OUTLINE

Basic Membrane models
1. HH formulation
2. I+F

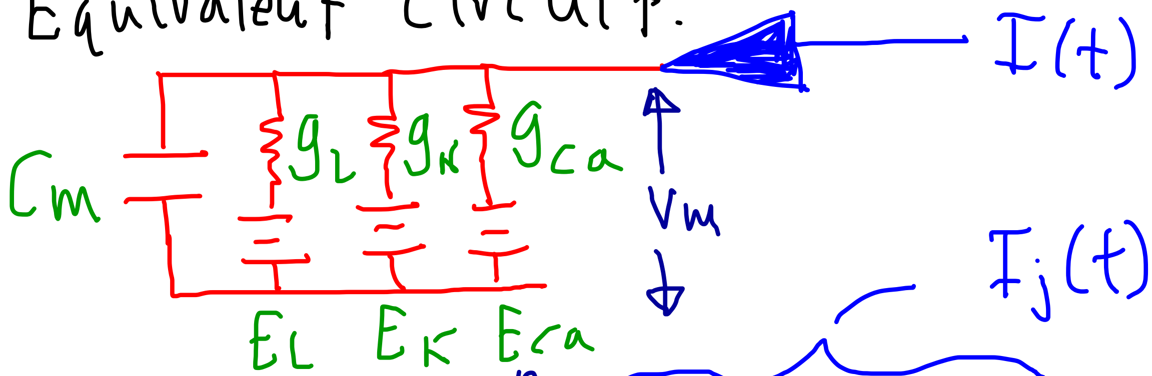
Neural Oscillators

1. Bifurcations to Oscillations
2. Phase resetting curves
3. Coupling & maps
4. Weak coupling
5. Phase models & noise

firing rate models
1. Wilson Cowan
2. Spatial stuff

Basic Models

Equivalent Circuit:

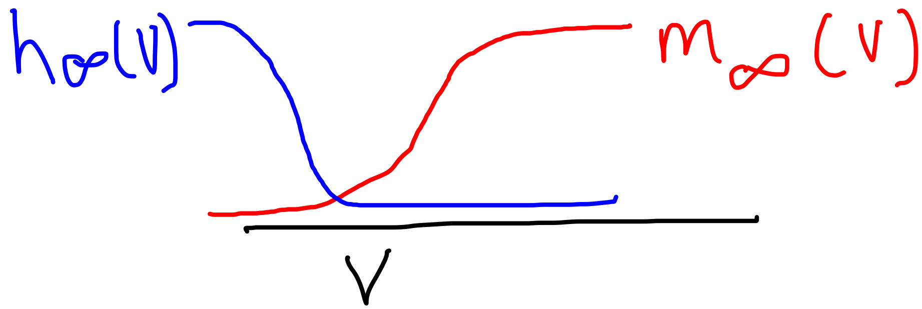


$$C_m \frac{dV_m}{dt} + \sum_{j=1}^{n} \overbrace{g_j(t)\left(V_m - E_j\right)}^{I_j(t) \,=\, \text{"active currents"}} = I(t)$$

Typically: $g_j(t) = m_j(t)^{\overset{\text{activation}}{p}}\, h_j(t)^{\overset{\text{inactivation}}{q}}$

$p, q \in \{0, 1, 2, \ldots\}$

$$\frac{dX}{dt} = \frac{X_\infty(V) - X}{\tau_X(V)}$$



Hodgkin-Huxley 1950's

Squid Axon

$$I_K = \bar{g}_K n^4 (V - E_K)$$

$$I_{Na} = \bar{g}_{Na} m^3 h (V - E_{Na})$$

$$I_L = \bar{g}_L (V - E_L)$$

$E_K \approx -90 - -70$ mV

$E_{Na} \approx +55$ mV

$E_L \approx -60$ mV

$E_{Ca} \approx +120$ mV

Simpler Models

$$\tau \frac{dV}{dt} = m(V) + R_m I(t)$$

$m(v) = -(V - E_L)$ Leaky I+F

$$m(v) = \frac{(V - E_L)(V - V_T)}{V_T - E_L}$$ Quad I+F $V_T > E_L$

$m(v) = -(V - E_L) + \Delta e^{\frac{V - V_T}{\Delta}}$ EIF

Typically There is a firing + reset:

When $V(t^-) = V_{spike}$, $V(t^+) = V_{reset}$

Can add slow negative feedback: $-\beta W$

$$\tau_W \frac{dW}{dt} = a(V - E_L) - W$$

Neural Models: Analysis

MORRIS-LECAR

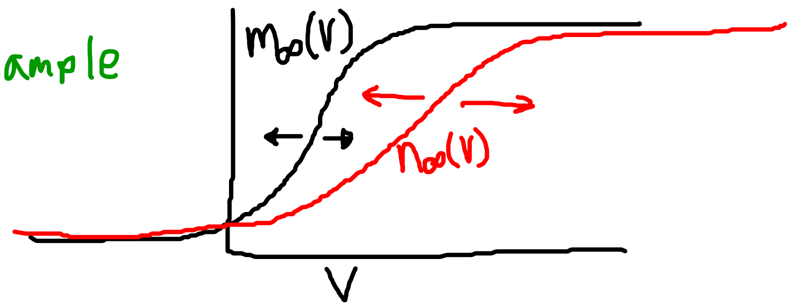
$C\frac{dV}{dt} = -I_{ionic} + I_{app}$ e.g. $I_{ionic} = g_L(V-E_L) + g_K n(V-E_K) + g_{Ca} m_\infty(V)(V-E_{Ca})$

$I_{ionic} = g_L(V-E_L) + g_K n^4(V-E_K) + g_{Na} m^3 h(V-E_{Na})$

Hodgkin-Huxley

$\frac{dn}{dt} = (n_\infty(V)-n)/\tau_n(V)$ etc (2 more eqns for HH)

Morris-Lecar example

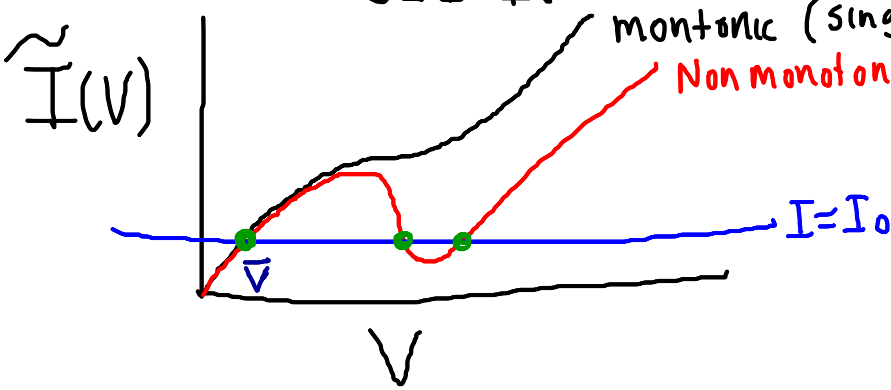


Fixed points $n = n_\infty(V)$, $0 = I - g_L(V-E_L) - g_K n_\infty(V)(V-E_K) - g_{Ca} m_\infty(V)(V-E_{Ca})$

$0 = I - \tilde{I}(V)$ ← ss I_V curve!!

montonic (single equlib)

Non monotonic (multiple equlib)



$I_0 - I_{ss}(\bar{V}) = 0$

Stability of Equilib

Hard for $n>2$ $\quad M \equiv \begin{pmatrix} a & -b \\ c & -d \end{pmatrix}$ $\quad b = g_K(\bar{V}-E_K)$ $\quad C = n'_\infty(\bar{V})/\tau(\bar{V})$

$d = 1/\tau(\bar{V})$ These 3 all positive

a can be +/− $\quad$ Clearly, if $a<0$, stable (det>0, Tr<0)

$a>0$ $\quad$ two cases $\quad$ (i) $\det<0$, $bc<ad$ $\quad$ (ii) $Tr>0$, $a>d$ $\quad$ depends on $\tau_n(\bar{V})$

Slope of $I_{ss}(V)<0$

magnitude, but not the sign of c, d depends on τ, the time constant of

$$a = -g_L - g_K \bar{n} - g_{CA} m_\infty(\bar{V}) + \underbrace{g_{CA} m'_\infty(\bar{V})(E_{Ca}-\bar{V})}_{+}$$

K^+ current.

If $a>0$, then Trace $\equiv a-d$ is positive if $d \equiv {}^{-1}/\tau_K(V)$

is sufficiently small. Get possibility of oscillations

<u>Recall</u> → Hopf bifurcation Theorem:

$\lambda(p) = \alpha(p) \pm i\omega(p)$ $\quad \alpha(0)=0$ $\quad \alpha'(0)>0$ $\quad \omega(0)\neq 0$, $\quad$ ONE MORE COND

$\exists$ L.C. $\quad Tr=0,\ Det>0 \Leftrightarrow i\,\omega_0$!

