Asymptotic Limit-cycle Analysis of the FitzHugh-Nagumo Equations

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The asymptotic limit-cycle analysis of the FitzHugh-Nagumo equations is presented. In this work, we obtain an explicit analytical expression for the relaxation-oscillation period that is accurate within 1% of their numerical values. In addition, we derive the critical parametric values leading to canard explosions and implosions in its associated limit cycles.

I. INTRODUCTION

The FitzHugh-Nagumo (FHN) equations [1,3] provide a simple model describing the activation and deactivation of spiking behavior in neurons. Nagumo [2] introduced an electric-circuit representation of the FitzHugh [1] model, in which a three-segment parallel circuit is built from a capacitor $C$ in one segment, in parallel with a tunnel diode (with an emf $\mathcal{E}_0$) in a second segment, and an LR-segment with a resistor $R$ connected in series with an inductor $L$.

The Kirchhoff junction equation for the Nagumo circuit is expressed as the sum of three currents equal to the constant external current $I$ that flows into the three-segment junction:

$$I = I_C + I_D(\varepsilon) + I_R,$$

where $I_C$ is the capacitor current, $I_D(\varepsilon)$ is the diode current (which depends on the potential difference $\varepsilon$ across the diode), and $I_R$ is the current flowing through the LR segment.

By denoting the potential difference across each segment as $V$, we obtain the capacitor current $I_C = C \frac{dV}{dt}$, and the LR current $I_R$ yields the relation

$$V = RI_R + L \frac{dI_R}{dt}.$$  \hfill (2)

Lastly, we define the potential difference across the tunnel diode as $\varepsilon = V - \mathcal{E}_0$, so that the tunnel-diode current is modeled as

$$I_D(\varepsilon) = I_0 - \frac{\Delta \varepsilon}{R_0} \left[ \left( \frac{\varepsilon - \mathcal{E}_0}{\Delta \varepsilon} \right) - \frac{1}{3} \left( \frac{\varepsilon - \mathcal{E}_0}{\Delta \varepsilon} \right)^3 \right],$$  \hfill (3)

where $I_0$ flows through the diode when the potential difference is $\mathcal{E}_0$, which defines the negative resistance $1/I_D' (\varepsilon_0) = -R_0 < 0$. The potential differences $\mathcal{E}_0 \pm \Delta \varepsilon$, on the other hand, are used to define the maximum and minimum $I_D(\varepsilon_0 \mp \Delta \varepsilon) = I_0 \pm \frac{2}{3} \Delta \varepsilon / R_0$ of the tunnel-diode current [3].

By introducing the following dimensionless variables: the diode potential $x = (\varepsilon - \mathcal{E}_0) / \Delta \varepsilon$ and the resistor current $y = (I_0 + I_R) R_0 / \Delta \varepsilon$, the Kirchhoff junction equation [1] becomes

$$\dot{x} = c + x \dot{x}^3 / 3 - x + y,$$

where $c = IR_0 / \Delta \varepsilon$ is the negative-resistance parameter, and we introduced the dimensionless time derivative $\dot{x} = R_0 C \frac{dx}{dt}$, which is normalized to the $R_0 C$ time constant. This equation is coupled to the resistor-current equation [2], now written in dimensionless form as

$$\dot{x} = b y - a + \epsilon^{-1} \dot{y},$$  \hfill (5)

where $a = (RI_0 + \mathcal{E}_0) / \Delta \varepsilon$ and $b = R / R_0$ are arbitrary constants, and the small dimensionless parameter is $\epsilon = \omega^2 (R_0 C)^2 \ll 1$, where $\omega = 1 / \sqrt{LC}$ is the natural $LC$ frequency (i.e., the LC period is chosen to be much longer than the $R_0 C$ time constant).

There is a large amount of literature on the FHN equations and its extensions [3]. As a simplification of the four-variable Hodgkin-Huxley model [4], the FHN model combines: (1) the membrane potential $V$ and the sodium activation variable $n$ as the membrane potential variable $x$; (2) the sodium inactivation variable $h$ and the potassium activation parameter $a$ as the recovery variable $y$; and (3) the membrane current is represented by the stimulus current $c$. Like the Van der Pol paradigm [5], these equations display a Hopf bifurcation at a critical value of the control parameter $c$, where a stable fixed point is replaced by a stable limit cycle. Once a stable limit cycle is created, a sudden transition from a small-amplitude oscillation to a large-amplitude relaxation oscillation is described as a canard explosion.

The remainder of the paper is organized as follows. In Sec. [II] we present the mathematical preliminary material that underlies the stability, bifurcation, and canard analysis of coupled first-order differential equations. In particular, we present the Fenichel geometric singular perturbation theory [6, 7], which is applied to the Van der Pol equations. In Sec. [III] we apply this analysis to the FHN equations, which yields an explicit analytical expression for the relaxation-oscillation period that is accurate within 1% of their numerical values, as well as critical parametric values leading to canard explosions and implosions in its associated limit cycles.

