DELAY-INDUCED SPIKING DYNAMICS IN INTEGRATE-AND-FIRE NEURONS

CHANG-YUAN CHENG
Department of Applied Mathematics, National Pingtung University, Pingtung, Taiwan, R.O.C.
No.4-18, Minsheng Rd., Pingtung City, Pingtung County 90003, Taiwan, R.O.C.

SHYAN-SHIOU CHEN*
Department of Mathematics, National Taiwan Normal University
No. 88, Sec. 4, Ting-chou Rd., Taipei 116, Taiwan

RUI-HUA CHEN
Department of Applied Mathematics, National Pingtung University, Pingtung, Taiwan, R.O.C.
Fang Liao High School, Pingtung, Taiwan, R.O.C.
No.3, Yimin Rd., Fangliao Township, Pingtung County 940, Taiwan, R.O.C.

(Dedicated to Prof. Sze-Bi Hsu in appreciation of his inspiring ideas)

ABSTRACT. Experiments showed that a neuron can fire when its membrane potential (an intrinsic quality related to its membrane electrical charge) reaches a specific threshold. On theoretical studies, there are two crucial issues in exploring cortical neuronal dynamics: (i) what model describes spiking dynamics of each neuron, and (ii) how the neurons are connected [E. M. Izhikevich, IEEE Trans. Neural Networks, 15 (2004)]. To study the first issue, we propose the time delay effect on the well-known integrate-and-fire (IF) model which is classically introduced to study the spiking behaviors in neural systems by using the spike-and-reset procedure. Under the consideration of delayed adaptation on the membrane potential, the parameter range for the IF model with spiking dynamics becomes wider due to undergoing subcritical Hopf bifurcation and the existence of an unstable orbit. To study the second issue, we consider the system with two coupled identical IF units where time delay takes place in the coupling structure. We also demonstrate spiking behaviors in the coupled system when the delay time is large enough, and it contributes an original viewpoint of the connection between neurons. In contrast with the emergence of delay-induced spiking in a single-neuron system, a coupled two-neuron system involve both emergence and death of spiking according to different values of delay times. We also discuss the ranges of different parameters in which it allows occurrence of spiking behaviors.

2020 Mathematics Subject Classification. Primary: 34K18, 34K20, 34K25.
Key words and phrases. Spiking dynamics, Integrate-and-fire, Delayed coupling, Hopf Bifurcation.

S. S. Chen and C. Y. Cheng were partially supported by the Ministry of Science and Technology of Taiwan, R.O.C. (Grant Nos. MOST 108-2115-M-003-011 and MOST 108-2115-M-153-003).

* Corresponding author: Shyan-Shiou Chen.
1. Introduction. Mathematical models can be used to mimic real nerve cell activities observed in experiments, from a basic isolated neuron to a large-scaled network of neurons. Two-variable spiking models introduced in lots of literature are structurally simple but reproduce a large number of electrophysiological features such as bursting and regular spiking [11, 18, 21]. Recent works [2, 3] also presented several of the most prominent signatures of biological spiking behaviors by using the 2-dimensional Hindmarsh-Rose type model. In addition, several papers have demonstrated that time delays can play important roles in neurobiological systems [1, 5, 14]. In the field of electrophysiology, time delays mainly come from two reasons: (a) the finite speed of an action potential propagating along an axon, (b) the finite spreading time of the post-synaptic potential through the dendritic tree of the neuron to the cell body. So far, how the spiking dynamics affected or even induced by time delays in a neuron system still lacks for a complete answer. Especially, it is important to study the influence of time delay on the corresponding parameter sets of particular neural behaviors.

The sequel comparison on numerous spiking models in [11] include from the simplest integrate-and-fire (IF) model up to the Hodgkin-Huxley model consisting of four equations and tens of parameters. Meanwhile, a spiking model proposed by Izhikevich exhibits rich and all twenty neuron-computational properties mentioned therein, and it is the simplest possible model that can exhibit all discussed firing patterns. By this way, the fine temporal structure of cortical spike trains and how the mammalian neocortex processes information are understood. To see self-sustained subthreshold oscillations that can describe a particular behavior different from spiking and bursting in cortical neurons for the precision and robustness of spiking generation patterns, author in [18] considered the quartic model and demonstrated a Bautin bifurcation which can produce self-sustained oscillations. Previous two models were described by the following ordinary differential equation

\[
\begin{align*}
\dot{v}(t) &= f(v) - w + I, \\
\dot{w}(t) &= a(bv - w),
\end{align*}
\]

where \(v\) indicates membrane potential of the nerve cell; \(w\) denotes the adaptation variable; \(a, b\) are real parameters respectively corresponding to the time constant ration between the adaptation variable and the membrane potential and to the coupling strength between these two variables; \(I\) is a real parameter modeling the input intensity of the neuron; \(f\) is a real function accounting for the leak and spike initiation currents. The real function \(f\) plays a key role in the two-variable spiking models, and are typically assumed to be regular (at least three times continuously differentiable), strictly convex, and its derivative to have a negative limit at \(-\infty\) and an infinite limit at \(+\infty\). In this paper, we also assume that

\[
(A) \quad f''(v) > 0 \quad \text{for all} \quad v; \quad \lim_{v \to -\infty} f'(v) < 0 \quad \text{and} \quad \lim_{v \to \infty} f'(v) = +\infty.
\]

Typical models include the quadratic adaptive model with \(f(v) = v^2\) that can be used to simulate very large scale neural networks [11], the adaptive exponential model with \(f(v) = e^v - v\) that describes the electrophysiology of the sodium current responsible for the generation of action potential [8], the quartic model with \(f(v) = v^4 + 2\sigma v\) that has the advantage of the self-sustained subthreshold oscillations [18, 19, 21]. As authors proved in literature, in the case with function \(f\) satisfying \(\lim_{v \to \infty} f(v)/v\) to be bounded (including the quadratic adaptive model), the adaptation variable blows up at the same time as the membrane potential,
yet in the case with function $f$ satisfying that there exist $\epsilon > 0$ and $\varsigma > 0$ such that $\lim_{v \to \infty} \frac{f(v)}{v^2} \geq \varsigma$ (including the adaptive exponential and the quartic models), the membrane potential blows up in infinite time, and at this explosion time the adaptation variable will converge [20, 21]. As mentioned in [18, 21], if the membrane potential blows up at finite time $t^*$, a spike is emitted and a spike-and-reset condition is applied for an electrophysiological reason:

$$v(t^*) = v_r, \quad w(t^*) = w(t^- + \vartheta),$$

(2)

where $v_r$ is the reset membrane potential and $\vartheta > 0$ is a real parameter. Eqs. (1) and (2) form a hybrid dynamical system combining a differential equation and a discrete reset, which reproduce a large number of electrophysiological features such as spike frequency adaptation and bursting. Bifurcations about transitions between different electrophysiological features and chaotic behavior were studied in [21] by introducing an adaptation map.

There are recent investigations regarding complicated dynamics of IF neurons with adaptation and seeing a variety of experimentally observed spiking patterns. One of them analyzed the transverse stability of orbits in the phase plane that leads to sufficient conditions for the occurrence of regular spiking [9]. Another result on chaotic firing has been established in a quadratic IF neuron with a nonlinear adaptive current by using Marotto’s Theorem where the main idea is to seek a snap-back repeller [22]. In [17], a quadratic IF model with a slow recovery variable was studied where a codimension two bifurcation represented the interaction of domain of attraction of a stable hyperpolarized rest state with the reset parameters, which reset the system state after spiking. Therein, authors also derived explicit approximations of instantaneous firing rates, and obtained asymptotic firing rates as a function of current and reset parameters by using the averaging theorem. When IF models are coupled through synaptic currents to form networks, it can display Hopf bifurcation and saddle-node collision of limit cycles that do not exist in an uncoupled oscillator [12]. The main idea is reducing the full network of neurons to a mean-field model which can describe the bifurcations that the full networks display. Furthermore, related neuron systems were extensively studied for different biological reasons, and certain dynamics were revealed for characterized systems; for example, subthreshold dynamics of a combination of the membrane potential and ion channels in a leaky integrate-and-fire (LIF) model constructed with a radial Ornstein-Uhlenbeck process and certain firing mechanism [6], synchronization behavior in a population of LIF neurons [7], bistability in a spatially extended LIF neuron [16], synchronization in a population of moving integrate-and-fire oscillators [13].