Class II Excitability

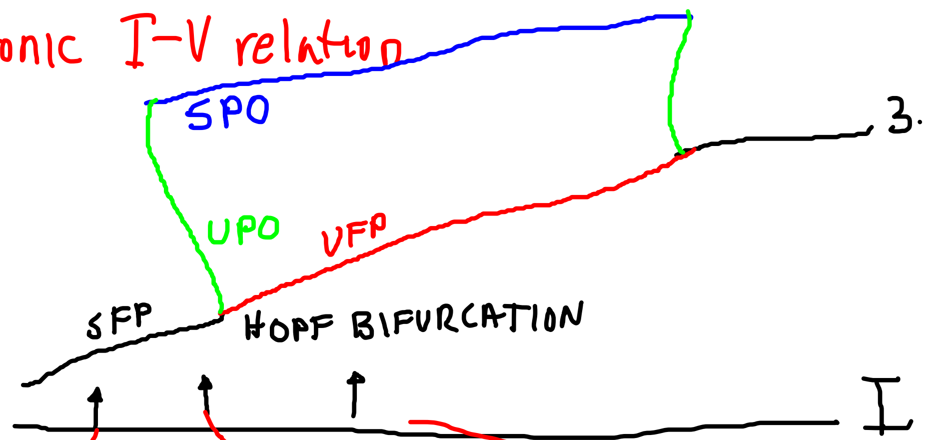
Examples: HH, ML, FN

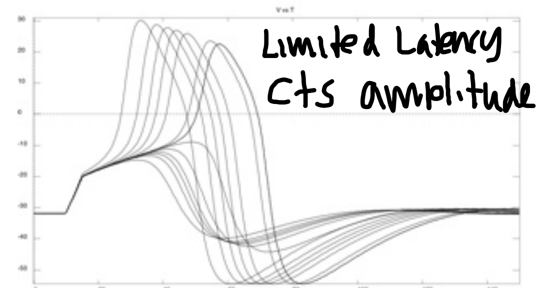
Treat I, the applied current as a parameter

Monotonic I-V relation

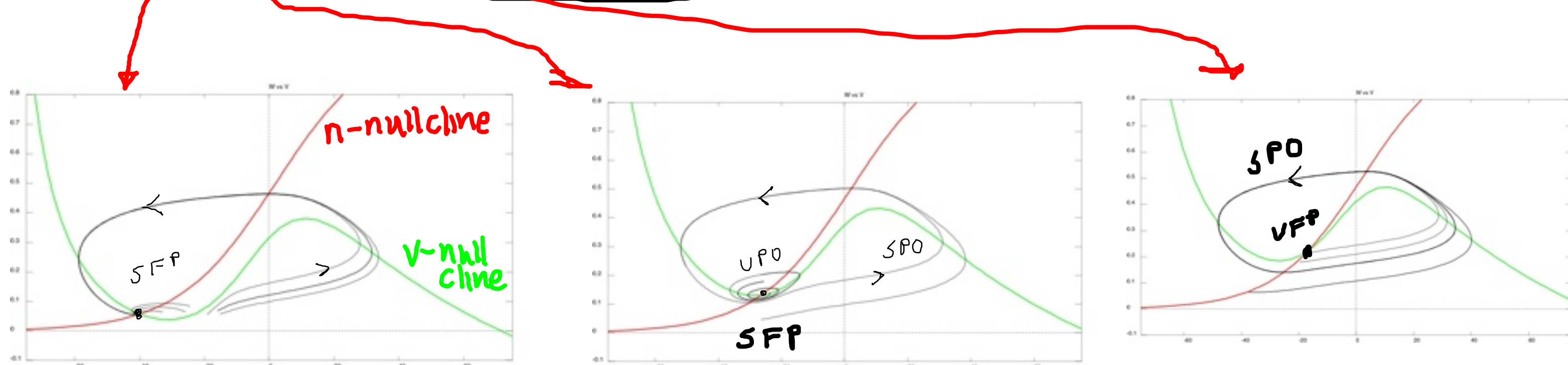
Properties

1. Abrupt onset of rhythmicity
2. Bistability





5 msec pulses between 44-46

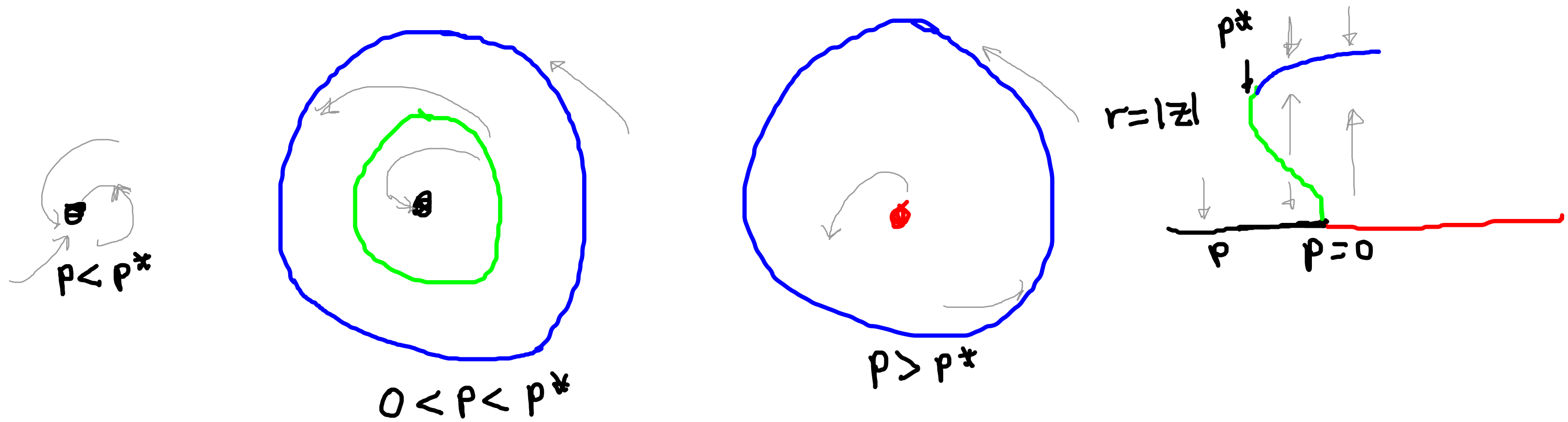


"Normal form"

Near a sub/supercritical HB, dynamics has form:

$$\dot{z} = z(p + i + a|z|^2 - |z|^4)$$

$a > 0$ sub
$a < 0$ super



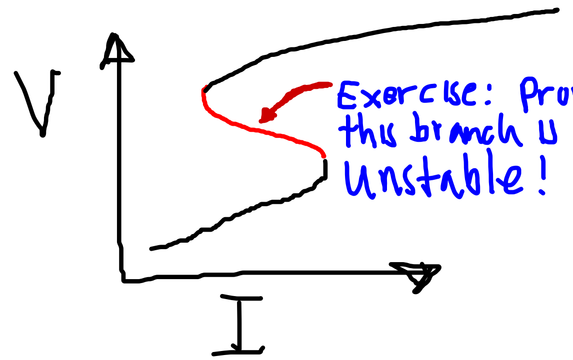
<u>Normal form</u> doesn't show excitability but illustrates the global dynamics

<u>Exercise</u> write $z = r e^{i\theta}$, where $p, a,$ real. Derive the BD above $(a>0)$

and also find the diagram when $a < 0$. For $a > 0$, compute p^*.
Don't forget to get stability!

Class I excitability

In the previous example the SS I-V curve was monotonic

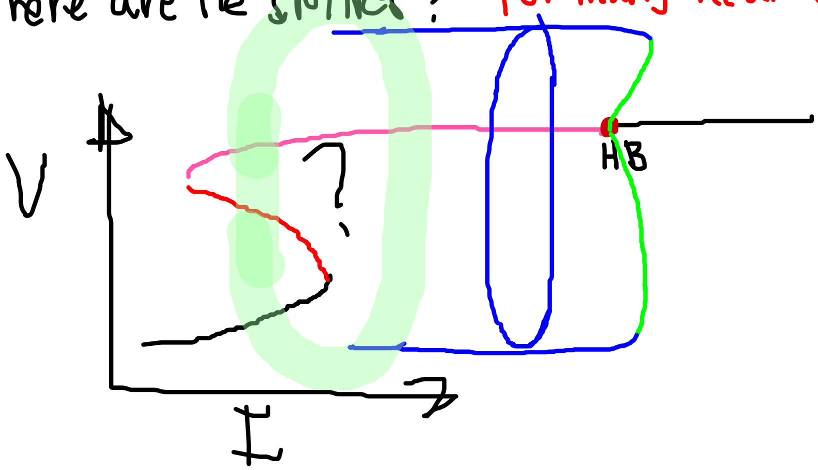


Exercise: Prove that this branch is always unstable!

I'll make it easy — just show for 2D system prove det $M < 0$

Where are the spikes?

