Reducing a Conductance-Based Neuron Model to Normal Form

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Objective

- Compute the normal form of a conductance-based neuron model at codimension-2 bifurcations using a method based on Lie transformations.
- Unfold the normal form in a neighborhood of the bifurcations.

A Conductance-Based Neuron Model

- We use the Morris-Lecar model, a planar system with three ionic currents:
  - a constant-conductance leak current I_ℓ,
  - an instaneous, persistent (non-inactivating) amplifying current I_m,
  - and a delayed-activating resonant (repolarizing) current I_n

  and the two dynamic variables:
  - v: membrane potential and
  - n: delayed-activating resonant current activation variable [1].

$$\frac{dv}{dt} = -[\overbrace{G_\ell(v-v_\ell)}^{\text{leak current}} + \overbrace{G_m m_\infty(v)(v-v_m)}^{\text{amplifying current}} + \overbrace{G_n n(t)(v-v_n)}^{\text{resonant current}} - I_{\text{app}}]/C$$
$$\frac{dn}{dt} = [n_\infty(v) - n]/\tau, \quad x_\infty(v) = [1+\exp(k_x(v-u_x))]^{-1} \tag{1}$$

- The model supports three types of excitability (Fig. 1).

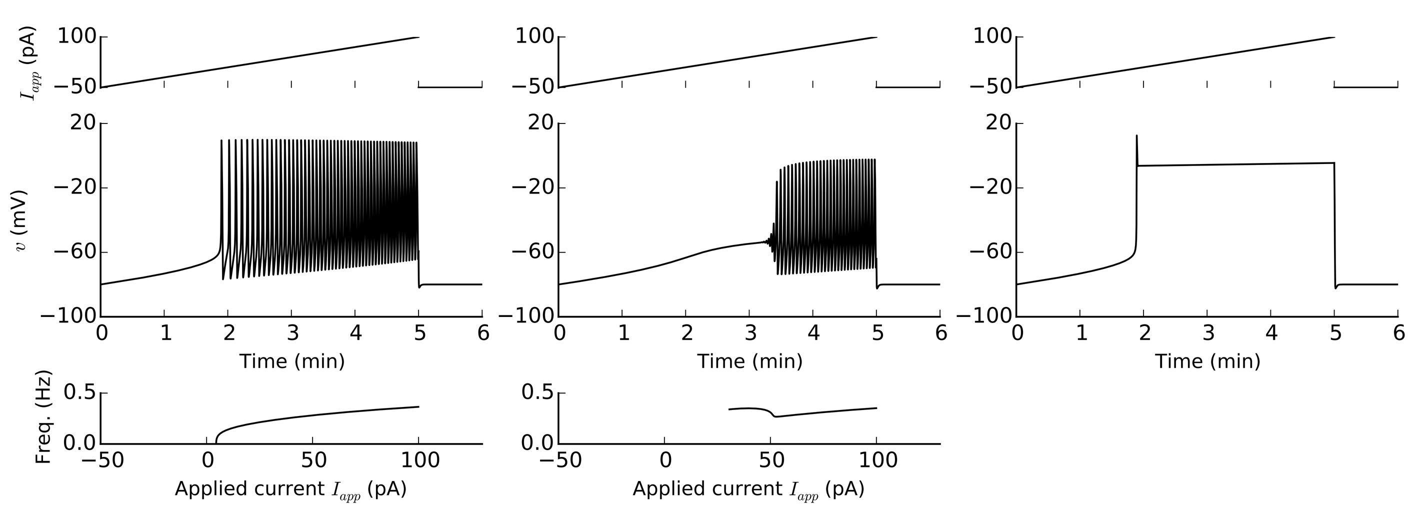

Figure 1: For different values of the resonant current half-activation potential u_n, the model (1) exhibits types 1 (left), 2 (center), and 3 (right) excitability in response to an applied current (I_{app}) ramp.

