Neural Oscillators: Weak Coupling

Part II:

Review of the previous talk, Bifurcations Analysis, Bifurcations and Adjoints, STRC

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- *Review of the previous talk*

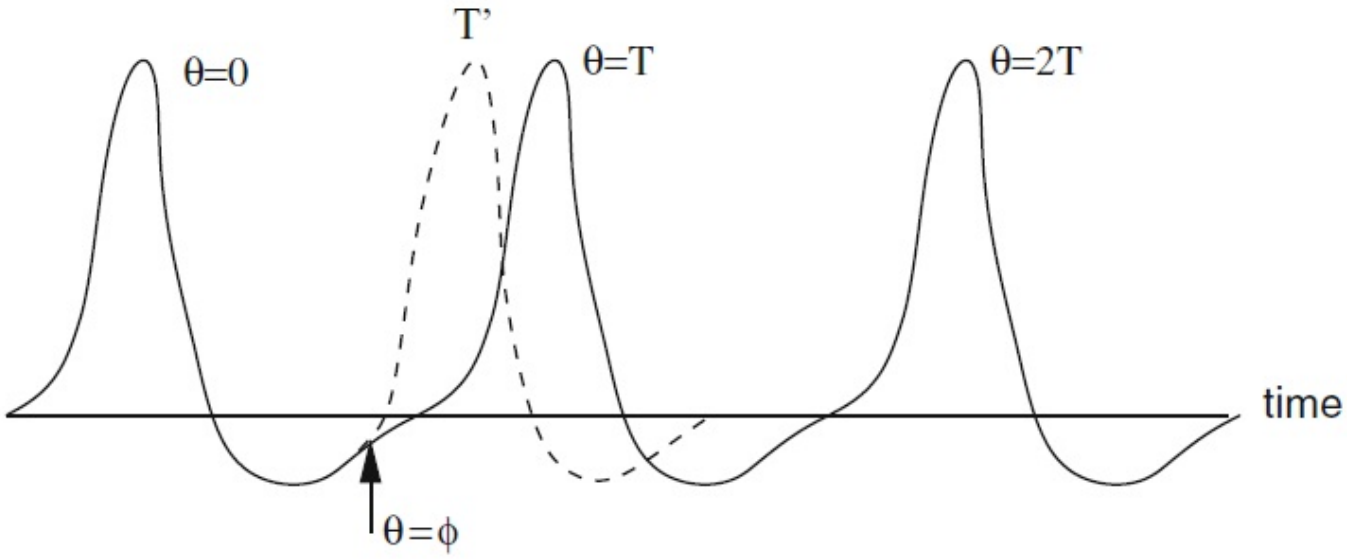
- **Single Neuron** to **Networks of Neurons**
- **Oscillators**:
  - The details of the action potentials (spikes) matter a great deal, and we need to understand how the spikes of one neuron affect the timing of the spikes of another neuron to which it is somehow (synaptically or ...) connected.
  - A neuron with slowly varying input current can be regarded as an oscillator.
  - Oscillatory networks arise in many areas of neuroscience, like motor patterns for repetitive activity such as locomotion, feeding, breathing, and mating.
  - **Central Pattern Generators (CPGs)** consist of networks of neurons which produce robust rhythmic output are easily modeled as networks of oscillators (neurons). (N. Kopell)

What is Isochron?

Consider the dynamical system derived by differential equation

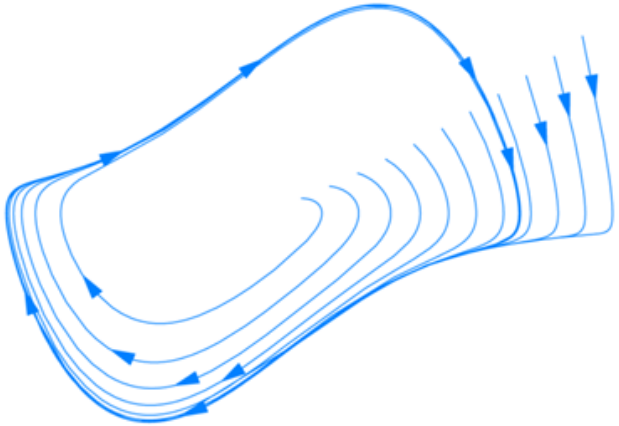
$$\frac{\mathrm{d}}{\mathrm{d}t}\mathrm{X} = \mathrm{F}(\mathrm{X}),$$

and let Γ be a T-periodic limit cycle. We can parameterize Γ by time and define a phase, $\theta \in [0, T)$ along the limit cycle.



What is Isochron?

So I can define $\Theta : \Gamma \to [0, T)$. Let Γ be a stable (attractive) limit cycle.



There exist a neighborhood of Γ, like U_Γ, such that for any $\mathrm{y} \in U_\Gamma$, we have

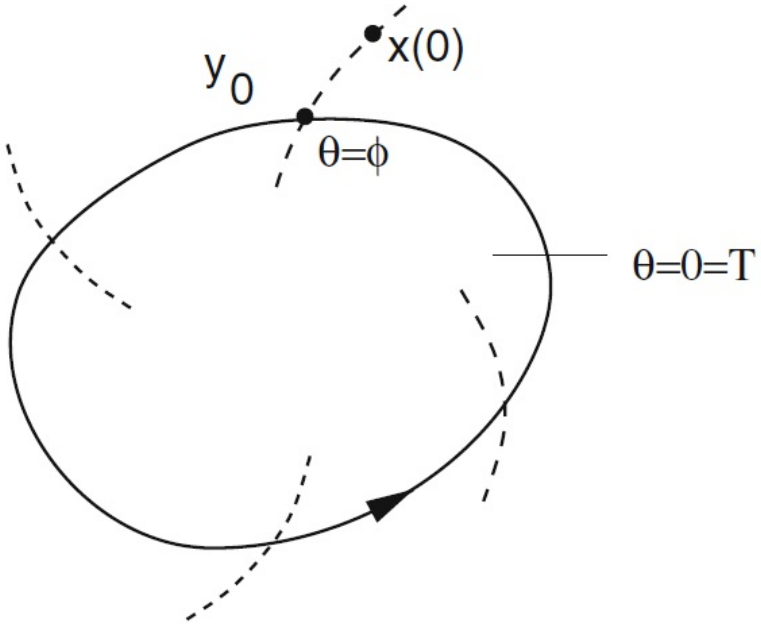
$$d(\Gamma, X(\mathrm{y}, t)) \to 0, \quad as\ t \to \infty.$$

What is Isochron?

So we can extend the function Θ over U_Γ, i.e. $\Theta : U_\Gamma \to [0, T)$, that is for any $y \in U_\Gamma$, we define $\Theta(\mathrm{y}) = \Theta(\mathrm{x})$, where $\mathrm{x} \in \Gamma$ such that

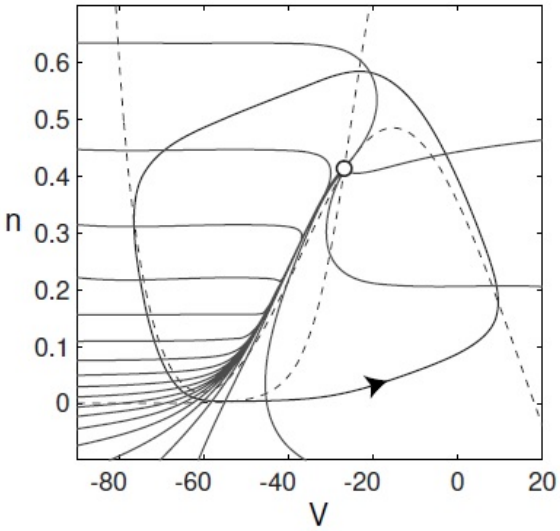
$$||X(\mathrm{x}, t) - X(\mathrm{y}, t)|| \to 0, \quad \textit{as } t \to \infty.$$

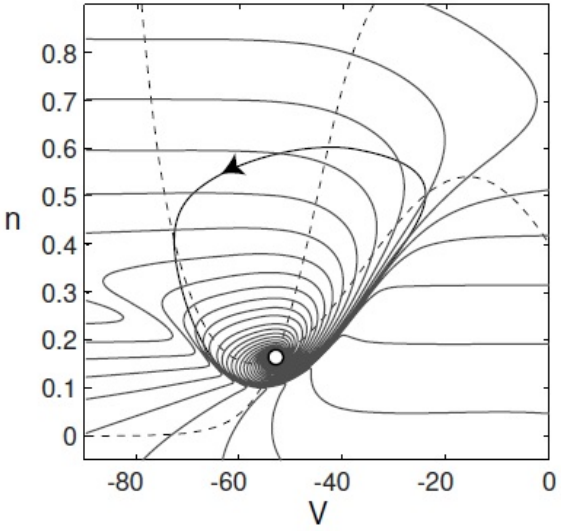
We call the level sets of Θ, set of points $\mathrm{y} \in U_\Gamma$ with the same asymptotic phase, the **isochron of the limit cycle** Γ.



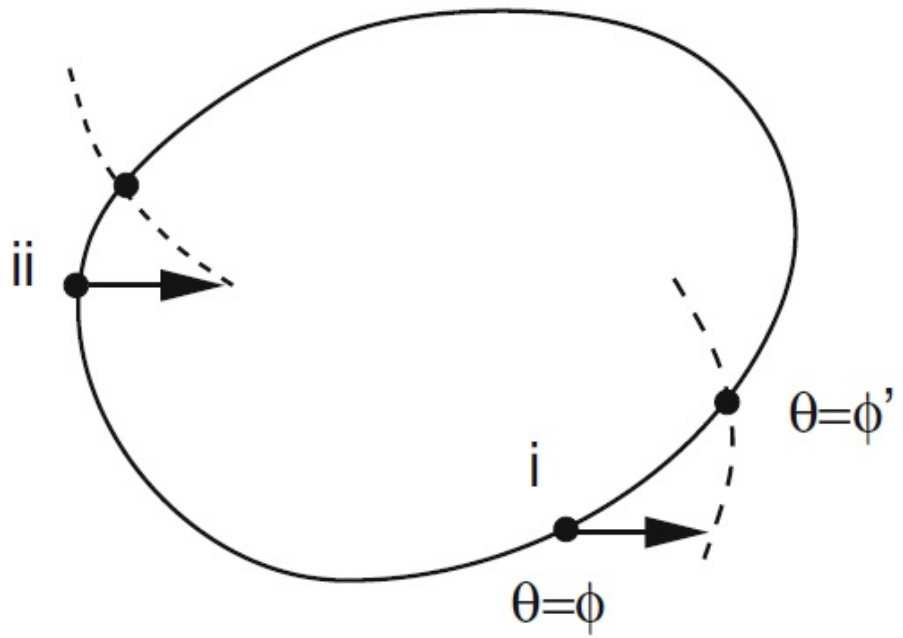
What is Isochron?

