

THE GEOMETRY OF HOPF AND SADDLE-NODE BIFURCATIONS FOR WAVES OF HODGKIN-HUXLEY TYPE

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ABSTRACT. We study a class of ordinary differential equations extending the Hodgkin-Huxley equations for the nerve impulse under a traveling wave condition. We obtain a geometrical description of the subset in parameter space where the stability of equilibria, parametrized by μ , is lost. This may happen in two ways: first, the linearization around the equilibrium may have a pair of purely imaginary eigenvalues with multiplicity j . This happens for parameters in the set N_j , the possible sites for Hopf bifurcation, where a branch of periodic solutions is created. The other way to lose stability is that a real eigenvalue changes sign at the site for a possible saddle-node bifurcation. This happens at parameter values in the sets K_l where there is a zero eigenvalue of multiplicity l . We show that the sets N_j and K_l are singular ruled submanifolds of the parameter space $\mathbf{R} \times \mathbf{R}^{M+2}$ with rulings contained in the codimension 1 affine subspaces where μ is constant. The subset of regular points in N_j has codimension $2j$ in $\mathbf{R} \times \mathbf{R}^{M+2}$ and its rulings have codimension $2j + 1$. The subset of regular points in K_l has codimension l in $\mathbf{R} \times \mathbf{R}^{M+2}$ with rulings of codimension $l + 1$.

1. INTRODUCTION — EQUATIONS OF HODGKIN-HUXLEY TYPE

The Hodgkin-Huxley model describes the variation of the difference $x \in \mathbf{R}$ of the electrical potential across a nerve cell membrane, as a function of the distance $s \in \mathbf{R}$ along an axon and of the time $t \in \mathbf{R}$, for an electrical stimulus of intensity $I \in \mathbf{R}$. Changes in the voltage x are due to the active transport of ions across the membrane through N *ionic channels* whose dynamics is controlled by M independent *gates* that open with probabilities $y_i, i = 1, \dots, M$. For the original Hodgkin-Huxley equations there are $N = 2$ channels controlled by $M = 3$ gates.

Key words and phrases. Hodgkin-Huxley; nerve impulse; boundary of stability; bifurcation; traveling waves; singularities; ruled manifolds.

The general model is a reaction-diffusion equation:

$$(HH) \begin{cases} C_m \frac{\partial x}{\partial t} &= a \frac{\partial^2 x}{\partial s^2} - I - c_0(x - V_0) - \sum_{j=1}^N c_j u_j(y)(x - V_j) \\ \frac{\partial y_i}{\partial t} &= (\gamma_i(x) - y_i) \tau_i(x), \quad i = 1, \dots, M \end{cases}$$

where $y = (y_1, \dots, y_M)$ and the constant $C_m \geq 0$ is the membrane capacity, $a > 0$ is half the axon radius divided by the electrical resistance of the axoplasm. The voltage x is the only dependent variable that may be observed directly in experiments. In many experimental settings the observed response to a stimulus is a voltage pulse (or train of pulses) that seems to propagate along the axon with constant speed. Thus we impose a traveling wave condition on (HH) and study the boundary of stability of its equilibria under very general assumptions, suitable for applications to different types of excitable tissue.

1.1. Overview. In the remainder of this section we state explicitly our assumptions on (HH), rewrite it under a traveling wave condition (HHW) and describe its equilibria. The parameter dependence of the linearization around equilibria and of the coefficients of its characteristic polynomial are described in section 2 where we introduce new parameters to simplify the expressions. In section 3 we describe the exchange of stability set for a general monic polynomial of fixed degree in terms of its coefficients. The main result appears in section 4: a description of the geometry of the exchange of stability set for (HHW).

1.2. General properties.

- (1) The expressions $\gamma_i(x)$ and $\tau_i(x)$ are fitted to experimental data, with $\tau_i(x) \geq 0$ and $\gamma_i(x) \in [0, 1]$. It follows that if $y_i(t_0, s) \in [0, 1]$ then $y_i(t, s) \in [0, 1]$ for $t > t_0$,
- (2) In the original Hodgkin-Huxley model the terms $c_j u_j(y)(x - V_j)$ are called the *ionic channels*, where the functions $u_j(y)$ are monomials and $c_j > 0$, V_j are constant. In some cases the form $c_j(u_j(y) - f_j(x))(x - V_j)$ is used instead, where the $f_j(x)$ are fitted to experimental data. The term $c_0(x - V_0)$ is called the *leakage channel*.

