DELAY-INDUCED MIXED-MODE OSCILLATIONS IN A 2D HINDMARSH-ROSE-TYPE MODEL

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(Communicated by Janet Best)

Abstract. In this study, we investigate a Hindmarsh-Rose-type model with
the structure of recurrent neural feedback. The number of equilibria and their
stability for the model with zero delay are reviewed first. We derive condi-
tions for the existence of a Hopf bifurcation in the model and derive equations
for the direction and stability of the bifurcation with delay as the bifurcation
parameter. The ranges of parameter values for the existence of a Hopf bifurca-
tion and the system responses with various levels of delay are obtained. When
a Hopf bifurcation due to delay occurs, canard-like mixed-mode oscillations
(MMOs) are produced at the parameter value for which either the fold bifurca-
tion of cycles or homoclinic bifurcation occurs in the system without delay.
This behavior can be found in a planar system with delay but not in a planar
system without delay. Therefore, the results of this study will be helpful for
determining suitable parameters to represent MMOs with a simple system with
delay.

1. Introduction. In many biological systems, the effects of delays are important
in understanding the dynamics of neural networks [4]. In one review paper [14],
the authors noted that the analysis of computational models at different space-time
scales shows the fundamental mechanisms that relate neural processes to neuro-
science data. Importantly, modeling at the microscopic level is necessary because
neural information is transmitted between the neurons of the brain. Delay factors
are inherent in many biological systems for two reasons: (1) the finite propagation
speed of the signals and (2) the finite processing time in the synapses. The time de-
lay is caused by the finite speed of signal transmission over a distance in processing
information from various sensory systems to form a coherent and unified perception
of the external world. Currently, relatively few studies have been conducted on bi-
ological systems with time delay. In mathematical biology, the effect of time delay
on dynamical behaviors, such as stability, firing mode, and mixed-mode oscillations
(MMOs), in a single neuron model remains unclear. Hence, it is important to study
the behavior of a single neuron with a differential-difference model.

2010 Mathematics Subject Classification. Primary: 34K18, 34K17; Secondary: 34K60.

Key words and phrases. Hindmarsh-Rose-type model, Hopf bifurcation, differential-difference
equation, mixed-mode oscillations, recurrent neural feedback.
To understand the behavior of neurons with time delay, it is important to clarify the behavior of reduced neuronal models. We begin by reviewing the Hindmarsh-Rose (HR) model, which was first introduced in the 1970s. Connor et al. [11, 12] were the first to establish a model for the alternative generation of action potentials. This model, which is similar to the classical four-dimensional Hodgkin-Huxley model [25], contains fast sodium, delayed rectifier potassium, leakage, and additional potassium conductance (i.e., the transient A-current). Rose and Hindmarsh [38] simplified the six-dimensional Connor-Stevens model to the two-dimensional Hindmarsh-Rose (2DHR) model by a transformation of variables. Furthermore, they extended the 2DHR model to a three-dimensional HR model with the addition of a slow variable to describe the subthreshold of the inward and outward currents. With suitable parameters, the models can simulate repetitive firing [23], bursting [24] and thalamic neurons [38] with detailed ionic currents, where repetitive firing is primarily induced through quadratic recovery. On a physiological level, the HR model can simulate the bursting neurons of the pond snail Lymnaea [7, 6, 9, 8, 40]. Zemanova [45] used the HR model to investigate the structural and functional clusters of a corticocortical network by modeling the cortical area of the network with a sub-network of interacting excitable neurons. Tsuji [42] proposed a 2DHR-type model that preserves both the time-scale parameter and the first component of the vector fields in the FitzHugh-Nagumo model [20, 35] and showed that the model has properties of both Class 1 and Class 2 neurons. Chen [10] studied the number and stability of equilibria and codimension-two bifurcations in the 2DHR-type model and the neurophysiological features of the model with spike-and-reset conditions. The aforementioned studies considered the 2DHR-type model without delay.

In the nervous systems of organisms, recurrent synaptic feedback plays an important role in recurrent inhibition and recurrent excitation. Feedback can be found in the nervous systems of vertebrates. Recurrent inhibition occurs in spinal motoneurons, in pyramidal cells of the hippocampus, in the cerebellum, thalamus and neocortex, and in the retina and olfactory bulb [1, 32, 44, 26, 18, 33, 43]. Recurrent excitation has been observed in the hippocampus, neocortical circuits, spiny stellate neurons and dendritic spines [16, 17, 41, 2, 34]. Plant [37] introduced the FitzHugh differential-difference equation with recurrent neural feedback in a planar system and studied the associated Hopf bifurcations with the strength of the feedback as the bifurcation parameter. From a biological perspective, it follows that a single nerve with monosynaptic recurrent feedback should be the simplest microcircuit in the nervous system. Recurrent feedback occurs after some finite delay due to the finite conduction velocity of the nerve axons and due to the synaptic delay. Castel-franco and Stech [5] demonstrated that stable periodic orbits for the Plant model emerge from a Hopf bifurcation through a period-doubling bifurcation. Double Hopf and fold-Hopf bifurcations in a three-dimensional HR model with recurrent feedback [31, 30] were recently studied. Zhang et al. [46] studied bursting solutions for two three-dimensional HR neurons with joint electrical and synaptic coupling using bifurcation analysis. However, to the best of our knowledge, few studies have considered a two-dimensional, single-neuron model in a differential-difference form. Therefore, we chose to study the dynamics of the 2DHR-type model [42, 10] in a differential-difference form.