For any $\mathrm{x} \in \Gamma$, We denote the isochron through a point x, as $N(\mathrm{x})$. Isochrons are local invariant sections; that is, for a point $\mathrm{y} \in N(\mathrm{x})$, we have $\mathrm{X}(T;\mathrm{y}) \in N(\mathrm{x})$.
The map $\mathrm{y} \to \mathrm{X}(T;\mathrm{y})$ is a Poincare map for the limit cycle which takes time exactly T to return.
Guckenheimer has proved generally the existence of isochrons.(J. Guckenheimer. Isochrons and phaseless sets. J. Math. Biol., 1(3):259273, 1974/75.) 2



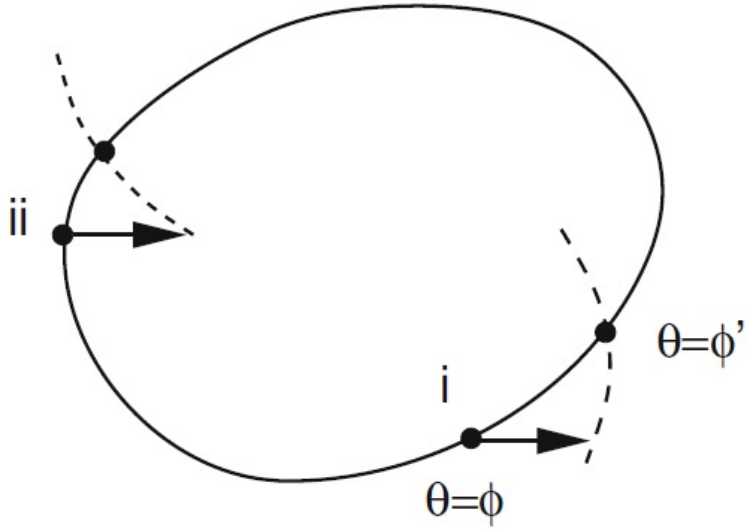


Phase resetting and transition curves



Rolling along the limit cycle, a brief stimulus is given, a perturbation to the vector field at phase ϕ. This perturbation puts us on the isochron for ϕ' so that the phase of the oscillator is reset to a different value which depends on its initial phase. For each phase ϕ at which the stimulus is applied, we get a new phase ϕ'.

Phase resetting and transition curves



Phase Transition Curve(PTC): The map $P : [0, T) \to [0, T)$, from old phase ϕ to new phase ϕ' is called the phase transition curve, i.e. $\phi' = P(\phi)$.

Phase Resetting Curve(PRC): Similarly, the map $\Delta : [0, T) \to [0, T)$ is defined as the difference between the new phase and the old phase:

$$\Delta(\phi) := \phi' - \phi = P(\phi) - \phi$$

Phase Resetting Curve and Phase function

Let $\mathrm{x} = \mathrm{X}_0(\phi) \in \Gamma$ be the point on the limit cycle, $\mathrm{X}_0(t)$, with phase (time) $\phi \in [0, T)$, i.e. $\Theta(\mathrm{x}) = \phi$. Consider an arbitrary perturbation, $\mathrm{y} \in \mathbb{R}^n$, of the vector field. The new phase is

$$\phi' = \Theta(\mathrm{x} + \mathrm{y}) = \phi + \nabla_{\mathrm{x}}\Theta(\mathrm{x}) \cdot \mathrm{y} + O(||y||^2).$$

Thus, for small perturbations

$$\Delta(\phi; \mathrm{y}) = \phi' - \phi = \nabla_{\mathrm{x}}\Theta(\mathrm{x}) \cdot \mathrm{y} + O(||y||^2) \approx \nabla_{\mathrm{x}}\Theta(\mathrm{x}) \cdot \mathrm{y}.$$

Define the vector function $\mathrm{Z} : [0, T) \to \mathbb{R}^n$ as

$$\mathrm{Z}(\phi) = \nabla_{\mathrm{x}}\Theta(\mathrm{X}_0(\phi))$$

Phase Resetting Curve and Phase function

As we have

$$\Delta(\phi; \mathrm{y}) \approx \nabla_{\mathrm{x}} \Theta(\mathrm{x}) \cdot \mathrm{y} = \mathrm{Z}(\phi) \cdot \mathrm{y},$$

where $\Theta(\phi) = \mathrm{x}$, the function Z provides a complete description of how infinitesimal perturbations of the limit cycle change its phase.

Calculation of Z: Let $\mathrm{X}_0(t)$ is a T-periodic limit cycle solution to

$$\frac{\mathrm{d}}{\mathrm{d}t}\mathrm{X} = \mathrm{F}(\mathrm{X})$$

and

$$A(t) := D_{\mathrm{X}}\mathrm{F}(\mathrm{X})|_{\mathrm{X}_0(t)}$$

be the $n \times n$ matrix resulting from linearizing around the limit cycle.

Phase Resetting Curve and Phase function

Then solutions to the linearized equation satisfy

$$(\mathbf{L}\mathrm{y})(t) := \frac{\mathrm{d}}{\mathrm{d}t}\mathrm{y}(t) - A(t)\mathrm{y}(t) = 0.$$

The adjoint of $\mathbf{L}$, satisfies $< \mathrm{u}, \mathbf{L}\mathrm{v} >=< \mathbf{L}^*\mathrm{u}, \mathrm{v} >$ and therefore

$$(\mathbf{L}^*\mathrm{y})(t) := -\frac{\mathrm{d}}{\mathrm{d}t}\mathrm{y}(t) - A^H(t)\mathrm{y}(t) = 0.$$

Regarding these all and some technical points, we have proved that $\mathrm{Z}(t)$ is the (unique) solution of

$$\begin{cases} \mathbf{L}^*\mathrm{Z}(t) = 0 \\ \mathrm{Z}(\phi) \cdot \frac{\mathrm{dX}_0(\phi)}{\mathrm{d}\phi} = 1 \end{cases}$$

Ring Models

Consider the differential equation

$$\mathrm{x}' = \mathrm{f}(\mathrm{x})$$

where $\mathrm{f}(\mathrm{x}) > 0$ and $\mathrm{x} \in \mathbb{S}^1$. Thus, $\mathrm{f}(\mathrm{x}+1) = \mathrm{f}(\mathrm{x})$. This equation has a T-periodic solution $\mathrm{x}_0(t)$ with period

$$T = \int_0^1 \frac{1}{\mathrm{f}(\mathrm{x})} \mathrm{d}x.$$

The adjoint is just

$$\mathrm{z}(t) = \frac{1}{\mathrm{f}(\mathrm{x}_0(t))},$$

since

$$\mathrm{z}(t)\frac{\mathrm{d}\mathrm{x}_0}{\mathrm{d}t} = 1.$$

Ring Models

Note that $\mathrm{z}(t)$ is always positive and one can only phase-advance the oscillator when the stimulus is positive. On the other hand, plotting $-\mathrm{z}(t)$ as would be the response to an inhibitory stimulus.

For example, consider the function $\mathrm{f}(\mathrm{x}) = 1 + a\cos(2\pi\mathrm{x})$, where $|a| < 1$. Then the period is

$$T = \frac{1}{\sqrt{1-a^2}}$$

and a bit of algebra shows that the adjoint is just

$$\mathrm{z}(t) = \frac{1 - a\cos(2\pi t/T)}{1-a^2}$$

Quadratic Integrate-and-FireModel

The quadratic integrate-and-fire model with infinite reset,

$$V' = V^2 + I,$$

is a singular example of a scalar ring model. The solution to this is

$$V = -\sqrt{I}\cot(\sqrt{I}t).$$

So the adjoint is

$$z(t) = \frac{1}{V'(t)} = \frac{\sin^2(\sqrt{I}t)}{I} = \frac{1-\cos(2\sqrt{I}t)}{I}.$$

$\lambda - \omega$ Systems and Hopf bifurcation

Kopell and Howard introduced a class of nonlinear oscillators described by

$$\begin{cases} u' &= \lambda(\sqrt{u^2+v^2})u - \omega(\sqrt{u^2+v^2})v \\ v' &= \lambda(\sqrt{u^2+v^2})v + \omega(\sqrt{u^2+v^2})u \end{cases}$$

Suppose $\lambda(1) = 0, \omega(1) = 1$ and $\lambda'(1) < 0$. Then there is a stable limit cycle solution

$$(u, v) = (\cos t, \sin t)$$

and the adjoint for this system is

$$(u^*, v^*) = (a \cos t - \sin t, a \sin t + \cos t)$$

where $a = \omega'(1)/\lambda'(1)$.

- *Review of the previous talk*

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- *Bifurcation Analysis*

Bifurcation theory is concerned with how solutions change as parameters in a model are varied.

Using bifurcation theory, we can **classify the types of transitions** that take place as we change parameters.

In particular, we can **predict** for which value of parameters the fixed point loses its stability and oscillations emerge.

There are, in fact, **several different types of bifurcations**; that is, there are different mechanisms by which stable oscillations emerge.

The most important types of bifurcations can be realized by the **MorrisLecar model**.

Morris-Lecar model

Morris-Lecar model:

$$\begin{aligned} C\frac{dV}{dt} &= I - g_{\mathrm{L}}(V - V_{\mathrm{L}}) - g_{\mathrm{Ca}} M_{\mathrm{ss}}(V - V_{\mathrm{Ca}}) - g_{\mathrm{K}} N(V - V_{\mathrm{K}}) \\ \frac{dN}{dt} &= \frac{N - N_{\mathrm{ss}}}{\tau_N} \end{aligned}$$

where

$$\begin{aligned} M_{\mathrm{ss}} &= \frac{1}{2} \cdot (1 + \tanh[\frac{V - V_1}{V_2}]) \\ N_{\mathrm{ss}} &= \frac{1}{2} \cdot (1 + \tanh[\frac{V - V_3}{V_4}]) \\ \tau_N &= 1/(\phi \cosh[\frac{V - V_3}{2V_4}]) \end{aligned}$$

and

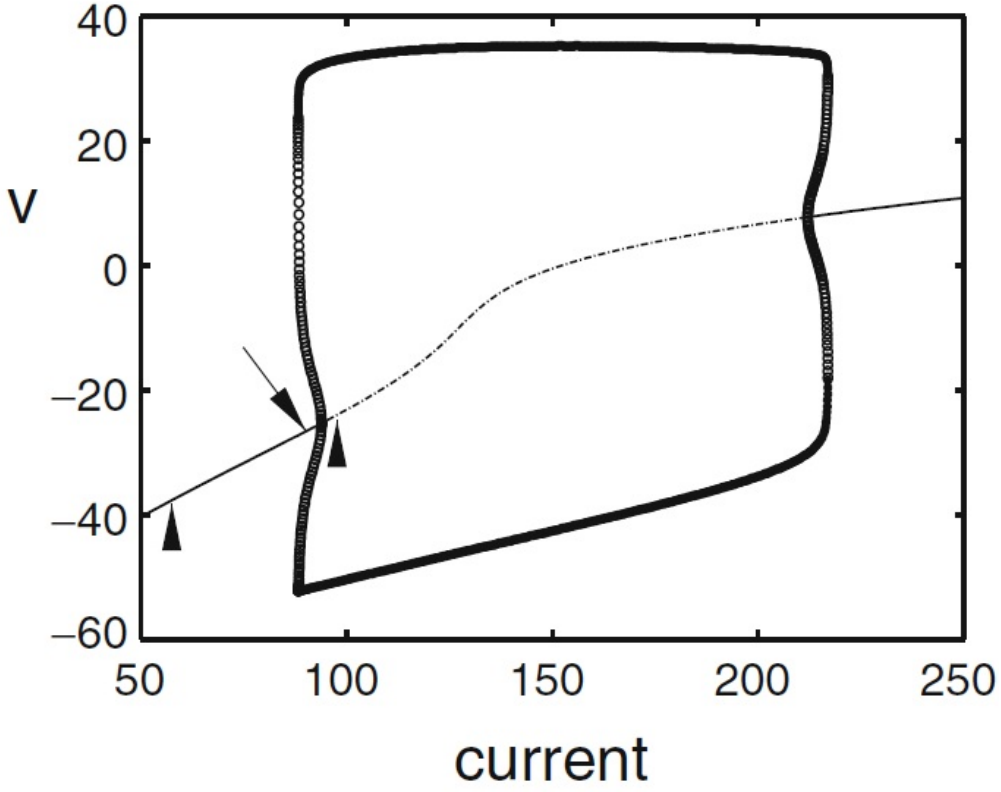
V : membrane potential,

N : recovery variable: the probability that the K^+ channel is conducting.

