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A CONDITION OF UNIQUENESS AND STABILITY IN A BURSTING MODEL

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ABSTRACT. We consider one class of bursting oscillation models, that is square-wave burster. One of the interesting features of these models is that periodic bursting solution need not to be unique or stable for arbitrarily small values of a singular perturbation parameter ϵ. Recent results show that the bursting solution is uniquely determined and stable for most of the ranges of the small parameter ϵ. In this paper, we present a condition of uniqueness and stability of periodic bursting solutions for all sufficiently small values of $\epsilon > 0$.

1. INTRODUCTION

The term *bursting* refers to the dynamic activity in which some variables undergo alternations between an active phase of rapid, spike-like oscillations and a silent phase of near steady state resting period as shown in Figure 1. This activity is observed in various electrically excitable biological systems such as nerve cells, secretory cells, and muscle fibers, as well as in chemical reactions (*cf.* Hudson, Hart & Marinko [9], Morris & Lecar [12], Plant & Kim [13], Rinzel & Ermentrout [15], Sherman, Rinzel & Keizer [17]). There are several different classes of bursting oscillations and there have been considerable efforts in trying to formulate and classify the underlying mechanisms responsible for these oscillations (*cf.* Bertram, Butte, Kiemel & Sherman [1], Rinzel [14], Rinzel & Lee [16]). For comprehensive reviews, see Izhikevich [10].

Mathematical models for bursting oscillations often involve a rich structure of dynamic behaviors. Besides periodic bursting solutions, the systems display other types of periodic solutions as well as more exciting behaviors including chaotic dynamics. The systems contain variables of different time scales and this often leads to interesting mathematical issues related to the theory of singular perturbations,

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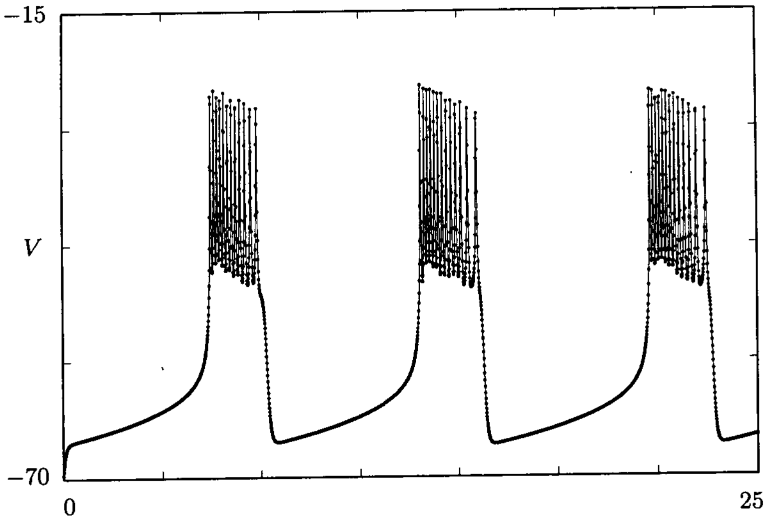


Figure 1. An example of a bursting solution. The solution is computed using the equations in the Appendix.

invariant manifold theories, or bifurcation problems (*cf.* Fenichel [6], Guckenheimer & Holmes [7], Hirsch, Pugh & Shub [8], Tihonov [21]).

In this paper we consider one class of models for bursting oscillations; this is the so-called square-wave burster. These bursting patterns arise in models for electrical activity in pancreatic β-cells (*cf.* Chay & Keizer [3], Chay & Rinzel [4], Sherman, Rinzel & Keizer [17]). This activity is believed to be correlated to the release of insulin from the cells. Square-wave bursting phenomena are also observed in recent models of respiratory rhythm generation and models for pattern generation based on synaptic depression (*cf.* Butera, Rinzel & Smith [2], Tabak, Senn, O'Donovan & Rinzel [18]).

Rigorous mathematical, qualitative analysis of these models was initiated by Terman [19, 20]. He proved the existence of periodic bursting solutions in these models. An interesting feature of these models is that the bursting solution is not always unique or stable. He also showed the existence of chaotic bursting behavior for some parameter ranges. Recently the ranges of singular perturbation parameter ϵ for which the periodic bursting solutions are uniquely determined were characterized in Lee & Terman [11].