For many neuron models, upper branch is unstable

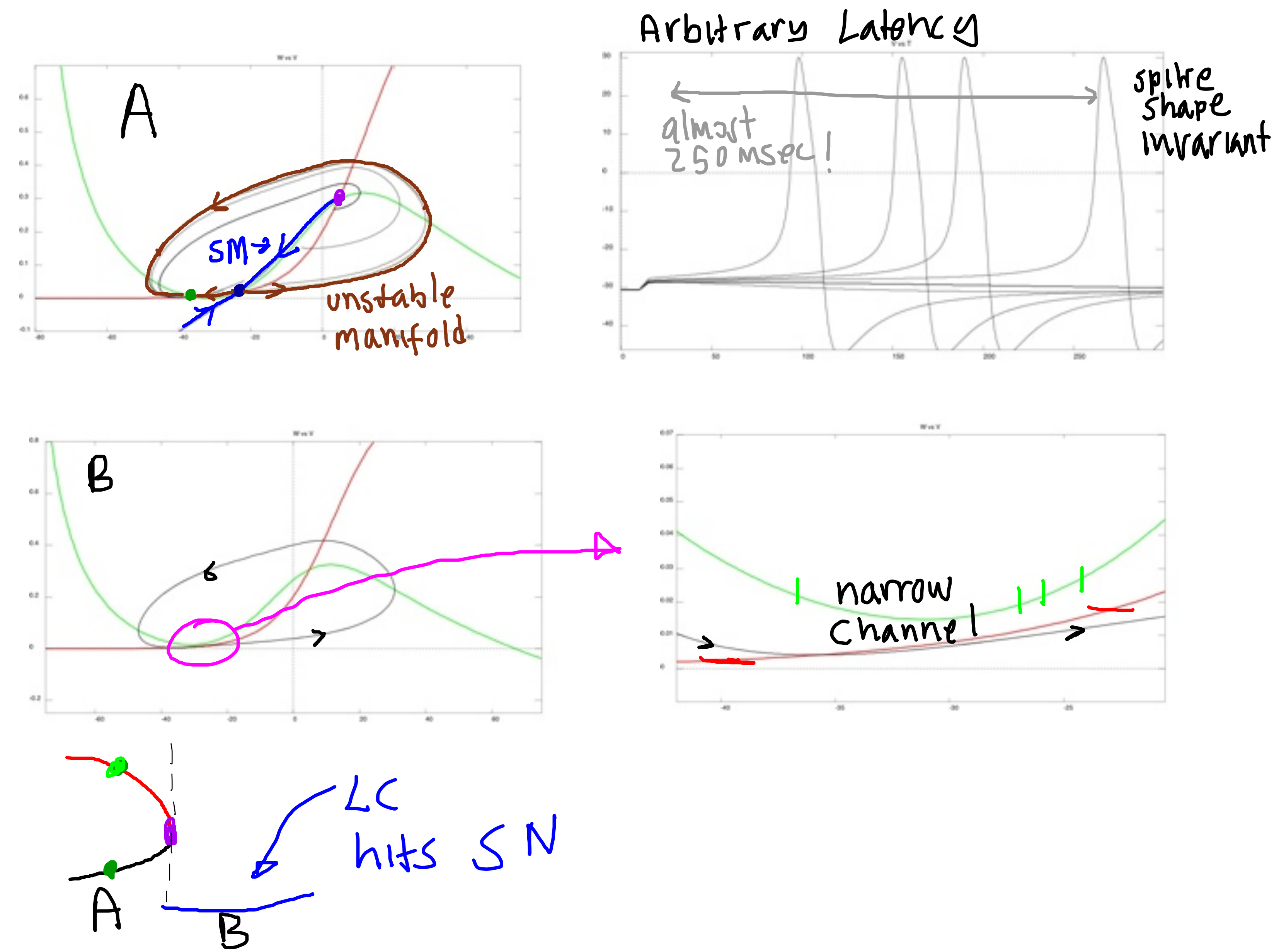


Two cases here

(1) SNIC

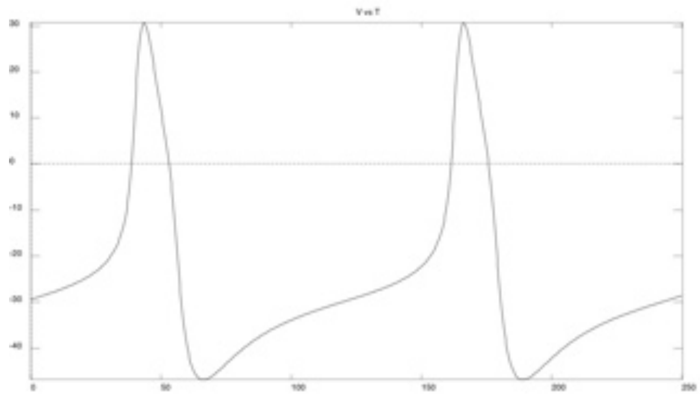
(2) Homoclinic

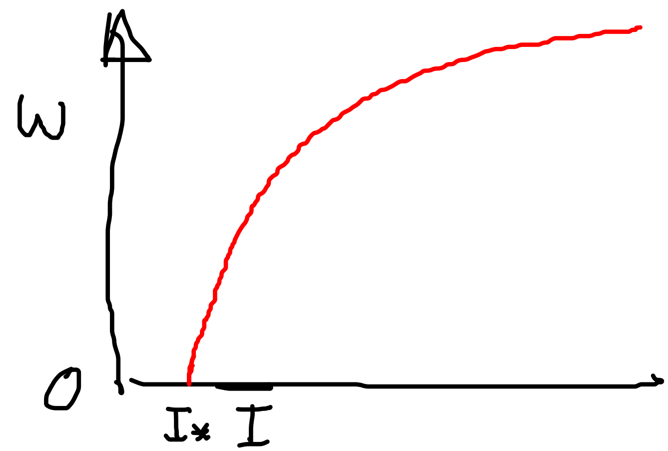
SNIC

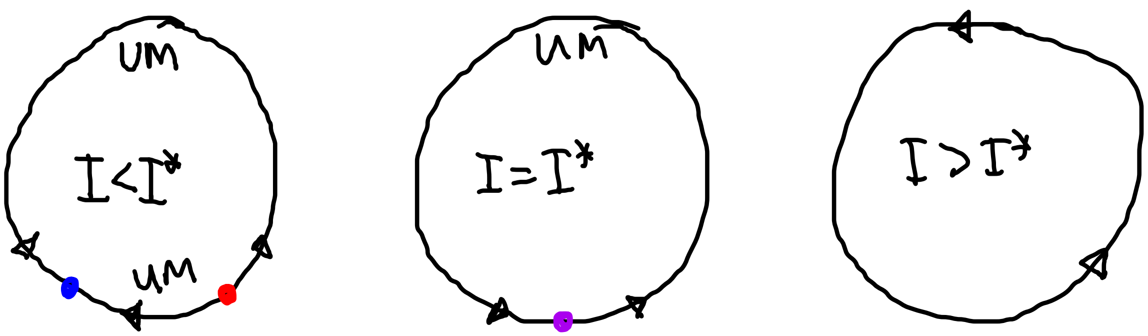

Arbitrary Latency
A
SM
unstable manifold
almost 250 msec!
spike shape invariant
B
narrow channel
LC hits SN
A
B

SNIC 2

arbitrarily low frequency







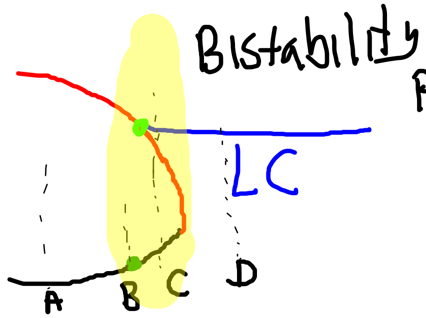
$\dot{\theta} = 1 - \cos\theta + (1+\cos\theta)(I - I_*)$ $\quad \omega \sim K\sqrt{I - I^*}$ Normal Form

Exercise: Find K

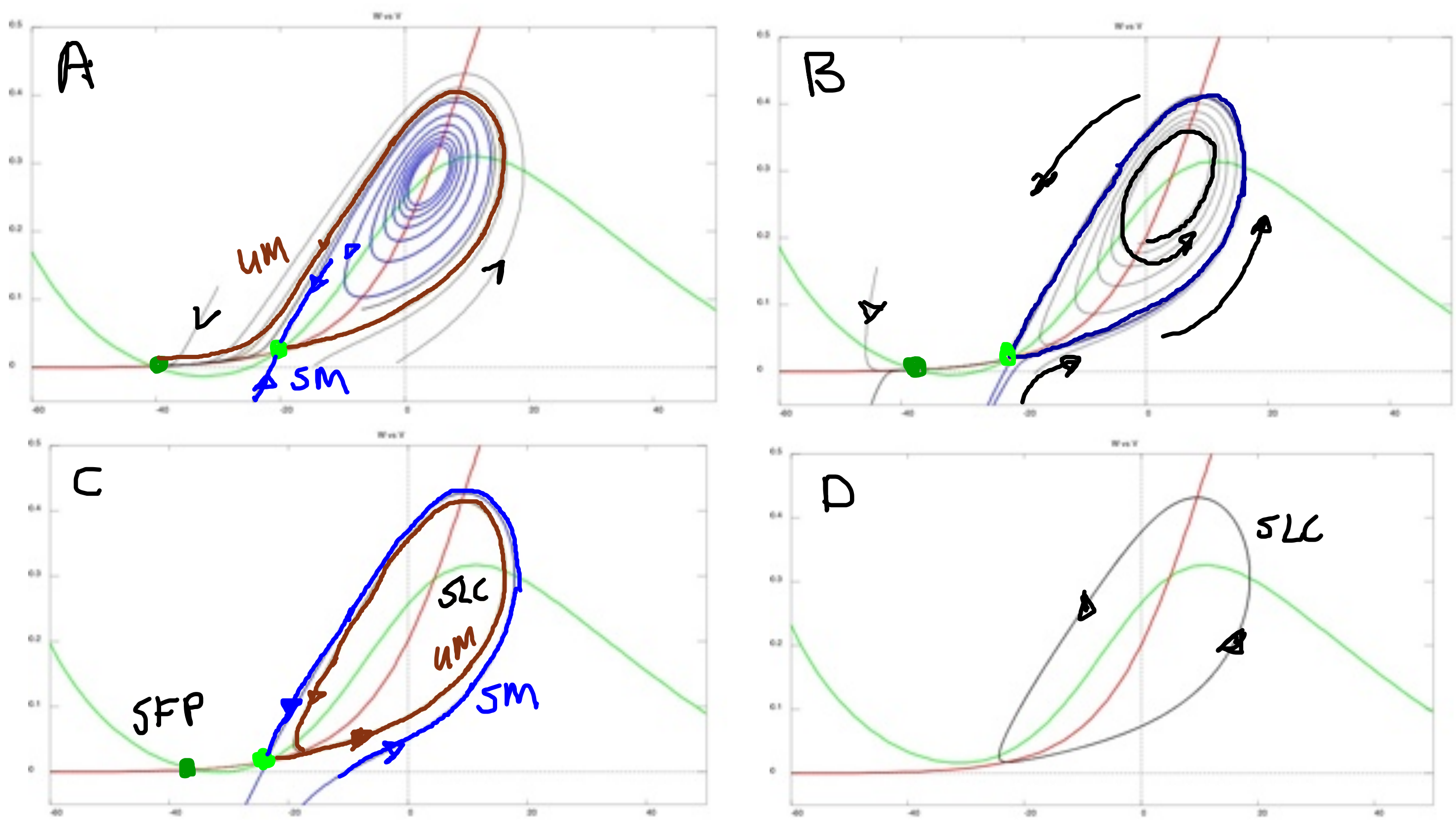
$\dot{x} = x^2 + (I - I^*)$ $\quad x = \tan\left(\frac{\theta}{2}\right)$ QIF

Exercise: Derive !

