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In a previous paper we have proposed a new method for proving the existence of "canard solutions" for three and four-dimensional singularly perturbed systems with only one *fast* variable which improves the methods used until now. The aim of this work is to extend this method to the case of four-dimensional singularly perturbed systems with two *slow* and two *fast* variables. This method enables to state a unique generic condition for the existence of "canard solutions" for such four-dimensional singularly perturbed systems which is based on the stability of *folded singularities* (*pseudo singular points* in this case) of the *normalized slow dynamics* deduced from a well-known property of linear algebra. This unique generic condition is identical to that provided in previous works. Applications of this method to the famous coupled FitzHugh-Nagumo equations and to the Hodgkin-Huxley model enables to show the existence of "canard solutions" in such systems.

Key Words: Geometric singular perturbation theory, singularly perturbed dynamical systems, canard solutions.

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1. INTRODUCTION

In the beginning of the eighties, Benoît and Lobry [5], Benoît [6] and then Benoît [7] in his PhD-thesis studied canard solutions in $\mathbb{R}^3$. In the article entitled "Systèmes lents-rapides dans $\mathbb{R}^3$ et leurs canards," Benoît [6, p. 170] proved the existence of canards solution for three-dimensional singularly perturbed systems with two *slow* variables and one *fast* variable while using "Non-Standard Analysis"according to a theorem which stated that canard solutions exist in such systems provided that the *pseudo singular point*[1] of the *slow dynamics*, *i.e.*, of the *reduced vector field* is of *saddle* type. Nearly twenty years later, Szmolyan and Wechselberger [25] extended "Geometric Singular Perturbation Theory[2]" to canards problems in $\mathbb{R}^3$ and provided a "standard version" of Benoît's theorem [6]. Very recently, Wechselberger [39] generalized this theorem for n-dimensional singularly perturbed systems with k *slow* variables and m *fast* (Eq. (1)). The method used by Szmolyan and Wechselberger [25] and Wechselberger [39] require to implement a "desingularization procedure" which can be summarized as follows: first, they compute the *normal form* of such singularly perturbed systems which is expressed according to some coefficients (a and b for dimension three and $\tilde{a}$, $\tilde{b}$ and $\tilde{c}_j$ for dimension four) depending on the functions defining the original vector field and their partial derivatives with respect to the variables. Secondly, they project the "desingularized vector field" (originally called "normalized slow dynamics" by Eric Benoît [6, p. 166]) of such a *normal form* on the tangent bundle of the critical manifold. Finally, they evaluate the Jacobian of the projection of this "desingularized vector field" at the *folded singularity* (originally called *pseudo singular points* by José Argémi [1, p. 336]). This lead Szmolyan and Wechselberger [25, p. 427] and Wechselberger [39, p. 3298] to a "classification of *folded singularities* (*pseudo singular points*)". Thus, they showed that for three-dimensional singularly perturbed systems such *folded singularity* is of *saddle type* if the following condition is satisfied: $a < 0$ while for four-dimensional singularly perturbed systems such *folded singularity* is of *saddle type* if $\tilde{a} < 0$. Then, Szmolyan and Wechselberger [25, p. 439] and Wechselberger [39, p. 3304] established their Theorem 4.1. which state that "*In the folded saddle and in the folded node case singular canards perturb to maximal canard for sufficiently small* ε". However, in their works neither Szmolyan and Wechselberger [25] nor Wechselberger [39] did not provide (to our knowledge) the expression of these constants (a and $\tilde{a}$) which are necessary to state the existence of canard solutions in such systems.

In a previous paper entitled: "Canards Existence in Memristor's Circuits" (see Ginoux & Llibre [17]) we first provided the expression of these

[1]This concept has been originally introduced by José Argémi [1]. See Sec. 1.8.
[2]See Fenichel [12, 15], O'Malley [23], Jones [20] and Kaper [21]

constants and then showed that they can be directly determined starting from the *normalized slow dynamics* and not from the projection of the "desingularized vector field" of the *normal form*. This method enabled to state a unique "generic" condition for the existence of "canard solutions" for such three and four-dimensional singularly perturbed systems which is based on the stability of *folded singularities* of the *normalized slow dynamics* deduced from a well-known property of linear algebra. This unique condition which is completely identical to that provided by Benoît [6] and then by Szmolyan and Wechselberger [25] and finally by Wechselberger [39] is "generic" since it is exactly the same for singularly perturbed systems of dimension three and four with only one *fast* variable.

The aim of this work is to extend this method to the case of four-dimensional singularly perturbed systems with $k = 2$ *slow* and $m = 2$ *fast* variables. Since the dimension of the system is $m = k + m$, such problem is known as "canards existence in $\mathbb{R}^{2+2}$". Moreover, in this particular case where $k = m = 2$, the *folded singularities* of Wechselberger [39, p. 3298] are nothing else but the *pseudo singular points* of the late José Argémi [1] as we will see below. Following the previous works, we show that for such four-dimensional singularly perturbed systems *pseudo singular points* are of *saddle type* if $\tilde{a} < 0$. Then, according Theorem 4.1. of Wechselberger [39, p. 3304] we provide the expression of this constant $\tilde{a}$ which is necessary to establish the existence of canard solutions in such systems. So, we can state that the condition $\tilde{a} < 0$ for existence of canards in such $\mathbb{R}^{2+2}$ is "generic" since it is exactly the same for singularly perturbed systems of dimension three and four with only one *fast* variable.

The outline of this paper is as follows. In Sec. 1, definitions of singularly perturbed system, critical manifold, reduced system, "constrained system", canard cycles, folded singularities and pseudo singular points are recalled. The method proposed in this article is presented in Sec. 2 for the case of four-dimensional singularly perturbed systems with two *fast* variables. In Sec. 3, applications of this method to the famous coupled FitzHugh-Nagumo equations and to the Hodgkin-Huxley model enables to show the existence of "canard solutions" in such systems.

2. DEFINITIONS

2.1. Singularly perturbed systems

According to Tikhonov [37], Jones [20] and Kaper [21] *singularly perturbed systems* are defined as:

$$\begin{aligned} \vec{x}' &= \varepsilon \vec{f}\,(\vec{x}, \vec{y}, \varepsilon)\,, \\ \vec{y}' &= \vec{g}\,(\vec{x}, \vec{y}, \varepsilon)\,. \end{aligned} \tag{1}$$

where $\vec{x} \in \mathbb{R}^k$, $\vec{y} \in \mathbb{R}^m$, $\varepsilon \in \mathbb{R}^+$, and the prime denotes differentiation with respect to the independent variable t'. The functions $\vec{f}$ and $\vec{g}$ are assumed to be C^∞ functions[3] of $\vec{x}$, $\vec{y}$ and ε in $U \times I$, where U is an open subset of $\mathbb{R}^k \times \mathbb{R}^m$ and I is an open interval containing $\varepsilon = 0$.

In the case when $0 < \varepsilon \ll 1$, *i.e.* ε is a small positive number, the variable $\vec{x}$ is called *slow* variable, and $\vec{y}$ is called *fast* variable. Using Landau's notation: $O(\varepsilon^p)$ represents a function f of u and ε such that $f(u,\varepsilon)/\varepsilon^p$ is bounded for positive ε going to zero, uniformly for u in the given domain.

In general we consider that $\vec{x}$ evolves at an $O(\varepsilon)$ rate; while $\vec{y}$ evolves at an $O(1)$ *slow* rate. Reformulating system (1) in terms of the rescaled variable $t = \varepsilon t'$, we obtain

$$\begin{aligned} \dot{\vec{x}} &= \vec{f}(\vec{x}, \vec{y}, \varepsilon), \\ \varepsilon \dot{\vec{y}} &= \vec{g}(\vec{x}, \vec{y}, \varepsilon). \end{aligned} \tag{2}$$

The dot represents the derivative with respect to the new independent variable t.

The independent variables t' and t are referred to the *fast* and *slow* times, respectively, and (1) and (2) are called the *fast* and *slow* systems, respectively. These systems are equivalent whenever $\varepsilon \neq 0$, and they are labeled *singular perturbation problems* when $0 < \varepsilon \ll 1$. The label "singular" stems in part from the discontinuous limiting behavior in system (1) as $\varepsilon \to 0$.

2.2. Reduced slow system

In such case system (2) leads to a differential-algebraic system (D.A.E.) called *reduced slow system* whose dimension decreases from $k + m = n$ to m. Then, the *slow* variable $\vec{x} \in \mathbb{R}^k$ partially evolves in the submanifold M_0 called the *critical manifold*[4]. The *reduced slow system* is

$$\begin{aligned} \dot{\vec{x}} &= \vec{f}(\vec{x}, \vec{y}, \varepsilon), \\ \vec{0} &= \vec{g}(\vec{x}, \vec{y}, \varepsilon). \end{aligned} \tag{3}$$

2.3. Slow Invariant Manifold

The *critical manifold* is defined by

$$M_0 := \left\{ (\vec{x}, \vec{y}) : \vec{g}(\vec{x}, \vec{y}, 0) = \vec{0} \right\}. \tag{4}$$

[3] In certain applications these functions will be supposed to be C^r, $r \geqslant 1$.

[4] It represents the approximation of the slow invariant manifold, with an error of $O(\varepsilon)$.

Such a normally hyperbolic invariant manifold (4) of the *reduced slow system* (3) persists as a locally invariant *slow manifold* of the full problem (1) for ε sufficiently small. This locally *slow invariant manifold* is $O(\varepsilon)$ close to the *critical manifold*.

When $D_{\vec{x}}\vec{f}$ is invertible, thanks to the Implicit Function Theorem, M_0 is given by the graph of a C^∞ function $\vec{x} = \vec{G}_0(\vec{y})$ for $\vec{y} \in D$, where $D \subseteq \mathbb{R}^k$ is a compact, simply connected domain and the boundary of D is a $(k-1)$–dimensional C^∞ submanifold[5].

According to Fenichel [12, 15] theory if $0 < \varepsilon \ll 1$ is sufficiently small, then there exists a function $\vec{G}(\vec{y}, \varepsilon)$ defined on D such that the manifold

$$M_\varepsilon := \left\{ (\vec{x}, \vec{y}) : \vec{x} = \vec{G}(\vec{y}, \varepsilon) \right\}, \tag{5}$$

is locally invariant under the flow of system (1). Moreover, there exist perturbed local stable (or attracting) M_a and unstable (or repelling) M_r branches of the *slow invariant manifold* M_ε. Thus, normal hyperbolicity of M_ε is lost via a saddle-node bifurcation of the *reduced slow system* (3). Then, it gives rise to solutions of "canard" type.

2.4. Canards, singular canards and maximal canards

A *canard* is a solution of a singularly perturbed dynamical system (1) following the *attracting* branch M_a of the *slow invariant manifold*, passing near a bifurcation point located on the fold of this *slow invariant manifold*, and then following the *repelling* branch M_r of the *slow invariant manifold*.

A *singular canard* is a solution of a *reduced slow system* (3) following the *attracting* branch $M_{a,0}$ of the *critical manifold*, passing near a bifurcation point located on the fold of this *critical manifold*, and then following the *repelling* branch $M_{r,0}$ of the *critical manifold*.

A *maximal canard* corresponds to the intersection of the attracting and repelling branches $M_{a,\varepsilon} \cap M_{r,\varepsilon}$ of the slow manifold in the vicinity of a non-hyperbolic point.

According to Wechselberger [39, p. 3302]:

"Such a maximal canard defines a family of canards nearby which are exponentially close to the maximal canard, *i.e.* a family of solutions of (1) that follow an attracting branch $M_{a,\varepsilon}$ of the slow manifold and then follow, rather surprisingly, a repelling/saddle branch $M_{r,\varepsilon}$ of the slow manifold for a considerable amount of slow time. The existence of this family of canards is a consequence of the non-uniqueness of $M_{a,\varepsilon}$ and $M_{r,\varepsilon}$. However, in the singular limit $\varepsilon \to 0$, such a family of canards is represented by a unique singular canard."

[5]The set D is overflowing invariant with respect to (2) when $\varepsilon = 0$. See Kaper [21] and Jones [20].

Canards are a special class of solution of singularly perturbed dynamical systems for which normal hyperbolicity is lost. Canards in singularly perturbed systems with two or more slow variables ($\vec{x} \in \mathbb{R}^k$, $k \geqslant 2$) and one fast variable ($\vec{y} \in \mathbb{R}^m$, $m = 1$) are robust, since maximal canards generically persist under small parameter changes[6].