In this paper, we are interested in the delay effect on the spiking dynamics of the IF model. Additionally, the author in [11] pointed out two crucial issues in studying neuronal dynamics: (I) what model describes spiking dynamics of each neuron and (II) how the neurons are connected. Therefore, we are motivated to study two subjects. From previous literature, rich dynamics occurs in the two-dimensional neural system (1), and then our first concern is how the time delay affects the occurrence of spiking dynamics in this simple system with time delay. Secondly, in two coupled IF neuronal systems, how the time delay and the coupling strength between two isolated units collaborate to affect the occurrence of spiking dynamics. Since Eq. (1) is a two-dimensional ordinary differential equation, the
blowing up dynamics can be demonstrated by ruling out stable stationary solution and periodic orbits. Although considering time delay in the IF neuronal system (1) will form an infinite-dimensional dynamical system, and then the blowing up dynamics can not be certified in the same way, analyzing local stability of equilibria and stability of periodic solutions generated through Hopf bifurcation provides an approach for seeking delay-induced spiking dynamics in this system. Namely, if the IF neuronal system undergoes the subcritical Hopf bifurcation by using delay time as the bifurcating parameter and the bifurcating periodic orbit is unstable, we naturally look forward to blowing up dynamics and the followed spiking behavior.

In the second section, we consider delayed adaptation acting on the membrane potential in the IF neuronal system. Based on the normal form approach and the center manifold theory, we derive the formula for determining the properties of Hopf bifurcation for a delayed IF system, including the direction of Hopf bifurcation and stability of the bifurcating periodic orbits. Using this approach and numerical simulations, we show that both quadratic and quartic models are able to reproduce certain feature of biological spiking behavior. In the third section, we consider the system with two identical unitary IF systems and diffusive coupling. Delay-induced spiking behaviors are also revealed in this model. In addition, how the delay time and the coupling strength between these two identical units collaborate to affect the occurrence of spiking dynamics are discussed. In contrast with the emergence of delay-induced spiking in a single-neuron system, a coupled two-neuron system involves both emergence and death of spiking according to different ranges of parameters. Numerical simulations are presented in these cases to demonstrate our theoretical results. Finally, we summarize our results and propose further questions on this subject in the last section.

2. Delayed single neuron model. In this paper, we incorporate the model in [18] with the time delay to study the delay effect of adaptation variable acting on the membrane potential. This consideration is formulated in a functional differential equation as the following:

\[
\begin{align*}
\dot{v}(t) &= f(v(t)) - w(t-s) + I, \\
\dot{w}(t) &= a(bv(t) - w(t)),
\end{align*}
\]  

(3)

where \( s \) is the delay time due to adaptation information. Herein, we also apply the spike-and-reset procedure (2) to the system (3).

In [18], the number of equilibria and their stability were studied for the case without delay, i.e. \( s = 0 \). Specifically, bifurcation of the model with the real function \( f(v) = dv^2, d > 0 \), is depicted in Fig. 1. When \( b^2 - 4dI < 0 \), there does not exist any equilibrium; when \( b^2 - 4dI = 0 \), there exists a unique equilibrium; when \( b^2 - 4dI > 0 \), there are two equilibria with the membrane potential \( v_+ = (b \pm \sqrt{b^2 - 4dI})/(2d) \) respectively. When there exist two equilibria, stability of each equilibrium was confirmed that

1. the equilibrium with \( v = v_+ \) is always a saddle;
2. if \( b < a \), the equilibrium with \( v = v_- \) is attractive; if \( b > a \), the equilibrium with \( v = v_- \) is attractive when \( I < \frac{ab}{2d} - \frac{a^2}{4d} \), and is repulsive when \( I > \frac{ab}{2d} - \frac{a^2}{4d} \).

Herein, we study the effect of the time delay and focus on the case with two equilibria. The linearized equation of the system (3) at an equilibrium \((\bar{v}, \bar{w})\) is the
following system with the original symbols
\[
\begin{align*}
\dot{v}(t) &= f'(\bar{v})v(t) - w(t - s) + I, \\
\dot{w}(t) &= abv(t) - aw(t).
\end{align*}
\] (4)

The characteristic equation of the linear system (4) reads
\[
\lambda^2 + A\lambda + B + Ce^{-\lambda s} = 0,
\] (5)

where
\[ A = a - f'(\bar{v}), \quad B = -af'(\bar{v}), \quad C = ab. \]

Eq. (5) can be studied as in [4] and then the stability of each equilibrium is obtained. We make a summary here for readers’ convenience. If \( \lambda = iw, \ w > 0, \) is a purely imaginary root of (5), it leads to\[
\cos sw = (w^2 - B)/C \quad \text{and} \quad \sin sw = Aw/C
\]
then
\[
w^4 + (A^2 - 2B)w^2 + B^2 - C^2 = 0.
\] (6)

There are four cases to study the roots of (6).

1. When \( B^2 > C^2 \) and \( 2B < A^2 \), there does not exist a positive root of (6).
2. When \( B^2 < C^2 \), there exists one positive root \( w_c = ((2B - A^2 + \sqrt{\Delta})/2)^{1/2} \) and \( s \) must be one of the values \( s_n = (\arcsin \frac{Aw_c}{C} + 2n\pi)/w_c, \ n = 0, 1, 2, \ldots \), where \( \arcsin \frac{Aw_c}{C} \) is chosen in the first or second quadrant according to the sign of \( \cos sw_c \). This root \( \lambda = iw_c \) is simple and

\[
\Re \frac{d\lambda}{ds} = \frac{C^2w_c^2(2w_c^2 - 2B + A^2)}{(AB + Aw_c^2 + C^2s)^2 + (2w_c^3 - 2Bw_c + A^2w_c)^2}.
\] (7)
3. When \( B^2 > C^2 \) and \( 2B > A^2 \), there are two positive values of \( w^2 \), \( w_1^2 = (2B - A^2 + \sqrt{\Delta})/2 \) and \( w_2^2 = (2B - A^2 - \sqrt{\Delta})/2 \).

4. When \( B^2 = C^2 \) and \( 2B > A^2 \), there is one positive value \( w^2 = 2B - A^2 \).

Accordingly, the local stability of equilibria in (3) is verified in the following.

**Theorem 2.1.** Suppose that there exist two equilibria in the system (3), i.e. \( b^2 > 4dI \). Let \( w_\pm = bw_\pm \). Then the equilibrium \((v_+, w_+)\) is unstable for all \( s > 0 \). In addition, if equilibrium \((v_-, w_-)\) is attractive when \( s = 0 \), i.e. \( b < a \) or \( b > a \) and \( I < \frac{ab}{2d} - \frac{a^2}{4d} \), then

(i) when \( B^2 \geq C^2 \), \((v_-, w_-)\) is stable for \( s > 0 \);

(ii) when \( B^2 < C^2 \), the system (3) undergoes Hopf bifurcation near \((v_-, w_-)\) when \( s = s_n \), where

\[
\begin{align*}
  s_n &= \frac{1}{w_c} \left( \arcsin \frac{Aw_c}{C} + 2n\pi \right), \quad n = 0, 1, 2, \ldots, \\
  w_c &= \left( 2B - A^2 + \sqrt{\Delta} \right)/2, \quad \Delta = (A^2 - 2B)^2 - 4(B^2 - C^2),
\end{align*}
\]

and the derivative of \( \lambda \) with respect to \( s \) satisfies that \( \operatorname{Re} \frac{d\lambda}{ds}(s_n) > 0 \).

**Proof.** At the equilibrium \((v_+, w_+)\), where \( v_+ = (b + \sqrt{b^2 - 4dI})/(2d) \), it is directly calculated that \( B^2 > C^2, 2B < A^2 \), and then the associated characteristic equation (5) has no purely imaginary root. Since the equilibrium \((v_+, w_+)\) is a saddle when \( s = 0 \), it is unstable for all \( s > 0 \). At the equilibrium \((v_-, w_-)\), where \( v_- = (b - \sqrt{b^2 - 4dI})/(2d) \), it satisfies that \( 2B < A^2 \). According to previous statements, the characteristic equation (5) has no purely imaginary root when \( B^2 > C^2 \), and has a pair of purely imaginary roots \( \pm w_c \) when \( B^2 < C^2 \) and \( s = s_n \). From (6) and (7), we see that \( \operatorname{Re} \frac{d\lambda}{ds}(s_n) > 0 \) for all \( n = 0, 1, 2, \ldots \). Therefore, when \( B^2 \geq C^2 \), the equilibrium \((v_-, w_-)\) is stable for all \( s > 0 \); when \( B^2 < C^2 \), \((v_-, w_-)\) is stable for \( s \in [0, s_0) \) and unstable for \( s \in (s_0, +\infty) \). \( \square \)

**Figure 2.** Left: Graphs of \( s_0(b) \) in different values of \( d \). The solid curve: \( d = 0.85 \), the dash curve: \( d = 1 \), the dot curve: \( d = 1.15 \). Right: Zoomed out graphs as in the left panel showing that \( s_0(b) \to 0 \) as \( b \to +\infty \).

