following conclusions hold:

Lemma 2.4 *(i) Let $\omega_j^+ \in \left(\frac{2(j-1)\pi}{\tau}, \frac{(2j-1)\pi}{\tau}\right)$, and $\omega_j^- \in \left(\frac{(2j-1)\pi}{\tau}, \frac{(4j-1)\pi}{2\tau}\right)$ $j = 1, 2, ...$ be the roots of the equation $\frac{(\mu_1+\mu_2)\omega}{\omega^2-\mu_1\mu_2} = \tan\omega\tau$, and $\nu_j^+ = \frac{(\mu_1+\mu_2)\omega_j^+}{\sin\omega_j^+\tau} > 0$, $\nu_j^- = \frac{(\mu_1+\mu_2)\omega_j^-}{\sin\omega_j^-\tau} < 0$, then Eq. (7), with $\nu = \nu_j^{\pm}$, has a pair of purely imaginary roots, $\pm i\omega_j^{\pm}$, which are both simple. (ii) Let $\lambda = \alpha(\nu) + i\omega(\nu)$ be a root of Eq. (7) satisfying $\alpha(\nu_j^{\pm}) = 0$, $\omega(\nu_j^{\pm}) = \pm i\omega_j^{\pm}$, then $\alpha'(\nu_j^+) > 0$ and $\alpha'(\nu_j^-) < 0$. (iii) Let $\nu_0 = \min\{\nu_j^+\}$, then for $\nu \in (-\mu_1\mu_2, \nu_0)$ all roots of Eq. (7) have negative real parts and when $\nu \notin [-\mu_1\mu_2, \nu_0]$ Eq. (7) has at least one root with positive real part.*

To prove the statements (i) and (ii) it is sufficient to use Lemmas 2.1 and 2.3 from the work Ruan and Wei [20]. To prove (iii) we notice that at $\nu = -\mu_1\mu_2$ Eq. (7) has the root $\lambda = 0$. Thus with $\lambda(\nu)$ being a root of Eq. (7) satisfying $\lambda(-\mu_1\mu_2) = 0$, we substitute it into Eq. (7) and taking the derivative with respect to ν we obtain

$$\frac{d\lambda(\nu)}{d\nu} = -\frac{e^{-\lambda(\nu)\tau}}{2\lambda(\nu)+\mu_1+\mu_2-\nu e^{-\lambda\tau}\tau},$$

and hence

$$\frac{d\lambda(-\mu_1\mu_2)}{d\nu} = -\frac{1}{\mu_1+\mu_2+\mu_1\mu_2\tau} < 0.$$

This implies that Eq. (7) has a positive real root when $\nu < -\mu_1\mu_2$ and close enough to $-\mu_1\mu_2$. On the other hand, we know that $\nu_j^- < -\mu_1\mu_2$, $\alpha'(\nu_j^-) < 0$ and Eq. (7) has no roots appearing on the imaginary axis when $\nu \notin \left\{-\mu_1\mu_2, \nu_j^-, \nu_j^+\right\}_{j=1,...}$. Thus Eq. (7) has at least one root with positive real part when $\nu < -\mu_1\mu_2$.

Since $\nu_0 = \min_{j\geqslant 1}\{\nu_j^+\}$ and $\alpha'(\nu_j^+) > 0$, together with the roots of the Eq. (7) with $\nu = 0$ satisfying $\mathrm{Re}\lambda_{1,2} < 0$, we also have that all roots of Eq. (7) have negative real parts when $\nu \in (-\mu_1\mu_2\,,\ \nu_0)$, and Eq. (7) has at least one root with positive real part when $\nu > \nu_0$. This completes the proof. ■

Then using Lemma 2.4, we have the following theorem.