Homoclinic



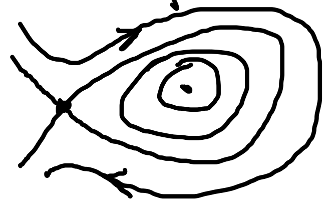
Periodic branch meets with saddle point



Homoclinic

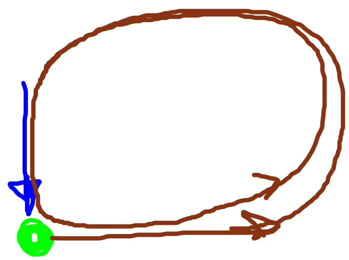
No simple normal form

$$\ddot{x} = x(1-x)$$

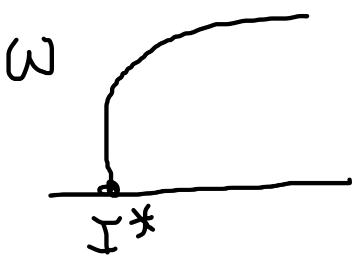


MR. FISH

Get close to saddle



$$\omega \sim 1/\log|I-I^*|$$



1. Arbitrarily low frequency
2. Bistability between SFP + SLC
3. No simple normal form

Transition I $\leftrightarrow$ II

Class I $\leftarrow$ SNIC $\leftarrow$ saddle node $\leftarrow$ det 0

Class II $\leftarrow$ HB $\leftarrow$ Tr = 0

Arrange parameters so that trace + det = 0

(Generalize to n-dimensions 0 is double eigenvalue)

TAKENS / BOGDANOV

$$\begin{pmatrix} a & b \\ -\frac{a^2}{b} & -a \end{pmatrix} \quad V = \begin{pmatrix} -b \\ a \end{pmatrix}$$ unique eigenvector

$$\begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}$$ Jordan Normal form

simple nonlinear system:

$$\dot{V} = V^2 + I - W \qquad \dot{W} = a(V - bW)$$

Izhikevich model

QIF + A

HW Find saddle node + HB as function of I, a, b

QIFA ctd

$\dot{V} = V^2 + I - W \qquad \dot{W} = a(V - bW)$

add reset: When $V = V_{spike}$ $\quad V \to C$

$W \to W + d$

Fun exercises:

$\dot{V} = V^2 + I$, $V = V_{spike}$, $V \to C$

$I < 0$, $V_{spike} = \infty$, $c > \sqrt{-I}$ sketch solutions

show bistable. Show LC

compute period as function of I for c fixed > 0

Sketch bifurcation diagram

Is there a Homoclinic ?

Try to find a "bursting" solution for QIFA

Summary, so far

Three ways that oscillations arise from FPs:

① HB $\rightarrow$ sub
   $\rightarrow$ super (bistable)

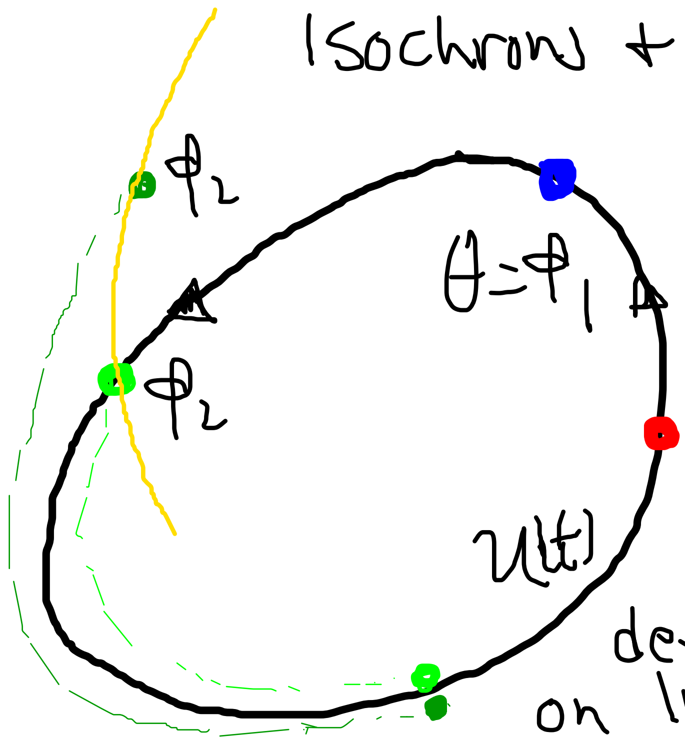
② SNIC

③ Homoclinic (bistable)

What happens in networks?

How does an oscillator respond to inputs

Isochrons + PRCs



Define a phase, θ
for T-periodic oscillator
as time since $\theta = 0 \mod T$
for any pt on LC

If near limit cycle,
define phase, ϕ_2, to be point
on limit cycle to which
you approach as $t \to \infty$

$$\phi_2 = \Theta(X) \Rightarrow \lim_{t \to \infty} |u(t+\phi_2) - X(t)| = 0$$

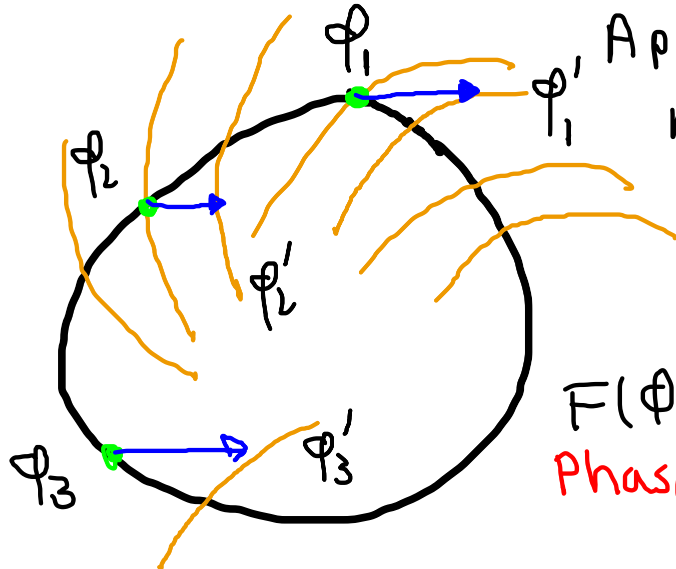
Isochron at ϕ

$$\{X \mid \Theta(X) = \phi\}$$

n-1 dimensional
manifold

$\Theta : N \to S^1$ maps a neighborhood, N, of
Limit cycle to asymptotic phase

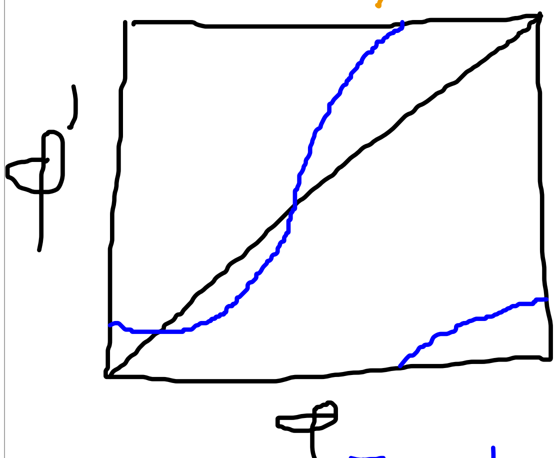
PRC's + perturbations



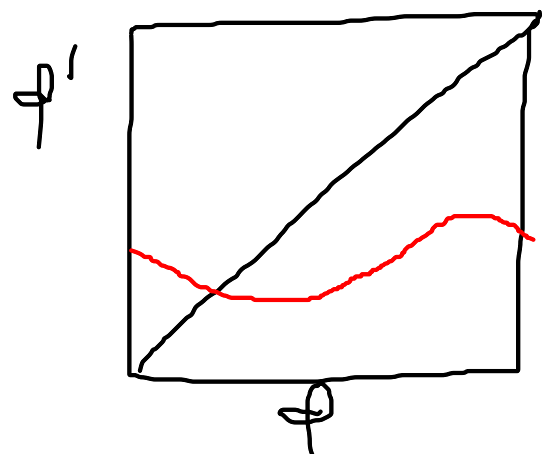
Apply perturbation at ϕ moves you to new isochron for ϕ'.

$$\phi' = F(\phi, Z)$$

$F(\phi, Z)$ is called the Phase transition curve

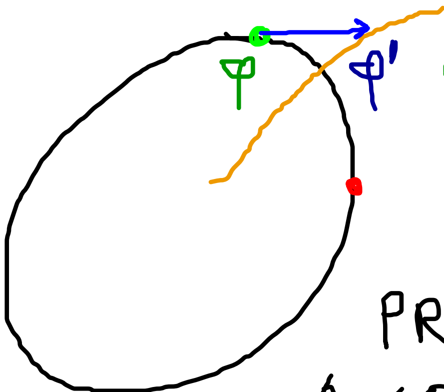


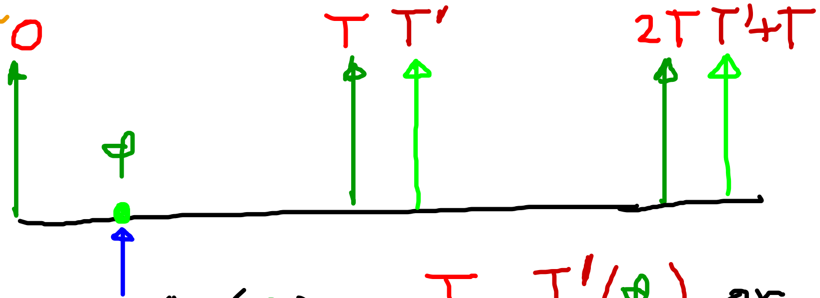
Topological Type 1
1:1 invertible
"Weak" resetting