II. MATHEMATICAL PRELIMINARIES

The FHN equations [4-5] are generically expressed as the nonlinear singular first-order ordinary differential equations

$$\begin{align*}
\dot{x} &= F(x, y; a) \\
\dot{y} &= \epsilon G(x, y; a)
\end{align*},$$  \hfill (6)

where
where $x$ and $y$ denote dimensionless dynamical variables, and each dimensionless time derivative is represented with a dot (e.g., $\dot{x} = dx/dt$). On the right side of Eq. (3), the dimensionless parameter $\epsilon$ plays an important role in the qualitative solutions of Eq. (6), while the functions $F(x, y; a)$ and $G(x, y; a)$ (which may depend on a dimensionless control parameter $a$) are used to define the nullcline equations: $F(x, y; a) = 0 = G(x, y; a)$, which yield separate curves $y = f(x; a)$ and $y = g(x; a)$ onto the $(x, y)$-plane. A simplifying assumption used here is that the functions $F$ and $G$ are at most separately linear in $y$ and $a$, with $\partial^2 F/\partial y \partial a = 0 = \partial^2 G/\partial y \partial a$.

By introducing a new time normalization $t' = \epsilon t$, the equations (6) may also be written as

$$
\begin{align*}
\epsilon x' &= F(x, y; a) \\
y' &= G(x, y; a)
\end{align*}
$$

where a prime now denotes a derivative with respect to $t'$ (e.g., $x' = dx/dt'$). According to standard terminology, the times $t'$ and $t$ are called the slow time and fast time, respectively, and Eqs. (6) and (7) are called the fast system and slow system, respectively.

We note that the slope function $m(x, y; a) \equiv \dot{y}/\dot{x} = y'/x' = \epsilon G(x, y; a)/F(x, y; a)$ is a useful qualitative tool as we follow an orbit in the $y(t)$-versus-$x(t)$ phase space. In particular, we see that the orbit crosses the $y$-nullcline horizontally ($m = 0$) while it crosses the $x$-nullcline vertically ($m = \pm \infty$). Hence, in the limit $\epsilon \ll 1$, the slope function is near zero (i.e., the orbit is horizontal) unless the orbit is near the $x$-nullcline, where $F(x, y; a) \simeq 0$. As the slope $m(x, y; a)$ depends on the model parameter $a$, the shape of the orbit solution will also change with $a$.

The dynamical equations (6) can exhibit a type of large-amplitude oscillations called relaxation oscillations (8). The paradigm for these large-amplitude oscillations is represented by the biased Van der Pol equation (3)

$$
\frac{d^2 x}{dt^2} - \nu (1 - x^2) \frac{dx}{dt} + \omega^2 x = \omega^2 a,
$$

where $\omega$ is the natural frequency of the linearized harmonic oscillator and $\nu$ is the negative dissipative rate, while the bias parameter $a$ represents an equilibrium value of the dimensionless oscillator displacement $x$. We note that the term $-\nu (1 - x^2) dx/dt$ yields negative dissipation in the range $x^2 < 1$, which leads to exponential growth in that range.

From Eq. (8), we obtain the coupled dimensionless equations

$$
\begin{align*}
\dot{x} &= x - x^3/3 - y \\
\dot{y} &= \epsilon (x - a)
\end{align*}
$$

where the dimensionless time is normalized to $\nu^{-1}$ (i.e., $\dot{x} = \nu^{-1} dx/dt$) and $\epsilon \equiv \omega^2/\nu^2$ (10). Here, the $x$-nullcline is $y(x) = x - x^3/3$ (which has a minimum at $x = -1$ and a maximum at $x = 1$) while the $y$-nullcline is a vertical line at $x = a$.

Figure 1 shows the solution of the Van der Pol equations (4) for $a = 0.5$ and $\epsilon = 0.001$ and the initial conditions $x(0) = 1$ and $y(0) = 0$. In the top plot, the solution $x(t)$ shows slow orbits (on time scales of order $\epsilon^{-1}$) from A to B and C to D, and fast (exponential) transitions (on time scales of order $\epsilon^2$, with $-1 < \alpha < 0$) from B to C and D to A. The bottom plot in Fig. 1 shows that the slow orbits occur near the $x$-nullcline (shown as a dashed curve). Figure 2, on the other hand, shows that the orbits from B to C and D to A include nonlinear exponential accelerations from $\pm 1$ to $\mp 1$, respectively, and then nonlinear exponential decays from $\mp 1$ to the turning points.
\[ x_C \simeq -2 \text{ and } x_A \simeq 2, \text{ respectively.} \]