2.5. Constrained system

In order to characterize the "slow dynamics", *i.e.* the slow trajectory of the *reduced slow system* (3) (obtained by setting $\varepsilon = 0$ in (2)), Floris Takens [28] introduced the "constrained system" defined as follows:

$$\begin{aligned} \dot{\vec{x}} &= \vec{f}\,(\vec{x},\vec{y},0)\,, \\ D_{\vec{y}}\vec{g}.\dot{\vec{y}} &= -(D_{\vec{x}}\vec{g}.\vec{f})\,(\vec{x},\vec{y},0)\,, \\ \vec{0} &= \vec{g}\,(\vec{x},\vec{y},0)\,. \end{aligned} \tag{6}$$

Since, according to Fenichel [12, 15], the *critical manifold* $\vec{g}\,(\vec{x},\vec{y},0)$ may be considered as locally invariant under the flow of system (1), we have:

$$\frac{d\vec{g}}{dt}\,(\vec{x},\vec{y},0) = 0 \quad \Longleftrightarrow \quad D_{\vec{x}}\vec{g}.\dot{\vec{x}} + D_{\vec{y}}\vec{g}.\dot{\vec{y}} = \vec{0}.$$

By replacing $\dot{\vec{x}}$ by $\vec{f}\,(\vec{x},\vec{y},0)$ leads to:

$$D_{\vec{x}}\vec{g}.\vec{f}\,(\vec{x},\vec{y},0) + D_{\vec{y}}\vec{g}.\dot{\vec{y}} = \vec{0}.$$

This justifies the introduction of the *constrained system*.

Now, let $adj(D_{\vec{y}}\vec{g})$ denote the adjoint of the matrix $D_{\vec{y}}\vec{g}$ which is the transpose of the co-factor matrix $D_{\vec{y}}\vec{g}$, then while multiplying the left hand side of (6) by the inverse matrix $(D_{\vec{y}}\vec{g})^{-1}$ obtained by the adjoint method we have:

$$\begin{aligned} \dot{\vec{x}} &= \vec{f}\,(\vec{x},\vec{y},0)\,, \\ det(D_{\vec{y}}\vec{g})\dot{\vec{y}} &= -(adj(D_{\vec{y}}\vec{g}).D_{\vec{x}}\vec{g}.\vec{f})\,(\vec{x},\vec{y},0)\,, \\ \vec{0} &= \vec{g}\,(\vec{x},\vec{y},0)\,. \end{aligned} \tag{7}$$

2.6. Normalized slow dynamics

Then, by rescaling the time by setting $t = -det(D_{\vec{y}}\vec{g})\tau$ we obtain the following system which has been called by Eric Benoît [6, p. 166] "normalized slow dynamics":

[6]See Benoît [6, 9], Szmolyan and Wechselberger [25] and Wechselberger [38, 39].

$$\begin{aligned}
\dot{\vec{x}} &= -det(D_{\vec{y}}\vec{g})\vec{f}\,(\vec{x},\vec{y},0)\,,\\
\dot{\vec{y}} &= (adj(D_{\vec{y}}\vec{g}).D_{\vec{x}}\vec{g}.\vec{f})\,(\vec{x},\vec{y},0)\,,\\
\vec{0} &= \vec{g}\,(\vec{x},\vec{y},0)\,.
\end{aligned} \tag{8}$$

where the overdot now denotes the time derivation with respect to τ.

Let's notice that José Argémi [1] proposed to rescale time by setting $t = -det(D_{\vec{y}}\vec{g})sgn(det(D_{\vec{y}}\vec{g}))\tau$ in order to keep the same flow direction in (8) as in (7).

2.7. Desingularized vector field

By application of the Implicit Function Theorem, let suppose that we can explicitly express from Eq. (4), say without loss of generality, x_1 as a function ϕ_1 of the other variables. This implies that M_0 is locally the graph of a function $\phi_1 : \mathbb{R}^k \to \mathbb{R}^m$ over the base $U = (\vec{\chi}, \vec{y})$ where $\vec{\chi} = (x_2, x_3, ..., x_k)$. Thus, we can span the "normalized slow dynamics" on the tangent bundle at the *critical manifold* M_0 at the *pseudo singular point*. This leads to the so-called *desingularized vector field*:

$$\begin{aligned}
\dot{\vec{\chi}} &= -det(D_{\vec{y}}\vec{g})\vec{f}\,(\vec{\chi},\vec{y},0)\,,\\
\dot{\vec{y}} &= (adj(D_{\vec{y}}\vec{g}).D_{\vec{x}}\vec{g}.\vec{f})\,(\vec{\chi},\vec{y},0)\,.
\end{aligned} \tag{9}$$

2.8. Pseudo singular points and folded singularities

As recalled by Guckenheimer and Haiduc [18, p. 91], *pseudo-singular points* have been introduced by the late José Argémi [1] for low-dimensional singularly perturbed systems and are defined as singular points of the "normalized slow dynamics" (8). Twenty-three years later, Szmolyan and Wechselberger [25, p. 428] called such *pseudo singular points*, *folded singularities*. In a recent publication entitled "A propos de canards" Wechselberger [39, p. 3295] proposed to define such singularities for n-dimensional singularly perturbed systems with k *slow* variables and m *fast* as the solutions of the following system:

$$\begin{aligned}
&det(D_{\vec{y}}\vec{g}) = 0,\\
&(adj(D_{\vec{y}}\vec{g}).D_{\vec{x}}\vec{g}.\vec{f})\,(\vec{x},\vec{y},0) = \vec{0},\\
&\vec{g}\,(\vec{x},\vec{y},0) = \vec{0}.
\end{aligned} \tag{10}$$

Thus, for dimensions higher than three, his concept encompasses that of Argémi. Moreover, Wechselberger [39, p. 3296] proved that *folded singularities* form a $(k-2)$-dimensional manifold. Thus, for $k = 2$ the *folded singularities* are nothing else than the *pseudo singular points* defined by

Argémi [1]. While for $k \geqslant 3$ the *folded singularities* are no more points but a $(k-2)$-dimensional manifold. Moreover, let's notice on the one hand that the original system (1) includes $n = k + m$ variables and on the other hand, that the system (10) comprises $p = 2m + 1$ equations. However, in the particular case $k = m = 2$, two equations of the system (10) are linearly dependent. So, such system only comprises$p = 2m = 2k$ equations. So, all the variables (unknowns) of system (10) can be determined. The solutions of this system are called *pseudo singular points*. We will see in the next Sec. 2 that the stability analysis of these *pseudo singular points* will give rise to a condition for the existence of canard solutions in the original system (1).

3. FOUR-DIMENSIONAL SINGULARLY PERTURBED SYSTEMS WITH TWO FAST VARIABLES

A four-dimensional *singularly perturbed dynamical system* (2) with $k = 2$ *slow* variables and $m = 2$ *fast* may be written as:

$$\dot{x}_1 = f_1(x_1, x_2, y_1, y_2), \tag{11a}$$
$$\dot{x}_2 = f_2(x_1, x_2, y_1, y_2), \tag{11b}$$
$$\varepsilon\dot{y}_1 = g_1(x_1, x_2, y_1, y_2), \tag{11c}$$
$$\varepsilon\dot{y}_2 = g_2(x_1, x_2, y_1, y_2), \tag{11d}$$

where $\vec{x} = (x_1, x_2)^t \in \mathbb{R}^2$, $\vec{y} = (y_1, y_2) \in \mathbb{R}^2$, $0 < \varepsilon \ll 1$ and the functions f_i and g_i are assumed to be C^2 functions of (x_1, x_2, y_1, y_2).

3.1. Critical Manifold

The critical manifold equation of system (11) is defined by setting $\varepsilon = 0$ in Eqs. (11c & 11d). Thus, we obtain:

$$g_1(x_1, x_2, y_1, y_2) = 0, \tag{12a}$$
$$g_2(x_1, x_2, y_1, y_2) = 0. \tag{12b}$$

By application of the Implicit Function Theorem, let suppose that we can explicitly express from Eqs. (12a & 12b), say without loss of generality, x_1 and y_1 as functions of the others variables:

$$x_1 = \phi_1(x_2, y_1, y_2), \tag{13a}$$
$$y_1 = \phi_2(x_1, x_2, y_2). \tag{13b}$$

3.2. Constrained system

The *constrained system* is obtained by equating to zero the time derivative of $g_{1,2}\left(x_1, x_2, y_1, y_2\right)$:

$$\frac{dg_1}{dt} = \frac{\partial g_1}{\partial x_1}\dot{x}_1 + \frac{\partial g_1}{\partial x_2}\dot{x}_2 + \frac{\partial g_1}{\partial y_1}\dot{y}_1 + \frac{\partial g_1}{\partial y_1}\dot{y}_2 = 0 \tag{14a}$$

$$\frac{dg_2}{dt} = \frac{\partial g_2}{\partial x_1}\dot{x}_1 + \frac{\partial g_2}{\partial x_2}\dot{x}_2 + \frac{\partial g_2}{\partial y_1}\dot{y}_1 + \frac{\partial g_2}{\partial y_1}\dot{y}_2 = 0 \tag{14b}$$

Eqs. (14a & 14b) may be written as:

$$\frac{\partial g_1}{\partial y_1}\dot{y}_1 + \frac{\partial g_1}{\partial y_1}\dot{y}_2 = -\left(\frac{\partial g_1}{\partial x_1}\dot{x}_1 + \frac{\partial g_1}{\partial x_2}\dot{x}_2\right) \tag{15a}$$

$$\frac{\partial g_2}{\partial y_1}\dot{y}_1 + \frac{\partial g_2}{\partial y_1}\dot{y}_2 = -\left(\frac{\partial g_2}{\partial x_1}\dot{x}_1 + \frac{\partial g_2}{\partial x_2}\dot{x}_2\right) \tag{15b}$$

By solving the system of two equations (15a & 15b) with two unknowns $(\dot{y}_1, \dot{y}_2)$ we find:

$$\dot{y}_1 = \frac{-\left(\frac{\partial g_1}{\partial x_1}\dot{x}_1 + \frac{\partial g_1}{\partial x_2}\dot{x}_2\right)\frac{\partial g_2}{\partial y_2} + \left(\frac{\partial g_2}{\partial x_1}\dot{x}_1 + \frac{\partial g_2}{\partial x_2}\dot{x}_2\right)\frac{\partial g_1}{\partial y_2}}{det\left[J_{(y_1,y_2)}\right]}, \tag{16a}$$

$$\dot{y}_2 = \frac{-\left(\frac{\partial g_1}{\partial x_1}\dot{x}_1 + \frac{\partial g_1}{\partial x_2}\dot{x}_2\right)\frac{\partial g_2}{\partial y_1} + \left(\frac{\partial g_2}{\partial x_1}\dot{x}_1 + \frac{\partial g_2}{\partial x_2}\dot{x}_2\right)\frac{\partial g_1}{\partial y_1}}{det\left[J_{(y_1,y_2)}\right]}. \tag{16b}$$

So, we have the following constrained system:

$$\begin{aligned}
\dot{x}_1 &= f_1\left(x_1, x_2, y_1, y_2\right), \\
\dot{x}_2 &= f_2\left(x_1, x_2, y_1, y_2\right), \\
\dot{y}_1 &= \frac{-\left(\frac{\partial g_1}{\partial x_1}\dot{x}_1 + \frac{\partial g_1}{\partial x_2}\dot{x}_2\right)\frac{\partial g_2}{\partial y_2} + \left(\frac{\partial g_2}{\partial x_1}\dot{x}_1 + \frac{\partial g_2}{\partial x_2}\dot{x}_2\right)\frac{\partial g_1}{\partial y_2}}{det\left[J_{(y_1,y_2)}\right]}, \\
\dot{y}_2 &= \frac{-\left(\frac{\partial g_1}{\partial x_1}\dot{x}_1 + \frac{\partial g_1}{\partial x_2}\dot{x}_2\right)\frac{\partial g_2}{\partial y_1} + \left(\frac{\partial g_2}{\partial x_1}\dot{x}_1 + \frac{\partial g_2}{\partial x_2}\dot{x}_2\right)\frac{\partial g_1}{\partial y_1}}{det\left[J_{(y_1,y_2)}\right]}, \\
0 &= g_1\left(x_1, x_2, y_1, y_2\right), \\
0 &= g_2\left(x_1, x_2, y_1, y_2\right).
\end{aligned} \tag{17}$$

3.3. Normalized slow dynamics

By rescaling the time by setting $t = -det\left[J_{(y_1,y_2)}\right]\tau$ we obtain the "normalized slow dynamics":

$$\begin{aligned}
\dot{x}_1 &= -f_1(x_1,x_2,y_1,y_2)\,det\left[J_{(y_1,y_2)}\right] = F_1(x_1,x_2,x_3,y_1),\\
\dot{x}_2 &= -f_2(x_1,x_2,y_1,y_2)\,det\left[J_{(y_1,y_2)}\right] = F_2(x_1,x_2,x_3,y_1),\\
\dot{y}_1 &= \left(\frac{\partial g_1}{\partial x_1}\dot{x}_1+\frac{\partial g_1}{\partial x_2}\dot{x}_2\right)\frac{\partial g_2}{\partial y_2}-\left(\frac{\partial g_2}{\partial x_1}\dot{x}_1+\frac{\partial g_2}{\partial x_2}\dot{x}_2\right)\frac{\partial g_1}{\partial y_2}\\
&= G_1(x_1,x_2,x_3,y_1),\\
\dot{y}_2 &= \left(\frac{\partial g_1}{\partial x_1}\dot{x}_1+\frac{\partial g_1}{\partial x_2}\dot{x}_2\right)\frac{\partial g_2}{\partial y_1}-\left(\frac{\partial g_2}{\partial x_1}\dot{x}_1+\frac{\partial g_2}{\partial x_2}\dot{x}_2\right)\frac{\partial g_1}{\partial y_1}\\
&= G_2(x_1,x_2,x_3,y_1),\\
0 &= g_1(x_1,x_2,y_1,y_2),\\
0 &= g_2(x_1,x_2,y_1,y_2).
\end{aligned} \tag{18}$$

where the overdot now denotes the time derivation with respect to τ.