Here we present a sufficient condition of uniqueness and stability of periodic bursting solutions for all sufficiently small values of $\epsilon > 0$. Hence, if the condition is satisfied, then chaotic behaviors do not arise in the models. Our approach to this problem is quite geometrical. We construct a Poincare return map for the periodic bursting solutions and determine when the return map is a contraction. To do this, we divide it into several different pieces and compute the contraction or expansion rate of the pieces.

2. The model

We consider a system of the form

$$\begin{aligned} x' &= f(x, y) \\ y' &= \epsilon g(x, y). \end{aligned} \tag{2.1}$$

Here $(x, y) \in \mathbb{R}^2 \times \mathbb{R}$ and f and g are sufficiently smooth functions and $\epsilon > 0$ is a small singular perturbation parameter.

If $\epsilon = 0$, then y is a constant, and we can consider y to be a parameter in the first equation of the system (2.1), i.e.,

$$x' = f(x, y). \tag{2.2}$$

We refer to (2.2) as the fast system (FS) and the second equation of (2.1) as the slow equation.

We now discuss the assumptions needed so that (2.1) exhibits bursting oscillations. These conditions are geometric in the sense that we make assumptions on the nature of the fixed points, periodic and other bounded solutions of (FS), and the slow equation. Most of these conditions are straightforward to verify for a specific model using numerical bifurcation and branch-tracking methods (*cf.* Doedel [5]).

An example of a specific set of equations which satisfy these assumptions is given in the Appendix. Our first three assumptions are concerned with (FS).

(A1) The set of fixed points of (FS) makes a 'Z-shaped' curve, denoted by $\mathcal{Z}$, as shown in Figure 2. That is, there exist $y_\rho < y_\lambda$ such that if $y < y_\rho$ or $y > y_\lambda$, then (FS) has exactly one fixed point, while if $y_\rho < y < y_\lambda$, then (FS) has precisely three fixed points. See also Figure 3.

(A2) The lower branch, denoted by $\mathcal{L}$, consists of fixed points which are sinks as solutions of (FS) and the middle branch consists of saddle fixed points.

(A3) There exists a one parameter family of asymptotically stable periodic solutions of (FS) as shown in Figure 2. This branch, denoted by $\mathcal{P}$, surrounds

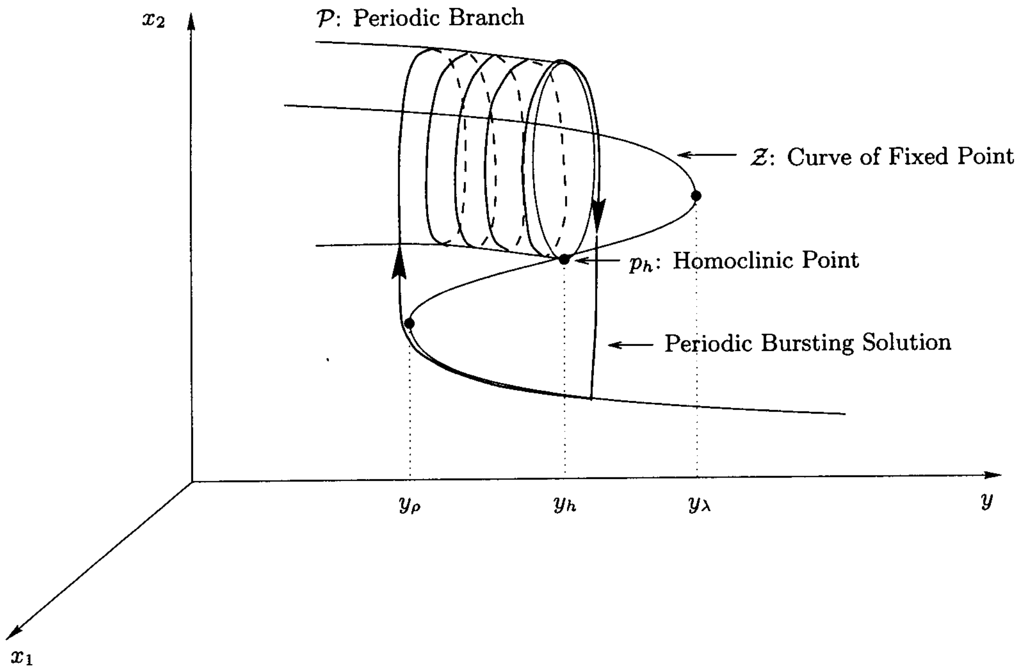


Figure 2. Geometric model for bursting. The fast system has a Z-shaped curve $\mathcal{Z}$ of fixed points and the branch $\mathcal{P}$ of stable periodic solutions. The bursting solution passes near the lower branch of fixed points in the silent phase and passes near the periodic branch $\mathcal{P}$ in the active phase.

a portion of the upper branch of fixed points and terminates at a solution which is homoclinic to one of the fixed points on the middle branch. We denote this homoclinic point by p_h.