A. Linear stability analysis

If the nullcline curves of Eq. (6) intersect at \((x_0, y_0)\), where \(x_0 = x_0(a)\) and \(y_0(a) = f(x_0) = g(x_0)\), the point \((x_0, y_0)\) is called a fixed point of Eq. (6). The stability of this fixed point is investigated through a standard normal-mode analysis \([3]\), where \(x = x_0 + \delta x \exp(\lambda t)\) and \(y = y_0 + \delta y \exp(\lambda t)\) are inserted into Eq. (6) to obtain the linearized matrix equation

\[
\begin{pmatrix}
\lambda - F_{x0} & F_{y0} \\
-\epsilon G_{x0} & \lambda - \epsilon G_{y0}
\end{pmatrix}
\begin{pmatrix}
\delta x \\
\delta y
\end{pmatrix}
= 0,
\]

where the constant eigenvector components \((\delta x, \delta y)\) are non-vanishing only if the determinant of the linearized matrix vanishes. Here, \((F_{x0}, F_{y0})\) and \((G_{x0}, G_{y0})\) are partial derivatives evaluated at the fixed point \((x_0, y_0)\) and the eigenvalues \(\lambda_{\pm} = \frac{1}{2} \tau \pm \sqrt{\tau^2 - 4\Delta}\) are roots of the quadratic characteristic equation \(\lambda^2 - \tau \lambda + \Delta = 0\), where \(\tau(a, \epsilon) = F_{x0} + \epsilon G_{y0} = \lambda_+ + \lambda_-\) and \(\Delta(a, \epsilon) = \epsilon (F_{x0} G_{y0} - F_{y0} G_{x0}) = \lambda_+ - \lambda_-\) are the trace and determinant of the Jacobian matrix, respectively.

The fixed point is a stable point \((\tau < 0 \text{ and } \Delta > 0)\) that is either a node \((\tau^2 > 4 \Delta)\), when the eigenvalues are real and negative: \(\lambda_- < \lambda_+ < 0\), or a focus \((\tau^2 < 4 \Delta)\), when the eigenvalues are complex-valued \((\lambda_+ = \lambda_- + i\delta)\) with a negative real part. Otherwise, the fixed point is either an unstable point \((\tau > 0 \text{ and } \Delta > 0)\) or a saddle point \((\Delta < 0)\). Periodic solutions of Eq. (6) exist when a Hopf bifurcation \([3]\) replaces an unstable fixed point with a stable limit cycle, which forms a closed curve in the \((x, y)\)-plane. Here, a limit cycle appears when the x-nullcline function \(f(x; a)\) has non-degenerate minimum and maximum points and it is stable whenever the trace \(\tau(a) > 0\) is positive in the range \(a_0 < a < a_u\).

For the Van der Pol equations \([3]\), we easily find the fixed point \((x_0, y_0) = (a, a - a^3/3)\) and the linear stability of that fixed point is described in terms of the trace \(\tau = 1 - a^2\) and the determinant \(\Delta = \epsilon > 0\). Here, the fixed point is stable if \(a^2 > 1\) and a limit cycle becomes stable in the range \(-1 < a < 1\) as a result of a Hopf bifurcation \([3]\) at \(a = \pm 1\), where the fixed point merges with the critical points of the x-nullcline.

B. Canard transition to relaxation oscillations

Whenever the fixed point \(x_0(a)\) of Eq. (6) comes close to a critical point \(x_c(a)\) of the x-nullcline, a sudden transition to a large-amplitude relaxation oscillation becomes possible. This transition, which occurs as the control parameter \(a\) crosses a critical value \(a_c(a)\), is referred to as a canard explosion or implosion, depending on whether the large-amplitude relaxation oscillation appears or disappears. For a brief review of the early literature on canard explosions, see Ref. \([3]\) and references therein. For a mathematical treatment, on the other hand, see Refs. \([3, 11]\).

We now present a perturbative calculation of the critical canard parameter \(a_c(\epsilon)\) as an asymptotic expansion in terms of the small parameter \(\epsilon\). For this purpose, we use the invariant-manifold solution \(y = \Phi(x, \epsilon)\) of geometric singular perturbation theory \([4, 5]\), which yields the generic canard perturbation equation

\[
y = \epsilon \xi\left(x, \Phi(x, \epsilon); a\right) = \frac{\partial \Phi(x, \epsilon)}{\partial x} \dot{x},
\]

where \(\Phi(x, \epsilon) = \sum_{k=0}^{\infty} \epsilon^k \Phi_k(x)\) and \(a_c(\epsilon) = \sum_{k=0}^{\infty} \epsilon^k a_k\).

At the lowest order \((\epsilon = 0)\), we find

\[
0 = F\left(x, \Phi_0(x); a_0\right),
\]

which yields the lowest-order x-nullcline

\[
\Phi_0(x) \equiv f(x; a_0).
\]