3.4. Desingularized system on the critical manifold

Then, since we have supposed that x_1 and y_1 may be explicitly expressed as functions of the others variables (13a & 13b), they can be used to project the normalized slow dynamics (18) on the tangent bundle of the critical manifold. So, we have:

$$\begin{aligned}
\dot{x}_2 &= -f_2(x_1,x_2,y_1,y_2)\,det\left[J_{(y_1,y_2)}\right] = F_2(x_2,y_2),\\
\dot{y}_2 &= \left(\frac{\partial g_1}{\partial x_1}\dot{x}_1+\frac{\partial g_1}{\partial x_2}\dot{x}_2\right)\frac{\partial g_2}{\partial y_1}-\left(\frac{\partial g_2}{\partial x_1}\dot{x}_1+\frac{\partial g_2}{\partial x_2}\dot{x}_2\right)\frac{\partial g_1}{\partial y_1} = G_2(x_2,y_2).
\end{aligned} \tag{19}$$

3.5. Pseudo singular points

Pseudo-singular points are defined as singular points of the "normalized slow dynamics", *i.e.* as the set of points for which we have:

$$det\left[J_{(y_1,y_2)}\right] = 0, \tag{20a}$$

$$\left(\frac{\partial g_1}{\partial x_1}\dot{x}_1+\frac{\partial g_1}{\partial x_2}\dot{x}_2\right)\frac{\partial g_2}{\partial y_2}-\left(\frac{\partial g_2}{\partial x_1}\dot{x}_1+\frac{\partial g_2}{\partial x_2}\dot{x}_2\right)\frac{\partial g_1}{\partial y_2} = 0, \tag{20b}$$

$$\left(\frac{\partial g_1}{\partial x_1}\dot{x}_1+\frac{\partial g_1}{\partial x_2}\dot{x}_2\right)\frac{\partial g_2}{\partial y_1}-\left(\frac{\partial g_2}{\partial x_1}\dot{x}_1+\frac{\partial g_2}{\partial x_2}\dot{x}_2\right)\frac{\partial g_1}{\partial y_1} = 0, \tag{20c}$$

$$g_1(x_1,x_2,y_1,y_2) = 0, \tag{20d}$$

$$g_2(x_1,x_2,y_1,y_2) = 0. \tag{20e}$$

Remark 1. Let's notice on the one hand that Eqs. (20b) & (20c) are linearly dependent and on the other hand that contrary to previous works we don't use the "desingularized vector field" (19) but the "normalized slow dynamics" (18).

The Jacobian matrix of system (18) reads:

$$J_{(F_1,F_2,G_1,G_2)} = \begin{pmatrix} \dfrac{\partial F_1}{\partial x_1} & \dfrac{\partial F_1}{\partial x_2} & \dfrac{\partial F_1}{\partial y_1} & \dfrac{\partial F_1}{\partial y_2} \\ \dfrac{\partial F_2}{\partial x_1} & \dfrac{\partial F_2}{\partial x_2} & \dfrac{\partial F_2}{\partial y_1} & \dfrac{\partial F_2}{\partial y_2} \\ \dfrac{\partial G_1}{\partial x_1} & \dfrac{\partial G_1}{\partial x_2} & \dfrac{\partial G_1}{\partial y_1} & \dfrac{\partial G_1}{\partial y_2} \\ \dfrac{\partial G_2}{\partial x_1} & \dfrac{\partial G_2}{\partial x_2} & \dfrac{\partial G_2}{\partial y_1} & \dfrac{\partial G_2}{\partial y_2} \end{pmatrix} \tag{21}$$

3.6. Extension of Benoît's generic hypothesis

Without loss of generality, it seems reasonable to extend Benoît's generic hypotheses introduced for the three-dimensional case to the four-dimensional case. So, first, let's suppose that by a "standard translation" the *pseudo singular point* can be shifted at the origin $O(0,0,0,0)$ and that by a "standard rotation" of y_1-axis that the *slow manifold* is tangent to (x_2, x_3, y_1)-hyperplane, so we have

$$\begin{aligned} &f_1(0,0,0,0) = g_1(0,0,0,0) = 0 \\ &\left.\frac{\partial g_1}{\partial x_2}\right|_{(0,0,0,0)} = \left.\frac{\partial g_1}{\partial x_3}\right|_{(0,0,0,0)} = \left.\frac{\partial g_1}{\partial y_1}\right|_{(0,0,0,0)} = 0 \end{aligned} \tag{22}$$

Then, let's make the following assumptions for the non-degeneracy of the *folded singularity*:

$$f_2(0,0,0,0) \neq 0 \quad ; \quad \left.\frac{\partial g_1}{\partial x_1}\right|_{(0,0,0,0)} \neq 0 \quad ; \quad \left.\frac{\partial^2 g_1}{\partial y_1^2}\right|_{(0,0,0,0)} \neq 0. \tag{23}$$

According to these generic hypotheses Eqs. (22-23), the Jacobian matrix (21) reads:

$$J_{(F_1,F_2,G_1,G_2)} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ -f_2\dfrac{\partial P}{\partial x_1} & -f_2\dfrac{\partial P}{\partial x_2} & -f_2\dfrac{\partial P}{\partial y_1} & -f_2\dfrac{\partial P}{\partial y_2} \\ a_{31} & a_{32} & a_{33} & a_{34} \\ a_{41} & a_{42} & a_{43} & a_{44} \end{pmatrix} \tag{24}$$

where

$$\begin{aligned}
P &= det\left[J_{(y_1,y_2)}\right], \\
a_{3i} &= -f_2\frac{\partial g_2}{\partial x_2}\frac{\partial^2 g_1}{\partial y_2 \partial x_i} + \frac{\partial g_2}{\partial y_2}\left(f_2\frac{\partial^2 g_1}{\partial x_2 \partial x_i} + \frac{\partial g_1}{\partial x_1}\frac{\partial f_1}{\partial x_i}\right) \text{ for } i = 1,2, \\
a_{3i} &= -f_2\frac{\partial g_2}{\partial x_2}\frac{\partial^2 g_1}{\partial y_2 \partial y_i} + \frac{\partial g_2}{\partial y_2}\left(f_2\frac{\partial^2 g_1}{\partial x_2 \partial y_i} + \frac{\partial g_1}{\partial x_1}\frac{\partial f_1}{\partial y_i}\right) \text{ for } i = 3,4, \\
a_{4i} &= f_2\frac{\partial g_2}{\partial x_2}\frac{\partial^2 g_1}{\partial y_1 \partial x_i} - \frac{\partial g_2}{\partial y_1}\left(f_2\frac{\partial^2 g_1}{\partial x_2 \partial x_i} + \frac{\partial g_1}{\partial x_1}\frac{\partial f_1}{\partial x_i}\right) \text{ for } i = 1,2, \\
a_{4i} &= f_2\frac{\partial g_2}{\partial x_2}\frac{\partial^2 g_1}{\partial y_1 \partial y_i} - \frac{\partial g_2}{\partial y_1}\left(f_2\frac{\partial^2 g_1}{\partial x_2 \partial y_i} + \frac{\partial g_1}{\partial x_1}\frac{\partial f_1}{\partial y_i}\right) \text{ for } i = 3,4.
\end{aligned}$$

Thus, we have the following Cayley-Hamilton eigenpolynomial associated with such a Jacobian matrix (24) evaluated at the *pseudo singular point*, *i.e.*, at the origin:

$$\lambda^4 - \sigma_1\lambda^3 + \sigma_2\lambda^2 - \sigma_3\lambda + \sigma_4 = 0 \tag{25}$$

where $\sigma_1 = Tr(J)$ is the sum of all first-order diagonal minors of J, *i.e.*, the the trace of the Jacobian matrix J, σ_2 represents the sum of all second-order diagonal minors of J and σ_3 represents the sum of all third-order diagonal minors of J. It appears that $\sigma_4 = |J| = 0$ since one row of the Jacobian matrix (24) is null. So, the eigenpolynomial reduces to:

$$\lambda\left(\lambda^3 - \sigma_1\lambda^2 + \sigma_2\lambda - \sigma_3\right) = 0 \tag{26}$$

But, according to Wechselberger [39], σ_3 vanishes at a *pseudo singular point* as it's easy to prove it. So, the eigenpolynomial (26) is reduced to

$$\lambda^2\left(\lambda^2 - \sigma_1\lambda + \sigma_2\right) = 0 \tag{27}$$

Let λ_i be the eigenvalues of the eigenpolynomial (27) and let's denote by $\lambda_{3,4} = 0$ the obvious double root of this polynomial. We have:

$$\begin{aligned}
\sigma_1 &= Tr(J_{(F_1,F_2,G_1,G_2)}) = \lambda_1 + \lambda_2 = \frac{\partial g_2}{\partial x_1}\frac{\partial g_1}{\partial y_1}\frac{\partial f_1}{\partial y_2}, \\
\sigma_2 &= \sum_{i=1}^{3}\left|J^{ii}_{(F_1,F_2,G_1,G_2)}\right| = \lambda_1\lambda_2 \\
&= \left(\frac{\partial g_1}{\partial y_1}\right)^2\left[f_2^2\left(\frac{\partial^2 g_2}{\partial x_2^2}\frac{\partial^2 g_2}{\partial y_2^2} - \left(\frac{\partial^2 g_2}{\partial x_2 \partial y_2}\right)^2\right)\right. \\
&\left. + f_2\frac{\partial g_2}{\partial x_1}\left(\frac{\partial^2 g_2}{\partial y_2^2}\frac{\partial f_1}{\partial x_2} - \frac{\partial^2 g_2}{\partial x_2 \partial y_2}\frac{\partial f_1}{\partial y_2}\right)\right]
\end{aligned} \tag{28}$$

where $\sigma_1 = Tr(J_{(F_1,F_2,G_1,G_2)}) = p$ is is the sum of all first-order diagonal minors of $J_{(F_1,F_2,G_1,G_2)}$, *i.e.* the trace of the Jacobian matrix $J_{(F_1,F_2,G_1,G_2)}$ and $\sigma_2 = \sum_{i=1}^{3}\left|J^{ii}_{(F_1,F_2,G_1,G_2)}\right| = q$ represents the sum of all second-order diagonal minors of $J_{(F_1,F_2,G_1,G_2)}$. Thus, the *pseudo singular point* is of saddle-type *iff* the following conditions C_1 and C_2 are verified:

$$\begin{aligned}
C_1: &\quad \Delta = p^2 - 4q > 0, \\
C_2: &\quad q < 0.
\end{aligned} \tag{29}$$

Condition C_1 is systematically satisfied provided that condition C_2 is verified. Thus, the *pseudo singular point* is of saddle-type *iff* $q < 0$.

3.7. Canard existence in $\mathbb{R}^{2+2}$

Following the works of Wechselberger [39] it can be stated, while using a standard polynomial change of variables, that any n-dimensional singularly perturbed systems with k *slow* variables ($k \geqslant 2$) and m *fast* ($m \geqslant 1$) (1) can be transformed into the following "normal form":

$$\begin{aligned}
\dot{x_1} &= \tilde{a}x_2 + \tilde{b}y_2 + O\left(x_1, \epsilon, x_2^2, x_2y_2, y_2^2\right), \\
\dot{x_2} &= 1 + O\left(x_1, x_2, y_2, \epsilon\right), \\
\epsilon\dot{y_1} &= \tilde{c}y_1 + O\left(\epsilon x_1, \epsilon x_2, \epsilon y_2, x_1^2, x_2^2, y_2^2, x_2y_2\right), \\
\epsilon\dot{y_2} &= -\left(x_1 + y_2^2\right) + O\left(\epsilon x_1, \epsilon x_2, \epsilon y_2, \epsilon^2, x_1^2y_2, y_2^3, x_1x_2y_2\right).
\end{aligned} \tag{30}$$

We establish in Appendix A for any four-dimensional singularly perturbed systems (11) with $k = 2$ *slow* and $m = 2$ *fast* variables that

$$\tilde{a} = \frac{1}{2}\left[f_2^2\left(\frac{\partial^2 g_2}{\partial x_2^2}\frac{\partial^2 g_2}{\partial y_2^2} - \left(\frac{\partial^2 g_2}{\partial x_2 \partial y_2}\right)^2\right) + f_2\frac{\partial g_2}{\partial x_1}\left(\frac{\partial^2 g_2}{\partial y_2^2}\frac{\partial f_1}{\partial x_2} - \frac{\partial^2 g_2}{\partial x_2 \partial y_2}\frac{\partial f_1}{\partial y_2}\right)\right]$$
$$\tilde{b} = -\frac{\partial g_2}{\partial x_1}\frac{\partial f_1}{\partial y_2},$$
$$\tilde{c} = \frac{\partial g_1}{\partial y_1}.$$

Thus, in his paper Wechselberger [39, p. 3304] provided in the framework of "standard analysis" a generalization of Benoît's theorem [6] for any n-dimensional singularly perturbed systems with k *slow* variables ($k \geqslant 2$) and m *fast* ($m \geqslant 1$). According to his Theorem 4.1 presented below he proved the existence of canard solutions for the original system (1).