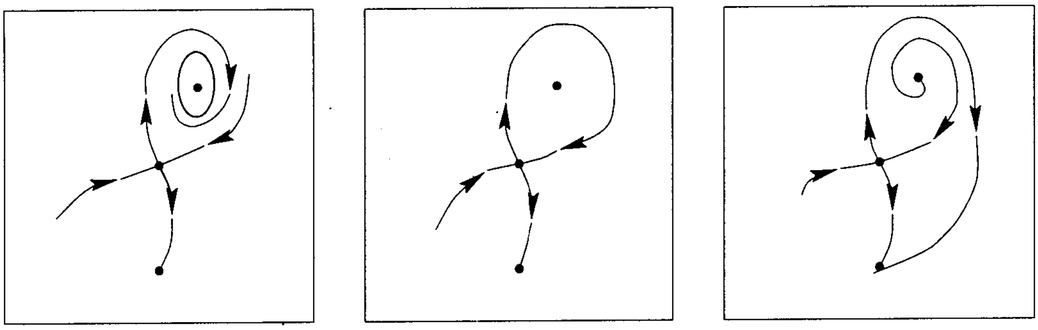
Our next two assumptions are concerned with the slow equation. Let the y-nullsurface $\mathcal{N} = \{(x,y) \in \mathbb{R}^3 \mid g(x,y) = 0\}$.

(B1) The set $\mathcal{N}$ defines a smooth surface which intersects the curve $\mathcal{Z}$ at a single point which lies on the middle branch of $\mathcal{Z}$ between the homoclinic point p_h and the left knee (the junction point of lower and middle branches).

(B2) $g < 0$ below $\mathcal{N}$, $g > 0$ above $\mathcal{N}$, and $\mathcal{N} \cap \mathcal{P} = \varnothing$.

Remark. There are some other technical assumptions required for our analysis, but most of these are generic ones. See Lee & Terman [11] for details.

We now give an intuitive explanation for why the system (2.1) will give rise to a bursting solution. Our description follows Terman [20] and the trajectory is shown



$y_p < y < y_h$ $\quad$ $y = y_h$ $\quad$ $h_h < y < y_\lambda$

Figure 3. The phase plane of (FS) for different values of y. For each $y \in (y_p, y_\lambda)$, one of the two trajectories in the unstable manifold of the fixed point along the middle branch approaches the stable fixed point on the lower branch. If $y < y_h$, then the other trajectory approaches the periodic solution; while, if $y > y_h$, then it ultimately approaches the lower stable fixed point.

in Figure 2. Assume that $\epsilon > 0$ is small and start the trajectory close to the lower branch. Because the lower branch consists of asymptotically stable fixed points of (FS), the trajectory will quickly approach a small neighborhood of the lower branch. Now $g < 0$ near the lower branch. Hence the solution tracks to the left along the lower branch. This continues until the slow dynamics pushes the trajectory past the left knee. The trajectory is then attracted to near the branch $\mathcal{P}$ of periodic solutions. This corresponds to the jump-up from the silent phase to the active phase. The fast spike-like oscillations of the bursting solution correspond to the trajectory passing near and around $\mathcal{P}$. The slow dynamics now forces the orbit to move slowly to the right. This continues until the trajectory passes near the homoclinic orbit of (FS). Once past this homoclinic orbit, the fast dynamics eventually forces the trajectory back to near the lower branch. This completes one cycle of the bursting solution.

3. The main theorem

We now derive a sufficient condition of uniqueness and stability of periodic bursting solutions by constructing a two-dimensional Poincare section Σ transverse to the flow defined by (2.1) and then considering the return map from Σ back into Σ. We denote this map by π_ϵ. The existence of periodic bursting solutions follows immediately from this construction by Brouwer fixed point theorem. Let the curves of periodic bursting solutions be denoted by γ_ϵ. We derive the uniqueness and stability results of periodic bursting solutions by determining when the map π_ϵ is a contraction with respect to the fixed point for all sufficiently small $\epsilon > 0$.