Large-scale oscillatory behavior in a cortex often involves large numbers of intrinsic single-neuron oscillations. The oscillatory dynamics involving oscillations of various amplitudes, such as MMOs, are important in neuron models [19] and
Several researchers have studied the bifurcation scenarios of MMOs. Koper [27] found that the MMOs occurred near two Hopf bifurcations, which were located near the saddle-node (SN) bifurcation in a cross-shaped phase diagram. These results differed from those of previous studies that showed MMOs occur in the vicinity of a Shil’nikov homoclinic orbit. Erchova and McGonigle [19] reviewed studies on MMOs in the brain. These studies included examples at the single-neuron level and possible instances of MMOs across local and global brain networks using a number of noninvasive techniques, such as electroencephalography and magnetoencephalography. Rubin and Wechselberger [39] investigated the generation of MMOs in a three-dimensional Hodgkin-Huxley neuron model. Krupa et al. [28] studied the generation of MMOs in a coupled system using a two-dimensional oscillator to model the dynamics of the membrane potential and the calcium concentration in dopaminergic neurons in the mammalian brain stem. Desroches et al. [15] investigated the organization of the MMOs in the self-coupled FitzHugh-Nagumo system and in a simplified model to study synchronization in a network of Hodgkin-Huxley neurons. However, relatively few studies have investigated MMOs in a two-dimensional, single-neuron model in a differential-difference form. Therefore, we chose to investigate the occurrence of MMOs in the 2DHR-type model with recurrent feedback.

The remainder of the paper is organized as follows. In Sec. 2, we introduce a general class of nonlinear neuron models in a differential-difference form. The model can be considered a generalization of the 2DHR-type model [42, 10]. From the characteristic equation of this model, we analyze the local stability of an equilibrium as a function of the time delay. In Sec. 3, the direction and stability of the Hopf bifurcations are analyzed by reducing the system on a center manifold. In Sec. 4, we provide results of numerical simulations to assess the accuracy of the theoretical analysis. In addition, we suggest a possible reason for the emergence of MMOs in the planar system. Finally, conclusions are presented in Sec. 5.

2. The delay Hindmarsh-Rose-type model. Let us consider that the simplest possible modification of the systems described in [42, 10] to simulate synaptic feedback is the following system of differential-difference equations:

\[
\begin{align*}
\dot{x}(t) &= c \left[ k_1 x(t) - \frac{x^3(t)}{3} - y(t) + k_2 (x(t - \tau) - v_0) + I \right], \\
\dot{y}(t) &= \left( x^2(t) + dx(t) - by(t) + a \right)/c.
\end{align*}
\]

where \( x \) and \( y \) denote the cell membrane potential and a recovery variable, respectively, and \( a, b, c, d, \tau \) and \( k_1 \) are positive constants. The parameter \( c \) represents the time scale. The parameter \( k_2 \) is positive for excitatory feedback and negative for inhibitory feedback, with the strength of the feedback given by the magnitude of \( k_2 \). Because the current is ionic, we expect that its magnitude will be approximately proportional to the difference between \( x \) and the “resting potential” \( v_0 \), which is similar to the assumption in [37]. The parameter \( I \) denotes the membrane current or an external stimulus. If the value of \( I \) is increased and the other parameters are unchanged, the cubic function is shifted up. However, if the value of the parameter \( a \) is reduced and the other parameter values are unchanged, the quadratic function is shifted down. Hence, the effect of \( I \) is reflected through parameter \( a \).
For convenience, the term $I - k_2v_0$ is replaced with $I$, and it is assumed that $k_1 + k_2 = 1$ and $k_1 = k$ in Eqs. (1) and (2). System (1)-(2) can be recast in the following form.

\[
\dot{x}(t) = c \left[ kx(t) - \frac{x^3(t)}{3} - y(t) + (1 - k)x(t - \tau) + I \right],
\]

\[
\dot{y}(t) = \left( x^2(t) + dx(t) - by(t) + a \right) / c.
\]

For $k = 1$, the system is the same as in [42, 10]. We can identify the number of equilibria and their stability and several codimension-one and codimension-two bifurcations, such as the SN, Hopf, Bautin and Bogdanov-Takens bifurcations. Let the point $(x_0, y_0)$ be an equilibrium, and let $x(t) = x(t) - x_0$ and $y(t) = y(t) - y_0$. To simplify the notation, the variable $x$ is replaced with $x$, and the equations can be transformed as follows:

\[
\dot{x}(t) = c \left[ (k - x_0^2)x(t) - y(t) + (1 - k)x(t - \tau) \right] - \frac{1}{3}cx^3(t) - cx_0x^2(t),
\]

\[
\dot{y}(t) = \left[ (2x_0 + d)x(t) - by(t) \right] / c + x^2(t) / c.
\]

The associated characteristic equation is

\[
\det \left( \begin{array}{cc}
(2x_0 + d) & -c \\
(2x_0 + d) / c & -b/c - \lambda
\end{array} \right) = 0,
\]

or

\[
[\lambda - c(k - x_0^2) + (1 - k)e^{-\lambda \tau}] (\lambda + \frac{b}{c}) + (2x_0 + d) = 0.
\]

Eq. (7) can be expressed as

\[
F(\lambda) + G(\lambda)e^{-\lambda \tau} = 0,
\]

where $F(\lambda) = \lambda^2 + a_1\lambda + a_0$ and $G(\lambda) = b_1\lambda + b_0$ with $a_0 = b(x_0^2 - k) + (2x_0 + d)$, $a_1 = b/c - c(k - x_0^2)$, $b_0 = b(k - 1)$ and $b_1 = c(k - 1)$. This characteristic equation determines the local stability of an equilibrium. That is, the equilibrium is stable if and only if all of the characteristic roots $\lambda$ have negative real parts.

The following two conditions determine whether the characteristic roots are purely imaginary.