The bifurcation value \( s_0 \) depends on each parameter. An example of graphs of \( s_0(b) \) in different values of \( d \) is depicted in Fig. 2. Herein, we focus on probing
the relationship between $s_0$ and the strength parameter $d$ and reveal the following properties. (I) With smaller $d$, smaller $b$ is permitted for the system (3) to perform Hopf bifurcation. Namely, denoting the range of $b$ for the system (3) to undergo Hopf bifurcation by $(b_*(d), +\infty)$, we have that $b_*(d)$ is decreasing in $d$. However, for fixed $b \in (b_*(d), +\infty)$, the system (3) with smaller $d$ needs larger delay time to undergo Hopf bifurcation. (II) For fixed $d$, there exists $b^*$ such that the bifurcation value $s_0(b)$ has the maximum at $b = b^*$, and $s_0(b)$ is increasing in $b$ for $b \in (b_*, b^*)$, decreasing in $b$ for $b \in (b^*, \infty)$. (III) With fixed $d$, the bifurcation value $s_0(b) \rightarrow 0$ as $b \rightarrow +\infty$.

In the rest of this section, we look forward to the occurrence of spiking behavior in the system (3) that comes from blowing up in finite time, and the reset mechanism offers a feasible approach. From the mathematical viewpoint, an unstable periodic orbit induced by the subcritical Hopf bifurcation is expected to trigger the blowing up behavior. Therefore, we present the formulae for determining the direction of the orbit induced by the subcritical Hopf bifurcation is expected to trigger the blowing up behavior. Therefore, we present the formulae for determining the direction of the Hopf bifurcation and stability of bifurcating periodic solutions of system (3) at $s_0$ by employing the normal form method and the center manifold theorem [10].

First, we denote $V(t) = v(t) - v_-$, $W(t) = w(t) - w_-$ and rewrite the delayed differential equation as a Taylor expansion

$$
\begin{align*}
\dot{V}(t) &= f'(v_-)V(t) - W(t - s) + \frac{f''(v_-)}{2}V^2(t) + \frac{f'''(v_-)}{6}V^3(t) + \text{h.o.t.}, \\
\dot{W}(t) &= a(bV(t) - W(t)).
\end{align*}
$$

For convenience, denote $s = s_0 + \mu$, then $\mu = 0$ is the bifurcation value of the system (3). Let $C = C([-s, 0], \mathbb{R}^2)$ be the Banach space of continuous functions with the supremum norm $\| \phi \| = \sup_{-s \leq \theta \leq 0} |\phi(\theta)|$ for $\phi \in C$. Rewrite the system (8) in an abstract form,

$$
\dot{x}(t) = L_\mu(x_t) + G(\mu, x_t),
$$

where $x(t) = (V(t), W(t))^T$, $x_t(\theta) = x(t + \theta) \in C$, $L_\mu : C \rightarrow \mathbb{R}^2$ is the linear part, which is given by

$$
L_\mu \phi = A_0 \phi(0) + A_1 \phi(-s),
$$

$$
A_0 = \begin{pmatrix} f'(v_-) & 0 \\ ab & -a \end{pmatrix}, \quad A_1 = \begin{pmatrix} 0 & -1 \\ 0 & 0 \end{pmatrix},
$$

for $\phi(\theta) = (\phi_1(\theta), \phi_2(\theta))^T \in C$, and $G : \mathbb{R} \times C \rightarrow \mathbb{R}^2$ is the nonlinear part, which is given by

$$
G(\mu, \phi) = \left( \frac{f''(v_-)}{2}V^2(t) + \frac{f'''(v_-)}{6}V^3(t) + \text{h.o.t.} \right).
$$

By the Reisz representation theorem, there exists a matrix whose entries are functions $\eta(\theta, \mu)$ of bounded variations on $[-s_0, 0]$, such that

$$
L_\mu \phi = \int_{-s_0}^0 d\eta(\theta, \mu)\phi(\theta).
$$

In fact, the following can be selected

$$
\eta(\theta, \mu) = \begin{cases} A_0, & \theta = 0, \\
A_1 \delta(\theta + s), & \theta \in [-s, 0),
\end{cases}
$$

1873
where $\delta(\theta)$ is the Dirac function. For $\phi \in C$, two operators

$$
(\Lambda(\mu)\phi)(\theta) = \begin{cases} 
    \frac{d\phi(\theta)}{d\theta}, & \theta \in [-s_0, 0), \\
    \int_{-s_0}^{0} d\eta(\zeta, \mu)\phi(\zeta), & \theta = 0,
\end{cases}
$$

and

$$
(\Upsilon(\mu)\phi)(\theta) = \begin{cases} 
    0, & \theta \in [-s_0, 0), \\
    G(\mu, \phi), & \theta = 0,
\end{cases}
$$

are defined. System (8) is easily transformed into an operator differential equation of the form

$$
\dot{x}_1 = \Lambda(\mu)x_1 + \Upsilon(\mu)x_1.
$$

For $\theta \in [-s_0, 0)$, Eq. (15) becomes the trivial equation $dx_1/d\theta = dx_1/dt$, and for $\theta = 0$ it is (8). The adjoint operator $\Lambda^*$ of $\Lambda$ is defined as

$$
(\Lambda^*(\mu)\psi)(\theta^*) = \begin{cases} 
    -\frac{d\psi(\theta^*)}{d\theta^*}, & \theta^* \in (0, s_0], \\
    \int_{-s_0}^{0} d\eta^T(\zeta, \mu)\psi(-\zeta), & \theta^* = 0,
\end{cases}
$$

where $\psi \in C^* = C([0, s_0], \mathbb{R}^2)$. To determine the coordinates of the center manifold near the trivial equilibrium, a bilinear form is defined:

$$
\langle \psi, \phi \rangle = \int_0^0 \int_{\theta = -s_0}^0 \int_0^\theta \psi^T(\xi - \theta)d\eta(\theta)\phi(\xi)d\xi,
$$

for $\phi \in C$, $\psi \in C^*$ and $\eta(\theta) = \eta(\theta, 0)$. Notably, the domains of $\Lambda$ and $\Lambda^*$ are $C$ and $C^*$, respectively. For convenience of computation, all functions are allowed to fall into $\mathbb{C}^2$ rather than $\mathbb{R}^2$. Let $q(\theta)$ be the eigenvector of $\Lambda(0)$ corresponding to $s_0$:

$$
\Lambda(0)q(\theta) = i\omega_c q(\theta).
$$

Therefore, $-i\omega_c$ is an eigenvalue of $\Lambda^*(0)$, and

$$
\Lambda^*(0)q^*(\theta^*) = -i\omega_c q^*(\theta^*),
$$

for some nonzero function $q^*(\cdot)$ on $[0, s_0]$. To obtain $q(\theta)$ and $q^*(\theta^*)$, (14) and (16) are substituted into (18) and (19) respectively to yield

$$
q(\theta) = q(0)e^{i\omega_c \theta}, \quad q^*(\theta^*) = q^*(0)e^{i\omega_c \theta^*},
$$

for $\theta \in [-s_0, 0)$, $\theta^* \in (0, s_0]$, and $q(0) = (1, \alpha)^T$, $q^*(0) = \frac{1}{\rho}(1, \alpha^*)^T$, where $\rho$ is with regard to normalization $\langle q^*, q \rangle = 1$. It is directly computed that $\alpha = \frac{ab}{i\omega_c + \frac{a}{b}}$ and $\alpha^* = -\frac{i\omega_c - f^*(-w_c)}{ab}$. From

$$
\langle q^*, q \rangle = \frac{\bar{q}^*(0) \cdot q(0) - \int_{\theta = -s_0}^0 \int_{\xi = 0}^{\theta} q^T(\xi - \theta)d\eta(\theta)q(\xi)d\xi}{\rho^2},
$$

it determines that $\rho = 1 + \frac{i\omega_c + f^*(-w_c)}{\rho}$, $\alpha s_0 e^{i\omega_c s_0}$. The condition $\langle q^*, \bar{q} \rangle = 0$ can be established through a direct calculation.

Next, a coordinate for the center manifold $\Omega_0$ near $\mu = 0$, which is a locally invariant and two-dimensional manifold, is constructed. The theory of the normal
form method and the center manifold theorem can be found in [10]. For \( x_t \) being a solution to (15), let

\[
\begin{align*}
    z(t) &= \langle q^*, x_t \rangle, \\
    W(t, \theta) &= x_t - 2\text{Re}[z(t)q(\theta)].
\end{align*}
\]

On the center manifold,

\[
W(t, \theta) = W(z, \bar{z}, \theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots. 
\]

(22)

In fact, \( z \) and \( \bar{z} \) are the local coordinates of the center manifold \( \Omega_0 \) in the directions \( q^* \) and \( \bar{q}^* \), respectively. Notably, \( W(t, \theta) \) is real if \( x_t(\theta) \) is real. Therefore, only real solutions are considered. The existence of the center manifold \( \Omega_0 \) enables (15) to be reduced to an ordinary differential equation in a single complex variable on \( \Omega_0 \).