Theorem 2.
In the folded saddle case of system (30) *singular canards perturb to maximal canards solutions for sufficiently small* $\varepsilon \ll 1$.

Proof. See Wechselberger [39]. ▌

Since our method doesn't use the "desingularized vector field" (19) but the "normalized slow dynamics" (18), we have the following proposition:

Proposition 3.
If the normalized slow dynamics (18) *has a pseudo singular point of saddle type, i.e. if the sum* σ_2 *of all second-order diagonal minors of the Jacobian matrix of the normalized slow dynamics* (18) *evaluated at the pseudo singular point is negative, i.e. if* $\sigma_2 < 0$ *then, according to Theorem 2, system* (11) *exhibits a canard solution which evolves from the attractive part of the slow manifold towards its repelling part.*

Proof.
By making some smooth changes of time and smooth changes of coordinates (see Appendix A) we brought the system (11) to the following "normal form":

$$\begin{aligned}
\dot{x_1} &= \tilde{a}x_2 + \tilde{b}y_2 + O\left(x_1, \epsilon, x_2^2, x_2y_2, y_2^2\right),\\
\dot{x_2} &= 1 + O\left(x_1, x_2, y_2, \epsilon\right),\\
\epsilon\dot{y_1} &= \tilde{c}y_1 + O\left(\epsilon x_1, \epsilon x_2, \epsilon y_2, x_1^2, x_2^2, y_2^2, x_2y_2\right),\\
\epsilon\dot{y_2} &= -\left(x_1 + y_2^2\right) + O\left(\epsilon x_1, \epsilon x_2, \epsilon y_2, \epsilon^2, x_1^2y_2, y_2^3, x_1x_2y_2\right),
\end{aligned}$$

Then, we deduce that the condition for the *pseudo singular point* to be of saddle type is $\tilde{a} < 0$. According to Eqs. (29) it is easy to verify that

$$\sigma_1 = Tr(J_{(F_1,F_2,G_1,G_2)}) = \lambda_1 + \lambda_2 = -\tilde{b}\tilde{c},$$
$$\sigma_2 = \sum_{i=1}^{3} \left| J^{ii}_{(F_1,F_2,G_1,G_2)} \right| = \lambda_1\lambda_2 = 2\tilde{a}\tilde{c}^2.$$

So, the condition for which the *pseudo singular point* is of saddle type, *i.e.* $\sigma_2 < 0$ is identical to that proposed by Wechselberger [39, p. 3298] in his theorem, *i.e.* $\tilde{a} < 0$. ▌

So, Prop. 3 can be used to state the existence of canard solution for such systems. Application of Proposition 3 to the coupled FitzHugh-Nagumo equations, presented in Sec. 4, which is a four-dimensional singularly perturbed system with two *slow* and two *fast* variables will enable to prove, as many previous works such as those of Tchizawa & Campbell [30] and Tchizawa [30, 31, 32, 33, 34, 35], the existence of "canard solutions" in such system. According to Tchizawa [36], it is very important to notice, on the one hand that the fast equation has 2-dimensional in the system $\mathbb{R}^{2+2}$ and, on the other hand that the fast system can give attractive, repulsive or attractive-repulsive at each *pseudo singular point*. Then, Tchizawa [36] has established that the jumping direction can be shown using the eigenvectors. In the same way we will find again the results of Rubin *et al.* [24] concerning the existence of "canard solutions" in the Hodgkin-Huxley model but with a set of more realistic parameters used in Chua *et al.* [10, 11].

4. COUPLED FITZHUGH-NAGUMO EQUATIONS

The FitzHugh-Nagumo model [16, 22] is a simplified version of the Hodgkin-Huxley model [19] which models in a detailed manner activation and deactivation dynamics of a spiking neuron. By coupling two FitzHugh-Nagumo models Tchizawa & Campbell [29] and Tchizawa [30, 35] obtained the following four-dimensional singularly perturbed system with two *slow* and two *fast* variables:

$$\frac{dx_1}{dt} = \frac{1}{c}\left(y_1 + bx_1\right), \tag{31a}$$

$$\frac{dx_2}{dt} = \frac{1}{c}\left(y_2 + bx_2\right), \tag{31b}$$

$$\varepsilon\frac{dy_1}{dt} = x_1 - \frac{y_1^3}{3} + y_2, \tag{31c}$$

$$\varepsilon\frac{dy_2}{dt} = x_2 - \frac{y_2^3}{3} + y_1. \tag{31d}$$

where $0 < \varepsilon \ll 1$ and b is the "canard parameter" or "duck parameter" while c is a scale factor.

4.1. Slow manifold and contrained system

The slow manifold equation of system (31) is defined by setting $\varepsilon = 0$ in Eqs. (31c & 31d). Thus, we obtain:

$$\begin{aligned}
\frac{dx_1}{dt} &= \frac{1}{c}\left(y_1 + bx_1\right),\\
\frac{dx_2}{dt} &= \frac{1}{c}\left(y_2 + bx_2\right),\\
\frac{dy_1}{dt} &= -\frac{\frac{1}{c}\left(y_2 + bx_2\right) + \frac{y_2^2}{c}\left(y_1 + bx_1\right)}{y_1^2y_2^2 - 1},\\
\frac{dy_2}{dt} &= -\frac{\frac{1}{c}\left(y_1 + bx_1\right) + \frac{y_1^2}{c}\left(y_2 + bx_2\right)}{y_1^2y_2^2 - 1},\\
0 &= x_1 - \frac{y_1^3}{3} + y_2,\\
0 &= x_2 - \frac{y_2^3}{3} + y_1.
\end{aligned} \tag{32}$$

4.2. Normalized slow dynamics

Then, by rescaling the time by setting $t = -det\left[J_{(y_1,y_2)}\right]\tau = -(y_1^2y_2^2-1)$ we obtain the "normalized slow dynamics":

$$\begin{aligned}
\frac{dx_1}{dt} &= -\frac{1}{c}\left(y_1+bx_1\right)\left(y_1^2y_2^2-1\right) = F_1\left(x_1,x_2,y_1,y_2\right),\\
\frac{dx_2}{dt} &= -\frac{1}{c}\left(y_2+bx_2\right)\left(y_1^2y_2^2-1\right) = F_2\left(x_1,x_2,y_1,y_2\right),\\
\frac{dy_1}{dt} &= \frac{1}{c}\left(y_2+bx_2\right)+\frac{y_2^2}{c}\left(y_1+bx_1\right) = G_1\left(x_1,x_2,y_1,y_2\right),\\
\frac{dy_2}{dt} &= \frac{1}{c}\left(y_1+bx_1\right)+\frac{y_1^2}{c}\left(y_2+bx_2\right)G_2\left(x_1,x_2,y_1,y_2\right),\\
0 &= x_1-\frac{y_1^3}{3}+y_2,\\
0 &= x_2-\frac{y_2^3}{3}+y_1.
\end{aligned} \tag{33}$$

4.3. Pseudo singular points

From Eqs. (20), the *pseudo-singular points* of system (31) are defined by:

$$det\left[J_{(y_1,y_2)}\right] = y_1^2y_2^2-1 = 0, \tag{34a}$$

$$\left(\frac{\partial g_1}{\partial x_1}\dot{x}_1+\frac{\partial g_1}{\partial x_2}\dot{x}_2\right)\frac{\partial g_2}{\partial y_2}-\left(\frac{\partial g_2}{\partial x_1}\dot{x}_1+\frac{\partial g_2}{\partial x_2}\dot{x}_2\right)\frac{\partial g_1}{\partial y_2} \tag{34b}$$

$$= \frac{1}{c}\left(y_2+bx_2\right)+\frac{y_2^2}{c}\left(y_1+bx_1\right) = 0,$$

$$\left(\frac{\partial g_1}{\partial x_1}\dot{x}_1+\frac{\partial g_1}{\partial x_2}\dot{x}_2\right)\frac{\partial g_2}{\partial y_1}-\left(\frac{\partial g_2}{\partial x_1}\dot{x}_1+\frac{\partial g_2}{\partial x_2}\dot{x}_2\right)\frac{\partial g_1}{\partial y_1} \tag{34c}$$

$$= \frac{1}{c}\left(y_1+bx_1\right)+\frac{y_1^2}{c}\left(y_2+bx_2\right) = 0,$$

$$g_1\left(x_1,x_2,y_1,y_2\right) = x_1-\frac{y_1^3}{3}+y_2 = 0, \tag{34d}$$

$$g_2\left(x_1,x_2,y_1,y_2\right) = x_2-\frac{y_2^3}{3}+y_1 = 0. \tag{34e}$$

According to Tchizawa & Campbell [29] and Tchizawa [30, 31], there are six *pseudo singular points*, the last four are depending on the parameter b.

$$(\tilde{x}_1, \tilde{x}_2, \tilde{y}_1, \tilde{y}_2) = \left(\pm\frac{4}{3}, \mp\frac{4}{3}, \pm 1, \mp 1 \right), \tag{35a}$$

$$\begin{aligned}(\tilde{x}_1, \tilde{x}_2, \tilde{y}_1, \tilde{y}_2) = \Bigg(& \pm\frac{\sqrt{\frac{3-\sqrt{9-4b^2}}{b}}\left(3+2\sqrt{9-4b^2}\right)}{3\sqrt{2}b}, \\ & \mp\frac{\sqrt{\frac{3-\sqrt{9-4b^2}}{b}}\left(9-8b^2+3\sqrt{9-4b^2}\right)}{6\sqrt{2}b^2}, \\ & \mp\sqrt{\frac{3-\sqrt{9-4b^2}}{2b}}, \mp\frac{\sqrt{2b}}{\sqrt{3-\sqrt{9-4b^2}}}\Bigg),\end{aligned} \tag{35b}$$

$$\begin{aligned}(\tilde{x}_1, \tilde{x}_2, \tilde{y}_1, \tilde{y}_2) = \Bigg(& \pm\frac{\left(3-2\sqrt{9-4b^2}\right)\sqrt{\frac{3+\sqrt{9-4b^2}}{b}}}{3\sqrt{2}b}, \\ & \mp\frac{\sqrt{\frac{3+\sqrt{9-4b^2}}{b}}\left(9-8b^2-3\sqrt{9-4b^2}\right)}{6\sqrt{2}b^2}, \\ & \mp\sqrt{\frac{3-\sqrt{9-4b^2}}{2b}}, \mp\frac{\sqrt{2b}}{\sqrt{3-\sqrt{9-4b^2}}}\Bigg).\end{aligned} \tag{35c}$$

4.4. Canard existence in coupled FitzHugh-Nagumo equations

The Jacobian matrix of system (33) evaluated at the *pseudo singular points* (35a) reads:

$$J_{(F_1,F_2,G_1,G_2)} = \begin{pmatrix} 0 & 0 & \frac{2(3+4b)}{3c} & -\frac{2(3+4b)}{3c} \\ 0 & 0 & -\frac{2(3+4b)}{3c} & \frac{2(3+4b)}{3c} \\ \frac{b}{c} & \frac{b}{c} & \frac{1}{c} & -\frac{3+8b}{3c} \\ \frac{b}{c} & \frac{b}{c} & -\frac{3+8b}{3c} & \frac{1}{c} \end{pmatrix} \tag{36}$$

Remark 4. Although the *pseudo singular points* have not been shifted at the origin extension of Benoît's generic hypotheses (22-23) are satisfied. In other words, we have $\sigma_4 = \sigma_3 = 0$.

According to Eqs. (28) we find that:

$$\begin{aligned} p = \sigma_1 &= Tr(J) = +\frac{2}{c}, \\ q = \sigma_2 &= -\frac{16b(3+4b)}{9c^2} \end{aligned} \tag{37}$$

Thus, according to Prop. 3, the *pseudo singular points* are of saddle-type if and only if:

$$-\frac{16b(3+4b)}{9c^2} < 0$$

So, we have the following conditions C_1 and C_2:

$$\begin{aligned} C_1: \quad \Delta &= \frac{4(3+8b)^2}{9c^2} > 0, \\ C_2: \quad q &= -\frac{16b(3+4b)}{9c^2} < 0. \end{aligned} \tag{38}$$

Let's choose arbitrarily b as the "canard parameter" or "duck parameter". Obviously, it appears that the condition C_1 is still satisfied. Finally, the *pseudo singular points* are of saddle-type if and only if we have:

$$b > 0 \quad \text{or} \quad b < -\frac{3}{4}. \tag{39}$$

Remark 5. Let's notice that the *pseudo singular points* are of node-type if $-\frac{3}{4} < b < 0$ as stated by Tchizawa & Campbell [29] and Tchizawa [30, 31].