Theorem 2.2 *For Eqs. (5), under the hypothesis (H_1) and fixed $\tau > 0$ we have: (i) the fixed point in the origin is asymptotically stable if $\nu \in (-\mu_1\mu_2, \nu_0)$, and unstable if $\nu \notin [-\mu_1\mu_2, \nu_0]$, (ii) the system (5) undergoes a Hopf bifurcation of the base state (0,0) when the coupling parameter crosses the sequence of values $\nu = \nu_j^\pm$, $j = 1, 2...$*

3 Global existence of periodic solutions

Let us now investigate the global existence of periodic solutions of the system (5). We introduce the oscillation period p and regard ν as the bifurcation parameter. To proceed further let us make the following assumptions about properties of the transfer functions F and G:

(H_2) *There exists a constant $L > 0$ such that $|F(x)| \leqslant L$ and $|G(x)| \leqslant L$ for all $x \in R$.*

From the above given Lemma 2.4 we have $\lim_{j\to\infty} \omega_j^\pm = \infty$, where we assume that $\omega_{j+1}^+ > \omega_j^+$ and $\omega_{j+1}^- > \omega_j^-$ for $j \geqslant 1$. Then there exist integers j_1 and j_2 such that $\frac{2\pi}{\omega_{j_1}^+} \leqslant \tau$, $\frac{2\pi}{\omega_j^+} > \tau$ for $j < j_1$, and $\frac{2\pi}{\omega_{j_2}^-} \leqslant \tau$, $\frac{2\pi}{\omega_j^-} > \tau$ for $j < j_2$.

Theorem 3.1 *Assuming that the hypotheses (H_1) and (H_2) are satisfied, and either $(b, F'(0), G'(0))$ or $(a, F'(0), G'(0))$ is fixed, we have:*
(i) for $\nu > \nu_{j_1}^+$, the system (5) has at least one periodic solution.
(ii) if $F(x)$ and $G(x)$ are both monotonically increasing functions, and $xF''(x) < 0$, $xG''(x) < 0$ for $x \neq 0$, then for $\nu < \nu_{j_2}^-$, the system (5) has at least one periodic solution.

To prove (i) let us assume that $\nu > \nu_{j_1}^+$ and take $\bar{\nu} > \nu$ to be fixed. Suffices to use Theorem 3.3 from the Ref. [27], which is based on the S^1-equivariant degree theory [19].

Regarding ν and p as parameters we have that $(0, \nu, p)$ is the only stationary solution of Eqs. (5). The corresponding characteristic function

$$\Delta_{(0,\nu,p)}(\lambda) = \lambda^2 + (\mu_1 + \mu_2)\lambda + \mu_1\mu_2 + \nu e^{-\lambda\tau}, \quad (12)$$

is continuous in $(\nu, p, \lambda) \in \mathbb{R} \times \mathbb{R}_+ \times \mathbb{C}$. Thus we can apply the above mentioned Theorem 3.3 by Wu [27]. In particular, $(0, \nu_j^+, \frac{2\pi}{\omega_j^+})$ and $(0, \nu_j^-, \frac{2\pi}{\omega_j^-})$ are centers. In fact, the set of centers is countable and can be expressed as $\left\{(0, \nu_j^\pm, \frac{2\pi}{\omega_j^\pm});\ j = 1, 2, ...\right\}$. Then, $(0, \nu_j^+, \frac{2\pi}{\omega_j^+})$ and $(0, \nu_j^-, \frac{2\pi}{\omega_j^-})$ are all isolated points due to the definition of $\nu_j^\pm$.

The above given Lemma 2.4 ensures that there exist $\varepsilon > 0$, $\delta > 0$ and a smooth curve $\lambda : \left(\nu_j^+ - \delta\,,\ \nu_j^+ + \delta\right) \to C$ such that $\Delta(\lambda(\nu)) = 0$, $\left|\lambda(\nu) - i\omega_j^+\right| < \varepsilon$ for all $\nu \in \left[\nu_j^+ - \delta\,,\ \nu_j^+ + \delta\right]$, and $\lambda\left(\nu_j^+\right) = i\omega_j^+$, $\frac{d}{d\nu}\mathrm{Re}\lambda(\nu)\big|_{\nu=v_j^+} > 0$.