1. First-order perturbation analysis

At the first order in \(\epsilon\), we now find from Eq. (11):

\[
G(x, \Phi_0; a_0) = \Phi_0'(x) \left[ F_{y0} \Phi_1(x) + F_{x0} a_1 \right],
\]

where \(F_{y0} = \partial F/\partial y|_{a_0} \neq 0\) and \(F_{x0} = \partial F/\partial a|_{a_0}\) are evaluated at \((x, \Phi_0; a_0)\). Here, \(\Phi_0'(x)\) can be factored as

\[
\Phi_0'(x) \equiv (x - x_c) \Psi_0(x),
\]

where \(\Psi_0(x)\) is assumed to be finite at the critical point \(x_0(a_0)\) (i.e., a minimum or a maximum of the x-nullcline). Since the right side vanishes at the critical point \(x_0(a_0)\), we find that \(G(x_c, \Phi_0; a_0) = 0\) implies the identity

\[
x_0(a_0) \equiv x_c(a_0),
\]

where the fixed point \(x_0\) has merged with the critical point \(x_c\) of the x-nullcline at a unique value \(a_0\), i.e., the fixed point \(x_0(a_0)\) is either at the maximum \(x_0(a_0) = x_B(a_0)\), which yields \(a_0 = a_{B0}\), or at the minimum \(x_0(a_0) = x_D(a_0)\), which yields \(a_0 = a_{D0}\). With this choice of \(a_0\), we can write the factorization

\[
G(x, \Phi_0; a_0) \equiv (x - x_c) H_1(x),
\]

where \(H_1(x)\) is finite at \(x = x_c(a_0)\).

Hence, from Eq. (14), we obtain the first-order solution

\[
\Phi_1(x) \equiv K_1(x) - h(x) a_1,
\]

where we introduced the definitions

\[
K_1(x) \equiv H_1(x)/[\Psi_0(x) F_{y0}(x)],
\]

\[
h(x) \equiv F_{x0}(x)/F_{y0}(x),
\]

which are both finite at \(x = x_c(a_0)\).
2. Second-order perturbation analysis

At the second order in $\epsilon$, we find from Eq. (11):

$$G_{y0} \Phi_1 + G_{a0} a_1 = \Phi'_0 \left( F_{y0} \Phi_2 + F_{a0} a_2 \right) + \Phi'_1 \left( F_{y0} \Phi_1 + F_{a0} a_1 \right)$$

$$= \Phi'_0 F_{y0} \left( \Phi_2 + h \, a_2 \right) + F_{y0} \left( K'_1 - h \, a_1 \right) K_1,$$

where $G_{y0} = (\partial G/\partial y)_0$ and $G_{a0} = (\partial G/\partial a)_0$ are evaluated at $(x, \Phi_0, a_0)$, and we have used the first-order solution (13). By rearranging terms in Eq. (20), we obtain the second-order equation

$$S_1(x) a_1 - R_2(x) = F_{y0} \Phi_2(x) + F_{a0} a_2,$$

where we introduced the definitions

$$R_2(x) = K_1(x) \left[ F_{y0} K'_1(x) - G_{y0} \right],$$

$$S_1(x) = G_{a0} - G_{y0} h(x) + F_{y0} h'(x) K_1(x),$$

which are both finite at $x_c(a_0)$.

Once again, since the right side of this equation vanishes at the critical point $x = x_c(a_0)$, the left side must also vanish at that point, and we obtain the first-order correction

$$a_1 = R_2(x_c)/S_1(x_c).$$

By factoring the left side of Eq. (21),

$$S_1(x) a_1 - R_2(x) = (x - x_c) H_2(x),$$

we now obtain the second-order solution

$$\Phi_2(x) = K_2(x) - h(x) a_2,$$

where $K_2(x) \equiv H_2(x)/[\Psi_0(x) F_{y0}(x)]$ and $h(x)$ is defined in Eq. (19).

3. Higher-order perturbation analysis

By continuing the perturbation analysis at higher order ($n \geq 3$), Eq. (11) yields the $n$th-order equation

$$S_1(x) a_{n-1} - R_n(x) = \Phi'_0(x) F_{y0} \left[ \Phi_n(x) + h(x) a_n \right],$$

where $S_1(x)$ is defined in Eq. (23) and

$$R_n(x) = K_1(x) F_{y0} K'_{n-1}(x) - G_{y0} K_{n-1}(x)$$

$$+ \sum_{k=1}^{n-2} F_{y0} \left[ K'_k(x) - h'(x) a_k \right] K_{n-k}(x).$$

Hence, the left side of Eq. (27) vanishes at $x_c$ if

$$a_{n-1} = R_n(x_c)/S_1(x_c),$$

and the $n$th-order solution is obtained by first obtaining the factorization

$$S_1(x) a_{n-1} - R_n(x) = (x - x_c) H_n(x),$$

so that

$$\Phi_n(x) = K_n(x) - h(x) a_n,$$

where $K_n(x) \equiv H_n(x)/[\Psi_0(x) F_{y0}(x)]$ and

$$a_n = R_{n+1}(x_c)/S_1(x_c),$$

is calculated from Eq. (29). We note that, once the function $R_n(x)$ is calculated in Eq. (28), the most computationally-intensive step is the factorization (30), with $a_{n-1}$ calculated from Eq. (29).