1.3. ODES. There are two standard ways of obtaining ODES from (HH). The first consists in taking $a = 0$ and reduces (HH) to ODES in $\mathbf{R} \times [0, 1]^M$, called the *clamped* equations of Hodgkin-Huxley type. The bifurcation of its equilibria was studied in [3] and the boundary of stability in [2].

Another way of obtaining an ODE from (HH) is to consider a solution $x(t, s)$ that is a wave propagating with constant speed δ . We may write

$x(t, s) = \xi(s - \delta t)$. For $\hat{t} = s - \delta t$ and $\dot{\xi} = d\xi/d\hat{t}$ we have

$$\frac{\partial^2 x}{\partial s^2} = \ddot{\xi} \quad \frac{\partial x}{\partial t} = -\delta \dot{\xi}$$

and the first equation in (HH) takes the form:

$$-C_m \delta \dot{\xi} = a \ddot{\xi} - I - c_0(\xi - V_0) - \sum_{j=1}^N c_j u_j(y)(\xi - V_j)$$

rewriting x for ξ we get:

$$-a \ddot{x} = C_m \delta \dot{x} - I - c_0(x - V_0) - \sum_{j=1}^N c_j u_j(y)(x - V_j)$$

or

$$(HHW) \begin{cases} \dot{x} = -z \\ \dot{y}_i = (\gamma_i(x) - y_i) \tau_i(x), & i = 1, \dots, M \\ a \dot{z} = -C_m \delta z - I - c_0(x - V_0) - \sum_{j=1}^N c_j u_j(y)(x - V_j) \end{cases}$$

1.4. Equilibria. We are interested in studying (HHW) for different values of the stimulus intensity I , treating I as a special bifurcation parameter. Equilibria of (HHW) satisfy $\dot{x} = -z = 0$ and $y_i = \gamma_i$. Thus $a \dot{z} = 0$ if and only if

$$(1) \quad \eta(x, I) = -I - c_0(x - V_0) - \sum_{j=1}^N c_j u_j(\gamma(x))(x - V_j) = 0$$

where $\gamma(x) = (\gamma_1(x), \dots, \gamma_M(x))$.

Equilibria may thus be parametrized by x and we may use the value of x at equilibrium as a new bifurcation parameter μ . The intensity I may be computed from the expression $\eta(\mu, I) = 0$ depending on the $2N + 2$ parameters $c = (c_0, \dots, c_N)$, $V = (V_0, \dots, V_N)$.

1.5. Bifurcation. A geometrical description of the subset in parameter space where the number of multiple solutions of (1) changes locally is given in [3] in the context of the clamped equations. This description may be applied to equilibria of (HHW) without any changes. It follows that for an equation with N channels and for generic ion dynamics (i.e. for generic functions $\psi_j(\mu) = u_j(\gamma(\mu))$), equilibria of (HHW) have multiplicity at most $2N + 2$ and that there are always equilibria of multiplicity $2N + 1$. Moreover, if for a fixed value of parameters $\eta(\mu, I)$ has a zero of order $k \leq 2N + 2$ at $\mu = \mu_0$ then, for any $l \leq k$, there are parameter values arbitrarily close to the initial one where η has a zero of order l at a point μ near μ_0 . In particular, it follows that there are nearby parameter values where η has k simple zeros near μ_0 .

2. LINEARIZATION

We are concerned with the way an equilibrium may lose stability when we vary the parameters in (HHW). This happens at parameter values where the linearization around the equilibrium has an eigenvalue whose real part changes sign. We are interested in the geometry of these parameter sets.