Let $\Omega_\varepsilon = \left\{(u, p) :\ 0 < u < \varepsilon,\ \left|p - \frac{2\pi}{\omega_j^+}\right| < \varepsilon\right\}$. Accordingly, if $\left|\nu - \nu_j^+\right| \leqslant \delta$ and $(u, p) \in \partial\Omega_\varepsilon$ such that $\Delta(0, \nu, p)\left(u + i\frac{2\pi}{p}\right) = 0$, then $\nu = \nu_j^+$, $u = 0$ and $p = \frac{2\pi}{\omega_j^+}$. Theorem 3.3 by Wu [27] can also be applied for $m = 1$. Moreover, if we put

$$H_m^\pm(0, \nu_j^+, \frac{2\pi}{\omega_j^+})(u, p) = \Delta\left(0, \nu_j^+ \pm \delta, p\right)(u + im\frac{2\pi}{p}),$$

then $m = 1$ and we have

$$\gamma_m\left(0, \nu_j^+, \tfrac{2\pi}{\omega_j^+}\right) = \deg_B\left(H_m^-\left(0, \nu_j^+, \tfrac{2\pi}{\omega_j^+}\right), \Omega_\varepsilon\right) - \deg_B\left(H_m^+\left(0, \nu_j^+, \tfrac{2\pi}{\omega_j^+}\right), \Omega_\varepsilon\right) = -1.$$

Using once more Theorem 3.3 from the Ref. [27] we can conclude that the connected component $C\left(0, \nu_j^+, \frac{2\pi}{\omega_j^+}\right)$ through $\left(0, \nu_j^+, \frac{2\pi}{\omega_j^+}\right)$ in Σ is nonempty, where $\Sigma = cl\{(x, \nu, p),\ x$ is a p-periodic solution of Eqs. (5)}. Using the same argument as above, we can show that the first crossing number of each center $\left(0, \nu_j^+, \frac{2\pi}{\omega_j^+}\right)$ is always -1.

On the other hand, if $\nu = 0$, from the assumption (H_1) either $a = 0$ or $b = 0$. Without loss of generality let us consider $a = 0$. Then Eqs. (5) become

$$\begin{aligned} \dot{x}(t) &= -\mu_1 x(t) \\ \dot{y}(t) &= -\mu_2 y(t) + bG(x(t)). \end{aligned} \tag{13}$$

For any initial conditions $(x_0, y_0) \in \mathbb{R}^2$, the solution of the system (13) passing through (x_0, y_0) satisfies $\lim_{t\to\infty} x(t, x_0, y_0) = 0$, $\lim_{t\to\infty} y(t, x_0, y_0) = 0$ hence decays to the fixed point in the origin. Thus Eqs. (5) with $\nu = 0$ have no periodic solution. This implies that no center $(0, \nu_j^-, \frac{2\pi}{\omega_j^-})$ exists in the connected component $C(0, \nu_j^+, \frac{2\pi}{\omega_j^+})$. Therefore, we can exclude alternative (ii) of Theorem 3.3 in the Ref. [27]. Thus we conclude that $C\left(0, \nu_j^+, \frac{2\pi}{\omega_j^+}\right)$ is unbounded.