The Hopf Bifurcation

For each value of I, there is a **unique fixed point**, $(V_R(I), n_R(I))$. Here, the fixed point is stable for $I < 94 = I_1$ and $I > 212 = I_2$; otherwise, it is unstable.

A **Hopf bifurcation** occurs at $I = I_1$ and $I = I_2$.



What do we mean by this?

Recall that a fixed point is **stable** if **all** of the *eigenvalues of the linearization* have a **negative real part**; the fixed point is **unstable** if **at least one** of the eigenvalues has a **positive real part**.

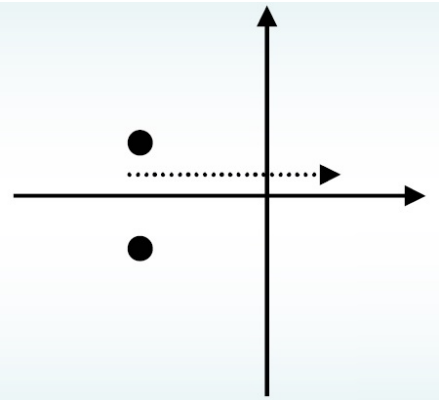
So, the fixed point may lose stability, as a parameter is varied, i.e. when **at least one eigenvalue crosses the imaginary axis**.

If the eigenvalues are all real numbers, then they can cross the imaginary axis only at the origin in the complex plane.

However, if an eigenvalue is complex, then it (and its complex conjugate) will cross the imaginary axis at some point that is not at the origin.

This latter case corresponds to the **Hopf bifurcation** and it is precisely what happens here.

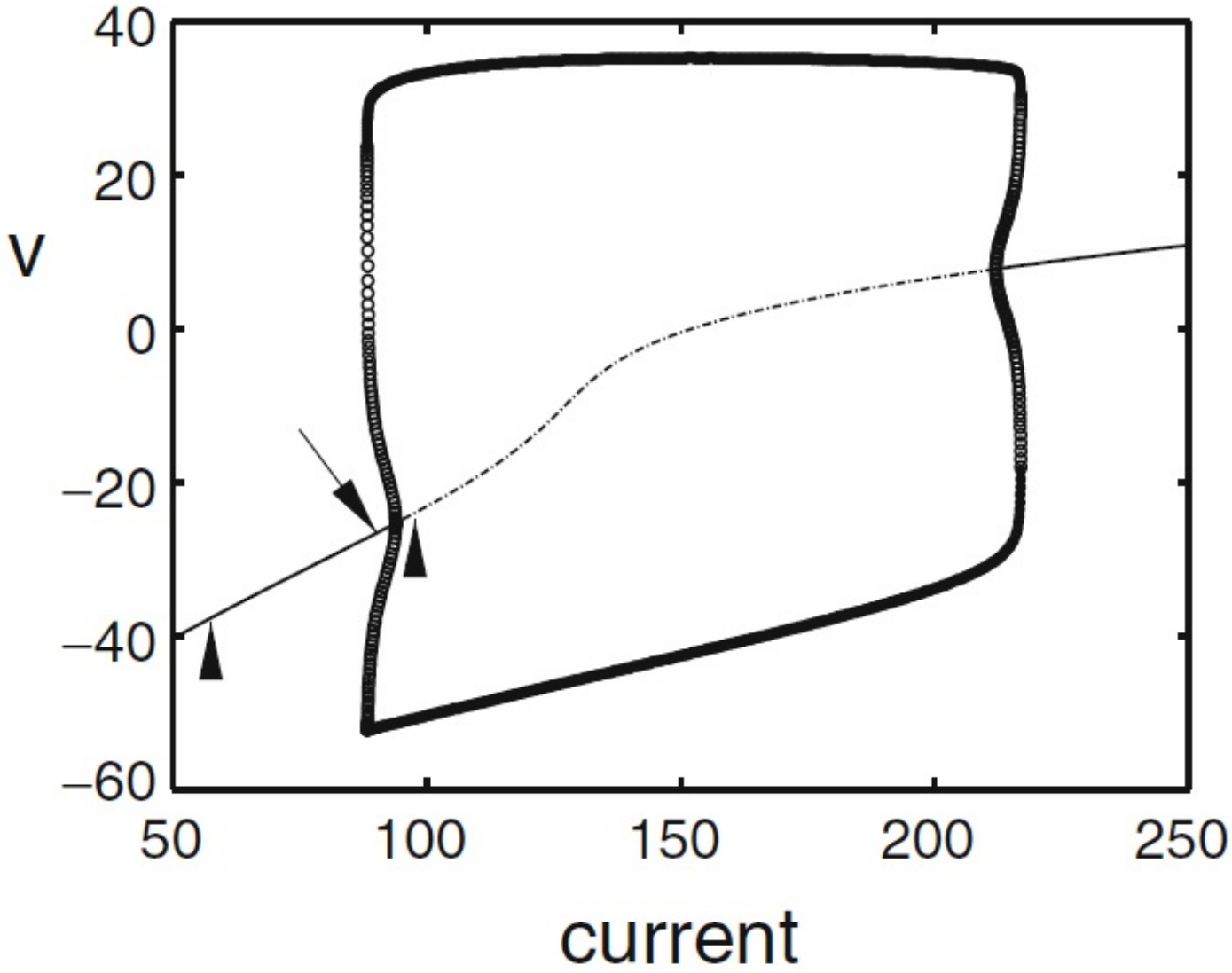
In this example, $(I_1, V_R(I_1), n_R(I_1))$ and $(I_2, V_R(I_2), n_R(I_2))$ are called **bifurcation points**. Sometimes, I_1 and I_2 are also referred to as bifurcation points.



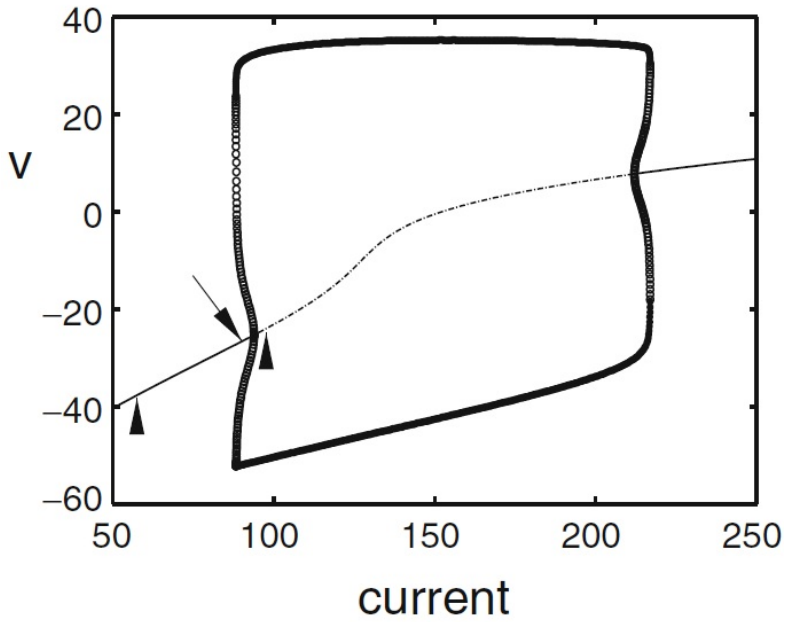
Theorem

If certain technical assumptions are satisfied, then there must exist values of the parameter I near I_1 and I_2 such that there exist periodic solutions that lie near the fixed points $(V_R(I), n_R(I))$.

This is an application of the famous **Hopf Bifurcation Theorem**.



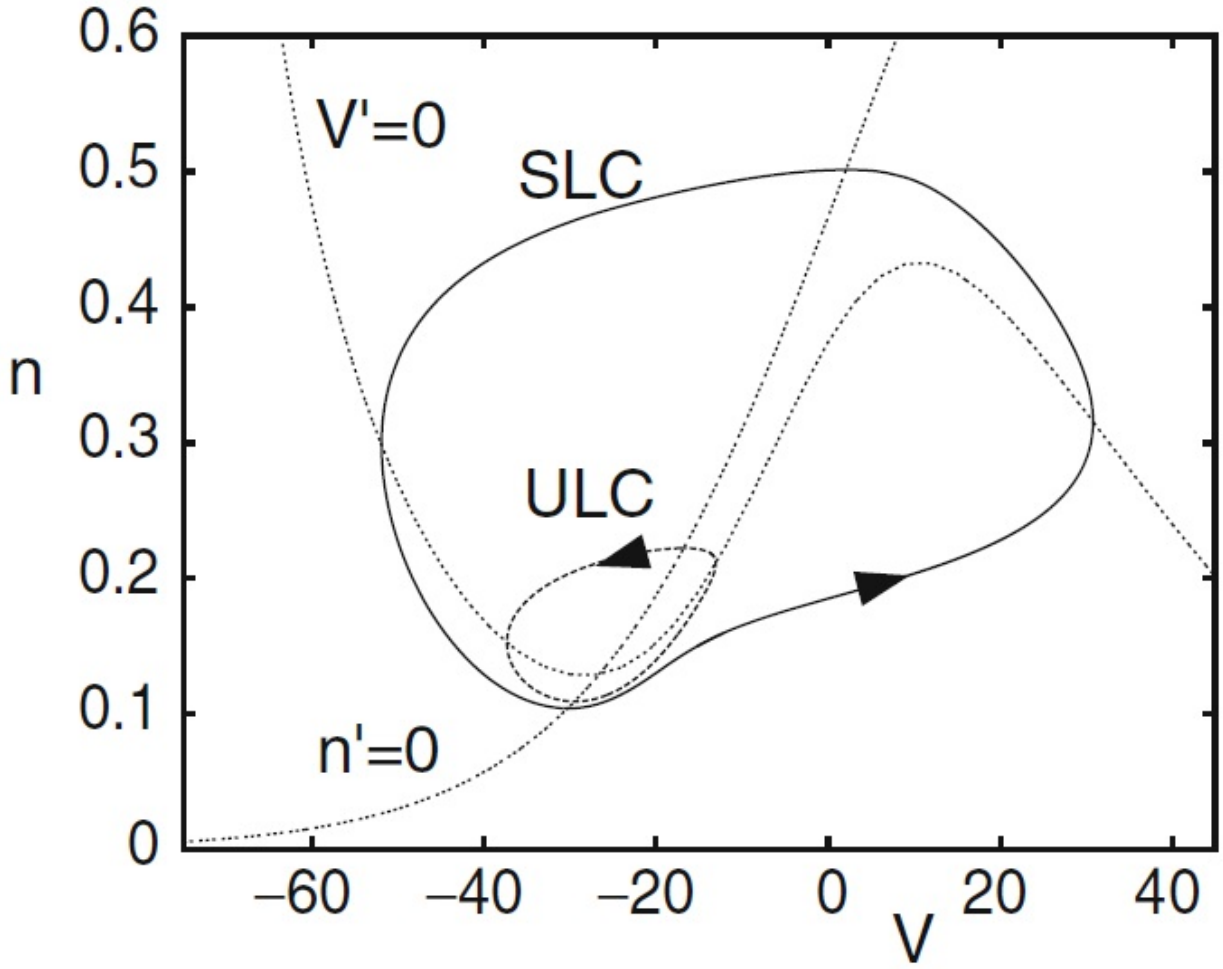
This **Bifurcation Diagram** is generated using the numerical software program **XPPAUT**.



These are both examples of **Subcritical Hopf Bifurcations**.