We consider new parameters $R = (R_0, R_1, \dots, R_M, R_{M+1})$ given by

$$R_0 = \frac{1}{a} \left(-c_0 - \sum_{j=1}^N c_j u_j(\gamma(\mu)) \right) \quad R_{M+1} = \frac{C_m \delta}{a}$$

and

$$R_i = \frac{1}{a} \left(- \sum_{j=1}^N c_j \frac{\partial u_j}{\partial y_i}(\gamma(\mu)) (\mu - V_j) \right) \quad i = 1, \dots, M.$$

The linearization of (HHW) around the equilibrium $(\mu, \gamma(\mu))$ is

$$L = \begin{pmatrix} 0 & 0 & 0 & \dots & -1 \\ \gamma'_1 \tau_1 & -\tau_1 & 0 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \gamma'_M \tau_M & 0 & \dots & -\tau_M & 0 \\ R_0 & R_1 & \dots & R_M & -R_{M+1} \end{pmatrix},$$

with characteristic polynomial given by

$$P_L(X) = \det(L - XI) = (-1)^M X (R_{M+1} + X) \prod_{i=1}^M (\tau_i(\mu) + X) + r(X)$$

$$\text{where } r(X) = \det \begin{pmatrix} \gamma'_1 \tau_1 & -\tau_1 - X & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ \gamma'_M \tau_M & 0 & \dots & -\tau_M - X \\ R_0 & R_1 & \dots & R_M \end{pmatrix}.$$

Writing

$$P_L(X) = (-1)^M \left(X^{M+2} + \sum_{i=0}^{M+1} \alpha_i X^i \right)$$

and defining the symmetric functions $s_0(\tau) = 1$ and

$$s_n(\tau) = \sum_{1 \leq i_1 < \dots < i_n \leq M} \tau_{i_1} \cdots \tau_{i_n}, \quad n = 1, \dots, M,$$

the coefficients α_0 and α_1 are given by

$$\begin{aligned}\alpha_0 &= R_0 s_M(\tau) + \sum_{i=1}^M R_i \gamma'_i \tau_i \frac{\partial s_M(\tau)}{\partial \tau_i}, \\ \alpha_1 &= R_0 s_{M-1}(\tau) + \sum_{i=1}^M R_i \gamma'_i \tau_i \frac{\partial s_{M-1}(\tau)}{\partial \tau_i} + R_{M+1} s_M(\tau),\end{aligned}$$

for $1 < j < M$

$$\alpha_j = R_0 s_{M-j}(\tau) + \sum_{i=1}^M R_i \gamma'_i \tau_i \frac{\partial s_{M-j}(\tau)}{\partial \tau_i} + R_{M+1} s_{M-j+1}(\tau) + s_{M-j+2}(\tau),$$

and

$$\begin{aligned}\alpha_M &= R_0 s_0(\tau) + R_{M+1} s_1(\tau) + s_2(\tau), \\ \alpha_{M+1} &= R_{M+1} s_0(\tau) + s_1(\tau).\end{aligned}$$

The expression $\alpha = (\alpha_0, \alpha_1, \dots, \alpha_{M+1})$ can be written in the form $\alpha^T = D + E \cdot R^T$, where $D^T = (0, 0, s_M, s_{M-1}, \dots, s_1)$, and

$$E = \begin{pmatrix} s_M(\tau) & \gamma'_1 \tau_1 \frac{\partial s_M(\tau)}{\partial \tau_1} & \cdots & \gamma'_M \tau_M \frac{\partial s_M(\tau)}{\partial \tau_M} & 0 \\ s_{M-1}(\tau) & \gamma'_1 \tau_1 \frac{\partial s_{M-1}(\tau)}{\partial \tau_1} & \cdots & \gamma'_M \tau_M \frac{\partial s_{M-1}(\tau)}{\partial \tau_M} & s_M(\tau) \\ \vdots & \vdots & & \vdots & \vdots \\ s_1(\tau) & \gamma'_1 \tau_1 \frac{\partial s_1(\tau)}{\partial \tau_1} & \cdots & \gamma'_M \tau_M \frac{\partial s_1(\tau)}{\partial \tau_M} & s_2(\tau) \\ s_0(\tau) & 0 & \cdots & 0 & s_1(\tau) \\ 0 & 0 & \cdots & 0 & s_0(\tau) \end{pmatrix}.$$