Let us now prove that the periodic solutions of Eqs. (5) are uniformly bounded for $\nu \in (0, \bar{\nu}]$. We assume that $(b, F'(0), G'(0))$ are fixed, and $M > \max\left\{1, \frac{L}{\mu}\left(\frac{\bar{\nu}}{|\nu|} + |b|\right)\right\}$ is a constant, where $\mu = \min\{\mu_1, \mu_2\}$. Now introducing the distance to the trajectory from the origin, $r(t) = \sqrt{x^2(t) + y^2(t)}$, and calculating its derivative along the solutions of Eqs. (5), we get

$$\begin{aligned} \dot{r}(t) &= \tfrac{1}{r(t)}[-\mu_1 x^2(t) - \mu_2 y^2(t) \\ &\quad + ax(t)F(y(t-\tau)) + by(t)G(x(t))] \\ &\leqslant \tfrac{1}{r(t)}\left[-\mu\, r^2(t) + L\left(|a|\,|x(t)| + |b|\,|y(t)|\right)\right]. \end{aligned}$$

If there is a $t_0 > 0$ such that $r(t_0) = A \geqslant M$, then we have

$$\begin{aligned} \dot{r}(t_0) &\leqslant \tfrac{1}{A}\left[-\mu A^2 + AL\left(|a| + |b|\right)\right] \\ &\leqslant \left[-\mu A + L\left(\tfrac{\bar{\nu}}{|bF'(0)\,G'(0)|} + |b|\right)\right] < 0. \end{aligned}$$

Hence if $(x(t)\ ,\ y(t))$ is a periodic solution of Eqs. (5), then either $r(t) < M$ or $r(t) > M$ for all t. In the later case from the discussion above it follows that $\dot{r}(t) < 0$ for all t, at variance with the fact that $(x(t), y(t))$ is periodic in time. Therefore, for each periodic solution of Eqs. (5), $r(t) < M$ for all t. When $(a, F'(0), G'(0))$ are held fixed, the proof is the same as above.

Let us now show that the period, p, of a periodic solution of Eqs. (5) with $\nu \in [0, \bar{\nu}]$ on $C\left(0, \nu_{j_1}^+, \frac{2\pi}{\omega_j^+}\right)$ is uniformly bounded. In fact Eqs. (5) have no τ-periodic solution. Otherwise, if Eqs. (5) have a τ-periodic solution, say $(x(t), y(t))$, then it satisfies the ordinary differential equations

$$\begin{aligned} \dot{x}(t) &= -\mu_1 x(t) + aF(y(t)) \triangleq P(x, y), \\ \dot{y}(t) &= -\mu_2 y(t) + bG(x(t)) \triangleq Q(x, y), \end{aligned} \tag{14}$$

which means that the system (14) has a periodic solution. On the other hand, on the (x, y)-plane we have

$$\frac{\partial P(x, y)}{\partial x} + \frac{\partial Q(x, y)}{\partial y} = -(\mu_1 + \mu_2) < 0.$$

Hence, due to Bendixson's criterion [26] we can conclude that the system (14) has no periodic solution. Accordingly, the system (5) has no $\frac{\tau}{n}$-periodic solution for any $n \geqslant 1$. By appropriately choosing ν_{j_1} we get that there exists $\kappa \geqslant 1$ such that $\frac{\tau}{\kappa+1} < \frac{2\pi}{\omega_{j_1}^+} < \frac{\tau}{\kappa}$. This shows that in order for $C\left(0, \nu_{j_1}^+, \frac{2\pi}{\omega_{j_1}^+}\right)$ to be unbounded, its projection onto the ν-space must be unbounded. As mentioned above, Eqs. (5) with $\nu = 0$ have no periodic solution. Consequently, the projection of $C\left(0, \nu_{j_1}^+, \frac{2\pi}{\omega_{j_1}^+}\right)$ onto the ν-space must include the interval $[\nu_0, \bar{\nu}]$ with $0 < \nu_0 \leqslant \nu_{j_1}^+$. This shows that for each $\nu > \nu_{j_1}^+$, Eqs. (5) have a periodic solution with the period in $\left(\frac{\tau}{\kappa+1}, \frac{\tau}{\kappa}\right)$. Note that, under the conditions (ii), Eqs. (5) have only one fixed point (0,0) for $\nu \geqslant -\mu_1\mu_2$, and altogether just three fixed points: (0,0), (x_1, y_1) and (x_2, y_2) when $\nu < -\mu_1\mu_2$. The coordinates of these fixed points can be found from

$$x_i = \tfrac{a}{\mu_1} F\left(\tfrac{b}{\mu_2} G(x_i)\right),\ y_i = \tfrac{b}{\mu_2} G(x_i), \quad i = 1, 2. \tag{15}$$