The Jacobian matrix $J_{(F_1,F_2,G_1,G_2)}$ of system (33) evaluated at the *pseudo singular points* (35b) reads:

$$\begin{pmatrix} 0 & 0 & -\frac{4\sqrt{9-4b^2}}{3c} & -\frac{2\left(-9+4b^2+3\sqrt{9-4b^2}\right)}{3bc} \\ 0 & 0 & \frac{2\left(-9+4b^2+3\sqrt{9-4b^2}\right)}{3bc} & \frac{4\sqrt{9-4b^2}}{3c} \\ \frac{3+\sqrt{9-4b^2}}{2c} & \frac{b}{c} & \frac{3+\sqrt{9-4b^2}}{2bc} & \frac{3-4\sqrt{9-4b^2}}{3c} \\ \frac{b}{c} & \frac{3-\sqrt{9-4b^2}}{2c} & \frac{3+4\sqrt{9-4b^2}}{3c} & \frac{3-\sqrt{9-4b^2}}{2bc} \end{pmatrix} \tag{40}$$

Remark 6. Although, the *pseudo singular points* have not been shifted at the origin extension of Benoît's generic hypotheses (22-23) are satisfied. In other words, we have $\sigma_4 = \sigma_3 = 0$.

According to Eqs. (28) we find that:

$$\begin{aligned} p = \sigma_1 = Tr(J) = +\frac{3}{bc}, \\ q = \sigma_2 = \frac{16\left(9-4b^2\right)}{9c^2} \end{aligned} \tag{41}$$

Thus, according to Prop. 3, the *pseudo singular points* are of saddle-type if and only if:

$$\frac{16\left(9-4b^2\right)}{9c^2} < 0$$

$$\Delta = p^2 - 4q > 0 \qquad \text{and} \qquad q < 0.$$

So, we have the following conditions C_1 and C_2:

$$\begin{aligned} C_1: \quad \Delta = \left(\frac{3}{bc}\right)^2 - \frac{64\left(9-4b^2\right)}{9c^2} > 0, \\ C_2: \quad q = \frac{16\left(9-4b^2\right)}{9c^2} < 0. \end{aligned} \tag{42}$$

Let's choose arbitrarily b as the "canard parameter" or "duck parameter". Obviously, it appears that if the condition C_2 is verified then the condition C_1 is *de facto* satisfied. Finally, the *pseudo singular points* are of saddle-type if and only if we have:

$$b > \frac{3}{2} \quad \text{or} \quad b < -\frac{3}{2}. \tag{43}$$

Remark 7. Because of the symmetry of this coupled FitzHugh-Nagumo equations, the Jacobian matrix of system (33) evaluated at the *pseudo singular points* (35c) provides the same result as just above.

5. HODGKIN-HUXLEY MODEL

The original Hodgkin-Huxley model [19] is described by the following system of four nonlinear ordinary differential equations:

$$\frac{dV}{dt} = \frac{1}{C_M}\left[I - \bar{g}_K n^4 (V - V_K) - \bar{g}_{Na} m^3 h (V - V_{Na}) - \bar{g}_L (V - V_L)\right] \tag{44a}$$

$$\frac{dn}{dt} = \alpha_n(V)(1-n) - \beta_n(V)n \tag{44b}$$

$$\frac{dm}{dt} = \alpha_m(V)(1-m) - \beta_m(V)m \tag{44c}$$

$$\frac{dh}{dt} = \alpha_h(V)(1-h) - \beta_h(V)h \tag{44d}$$

where:

$$\alpha_n(V) = 0.01(V+10)/\left(\exp\frac{V+10}{10} - 1\right), \tag{45a}$$

$$\beta_n(V) = 0.125\exp\left(V/80\right), \tag{45b}$$

$$\alpha_m(V) = 0.1(V+25)/\left(\exp\frac{V+25}{10} - 1\right), \tag{45c}$$

$$\beta_m(V) = 4\exp(V/18), \tag{45d}$$

$$\alpha_h(V) = 0.07\exp(V/20), \tag{45e}$$

$$\beta_n(V) = 1/\left(\exp\frac{V+30}{10} + 1\right) \tag{45f}$$

The first equation (44a) results from the application of Kirchhoff's law to the space clamped squid giant axon. Thus, the total membrane current $C_M dV/dt$ for which C_M represents the specific membrane capacity and V the displacement of the membrane potential from its resting value, is equal to the sum of the following intrinsic currents:

$$\begin{aligned} I_K &= \bar{g}_K n^4 (V - V_K) \\ I_{Na} &= \bar{g}_{Na} m^3 h (V - V_{Na}) \\ I_L &= \bar{g}_L (V - V_L) \end{aligned}$$

where I_K is a delayed rectifier potassium current, I_{Na} is fast sodium current and I_L is the "leakage current". The parameter I is the total

membrane current density, inward positive, *i.e.* the total current injected into the space clamped squid giant axon and V_K, V_{Na} and V_L are the equilibrium potentials of potassium, sodium and "leakage current" respectively. The maximal specific conductances of the ionic currents are denoted $\bar{g}_K$, $\bar{g}_{Na}$ and $\bar{g}_L$ respectively. Functions $\alpha_{n,m,h}$ and $\beta_{n,m,h}$ are gates' opening and closing rates depending on V. Variable m denotes the activation of the sodium current, variable h the inactivation of the sodium current and variable n the activation of the potassium current. These dimensionless gating variables vary between $[0, 1]$.

Let's notice that the variables and symbols in Eqs. (44 & 45) originally chosen by Hodgkin-Huxley and are different from those found in recent literatures where the reference polarity of the voltage V, and the reference direction of the current I are defined as the negative of the voltages and currents. We have opted to adopt the reference assumption in Hodgkin & Huxley [19] for ease in comparison of our results with those from Hodgkin and Huxley[7]. The parameter values are exactly those chosen in the original Hodgkin-Huxley [19] works:

$$\begin{aligned} C_M &= 1.0\ \mu F/cm^2 \\ V_{Na} &= -115\ mV \\ V_K &= 12\ mV \\ V_L &= -10.613\ mV \\ \bar{g}_{Na} &= 120\ mS/cm^2 \\ \bar{g}_K &= 36\ mS/cm^2 \\ \bar{g}_L &= 0.3\ mS/cm^2 \end{aligned}$$

According to Suckley and Biktashev [26] and Suckley [27], dimensionless functions $\bar{n}$, $\bar{h}$ and $\bar{m}$ called gates' instant equilibrium values, *i.e.*, steady-state relation for gating variable n, h and m respectively as well as τ_n, τ_h and τ_m called gates dynamics time scales in ms, *i.e.*, time constant for gating variable n, h and m respectively may be defined as follows:

[7]For more details see Chua *et al.* [10, 11]

$$\bar{n}(V) = \frac{\alpha_n(V)}{\alpha_n(V) + \beta_n(V)} \tag{46a}$$

$$\bar{h}(V) = \frac{\alpha_h(V)}{\alpha_h(V) + \beta_h(V)} \tag{46b}$$

$$\bar{m}(V) = \frac{\alpha_m(V)}{\alpha_m(V) + \beta_m(V)} \tag{46c}$$

$$\tau_n(V) = \frac{1}{\alpha_n(V) + \beta_n(V)} \tag{46d}$$

$$\tau_h(V) = \frac{1}{\alpha_h(V) + \beta_h(V)} \tag{46e}$$

$$\tau_m(V) = \frac{1}{\alpha_m(V) + \beta_m(V)} \tag{46f}$$

By using Eqs. 46, the original Hodgkin-Huxley model [19] reads:

$$\frac{dV}{dt} = \frac{1}{C_M}\left[I - \bar{g}_K n^4 (V - V_K) - \bar{g}_{Na} m^3 h (V - V_{Na}) - \bar{g}_L (V - V_L)\right] \tag{47a}$$

$$\frac{dn}{dt} = \frac{\bar{n} - n}{\tau_n} \tag{47b}$$

$$\frac{dh}{dt} = \frac{\bar{h} - h}{\tau_h} \tag{47c}$$

$$\frac{dm}{dt} = \frac{\bar{m} - m}{\tau_m} \tag{47d}$$

Now, in order to apply the *singular perturbation method* to the Hodgkin-Huxley model, two small multiplicative parameters $\varepsilon \ll 1$ are introduced. According to Suckley and Biktashev [26], Suckley [27] and Rubin and Wechselberger [24], the existence of two different time scales of evolution for the couples of dynamic variables (n, h) and (m, V) enables to justify such an introduction. So, in order to differentiate *slow* variables from *fast* variables, Suckley and Biktashev [26], Suckley [27] and Rubin and Wechselberger [24] have plotted the inverse of "time constant for gating variable i", *i.e.*, ${\tau_i}^{-1}$ according to V with $i = n, h, m$. In Fig. 1, they have been plotted for the original functions α_i and β_i (Eqs. 45a). However, let's notice that this plot is exactly the same as those presented by Rubin and Wechselberger [24] (Fig. 1) for a nondimensionalized three-dimensional Hodgkin-Huxley singularly perturbed system obtained after the following variable changes: $V \to -V$ and $\bar{I} \to -\bar{I}$, then $V \to V + 65$ and finally $V \to V/100$.

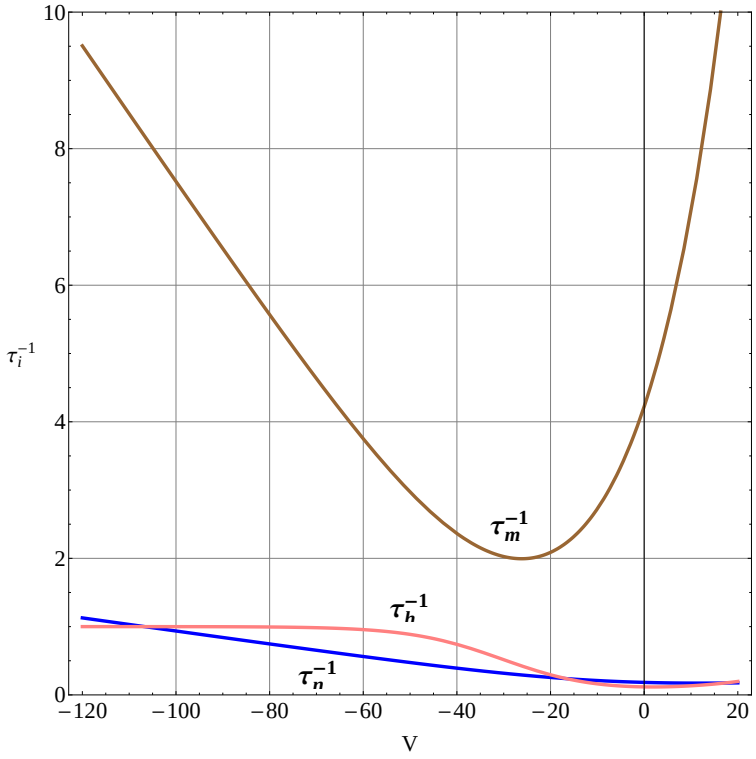

FIG. 1. Graph of $1/\tau_i$ (ms^{-1}) against V (mV).

Fig. 1 shows a plot of the functions ${\tau_i}^{-1}$ according to V with $i = n, h, m$ over the physiological range. We observe that ${\tau_m}^{-1}$ is of an order of magnitude bigger than ${\tau_h}^{-1}$ and ${\tau_n}^{-1}$, which are of comparable size. Indeed, we can deduce that the values of times scales are approximately ${\tau_m}^{-1} \approx 10ms^{-1}$ while ${\tau_n}^{-1} \approx {\tau_h}^{-1} \approx 1ms^{-1}$. Then, it appears that m corresponds to the *fast* variable while n and h correspond to *slow* variables. Moreover, since the activation of the sodium channel m is directly related to the dynamics of the membrane (action) potential V, Rubin and Wechselberger [24] consider that m and V evolve on the same *fast* time scale. So, the Hodgkin-Huxley model may be transformed into a *singularly perturbed system* with two time scales in which the *slow* variables are (n, h) and the *fast* variables are (m, V).