Topological type 0
non invertible
STRONG RESETTING

Phase Response Curve (PRC)





PRC: $\Delta(\phi) = T - T'(\phi)$ or $2\pi\left[1 - \frac{T'(\frac{2\pi\phi}{T})}{T}\right]$

$\Delta < 0$ delay next spike

$\Delta > 0$ advance next spike

$\frac{d\theta}{dt} = 1$, if T' is time to next spike and "time" of stimulus is ϕ, then, new phase, ϕ' after stimulus must be such that $\phi' + T' - \phi = T$

ϕ': phase after stimulus; T': Total time elapsed; ϕ: phase of spike

that is: $F(\phi) \equiv \phi' = T - T' + \phi$

$= \Delta(\phi) + \phi$

$F(\phi) = \Delta(\phi) + \phi$ or $\Delta(\phi) = F(\phi) - \phi$

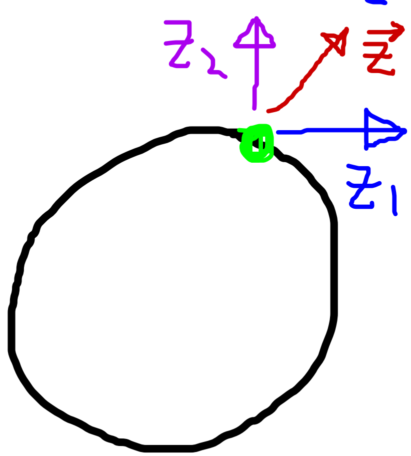
Infinitesimal PRC

$\Delta(\varphi_j; z)$ is PRC with stimulus magnitude z

$\Delta(\varphi_j; 0) = 0$ (Duh!)

so, $\Delta(\varphi_j; z) \approx \hat{\Delta}(\varphi)\, z$ for z small

$$\hat{\Delta}(\varphi) = \lim_{z \to 0} \frac{\Delta(\varphi_j; z)}{z}$$



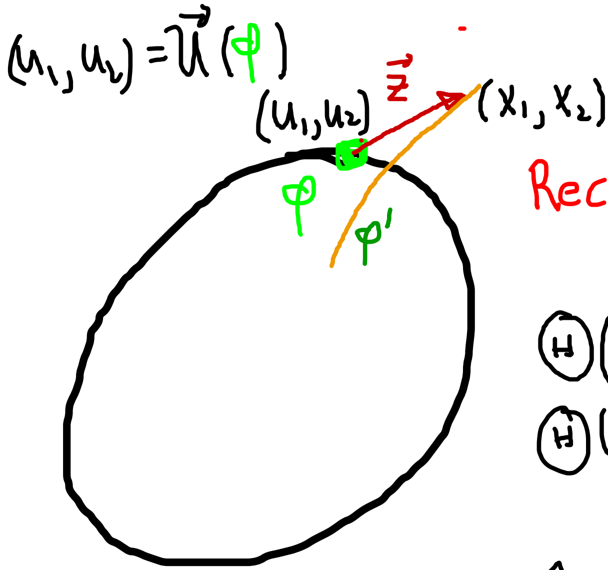
perturbation in any direction can be decomposed (if small) into

$$\left(\hat{\Delta}_1(\varphi)\, z_1,\ \hat{\Delta}_2(\varphi)\, z_2\right)$$

with net change in phase

$$\Delta(\varphi_j; \vec{z}) \approx \hat{\Delta}_1(\varphi)\, z_1 + \hat{\Delta}_2(\varphi)\, z_2$$

Adjoint



$x_1 = u_1 + z_1, \quad x_2 = u_2 + z_2$

Recall: $\Theta : N \to S^1$ maps nbhd $N \ni (x_1, x_2)$ to phase on limit cycle

$\Theta(u_1 + z_1, u_2 + z_2) = \varphi'$

$\Theta(u_1, u_2) = \varphi$

$$\hat{\Delta}_1(\varphi) z_1 + \hat{\Delta}_2(\varphi) z_2 \approx \Delta(\varphi; \vec{z}) = \varphi' - \varphi$$

$$= \Theta(u_1 + z_1, u_2 + z_2) - \Theta(u_1, u_2)$$

$$\approx \partial_1 \Theta(u_1, u_2) z_1 + \partial_2 \Theta(u_1, u_2) z_2$$

So,

$$\boxed{\begin{bmatrix} \hat{\Delta}_1(\varphi) \\ \Delta_2(\varphi) \end{bmatrix} = \nabla \Theta \Big|_{\vec{u}(\varphi)}}$$

Thus, if we can compute $\nabla \Theta$, we can approximate the PRC for any type of perturbation!

Adjoints (Analysis part)

Let $\frac{du}{dt} = F(u)$ be the stable limit cycle w/ period T, $u(t+T) = u(t)$

Define $A(t) := D_u F(u(t))$ be the Jacobi matrix evaluated at LC

$\frac{dy}{dt} = A(t) Y(t)$ has a periodic solution, $\dot{u}(t)$ (Prove this!)

$\langle v(t), w(t) \rangle := \int_0^T v(s) \cdot w(s)\, ds$ defines the usual inner product on periodic fns

Under this inner product, $Ly := \frac{dy}{dt} - A(t) y$, has an adjoint L^*

(recall, $\langle v, Lw \rangle = \langle L^* v, w \rangle$ defines the adjoint)

$L^* y^* = -\frac{dy^*}{dt} - A(t)^T y^*$

defines $Z(t)$, adjoint

Define $Z(t)$ as the unique solution to $\boxed{\frac{dZ}{dt} = -A(t)^T Z, \quad Z(t) \cdot \dot{u}(t) = 1}$

$$\boxed{\nabla \Theta \big|_{u(t)} = Z(t)}$$

Fundamental relationship

Proof

$\Theta(u+y) - \Theta(u)$ is the change in phase due to $y(t)$ and is independent of time

But, $\Theta(u+y) - \Theta(u) \simeq \nabla\Theta \cdot y$, thus $\frac{d}{dt}\left[\nabla\Theta\cdot y\right] = 0$,

$$\boxed{\frac{d\nabla\Theta}{dt}\cdot y + \nabla\Theta\cdot\frac{dy}{dt} = 0.}$$

y is a small perturbation off LC

so, $\boxed{\frac{dy}{dt} = A(t)y}$

$$\frac{d}{dt}\nabla\Theta\cdot y + \nabla\Theta\cdot A(t)y = 0 \qquad (x\cdot Ay = A^T x\cdot y)$$

$$\left[\frac{d}{dt}\nabla\Theta + A(t)^T\nabla\Theta\right]\cdot y(t) = 0$$

since y is an arbitrary perturbation, we must have

$$\boxed{\frac{d}{dt}\nabla\Theta = -A(t)^T\nabla\Theta}$$

note, $\Theta(U(\varphi)) = \varphi$ so

$\frac{d}{d\varphi}\left(\Theta(U(\varphi))\right) = 1$ or $\boxed{\nabla\Theta\cdot\dot{U}(\varphi) = 1} \Longrightarrow \boxed{\nabla\Theta = Z}$

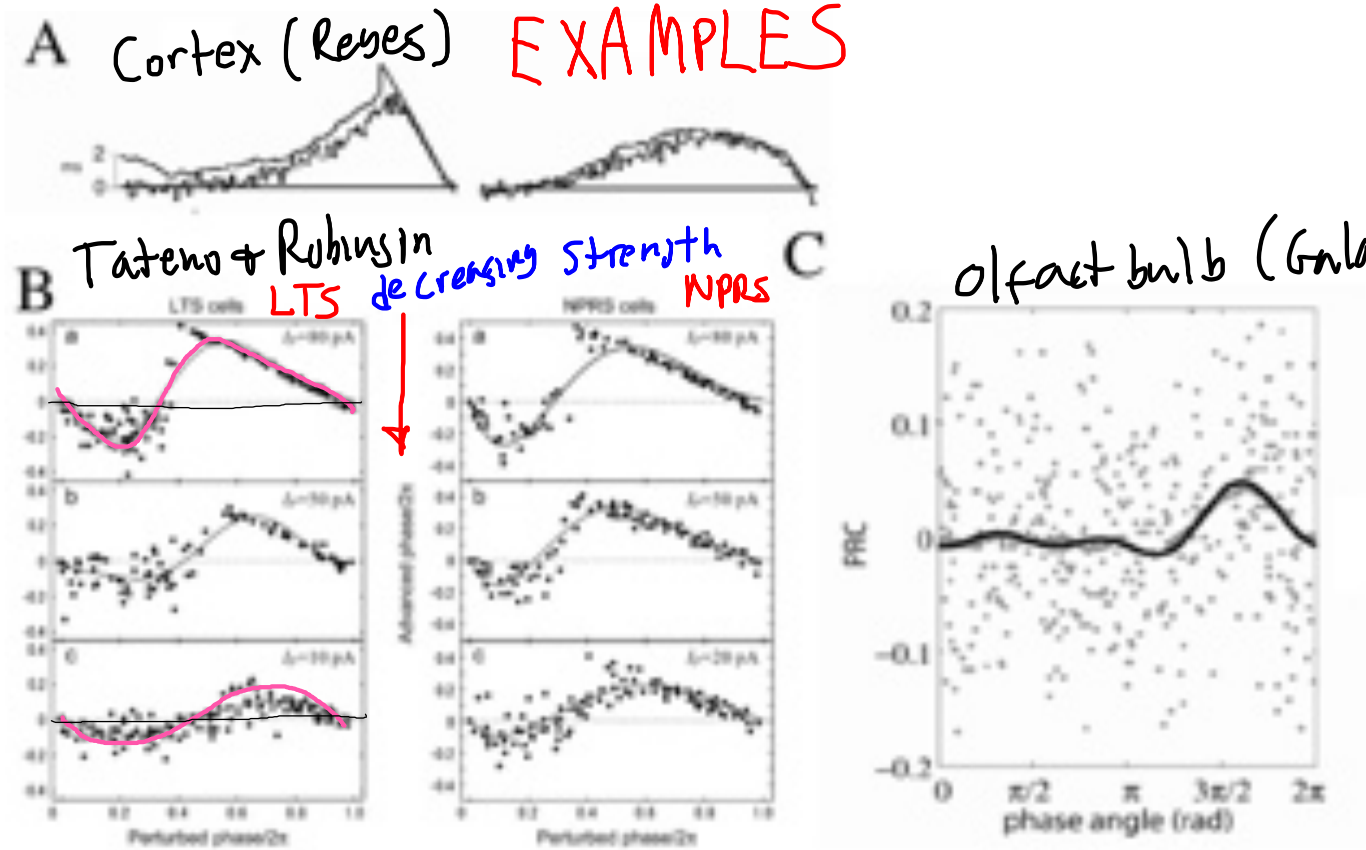
Compute $Z(t)$ by solving $\frac{dW}{dt} = A(-t)^T W$, $Z(t) = K\,W(-t)$