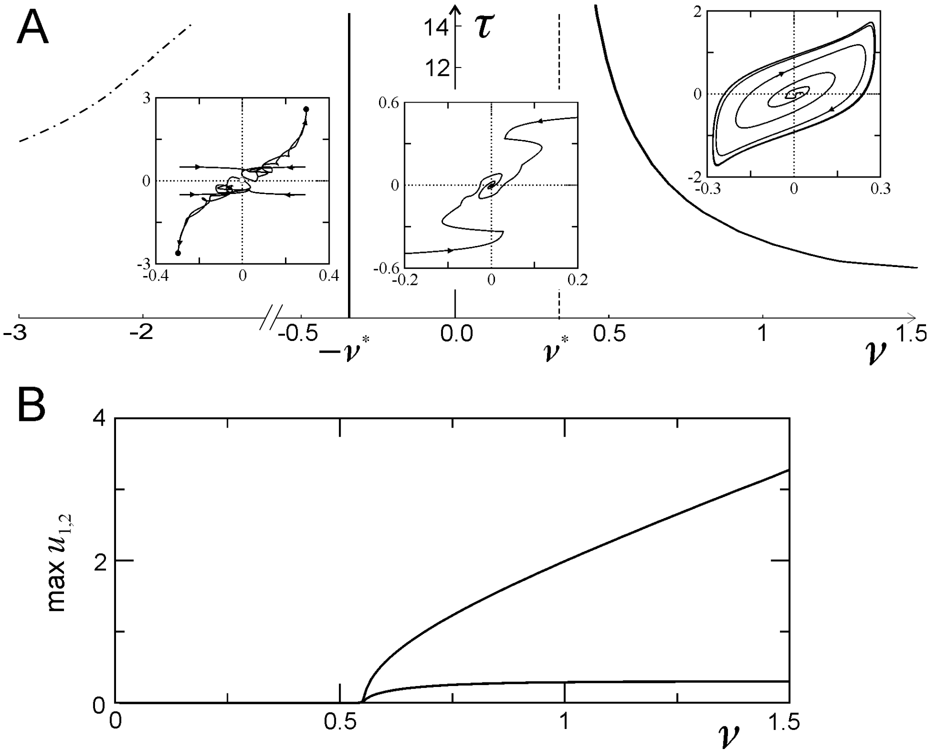

Fig. 3. Bifurcation diagram of Eqs. (16). A). (ν, τ)-plane divided by two solid lines corresponding to pitchfork and first Hopf bifurcations. Dashed straight line shows asymptotic behavior and dash-dot line corresponds to a Hopf bifurcation of the $(0,0)$ fixed point in the negative region of the composite coupling parameter. Insets showing trajectories on the (u_1, u_2)-plane for all three regions where obtained for $\tau_1 = 7.5$, $\tau_2 = 2.5$, $\alpha_1 = 0.6$, and $\nu = -0.9$, 0.2, and 0.9, respectively. B). Maxima of stationary motions on the (u_1, u_2)-plane (amplitudes) as functions of the composite coupling parameter ν. At $\nu \approx 0.53$ Hopf bifurcation occurs, hence for $\nu > 0.53$ nonzero oscillations can be observed. The amplitude of the first unit is lower than the amplitude of the second one.