Lemma 2.1. *The determinant of E satisfies*

$$\det(E) = \pm \left(\prod_{i=1}^M \gamma'_i \tau_i \right) \prod_{1 \leq i < j \leq M} (\tau_i - \tau_j).$$

Proof. Developing the determinant along the last row of E and again along the last row of the minor we obtain

$$\det(E) = \pm s_0(\tau)^2 \left(\prod_{j=1}^M \gamma'_j \tau_j \right) \det(E')$$

where

$$E' = \begin{pmatrix} \frac{\partial s_M(\tau)}{\partial \tau_1} & \cdots & \frac{\partial s_M(\tau)}{\partial \tau_M} \\ \frac{\partial s_{M-1}(\tau)}{\partial \tau_1} & \cdots & \frac{\partial s_{M-1}(\tau)}{\partial \tau_M} \\ \vdots & & \vdots \\ \frac{\partial s_1(\tau)}{\partial \tau_1} & \cdots & \frac{\partial s_1(\tau)}{\partial \tau_M} \end{pmatrix}.$$

Note that $\det E'$ is a homogeneous polynomial of degree $\frac{M(M-1)}{2}$ on the variables τ_j and that it is divisible by all the terms $(\tau_i - \tau_j)$, $i \neq j$. Therefore, by Lemma 1 of [2], $\det(E') = \pm \prod_{1 \leq i < j \leq M} (\tau_i - \tau_j)$, completing the proof. \square

3. THE EXCHANGE OF STABILITY SET

The loss of stability of an equilibrium point happens where the linearization around the equilibrium has an eigenvalue whose real part changes sign. For complex eigenvalues this may happen at parameter values where the linearization has a pair of purely imaginary eigenvalues. These points are the possible sites for Hopf bifurcations, where a branch of periodic solutions is created. The other possibility is that a real eigenvalue changes sign at the site for a possible saddle-node bifurcation.

We address the general problem of describing the set of coefficients where a real polynomial $P(X)$ has purely imaginary roots in a form suitable for application to our problem. When $P(X)$ is the characteristic polynomial of a Jacobian matrix these roots indicate a change in stability. Consider the polynomial $P_\alpha(X)$ with real coefficients

$$P_\alpha(X) = \alpha_0 + \alpha_1 X + \dots + \alpha_N X^N.$$

We want to study the *exchange of stability set* Σ_0 of parameters $\alpha \in \mathbf{R}^{N+1}$ such that $P_\alpha(i\sqrt{B}) = 0$ for some $B \geq 0$. There is a natural decomposition $\Sigma_0 = A_1 \cup S_1$ where the subset

$$A_1 = \left\{ \alpha \in \mathbf{R}^{N+1} : \exists B > 0 : P_\alpha(i\sqrt{B}) = 0 \right\},$$

corresponds to possible Hopf bifurcations and S_1 is the subspace $\alpha_0 = 0$, where saddle-node bifurcations occur. Denoting the integer part of x by $[x]$, we define the *singular set* A_j , $1 \leq j \leq [N/2]$ as the set of parameters α where $P_\alpha(X)$ has roots $X = i\sqrt{B}$, $B > 0$ of multiplicity at least j . Using the symbol $|$ for polynomial divisibility we have

$$A_j = \left\{ \alpha \in \mathbf{R}^{N+1} : \exists B > 0 : (X^2 + B)^j | P_\alpha(X) \right\}.$$

A *ruled submanifold of \mathbf{R}^l with codimension j rulings* is a submanifold of \mathbf{R}^l that is also a parametrized family of affine subspaces of codimension j . A *cone* $C \subset \mathbf{R}^l$ is a set invariant under scalar multiplication. The cone C is *regular* if $C - \{0\}$ is a smooth manifold, otherwise C is a *singular cone*. If every point of the cone belongs to a vector subspace of codimension j in \mathbf{R}^l , we say that the cone has *rulings of codimension j* .