Lie Theory and Computing the Normal Form

- Let $\mathcal{V}_i^2$ be the vector space of homogenous i^{th} degree polynomial vector fields on $\mathbb{R}^2$ and let $\mathrm{L}_g = [\cdot, g]$ be the Lie bracket with a particular $g \in \mathcal{V}_i^2$, so $\mathrm{L}_g f = [f,g] = f'g - g'f$.
- If ψ is the flow generated by g, the substitution $(v,n) = \psi(\tilde{v},\tilde{n})$ transforms $(\dot{v},\dot{n})^T = f(v,n)$ locally to $(\dot{\tilde{v}},\dot{\tilde{n}})^T = e^{\mathrm{L}_g} f(\tilde{v},\tilde{n})$ [2].
- If $g = g_j$ has degree j, f is unaltered up to degree $j-1$:

$$\begin{aligned}(\dot{\tilde{v}},\dot{\tilde{n}})^T &= \left(I + \mathrm{L}_{g_j} + \mathrm{L}_{g_j}^2/2! + \cdots\right)(f_1+f_2+f_3+\cdots) \\ &= f_1 + \cdots + f_{j-1} + f_j + \mathrm{L}_{g_j} f_1 + \cdots\end{aligned} \tag{2}$$

- The difference of the former (f_j) and the modified ($h_j \overset{\text{def}}{=} f_j + \mathrm{L}_{g_j} f_1$) j^{th} degree terms satisfies the linear equation $\mathrm{L}_{f_1} g_j = f_j - h_j$.
- This equation can be solved and (2) can be calculated numerically by representing the f_i as $2(i+1)$-dim vectors of their coefficients and the restrictions $\mathrm{L}_{g_j}\big|_{\mathcal{V}_i^2}$ as $2(i+j)\times 2(i+1)$ matrices with respect to the bases

$$\left\{\begin{bmatrix}v^i\\0\end{bmatrix}, \begin{bmatrix}v^{i-1}n\\0\end{bmatrix}, \ldots, \begin{bmatrix}vn^{i-1}\\0\end{bmatrix}, \begin{bmatrix}n^i\\0\end{bmatrix}, \begin{bmatrix}0\\v^i\end{bmatrix}, \begin{bmatrix}0\\v^{i-1}n\end{bmatrix}, \ldots, \begin{bmatrix}0\\vn^{i-1}\end{bmatrix}, \begin{bmatrix}0\\n^i\end{bmatrix}\right\}.$$

Motivation

- Codimension-2 bifurcations, such as *Bogdanov-Takens* where loci of saddle homoclinic and Hopf bifurcations meet, and *generalized Hopf*, where Hopf bifurcations switch criticality, organize the dynamics of (1) (Fig. 2).