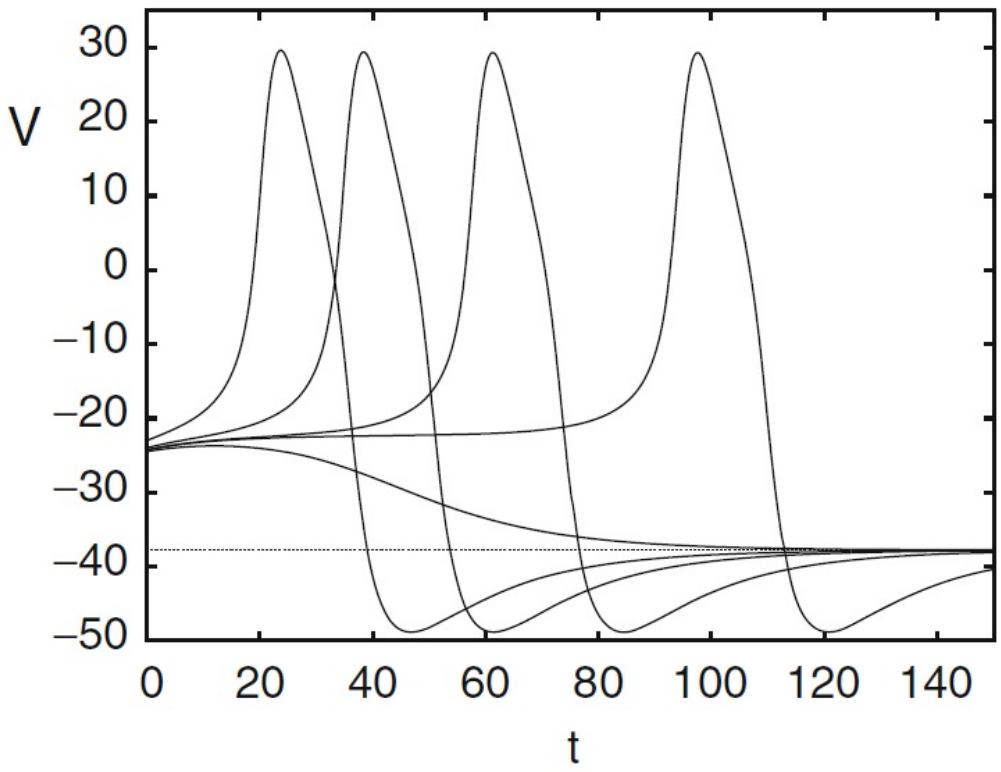
At a **Supercritical Hopf Bifurcation**, the small-amplitude periodic solutions near the Hopf bifurcation point are stable and lie on the side opposite the branch of stable fixed points.

If $88,3 < I < I_1$ or $I_2 < I < 217$, then the MorrisLecar model is **bistable**. For these values of I, there *exist both a stable fixed point and a stable periodic solution*.

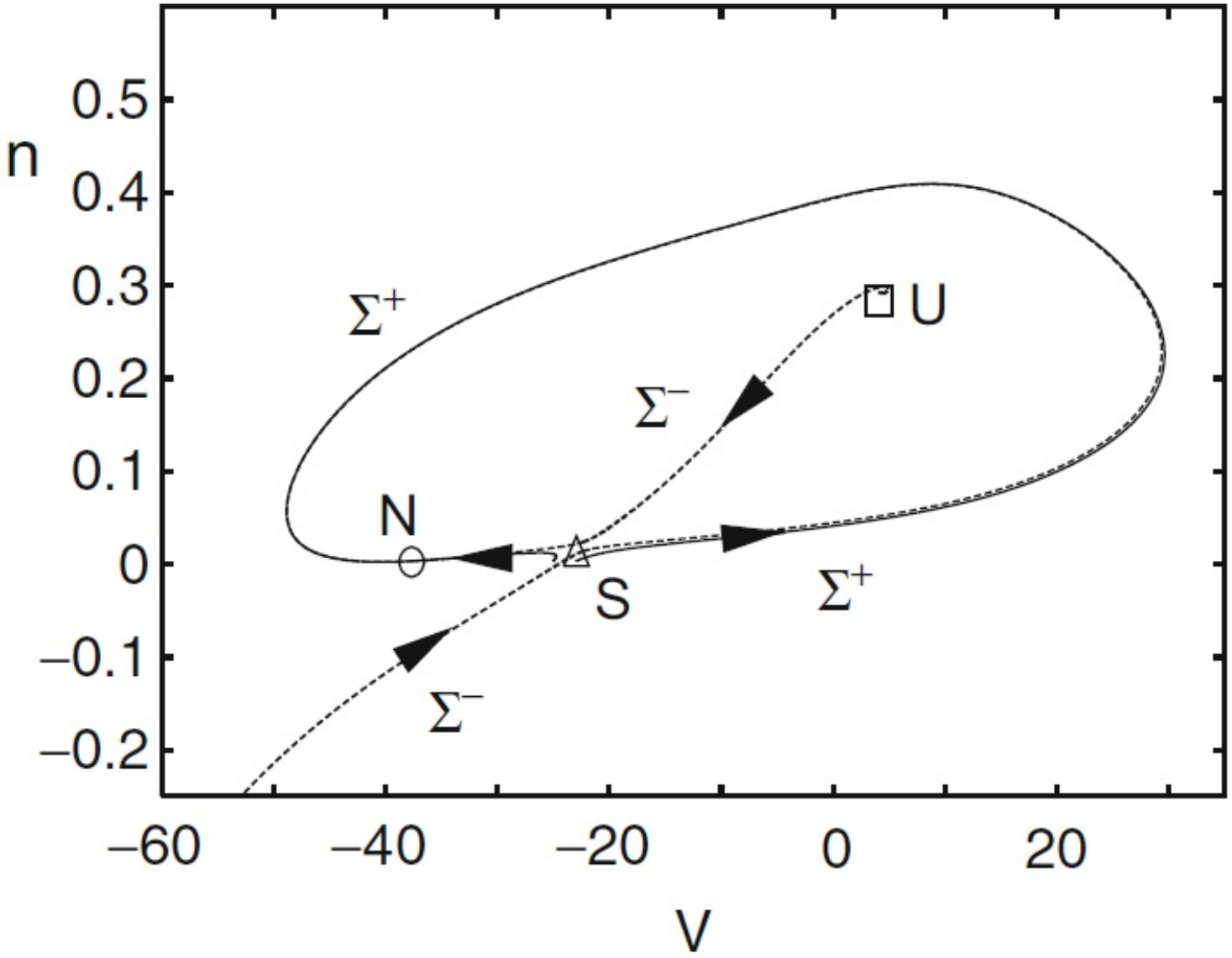


Small perturbations of initial conditions from the resting state will **decay back** to rest; however, **large perturbation** from rest will generate solutions that approach the **stable limit cycles**.

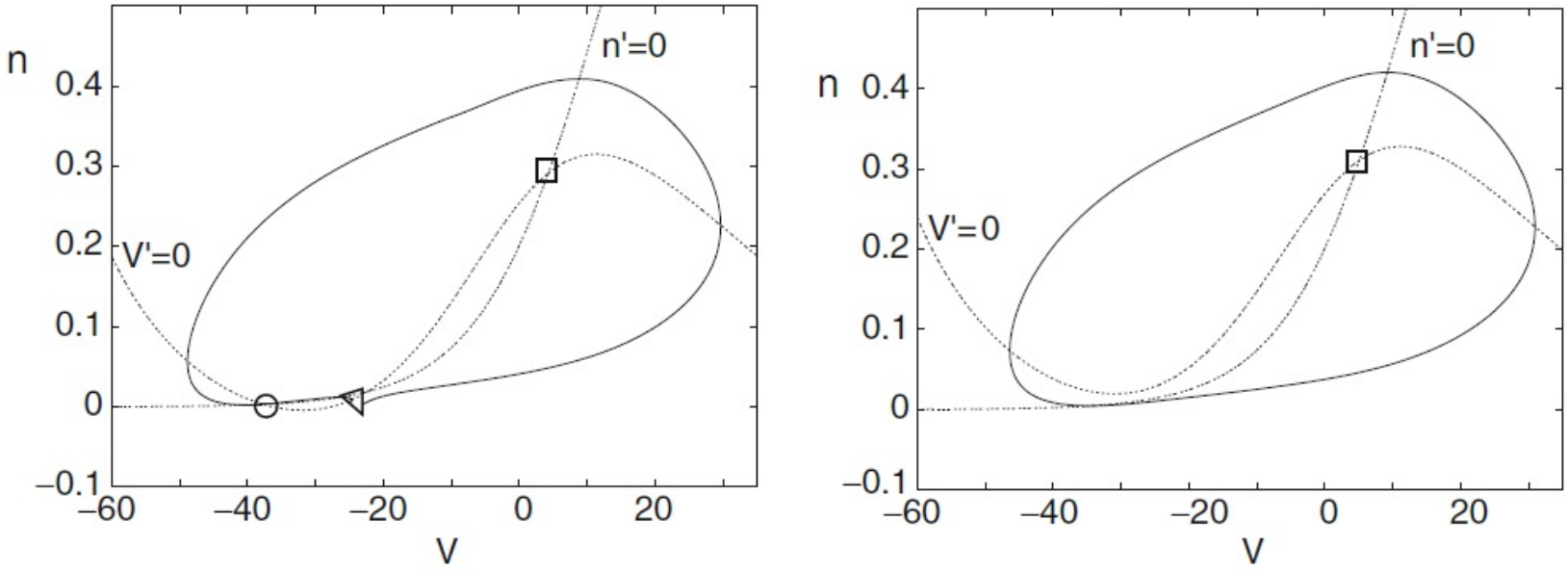
Saddle-Node on a Limit Cycle



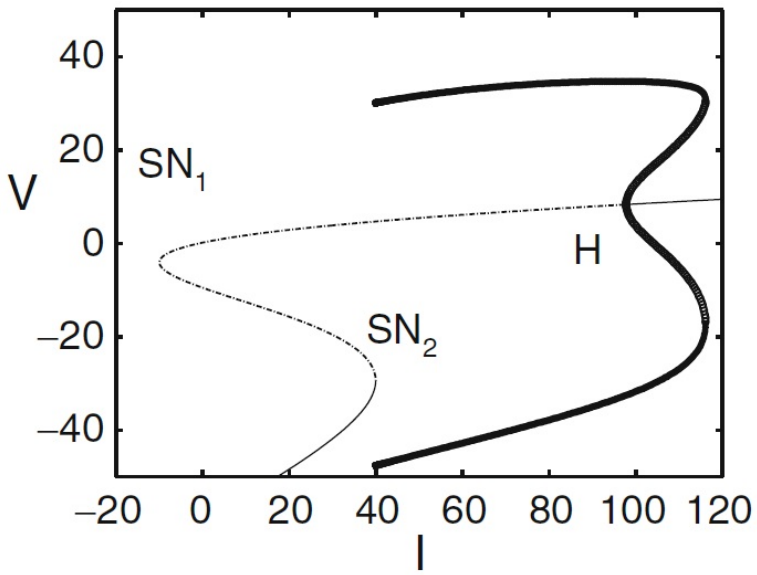
The action potentials appear to occur with **arbitrary delay** after the end of the stimulus, however, the **shape** of the action potentials is much less variable.



The two branches of the unstable manifold, Σ^+, form a loop with the stable node N and the saddle point S.