Proposition 3.1. *The exchange of stability set Σ_0 is the union of the hyperplane $S_1 \subset \mathbf{R}^{N+1}$ and the singular cone A_1 of codimension 1 in \mathbf{R}^{N+1} that has rulings of codimension 2. Each A_j , $1 \leq j \leq [N/2]$ is a singular cone of codimension $2j - 1$ with rulings of codimension*

$2j+1$ and, for $j < [N/2]$ singularities lying in A_{j+1} . The cone $A_{[N/2]}$ is regular. The closure $\overline{A_j}$ of A_j meets the hyperplane S_1 at the subspace $S_{2j} = \{\alpha_0 = \dots = \alpha_{2j-1} = 0\}$ and is given by $\overline{A_j} = S_{2j} \cup A_j$.

Proof. The projection $\pi : \mathbf{R}^+ \times \mathbf{R}^{N+1} \longrightarrow \mathbf{R}^{N+1}$, given by $\pi(B, \alpha) = \alpha$, maps each set

$$\Lambda_j = \{(B, \alpha) \in \mathbf{R}^+ \times \mathbf{R}^{N+1} : (X^2 + B)^j | P_\alpha(X)\}$$

into $\pi(\Lambda_j) = A_j$. These sets may be rewritten in a more convenient way if we divide \mathbf{R}^{N+1} into even and odd coordinates with the maps $q_E : \mathbf{R}^{N+1} \longrightarrow \mathbf{R}^{n_E+1}$ and $q_O : \mathbf{R}^{N+1} \longrightarrow \mathbf{R}^{n_O+1}$, with $n_E = [\frac{N}{2}]$ and $n_O = [\frac{N-1}{2}]$, given by

$$\begin{aligned} \alpha_E &= q_E(\alpha) = (\alpha_0, -\alpha_2, \alpha_4, \dots, (-1)^{n_E} \alpha_{2n_E}) \\ \alpha_O &= q_O(\alpha) = (\alpha_1, -\alpha_3, \alpha_5, \dots, (-1)^{n_O} \alpha_{2n_O+1}), \end{aligned}$$

Then $P_\alpha(i\sqrt{B}) = P_{\alpha_E}(B) + i\sqrt{B}P_{\alpha_O}(B)$ and $P_\alpha(i\sqrt{B}) = 0$ with $B > 0$ if and only if $P_{\alpha_E}(B) = P_{\alpha_O}(B) = 0$: in order to decide the divisibility of $P_\alpha(X)$ by powers of $X^2 - B$ it is sufficient to study the common positive real roots B of $P_{\alpha_E}(X)$ and $P_{\alpha_O}(X)$.

We claim that

$$\Lambda_1 = \{(B, \alpha) \in \mathbf{R}^+ \times \mathbf{R}^{N+1} : r_1^{n_E}(B) \cdot \alpha_E = 0 = r_1^{n_O}(B) \cdot \alpha_O\}$$

and that

$$\Lambda_j = \{(B, \alpha) \in \Lambda_{j-1} : r_j^{n_E}(B) \cdot \alpha_E = 0 = r_j^{n_O}(B) \cdot \alpha_O\},$$

for $1 < j \leq [N/2]$, where

$$r_1^n(B) = (1, B, B^2, \dots, B^n)$$

and

$$r_{j+1}^n(B) = \frac{dr_j^n(B)}{dB}.$$

Let γ and n be either α_E and n_E or α_O and n_O , respectively. Using $P_\gamma(B) = r_1^n(B) \cdot \gamma$ we obtain the expression for Λ_1 . For Λ_j , $j > 1$, note that $P_\gamma(B)$ is divisible by $(X - B)^j$ if and only if $P_\gamma(B) \in \Lambda_{j-1}$ and $\frac{d^j P_\gamma}{dB^j} = 0$.

Let $f_j : \mathbf{R}^+ \times \mathbf{R}^{N+1} \longrightarrow \mathbf{R}^{2j}$, $1 \leq j \leq N/2$ be the maps

$$\begin{aligned} f_1(B, \alpha) &= (r_1^{n_E}(B) \cdot \alpha_E, r_1^{n_O}(B) \cdot \alpha_O) \\ f_j(B, \alpha) &= (f_{j-1}(B, \alpha), r_j^{n_E}(B) \cdot \alpha_E, r_j^{n_O}(B) \cdot \alpha_O) \end{aligned}$$

Since $\frac{\partial f_j}{\partial \alpha}$ has maximum rank $2j$, using the implicit function theorem it follows that the Λ_j are smooth codimension $2j$ submanifolds of \mathbf{R}^{N+2} .