So, according to Awiszus *et al.* [2], Suckley and Biktashev [26], Suckley [27] and Rubin and Wechselberger [24] small multiplicative parameters $0 < \varepsilon \ll 1$ in the original vector field of the Hodgkin-Huxley Eqs. (47) may be identified while factorizing the right hand side of Eq. (47a) by $\bar{g}_{Na}$ and set:

$$\bar{g}_{Na} \ \rightarrow \ \frac{\bar{g}_{Na}}{\bar{g}_{Na}} = 1, \ \bar{g}_K \rightarrow \frac{\bar{g}_K}{\bar{g}_{Na}} = 0.3, \ \bar{g}_L \rightarrow \frac{\bar{g}_L}{\bar{g}_{Na}} = 0.0025.$$

other parameters are kept as for the original Hodgkin-Huxley model [19]:

$$C_M \ = \ 1.0 \ \mu F/cm^2, \ \bar{V}_{Na} = -115 \ mV, \ \bar{V}_K = 12 \ mV, \ \bar{V}_L = -10.613 \ mV.$$

Then, by posing $\bar{I} \rightarrow \dfrac{\bar{I}}{\bar{g}_{Na}}$, $\varepsilon = \dfrac{C_M}{\bar{g}_{Na}} = \dfrac{1}{120}$ and $(n, h, m, V) = (x_1, x_2, y_1, y_2)$ to consistent with the notations of Sec. 3, we obtain:

$$\frac{dx_1}{dt} = \frac{\bar{x}_1 - x_1}{\tau_1} = f_1\left(x_1, x_2, y_1, y_2\right) \tag{48a}$$

$$\frac{dx_2}{dt} = \frac{\bar{x}_2 - x_2}{\tau_2} = f_1\left(x_1, x_2, y_1, y_2\right) \tag{48b}$$

$$\varepsilon\frac{dy_1}{dt} = \frac{\bar{y}_1 - y_1}{\tau_3} = g_1\left(x_1, x_2, y_1, y_2\right) \tag{48c}$$

$$\begin{aligned}\varepsilon\frac{dy_2}{dt} &= \bar{I} - \bar{g}_K x_1^4(y_2 - V_K) - \bar{g}_{Na} y_1^3 x_2(y_2 - V_{Na}) - \bar{g}_L(y_2 - V_L) \\ &= g_2\left(x_1, x_2, y_1, y_2\right)\end{aligned} \tag{48d}$$

where $(\bar{x}_1, \bar{x}_2, \bar{y}_1) = (\bar{n}, \bar{h}, \bar{m})$ and $\tau_{1,2,3} = \tau_{n,h,m}$.

Let's notice that the multiplicative parameter ε has been introduced artificially in Eq. (48c). This is due to the fact that it has been stated above that the time scale of variable m, *i.e.*, y_1 is tenth times greater than the time scale of variables n and h, *i.e.* of variables x_1 and x_2. Moreover, this parameter is identical to those use in Eq. (48d) since it has been also considered that m and V, *i.e.*, y_1 and y_2 evolve on the same *fast* time scale.

According to the *Geometric Singular Perturbation Theory*, the zero-order approximation in ε of the *slow manifold* associated with the Hodgkin-Huxley model (48) is obtained by posing $\varepsilon = 0$ in Eqs. (48c & 48d). So, the *slow manifold* is given by:

$$x_2 = \frac{\bar{I} - \bar{g}_K x_1^4 (y_2 - V_K) - \bar{g}_L (y_2 - V_L)}{\bar{g}_{Na} \bar{y}_1^3 (y_2 - V_{Na})} \tag{49a}$$

$$y_1 = \bar{y}_1(y_2) \tag{49b}$$

Then, the *fast foliation* is within the planes $x_1 = constant$ and $x_2 = constant$.

The *fold curve* is defined as the location of the points where $g_1(x_1, x_2, y_1, y_2) = 0$, $g_2(x_1, x_2, y_1, y_2) = 0$ and $det\left[J_{(g_1,g_2)}\right] = 0$. For the Hodgkin-Huxley model (48), the *fold curve* is thus given by Eqs. (49a & 49b) and by the determinant of the Jacobian matrix of the following *fast foliation*:

$$\frac{dy_1}{dt} = \frac{\bar{y}_1 - y_1}{\tau_3} = g_1(x_1, x_2, y_1, y_2) \tag{50a}$$

$$\begin{aligned} \frac{dy_2}{dt} &= \bar{I} - \bar{g}_K x_1^4 (y_2 - V_K) - \bar{g}_{Na} y_1^3 x_2 (y_2 - V_{Na}) - \bar{g}_L (y_2 - V_L) \\ &= g_2(x_1, x_2, y_1, y_2) \end{aligned} \tag{50b}$$

The Jacobian matrix of the *fast foliation* (50) reads:

$$J_{(g_1,g_2)} = \begin{pmatrix} \dfrac{\bar{y_1}'\tau_3 - \tau_3'(\bar{y_1} - y_1)}{\tau_3^2} & -\dfrac{1}{\tau_3} \\ -(\bar{g}_K x^4 + \bar{g}_{Na} y_1^3 x_2 + \bar{g}_L) & -3\bar{g}_{Na} y_1^2 x_2 (y_2 - V_{Na}) \end{pmatrix} \tag{51}$$

where the $(')$ denotes the derivative with respect to y_2. Then, taking into account Eqs. (49b), *i.e.*, $y_1 = \bar{y}_1$ we have:

$$J_{(g_1,g_2)} = \begin{pmatrix} \dfrac{\bar{y_1}'}{\tau_3} & -\dfrac{1}{\tau_3} \\ -(\bar{g}_K x_1^4 + \bar{g}_{Na}\bar{y}_1^3 x_2 + \bar{g}_L) & -3\bar{g}_{Na}\bar{y}_1^2 x_2 (y_2 - V_{Na}) \end{pmatrix} \tag{52}$$

So, the determinant of the Jacobian matrix of the *fast foliation* (50) is:

$$det\left(J_{(g_1,g_2)}\right) = -\frac{1}{\tau_3}\left[\bar{g}_K x_1^4 + \bar{g}_{Na}\bar{y}_1^3 x_2 + \bar{g}_L + 3\bar{g}_{Na}\bar{y_1}'\bar{y}_1^2 x_2 (y_2 - V_{Na})\right] \tag{53}$$

Thus, the condition for the *fold curve* is $det\left(J_{(g_1,g_2)}\right) = 0$, which gives:

$$\bar{g}_K x_1^4 + \bar{g}_{Na}\bar{y}_1^3 x_2 + \bar{g}_L + 3\bar{g}_{Na}\bar{y_1}'\bar{y}_1^2 x_2 (y_2 - V_{Na}) = 0 \tag{54}$$

Therefore:

$$x_2 = -\frac{\bar{g}_K x_1^4 + \bar{g}_L}{\bar{g}_{Na}\bar{y}_1^2\left(\bar{y}_1 + 3\bar{y_1}'(y_2 - V_{Na})\right)} \tag{55}$$

By subtracting Eq. (49a) from Eq. (55) we obtain x_1:

$$x_1 = x_{1f} = \left[\frac{-\bar{I}\left[\bar{y}_1 + 3\bar{y_1}'(y_2 - V_{Na})\right] + \bar{g}_L(V_{Na} - V_L)\bar{y}_1 + 3\bar{y_1}'(y_2 - V_{Na})(y_2 - V_L)}{\bar{g}_K\left[(V_K - V_{Na})\bar{y}_1 - 3\bar{y_1}'(y_2 - V_{Na})(y_2 - V_K)\right]}\right]^{1/4} \tag{56}$$

Plugging this value of x_1 (56) into Eq. (55) provides:

$$x_2 = x_{2f} = \frac{\bar{I} + \bar{g}_L(V_K - V_L)}{\bar{g}_{Na}\bar{y}_1^2\left[(V_{Na} - V_K)\bar{y}_1 + 3\bar{y_1}'(y_2 - V_{Na})(y_2 - V_K)\right]} \tag{57}$$

So, the *fold curve* is given by the set of parametric equations (56-57) in terms of y_2.

The *pseudo singular points* are given by Eqs. (20) which reads for the Hodgkin-Huxley model (48):

$$\frac{\bar{y}_1 - y_1}{\tau_3} = 0, \tag{58a}$$

$$\bar{I} - \bar{g}_K x_1^4 (y_2 - V_K) - \bar{g}_{Na} y_1^3 x_2 (y_2 - V_{Na}) - \bar{g}_L (y_2 - V_L) = 0, \tag{58b}$$

$$\left[\frac{4\bar{g}_K x_1^3 (y_2 - V_K)(x_1 - \bar{x}_1)}{\tau_1} + \frac{\bar{g}_{Na} y_1^3 (y_2 - V_{Na})(x_2 - \bar{x}_2)}{\tau_2} \right] = 0, \tag{58c}$$

$$\left[\frac{4\bar{g}_K x_1^3 (y_2 - V_K)(x_1 - \bar{x}_1)}{\tau_1} + \frac{\bar{g}_{Na} y_1^3 (y_2 - V_{Na})(x_2 - \bar{x}_2)}{\tau_2} \right] \frac{1}{\tau_3} = 0, \tag{58d}$$

$$\tau_3 \left(\bar{g}_K x_1^4 + \bar{g}_{Na} y_1^3 x_2 + \bar{g}_L \right) + 3\bar{g}_{Na} y_1^2 x_2 (y_2 - V_{Na})(\tau_3 y_1' + (y_1 - \bar{y}_1)\tau_3') = 0. \tag{58e}$$

Let's notice that Eqs. (58c) and (58d) are identical. Moreover, the definition of τ_3 (46f) enables to simplify the above system (58). Thus, we have:

$$\bar{I} - \bar{g}_K x_1^4 (y_2 - V_K) - \bar{g}_{Na} \bar{y}_1^3 x_2 (y_2 - V_{Na}) - \bar{g}_L (y_2 - V_L) = 0, \tag{59a}$$

$$\frac{4\bar{g}_K x_1^3 (y_2 - V_K)(x_1 - \bar{x}_1)}{\tau_1} + \frac{\bar{g}_{Na} \bar{y}_1^3 (y_2 - V_{Na})(x_2 - \bar{x}_2)}{\tau_2} = 0, \tag{59b}$$

$$\bar{g}_K x_1^4 + \bar{g}_{Na} \bar{y}_1^3 x_2 + \bar{g}_L + 3\bar{g}_{Na} \bar{y}_1^2 \bar{y}_1' x_2 (y_2 - V_{Na}) = 0. \tag{59c}$$

Moreover, Eqs. (59a) and (59c) indicate that the *pseudo singular point* belongs to the *slow manifold* and to the *fold curve*. So, let's replace in Eq. (59b) the variables x_1 and x_2 by the variables x_{1f} and x_{2f} given by Eq. (56) and Eq. (57) respectively which represent the parametric equations of *fold curve*.

$$\frac{4g_K x_{1f}^3 (y_2 - V_K)(x_{1f} - \bar{x}_1)}{\tau_1} + \frac{\bar{y}_1^3 (y_2 - V_{Na})(x_{2f} - \bar{x}_2)}{\tau_2} = 0. \tag{60}$$

Thus, it appears that Eq. (60) depends on the variable y_2, on the functions gates dynamics time scales $\tau_1(y_2)$ and $\tau_2(y_2)$ and on the bifurcation parameter $\bar{I}$. According to Rubin and Wechselberger [24], the function $y_2(\bar{I})$, solution of (60) is independent of time multiplicative constants k_1 and k_2 that one could set in factor of $\tau_1(y_2)$ and $\tau_2(y_2)$.

So, following their works, let's plot the function $y_2(\bar{I})$ solution of (60) for various values of these time constants by posing successively in (60) $k_1 = 1$, 3, 4.75 and 7 and while fixing $k_2 = 1$. The result is presented in Fig. 2.

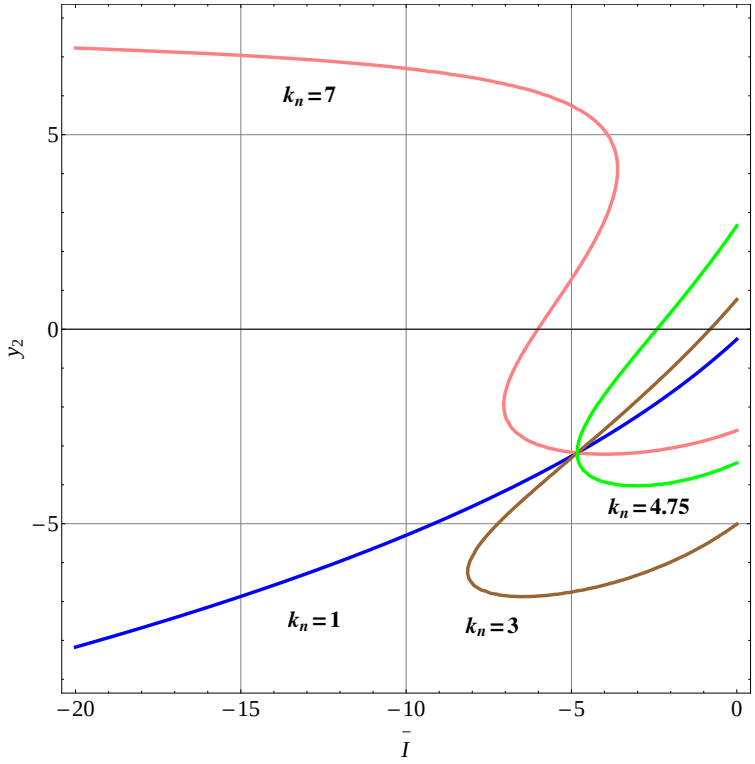

FIG. 2. Function $y_2(\bar{I})$ for various values of parameter $k_n = 1, 3, 4.75, 7$ exhibiting the the bifurcation parameter value $\bar{I}_C \approx -4.8$.