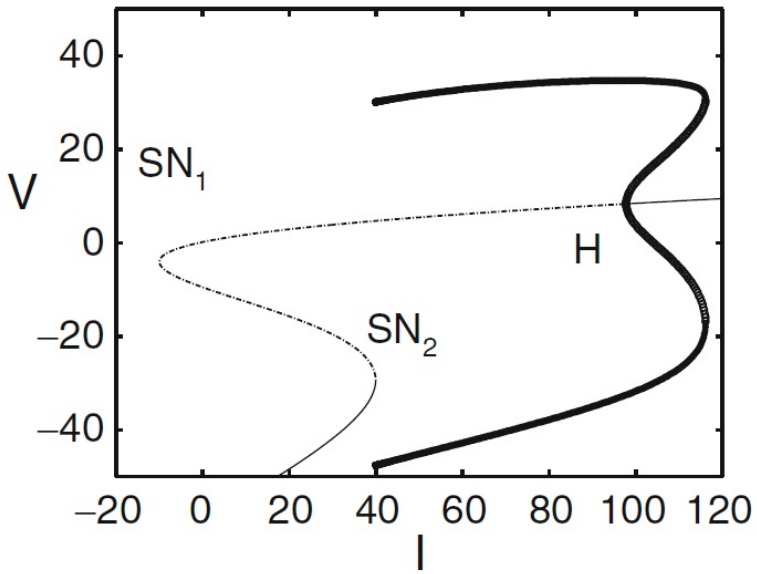


There exists a stable limit cycle for sufficient current; Note to the nullclines.



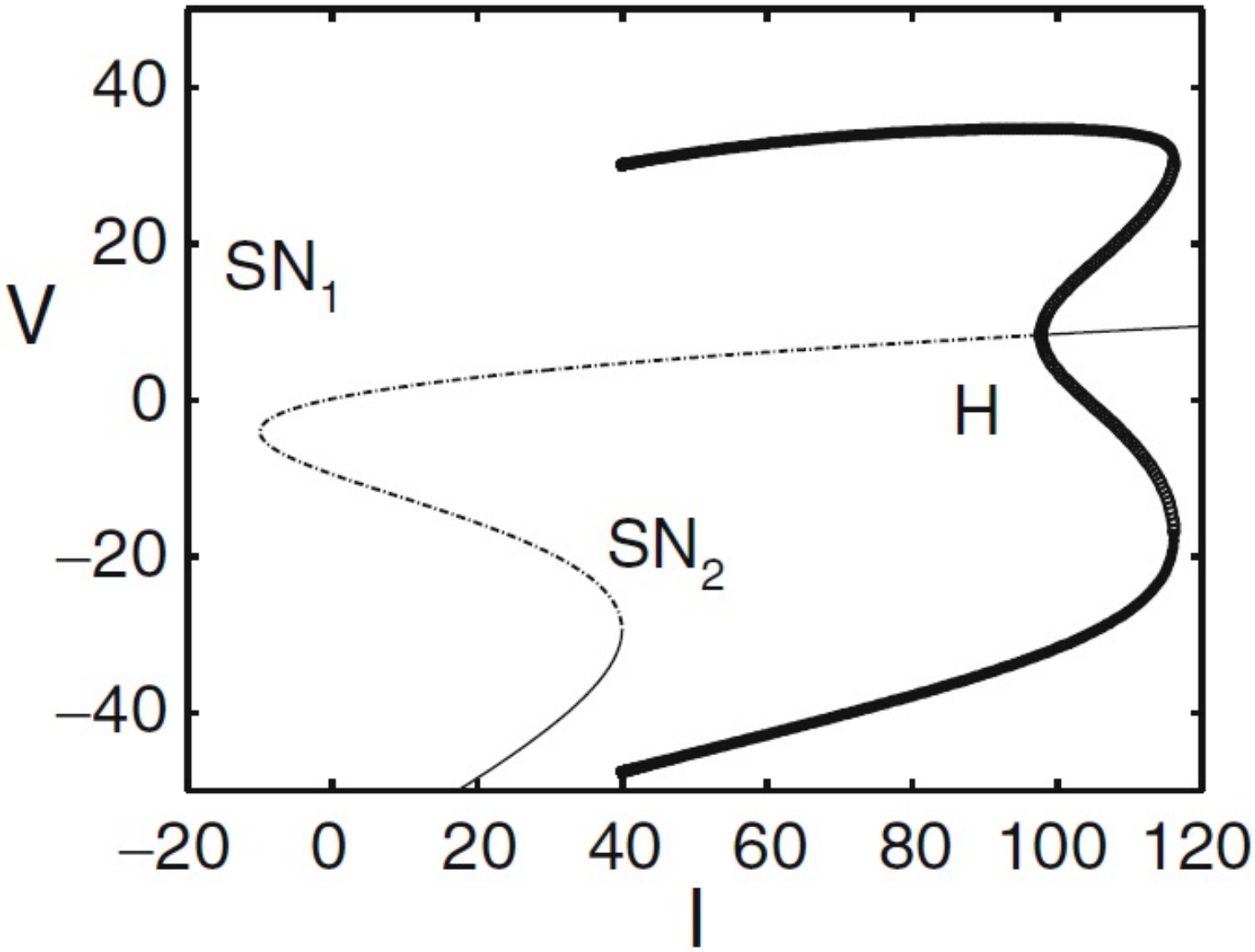
The steady-state voltage shows a region where there are **three equilibria** for I between about -15 and 40. *Only the lower fixed point is stable.*

As I increases, the saddle point and the stable node merge together at a **saddle-node bifurcation**, labeled SN_2. When $I = I_{SN_2}$, the invariant loop formed from Σ^+ becomes a **homoclinic orbit**, i.e a single trajectory that approaches a single fixed point in both forward and backward time.

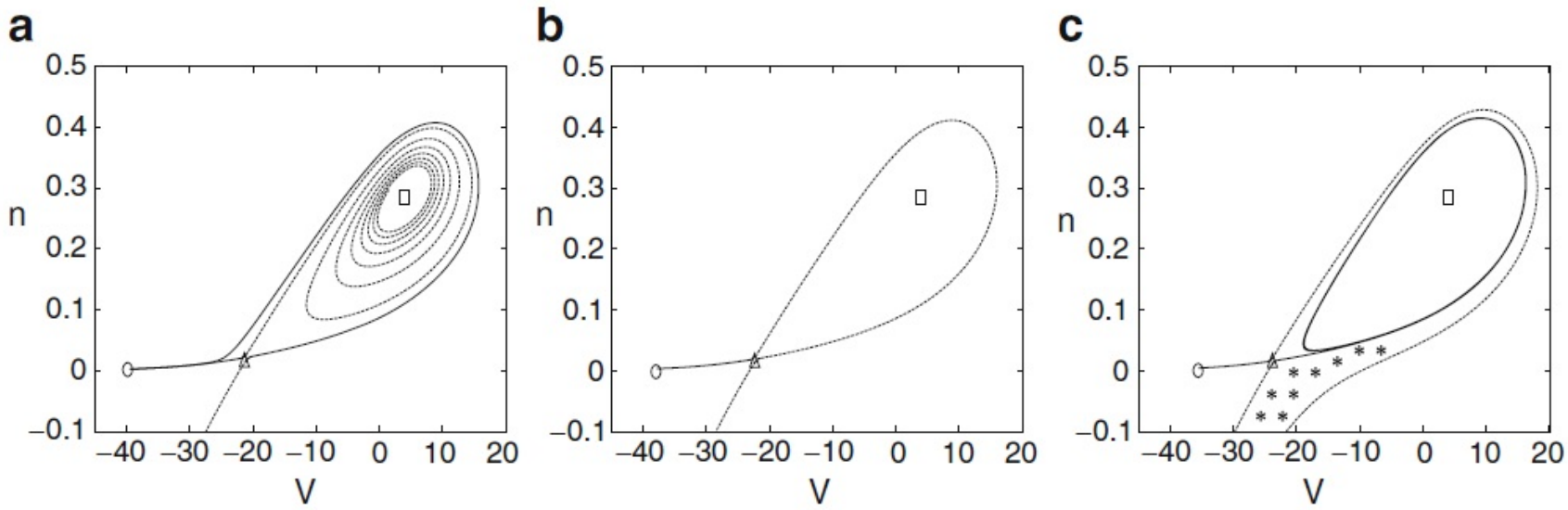


As I increases past $I = I_{SN_2}$, the saddle point and node disappear; the invariant loop formed from Σ^+ becomes a **stable limit cycle**.

The branch of limit cycles persists until it meets a branch of unstable periodic solutions emerging from a **subcritical Hopf bifurcation**.


40
20
0
−20
−40
V
SN1
SN2
H
−20
0
20
40
60
80
100
120
I

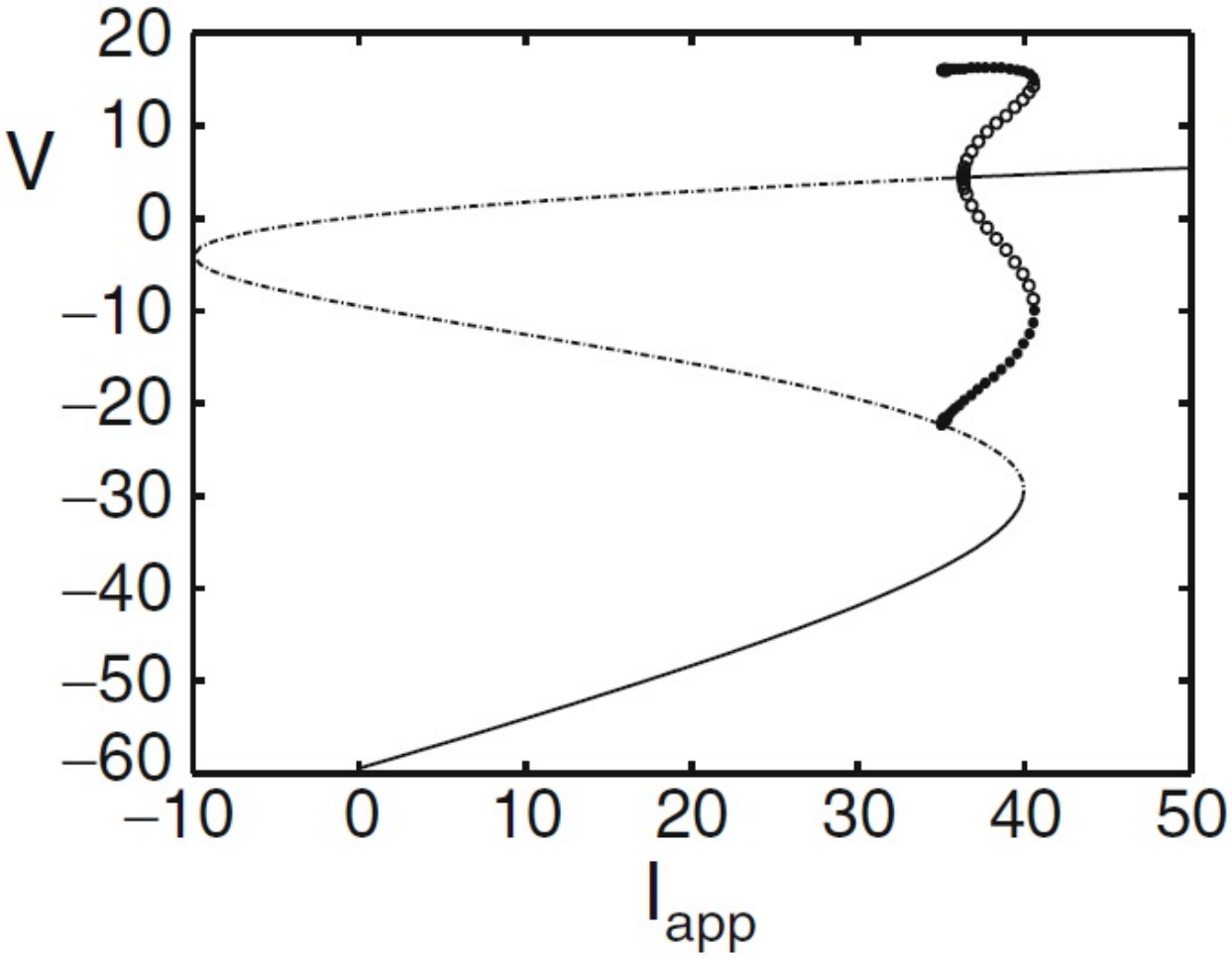
Saddle-Homoclinic Bifurcation



(a) $I < I_{Hc}$,
(b) $I = I_{Hc}$, and
(c) $I > I_{Hc}$.