We choose the section Σ just above the left knee such in a way that trajectories cross Σ transversely as they jump up to the active phase. The distance between Σ and the left knee is assumed to be small, but still independent of ϵ. In order to determine when the return map is a contraction, we write it as the composition of several other maps; these maps correspond to the different pieces of the trajectories as they move around in phase space. The different pieces are

(P1) the jump up,
(P2) tracking near the branch $\mathcal{P}$ of periodic solutions,
(P3) motion near the homoclinic orbit and interaction with the middle branch,
(P4) the jump down,
(P5) tracking near the lower branch, and
(P6) passing near the left knee.

We need to estimate the amount of expansion or contraction induced by each of these pieces of the flow. We will show that there is a huge amount of contraction as trajectories pass near the lower branch. This contraction will be of the order $e^{-k_0/\epsilon}$ for some constant $k_0 > 0$. This contraction in (P5) easily dominate any possible expansion that can occur over the pieces (P1), (P2), (P4) or (P6). Hence, the only possible expansion that can ultimately destroy the contraction of the map π_ϵ must occur during the piece labeled (P3). It will, in fact, be possible for exponential expansion to occur as the trajectories pass near the middle branch, just before they jump down to the silent phase. See Lee & Terman [11] for more details.

It remains to estimate the contraction rate of trajectories during the piece (P5) and the possible maximum expansion rate during the piece (P3).

3.1. The contraction at the lower branch.

In the lower branch, (FS) has a fixed point for each $y > y_\rho$. Denote the fixed point by $(x_*(y), y)$. Since the fixed points of the lower branch are attracting in (FS), both of the two eigenvalues of $A(y) = D_x f(x_*(y), y)$ have negative real parts for $y > y_\rho$. Hence it follows that the fixed point $x_*(y)$ of (FS) has a domain of attraction $G(y)$;

any solution of (FS) with the initial point in $G(y)$ tends to the fixed point $(x_*(y), y)$. By the rescaling $\tau = \epsilon t$, system (2.1) can be put into an equivalent system

$$\begin{aligned} \epsilon \dot{x} &= f(x, y) \\ \dot{y} &= g(x, y), \end{aligned} \tag{3.1}$$

where $\cdot$ indicates differentiation with respect to τ. We designate by $(x(\tau, \epsilon),\ y(\tau, \epsilon))$ the solution of (3.1) with an initial point (x_0, y_0), $x_0 \in G(y_0)$. When $\epsilon = 0$, (3.1) is reduced to the following Slow Equation System (SES):

$$\frac{d\bar{y}}{d\tau} = g(x_*(\bar{y}), \bar{y}). \tag{3.2}$$

Let the solution of (SES) with the initial value $\bar{y}(0) = y_0$ be denoted by $\bar{y}(\tau)$. Since $g < 0$ in the lower branch, we must have $\bar{y}(T) = y_\rho$ for some time T. Then, we have the following result due to Tihonov [21]. If $\delta_1, \delta_2 > 0$, then for $\delta_1 \le \tau \le T - \delta_2$

$$\begin{aligned} |x(\tau, \epsilon) - x_*(\bar{y}(\tau))| &= O(\epsilon) \\ |y(\tau, \epsilon) - \bar{y}(\tau)| &= O(\epsilon). \end{aligned} \tag{3.3}$$

uniformly with respect to τ.

The contraction rate at the lower branch is determined by the real parts of the eigenvalues of $A(y)$ and (SES). To estimate the contraction rate, let $\lambda_1(y)$, $\lambda_2(y)$ be the two eigenvalues of $A(y)$ and define

$$\alpha(y) = \max\{\text{Re } \lambda_1(y), \text{Re } \lambda_2(y)\}.$$

Since the bursting solutions fall from the periodic branch to the lower branch after passing near the homoclinic point, we compute the contraction rate of trajectories at the lower branch from $y = y_h$ to $y = y_\rho$ (except for small neighborhoods of both end points). Let τ_1 be the time when the solution of (SES) with $\bar{y}(0) = y_h$ attains $\bar{y}(\tau_1) = y_\rho$. Let the solution $(x(\tau, \epsilon), y(\tau, \epsilon))$ to (3.1) be with initial point $y_0 = y_h$ and $x_0 \in G(y_0)$.