(C1) $a_0^2 < b_0^2$,
(C2) $a_0^2 > b_0^2$, $b_1^2 - a_1^2 + 2a_0 > 0$, $(b_1^2 - a_1^2 + 2a_0)^2 > 4(a_0^2 - b_0^2)$

Applying the lemma in [13], we obtain the following results for Eq. (9): if Condition (C1) holds and $\tau = \tau^+_n$, then Eq. (9) has a pair of purely imaginary roots $\pm i\omega_+$; if Condition (C2) holds for $\tau = \tau^+_n$ (resp. $\tau = \tau^-_n$), then Eq. (9) has a pair of imaginary roots $\pm i\omega_+$ (resp. $\pm i\omega_-$); if neither (C1) nor (C2) and $\tau > 0$, then Eq. (9) has no purely imaginary roots, where

\[
\omega_+^2 = \frac{1}{2} \left( b_1^2 - a_1^2 + 2a_0 \right) \pm \sqrt{\frac{1}{4} \left( b_1^2 - a_1^2 + 2a_0 \right)^2 - (a_0^2 - b_0^2)},
\]

\[
\cos(\tau^+_n \omega_+) = \frac{b_0(\omega_+^2 - a_0) - \omega_+^2 a_1b_1}{b_1^2 \omega_+^2 + b_0^2},
\]

\[
\sin(\tau^+_n \omega_+) = \frac{a_1b_0\omega_+ + (a_0 - \omega_+^2)b_1\omega_+}{b_1^2 \omega_+^2 + b_0^2},
\]

\[
\omega_+^2 = \frac{1}{2} \left( b_1^2 - a_1^2 + 2a_0 \right) \pm \sqrt{\frac{1}{4} \left( b_1^2 - a_1^2 + 2a_0 \right)^2 - (a_0^2 - b_0^2)},
\]

\[
\cos(\tau^-_n \omega_-) = \frac{b_0(\omega_-^2 - a_0) - \omega_-^2 a_1b_1}{b_1^2 \omega_-^2 + b_0^2},
\]

\[
\sin(\tau^-_n \omega_-) = \frac{a_1b_0\omega_- + (a_0 - \omega_-^2)b_1\omega_-}{b_1^2 \omega_-^2 + b_0^2},
\]
Let \( \lambda_{\ell,n}(\tau) = \alpha_{\ell,n}(\tau) + i\omega_{\ell,n}(\tau) \) with \( \ell = -\) or \( + \) and \( n = 0, 1, 2, \cdots \), where the root of Eq. (9) satisfies \( \alpha_{-n}(\tau_n^-) = 0, \omega_{-n}(\tau_n^-) = \omega_- \) and \( \alpha_{+n}(\tau_n^+) = 0, \omega_{+n}(\tau_n^+) = \omega_+ \). If \( \tau_n^+ \) and \( \tau_n^- \) are bifurcation values, we must verify that the transversality conditions hold. In other words, we obtain the following transversality conditions:

\[
\begin{align*}
&\left( T \right) \frac{d\text{Re} \lambda_{-n}(\tau_n^-)}{d\tau} < 0, \\
&\frac{d\text{Re} \lambda_{+n}(\tau_n^+)}{d\tau} > 0,
\end{align*}
\]

where

\[
\text{sign} \left( \frac{d\text{Re} \lambda_{\pm n}(\tau_n^{\pm})}{d\tau} \right) = \text{sign} \left( a_1^2 - b_1^2 - 2a_0 + 2\omega_2 \right). \tag{13}
\]

As an example, we list several Hopf points in Table 1 when the parameters vary in \( \tau \) space for two values of \( a \). A bifurcation diagram of the local maxima of \( x \) with respect to \( \tau \) is shown in Fig. (1) for \( a = 0.2 \). If \( 0 \leq \tau < 1.7377 \), a stable equilibrium exists, and for \( \tau > 1.7377 \), the equilibrium is unstable. For convenience, the stability of the equilibrium is not shown in Fig. (1).

| \( a = 0.2 \) | \( a = 0.22 \) |
|---|---|
| \( i \) | \( h \) | \( \tau_i^- \) | \( \text{sign} \) | \( i \) | \( h \) | \( \tau_i^+ \) | \( \text{sign} \) |
| 0 | 1 | 1.7377 | 1 | 0 | 1 | 3.0544 | 1 |
| 1 | 1 | 10.1531 | 1 | 0 | 2 | 6.4068 | -1 |
| 0 | 2 | 11.9329 | -1 | 1 | 1 | 12.4303 | 1 |
| 2 | 1 | 18.5685 | 1 | 1 | 2 | 20.3581 | -1 |
| 3 | 1 | 26.9839 | 1 | 2 | 1 | 21.8061 | 1 |
| 1 | 2 | 34.6035 | -1 | 3 | 1 | 31.182 | 1 |
| 4 | 1 | 35.3993 | 1 | 2 | 2 | 34.3094 | -1 |
| 5 | 1 | 43.8147 | 1 | 4 | 1 | 40.5579 | 1 |
| 6 | 1 | 52.2301 | 1 | 3 | 2 | 48.2607 | -1 |
| 2 | 2 | 57.2741 | -1 | 5 | 1 | 49.9338 | 1 |
| \vdots | \vdots | \vdots | \vdots | \vdots | \vdots | \vdots | \vdots |

Table 1. Hopf bifurcations and stability switches with \( \tau \) as the bifurcation parameter. We chose the following values for the parameters: \( b = 2, c = 3, d = 2.55 \) and \( k = 1.1 \). A Hopf bifurcation occurs at \( \tau_i^h \), where \( i \in \{0\} \cup \mathbb{N} \) and \( h \in \{1, 2\} \). The index \( h = 1 \) (resp. \( h = 2 \)) corresponds to \( \omega_+ \) (resp. \( \omega_- \)). For \( a = 0.2 \), one switch, from stability to instability, occurs. For \( a = 0.22 \), two switches, from stability to instability and back to stability, occur. The last column, labeled “sign”, indicates the sign of the transversality condition.