Implications for neurons

Compute PRC with current perturbations which affect voltage

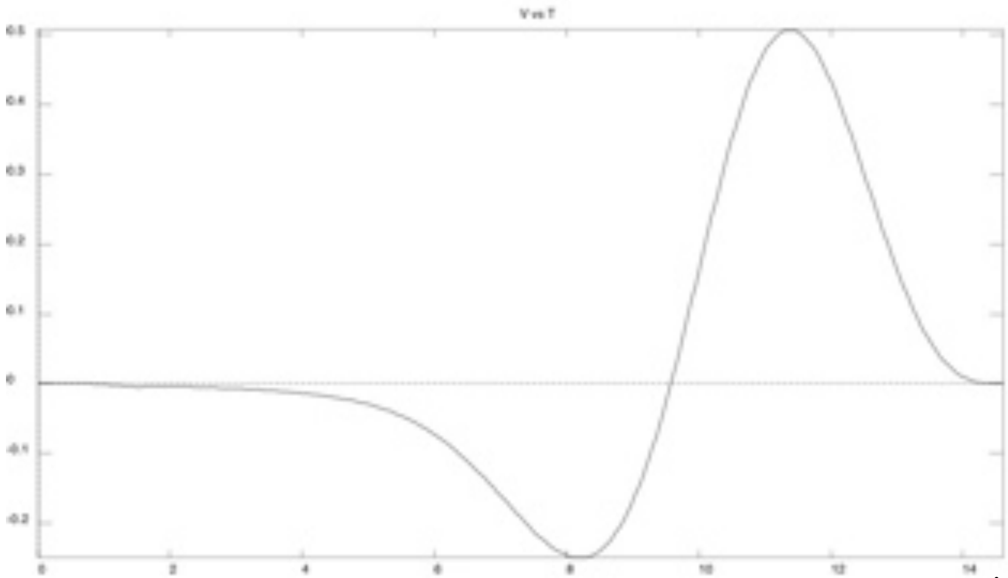
so, $\Delta(\phi) \simeq \alpha Z_V(t)$ ← voltage component of Z, the adjoint

Experimentally compute PRC's with stimuli



HH equation, numerically

$Z_v(t)$



0 peak of AP   time   14.4

"Type II" PRC
has positive + negative reset

Can we say anything about PRC's in general?

usually compute numerically. XPP automates the process

1\. One dimensional models $\frac{dx}{dt} = f(x)$; $f(x+2\pi) = f(x)$; $f(x) > 0$

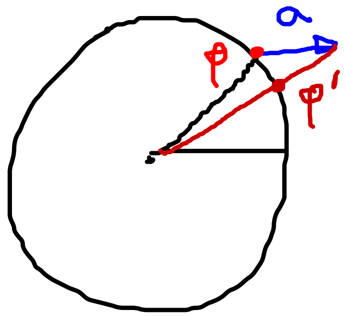
$T = \int_0^{2\pi} \frac{dy}{f(y)}$, $x(t+T) = x(t) + 2\pi$ called ring model

$\dot{x}(t)\, z(t) = 1 \Rightarrow z(t) = 1/\dot{x}(t)$

example $\dot{x} = 1 - a\cos x$, $|a| < 1$; $x(t) = 2\,\mathrm{atan}\left[\sqrt{\frac{1-a}{1+a}}\tan\left(\frac{\sqrt{1-a^2}}{2}t\right)\right]$

$z(t) = a\left(\cos\sqrt{1-a^2}\,t + 1\right)/(1-a^2)$

2\. Radial isochron clock



Exercise: compute $\varphi' = F(\varphi, a)$ using trig

compute $\displaystyle\lim_{a \to 0} \frac{F(\varphi, a) - \varphi}{a} = \Delta_x(\varphi)$

3\. Normal form for SNIC:

$\dot{x} = 1 - \cos x + (1 + \cos x)a, \quad a > 0$ (this is a ring model!)

4\. Normal form near HB

$\dot{x} = x\lambda(r) - y\,\omega(r) \qquad \lambda(1) = 0, \; \lambda'(1) < 0, \; \omega(1) = 1$

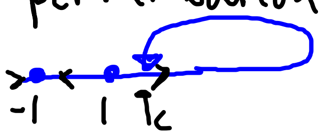
$\dot{y} = y\lambda(r) + x\,\omega(r) \qquad r = \sqrt{x^2 + y^2}$

$[x(t), y(t)] = (\cos t, \sin t)$

Exercise: compute $(x^*(t), y^*(t))$ (see K+E 1984)

5\. $\dot{x} = x^2 - 1$; $x(0) > 1$; when $x(t) = +\infty$, $x(t)$ is reset to $a > 1$.

perturbation of size $b > 0$ at time $t \in [0, T)$



Compute T, + the $PRC(t; b, c)$

Compute $\displaystyle\lim_{b \to 0} \frac{PRC(t; b, c)}{b} = Z$ (still a ring model!)

Pulse Coupled Oscillators

Two identical oscillators.
Each time one oscillator "fires" it gives a brief pulse to the other one

$$\dot{\Theta}_1 = 1 + \delta(\mathrm{mod}(\theta_2, T))\,\Delta(\theta_1)$$

moves around @ uniform speed

kick from 2

shift by PRC

We will construct a map. Let ϕ be phase of #2 when #1 hits T.

1. $\Theta_2 \to \phi + \Delta(\phi) \equiv F(\phi)$, $\Theta_1 \to 0$

2. Assume $F(0)=0$, $F(T)=T$, $F'(\phi)>0$

Takes $T - F(\phi)$ for Θ_2 to fire, at which point

$\Theta_1 = T - F(\phi)$ since $\theta_1' = 1$, $\theta_1(0) = 0$

$\Theta_1 \to F(T - F(\phi))$, $\Theta_2 \to 0$

kick from 2

Map, cont'd

3. $\theta_2 = 0$, $\theta_1 = F(T - F(\phi))$, so it takes θ_1 $T - F(T - F(\phi))$ to fire, & $\theta_2 = T - F(T - F(\phi))$

4. $\phi_{new} = T - F(T - F(\phi))$ our map!

$\phi_{n+1} = M(\phi_n)$; $M(\phi) = T - F(T - F(\phi))$

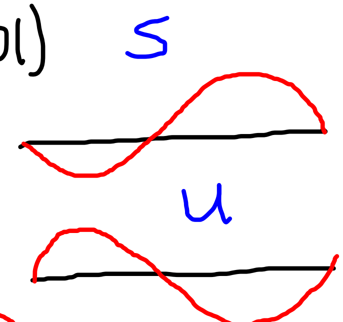
Fixed points $\bar{\phi} = M(\bar{\phi})$

stable iff $|M'(\bar{\phi})| < 1$

$M(0) = 0$ (synchrony) $\quad T - F(T - F(0))$

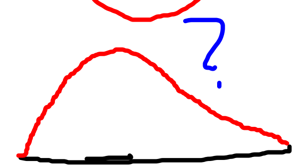
$= T - F(T)$

$= 0$



$M'(0) = F'(T)\,F'(0)$

$= (1 + \Delta'(T))(1 + \Delta'(0))$



Shape of PRC matters!

HW ① Try $\Delta(\varphi) = a\sin\varphi + b\sin 2\varphi$ $T = 2\pi$

② $\Delta(\varphi) = \varphi^\alpha (1-\varphi)^\beta$, $T = 1$, $\alpha, \beta \geq 1$

PRC shape is tightly tied to the ionic conductances in neurons. For example:

1) M-current can cause negative lobe near 0
2) A-current can cause positive PRC
3) Persistent sodium can alter skew
4) Ca-dep K can flatten PRC near 0

Weak Coupling

$$\dot{X}_1 = F(X_1) + \varepsilon G_1(X_2, X_1)$$
$$\dot{X}_2 = F(X_2) + \varepsilon G_2(X_1, X_2)$$

Assume: $\dot{u} = F(u)$ has exponentially stable LC

Preliminaries: $A(t) = D_X F(X)\big|_{u(t)}$

$$\dot{Z}(t) = -A(t)^T Z(t), \quad Z(t) \cdot \dot{u}(t) = 1$$

Fredholm alternative:
$Lx = b$ has a solution if and only if $\langle z, b \rangle = 0$ for all z s.t. $L^* z = 0$

$$R_L = (N_{L^*})^\perp$$ Fundamental thm of L.A.