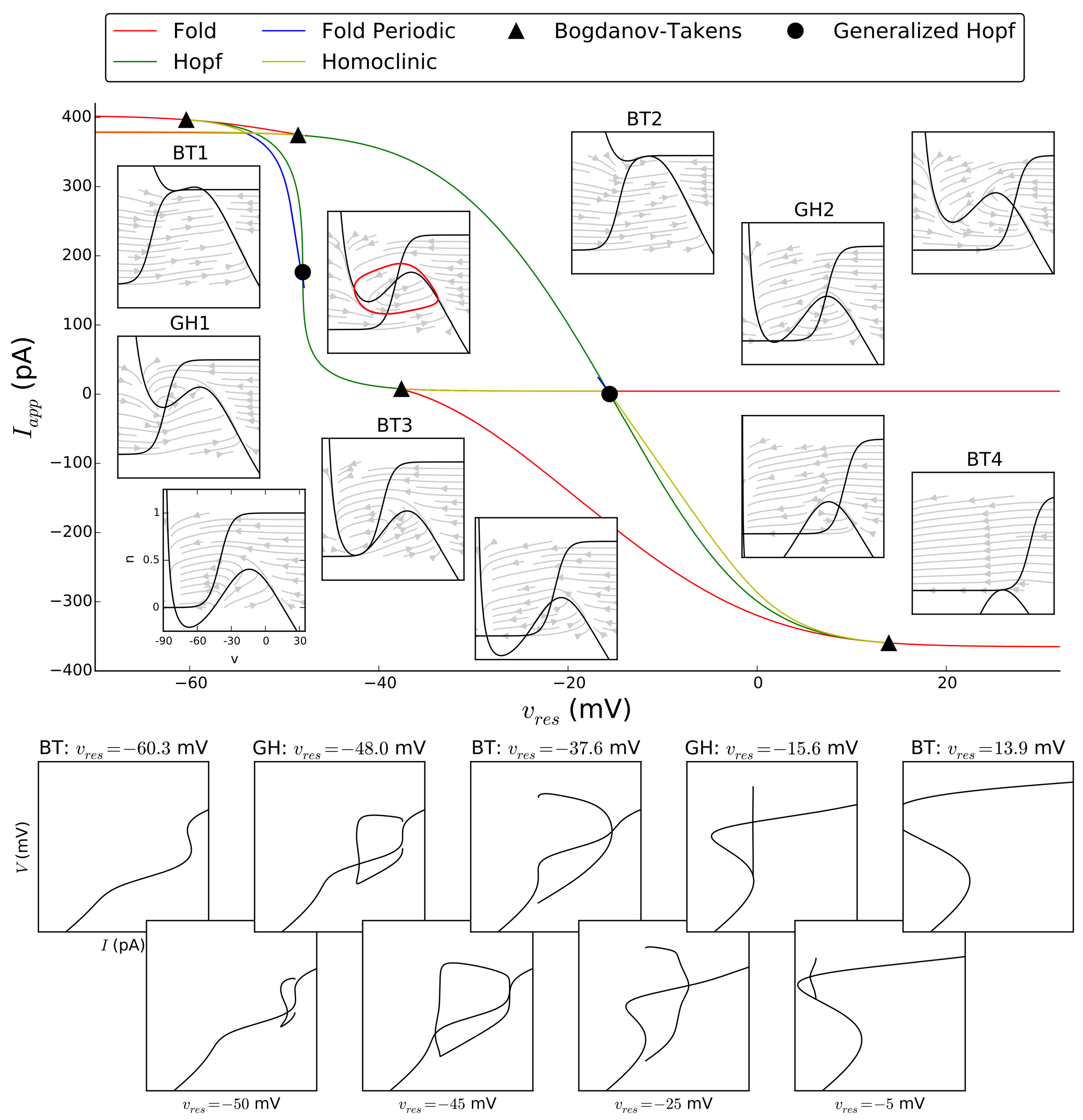

Figure 2: Top: A two-parameter unfolding of (1). Bottom: I-V curves and periodic branches for various values of the resonant current half-activation potential v_{res}.

An Algorithm for Computing the Normal Form

1. Expand (1) in a Taylor series about a bifurcation equilibrium point (v_0, n_0).
2. Perform a linear subsitution for (v,n) that transforms f_1' to a canonical form.
3. Choose a basis $\mathcal{N}$ for the complement of im L_{f_1}.
4. Repeat for $j = 2, 3, 4, \ldots$
   - Set h_j to the projection of f_j onto $\mathcal{N}$.
   - Solve $\mathrm{L}_{f_1} g_j = f_j - h_j$ for g_j.
   - Calculate (2).

The resulting system is of the form $(\dot{v},\dot{n})^T = f_1 + h_2 + h_3 + h_4 + \cdots$

The Form of the Normalized System

- Canonical forms for the Jacobian matrix (f_1'), associated linear operators (L_{f_1}), bases ($\mathcal{N}$) and normal form terms (h_i) for Bogdanov-Takens and Generalized Hopf bifurcations are:

	Bogdanov-Takens	Generalized Hopf
$f_1',\ L_{f_1}\|_{\mathcal{V}_i^2}$	$\begin{bmatrix}0&1\\0&0\end{bmatrix}, \begin{bmatrix}L&-I\\0&L\end{bmatrix}$	$\begin{bmatrix}0&-1\\1&0\end{bmatrix}, \begin{bmatrix}U-L&I\\-I&U-L\end{bmatrix}$
$\mathcal{N}$	$\left\{(0,v^i)^T, (0,v^{i-1}n)^T\right\}$	$\left\{(v^2+n^2)^{i-1}(v,n)^T, (v^2+n^2)^{i-1}(-n,v)^T\right\}$
h_i	$v^{i-1}\left(a_i\begin{bmatrix}0\\v\end{bmatrix} + b_i\begin{bmatrix}0\\n\end{bmatrix}\right)$	$(v^2+n^2)^{\frac{i-1}{2}}\left(c_i\begin{bmatrix}v\\n\end{bmatrix} + d_i\begin{bmatrix}-n\\v\end{bmatrix}\right)$ (i odd)

for $L_{jk} = k$ if $j = k+1$, $U_{jk} = j$ if $k = j+1$, and 0 otherwise, $1 \le j,k \le i+1$.

Normal Form Coefficients

- Analytic formulas expressed in the biophysical parameters of (1) for the first coefficients in the Bogdanov-Takens normal form are

$$a_2 = -\frac{1}{2\tau^3}\frac{n''(v_0)}{n'(v_0)} - \frac{G_m}{\tau^2 C}[m'(v_0) + m''(v_0)(v_0-v_1)/2] - \frac{G_n}{\tau C}n'(v_0)$$
$$b_2 = \left(\frac{1}{\tau^3} - \frac{1}{\tau^2}\right)\frac{n''(v_0)}{n'(v_0)} - \frac{G_m}{\tau C}[2m'(v_0) + m''(v_0)(v_0-v_1)] - \frac{G_n}{\tau C}n'(v_0)$$

- Numerical values for the first coefficients of the normal form at the bifurcations depicted in Fig. 2 are

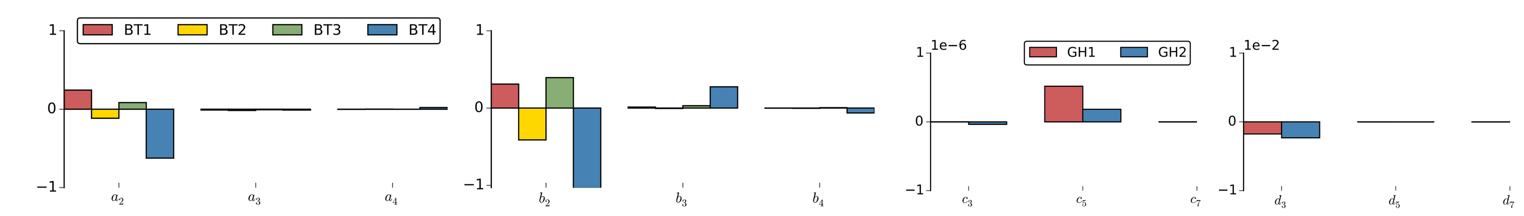

Figure 3: Normal form coefficients for the bifurcations depicted in Fig. 1.

Unfolding the Normal Forms

- The normal form dynamics in a neighborhood of the bifurcation can be studied by inserting parameters (μ_1, μ_2 and ν_1, ν_2 below) in low-degree terms that are otherwise zero:

$$\text{BT:}\quad \begin{bmatrix}\dot{v}\\\dot{n}\end{bmatrix} = \begin{bmatrix}0&1\\\mu_1&\mu_2\end{bmatrix}\begin{bmatrix}v\\n\end{bmatrix} + \sum_{i\ge 2} v^{i-1}\left(a_i\begin{bmatrix}0\\v\end{bmatrix} + b_i\begin{bmatrix}0\\n\end{bmatrix}\right)$$

$$\text{GH:}\quad \begin{bmatrix}\dot{v}\\\dot{n}\end{bmatrix} = \begin{bmatrix}\nu_1&-1\\1&\nu_1\end{bmatrix}\begin{bmatrix}v\\n\end{bmatrix} + \sum_{\substack{i\ge 3\\ i\text{ odd}}} (v^2+n^2)^{\frac{i-1}{2}}\left(c_i\begin{bmatrix}v\\n\end{bmatrix} + d_i\begin{bmatrix}-n\\v\end{bmatrix}\right), \nu_2 = c_3$$