In what follows $\delta_1, \delta_2, \cdots, \delta_6$ are small finite (independent of ϵ) constants. Let the interval $[y_\rho + \delta_1, y_h - \delta_1]$ be denoted by I. The distance between the lower branch $\mathcal{L}$ and the periodic bursting solution curve γ_ϵ is $O(\epsilon)$ uniformly for y in I. Trajectories near $\mathcal{L}$ are attracted to γ_ϵ at an exponential rate. To estimate the contraction rate of trajectories around γ_ϵ at the lower branch, let the curve γ_ϵ be expressed by $x = \phi(y, \epsilon)$ for some function ϕ in I. Using the coordinate change $u = x - \phi(y, \epsilon)$, system (3.1) is transformed into the form

$$\begin{aligned} \epsilon \dot{u} &= \tilde{f}(u, y, \epsilon) \\ \dot{y} &= g(u + \phi(y, \epsilon), y), \end{aligned} \tag{3.4}$$

where

$$\tilde{f}(u,y,\epsilon) = f(u+\phi(y,\epsilon),y) - \epsilon\frac{d\phi}{dy}(y,\epsilon)g(u+\phi(y,\epsilon),y).$$

Note $\tilde{f}(0,y,\epsilon) \equiv 0$ for all y in I. Let $A(y,\epsilon) = D_u\tilde{f}(0,y,\epsilon)$, then

$$\tilde{f}(u,y,\epsilon) = A(y,\epsilon)u + O(|u|^2).$$

For each y in I, there can be found a Liapunov function $W(u,y)$, a quadratic function of u, with the property that the derivative of W along the solution to the system $u' = A(y)u$ satisfies

$$W' = D_uW \cdot A(y)u \leq 2[\alpha(y) + \delta_2]W.$$

Furthermore, it can be achieved that

$$c_1\sqrt{W} \leq |u| \leq c_2\sqrt{W}.$$

in which the constants $c_1, c_2 > 0$ can be chosen independent of y in I. Then, the derivative of W along the solution to (3.4) is given by

$$\begin{aligned} \epsilon\dot{W} &= D_uW \cdot \tilde{f}(u,y,\epsilon) + \epsilon D_yWg(u+\phi(y,\epsilon),y) \\ &= D_uW \cdot A(y,\epsilon)u + O(|u|^3) + \epsilon O(|u|^2). \end{aligned}$$

From $\|A(y,\epsilon) - A(y)\| = O(\epsilon)$, it follows that for small $|u|$,

$$\epsilon\dot{W} \leq 2[\alpha(y) + \delta_3]W.$$

Since $|\bar{y}(\tau) - y(\tau,\epsilon)| = O(\epsilon)$ for $\tau \in [\delta_4, \tau_1 - \delta_5]$, we obtain

$$\frac{d}{d\tau}\log\sqrt{W(u(\tau,\epsilon),y(\tau,\epsilon))} \leq \frac{1}{\epsilon}[\alpha(\bar{y}(\tau)) + \delta_6].$$

It follows from integration that

$$\sqrt{W(u(\tau,\epsilon),y(\tau,\epsilon))} \leq \sqrt{W(u(\delta_4,\epsilon),y(\delta_4,\epsilon))}\exp\Big(\frac{1}{\epsilon}\int_{\delta_4}^{\tau}[\alpha(\bar{y}(s)) + \delta_6]ds\Big)$$

until $\tau \leq \tau_1 - \delta_5$. By letting

$$k_1 = \int_0^{\tau_1}\alpha(\bar{y}(\tau))d\tau < 0,$$

we conclude that for any small $\delta > 0$

$$|u(\tau_1,\epsilon)| \leq |u(0)|e^{\frac{1}{\epsilon}(k_1+\delta)}. \tag{3.5}$$

3.2. The expansion at the middle branch.

The typical bursting solutions are expected to jump from the periodic branch to the lower branch near the homoclinic orbit. But this is not always the case. The number of spikes per burst increases as the singular perturbation parameter ϵ decreases to 0. During the transition from n to $n+1$ spikes per burst, the bursting solution does not behave in this typical way. The dynamics during the transition can be quite complicated and we outline the analysis (see Lee & Terman [11], Terman [20] for detailed analysis).