Weak Coupling II

To study weak coupling, we introduce a simple series expansion using the method of multiple scales:

Let $\tau = \varepsilon t$ be a slow time scale

Write $X_j(t) = U(t+\theta_j(\tau)) + \varepsilon Y_j(t;\tau) + \ldots$

Then we get to $O(\varepsilon)$

$$\dot{U}(t+\theta_j)\frac{\partial\theta_j}{\partial\tau} + \dot{Y}_j = A(t+\theta_j)Y_j + G_j(U(t+\theta_k), U(t+\theta_j))$$

which we rewrite as

$$L(t+\theta_j)Y_j(t+\theta_j) = -\dot{U}(t+\theta_j)\frac{\partial\theta_j}{\partial\tau} + G_j(\cdots)$$

Weak coupling III

$$L(t+\theta_j)Y_j(t+\theta_j) = -\dot{u}(t+\theta_j) + G_j(t+\theta_n, t+\theta_j)$$

$$L(t)Y(t) := \frac{dY}{dt} - A(t)Y(t), \quad A(t) = D_x F(u(t))$$

We have an equation of the form

$$L(t)y(t) = f(t) \quad (\star)$$

in the space of periodic functions

$L(t)\dot{u}(t) = 0$ so $L(t)$ has a nontrivial nullspace

Thus we can solve $(\star)$ iff

$$\int_0^T Z(t)\cdot f(t)\,dt \equiv \langle Z, f\rangle = 0$$

Recall $L^*(t)Z(t) = 0$

Apply to our problem!

$$L(t+\theta_j)Y(t+\theta_j) = -\dot{u}(t+\theta_j)\frac{d\theta_j}{d\tau} + G_j(u(t+\theta_k), u(t+\theta_j))$$

$$L^*(t+\theta)\,Z(t+\theta) = 0$$

$$\int_0^T -Z(t+\theta_j)\cdot\dot{u}(t+\theta_j)\frac{d\theta_j}{d\tau} + Z(t+\theta_j)\cdot G_j(u(t+\theta_k), u(t+\theta_j))\,dt$$

$Z(t)\cdot\dot{u}(t) = 1$, so we get

$$\frac{d\theta_j}{dt} = \frac{1}{T}\int_0^T Z(t+\theta_j)\cdot G_j(u(t+\theta_k), u(t+\theta_j))\,dt$$

$$= \frac{1}{T}\int_0^T Z(t)\cdot G_j(u(t+\theta_k-\theta_j), u(t))\,dt \equiv H_j(\theta_k-\theta_j)$$

MAIN POINT

$$\frac{d\theta_j}{d\tau} = \sum_k H_{jk}(\theta_k - \theta_j)$$

Phase model
Weak coupling

define $H_{jj}(0) \equiv \omega_j$ as heterogeneity in par's

$$\frac{d\theta_j}{dt} = \omega_j + \sum_{k \neq j} H_{jk}(\theta_k - \theta_j)$$

Phase locked solution $\theta_j(\tau) = \Omega\tau + \phi_j, \quad \phi_1 = 0$

$$\Omega = \omega_j + \sum_{k \neq j} H_{jk}(\phi_k - \phi_j)$$

N equations in
$\Omega, \phi_2, \ldots, \phi_N$
N unknowns

Stability theory

"Master Stability Thm!"

Consider:

$$\theta_j' = H_j(\theta_1-\theta_j, \ldots, \theta_N-\theta_j), \quad j=1,\ldots,N$$

$$\text{"}\xi_1, \ldots, \xi_N\text{"}$$

Suppose $\theta_j = \Omega t + \phi_j$ is a phaselocked solution

Let $a_{jk} = \left.\dfrac{\partial H_j}{\partial \xi_k}\right|_{(\phi_1,\ldots,\phi_N)}$ (0)

Suppose $a_{jk} \geq 0$ and (a_{jk}) is irreducible

Then the locked solution is exponentially stable

Remark Draw N nodes + draw a directed $\longrightarrow$ line from j to k if $a_{jk} > 0$.

(a_{jk}) is irreducible iff you can go from any l to any k

Examples

$\theta_1' = \omega_1 + H(\theta_2 - \theta_1)$ Let $\phi = \theta_2 - \theta_1$

$\theta_2' = \omega_2 + H(\theta_1 - \theta_2)$

$\phi' = \omega_2 - \omega_1 + H(-\phi) - H(\phi)$

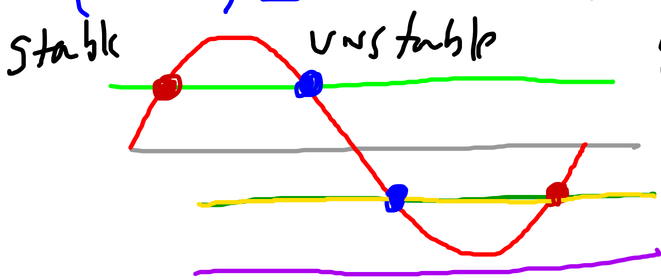
$= \delta - 2g(\phi)$ g is odd part of $H(\phi)$

Let $g(\bar\phi) = \delta/2$

$\bar\phi$ is stable when $\boxed{g'(\bar\phi) > 0}$

If $\delta = 0$, then $\exists$ at least two roots: $\bar\phi = 0$ (sync)

$\bar\phi = T/2$ "anti phase"



$\delta/2 > 0$ $\bar\phi > 0$, #2 leads

$\delta/2 = 0$ sync

$\delta/2 < 0$ $\bar\phi < 0$, #2 lags

no roots $\dot\phi < 0$ #2 falls behind

H H revisited

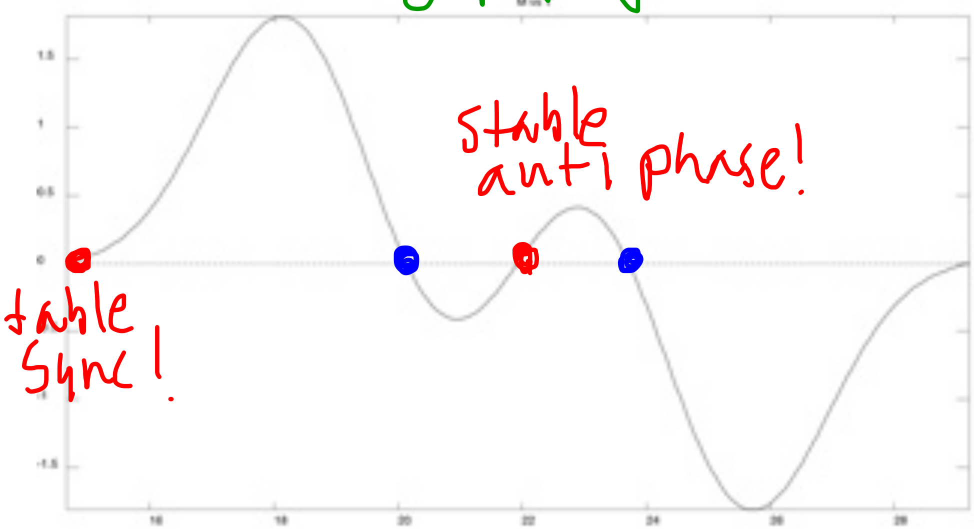
$$\dot{S} = f(V)(1-S) - \beta S$$

$$I^j_{syn} = -g_{syn} S_k (V_j - E_{rev})$$

or $\quad -g_{gap}(V_j - V_k)$

GAP junction

$g(\phi)$

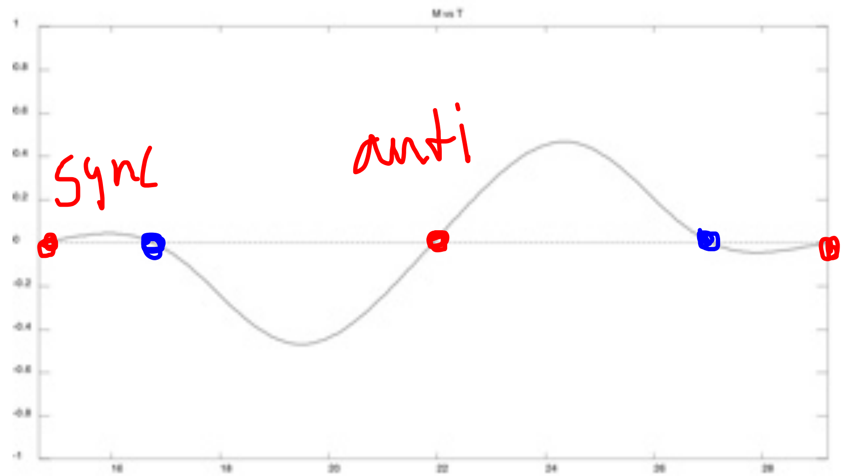


stable anti phase!

stable sync!