For the solution \( x_t \in \Omega_0 \) of (15) and \( \mu = 0 \),

\[
\dot{z}(t) = \langle q^*, \dot{x}_t \rangle = \langle q^*, \Lambda(0)x_t \rangle + \langle q^*, \Upsilon(0)x_t \rangle = iw_c z(t) + q^*(0)^T \cdot G(0, x_t). 
\]

(23)

Rewrite (23) as

\[
\dot{z}(t) = iw_c z(t) + g(z, \bar{z}),
\]

where

\[
g(z, \bar{z}) = g_{02}\frac{z^2}{2} + g_{11}z\bar{z} + g_{21}\frac{\bar{z}^2}{2} + \cdots. 
\]

(24)

Next, it is sufficient to expand \( g \) in powers of \( z \) and \( \bar{z} \) and then obtain, from the coefficients of expansion, the critical values determining the direction of Hopf bifurcation and stability of bifurcating periodic solutions by using algorithm presented in [10]. From (21), (23) and denoting \( \Lambda = \Lambda(0) \) and \( \Upsilon = \Upsilon(0) \), we have

\[
\begin{align*}
\dot{W} &= \dot{x}_t - \dot{z}q - \dot{\bar{q}}q \\
&= \Lambda x_t + \bar{\Upsilon} x_t - [is_0w_c z + q^*(0) \cdot G(0, W + 2\text{Re}(zq))]q - \\
&\quad - [is_0w_c \bar{z} + \bar{q}^*(0) \cdot \bar{G}(0, W + 2\text{Re}(zq))]\bar{q} \\
&= \Lambda W - 2\text{Re}[\bar{q}^*(0) \cdot G(0, W + 2\text{Re}(zq))]q + \bar{T} x_t. 
\end{align*}
\]

(25)

Let

\[
\dot{W} = \Lambda W + H(z, \bar{z}, \theta),
\]

(26)

where

\[
H(z, \bar{z}, \theta) = H_{20}(\theta)\frac{z^2}{2} + H_{11}(\theta)z\bar{z} + H_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots. 
\]

(27)

From (22) and (23), we have

\[
\begin{align*}
\dot{W} &= W_{z} \dot{z} + W_{\bar{z}} \dot{\bar{z}} = (W_{20} z + W_{11} \bar{z} + \cdots)(is_0w_c z + g(z, \bar{z})) \\
&\quad + (W_{11} \bar{z} + W_{02} \bar{z} + \cdots)(-is_0w_c \bar{z} + \bar{g}(z, \bar{z})). 
\end{align*}
\]

(28)

From (22) and (26), we obtain

\[
\dot{W} = (\Lambda W_{20} + H_{20})\frac{z^2}{2} + (\Lambda W_{11} + H_{11})z\bar{z} + (\Lambda W_{02} + H_{02}). 
\]

(29)

Comparing the coefficients of (28) and (29), the following results are derived

\[
\begin{align*}
(\Lambda - 2is_0w_c)W_{20}(\theta) &= -H_{20}(\theta), \\
\Lambda W_{11}(\theta) &= -H_{11}(\theta). 
\end{align*}
\]

(30)

On the other hand,

\[
q^*(0)^T \cdot G(0, x_t) = \frac{1}{\rho}(1, \bar{\alpha}^*)^T \cdot \left( \frac{f''(v_-)}{2} V^2(t) + \frac{f'''(v_-)}{6} V^3(t) + \text{h.o.t.}, 0 \right)^T.
\]
From (24), it reveals that
\[ g_{20} = g_{11} = g_{02} = \frac{f''(v_-)}{\rho}, \]
\[ g_{21} = \frac{f''(v_-)}{\rho} (1 + 2W^{(1)}_{11}(0) + W^{(1)}_{20}(0)), \]  
(31)
where \( W^{(l)}_{ij}(\theta) = (W^{(l)}_{ij}(\theta), W^{(l)}_{ij}(\theta))^T \). Next, we compute \( W_{20}(\theta) \) and \( W_{11}(\theta) \). From (25) and (26),
\[ H(z, \bar{z}, \theta) = -2\text{Re}[\bar{q}^*(0) \cdot G(0, W + 2\text{Re}(zq))q] + \Upsilon x_t \]
\[ = -gq(\theta) - \bar{g}q(\theta) + \Upsilon x_t \]
\[ = -(g_{20}z^2/2 + g_{11}z\bar{z} + g_{02}\bar{z}^2/2 + \cdots)q(\theta) \]
\[ - (\bar{g}_{20}z^2/2 + \bar{g}_{11}z\bar{z} + \bar{g}_{02}\bar{z}^2/2 + \cdots)\bar{q}(\theta) + \Upsilon x_t. \]  
(32)
Comparing the coefficients in (27) and (32), it leads to
\[ H_{20}(\theta) = -g_{20}q(\theta) - \bar{g}_{20}\bar{q}(\theta), \]  
\[ H_{11}(\theta) = -g_{11}q(\theta) - \bar{g}_{11}\bar{q}(\theta), \quad \theta \in [-s_0, 0). \]  
(33)
From (30) and (33), we obtain the following ODEs
\[ \dot{W}_{20}(\theta) = 2iw_c W_{20}(\theta) + g_{20}q(0)e^{iw_c \theta} + \bar{g}_{20}\bar{q}(0)e^{-iw_c \theta}, \]
\[ \dot{W}_{11}(\theta) = g_{11}q(0)e^{iw_c \theta} + \bar{g}_{11}\bar{q}(0)e^{-iw_c \theta}, \]
and it is easy to obtain the solutions
\[ W_{20}(\theta) = E_1 e^{2iw_c \theta} - \frac{g_{20}}{iw_c} q(0)e^{iw_c \theta} - \frac{\bar{g}_{20}}{3iw_c} \bar{q}(0)e^{-iw_c \theta}, \]
\[ W_{11}(\theta) = E_2 + \frac{g_{11}}{iw_c} q(0)e^{iw_c \theta} - \frac{\bar{g}_{11}}{iw_c} \bar{q}(0)e^{-iw_c \theta}, \]  
(34)
where \( E_1 \) and \( E_2 \) will be calculated in the following. From (10), (12), (14) and (34), we derive
\[ \Lambda W_{20}(0) = \int_{-s_0}^0 dq(\theta)W_{20}(\theta) = A_0 W_{20}(0) + A_1 W_{20}(-s_0) \]
\[ = A_0 E_1 + A_1 E_1 e^{-2iw_c s_0} - g_{20}q(0) + \frac{\bar{g}_{02}}{3} \bar{q}(0). \]  
(35)
From (27) and (32), we derive
\[ H_{20}(0) = -g_{20}q(0) - \bar{g}_{20}\bar{q}(0) + (f''(v_-), 0)^T. \]  
(36)
Substituting (34), (35) and (36) into (30), we obtain
\[ E_1 = (A_0 + A_1 e^{-2iw_c s_0} - 2iw_c J_{2\times 2})^{-1}(-f''(v_-), 0)^T. \]
Similarly,
\[ E_2 = (A_0 + A_1)^{-1}(-f''(v_-), 0)^T. \]
Based on the above analysis, the parameters and delays in system (3) determine each \( g_{ij} \). Accordingly, we can compute the following quantities:
\[ C_1(0) = \frac{i}{2w_c} \left( g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3} |g_{02}|^2 \right) + \frac{g_{21}}{2}, \]
\[ \mu_2 = \frac{\text{Re}C_1(0)}{\text{Re}\lambda(s_0)}, \quad \beta_2 = 2\text{Re}C_1(0), \]  
(37)
which refer to the bifurcation near the equilibrium $\xi$ of the system (3) at $s = s_0$ \[10\]. Specifically, $\mu_2$ determines the direction of the Hopf bifurcation: if $\mu_2 > 0(< 0)$, then the Hopf bifurcation is supercritical (subcritical) and the bifurcating periodic solutions occur when $s > s_0(s < s_0)$; $\beta_2$ specifies the stability of the bifurcating periodic solutions: the periodic solutions are orbitally stable (unstable) if $\beta_2 < 0(> 0)$.

Finally, the following results are obtained.

**Theorem 2.2.** If the conditions in Theorem 2.1(ii) hold, then the system (3) undergoes a Hopf bifurcation at $s = s_0$. More precisely,

(i) the direction of the Hopf bifurcation is determined by the sign of $\mu_2$, defined in (37); if $\mu_2 > 0(< 0)$, the Hopf bifurcation is supercritical (subcritical) and a bifurcating periodic solution exists for $\tau > \tau_c(< \tau_c)$;

(ii) the stability of the bifurcating periodic solutions is determined by the sign of $\beta_2$, defined in (37); if $\beta_2 < 0(> 0)$, then the periodic solutions are stable (unstable).