Perturbations from rest that lie in the starred region shown in (c) will approach the stable limit cycles.

Saddle-Homoclinic Bifurcation



Class I and Class II

In the 1940s, Hodgkin classified three types of axons according to their properties. He called these classes I and II, with class III being somewhere in-between the first two classes which we describe:

- Class I: Axons have sharp thresholds, can have long latency to firing, and can fire at arbitrarily low frequencies (**SNIC**).
- Class II: Axons have variable thresholds, short latency, and a positive minimal frequency (**Hopf**).
- Class III: The relative behaviors is somehow between class I and class II.

- *Review of the previous talk*
- *Bifurcation Analysis*

- *Review of the previous talk*
- *Bifurcation Analysis*
- *Bifurcations and Adjoints*

In general, except for the some few cases, it is not possible to find the adjoint explicitly for a limit cycle. Certainly, the minimal condition is that **an explicit solution for the limit cycle** should be provided and there are very few examples of that.

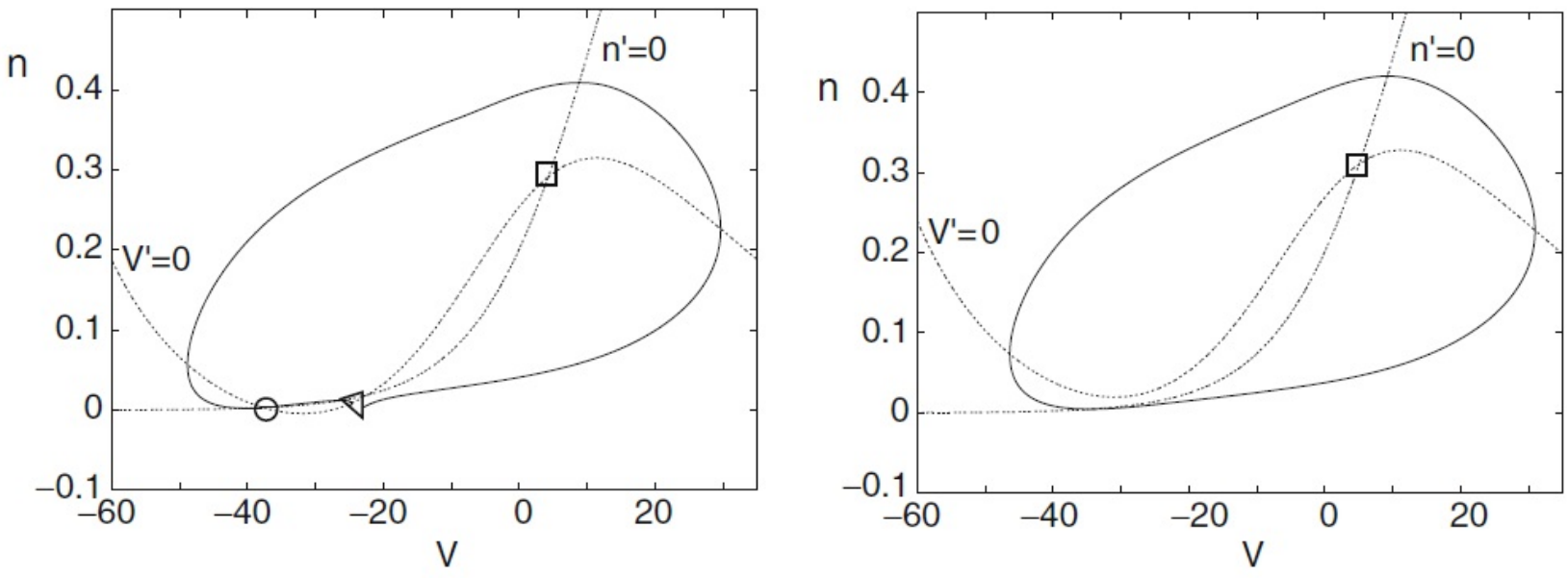
In class I excitability, the behavior near the bifurcation is the same as that of the **quadratic integrate-and-fire/theta model**. Thus, we **expect** that near the onset of rhythmicity, the adjoint of any class I oscillator should look like $1 - \cos t$.

Is it true? Is there a general idea? How well does this actually work in practice?

We can **numerically compute the adjoint** for any oscillator and compare the shape with that **(approximate) prediction** near the bifurcation point. Lets try!

Class I Excitability

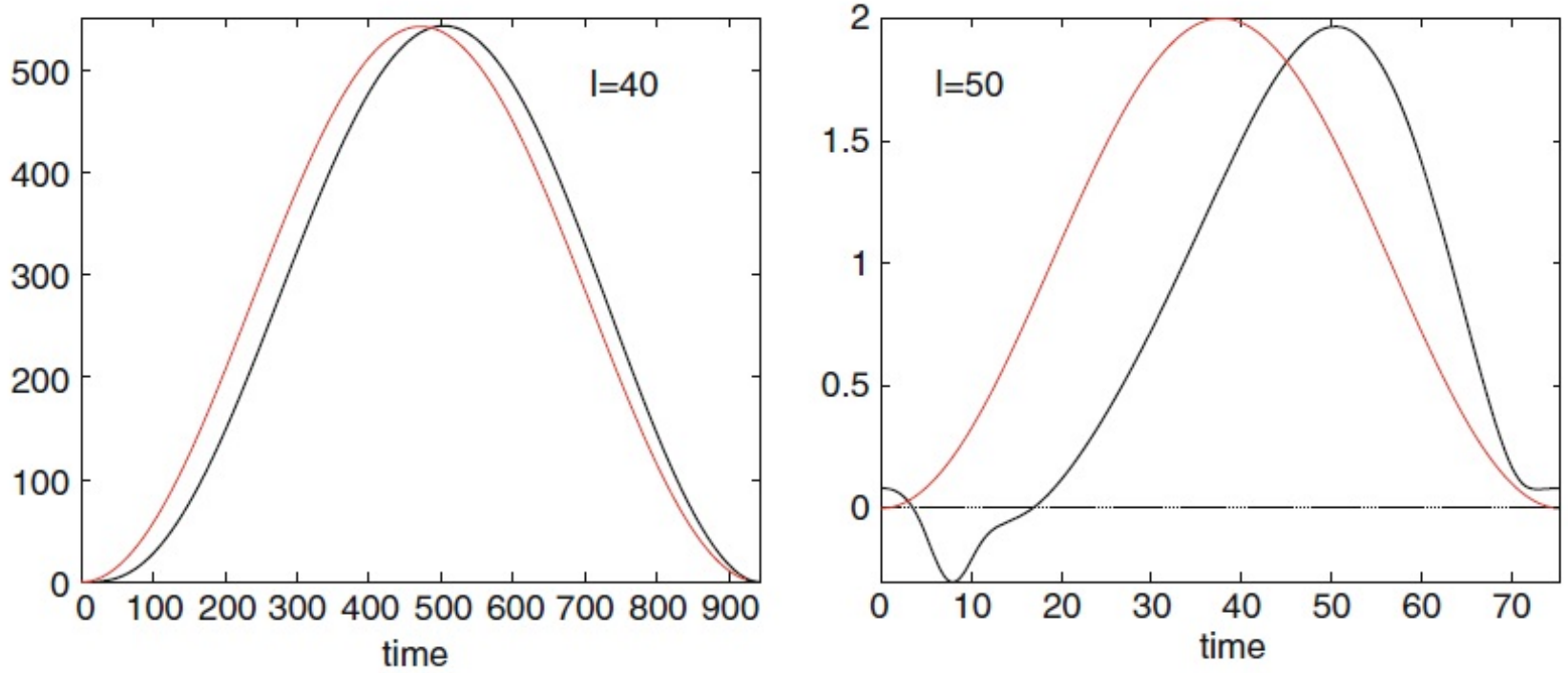
In class I excitability, the behavior is similar to a saddle-node invariant circle bifurcation:



Class I Excitability

So, we expect that near a saddle-node on an invariant circle bifurcation, the adjoint should be proportional to $1 - \cos\theta$.

(Left: $T_{I=40} = 1000ms$, Right: $T_{I=50} = 75.5ms$)

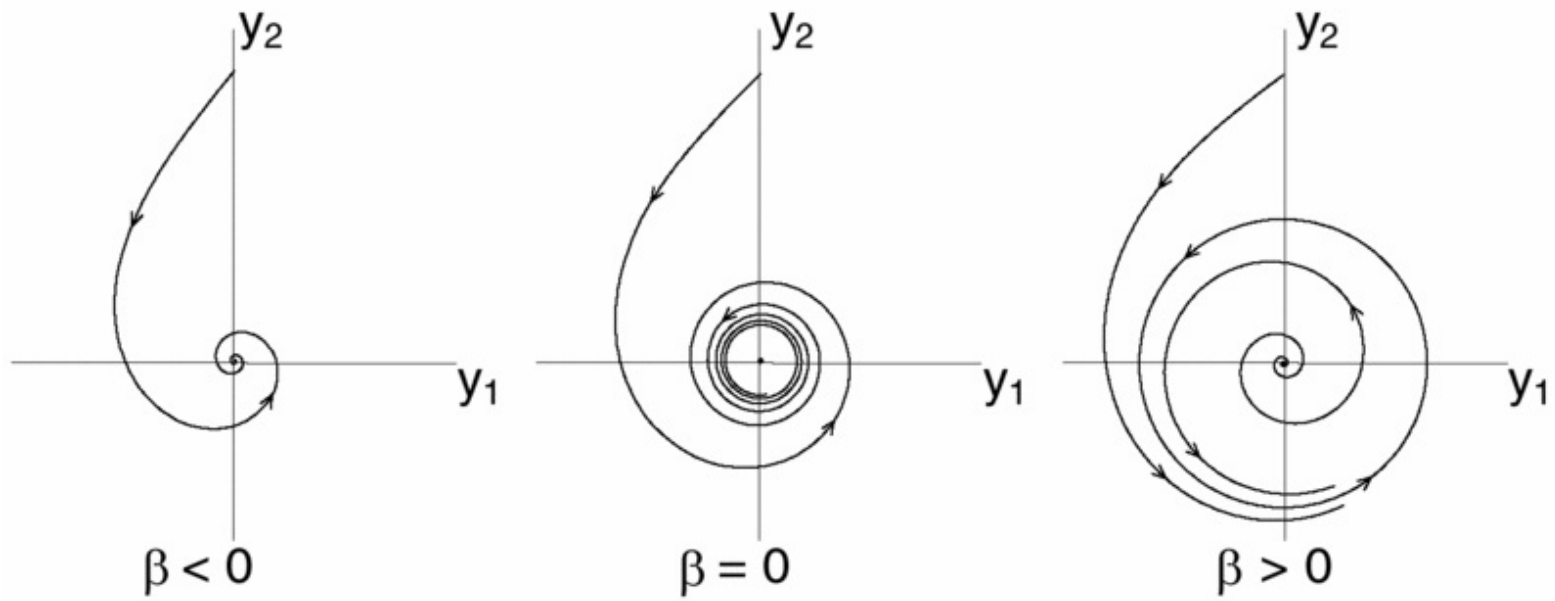


Supercritical Hopf Bifurcation

The normal form of supercritical hopf bifurcation is:

$$\begin{cases} \dot{y}_1 &= y_1(\beta - y_1^2 - y_2^2) - y_2 \\ \dot{y}_2 &= y_2(\beta - y_1^2 - y_2^2) - y_1 \end{cases}$$

We have:



$\lambda - \omega$ Systems and Hopf bifurcation

Kopell and Howard introduced a class of nonlinear oscillators described by

$$\begin{cases} u' &= \lambda(\sqrt{u^2+v^2})u - \omega(\sqrt{u^2+v^2})v \\ v' &= \lambda(\sqrt{u^2+v^2})v + \omega(\sqrt{u^2+v^2})u \end{cases}$$

Suppose $\lambda(1) = 0, \omega(1) = 1$ and $\lambda'(1) < 0$. Then there is a stable limit cycle solution

$$(u, v) = (\cos t, \sin t)$$

and the adjoint for this system is

$$(u^*, v^*) = (a \cos t - \sin t, a \sin t + \cos t)$$

where $a = \omega'(1)/\lambda'(1)$.