Let's notice that this plot[8] is exactly the same as those presented by Rubin and Wechselberger [24] (Fig. 8-9) for a nondimensionalized three-dimensional Hodgkin-Huxley singularly perturbed system which had been obtained after the following variable changes: $V \to -V$ and $\bar{I} \to -I$, then $V \to V + 65$ and finally $V \to V/100$.

We observe from Fig. 2 that the bifurcation parameter value $\bar{I}_C \approx -4.8$ is exactly identical (in absolute value) to those obtained by Rubin and Wechselberger [24]. Numerical resolution[9] of Eq. (60) provides a better approximation of the bifurcation parameter value:

$$\bar{I}_C = -4.82988 \ \mu A$$

This value corresponds to a voltage $y_2 = -3.18136 \ mV$.

For $\bar{I} \approx -4.1$, the coordinate of the *pseudo singular point* can be computed numerically:

$$(x_1, x_2, y_1, y_2) = (0.362513, 0.521793, 0.0733782, -2.81908)$$

According to Proposition 3 we can state that the eigenpolynomial of the Jacobian matrix associated with the "normalized slow dynamics" of the Hodgkin-Huxley model (48) reads:

$$\lambda^4 - \sigma_1\lambda^3 + \sigma_2\lambda^2 - \sigma_3\lambda + \sigma_4 = 0$$

for which it is easy to prove that $\sigma_4 = \sigma_3 = 0$. So, this eigenpolynomial reduces to:

$$\lambda^2\left(\lambda^2 - \sigma_1\lambda + \sigma_2\right) = 0$$

According to Eqs. (28) we find that:

$$\begin{aligned} p &= Tr(J) = 144.933, \\ q &= \sigma_2 = -362.924 \end{aligned}$$

Thus, according to Prop. 3, the *pseudo singular points* is of saddle-type. Moreover, numerical computation of the eigenvalues of this Jacobian matrix evaluated at the *pseudo singular point* provides:

[8]The function $y_2(\bar{I})$ solution of (59) has been plotted with Mathematica© while using the ContourPlot function used for representing implicit function since such function cannot be expressed explicitly.

[9]This resolution has been made while using the function FindRoot in Mathematica©.

$$(\lambda_1, \lambda_2, \lambda_3, \lambda_4) = (-2.46224, 147.396, 0, 0)$$

So, according to Proposition 3, this *pseudo singular point* is of saddle-type and canard solution may occur in the four-dimensional Hodgkin-Huxley singularly perturbed system (48) for the original set of parameter values.

In Fig. 3, 4 & 5 canard solution of the four-dimensional Hodgkin-Huxley singularly perturbed system for the "canard value" of $\bar{I} \approx -4.1$ has been plotted in the (x_1, x_2, y_2) phase-space and then in the (x_1, y_2) phase plane. The green point represents the *pseudo singular point*. The trajectory curve, *i.e.*, the canard solution has been plotted in red while the *fold curve* is in yellow. We observe on Fig. 3 that when the trajectory curve reaches the *fold* at the *pseudo singular point* it "jump" suddenly to the other part of the *slow manifold* before being reinjected towards the *pseudo singular point*.

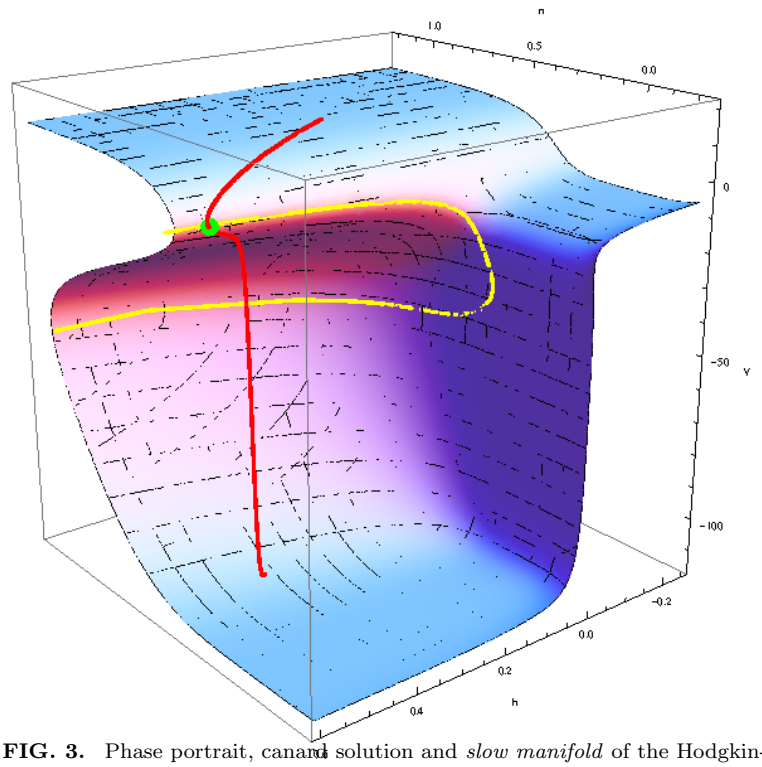

FIG. 3. Phase portrait, canard solution and *slow manifold* of the Hodgkin-Huxley system (48) in the (n, h, V) phase space.

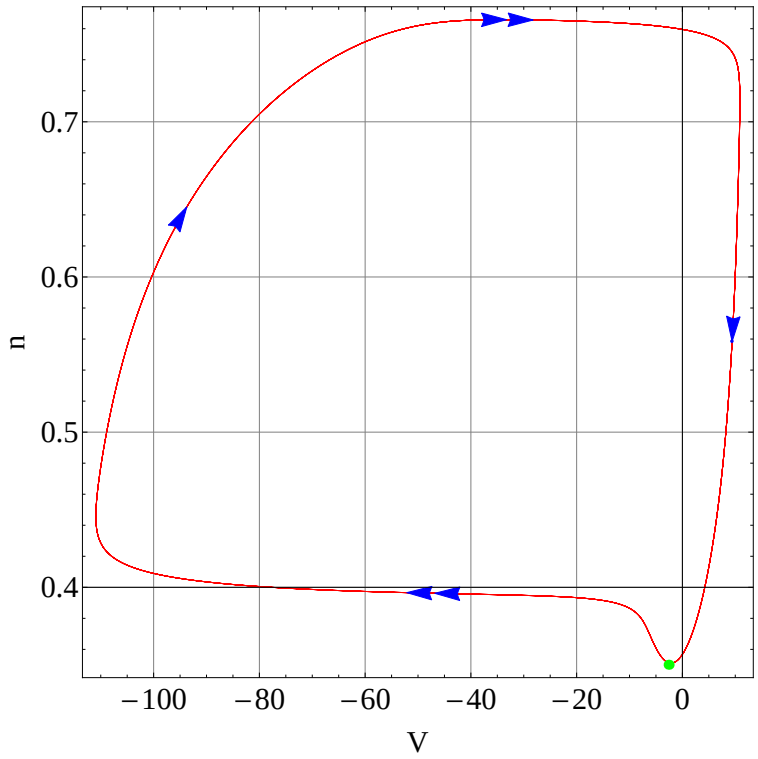

FIG. 4. Phase portrait, canard solution and *slow manifold* of the Hodgkin-Huxley system (48) in the (V, n) phase plane.

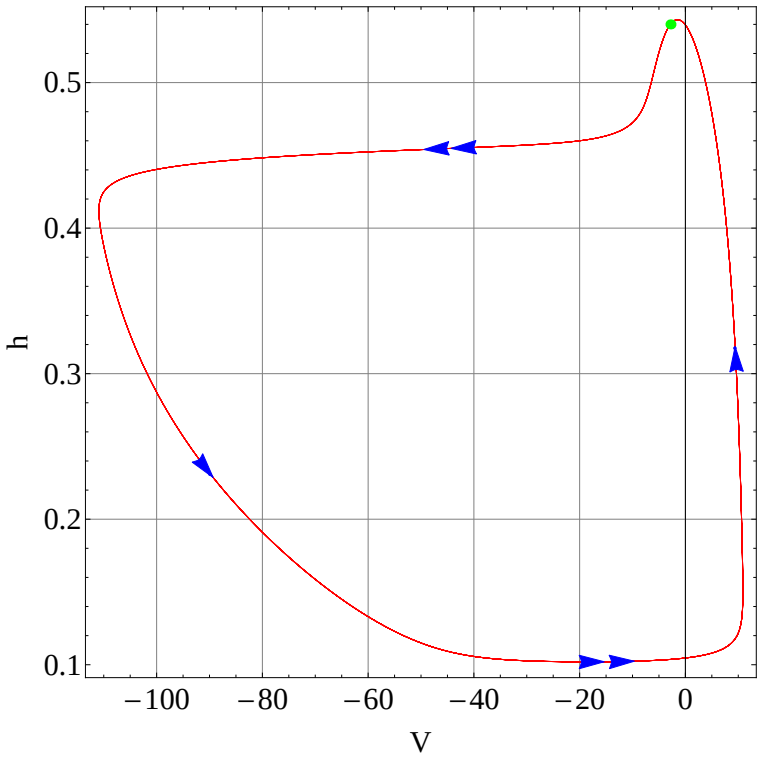

FIG. 5. Phase portrait, canard solution and *slow manifold* of the Hodgkin-Huxley system (48) in the (V, h) phase plane.

6. DISCUSSION

In a previous paper entitled: "Canards Existence in Memristor's Circuits" (see Ginoux & Llibre [17]) we have proposed a new method for proving the existence of "canard solutions" for three and four-dimensional singularly perturbed systems with only one *fast* variable which improves the methods used until now. This method enabled to state a unique "generic" condition for the existence of "canard solutions" for such three and four-dimensional singularly perturbed systems which is based on the stability of *folded singularities* of the *normalized slow dynamics* deduced from a well-known property of linear algebra. This unique condition which is completely identical to that provided by Benoît [6] and then by Szmolyan and Wechselberger [25] and finally by Wechselberger [39] was considered as "generic" since it was exactly the same for singularly perturbed systems of dimension three and four with only one *fast* variable. In this work we have extended this new method to the case of four-dimensional singularly perturbed systems with two *slow* and two *fast* variables and we have stated that the condition for the existence of "canard solutions" in such systems is exactly identical to those proposed in our previous paper. This result confirms the genericity of the condition ($\sigma_2 < 0$) we have highlighted and provides a simple and efficient tool for testing the occurrence of "canard solutions" in any three or four-dimensional singularly perturbed systems with one or two *fast* variables. Applications of this method to the famous coupled FitzHugh-Nagumo equations and to the Hodgkin-Huxley model has enabled to show the existence of "canard solutions" in such systems. However, in this paper, only the case of *pseudo singular points* or *folded singularities* of saddle-type has been analyzed. Of course, the case of of *pseudo singular points* or *folded singularities* of node-type and focus-type could be also studied with the same method.

7. ACKNOWLEDGEMENTS

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APPENDIX

Change of coordinates leading to the *normal forms* of four-dimensional singularly perturbed systems with two fast variables are given in the following section.