This implies that at $\nu = -\mu_1\mu_2$ a supercritical pitchfork bifurcation occurs. Besides, $xF''(x) < 0$ and $xG''(x) < 0$, for $x \neq 0$, guarantee that $abF'(y_i)\,G'(x_i) < \mu_1\mu_2$, $i = 1, 2$. Hence the characteristic equation associated with the linearization of Eqs. (5) around either of the fixed points, (x_i, y_i), is

$$\lambda^2 + (\mu_1 + \mu_2)\,\lambda + \mu_1\mu_2 - abF'(x_i)\,G'(y_i)\,e^{-\lambda\tau} = 0, \quad i = 1, 2,$$

and it has no purely imaginary roots.

The remainder of the proof of (ii) is similar to that of (i), hence we omit it. ■

4 Computer simulations

To illustrate the analytical results found let us consider the following particular case of Eqs. (5)

$$\begin{aligned} \dot{u}_1(t) &= -\tfrac{1}{T_1}u_1(t) + \alpha_1 \tanh(u_2(t-\tau_2)) \\ \dot{u}_2(t) &= -\tfrac{1}{T_2}u_2(t) + \alpha_2 \tanh(u_1(t-\tau_1)) \,. \end{aligned} \tag{16}$$

Related models have been studied in the literature [17, 18, 20, 28, 29, 30, 31].

In the numerical integration we set $T_1 = 0.5$ and $T_2 = 6$, hence we consider neurons with strongly different input properties. As the bifurcation characteristics of Eqs. (16) depend on the composite coupling parameter $\nu = -\alpha_1\alpha_2$ only, we fix $\alpha_1 = 0.6$ and then use α_2 as free parameter. The hypotheses

(H_1) and (H_2) on the properties of the transfer functions in Eqs. (16) are satisfied. Then from Theorem 2.1, follow a number of consequences:

(i) the base state (0,0) is unstable for all delay values $\tau = \tau_1 + \tau_2 \geqslant 0$ if $T_1 T_2 \nu < -1$. Besides the fixed point at the origin there exist two other stable fixed points. Thus the system (16) is bistable and the final state of the system depends on initial conditions. Since $\nu < 0$, the two parameters α_1 and α_2 have the same sign (in our case positive). Such a possibility can be realized in the network only with identical type of coupling (inhibitory-inhibitory or excitatory-excitatory).

(ii) If $-1 < \nu T_1 T_2 \leqslant 1$ then the origin is absolutely stable (whatever the value of τ). At $\nu = -1/T_1 T_2 = -1/3$ a supercritical pitchfork bifurcation occurs.

(iii) If $\nu T_1 T_2 > 1$, then there exists $\hat{\tau}_0 > 0$ such that the origin is asymptotically stable when $\tau \in [0, \hat{\tau}_0)$, and unstable when $\hat{\tau} > \tau_0$. The system (16) undergoes a Hopf bifurcation at the origin when $\tau = \hat{\tau}_j$, $j = 0, 1, 2, ...$ The value $\hat{\tau}_0$ is calculated using Eq. (10). Applying the above given Theorem 3.1 we have that, for $\nu > \nu^+_{j_1}$ the system (16) has at least one periodic solution. This coincides with the results about the Hopf bifurcation at $\tau = \hat{\tau}_j$. Moreover, the system (16) has at least one periodic solution for negative values of the composite coupling parameter $\nu < \nu^-_{j_2}$. Note, for $\nu < -\nu^*$ due to the pitchfork bifurcation the base state is unstable (the characteristic equation has one positive root) and thus the periodic solution born at the Hopf bifurcation at $\nu = \nu^-_{j_2}$ is hyperbolic (unstable).