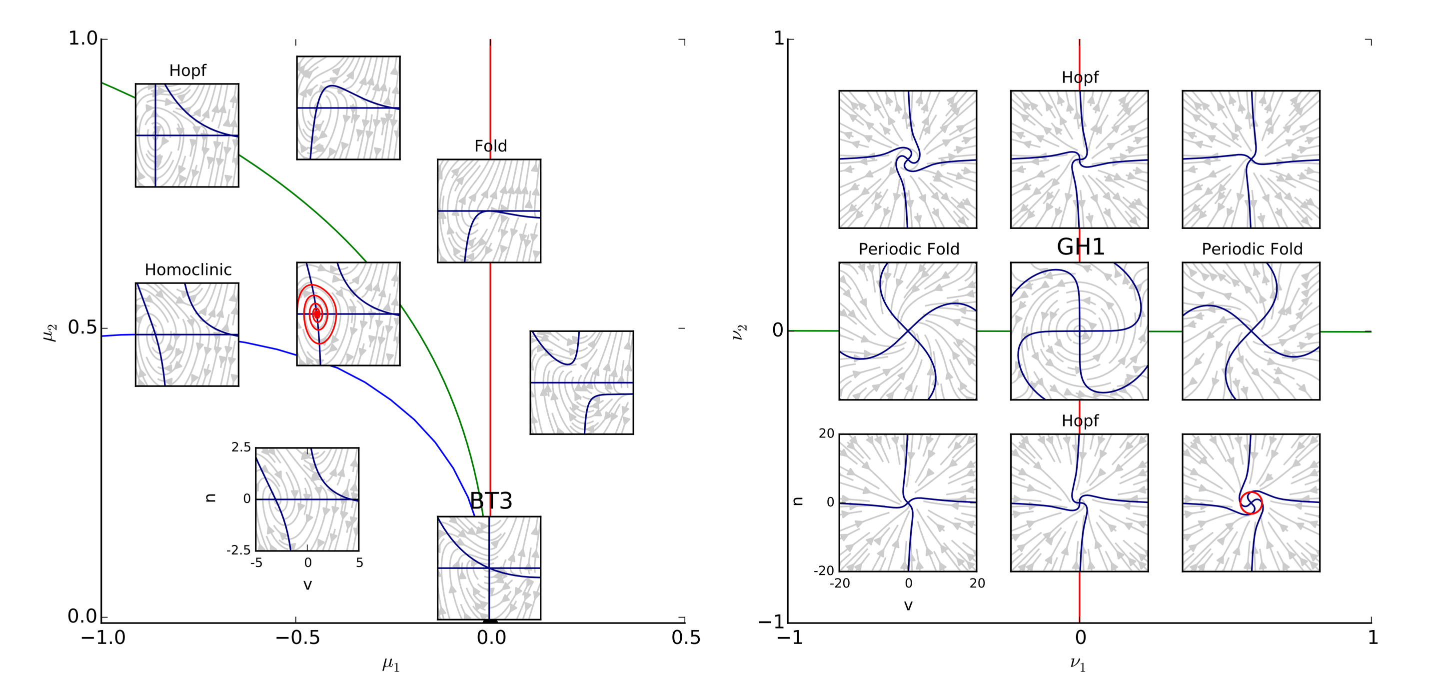

Figure 4: Two-parameter unfoldings of the normal form with bifurcations 'BT3' and 'GH2' from Fig. 2 as organizing centers.

Conclusion

- We simplified the Morris-Lecar model by reducing it to normal form at the codimension-2 bifurcations that organize its dynamics.
- Since the normal form exhibits the same dynamics in a neighborhood of the bifurcation at which the transformation was performed, it is a useful analytic tool for studying the original system.

References

[1] E. M. Izhikevich, *Dynamical systems in neuroscience*, MIT press, 2007.

[2] J. Murdock, *Normal forms and unfoldings for local dynamical systems*, Springer Science & Business Media, 2006.