3. **Direction and stability of the Hopf bifurcation.** In this section, we examine the direction and stability of Eqs. (5)-(6) using Hopf bifurcation theory \([21, 22]\).

Let the phase space \( C_2 := C([\tau, 0], \mathbb{R}^2) \) be the Banach space of continuous functions from \( [\tau, 0] \) to \( \mathbb{R}^2 \) with the supremum norm. In the following, the superscript \( T \) denotes the transpose. For \( \phi = (\phi_1, \phi_2)^T \in C_2 \), the operator \( \Pi \) is defined as

\[
\Pi \phi(\theta) = \begin{cases} 
    d\phi(\theta)/d\theta, & \text{if } \theta \in [-\tau, 0), \\
    L\phi(\theta), & \text{if } \theta = 0,
\end{cases}
\]
where $L$ is defined as

$$L \phi = \int_{-\tau}^{0} [d\eta(\theta)] \phi(\theta),$$  \hspace{1cm} (14)

and $\eta : [-\tau, 0] \to \mathbb{R}^2 \times \mathbb{R}^2$ is a real-valued function of bounded variation in $[-\tau, 0]$ satisfying

$$d\eta(\theta) = (\Pi_0 \delta(\theta) + \Pi_1 \delta(\theta + \tau)) d\theta,$$

with

$$\Pi_0 = \begin{bmatrix} A & D \\ B & F \end{bmatrix}, \quad \text{and} \quad \Pi_1 = \begin{bmatrix} \hat{C} & 0 \\ 0 & 0 \end{bmatrix},$$

$A = ck - cx_0^2$, $B = (2x_0 + d)/c$, $\hat{C} = c(1 - k)$, $D = -c$, and $F = -b/c$. For the nonlinear part, let $R$ be defined as

$$R \phi = \begin{cases} 0, & \text{if } \theta \in [-\tau, 0), \\ \tilde{R}(\phi), & \text{if } \theta = 0, \end{cases}$$

with

$$\tilde{R}(\phi) = \left( \frac{-c\phi_1^2(0)}{3} - cx_0\phi_1^2(0) \phi_2^2(0)/c \right).$$
Therefore, Eqs. (5) and (6) are equivalent to the following operator equation:

\[ \dot{u}_t = \Pi u_t + R u_t, \]

where \( u = (x, y)^T \) and \( u_t = u(t + \theta) \) for \( \theta \in [-\tau, 0] \).

For \( \psi \in C^2([-\tau, 0], \mathbb{R}^2) \), the operator \( \Pi^* \) is defined as

\[
\Pi^* \psi(s) = \begin{cases} 
-d\psi(s)/ds, & \text{if } s \in (0, \tau], \\
\int_{-\tau}^{0} [d\eta(s, 0)]^T \psi(-s), & \text{if } s = 0.
\end{cases}
\]

Let \( \phi \in C([-\tau, 0], \mathbb{C}^2) \) and \( \psi \in C([0, \tau], \mathbb{C}^2) \). We use the formal duality in \( C^* \times C \) with the bilinear form

\[
\langle \psi, \phi \rangle = \bar{\psi}^T(0) \phi(0) - \int_{-\tau}^{0} \int_{\xi=0}^{\theta} \bar{\psi}^T(\xi - \theta)d\eta(\theta)\phi(\xi)d\xi.
\]

(15)

The two operators \( \Pi^* \) and \( \Pi \) are adjoint. That is, \( \langle \psi, \Pi\phi \rangle = \langle \Pi^*\psi, \phi \rangle \) for \( \phi \in D(\Pi) \) and \( \psi \in D(\Pi^*) \).

Without loss of generality, we write \( \pm i\omega_\ell \) as \( \pm i\omega_0 \). Let \( q(\theta) \) be the eigenfunction for \( \Pi \) corresponding to \( i\omega_0 \). That is,

\[
\Pi q(\theta) = i\omega_0 q(\theta), \quad \Pi^* q^*(s) = -i\omega_0 q^*(s).
\]

One can easily verify that the vector \( q(\theta) = (1, q_2)^T e^{i\omega_0 \theta} \) is the right eigenvector of \( \Pi \) corresponding to the eigenvalue \( i\omega_0 \) and \( q^*(s) = N(1, q_2^*) e^{i\omega_0 s} \) is the left eigenvector of \( \Pi^* \) corresponding to the eigenvalue \(-i\omega_0 \), where \( \theta \in [-\tau, 0] \) and \( s \in [0, \tau] \). It follows from the definition of \( \Pi \) and Eq. (14) that \( M_0 \times (1, q_2)^T = (0, 0)^T \), where

\[
M_0 = \begin{bmatrix} A + \hat{C} e^{-\tau i\omega_0} - i\omega_0 & D \\ B & F - i\omega_0 \end{bmatrix}.
\]

By direct computation, we obtain \( q_2 = -B/(F - i\omega_0) \). Similarly, we have \( (1, q_2^*) \times M^* = (0, 0)^T \), where

\[
M^* = \begin{bmatrix} A + \hat{C} e^{\tau i\omega_0} + i\omega_0 & D \\ B & F + i\omega_0 \end{bmatrix}
\]

and \( q_2^* = -D/(F + i\omega_0) \). From Eq. (15), we can choose

\[
\langle q^*, q \rangle = N \left\{ \left( \begin{array}{c} 1 \\ q_2^* \end{array} \right)^T \left( \begin{array}{c} 1 \\ q_2 \end{array} \right) \right. \\
- \int_{-\tau}^{0} \int_{\xi=0}^{\theta} \left( \begin{array}{c} 1 \\ q_2^* \end{array} \right)^T e^{-i\omega_0(\xi - \theta)} d\eta(\theta) \left( \begin{array}{c} 1 \\ q_2 \end{array} \right) e^{i\omega_0 \xi} d\xi \left\} \right. \\
= N \left( 1 + \frac{BD}{F - i\omega_0} + C_T e^{-i\omega_0 \tau} \right).
\]