Figure 3 summarizes the results. All insets have been obtained by integration of Eqs. (16) with $\tau_1 = 7.5$, and $\tau_2 = 2.5$ using three significantly different values of ν. For $\nu < -\nu^* = -1/3$, depending on the initial conditions, trajectories tend to either the fixed point with positive values of voltages or to the fixed point with negative voltage values while the base state (0,0) is unstable (left inset in Fig. 3A). In this region there also exists a sequence of Hopf bifurcations (the first one is shown by the dash-dot line). However, as mentioned above, the limit cycle born at the first bifurcation is unstable and cannot be observed experimentally. In the middle region the origin is the only fixed point attractor (middle inset in Fig. 3A). Increasing further the value of ν the origin becomes unstable and a stable limit cycle appears (right inset in Fig. 3A). Figure 3B shows the amplitudes of stationary oscillations as a function of parameter ν. The increase of ν leads to higher oscillation amplitude and to steeper oscillations. Due to the difference in the decay characteristics (T_1 and T_2) the amplitude of oscillations in the first neuron is lower than in the second one. We have numerically obtained that the periodic orbit born due to the Hopf bifurcation is, indeed, stable.

5 Conclusions

Delays occur both in the signal transmission between neurons or electronic-model-neurons due to finite propagation velocity of action potentials (axonal delay), non-negligible time of a signal from a neuron to reach the receiving state of a postsynaptic neuron, and due to finite switching speed. An important issue is how delays change the stability of neural network states, steady or oscillatory, causing further oscillations and hence inducing delay-controlled periodic behavior. Furthermore, even for a simple *two-neuron* system delays may induce chaotic evolution. In this paper we have considered a simple *two-neuron* network model with delays in signal propagation between neurons. We have introduced appropriate variables to transform the model originally with two delayed variables (τ_1 and τ_2 denote the delays) into a system having a single delayed variable ($\tau = \tau_1 + \tau_2$, τ_1 need not be equal to $m\tau_2$). We have studied the stability of its base state. By studying the distribution of the roots of the characteristic equation of the linearized system around the base state we have obtained the bifurcation diagram of the system. Then we have studied the global existence of periodic solutions in terms of the overall coupling, ν, and delay parameters of the problem. We show that the Eqs. (3) have a periodic solution not only when the composite coupling parameter $\nu > 0$ is large enough but also when $\nu < 0$ is large enough in absolute value. Numerical simulations support the analytical results found.

The modest results found may, however, be of interest in the understanding of how does a neuron integrate the tens of thousands of synaptic inputs received in its dendritic tree coming from other neurons. It is known that back propagation signals along dendrites regulate the arrival of such inputs into the soma (a chemical reactor) and hence delays seems to play a significant role in the integration process before a single overall response is given by the neuron. Changes in excitatory connections between neurons are believed to mediate most forms of neural learning and memory. The problem is indeed complex as at any given time, tens or hundreds of synapses are firing at a rate of tens or hundreds of times per second all across the dendritic tree.

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References

[1] N. MacDonald. *Biological Delay Systems: Linear Stability.* (Cambridge Univ. Press, 1989).

[2] H. Haken. *Principles of brain functioning.* (Springer, 1996).

[3] H. Haken. Delay, noise and phase locking in pulse coupled neural networks. Biosystems. **63**, 15-20 (2001).

[4] H. Haken. *Brain Dynamics. Synchronization and Activity Patterns in Pulse-Coupled Neural Nets with Delays and Noise.* (Springer, 2002).

[5] X. J. Wang, and J. Rinzel. Spindle rhythmicity in the reticularis thalami nucleus: Synchronization among mutually inhibitory neurons. Neuroscience. **53**, 899-904 (1993).

[6] C. van Vreeswijk, L. F. Abbott, and G. B. Ermentrout. When inhibition not excitation synchronizes neural firing. J. Computational Neuroscience. **1** , 313-322 (1994).

[7] G. B. Ermentrout, and N. Kopell. Inhibition produced patterning in chains of coupled nonlinear oscillators. J. Applied Mathematics. **54**, 478-605 (1994).

[8] R. E. Plant. A FitzHugh differential-difference equation modeling recurrent neural feedback. J. Applied Mathematics. **40**, 150-162 (1981).