From the expressions for Λ_j it follows that, for fixed B , the set $f_j^{-1}(0)$ is an affine subspace of $\mathbf{R}^+ \times \mathbf{R}^{N+1}$ of codimension $2j+1$, having the form $\{B\} \times V^\perp$, where V is a $2j$ -dimensional subspace of \mathbf{R}^{N+1} . Thus

the sets Λ_j are smooth ruled manifolds, with rulings of codimension $2j + 1$ contained in hyperplanes $B = \text{const}$.

The projection π is singular at the points in Λ_j where $\frac{\partial f_j}{\partial B} = 0$. Since

$$\begin{aligned} f_{j+1}(B, \alpha) &= (f_j(B, \alpha), r_{j+1}^{n_E}(B) \cdot \alpha_E, r_{j+1}^{n_O}(B) \cdot \alpha_O) \\ &= \left(f_1(B, \alpha), \frac{\partial f_j}{\partial B}(B, \alpha) \right) \end{aligned}$$

it follows that singular points of $\pi|_{\Lambda_j}$ lie on Λ_{j+1} for $1 \leq j < \lfloor \frac{N}{2} \rfloor$ and that π is regular on $\Lambda_{\lfloor N/2 \rfloor}$.

Each one of the rulings of Λ_j is projected into a vector subspace of codimension $2j$ orthogonal to the subspaces V discussed above. \square

For the study of the characteristic polynomial of a matrix we are interested in monic polynomials $P_\alpha(X)$ with $\alpha_N = 1$. Let $\widehat{\Sigma} \subset \mathbf{R}^N$ and H_j , $1 \leq j \leq \lfloor N/2 \rfloor$, be given by

$$\begin{aligned} \widehat{\Sigma} &= \{ \alpha \in \mathbf{R}^N : \exists B \geq 0 : P_{(\alpha, 1)}(i\sqrt{B}) = 0 \} \\ H_j &= \{ \alpha \in \mathbf{R}^N : \exists B > 0 : (X^2 + B)^j | P_{(\alpha, 1)}(X) \}. \end{aligned}$$

Then, $\widehat{\Sigma}$ (resp. H_j) is the transverse intersection of Σ_0 (resp. A_j) with the hyperplane $\alpha_N = 1$.

Corollary 3.1. *The sets $H_j \subset \mathbf{R}^N$, $1 \leq j < \lfloor N/2 \rfloor$ are singular ruled submanifolds of codimension $2j - 1$ with rulings of codimension $2j$. All the singularities of H_j lie in H_{j+1} and $\overline{H_j} = H_j \cup S_{2j}$. The set $\widehat{\Sigma}$ is a ruled manifold of codimension 1, with rulings of codimension 2. Its singularities lie in $H_2 \cup S_2$.*

4. THE EXCHANGE OF STABILITY SET IN (HHW)

The description of the set of parameters μ, R where the linearization of (HHW) has either pure imaginary or zero eigenvalues can now be completed. For $j = 1, \dots, \lfloor M/2 \rfloor + 1$, let N_j be given by

$$N_j = \{ (\mu, R) \in \mathbf{R} \times \mathbf{R}^{M+2} : \exists B > 0 : (X^2 + B)^j | P_L(X) \}$$

and let

$$K_j = \{ (\mu, R) \in \mathbf{R} \times \mathbf{R}^{M+2} : X^j | P_L(X) \}$$

then

$$\widetilde{\Sigma} = \left\{ (\mu, R) \in \mathbf{R} \times \mathbf{R}^{M+2} : \exists B \geq 0 : P_L(i\sqrt{B}) = 0 \right\} = N_1 \cup K_1.$$

Theorem 4.1. *Assume that $M \geq 3$. For a residual set of functions $\tau_i(\mu) > 0$ and for all functions $\gamma_i(\mu)$ such that $\gamma_i'(\mu) \neq 0$, where $i = 1, \dots, M$, the sets N_j , where $j = 1, \dots, \lfloor M/2 \rfloor + 1$, and K_l , where $l = 1, \dots, M+1$, are singular ruled submanifolds of $\mathbf{R} \times \mathbf{R}^{M+2}$ with rulings contained in the codimension 1 affine subspaces where μ is constant. Singular points of N_j (resp. K_l) occur both for $(\mu, R) \in N_{j+1}$ (resp.*

K_{l+1}) and for isolated values of $\mu = \mu_*$, where $\tau_i(\mu_*) = \tau_k(\mu_*)$ for some $i \neq k$. Moreover, $\overline{N_j} = N_j \cup K_{2j}$.