A Homework!!!

Davis Cope (personal communication) derived a formula for the adjoint equation for arbitrary nonlinear planar systems

$$\begin{cases} u' &= f(u,v) \\ v' &= g(u,v) \end{cases}$$

which is

$$\begin{pmatrix} u^*(t) \\ v^*(t) \end{pmatrix} = \begin{pmatrix} \frac{u'(t)}{u'(t)^2+v'(t)^2} \\ \frac{v'(t)}{u'(t)^2+v'(t)^2} \end{pmatrix} + c(t) \begin{pmatrix} -v'(t) \\ u'(t) \end{pmatrix}$$

where

$$\frac{\mathrm{d}c}{\mathrm{d}t} = -(f_u+g_v)c + \frac{2u'(t)v'(t)[f_u - g_v] + (v'(t)^2 - u'(t)^2)[f_v + g_u]}{u'(t)^2 + v'(t)^{2^2}}.$$

Golomb-Amitai Model:

$$\begin{cases} \dot{V} &= (-g_L(V-V_L) - g_{Na}\,\Gamma_F(V,\theta_m,\sigma_m)^3\; h(V-V_{Na}) \\ & \quad -g_{NaP}\,\Gamma_F((V,\theta_p,\sigma_p)\;(V-V_{Na}) - g_{Kdr}\;n^4(V-V_K) - \\ & \quad g_A\,\Gamma_F((V,\theta_a,\sigma_a)^3\;b\;(V-V_K) - g_Z\;z(V-V_K) + I(t)) \\ \dot{h} &= \phi(\Gamma_F(V,\theta_h,\sigma_h) - h)/(1.0 + 7.5\Gamma_F(V,t_{\tau_h},-6.0)) \\ \dot{n} &= \phi(\Gamma_F(V,\theta_n,\sigma_n) - n)/(1.0 + 5.0\Gamma_F(V,t_{\tau_n},-15.0)) \\ \dot{b} &= (\Gamma_F(V,\theta_b,\sigma_b) - b)/\tau_B \\ \dot{z} &= (\Gamma_F(V,\theta_z,\sigma_z) - z)/\tau_Z \end{cases}$$

where

$$\Gamma_F(V,\theta,\sigma) = \frac{1}{1+e^{-(V-\theta)/\sigma}}.$$

The Golomb-Amitai Model has a **Supercritical Hopf bifurcation** at high applied currents.(D. Golomb and Y. Amitai. *Propagating neuronal discharges in neocortical slices: computational and experimental study*. J. Neurophysiol., 78:1199-1211, Sep 1997)

Golomb-Amitai Model and Supercritical Hopf Bifurcation

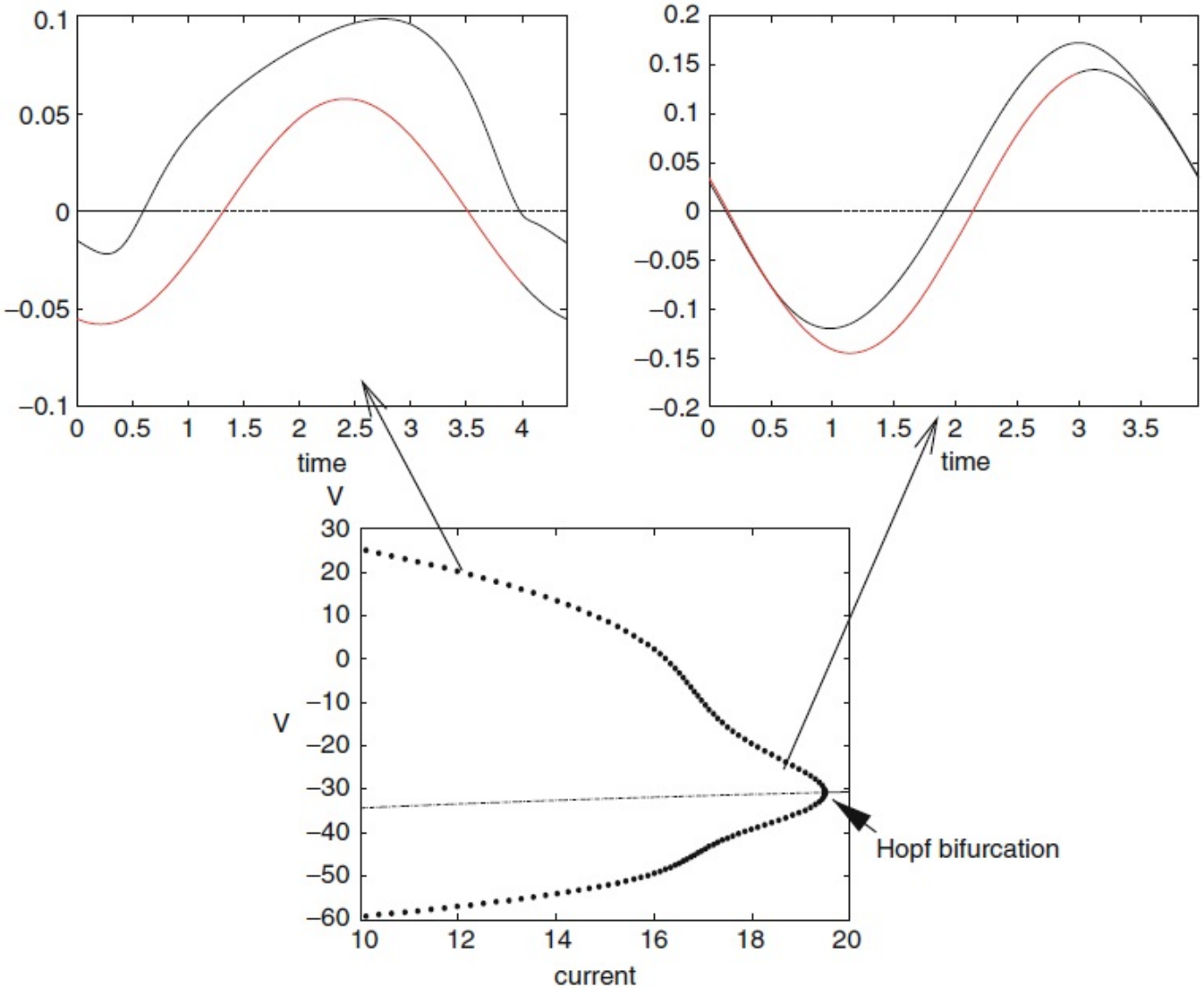
For this model, each component of the adjoint is a pure sinusoid:

$$\mathrm{u}^* = \alpha \sin\theta + \beta \cos\theta$$

We compute the adjoint numerically and see how well it is approximated by pure sinusoids. Models near a Hopf bifurcation

have regimes of phase advance and phase delay in contrast to class I models, which are dominated by phase-advance dynamics.

Hopf Bifurcation



Takens-Bogdanov

The **M-type potassium channel** (an outward current which acts at voltages near rest) can convert the transition to oscillations from class I (saddlenode on an invariant circle) to class II (Hopf bifurcation).
The quadratic integrate-and-fire model with an adaptation is :

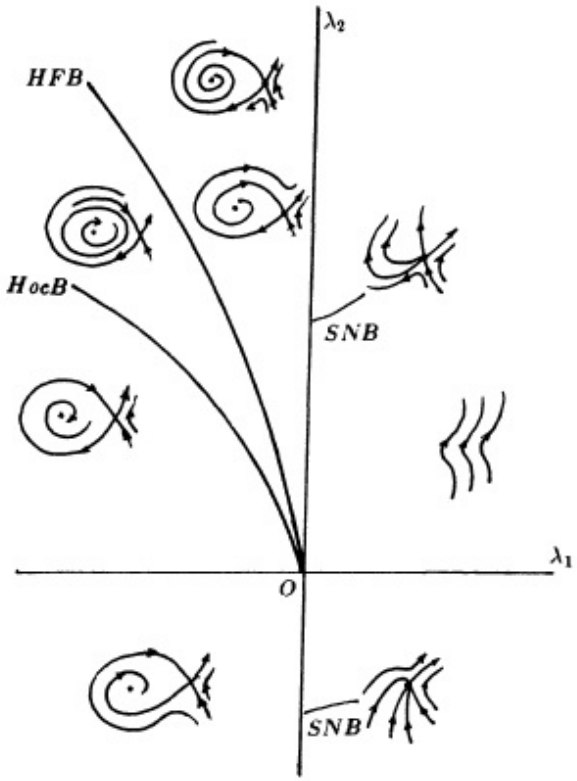
$$\begin{cases} \dot{V} &= I + V^2 - u \\ \dot{u} &= a(bV - u) \end{cases}$$

with reset of V to c when there is a spike, $V(t_{spike}) = V_{spike}$, and at the same time the variable u is increased by an amount d.

Takens-Bogdanov

This model is locally equivalent to the normal form for the **Takens-Bogdanov bifurcation**:

$$\begin{cases} \dot{x} &= y \\ \dot{y} &= \lambda_1 + \lambda_2 y + x^2 + xy \end{cases}$$



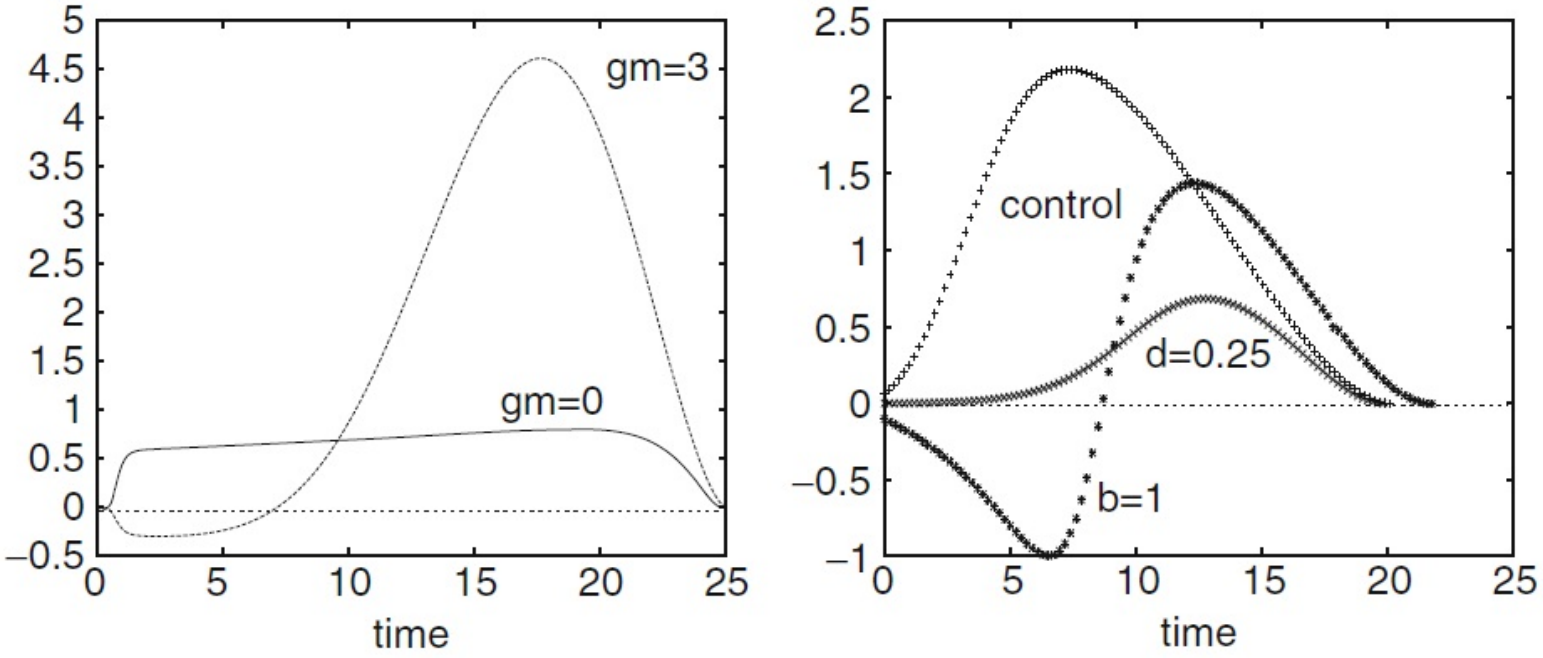
The adaptation is manifested in two ways:

- the parameter b governs **subthreshold effects**, and
- the parameter d governs **effects due to spikes**.