[9] V. Menon. Interaction of neuronal populations with delay: effect of frequency mismatch and feedback gain. Int. J. Neural Systems. **6** , 3-17 (1995).

[10] P. Bush, and T. Sejnowski. Inhibition synchronizes sparsely connected cortical neurons within and between columns in realistic network models. J. Computational Neuroscience. **3**, 91-110 (1996).

[11] S. M. Crook, G. B. Ermentrout, M. C. Vanier, and J. M. Bower. The role of axonal delay in the synchronization of networks of coupled cortical oscillators. J. Computational Neuroscience. **4**, 161-172 (1997).

[12] L. Wang, and X. Zou. Harmless delays in Cohen-Grossberg neural networks. Physica D. **170** , 162-173 (2002).

[13] J. Hopfield. Neurons with graded response have collective computational properties like those of two-state neurons. Proc. National Academy Science USA. **81**, 3088-3092 (1984).

[14] C. M. Marcus, and R. M. Westervelt. Stability of analog neural network with delay. Physical Review A. **39** , 347-359 (1989).

[15] A. Atiya, and P. Baldi. Oscillations and synchronizations in neural networks: An exploration of the labeling hypothesis. J. Neural Systems. **1** , 102-124 (1989).

[16] P. Baldi, and A. Atiya. How delays affect neural dynamics and learning. IEEE Trans. Neural Networks. **5**, 612-621 (1994).

[17] K. Gopalsamy, and I. Leung. Delay induced periodicity in a neural network of excitation and inhibition. Physica D. **89**, 395-426 (1996).

[18] J. Wei, and S. Ruan. Stability and bifurcation in a neural network model with two delays. Physica D. **130**, 255-272 (1999).

[19] L. H. Erbe, W. Krawcewicz, K. Geba, and J. Wu. S^1-degree and global Hopf bifurcation theory

of functional differential equations. J. Differential Equations. **98**, 277-298 (1992).

[20] S. Ruan, and J. Wei. Periodic solutions of planar systems with two delays. Proc. Royal Society, Edinburgh A. **129**, 1017-1032 (1999).

[21] J. Mallet-Paret, and G. Sell. Systems of differential delay equations: Floquet multipliers and discrete Lyapunov functions. J. Differential Equations. **125**, 385-440 (1996).

[22] J. Mallet-Paret, and G. Sell. The Poincaré-Bendixson theorem for a monotonic cyclic feedback system with delay. J. Differential Equations. **125**, 441-489 (1996).

[23] Y. Chen, and J. Wu. Slowly oscillating periodic solutions for a delayed frustrated network of two neurons. J. Math. Anal. Appl. **259**, 188-208 (2001).

[24] S. Ruan, and J. Wei. On the zeros of transcendental functions with applications to stability of delay differential equations. *Dynamics of Continuous, Discrete and Impulsive Systems.* (2002 submitted).

[25] J. Hale, and S. Verduyn Lunes. *Introduction to Functional Differential Equations.* (Springer, 1993).

[26] J. Guckenheimer, and R. Holmes. *Nonlinear Oscillations, Dynamical Systems. Bifurcations of Vector Fields.* (Springer, 1986).

[27] J. Wu. Symmetric functional differential equations and neural networks with memory. Transaction American Mathematical Society. **350**, 4799-4838 (1998).

[28] Y. Chen, and J. Wu. Minimal instability and unstable set of a phase-locked periodic orbit in a delayed neural network. Physica D. **134**, 185-199 (1999).

[29] L. Olien, and J. Belair. Bifurcations, stability and monotonicity properties of a delayed neural network model. Physica D. **102**, 349-363 (1997).

[30] T. Faria. On a planar system modeling a neuron network with memory. J. Differential Equations. **168**, 129-149 (2000).

[31] P. van der Driessche, J. Wu, and X. Zou. Stabilization role of inhibitory self-connections in a delayed neural network. Physica D. **150**, 84-90 (2001).