Because \( \langle q^*, q \rangle = 1 \),

\[
N = \left( 1 + \frac{BD}{F - i\omega_0} + C_T e^{-i\omega_0 \tau} \right)^{-1}.
\]

Using the same notation as in [22], we define

\[
z(t) = \langle q^*, u_t \rangle,
W(t, \theta) = u_t(\theta) - 2\text{Re}\{z(t)q(\theta)\},
\]

(16)
where \( \text{Re}\{z(t)q(\theta)\} = (z(t)q(\theta) + \bar{z}(t)\bar{q}(\theta))/2 \) and \( W = (W^{(1)}, W^{(2)}) \). On the center manifold \( C_0 \), we have
\[
W(t, \theta) = W(z(t), \bar{z}(t), \theta),
\]
where
\[
W(z, \bar{z}, \theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{21}(\theta)\frac{\bar{z}^2}{2} + W_{30}(\theta)\frac{z^3}{6} + \cdots,
\]
and \( z \) and \( \bar{z} \) are local coordinates on the center manifold in the directions of \( q^* \) and \( \bar{q}^* \), respectively. \( W \) is real if \( u_t \) is real. We consider only real solutions. For a solution \( u_t \in C_0 \), because \( \mu = 0 \),
\[
\dot{z}(t) = i\omega_0 z(t) + g(z, \bar{z}),
\]
where
\[
g(z, \bar{z}) = \bar{q}^*(0)F(W(z, \bar{z}, 0) + 2\text{Re}\{z(t)q(0)\})
\]
\[
= g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2} + \cdots. \quad (17)
\]
From Eq. (16), we can write
\[
W(t, -\tau) = u_t(-\tau) - 2\text{Re}\{z(t)q(-\tau)\}
\]
\[
= u(t - \tau) - z(t)q(-\tau) - \bar{z}(t)\bar{q}(-\tau)
\]
\[
= u(t - \tau) - z(t)\left(1, \frac{1}{q_2}\right)e^{-i\omega_0\tau}
\]
\[
- \bar{z}(t)\left(1, \frac{1}{\bar{q}_2}\right)e^{i\omega_0\tau}.
\]
Therefore,
\[
x(t - \tau) = e^{-i\omega_0\tau}z(t) + e^{i\omega_0\tau}\bar{z}(t) + W^{(1)}(t, -\tau),
\]
where
\[
W^{(1)}(t, -\tau) = W_{20}^{(1)}(-\tau)\frac{z^2}{2} + W_{11}^{(1)}(-\tau)z\bar{z} + W_{21}^{(1)}(-\tau)\frac{\bar{z}^2}{2} + \cdots.
\]
If \( \tau = 0 \), then we have \( x(t) = z(t) + \bar{z}(t) + W^{(1)}(t, 0) \). Furthermore, we have
\[
g(z, \bar{z}) = \bar{q}^*(0)\tilde{R}_0
\]
\[
= \tilde{N}(1, \tilde{q}_2^*)\tilde{R}_0,
\]
where
\[
\tilde{R}_0 = \left(-cx_0x^2 - \frac{1}{3}cx^3\right).
\]
Comparing the coefficients in Eq. (17) with those in Eq. (18), we have
\[
g_{20} = \tilde{N}(-2cx_0 + \tilde{q}_2^*),
\]
\[
g_{21} = \tilde{N}\left(-2c - 2(cx_0 - \tilde{q}_2^*)\left(2W_{11}^{(1)}(0) + W_{20}^{(1)}(0)\right)\right),
\]
and \( g_{02} = g_{11} = g_{20} \).
Next, we compute \( W_{11}(\theta) \) and \( W_{20}(\theta) \) for \( \theta \in [-\tau, 0) \). We can write
\[
\dot{W} = HW + H(z, \bar{z}, \theta),
\]
where
\[
H(z, \bar{z}, \theta) = \begin{cases} 
-\text{Re}\{\bar{q}^*(0) \cdot R_0q(\theta)\}, & \text{if } \theta \in [-\tau, 0), \\
-\text{Re}\{\bar{q}^*(0) \cdot R_0q(0)\} + \tilde{R}_0, & \text{if } \theta = 0.
\end{cases}
\]
Therefore, we have
\[
H(z, \bar{z}, \theta) = \frac{1}{2} H(\theta) z^2 + H_{11}(\theta) \bar{z} \bar{z} + \frac{1}{2} H_{02}(\theta) \bar{z}^2 + \cdots.
\]
Comparing the coefficients in Eq. (19) with those in Eq. (20), we obtain
\[
H_{20}(\theta) = -g_{20} q(\theta) - \bar{g}_{02} \bar{q}(\theta)
\]
and
\[
H_{11}(\theta) = -g_{11} q(\theta) - \bar{g}_{11} \bar{q}(\theta).
\]
It follows from \((\Pi - 2i\omega_0)W_{20}(\theta) = -H_{20}(\theta)\) that
\[
\begin{align*}
\Pi W_{20}(\theta) &= 2i\omega_0 W_{20}(\theta) - H_{20}(\theta), \\
\dot{W}_{20}(\theta) &= 2i\omega_0 W_{20}(\theta) + \bar{g}_{20} q(0) e^{i\omega_0 \theta} + \bar{g}_{02} \bar{q}(0) e^{-i\omega_0 \theta}.
\end{align*}
\]
Solving the ordinary differential equation (22) for \(W_{20}(\theta)\), we obtain
\[
W_{20}(\theta) = -\frac{g_{20}}{i\omega_0} q(0) e^{i\omega_0 \theta} - \frac{\bar{g}_{02}}{3i\omega_0} \bar{q}(0) e^{-i\omega_0 \theta} + E_1 e^{2i\omega_0 \theta},
\]
and similarly
\[
W_{11}(\theta) = \frac{g_{11}}{i\omega_0} q(0) e^{i\omega_0 \theta} - \frac{\bar{g}_{11}}{i\omega_0} \bar{q}(0) e^{-i\omega_0 \theta} + E_2,
\]
where \(E_1\) and \(E_2\) are both two-dimensional undetermined coefficients that can be determined by setting \(\theta = 0\) in \(H\). In fact, because
\[
H(z, \bar{z}, 0) = -2\text{Re}\{\bar{q}^*(0) \cdot R_0q(0)\} + \tilde{R}_0,
\]
we have
\[
H_{20}(0) = -g_{20} q(0) - \bar{g}_{02} \bar{q}(0) + \left( \frac{-2c_{x_0}}{2/c} \right),
\]
and
\[
H_{11}(0) = -g_{11} q(0) - \bar{g}_{11} \bar{q}(0) + \left( \frac{-2c_{x_0}}{2/c} \right).
\]
From Eq. (21) with \(\theta = 0\), we have
\[
\Pi_0 W_{20}(0) + \Pi_1 W_{20}(-\tau) = 2i\omega_0 W_{20}(0) - H_{20}(0),
\]
and
\[
\Pi_0 W_{11}(0) + \Pi_1 W_{11}(-\tau) = -H_{11}(0).
\]
Substituting Eq. (23) into Eq. (24), the left side of Eq. (24) can be expressed as