As a result of the perturbative solution of Eq. (11), we have, therefore, calculated the perturbation expansion of the canard critical parameter

$$a_c(\epsilon) = a_0 + \frac{1}{S_1(x_c)} \sum_{k=1}^{\infty} \epsilon^k R_{k+1}(x_c).$$

For most applications, however, Eq. (33) can be truncated at first order in the asymptotic limit $\epsilon \ll 1$: $a_c(\epsilon) \approx a_0 + a_1 \epsilon$, where $a_1 > 0$ for a canard explosion, while $a_1 < 0$ for a canard implosion.

4. Van der Pol canard perturbation analysis

Figure 3 shows that the biased Van der Pol equations (13) undergo canard explosion and implosion, when a small change in the bias parameter $a = -0.998740 \to -0.998739$ leads to the appearance of a large-amplitude relaxation oscillation from small-amplitude oscillations about the fixed point, while a small change in the bias parameter $a = 0.998739 \to 0.998740$ leading to the disappearance of large-amplitude oscillations in $x(t)$ and $y(t)$ for the case $\epsilon = 0.01$.

The canard perturbation equation (11) for the Van der Pol equations (9) is

$$\epsilon \left[ x - a(\epsilon) \right] = \frac{\partial \Phi(x, \epsilon)}{\partial x} \left[ \Phi_0(x) - \Phi(x, \epsilon) \right],$$

where the partial derivatives evaluated at $\epsilon = 0$ are

$$\left( F_{y0}, F_{a0} \right) = (-1, 0)$$

and

$$\left( G_{y0}, G_{a0} \right) = (0, -1).$$

Here, the lowest-order solution $\Phi_0(x) = x - x^3/3$ has critical points at $x_c = \pm 1$ where $\Phi'_0(x) = 1 - x^2$ vanishes. Hence, the lowest-order fixed point $x_0 = a_0$ merges with
the critical point $x_c$ when $a_0 = \pm 1$. Because $F_{a0} = 0$, the function $h(x) = 0$ in Eq. (19), while $\Psi_0(x) = x + a_0$ and $H_1(x) = -1$, so that $K_1(x) = 1/(x + a_0) = \Phi_1(x)$.

Next, in Eqs. (22), we have $R_2 = -K_1 K_1' = 1/(x + a_0)^2$ and $S_1 = -1$, so that at $x = a_0 = \pm 1$, we find the first-order correction $a_1 = -1/(8 a_0^2)$, i.e., $a_1 = -1/8$ for the canard implosion at $a_0 = 1$, and $a_1 = 1/8$ for the canard explosion at $a_0 = -1$.

For the canard explosion, the calculated critical parameter (truncated at first order) $a_c(\epsilon) = -1 + \epsilon/8$ yields $a_c(0.01) = -0.99875$, which is in excellent agreement with the numerical value $-0.998740$, shown in Fig. 3. Because of the symmetry of the Van der Pol model, the calculated critical parameter (truncated at first order) $a_c(\epsilon) = 1 - \epsilon/8$ for the canard implosion yields $a_c(0.01) = 0.99875$, which is again in excellent agreement with the numerical value $0.998740$, shown in Fig. 3. Higher-order corrections to the Van der Pol canard parameter $a_c(\epsilon) = 1 - \epsilon/8 - 3\epsilon^2/32 - 173\epsilon^3/1024 - \cdots$ can be computed up to arbitrary order [12], but they are not needed in what follows.

C. Asymptotic limit-cycle period

We saw in Figs. 1-2 that, in the asymptotic limit $\epsilon \ll 1$, the limit-cycle curve of Eq. (6) is composed of slow segments that are close to the $x$-nullcline. In this limit, the asymptotic period can be calculated as follows. First, we begin with the $x$-nullcline $y = f(x; a)$ on which we obtain $dy/dt = f'(x; a) dx/dt$. Next, we use the $y$-equation $dy/dt = \epsilon G(x, y; a)$, into which we substitute the $x$-nullcline equation: $dy/dt = \epsilon G(x, f(x; a); a)$.

By combining these equations, we obtain the infinitesimal asymptotic-period equation

$$\epsilon dt = f'(x; a) dx/G(x, f(x; a); a),$$

which yields the asymptotic limit-cycle period

$$\epsilon T_{\text{ABCDA}}(a) = \int_{x_A(a)}^{x_B(a)} f'(x; a) dx - \frac{f'(x; a) dx}{G(x, f(x; a); a)}.$$

Here, the asymptotic limit cycle ABCDA combines the slow $x$-nullcline orbits $x_A \rightarrow x_B$ and $x_C \rightarrow x_D$ and the fast horizontal transitions $x_B \rightarrow x_C$ and $x_D \rightarrow x_A$, which are ignored in Eq. (36). Generically, the values $x_D(a) < x_B(a)$ are the minimum and maximum of the $x$-nullcline $y = f(x; a)$, respectively, where $f'(x; a)$ vanishes. The points $x_C(a) = x_A(a)$, on the other hand, are the minimum and maximum of the asymptotic limit cycle.