The subset of regular points in N_j has codimension $2j$ in $\mathbf{R} \times \mathbf{R}^{M+2}$ and its rulings have codimension $2j + 1$.

The subset of regular points in K_l has codimension l in $\mathbf{R} \times \mathbf{R}^{M+2}$ with rulings of codimension $l + 1$. The sets K_1 and K_2 are singular cones and K_{M+2} is the union of a set of isolated lines and a curve whose singular points lie on those lines.

Proof. From Lemma 2.1 it follows that the set

$$T = \{\tau \in \mathbf{R}^M : \det(E) \neq 0\}$$

is an algebraic variety of codimension one in \mathbf{R}^M . By a direct application of Thom's transversality theorem, the set of functions $\tau_i(\mu)$ whose 0-jet is transverse to this set is residual in $C^\infty(\mathbf{R}, \mathbf{R})$. Since T has codimension one, transversality to T means that $\det(E) = 0$ only at isolated values μ_* of μ . Therefore, for generic functions $\tau_i(\mu) > 0$ and for all functions $\gamma_i(\mu)$, $i = 1, \dots, M$, such that $\gamma_i'(\mu) \neq 0$, the map $R \mapsto E \cdot R^T$ is invertible, except at isolated values μ_* of μ such that $\tau_i(\mu_*) = \tau_k(\mu_*)$, $i \neq k$. Moreover, the subset of points in T where more than two τ_i have the same value has codimension one in T , and therefore transversality to T means the set of functions may be refined to ensure that $\tau(\mu)$ does not meet this subset. Thus, E has corank at most 1 for all values of μ . From now on, we suppose the $\tau_i(\mu)$ are in this residual set.

Let $F : \mathbf{R} \times \mathbf{R}^{M+2} \rightarrow \mathbf{R}^{M+2}$ be the map $F(\mu, R) = F_\mu(R)$ where $F_\mu : \mathbf{R}^{M+2} \rightarrow \mathbf{R}^{M+2}$ is the affine map $F_\mu(R) = E(\mu) \cdot R^T + D(\mu)$ that sends parameters R into the coefficients of the characteristic polynomial of the linearization L . Then $N_j = F^{-1}(H_j)$. For most values of μ the map F_μ is invertible, the rulings of N_j are the preimage by F_μ of the rulings of H_j and the result follows from Corollary 3.1.

In order to complete the description of the N_j it remains to see that at the isolated values μ_* of μ where the determinant of $E(\mu_*)$ is zero the preimage of the rulings still has the correct dimension. At these values of μ the image of F_{μ_*} is an affine hyperplane in \mathbf{R}^{M+2} . We claim that the residual set of functions $\tau(\mu)$ may be refined in such a way that the image of F_{μ_*} meets all the rulings of H_j in general position, and their inverse image by F are rulings of N_j of codimension $2j$, as for other values of μ .

To see this let $v(\mu_*) \neq 0$ be a vector in the kernel of $(E(\mu_*))^T$, so that the image of F_{μ_*} is orthogonal to $v(\mu_*)$ (Figure 1). From the proof of Proposition 3.1 we obtain $2j$ vectors $v_j^E(B)$ and $v_j^O(B) \in \mathbf{R}^{M+2}$ that generate the subspace orthogonal to the rulings of $A_j = \pi(\Lambda_j)$ given by $v_1^E(B) = (1, 0, -B, 0, B^2, 0, \dots)$, $v_1^O(B) = (0, 1, 0, -B, 0, B^2, 0, \dots)$ with $v_j^E(B)$ and $v_j^O(B)$ their j^{th} derivatives. The cone swept by these subspaces as B varies has codimension at least one in \mathbf{R}^{M+2} , for $M \geq$