The supercritical bifurcating case ($\mu_2 > 0$) with a stable periodic orbit ($\beta_2 < 0$) indicates a tendency to oscillations in neural systems whereas the subcritical bifurcating case ($\mu_2 < 0$) and unstable periodic orbit ($\beta_2 > 0$) incorporated with the reset process generates neural spiking. Herein, we present an example with fixed parameters $a = 1$, $b = 1.2$, $d = 1$ and $I = 0.2$ in the system (3). It is directly calculated that $I < \frac{\nu^2}{4d} = 0.36$, $B^2 = 0.16 < C^2 = 1.44$, the bifurcating value is $s_0 \approx 0.5157$, and the critical values are $\mu_2 \approx -7.2696 < 0$, $\beta_2 \approx 6.9292 > 0$ respectively. Therefore, the system (3) with (2) undergoes subcritical Hopf bifurcation when $s = s_0$ and the bifurcating periodic orbit is unstable. We choose $s = 0.5 < s_0$ in the left panel of Fig. 3 and it shows a stable equilibrium and a blow up solution that with initial value not near this equilibrium. With $s = 0.52 > s_0$ in the right panel of Fig. 3, the equilibrium becomes unstable and a solution with initial values near it blows up in finite time due to the effect of time delay. Considering the additional spike-and-reset condition (2), a spiking behavior can emerge in this neural system.

In Fig. 4, by increasing the time delay, dynamics of the neural system changes from the stabilization of the membrane potential to emergence of spiking behavior, and it demonstrates the delay-induced spiking in a neural system.

3. **Delayed coupled model.** In this section, we consider the system with two identical unitary IF subsystems and diffusive coupling to study how the connection of neurons is constructed to perform spiking phenomenon. To this purpose, the time delay is taken into account at the diffusive coupling, and this concern is formulated into the functional differential equation

\[
\begin{align*}
\dot{v}_1 &= f(v_1) - w_1 + I + c(v_2(t - \tau) - v_1(t)), \\
\dot{w}_1 &= a(bv_1 - w_1), \\
\dot{v}_2 &= f(v_2) - w_2 + I + c(v_1(t - \tau) - v_2(t)), \\
\dot{w}_2 &= a(bv_2 - w_2),
\end{align*}
\]

(38)

where $c$ is the coupling strength.
Figure 3. Two trajectories near and not near the equilibrium $\xi$ of the system (3) without the reset process and under fixed parameters $a = 1, b = 1.2, d = 1, I = 0.2$. Left: Choosing delay time $s = 0.5$, the equilibrium $\xi$ is locally stable. Right: Choosing delay time $s = 0.52$, the equilibrium $\xi$ becomes unstable, and two solutions blow up in finite time.

Figure 4. Delay-induced spiking in the equation (3). (a) The membrane potential tends to silence when $s = 5$; (b) a spiking emerges when $s = 5.2$ (due to the reset process).

An equilibrium $(v_1^*, w_1^*, v_2^*, w_2^*)$ of (38) satisfies the following equation
\begin{align*}
v_1^* &= \frac{-f(v_2^*) + (b + c)v_2^* - I}{c} \equiv F(v_2^*), \quad (39) \\
v_2^* &= \frac{-f(v_1^*) + (b + c)v_1^* - I}{c} \equiv F(v_1^*), \quad (40) \\
w_1^* &= bv_1^*, \quad w_2^* = bv_2^*. \quad (41)
\end{align*}

From the assumption (A), the function $F(v)$ satisfies that $F''(v) = -f''(v)/c < 0$ for all $v$ and then $F$ is strictly convex. In addition, the derivative of $F$ satisfies that
\[
\lim_{v \to -\infty} F'(v) \geq 1, \quad \lim_{v \to +\infty} F'(v) = -\infty.
\]

Hence, there exists unique value $\tilde{v}$ such that
\[
F'(\tilde{v}) = 1.
\]

Note that the graphs of $v_1 = F(v_2)$ and $v_2 = F(v_1)$ are symmetric with respect to $v_1 = v_2$. Based on previous properties and notations, we obtain the following cases of equilibria in (38). If $F(\tilde{v}) < \tilde{v}$, there does not exist equilibrium. If $F(\tilde{v}) = \tilde{v}$, there exists a unique equilibrium. If $F(\tilde{v}) > \tilde{v}$, there exist two equilibria in the synchronized space \{(v_1, w_1, v_2, w_2)|v_1 = v_2, w_1 = w_2\}, say $\xi = (v, w, v, w)$ and
\( \tilde{\xi} = (\bar{v}, \bar{\bar{v}}, \bar{\bar{v}}, \bar{\bar{v}}) \) with \( \bar{v} < \bar{\bar{v}} < \bar{\bar{v}} \). In addition, if \( F''(\bar{\bar{v}}) \geq -1 \), then there is no more equilibrium than \( \xi \) and \( \tilde{\xi} \); if \( F''(\bar{\bar{v}}) < -1 \), then there exist four equilibria \( \xi, \tilde{\xi}, \xi_1 = (\bar{v}, \bar{\bar{v}}, \bar{\bar{v}}, \bar{\bar{v}}) \) and \( \tilde{\xi}_1 = (\bar{v}, \bar{\bar{v}}, \bar{\bar{v}}, \bar{\bar{v}}) \) with \( \bar{v} < \bar{\bar{v}} < \bar{\bar{v}} \). An example showing different numbers of equilibria for variant parameters is depicted in Fig. 5.

![Figure 5](image-url) Graphs of \( v_1 = F(v_2) \) and \( v_2 = F(v_1) \). Herein, parameters \( b = 1 \) and \( d = 0.3 \) are fixed. (a) \( c = 2 \) and \( I = 1.2 \), (b) \( c = 1 \) and \( I = 0.3 \), (a) \( c = 0.3 \) and \( I = 0.3 \).

The linearized equation of \( (38) \) at an equilibrium \( (v_1^*, w_1^*, v_2^*, w_2^*) \) is
\[
\begin{align*}
v_1 &= f'(v_1^*) v_1(t) - w_1 + c(v_2(t - \tau) - v_1(t)), \\
\dot{w}_1 &= a(b v_1 - w_1), \\
\dot{v}_2 &= f'(v_2^*) v_2(t) - w_2 + c(v_1(t - \tau) - v_2(t)), \\
\dot{w}_2 &= a(b v_2 - w_2),
\end{align*}
\]
and then the characteristic equation reads
\[
[(\lambda + a)(\lambda - f'(v_1^*) + c) + ab] \times \frac{[(\lambda + a)(\lambda - f'(v_2^*) + c) + ab] - (\lambda + a)^2(ce^{-\lambda \tau})^2}{[(\lambda + a)(\lambda - f'(v_1^*) + c) + ab] - (\lambda + a)^2(ce^{-\lambda \tau})^2} = 0.
\]
First, we study the local stability of the equilibria on the identical phase, i.e. \( \tilde{\xi} \) and \( \bar{\xi} \). At these two equilibria, the characteristic equation \( (43) \) is written into
\[
P(\lambda) \tilde{P}(\lambda) \equiv \left[ \lambda^2 + p \lambda + q + (r \lambda + s) e^{-\lambda \tau} \right] \times \\
\left[ \lambda^2 + \tilde{p} \lambda + \tilde{q} + (\tilde{r} \lambda + \tilde{s}) e^{-\lambda \tau} \right] = 0,
\]
where
\[
\begin{align*}
p &= \tilde{p} = a + c - f(v^*), \\
q &= \tilde{q} = a (b + c - f(v^*)), \\
r &= c, \quad \tilde{r} = -c, \quad s = ac, \quad \tilde{s} = -ac, \\
v^* &= v_1^* = v_2^*.
\end{align*}
\]
Now, we consider the equation \( P(\lambda) = 0 \) and denote the following conditions and values,
\[
\begin{align*}
(H_1) & \quad p + r > 0 \text{ and } q + s > 0, \\
(H_1') & \quad q + s < 0, \\
(H_2) & \quad r^2 - p^2 + 2q < 0 \text{ and } q^2 - s^2 > 0, \text{ or } (r^2 - p^2 + 2q)^2 < 4(q^2 - s^2), \\
(H_3) & \quad q^2 - s^2 < 0, \text{ or } r^2 - p^2 + 2q > 0 \text{ and } (r^2 - p^2 + 2q)^2 = 4(q^2 - s^2), \\
(H_4) & \quad q^2 - s^2 > 0, \text{ or } r^2 - p^2 + 2q > 0 \text{ and } (r^2 - p^2 + 2q)^2 > 4(q^2 - s^2).
\end{align*}
\]
\[\tau_j^\pm = \begin{cases} 
\arccos \left\{ \frac{(s-b_2 q - pr \beta_2^2)}{r^2 \tau^2 + s^2} \right\} + 2j\pi / \beta_\pm, & \text{if } \frac{r^2 \beta_2^2 - r q \beta_2 + s p \beta_2^2}{r^2 \tau^2 + s^2} \geq 0, \\
2\pi - \arccos \left\{ \frac{(s-b_2 q - pr \beta_2^2)}{r^2 \tau^2 + s^2} \right\} + 2j\pi / \beta_\pm, & \text{if } \frac{r^2 \beta_2^2 - r q \beta_2 + s p \beta_2^2}{r^2 \tau^2 + s^2} < 0, 
\end{cases}\]

where

\[\beta_\pm^2 = \frac{(r^2 - p^2 + 2q) \pm \sqrt{(r^2 - p^2 + 2q)^2 - 4(q^2 - s^2)}}{2},\]

and the roots of equation \(P(\lambda) = 0\), \(\lambda(\tau) = \alpha(\tau) + \beta(\tau)\). From [4, 15], we have the following results.