In the limit $\epsilon \ll 1$, the phase-space portrait for the Van der Pol equations [12] shown in Fig. 1 has slow segments $A(x_A = 2) \rightarrow B(x_B = 1)$ and $C(x_C = -2) \rightarrow D(x_D = -1)$ on the $x$-nullcline (shown as a dashed curve) and fast horizontal transitions $B(x_B = 1) \rightarrow C(x_C = -2)$ and $D(x_D = -1) \rightarrow A(x_A = 2)$.
for the Van der Pol limit-cycle ABCDA is calculated as
\[ \epsilon T_{\text{VdP}}(a) = \int_{2}^{1} \frac{(1-x^2) \, dx}{x-a} + \int_{-2}^{-1} \frac{(1-x^2) \, dx}{x-a} \]
\[ = 3 - (1-a^2) \ln \left( \frac{4-a^2}{1-a^2} \right), \quad (37) \]
which is shown in Fig. 4 as a solid curve. We note that the asymptotic Van der Pol period \( (37) \) is symmetric in \( a \), i.e., \( T_{\text{VdP}}(-a) = T_{\text{VdP}}(a) \).

The next term in the asymptotic expansion of the Van der Pol period \( (37) \) involves a nontrivial correction associated with the complex orbits seen in Fig. 2 on their way to the turning points at \( x_{A,C} \approx \pm 2 \). This correction is expressed as \( 3 \alpha \epsilon^{2/3} \), where \( \alpha = 2.338107... \) denotes the lowest zero of the Airy function \( \text{Ai}(-x) \). If we add this correction to the Van der Pol asymptotic period \( (37) \), we obtain
\[ \epsilon T_{\text{VdP}}(a, \epsilon) \equiv 3 - (1-a^2) \ln \left( \frac{4-a^2}{1-a^2} \right) + 3 \alpha \epsilon^{2/3}, \quad (38) \]
where the correction is assumed to be independent of the bias parameter \( a \) (a more thorough calculation, which is omitted here, would be required to explore this dependence).

The numerical periods \( \epsilon T_{\text{num}}(a, \epsilon) \), which are shown in Fig. 4 as dots, are within 4\% higher than the asymptotic Van der Pol period \( (37) \) and are within 1\% of the corrected asymptotic Van der Pol period \( (38) \). These numerical results show that the asymptotic limit \( \epsilon \ll 1 \) enables us to evaluate the limit-cycle period according to Eq. \( (38) \) with excellent accuracy, on both qualitative and quantitative basis.

### III. FITZHUGH-NAGUMO EQUATIONS

The FHN equations \[ (3) \] offer a simple model used to study the conditions leading to firing of neuron cells. Here, the FHN equations are expressed as
\[ \dot{x} = x - x^3/3 + c - y, \quad (39) \]
\[ \dot{y} = \epsilon \left( x + a - b y \right), \quad (40) \]
where \((a, b, c)\) are constants and \( \epsilon \ll 1 \). In what follows, we will use the model parameters \((a, b) = (3/5, 4/5)\) for the purpose of explicit calculations and numerical simulations, and the control parameter \( c \) will determine the type of solutions for Eqs. \((39)-(40)\).

The FHN nullcline equations are
\[ x - \text{nullcline} : f(x) = x - x^3/3 + c \]
\[ y - \text{nullcline} : g(x) = (5x + 3)/4 \]
which intersect at a single fixed point \((x_0, y_0)\), where \( x_0(c) \) is the single real root of the cubic equation
\[ 4x^3 + 3x - (12c - 9) = 0. \quad (42) \]

![FIG. 5: Plot of the fixed point \( x_0(c) = \sinh[\psi(c)/3] \) as a function of the control parameter \( c \). The fixed point reaches the critical points \( \pm 1 \) (dashed lines) of the \( x \)-nullcline at \( c = 1/6 \) and \( c = 4/3 \).](image)

![FIG. 6: Linear stability diagram for the FHN equations for \( \epsilon = 0.001 \). Trace \( \tau(c) \) versus \( c \), showing a stable limit cycle in the range \( c_0(\epsilon) < c < c_0(\epsilon) \).](image)

The three roots of this equation \[ (4) \] are
\[ x_1(c) = i \cos \left( \frac{\pi}{6} - i \frac{\psi(c)}{3} \right), \quad (43) \]
\[ x_2(c) = -i \cos \left( \frac{\pi}{2} - i \frac{\psi(c)}{3} \right) = \sinh \left( \frac{1}{3} \psi(c) \right), \quad (44) \]
\[ x_3(c) = -i \cos \left( \frac{\pi}{6} + i \frac{\psi(c)}{3} \right) = x_1^*(c), \quad (45) \]
where \( \psi(c) \equiv \arcsinh(12c - 9) \). Here, the fixed point \( x_0(c) = x_2(c) = \sinh[\psi(c)/3] \) reaches the critical points \( \pm 1 \) of the \( x \)-nullcline at \( c = 1/6 \) and \( c = 4/3 \), respectively (see Fig. 5).