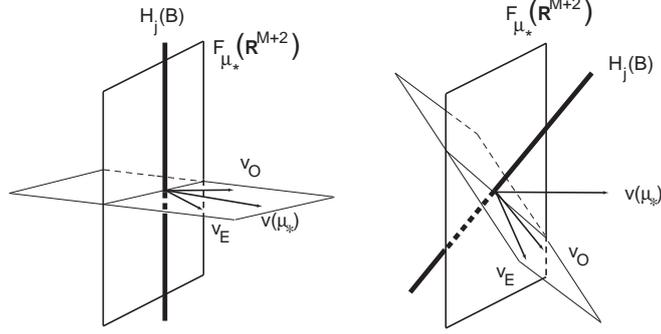


FIGURE 1. The situation on the left, where the rulings of A_j are contained in the image of F_{μ_*} , may be avoided by a small perturbation of the $\tau_i(\mu)$ (right) that tilts rulings slightly.

3. The residual set of functions $\tau(\mu)$ may be refined to satisfy the condition that $v(\mu_*)$ does not meet this cone. Therefore we may assume that the rulings of A_j are transverse to $v(\mu_*)^\perp$ and that the codimension of the intersection of $v(\mu_*)^\perp$ with the rulings of A_j is one plus the codimension of the rulings of A_j .

The claim will be proved if we show that the image of F_{μ_*} meets all the rulings of H_j in general position. Since $H_j = A_j \cap \{\alpha_{M+2} = 1\}$, it is sufficient to show that $\{\alpha_{M+2} = 1\}$ is transverse both to the rulings of A_j and to $v(\mu_*)^\perp$. The first statement is immediate from the preceding paragraph. The second would fail when $\{\alpha_{M+2} = 1\}$ is parallel to $v(\mu_*)^\perp$ and this may be avoided by refining the residual set again.

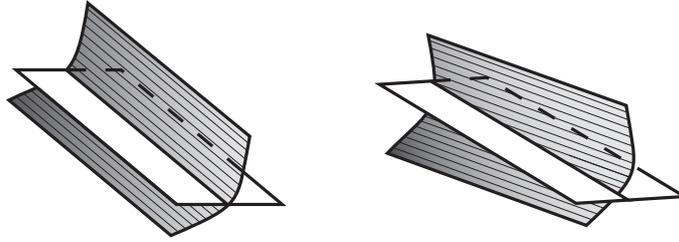


FIGURE 2. Left: rulings of H_j are not in general position with respect to the image of F_{μ_*} (white plane); on the right they are, after a small perturbation of the $\tau_i(\mu)$.

Intersecting the rulings of H_j with $v(\mu_*)^\perp$ increases the codimension by one, by transversality to $\{\alpha_{M+2} = 1\}$. Therefore the codimension of the preimage of $H_j \cap v(\mu_*)^\perp$ by F_{μ_*} is still $2j$.

Finally, we note that $K_l = F^{-1}(S_l)$. Refining the residual set again, the proofs for K_l are entirely analogous (and simpler) to those for H_j . The only point that remains is to check that both K_1 and K_2 are cones, which follows from the fact that the first two coordinates of $D(\mu)$ are zero, so each $F_\mu^{-1}(S_l)$ is a vector subspace for $l = 1, 2$.

The remaining assertions follow directly from Corollary 3.1. \square

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REFERENCES

- [1] A.L. Hodgkin and A.F. Huxley, 1952, *A quantitative description of membrane current and its application to conduction and excitation in nerve*, Journal of Physiology **117** pages 500–544
- [2] I.S. Labouriau and C.M.S.G. Rito, 2004, *Stability of equilibria in equations of Hodgkin-Huxley type*, in: T. Gaffney e M.A.S. Ruas (eds.), “Real and Complex Singularities”, Contemporary Mathematics, vol 354, American Mathematical Society pages 137–143
- [3] I.S. Labouriau and M.A.S. Ruas, 1996, *Singularities of equations of Hodgkin-Huxley type*, Dynamical Systems **11–2** pages 138–148

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