**Proposition 1.**

(i) If \((H_1)\) holds, then all roots of \(P(\lambda) = 0\) have negative real parts for \(\tau = 0\).

(ii) If \((H_2)\) holds, then the equation \(P(\lambda) = 0\) has no purely imaginary root for all \(\tau \geq 0\).

(iii) If \((H_3)\) holds, then the equation \(P(\lambda) = 0\) has a pair of purely imaginary roots \(\pm i\beta_\pm\) when \(\tau = \tau_j^+\) for \(j = 0, 1, 2, \ldots\).

(iv) If \((H_1)\) and \((H_4)\) hold, then there is a positive integer \(k\) such that when \(\tau \in [0, \tau_j^+), (\tau_0^-, \tau_1^+), \ldots, (\tau_{k-1}^-, \tau_k^+),\)

all roots of \(P(\lambda) = 0\) have negative real parts, and when \(\tau \in (\tau_0^+, \tau_1^-), (\tau_1^+, \tau_1^-), \ldots, (\tau_{k-1}^+, \tau_{k-1}^-), (\tau_k^+, +\infty),\)

\(P(\lambda) = 0\) has at least one root with positive real part.

(v) If \((H_1')\) and \((H_4)\) hold, then there is a positive integer \(l\) such that when \(\tau \in [0, \tau_0^-), (\tau_0^+, \tau_1^-), \ldots, (\tau_{l-1}^-, \tau_l^+), (\tau_l^+, +\infty),\)

\(P(\lambda) = 0\) has at least one root with positive real part, and when \(\tau \in (\tau_0^-, \tau_0^+), (\tau_1^-, \tau_1^+), \ldots, (\tau_{l-1}^-, \tau_l^+), (\tau_l^-, \tau_l^+),\)

all roots of \(P(\lambda) = 0\) have negative real parts.

(vi) In (iii), (iv) and (v), the following transversality conditions hold:

\[
\frac{d}{d\tau} \Re(\lambda^{\pm}_j) > 0, \quad \frac{d}{d\tau} \Re(\lambda^{-}_j) < 0 \text{ for } j = 0, 1, 2, \ldots.
\]

**Remark 1.** The statement (v) is derived from the theory in [4, 15]. Note that when \((H_1')\) holds, the equation \(P(\lambda) = 0\) at \(\tau = 0\) has exactly one root with positive real part. With further condition \((H_4)\), this root will cross the imaginary axis when we increase the delay time \(\tau\) to \(\tau_0^+\).

There are parallel results about the roots of \(\tilde{P}(\lambda) = 0\), and we denote the corresponding notations by \((\tilde{H}_1) - (\tilde{H}_4), \tilde{\beta}_\pm^j\) and \(\tilde{\beta}_\pm\). When \(\tau = 0\), all the roots of (44) have negative real parts if \((H_1)\) and \((\tilde{H}_1)\) hold. In fact, the condition \((\tilde{H}_1)\) implies \((H_1)\) and the condition \((H_i)\) is equivalent to \((\tilde{H}_i)\), for \(i = 2, 3, 4\), since \(p = \tilde{p}, q = \tilde{q}, r^2 = \tilde{r}^2\) and \(s^2 = \tilde{s}^2\).

First, we study the case that the coupled system (38) has at least two equilibria and obtain the local stability of each synchronized equilibrium.

**Theorem 3.1.** Assume \(F'(\tilde{v}) > \tilde{v}\) where \(\tilde{v}\) satisfies \(F'(\tilde{v}) = 1\). Then the system (38) has at least two equilibria, \(\tilde{\xi}\) and \(\xi\). Furthermore,

(i) the equilibrium \(\tilde{\xi}\) is always unstable;

(ii) if \((H_1)\) and \((H_2)\) hold, the equilibrium \(\xi\) is locally asymptotically stable for all \(\tau \geq 0\);
(iii) if $(\bar{H}_1)$ and $(H_3)$ hold, the equilibrium $\bar{\xi}$ is locally asymptotically stable for $\tau \in [0, \tau^*)$, where $\tau^* = \min\{\bar{\tau}_0, \bar{\tau}_1\}$, and unstable for $\tau \in (\tau^*, +\infty)$;

(iv) if $(\bar{H}_1)$ is violated and $(H_2)$ or $(H_3)$ holds, the equilibrium $\bar{\xi}$ is locally unstable for all $\tau \geq 0$;

(v) if $(H_1)$ and $(H_4)$ hold, then the equilibrium $\bar{\xi}$ is locally asymptotically stable for $\tau = 0$, and a finite switches of stability occurs when the delay time increases and the equilibrium $\bar{\xi}$ is unstable when the delay time is large enough; that is, there is a positive integer $m$ such that the equilibrium $\bar{\xi}$ is locally asymptotically stable when

$$\tau \in [0, \bar{\tau}_0), (\bar{\tau}_1, \bar{\tau}_2), \cdots, (\bar{\tau}_{m-1}, \bar{\tau}_m),$$

and the equilibrium $\bar{\xi}$ is locally unstable when

$$\tau \in (\bar{\tau}_0, \bar{\tau}_1), (\bar{\tau}_2, \bar{\tau}_3), \cdots, (\bar{\tau}_{m-2}, \bar{\tau}_{m-1}), (\bar{\tau}_m, +\infty);$$

(vi) if $(H_1)$, $(\bar{H}_1)$, and $(H_4)$ hold, then the equilibrium $\bar{\xi}$ is locally unstable for $\tau = 0$, and a finite switches of stability occurs when the delay time increases and the equilibrium $\bar{\xi}$ is unstable when the delay time is large enough; that is, there is a positive integer $n$ such that the equilibrium $\bar{\xi}$ is locally unstable when

$$\tau \in [0, \bar{\tau}_0), (\bar{\tau}_1, \bar{\tau}_2), \cdots, (\bar{\tau}_{n-1}, \bar{\tau}_n),$$

and the equilibrium $\bar{\xi}$ is locally asymptotically stable when

$$\tau \in (\bar{\tau}_0, \bar{\tau}_1), (\bar{\tau}_2, \bar{\tau}_3), \cdots, (\bar{\tau}_{n-1}, \bar{\tau}_n).$$

We have a similar result when $(\bar{H}_1)$, $(H'_1)$ and $(H_4)$ hold.

Proof. First, we study roots of the characteristic equation $P(\lambda)\hat{P}(\lambda) = 0$ that associated to the equilibrium $\bar{\xi}$. When $\tau = 0$, it reads

$$[\lambda^2 + (p + r)\lambda + q + s][\lambda^2 + (\bar{p} + \bar{r})\lambda + \bar{q} + \bar{s}] = 0.$$

Since $F'(\bar{\upsilon}) = 1$ where $\bar{\upsilon} = b/(2d)$ and $\bar{\upsilon} > \bar{\upsilon}$, we have $b < f'(\bar{\upsilon})$ and then $\bar{q} + \bar{s} < 0$. Thus, $\bar{\xi}$ is unstable when $\tau = 0$. For $\tau > 0$, since the transversality condition holds that $\bar{q} \Re \lambda(\tau) > 0$ under (H3), the stability of $\bar{\xi}$ would not change except that the criterion $(H_4)$ is true. In fact, when the inequality $q^2 - s^2 > 0$ holds, it leads to $|b - f'(\bar{\upsilon})|[b + 2c - f'(\bar{\upsilon})] > 0$. Since $b - f'(\bar{\upsilon}) < 0$, we have

$$b + c - f'(\bar{\upsilon}) < 0. \quad (45)$$

On the other hand, we have

$$f'(\bar{\upsilon})[2c - f'(\bar{\upsilon})] < b[b + 2c - f'(\bar{\upsilon})] - bf'(\bar{\upsilon}). \quad (46)$$

From (45) and (46), it yields that

$$\begin{align*}
\tau^2 + p^2 + 2q & = f'(\bar{\upsilon})[2c - f'(\bar{\upsilon})] + a(2b - a) \\
& < b(b + 2c - f'(\bar{\upsilon})) - bf'(\bar{\upsilon}) + b^2 \\
& = 2b[b + c - f'(\bar{\upsilon})] \\
& < 0.
\end{align*}$$

Therefore, the criterion $(H_4)$ does not hold for $v^* = \bar{\upsilon}$ and $\bar{\xi}$ is unstable for all $\tau \geq 0$.