Normal form of 4D singularly perturbed systems with two fast variables

Let's consider the four-dimensional *singularly perturbed dynamical system* (11) with $k = 2$ *slow* variables and $m = 2$ *fast* and let's make the following change of variables:

$$x_1 = \alpha^2 x, \quad x_2 = \alpha y, \quad y_1 = \alpha^2 z, \quad y_2 = \alpha u \quad \text{where} \quad \alpha \ll 1. \tag{A-1}$$

By taking into account extension of Benoît's generic hypothesis Eqs. (22,23) and while using Taylor series expansion the system (11) becomes:

$$\begin{aligned}
\dot{x} &= \frac{\partial f_1}{\partial y} y + \frac{\partial f_1}{\partial u} u, \\
\dot{y} &= f_2(x, y, z, u), \\
\left(\frac{\varepsilon}{\alpha}\right) \dot{z} &= \frac{\partial g_1}{\partial z} z + \frac{1}{2}\frac{\partial^2 g_1}{\partial y^2} y^2 + \frac{1}{2}\frac{\partial^2 g_1}{\partial u^2} u^2 + \frac{\partial^2 g_1}{\partial y \partial u} yu, \\
\left(\frac{\varepsilon}{\alpha}\right) \dot{u} &= \frac{\partial g_2}{\partial x} x + \frac{1}{2}\frac{\partial^2 g_2}{\partial y^2} y^2 + \frac{1}{2}\frac{\partial^2 g_2}{\partial u^2} u^2 + \frac{\partial^2 g_2}{\partial y \partial u} yu.
\end{aligned} \tag{A-2}$$

Then, let's make the standard polynomial change of variables:

$$\begin{aligned}
X &= Ax + By^2, \\
Y &= \frac{y}{f_2}, \\
Z &= Cy + Dz + Eu, \\
U &= Fy + Gu.
\end{aligned} \tag{A-3}$$

From (A-3) we deduce that:

$$\begin{aligned} x &= \frac{X - Bf_2^2Y^2}{A}, \\ y &= f_2Y, \\ z &= \frac{1}{D}\left[Z - Cf_2Y - \frac{E}{G}\left(U - Ff_2Y\right)\right], \\ u &= \frac{U - Ff_2Y}{G}. \end{aligned} \tag{A-4}$$

The time derivative of system (A-3) gives:

$$\begin{aligned} \dot{X} &= A\dot{x} + 2By\dot{y}, \\ \dot{Y} &= \frac{\dot{y}}{f_2}, \\ \dot{Z} &= C\dot{y} + D\dot{z} + E\dot{u}, \\ \dot{U} &= F\dot{z} + G\dot{u}. \end{aligned} \tag{A-5}$$

Then, multiplying the third and fourth equation of (A-5) by (ε/α) and while replacing in (A-5) $\dot{x}$, $\dot{y}$, $\dot{z}$ and $\dot{u}$ by the right-hand-side of system (A-2) leads to:

$$\begin{aligned} \dot{X} &= A\dot{x} + 2By\dot{y}, \\ \dot{Y} &= \frac{\dot{y}}{f_2}, \\ \left(\frac{\varepsilon}{\alpha}\right)\dot{Z} &= \left(\frac{\varepsilon}{\alpha}\right)C\dot{y} + \left(\frac{\varepsilon}{\alpha}\right)D\dot{z} + \left(\frac{\varepsilon}{\alpha}\right)E\dot{u}, \\ \left(\frac{\varepsilon}{\alpha}\right)\dot{U} &= \left(\frac{\varepsilon}{\alpha}\right)F\dot{y} + \left(\frac{\varepsilon}{\alpha}\right)G\dot{u}. \end{aligned} \tag{A-6}$$

Since $\varepsilon/\alpha \ll 1$, the first terms of the right-hand-side of the third and fourth equation of (A-16) can be neglected. So we have:

$$\begin{aligned} \dot{X} &= A\left(\frac{\partial f_1}{\partial y}y + \frac{\partial f_1}{\partial u}u\right) + 2Bf_2y, \\ \dot{Y} &= 1, \\ \left(\frac{\varepsilon}{\alpha}\right)\dot{Z} &= D\left(\frac{\partial g_1}{\partial z}z + \frac{1}{2}\frac{\partial^2 g_1}{\partial y^2}y^2 + \frac{1}{2}\frac{\partial^2 g_1}{\partial u^2}u^2 + \frac{\partial^2 g_1}{\partial y \partial u}yu\right) \\ &\quad + E\left(\frac{\partial g_2}{\partial x}x + \frac{1}{2}\frac{\partial^2 g_2}{\partial y^2}y^2 + \frac{1}{2}\frac{\partial^2 g_2}{\partial u^2}u^2 + \frac{\partial^2 g_2}{\partial y \partial u}yu\right), \\ \left(\frac{\varepsilon}{\alpha}\right)\dot{U} &= G\left(\frac{\partial g_2}{\partial x}x + \frac{1}{2}\frac{\partial^2 g_2}{\partial y^2}y^2 + \frac{1}{2}\frac{\partial^2 g_2}{\partial u^2}u^2 + \frac{\partial^2 g_2}{\partial y \partial u}yu\right). \end{aligned} \tag{A-7}$$

Then, by replacing in (A-7) x, y, z and u by the right-hand-side of (A-4) and by identifying with the following system in which we have posed: $(\varepsilon/\alpha) = \epsilon$:

$$\begin{aligned}
\dot{X} &= \tilde{a}Y + \tilde{b}U + O\left(X, \epsilon, Y^2, YU, U^2\right), \\
\dot{Y} &= 1 + O\left(X, Y, U, \epsilon\right), \\
\epsilon\dot{Z} &= \tilde{c}Z + O\left(\epsilon X, \epsilon Y, \epsilon U, X^2, y^2U, U^2, YU\right), \\
\epsilon\dot{U} &= -\left(X + U^2\right) + O\left(\epsilon X, \epsilon Y, \epsilon U, \epsilon^2, X^2U, U^3, XYU\right),
\end{aligned} \tag{A-8}$$

we find:

$$\begin{aligned}
\tilde{a} &= A\left(\frac{\partial f_1}{\partial y} - \frac{F}{G}\frac{\partial f_1}{\partial u}\right) f_2 + 2Bf_2^2, \\
\tilde{b} &= \frac{A}{G}\frac{\partial f_1}{\partial u}, \\
\tilde{c} &= \frac{\partial g_1}{\partial z}.
\end{aligned} \tag{A-9}$$

where

$$\begin{aligned}
A &= \frac{1}{2}\frac{\partial g_2}{\partial x}\frac{\partial^2 g_2}{\partial u^2}, \\
B &= \frac{1}{4}\left[\frac{\partial^2 g_2}{\partial u^2}\frac{\partial^2 g_2}{\partial y^2} - \left(\frac{\partial^2 g_2}{\partial y \partial u}\right)^2\right], \\
G &= -\frac{1}{2}\frac{\partial^2 g_2}{\partial u^2}.
\end{aligned} \tag{A-10}$$

Finally, we deduce:

$$\begin{aligned}
\tilde{a} &= \frac{1}{2}\left[f_2^2\left(\frac{\partial^2 g_2}{\partial x_2^2}\frac{\partial^2 g_2}{\partial y_2^2} - \left(\frac{\partial^2 g_2}{\partial x_2 \partial y_2}\right)^2\right) + f_2\frac{\partial g_2}{\partial x_1}\left(\frac{\partial^2 g_2}{\partial y_2^2}\frac{\partial f_1}{\partial x_2} - \frac{\partial^2 g_2}{\partial x_2 \partial y_2}\frac{\partial f_1}{\partial y_2}\right)\right] \\
\tilde{b} &= -\frac{\partial g_2}{\partial x_1}\frac{\partial f_1}{\partial y_2}, \\
\tilde{c} &= \frac{\partial g_1}{\partial y_1}.
\end{aligned} \tag{A-11}$$

This is the result we established in Sec. 2.7.

REFERENCES

1. J. Argémi, *Approche qualitative d'un problème de perturbations singulières dans* $\mathbb{R}^4$, in Equadiff 1978, ed. R. Conti, G. Sestini, G. Villari (1978), 330–340.
2. F. Awiszus, J. Dehnhardt & T. Funke, *The singularly perturbed Hodgkin-Huxley equations as a tool for the analysis of repetitive nerve activity*, J. Math. Biol. **28** (1990) 177–195.
3. E. Benoît, *Tunnels et entonnoirs*, CR. Acad. Sc. Paris **292**, Série I (1981) 283–286.
4. E. Benoît, *Équations différentielles : relation entrée-sortie*, CR. Acad. Sc. Paris **293**, Série I (1981) 293–296.
5. E. Benoît and C. Lobry, *Les canards de* $\mathbb{R}^3$, CR. Acad. Sc. Paris **294**, Série I (1982) 483–488.
6. E. Benoît, *Systèmes lents-rapides dans* $\mathbb{R}^3$ *et leurs canards*, Société Mathématique de France, Astérisque, (190–110) (1983) 159–191.
7. E. Benoît, Canards de $\mathbb{R}^3$, Thèse d'état (PhD), Université de Nice, 1984.
8. E. Benoît, *Canards et enlacements*, Publications de l'Institut des Hautes Etudes Scientifiques, **72** (1990) 63–91.
9. E. Benoît, *Perturbation singulière en dimension trois : Canards en un point pseudo singulier noeud*, Bulletin de la Société Mathématique de France, (129-1) (2001) 91–113.
10. L.O. Chua, V.I. Sbitnev & H. Kim, *Hodgkin-Huxley Axon is Made of memristors*, Int. J. of Bifurcation and Chaos, 22(3) (2012) p. 1250098.
11. L.O. Chua, V.I. Sbitnev & H. Kim, *Neurons are Poised Near the Edge of Chaos*, Int. J. of Bifurcation and Chaos, 22(4) (2012) p. 1230011.
12. N. Fenichel, *Persistence and smoothness of invariant manifolds for flows*, Ind. Univ. Math. J., **21** (1971) 193–225.
13. N. Fenichel, *Asymptotic stability with rate conditions*, Ind. Univ. Math. J., **23** (1974) 1109–1137.
14. N. Fenichel, *Asymptotic stability with rate conditions II*, Ind. Univ. Math. J., **26** (1977) 81–93.
15. N. Fenichel, *Geometric singular perturbation theory for ordinary differential equations*, J. Diff. Eq. (1979) 53–98.
16. R. FitzHugh, *Impulses and physiological states in theoretical models of nerve membranes*, Biophys. J., **1** (1961) 445–466.
17. J.M. Ginoux & J. Llibre, *Canards in Memristor's Circuits*, Qualitative Theory of Dynamical Systems, September 2015, 1–49.
18. J. Guckenheimer and R. Haiduc, *Canards at folded nodes*, Mosc. Math. J., **5**(1) (2005) 91–103.
19. A. L. Hodgkin & A.F. Huxley *A quantitative description of membrane current and its application to conduction and excitation in nerve*, J. Physiol., 117(4) (1952) 500–544.
20. C.K.R.T. Jones, *Geometric Singular Perturbation Theory in Dynamical Systems*, *Montecatini Terme*, L. Arnold, Lecture Notes in Mathematics, vol. 1609, Springer-Verlag (1994) 44–118.
21. T. Kaper, *An Introduction to Geometric Methods and Dynamical Systems Theory for Singular Perturbation Problems*, in Analyzing multiscale phenomena using singular perturbation methods, Baltimore, MD, (1998) 85–131. Amer. Math. Soc., Providence, RI.

22. J.S. Nagumo, S. Arimoto & S. Oshizawa, *An active pulse transmission line simulating nerve axon*,Proc. Inst. Radio Engineers, **50** (1962) 2061–2070.

23. R.E. O'Malley, *Introduction to Singular Perturbations*, Academic Press, New York, 1974.

24. J. Rubin & M. Wechselberger, *Giant squid-hidden canard: the 3D geometry of the Hodgkin-Huxley model*, Biol. Cybern., 97 (2007) 5–32.

25. P. Szmolyan and M. Wechselberger, *Canards in* $\mathbb{R}^3$, J. Dif. Eqs., **177** (2001) 419–453.

26. R. Suckley & V.N. Biktashev, *The asymptotic Structure of the Hodgkin-Huxley Equations*, Int. J. of Bifurcation and Chaos, 13(12) (2003) 3805–3825.

27. R. Suckley, *The Asymptotic Structure of Excitable Systems*, PhD Thesis of the University of Liverpool (2004).

28. F. Takens, *Constrained equations, a study of implicit differential equations and their discontinuous solutions*, in *Structural stability, the theory of catastrophes and applications in the sciences*, *Springer Lecture Notes in Math.*, **525** (1976) 143–234.

29. K. Tchizawa & S.A. Campbell, *On winding duck solutions in* $\mathbb{R}^4$,Proceedings of Neural, Parallel, and Scientific Computations, **2** (2002) 315–318.

30. K. Tchizawa, *On duck solutions in* $\mathbb{R}^4$, Kyoto Univ RIMS Kokyuroku, 1254 (2002), 160–162.

31. K. Tchizawa, *A direct method for finding ducks in* $\mathbb{R}^4$, Kyoto Univ RIMS Kokyuroku, 1372 (2004), 97–103.

32. K.Tchizawa, *Generic conditions for duck solutions in* $\mathbb{R}^4$, Kyoto Univ RIMS Kokyuroku, 1547 (2007), 107–113.

33. K. Tchizawa, *On the transversality conditions for 4-dim duck solutions*, Kyoto Univ RIMS Kokyuroku, 1582 (2008), 144–150.

34. K. Tchizawa, *On a Local Model for Finding 4-Dimensional Duck Solutions*, Selected Topics in Mathematical Methods and Computational Techniques in Electrical Engineering, (2010) 177–183.

35. K. Tchizawa, *On Relative Stability in 4-Dimensional Duck Solution*, Journal of Mathematics and System Science, (2) (2012), 558–563.

36. K. Tchizawa, *On the two methods for finding 4-dimensional duck solutions*, Applied Mathematics, (5) (2014), 16–24.

37. A.N. Tikhonov, *On the dependence of solutions of differential equations on a small parameter*, Mat. Sbornik N.S., **31** (1948) 575–586.

38. M. Wechselberger, *Existence and Bifurcation of Canards in* $\mathbb{R}^3$ *in the case of a Folded Node*, SIAM J. Applied Dynamical Systems, **4** (2005) 101–139.

39. M. Wechselberger, *À propos de canards*, Trans. Amer. Math. Soc., **364** (2012) 3289–3309.