Since only the parameter b (which acts at rest) can **switch the cell from class I to class II**, we expect that this parameter will produce a **negative component** in the *PRC*:

$$\begin{cases} \dot{V} &= I + V^2 - u, \\ \dot{u} &= a(bV - u). \end{cases}$$

With no adaptation ($b = d = 0$), the *PRC* is close to the canonical form, $1 - \cos t$. When $b = 1$, the resting state loses stability at a Hopf bifurcation and the excitability class is II. The *PRC* shows a pronounced negative component. However, if $b = 0$ and d is nonzero, then the *PRC* stays positive but is flattened in the early part of the cycle.



- *Review of the previous talk*
- *Bifurcation Analysis*
- *Bifurcations and Adjoints*

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- *Bifurcation Analysis*
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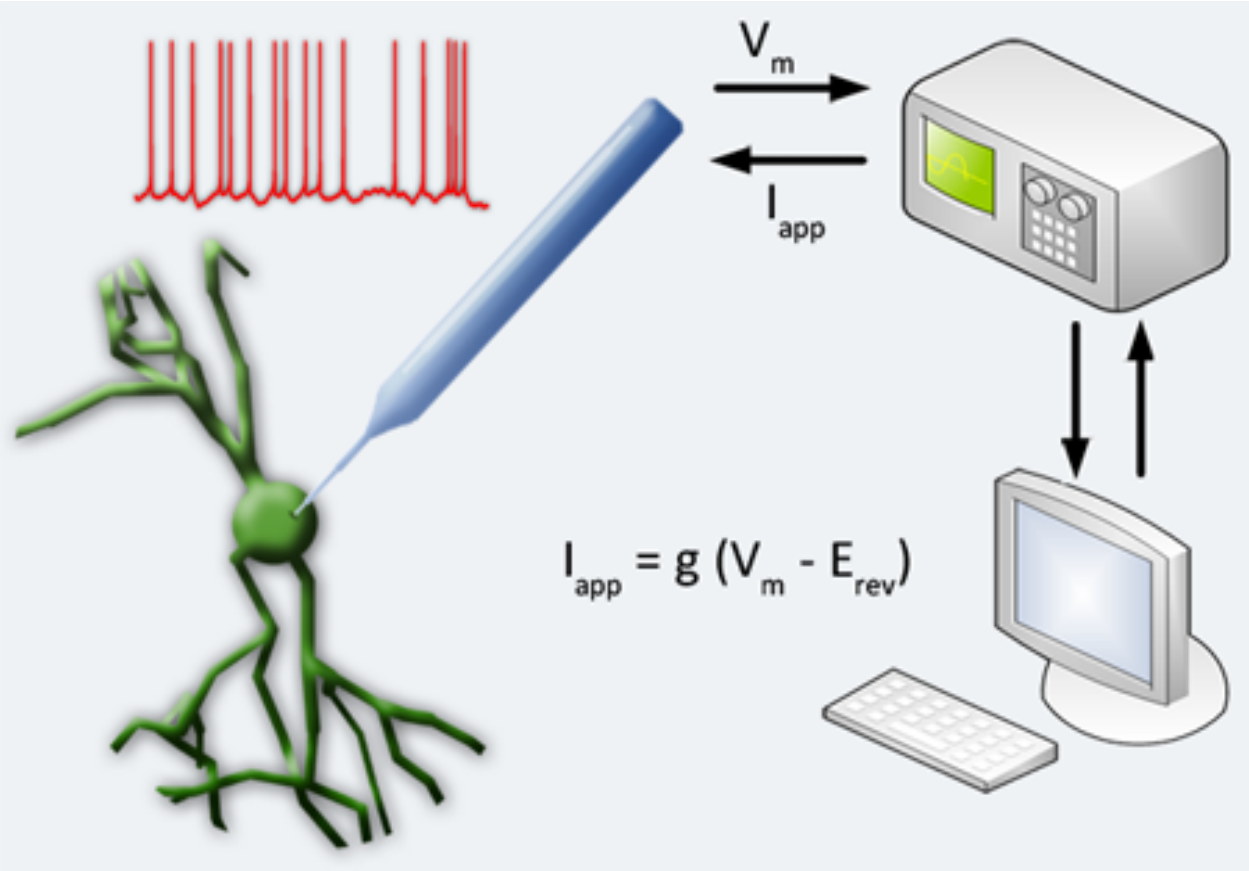
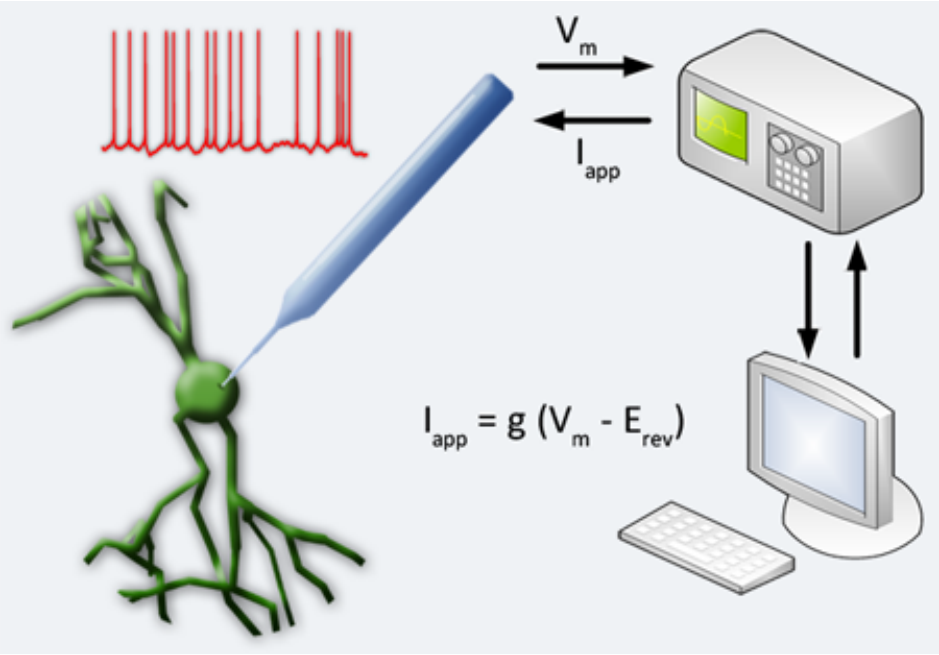
- *Spike - Time Response Curves*

Dynamic Clamp:



Astrid A. Prinz and Robert H. Cudmore (2011), "Dynamic clamp". Scholarpedia, 6(5):1470.



Dynamic Clamp:
The dynamic clamp is an experimental method in which the potential of a neuron is fed into a computer model for a channel and the resulting current is injected into the cell. Thus, it is possible to **add channels** to and **remove channels** from real neurons in real time.

Several **experimental groups** use the dynamic clamp to investigate the **behavior between two or more neurons** when they are coupled via these **artificial synapses**.

The **first step** in understanding the behavior of these coupled neurons is to understand how a **single neuron responds to a synaptic current**.

If this current is an **infinitesimal perturbation** of the membrane potential, then we know that the response is precisely the **adjoint**.

More generally, we can compute a **PRC** to any stereotypical input.

It is used this idea to compute the PRC for the **quadratic integrate-and-fire model** by applying a small rectangular pulse of current at different times.

Let

$$\frac{\mathrm{d}}{\mathrm{d}t}\mathrm{X} = \mathrm{F}(\mathrm{X}),$$

and also let $\mathrm{G}(t, t_0)$ be the vector of inputs parameterized by the time t_0, then the resulting system is

$$\frac{\mathrm{d}}{\mathrm{d}t}\mathrm{X} = \mathrm{F}(\mathrm{X}) + \mathrm{G}(t, t_0).$$

Assume that $\frac{\mathrm{d}}{\mathrm{d}t}\mathrm{X} = \mathrm{F}(\mathrm{X})$ has a stable limit cycle. As we have

$$\mathrm{Z}(\phi) = \nabla_{\mathrm{x}}\Theta(\mathrm{X}_0(\phi)),$$

we will have

$$\frac{\mathrm{d}}{\mathrm{d}t}\theta = 1 + \mathrm{Z}(t) \cdot \mathrm{G}(t, t_0).$$

Let $\theta(0) = 0$, T be period of solution θ and T' be such that $\theta(T') = T$. In fact, T' is a function of t_0 and is the time of the spike.
If $G(t; t_0) \equiv 0$, we have $T'(t_0) \equiv T$.
By integration from

$$\frac{\mathrm{d}}{\mathrm{d}t}\theta = 1 + \mathrm{Z}(t) \cdot \mathrm{G}(t, t_0),$$

we will have

$$\theta(T') = T' + \int_0^{T'} \mathrm{Z}(t) \cdot \mathrm{G}(t, t_0)\mathrm{d}t = T.$$

Solving this equation for T' tells us when the next spike occurs.

The PRC for a stimulus $\mathrm{G}(t, t_0)$ is just $PRC(t_0) = T - T'(t_0)$, which tells us how much the stimulus advances or delays the next spike.

Suppose $\mathrm{G}(t, t_0)$ is small, say, $\mathrm{G}(t, t_0) = \epsilon \mathrm{g}(t, t_0)$. Then we can expand $T'(t_0)$ as

$$T'(t_0) = T + \epsilon\tau(t_0) + \dots.$$

So we will have

$$0 \approx \tau + \int_0^T \mathrm{Z}(t) \cdot \mathrm{g}(t, t_0)\mathrm{d}t.$$

Therefore, to lowest order

$$PRC(t_0) \approx \int_0^T \mathrm{Z}(t) \cdot \mathrm{G}(t, t_0)\mathrm{d}t.$$

Note that if $\mathrm{G}(t)$ is a Dirac delta function along one of the components of X, then the PRC is exactly the same as the adjoint as it is just a component of Z.

When $\mathrm{X}(t)$ is a **membrane** equation and $\mathrm{G}(t, t_0)$ is a **synaptic current** generated by an alpha function type of synapse,

$$\mathrm{G}(t, t_0) = \alpha(t - t_0)(V_{syn} - V(t)).$$

then function

$$PRC(t_0) \approx \int_0^T \mathrm{Z}(t) \cdot \mathrm{G}(t, t_0) \mathrm{d}t.$$

is called the **spike-time response curve (STRC)**. It tells us how the spike time of a neuron is changed by a stereotypical input as a function of when that input arrives.

Thanks for your patience!