The statement (ii) follows from Proposition 1 (i) and (ii).
Assume that \((H_1)\) and \((H_2)\) hold. Again, from the transversality condition \(\frac{d}{d\tau} \text{Re} \lambda(\tau) > 0\), all roots of \(P(\lambda) = 0\) \((\hat{P}(\lambda) = 0)\) have negative real parts when \(\tau \in \left[0, \tau_0^-\right)\) \((\tau \in \left[0, \tilde{\tau}_0^-\right)\), \(P(\lambda) = 0\) \((\hat{P}(\lambda) = 0)\) has a pair of purely imaginary roots \(\pm i\beta_j\) \((\pm i\tilde{\beta}_j)\) when \(\tau = \tau_0^+\) \((\tilde{\tau}_0^+)\), and \(P(\lambda) = 0\) \((\hat{P}(\lambda) = 0)\) has at least one root with positive real part when \(\tau > \tau_0^+\) \((\tilde{\tau}_0^+)\). Hence, the equilibrium \(\xi\) is locally asymptotically stable for \(\tau \in [0, \tau_c)\), where \(\tau_c = \min\{\tau_0^+, \tilde{\tau}_0^+\}\), and unstable for \(\tau \in (\tau_c, +\infty)\).

Now, assume that \((H_1)\) and \((H_4)\) hold. From Proposition 1 \((iv)\), the equations \(P(\lambda) = 0\) \((\hat{P}(\lambda) = 0)\) have purely imaginary roots at \(\tau = \tau_j^+\), \(\tau_j^-\) for \(j = 1, 2, \ldots, \), respectively. Note that all roots of \(P(\lambda) = 0\) \((\hat{P}(\lambda) = 0)\) have negative real parts or exactly one root has a positive real part for \(\tau\) in intervals formed by \(\tau_j^-\) \((\tilde{\tau}_j^-)\) as in Proposition 1 \((iv)\). In addition, all roots of \(P(\lambda)\) \((\hat{P}(\lambda)\) have negative real parts for \(\tau \in (0, \min\{\tau_0^+, \tilde{\tau}_0^+\})\) and at least one root has a positive real part for \(\tau\) large enough. Therefore, the equilibrium \(\xi\) is locally asymptotically stable for \(\tau = 0\), and a finite number of stability switches occur when the delay time increases and the equilibrium \(\xi\) is unstable when the delay time is large enough. When \((H_1)\) and \((H_4')\) hold, all roots of the equation \(P(\lambda) = 0\) at \(\tau = 0\) are negative and exactly one of the roots of \(\hat{P}(\lambda) = 0\) at \(\tau = 0\) has a positive real part. Therefore, the statement \((vi)\) is proved by a similar method to that for the statement \((v)\).

Hereafter, we study the specific case with \(f(v) = dv^2\), then a synchronized equilibria \((v^*, w^*, v^*, w^*)\) satisfies

\[
dv^{*2} - b v^* + I = 0, \tag{47}
\]

which has roots if and only if \(b^2 - 4dI \geq 0\). When \(b^2 - 4dI > 0\), the equation \(\tag{47}\) has two roots, say \(\bar{v}\) and \(\hat{v}\) with \(\bar{v} < \hat{v}\). Since the graphs of \(v_1 = F(v_2)\) and \(v_2 = F(v_1)\) are symmetric with respect to \(v_1 = v_2\) and the function \(F\) satisfies \(F''(\bar{v}) > 0\), the equations \(\tag{39}\) and \(\tag{40}\) has four solutions, two with \(v_1 = v_2\) and two with \(v_1 \neq v_2\), whenever \(F''(\bar{v}) < -1\). Therefore, the number of equilibria in system \(\tag{38}\) is classified as following.

**Theorem 3.2.** Consider the coupled IF neurons \(\tag{38}\),

\(\text{(i)}\) if \(b^2 - 4dI < 0\), then the system \(\tag{38}\) has no equilibrium,

\(\text{(ii)}\) if \(b^2 - 4dI = 0\), then the system \(\tag{38}\) has unique equilibrium,

\(\text{(iii)}\) if \(b^2 - 4dI > 0\), then the system \(\tag{38}\) has at least two equilibrium \(\bar{v}, \hat{v}\) \((\bar{v}, \hat{v})\) with \(\bar{v} = (b - \sqrt{b^2 - 4dI})/(2d) < \hat{v} = (b + \sqrt{b^2 - 4dI})/(2d)\). In addition, there exists no more equilibria if \(F''(\bar{v}) \geq -1\) and there exists two more equilibria each with \(v_1 \neq v_2\) if \(F''(\bar{v}) < -1\).

In the symbols of \(\tag{38}\) with \(f(v) = dv^2\), the conditions \((H_i)\), \(i = 1, \ldots, 4\) and \((H_i')\) become

\(\text{(A1)}\): \(a - 2dv^*> 0\) and \(b - 2dv^* > 0\),

\(\text{(A1')}\): \(b - 2dv^* < 0\),

\(\text{(A2)}\): \(4dv(c - dv) + a(2b - a) < 0\) and \((b - 2dv)^2 + 2c(b - 2dv) > 0\),

or \[4dv(c - dv) + a(2b - a)]^2 < 4a^2(b + 2c - 2dv)(b - 2dv),

\(\text{(A3)}\): \((b - 2dv)^2 + 2c(b - 2dv) < 0\), or \(4dv(c - dv) + a(2b - a) > 0\),

or \[4dv(c - dv) + a(2b - a)]^2 = 4a^2(b + 2c - 2dv)(b - 2dv),

\(\text{(A4)}\): \((b - 2dv)^2 + 2c(b - 2dv) > 0\), \(4dv(c - dv) + a(2b - a) > 0\),

and \[4dv(c - dv) + a(2b - a)]^2 > 4a^2(b + 2c - 2dv)(b - 2dv),
is locally asymptotically stable for all \( \tau \geq 0 \);

(iii) if (A₁) and (A₃) hold, the equilibrium \( \xi \) is locally asymptotically stable for \( \tau \in [0, \tau_c) \), where \( \tau_c = \min\{\tau_0^+, \tau_0^{±}\} \), and unstable for \( \tau \in (\tau_c, +\infty) \);

(iv) if (A₁) and (A₂) or (A₃) hold, the equilibrium \( \xi \) is locally unstable for all \( \tau \geq 0 \);

(v) if (A₁) and (A₄) hold, then the equilibrium \( \xi \) is locally asymptotically stable for \( \tau = 0 \), and a finite switches of stability occurs when the delay time increases and the equilibrium \( \xi \) is unstable when the delay time is large enough; that is, there is a positive integer \( m \) such that the equilibrium \( \xi \) is locally asymptotically stable when

\[
\tau \in [0, \tau_0), (\tau_1, \tau_2), \ldots, (\tau_{m-1}, \tau_m),
\]

and the equilibrium \( \xi \) is locally unstable when

\[
\tau \in (\tau_0, \tau_1), (\tau_2, \tau_3), \ldots, (\tau_{m-2}, \tau_{m-1}), (\tau_m, +\infty);
\]

(vi) if (A₁), (A₁') and (A₄) hold, then the equilibrium \( \xi \) is locally unstable for \( \tau = 0 \), and a finite switches of stability occurs when the delay time increases and the equilibrium \( \xi \) is unstable when the delay time is large enough; that is, there is a positive integer \( n \) such that the equilibrium \( \xi \) is locally unstable when

\[
\tau \in [0, \bar{\tau}_0), (\bar{\tau}_1, \bar{\tau}_2), \ldots, (\bar{\tau}_{n-2}, \bar{\tau}_{n-1}), (\bar{\tau}_n, +\infty),
\]

and the equilibrium \( \xi \) is locally asymptotically stable when

\[
\tau \in (\bar{\tau}_0, \bar{\tau}_1), (\bar{\tau}_2, \bar{\tau}_3), \ldots, (\bar{\tau}_{n-1}, \bar{\tau}_n).
\]

We have a similar result when (A₁), (A₁') and (A₄) hold.

Compared to that in the case of the single-neuron system, not only the emergence of spiking behaviors can be seen in the delayed coupled two-neuron system but also the death of spiking behaviors occurs due to Hopf bifurcation. The cases of Theorem 3.3 (v) and (vi) indicate coexistence of induction and death of spikes in a model with two coupled IF subsystems and fixed parameters except changing the delay time. To show our theoretical results, two sequences of bifurcation values in different parameter \( a \) are listed in Table 1.