\[
\begin{align*}
\Pi_0 \left( \frac{-g_{20}}{i\omega_0} q(0) - \frac{g_{02}}{3i\omega_0} \bar{q}(0) + E_1 \right) + \\
\Pi_1 \left( \frac{-g_{20}}{i\omega_0} q(-\tau) - \frac{g_{02}}{3i\omega_0} \bar{q}(-\tau) + E_1 e^{-2i\omega_0\tau} \right)
\end{align*}
\]

\[= -g_{20}q(0) + \frac{1}{3}g_{02}\bar{q}(0) + \Pi_0 E_1 + \Pi_1 E_1 e^{-2i\omega_0\tau},\]

and the right side can be expressed as

\[
2i\omega_0 \left( \frac{-g_{20}}{i\omega_0} q(0) - \frac{g_{02}}{3i\omega_0} \bar{q}(0) + E_1 \right) - H_{20}(0)
\]

\[= \left( -2g_{20}q(0) - \frac{2}{3}g_{02}\bar{q}(0) + 2i\omega_0 E_1 \right) - H_{20}(0).
\]

Therefore,

\[\left( \Pi_0 + \Pi_1 e^{-2i\omega_0\tau} - 2i\omega_0I_2x2 \right) E_1 = \begin{pmatrix} 2cx_0 \\ -2/c \end{pmatrix}.
\]

So,

\[E_1 = \left( \Pi_0 + \Pi_1 e^{-2i\omega_0\tau} - 2i\omega_0I_2x2 \right)^{-1} \begin{pmatrix} 2cx_0 \\ -2/c \end{pmatrix}.
\]

Similarly,

\[E_2 = \left( \Pi_0 + \Pi_1 \right)^{-1} \begin{pmatrix} 2cx_0 \\ -2/c \end{pmatrix}.
\]

Therefore, \(W_{20}(\theta), W_{11}(\theta), E_1 \) and \(E_2\) can be determined.

We use the following definitions [22]:

\[
c_1(0) = i \frac{2\omega_0}{2\omega_0} \left( \frac{g_{20}}{2} \right) \left( g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2 \right) + \frac{g_{21}}{2},
\]

\[
\mu_2 = -\frac{\text{Re}\{c_1(0)\}}{\text{Re}\lambda'(0)},
\]

\[
T_2 = -\frac{\text{Im}\{c_1(0)\} + \mu_2\text{Im}\lambda'(0)}{\omega_0},
\]

\[
\beta_2 = 2\text{Re}\{c_1(0)\}.
\]

**Theorem 3.1.** If Condition \((C_1)\) or \((C_2)\) holds and the transversality conditions \((T)\) hold, then the system in (3) and (4) undergoes a Hopf bifurcation at \(\tau = \tau_c\). The sign of \(\mu_2\) determines the direction of bifurcation, and the sign of \(\beta_2\) determines the stability of the bifurcating periodic solutions. They are asymptotically, orbitally stable if \(\beta_2 < 0\) and unstable if \(\beta_2 > 0\).

4. **Numerical simulations.** In this section, we will examine the stability of the equilibria and their behaviors based on Eqs. (10)-(13) and condition \((T)\) in Sec. 2 and Theorem 3.1 in Sec. 3. We first review the number and stability of the equilibria for the system in Eqs. (3) and (4) with \(k = 1\). For \(k \neq 1\) and \(\tau \neq 0\), we will obtain the range of parameter values for which a Hopf bifurcation exists and discuss possible reasons for the occurrence of MMOs. In the following, we define \(b = 2\) and \(c = 3\), as in [10].