#### A. Linear stability of the fixed point

The linear stability of the fixed point \((x_0, y_0)\) is determined from the Jacobian matrix
\[ J_0(c, \epsilon) = \begin{pmatrix} 1 - x_0^2(c) & -1 \\ \epsilon & -4 \epsilon/5 \end{pmatrix}, \quad (46) \]
where the trace is \( \tau = (1 - 4 \epsilon/5) - x_0^2 \) and the determinant is \( \Delta = \epsilon (1 + 4 x_0^2)/5 > 0 \). Marginal stability \((\tau = 0)\)

...
occurs at \( c_u(\epsilon) = 3/4 - 7/12 \) and \( c_u(\epsilon) = 3/4 + \delta(\epsilon)/12 \), where \( \delta(\epsilon) = (7 - 16 \epsilon/5) \sqrt{1 - 4\epsilon/5} < 7 \) for \( \epsilon > 0 \). Here, the fixed point is stable if \( c < c_u(\epsilon) \) and \( c > c_u(\epsilon) \), while a limit cycle is stable (for \( \epsilon = 0.001 \)) in the range

\[
c_u(\epsilon) = 0.167167 < c < c_u(\epsilon) = 1.33283.
\]

Here, we note that \( c_u(\epsilon) > 3/4 - 7/12 = 1/6 \) and \( c_u(\epsilon) < 3/4 + 7/12 = 4/3 \), i.e., the fixed point loses stability after it has reached the \( x \)-nullcline minimum at \( x = -1 \), while it regains stability before it has reached the \( x \)-nullcline maximum at \( x = 1 \).

Figure 7 shows a path in the stability (trace-versus-determinant) space for \( 0 < c < 3/2 \). The path begins at \( c = 0 \) (A), where the fixed point is stable (\( \tau < 0 \)). As \( c \) increases, it first reaches \( c = 1/6 \) (B) where the fixed point is at the critical point \( x_0 = -1 \) of the \( x \)-nullcline. At \( c = c_u(\epsilon) = 0.167167 \) (C), the fixed point becomes marginally stable (\( \tau = 0 \)). A Hopf bifurcation yields a stable limit cycle for \( c > c_u(\epsilon) \) as we go through \( c = 3/4 \) (D) until we return to marginal stability at \( c = c_u(\epsilon) = 1.33283 \) (E). As \( c \) continues to increase, we reach \( c = 4/3 \) (F), when the fixed point is at the critical point \( x_0 = +1 \) of the \( x \)-nullcline, and then ultimately we return to the starting point of the path at \( c = 3/2 \) (G). We note that at point D (\( c = 3/4 \)), the trace \( \tau \) reaches its highest (positive) value, which corresponds to the fastest firing rate.

B. Canard behavior of the FHN Solutions

The singular canard perturbation equation \([11]\) for the FHN equations \([39]-[43]\) is

\[
\epsilon (x + a - b \Phi) = \frac{\partial \Phi}{\partial x} \left( x - \frac{x^3}{3} + c - \Phi \right),
\]

where \( \Phi(x, \epsilon) = \sum_{k=0}^{\infty} \epsilon^k \Phi_k(x) \) and \( c(\epsilon) = \sum_{k=0}^{\infty} \epsilon^k c_k \), and we use \((a, b) = (3/5, 4/5)\). Here, the partial derivatives evaluated at \( \epsilon = 0 \) are

\[
\begin{align*}
F_{\gamma 0} &= -1 \\
F_{\epsilon 0} &= 1 \\
G_{\gamma 0} &= -b \\
G_{\epsilon 0} &= 0
\end{align*}
\]

At lowest order (\( \epsilon = 0 \)), we find \( \Phi_0(x) = x - x^3/3 + c_0 \), which has two critical points at \( x_c = \pm 1 \).

At first order, we find

\[
x + a - b \Phi_0(x) = \Phi'_0(x) \left( c_1 - \Phi_1(x) \right),
\]

where the right side vanishes at the critical point \( x = \pm 1 \) of \( \Phi_0(x) \). In order for \( \Phi_1(x) \) to be regular at the critical points, we require the left side to also vanish at \( x = \pm 1 \). Hence, we find \( 12 c_0^3 - 9 = \pm 7 \), which yields \( c_0^3 = c_0(0) = 4/3 \) at \( x_c = +1 \) and \( c_0^3 = c_0(0) = 1/6 \) at \( x_c = -1 \). By factoring both sides by \( x \mp 1 \), we find

\[
H^\pm_1(x) = -\Psi^\pm_0(x) \left( c_1 - \Phi_1(x) \right),
\]

where \( H^\pm_1(x) = (4x^2 \pm 4x + 7)/15 \) and \( \Psi^\pm_0(x) = (x \pm 1) \).

Hence, the first-order solution is

\[
\Phi_1(x) = c_1 + K_1(x),
\]

where \( K_1(x) = (4x^2 \pm 4x + 7)/15 (x \pm 1) \).