One of our purposes is to investigate how two identical IF neural subsystems can be coupled to form the simplest network and behaves the spiking dynamics. Based on the results in Theorem 3.3, we fix all parameters of (38) except the coupling strength \( c \) to probe how the value of \( c \) and the delay time collaborate to affect the emergence and death of spikes. An example of (38) with \( a = 0.22, b = 1, d = 0.3 \) and \( I = 0.3 \) is considered, then the bifurcation values \( \tau_j^{±} \) and \( \bar{\tau}_j^{±} \) depending on \( c \) are directly calculated and the region of local stability of the equilibrium \( \xi \) is depicted in Fig. 6. Under the previous settings, there exists a critical value \( c^* \approx 0.1874 \) such
that the criteria $(A_1)$ and $(A_4)$ hold for $c > c^*$. From Theorem 3.3 $(v)$, it reveals that the equilibrium $\xi$ is stable for all $\tau \geq 0$ when $c < c^*$, and stability of the equilibrium $\xi$ switches as the delay time increases for $c > c^*$. Therefore, emergence and death of spikes switches in the system (38) with the spike-and-reset condition (2) for $c > c^*$. On the other hand, it shows that, for a fixed $\tau$, increasing the coupling strength $c$ not only changes the location of $\xi$ but also switches the local stability of $\xi$. Therefore, we confirm that the mechanism of delayed coupling between two identical IF subsystems triggers spiking behaviors in the coupled system due to both delay time and coupling strength.

Recall that the parameter $a$ indicates the time constant ration between the adaptation variable and the membrane potential. We also present an example with relatively larger time ration, $a = 1$, and other parameters $b = 1$, $c = 0.3$, $d = 2.4$ and
Figure 6. Regions of local stability of the equilibrium $\xi$ in Eq. (38) with $a = 0.22$, $b = 1$, $d = 0.3$, $I = 0.3$ and other parameter values as indicated. Herein, we fix all parameters except the coupling strength $c$ to observe how the bifurcation values $\tau_j^{\pm}$ and $\tilde{\tau}_j^{\pm}$ depend on $c$. Colored curves are $\tau_j^{\pm}(c)$ and $\tilde{\tau}_j^{\pm}(c)$ respectively and $\Omega$ is the curve $\tau_0^{+}$. The equilibrium $\xi$ is stable (unstable) with $(c, \tau)$ locating in the s (u) regions. When $c < c^* \approx 0.1874$ the equilibrium $\xi$ is stable for all $\tau \geq 0$; when $c > c^*$ stability of the equilibrium $\xi$ switches as the delay time increases.

$I = 0.1$. It is directly calculated that assumptions $(A_1)$ and $(A_4)$ hold and the sequential bifurcation values are $\{7.0518, 10.8531, 16.6675, 22.4819, \cdots\}$. Emergence and death of spiking behaviors are depicted in Fig. 7.

4. Conclusion. In this paper, we have formulated two delayed IF models to capture a scenario from which delayed adaptation acts on the membrane potential in a single-neuron system or the diffusive coupling between two identical units in a network. Several papers have recently used the two-dimensional IF model without time delay but collaborated with the spike-and-reset procedure to study the patterns of spikes displayed by real neurons. Mathematically, these are hybrid dynamical systems in the sense that they are defined by combining a continuous dynamical system (the original IF model) and a discrete dynamical system (the spike-and-reset procedure). Our consideration on time delay leads to Hopf bifurcation and proposes a new mechanism for IF models to generate spiking dynamics. In mathematical viewpoint, the essentiality includes two points. First, to see Hopf bifurcation, existence of purely imaginary roots for characteristic equations of related linear system were studied for both single-neuron model and coupled two-neuron model. Secondly, in order to generate neural spiking, we formulated the conditions to decide the direction of bifurcation and then apply the reset process to the case with subcritical
Figure 7. Emergence and death of spiking behaviors in the system (38). (a) The membrane potential tends to silence when $\tau = 6.5$; (b) a spiking emerges when $\tau = 7.1$; (c) death of spiking occurs when $\tau = 13$; (d) a spiking emerges again when $\tau = 18$.

bifurcation and unstable periodic orbit. Several numerical simulations were presented to demonstrate our theoretical results and discuss how certain parameters and the time delay affect the neural spiking. Namely, in a single-neuron model, we discuss how the strength parameter $b$ and the characteristic value $d$ for a specific real function incorporate to decide the occurrence of Hopf bifurcation. In a system with two coupled IF units, we have shown that the stability of equilibria switches by changing the time delay or the coupling strength, and then the model undergoes emergence and death of spiking behaviors. With these results, we partially answered the questions proposed by E. M. Izhikevich that what model describes the spiking dynamics of each neuron and how the neurons are connected. However, there are other aspects not considered in this paper. For example, simultaneously considering time delays at the acting of adaptation variable on the membrane potential and the diffusive coupling between two neurons will make the characteristic equation more complicated so that analyzing local stability of an equilibrium becomes challenging. Moreover, all previous subjects and additional synchronization property of the system with two coupled non-identical IF units will generalize the applications on real neuronal systems. All these unsolved problems remain as our future works.

Conflict of interest. All authors declare no conflicts of interest in this paper.

REFERENCES
[1] S. A. Campbell, Time delays in neural systems. In Handbook of Brain Connectivity (eds A. R. McIntosh & V. K. Jirsa), 65–90, Berlin, Germany: Springer, 2007.
[2] S. S. Chen, C. Y. Cheng and Y. R. Lin, Application of a two-dimensional Hindmarsh-Rose type model for bifurcation analysis, Int. J. Bifurcation and Chaos, 23 (2013), 1350055, 21pp.
[3] S. S. Chen and C. Y. Cheng, Delay-induced mixed-mode oscillations in a 2d Hindmarsh-Rose type model with recurrent neural feedback, Discrete Conti. Dyn. Sys.-B, 21 (2016), 37–53.
[4] K. L. Cooke and Z. Grossman, Discrete delay, distributed delay and stability switches, J. Math. Anal. Appl., 86 (1982), 592–627.
[5] S. Coombes and C. Laing, Delays in activity-based neural networks, Phil. Trans. R. Soc. A, 367 (2009), 1117–1129.
[6] S. Ditlevsen and P. Greenwood, The Morris-Lecar neuron model embeds a leaky integrate-and-fire model, J. Math. Biol., 67 (2013), 239–259.
[7] G. Dumont and J. Henry, Synchronization of an excitatory integrate-and-fire neural network, Bull. Math. Biol., 75 (2013), 629–648.
[8] N. Fourcaud-Trocmé, D. Hansel, C. van Vreeswijk and N. Brunel, How spike generation mechanisms determine the neuronal response to fluctuating inputs, J. Neurosci, 23 (2003), 11628–11640.
[9] E. Foxall, R. Edwards, S. Ibrahim and P. van den Driessche, A contraction argument for two-dimensional spiking neuron models, SIAM J. Appl. Dyn. Sys., 11 (2012), 540–566.
[10] B. D. Hassard, N. D. Kazarinoff and Y. H. Wan, Theory and Application of Hopf Bifurcation, Cambridge Univ. Press, Cambridge, 1981.
[11] E. M. Izhikevich, Which model to use for cortical spiking neurons?, IEEE Trans. Neural Networks, 15 (2004), 1063–1070.
[12] W. Nicola and S. A. Campbell, Bifurcations of large networks of two-dimensional integrate and fire neurons, J. Comp. Neurosci., 35 (2013), 87–108.
[13] L. Prignano, O. Sagarr and A. Díaz-Guilera, Tuning synchronization of integrate-and-fire oscillators through mobility, Phys. Rev. Lett., 110 (2013), 114101.
[14] I. Ratas and K. Pyragas, Macroscopic oscillations of a quadratic integrate-and-fire neuron network with global distributed-delay coupling, Phys. Rev. E, 98 (2018), 052224, 11pp.
[15] S. Ruan, Absolute stability, conditional stability and bifurcation in Kolmogorov-type predator-prey systems with discrete delays, Quart. Appl. Math., 59 (2001), 159–173.
[16] M. A. Schwemmer and T. J. Lewis, Bistability in a leaky integrate-and-fire neuron with a passive dendrite, SIAM J. Appl. Dyn. Sys., 11 (2012), 507–539.
[17] E. Shlizerman and P. Holmes, Neural dynamics, bifurcations and firing rates in a quadratic integrate-and-fire model with a recovery variable. I: Deterministic behavior, Neural Comput., 24 (2012), 2078–2118.
[18] J. Touboul, Bifurcation analysis of a general class of nonlinear integrate-and-fire neurons, SIAM J. Appl. Math., 68 (2008), 1045–1079.
[19] J. Touboul and R. Brette, Dynamics and bifurcations of the adaptive exponential integrate-and-fire model, Biol. Cybern., 99 (2008), 319–334.
[20] J. Touboul, Importance of the cutoff value in the quadratic adaptive integrate-and-fire model, Neural Comput., 21 (2009), 2114–2122.
[21] J. Touboul and R. Brette, Spiking dynamics of bidimensional integrate-and-fire neurons, SIAM J. Appl. Dyn. Sys., 8 (2009), 1462–1506.
[22] G. Zheng and A. Tonnelier, Chaotic solutions in the quadratic integrate-and-fire neuron with adaptation, Cogn. Neurodyn., 3 (2009), 197–204.

Received August 2020; revised October 2020.

E-mail address: cycheng@mail.nptu.edu.tw
E-mail address: sschen@ntnu.edu.tw
E-mail address: tsdtest0524@gmail.com