To begin, we recall several results for \(k = 1\) from [10]. This is the case without any delay. For \(k \neq 1\) and \(\tau = 0\), the system is the same as for \(k = 1\). In Fig. (2), the four lines \(AH^-, AH^+, SN^-\) and \(SN^+\) separate the parameter domain \((a, d)\) into
The number and stability of equilibria in the $a$-$d$ parameter space with $b = 2$, $c = 3$, and $\tau = 0$. The number and stability of the equilibria for the six areas $\Omega_1$-$\Omega_6$ are as follows: $\Omega_1$ has one stable equilibrium, $\Omega_2$ has two stable equilibria and one saddle equilibrium, $\Omega_3$ has one stable equilibrium, $\Omega_4$ has one unstable and one saddle equilibrium, $\Omega_5$ has one stable equilibrium, and $\Omega_6$ has two unstable equilibria and one saddle equilibrium. The line $\text{SN}^-$ indicates a SN bifurcation for a saddle and an unstable node, the line $\text{SN}^+$ indicates a SN bifurcation for a saddle and a stable node, and the lines $\text{AH}^\pm$ indicate AH bifurcations.

The six areas denoted by $\Omega_1$-$\Omega_6$. The number and stability of the equilibria for the six areas are indicated in Fig. (2). A codimension-one bifurcation can occur when the values of the parameters $(a, d)$ cross one of these four lines. For example, when the parameter values cross the line $\text{AH}^+$ from $\Omega_3$ to $\Omega_5$, the stability of the equilibrium changes. If the transversality conditions hold, this is a Hopf bifurcation. Similarly, when the parameter values cross the line $\text{SN}^-$ from $\Omega_1$ to $\Omega_2$, one stable and one saddle equilibrium emerge. If the transversality conditions hold, this is a SN bifurcation with a stable node. By [10], the Hopf (resp. Hopf, SN and SN) bifurcation in fact occurs at the point belongs to the line $\text{AH}^+$ (resp. $\text{AH}^+$, $\text{SN}^-$ and $\text{SN}^+$). The locus of the saddle-homoclinic bifurcation, which is based on the BT bifurcation [29], is represented by the blue dashed line in Fig. (3). The Bautin bifurcation occurs at $d = 2b - b^2/c^2 = 32/9 \approx 3.56$. Hence, for $d < 32/9$, the Hopf bifurcation is subcritical, and for $d > 32/9$, the Hopf bifurcation is supercritical. A nondegenerate fold bifurcation of the cycles originating from the Bautin point occurs to the right of $\text{AH}^+$ and lower than $d < 32/9$; this condition is represented by the blue line in Fig. (3). Therefore, the number and stability of equilibria, the conditions for codimension-one bifurcations for $\text{SN}^\pm$, $\text{AH}^\pm$, the homoclinic bifurcations based on the BT bifurcation and fold bifurcations of cycles are known for the case $k = 1$.

Next, we examine the parameter values that lead to the existence of Hopf bifurcations and switching stability in Eqs. (5) and (6) with $\tau$ as the bifurcation parameter. For $k > 1$, the model has the form of recurrent excitation, and for $k < 1$, the model possesses the structure of recurrent inhibition. For these two recurrent feedback cases, we choose two value, $k = 1.1$ and $k = 0.9$. The parameters corresponding
Figure 3. The number of distinct pairs of complex conjugate roots and the regions of mixed-mode states in the $a$-$d$ parameter space for the elliptic region in Fig. (2). For the region shaded in pale gray, there is only one imaginary solution, $i\omega_+$. For the region shaded in dark gray, there are two imaginary solutions, $i\omega_{\pm}$. Notably, in the cusp of the dark gray area, one imaginary and two imaginary solutions coexist for different equilibria. In other words, the pale gray region and dark gray region overlap. The parameter values for which the MMOs occur are indicated with black dots. The locus of homoclinic bifurcations is shown by the dashed blue line. The locus of fold bifurcations of cycles is shown by the blue line.

to the Hopf bifurcations are shown in Figs. (3(a)) and (3(b)) for the two values. The parameter regions corresponding to one pair of purely imaginary roots $\omega_+$ and two pairs of purely imaginary roots $\omega_{\pm}$ are shown in pale gray and dark gray, respectively, in Fig. (3(a)). As the value of $k$ approaches 1, the two regions reduce to the lines $SN^\pm$ and $AH^+$, respectively, in the $a$-$d$ parameter domain. The regions of switching stability are shown in Fig. (4), which shows the maximum number of stability switches for $k = 1.1$, where the region for one switch is shown in blue and the region for two switches is shown in pale blue. Regions with greater numbers of switches are shown in black near the boundary. Therefore, the parameter regions for Hopf bifurcations with $\tau$ as the bifurcation parameter in the parameter space $(a, d)$ are known for the system (5) and (6) for both recurrent inhibition and recurrent excitation.

To demonstrate the stability switches of the equilibria and dynamical behavior of the Hopf bifurcations, we will show results for two pairs of parameters, labeled ROI$_1$ and ROI$_2$ in Fig. (3(a)), where we have listed the Hopf bifurcations in Table 1. For the first pair, two switches, from stability to instability and back to stability, occur. For the second pair, only one switch, from stability to instability, occurs. The dynamical behavior for the parameter values $d = 2.55$ and $a = 0.2$ (i.e., ROI$_2$) is presented in Fig. (5); the results for ROI$_1$ are similar and are thus not shown. It follows from Fig. (2) that the system with the given parameter values has only one stable equilibrium $(x_0, y_0)$, where $x_0 \approx -0.968$ and $y_0 \approx -0.666$, when $\tau = 0$. One switch from stability to instability occurs when $a = 0.2$, where delay parameters are listed in Table 1. For these parameters, we obtain $\beta_2 \approx 6.81 > 0$ and $\mu_2 \approx -26.7 < 0$ at $\tau_0^+ \approx 1.7377$. It follows from Theorem 3.1 that the Hopf bifurcation at $\tau_0^+$ is
Figure 4. The maximum number of stability switches in the a-d parameter space with $b = 2$, $c = 3$ and $k = 1.1$. The colored regions indicate the existence of a pair of purely imaginary roots, $\lambda_\pm = i\omega_\pm$ with $\omega_+ > \omega_- > 0$, for Eq. (10). In other words, there exists a stability switch. The dark blue, blue, and green regions indicate those values for which the maximum number of stability switches is 1, 2 and 3, respectively. The number of stability switches is greater than 4 in the red region.