At the second order, we find

\[
-(4/5) \Phi_1 = \Phi'_0 (c_2 - \Phi_2) + \Phi'_1 (c_1 - \Phi_1),
\]

which can be expressed as

\[
R_2(x) - (4/5) c_1 = \Phi'_0 (c_2 - \Phi_2),
\]

where \( R_2(x) = K_1(x) [K'_1(x) - 4/5] \). Once again, since the right side vanishes at the critical point \( x = \pm 1 \) of \( \Phi_0(x) \), we require that \( c_1^7 = R_2(\pm 1)/b = 13/32 \),

Hence, when truncated at first order in \( \epsilon \), the canard explosion and implosion occur at

\[
\begin{align*}
\epsilon^- &= 1/6 + 13 \epsilon/32 = 0.167073 \\
\epsilon^+ &= 4/3 - 13 \epsilon/32 = 1.33293
\end{align*}
\]

respectively, where we used \( \epsilon = 0.001 \). These values agree very well with the numerical results shown in Fig. 8. We note that the canard explosion occurs between points B \((c = 1/6)\) and C \((c = c_u)\) in Fig. 7 while the canard implosion occurs between points E \((c = c_u)\) and F \((c = 4/3)\), i.e., these canard events occur between marginal stability and the fixed point located at the critical points \( \pm 1 \) of the \( x \)-nullcline.
We now construct the asymptotic limit-cycle integral \( \int c \) with the \( x \)-nullcline equation \( y = x - x^3/3 + c \), which yields \( \dot{y} = (1-x^2) \dot{x} \), and the \( y \)-equation \( \dot{y} = \epsilon (x+a-b \ y) \) evaluated on the \( x \)-nullcline: \( \dot{y} = \epsilon [x+a-b(x-x^3/3+c)] \).

We then obtain the infinitesimal equation
\[
\epsilon \ dt = \frac{(1 - x^2) \, dx}{b \, x^3/3 + (1 - b) \, x - (bc - a)} = \frac{(3/b) \, (1 - x^2) \, dx}{(x - x_1)(x - x_2)(x - x_3)},
\]
where \( x_1(c) = x_3^a(c) \) and \( x_2(c) \) are the roots defined in Eqs. 43-45.

The asymptotic limit-cycle period for the FHN equations is thus given by the integrals
\[
\epsilon T_{\text{FHN}}(c) = \frac{3}{b} \int_{x_2}^{x_1} \frac{(1 - x^2) \, dx}{(x - x_1)(x - x_2)(x - x_3)} + \frac{3}{b} \int_{x_3}^{-1} (1 - x^2) \, dx.
\]

We now introduce the partial-fraction decomposition
\[
\frac{(1 - x^2)}{(x - x_1)(x - x_2)(x - x_3)} = \frac{p_1}{x - x_1} + \frac{p_2}{x - x_2} + \frac{p_3}{x - x_3},
\]
with the coefficients

\[ p_1(c) = -\frac{(x_2 - x_3)}{\Delta} \left(1 - x_1^2\right), \quad (56) \]

\[ p_2(c) = -\frac{(x_3 - x_1)}{\Delta} \left(1 - x_2^2\right), \quad (57) \]

\[ p_3(c) = -\frac{(x_1 - x_2)}{\Delta} \left(1 - x_3^2\right), \quad (58) \]

where \( \Delta = (x_1 - x_2)(x_2 - x_3)(x_3 - x_1) \) and we used \( x_1 + x_2 + x_3 = 0 \). Hence, Eq. (55) can be written as

\[ \epsilon T_{\text{FHN}}(c) = -\frac{3}{\epsilon^2} \sum_{k=1}^{3} p_k \ln \left(\frac{4-x_k^2}{1-x_k^2}\right). \quad (59) \]

If we add the same nontrivial Van der Pol correction \( 3\alpha \epsilon^{2/3} \) [see Eq. (38)] to the asymptotic FHN period (59), we can define the corrected period

\[ T_{\text{FHN}}^\alpha(c, \epsilon) \equiv T_{\text{FHN}}(c) + 3\alpha/\epsilon^{1/3}. \quad (60) \]

Figure 11 shows that the exact numerical periods (shown as dots) are all within 4% above the period \( T_{\text{FHN}}(c) \), while they are within 1% of the \( \alpha \)-corrected period \( T_{\text{FHN}}^\alpha(c, \epsilon) \).

IV. SUMMARY

In the present paper, we have shown how the asymptotic limit-cycle properties of the FHN equations (4)-(5) can be accurately calculated. Indeed, we have shown in Sec. II B how the singular perturbation theory of Fenichel [6] can be used to accurately predict the appearance (canard explosion) and disappearance (canard implosion) of large-amplitude relaxation oscillations (see Fig. 8) in the FHN equations (4)-(5). In addition, once large-amplitude relaxation oscillations are excited, the period of these oscillations can be accurately calculated in Eq. (59), where explicit formulas for the cubic roots (43)-(45) of the polynomial (42). The accuracy of Eq. (60) is clearly demonstrated in Fig. 11 when the nontrivial Van der Pol correction \( 3\alpha \epsilon^{2/3} \) is added to the FHN period (59).

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