In the middle branch, (FS) has a saddle point $(x^*(y), y)$ for each $y \in (y_\rho, y_\lambda)$. Each saddle point has one-dimensional stable and unstable manifolds. Let W_0^s and W_0^u be the union of all the stable and unstable manifolds to the fixed points along the middle branch when $\epsilon = 0$. These manifolds perturb to smooth, two-dimensional, invariant manifolds W_ϵ^s and W_ϵ^u for small $\epsilon > 0$. If the trajectory passes very close to the center-stable manifold W_ϵ^s, then it tracks close to the middle branch for some finite distance before jumping down to the lower branch. It is actually possible for the periodic bursting solutions to lie precisely on W_ϵ^s and track the middle branch up to the right knee. This is when the strongest expansion of trajectories occurs at the middle branch which may destroy the uniqueness and stability of periodic bursting solutions. Therefore we estimate the expansion rate when the periodic bursting solution curves γ_ϵ lie $O(\epsilon)$ close to the middle branch (except for the small neighborhoods of the homoclinic point p_h and the right knee).

The expansion rate at the middle branch is determined by the positive eigenvalue of the matrix $B(y) = D_x(x^*(y), y)$ along the middle branch and the following (SES)

$$\frac{d\bar{y}}{d\tau} = g(x^*(\bar{y}), \bar{y}). \tag{3.6}$$

We denote by $\beta(y)$ the positive eigenvalue of $B(y)$ for $y_h < y < y_\lambda$. Let τ_2 be the time when the solution $\bar{y}(\tau)$ of (3.6) with $\bar{y}(0) = y_h$ becomes $\bar{y}(\tau_2) = y_\lambda$. We express γ_ϵ by $x = \psi(y, \epsilon)$ for some function ψ at the middle branch and introduce the coordinate change $u = x - \psi(y, \epsilon)$. Letting

$$k_2 = \int_0^{\tau_2} \beta(\bar{y}(\tau))d\tau > 0,$$

and utilizing Liapunov function exactly as in the computation of contraction rate at the lower branch, we can show that for any small $\delta > 0$

$$|u(\tau_2, \epsilon)| \leq |u(0)| e^{\frac{1}{\epsilon}(k_2 + \delta)} \tag{3.7}$$

By the estimates (3.5) and (3.7), we now obtain our main result.

Theorem 3.1. *If $k_1 + k_2 < 0$, then the periodic bursting solutions are uniquely determined and asymptotically stable for all sufficiently small values of $\epsilon > 0$.*

APPENDIX

The system of differential equations used for our numerical computations are

$$\begin{aligned} C_m \frac{dV}{dt} &= -I_K - I_{Ca} - I_{K-Ca} \\ &= -\bar{g}_K n(V - V_K) - \bar{g}_{Ca} m_\infty(V) h(V)(V - V_{Ca}) - g_{K-Ca}(V - V_K) \\ \frac{dn}{dt} &= \lambda \left[\frac{n_\infty(V) - n}{\tau_n(V)} \right] \\ \frac{dCa_i}{dt} &= f(-\alpha I_{Ca} - k_{Ca} Ca_i) \end{aligned}$$

where

$$\begin{aligned} m_\infty(V) &= \frac{1}{1 + \exp[(V_m - V)/S_m]} \\ n_\infty(V) &= \frac{1}{1 + \exp[(V_n - V)/S_n]} \\ \tau_n(V) &= \frac{c}{\exp[(V - \bar{V})/a] + \exp[(\bar{V} - V)/b]} \\ h(V) &= \frac{1}{1 + \exp[(V - V_h)/S_h]} \\ g_{K-Ca}(Ca_i) &= \bar{g}_{K-Ca} \frac{Ca_i}{K_d + Ca_i} \\ \alpha &= \frac{1}{2 V_{\text{cell}} F} \end{aligned}$$

The equations were proposed for the electrical activities in the pancreatic β-cells (see Sherman, Rinzel & Keizer [17]). The parameters for Figure 1 are as follows:

$$\begin{array}{lll} C_m(\mu m) = 5,310, & V_{\text{cell}}(\mu m^3) = 1,150, & F(Coul/mMol) = 96,487, \\ \bar{g}_K(pS) = 2,500, & \bar{g}_{Ca}(pS) = 1,400, & \bar{g}_{K-Ca}(pS) = 30,000, \\ V_K(mV) = -75, & V_{Ca}(mV) = 110, & \bar{V}(mV) = -75, \\ V_m(mV) = 4, & S_m(mV) = 14, & V_n(mV) = -15, \end{array}$$

$$S_n(mV) = 5.6, \quad a(mV) = 65, \quad b(mV) = 20,$$
$$c(mV) = 60, \quad V_h(mV) = -10, \quad S_h(mV) = 10,$$
$$K_d(\mu M) = 100, \quad k_{Ca}(ms^{-1}) = 0.03, \quad \lambda = 1.7,$$
$$f = 0.002.$$

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