The range of parameter values leading to the occurrence of MMOs is indicated with the dotted black line in Figs. (3(a)) and (3(b)). We consider only the parameter values $-5 \leq a \leq 5$ and $-2 \leq d \leq 5$, as shown in Fig. (3(a)). The range of delay resulting in MMOs is between 0 and 5. For example, with the parameter values $a = 0.2$ and $d = 2.55$, 7 different MMOs are shown, i.e., from $1^1$ to $1^7$, in Fig. (7(a)). Fig. (7(a)) shows two regions, “Non-Periodic” and “Non-MMO”. The former is the area where only one stable equilibrium exists, and the latter is the area where there is an unstable equilibrium and a stable periodic orbit. In Fig. (7(b)), the fold bifurcation of cycles occurs at $\tau_c \approx 1.6616$. The first Hopf bifurcation occurs at $\tau \approx 1.7377$, as shown in Table 1. The parameter pairs $(a,b)$ shown with black dots in the parameter space are those for which MMOs exist. It follows from [10] that for the system without delay, the bifurcation of the limit cycle occurs near $AH^+$ and to the right of $AH^+$, and the bifurcation of the homoclinic orbit occurs between $SN^+$ and $SN^-$ in Fig. (3(a)). When the Hopf bifurcation with delay $\tau$ as the bifurcation
Figure 5. Responses of the membrane potential in Eqs. (1)-(2) for four values of delay. The system parameters had the following values: \(a = 0.2\), \(b = 2\), \(c = 3\), \(d = 2.55\) and \(k = 1.1\). (a) For \(\tau = 1.6\), the system has a stable equilibrium. (b) For \(\tau = 1.7\), there exist a stable equilibrium, an unstable limit cycle and a stable \(1^3\) MMO. (c) For \(\tau = 1.75\), there exist an unstable equilibrium and a stable \(1^2\) MMO. (d) For \(\tau = 1.79\), there exist a stable limit cycle and an unstable equilibrium.

Figure 6. Trajectories in the x-y phase space for Eqs. (1)-(2) for two values of delay: (a) \(\tau = 1.7\) and (b) \(\tau = 1.75\). The two nullclines, \(\dot{x} = 0\) and \(\dot{y} = 0\), are shown by thick black lines, the trajectories for 8 sets of initial conditions are shown by thin gray lines, and a limit cycle is shown with a thick black line. The ratio between the two timescales is \(1/9\) because the value of the parameter \(c\) was 3. The values of the other parameters were as follows: \(a = 0.2\), \(b = 2\), \(d = 2.55\) and \(k = 1.1\).

parameter occurs for certain values of the parameters \(a\), \(b\), \(c\), \(d\), \(k\) and \(\tau\), the MMOs can occur in two cases with \(\tau = 0\): the parameter is near the fold bifurcation of the limit cycle, or the parameter is near the bifurcation of the homoclinic orbit.

Finally, we suggest a possible reason for the occurrence of MMOs. Eqs. (1) and (2) can be considered a fast-slow (i.e., singularly perturbed) system because the system involves two variables with dynamics on different timescales. The ratio between the two timescales is given by \(1/c^2\). For example, if we take \(c = 3\), the ratio is \(1/9\). Hence, we can call the variables \(x\) and \(y\) fast and slow variables, respectively. The set of points that satisfy \(g(x, y) = 0\) is a slow manifold of the differential-difference equation in the singular case. One solution of the singularly
perturbed system is a canard that follows an attracting slow manifold and then follows a repelling slow manifold near a bifurcation point. MMOs may also occur through the canard phenomenon [3]. The canard-induced MMO is a limit cycle resulting from a Hopf bifurcation that transitions from a small, nearly harmonic cycle to a large relaxation oscillation in a narrow parameter interval. For a two-dimensional system with additional variables or noise, MMOs may occur in larger regions as the dynamics switch between small- and large-amplitude oscillations. In our study, the canard-induced MMOs of the two-variable differential-difference equation may occur in a Hopf bifurcation with delay.

5. Conclusions. In this study, we analyzed Hopf bifurcations in a 2DHR-type model with recurrent feedback, where delay was the bifurcation parameter. This model is a generalization of the model presented in [42, 10]. Depending on the parameters of the model, the number of equilibria and their stability may be the same as those of the model without delay [10]. The conditions for the existence of purely imaginary roots of the characteristic equation for the system were studied, and the ranges of parameter values for these conditions were obtained for two cases, \( k = 0.9 \) and \( k = 1.1 \). When the parameter values were near the values corresponding
to the first Hopf bifurcation with delay as the bifurcation parameter, we observed canard-induced MMOs near the parameter values corresponding to either the Bautin bifurcation or homoclinic bifurcation in the system without delay. Therefore, the 2DHR-type model with recurrent feedback exhibits more complex behavior than the same model without recurrent feedback.

Acknowledgments. This work is partially supported by the Ministry of Science and Technology of the Republic of China, the National Taiwan Normal University, and the National Center for Theoretical Sciences of R.O.C. in Taiwan.

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Received February 2013; 1st revision November 2014; 2nd revision May 2015.
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