HH, Erev = -85

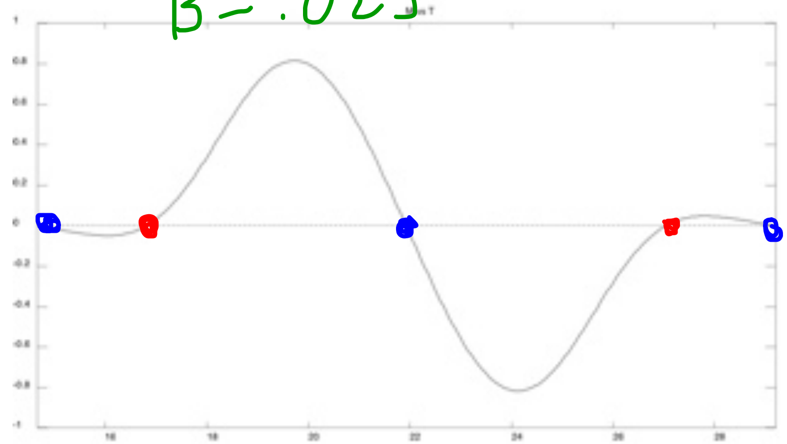
slow decaying S



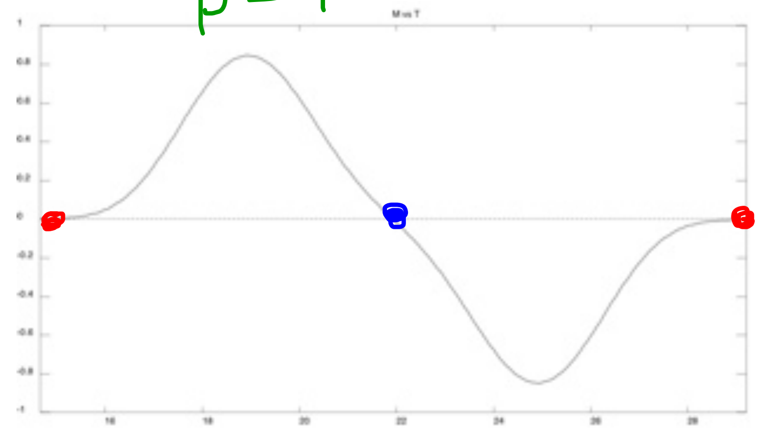
fast decay syn

$E_{rev} = 0$ mV

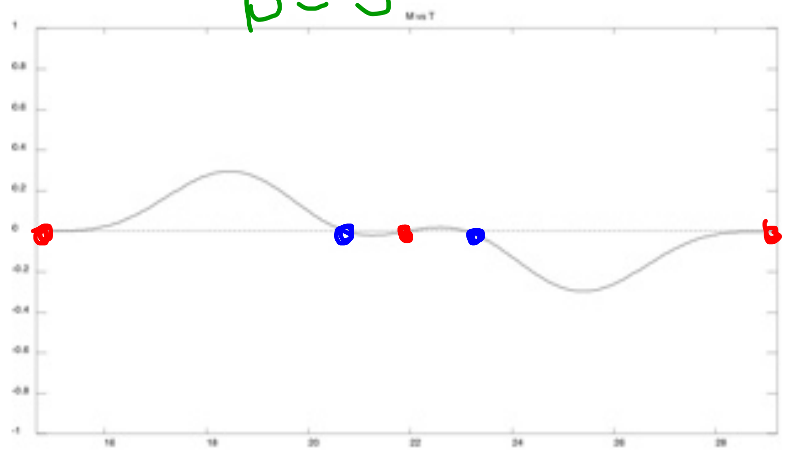
$\beta = .025$



$\beta = 1$

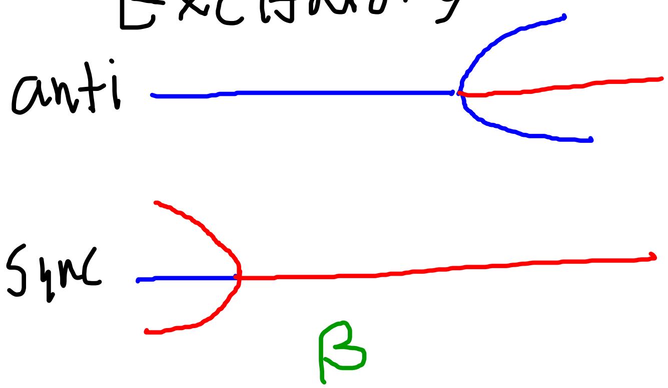


$\beta = 3$

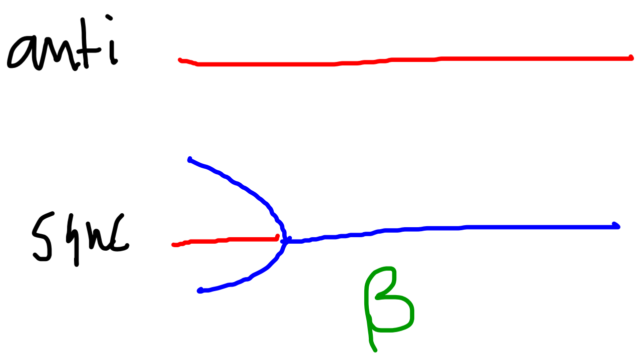


Summary weak syn coupling HH

Excitatory



Inhibitory



1. Nature of coupling matters
   - time scale
   - "sign"
2. Shape of PRC matters
   - determined by local bifurcations
   - which, in turn, determ'd by ionic conductance, frequency, etc etc!

Networks

1-d chains:

$$\theta_j' = \omega_j + H(\theta_{j+1} - \theta_j) + H(\theta_{j-1} - \theta_j), \quad j = 1, \ldots, N$$

($j=1, N$, terms deleted)

There are a few solvable examples

Let $\phi_j = \theta_{j+1} - \theta_j$ $\quad \phi_1' = \delta_1 + H(\phi_2) + H(-\phi_1) - H(\phi_1)$

$$\phi_j' = \delta_j + H(\phi_{j+1}) - H(-\phi_{j-1}) - H(\phi_j) + H(-\phi_j)$$

$$\phi_n' = \delta_n - H(\phi_n) + H(-\phi_n) - H(-\phi_{n-1}), \quad n = N-1, \quad \delta_j = \omega_{j+1} - \omega_j$$

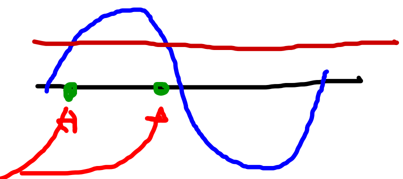
Suppose $H(-\phi) = -H(\phi)$, so $H(\phi)$ is odd

Locked solutions satisfy

$$0 = \vec{\delta} + D\vec{V}, \quad \vec{V} = \begin{bmatrix} H(\phi_1) \\ \vdots \\ H(\phi_n) \end{bmatrix}, \quad \delta = \begin{bmatrix} \delta_1 \\ \vdots \\ \delta_n \end{bmatrix} \quad D = \begin{bmatrix} -2 & 1 & 0 & \cdots & & 0 \\ 1 & -2 & 1 & 0 & \cdots & \\ & & \ddots & \ddots & & \\ & & & 1 & -2 & 1 \\ 0 & 0 & \cdots & \cdots & 1 & -2 \end{bmatrix}$$

Chains, cont'd

$H(\phi_j) = (D^{-1}\vec{\delta})_j$ (D is invertible)



$(D^{-1}\vec{\delta})_j$

This has at least 2^n solutions

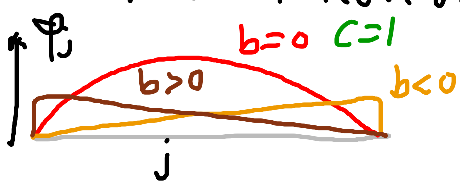
Only those with a positive slope are stable

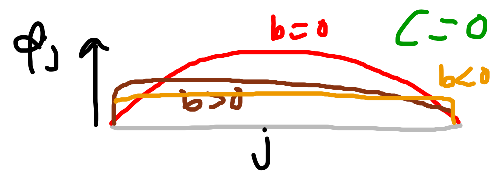
Thus, of the 2^n solutions, only 1 is stable!

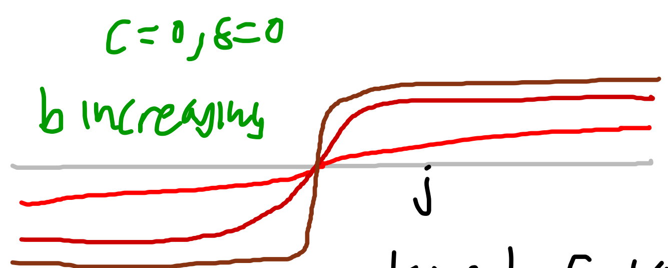
Example $H(\phi) = \sin\phi$, $\vec{\delta} = \delta\vec{1}$, fixed gradient

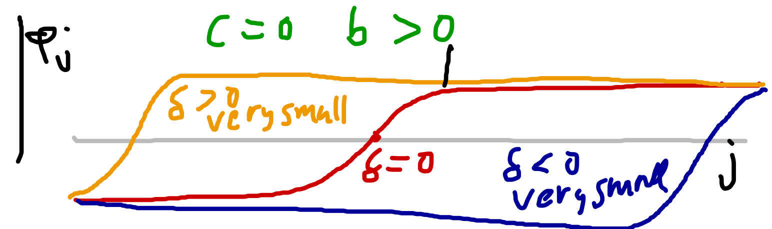
$$\sin\phi_j = \delta\,\frac{j(N-j)}{2} \Rightarrow |\delta| \lesssim \frac{N^2}{4} \Rightarrow$$ Can support very weak gradients

What about non odd: $H(\phi) = \sin\phi + b\,(c - \cos\phi)$ ($c=1$ Diffusive coupling)









Kopell + E 1980's

Rings

$$\dot\theta_j = \omega_j + H(\theta_{j+1}-\theta_j) + H(\theta_{j-1}-\theta_j) \quad j=1,\ldots,N$$

$0 \leftarrow N, \; N+1 \to 1$

Suppose $\omega_j = \omega$. $\theta_j = \Omega_m t + \frac{2\pi j m}{N}$ Travelling wave!

$$\Omega_m = \omega + H\left(\frac{2\pi m}{N}\right) + H\left(\frac{-2\pi m}{N}\right) \quad \text{DISPERSION RELATION}$$

If $H(\phi) = -H(-\phi)$ (H, odd), then $\Omega_m = \omega \; \forall m$

When there are even components, then there are frequency diffs

STABILITY

$$\dot y_j = H'(\psi_m)[y_{j+1}-y_j] + H'(-\psi_m)[y_{j-1}-y_j], \quad \psi_m = \frac{2\pi m}{N}$$

$$y_j = e^{\lambda t} e^{2\pi i j n/N}$$

$$\mathrm{Re}\,\lambda = H'(\psi_m)\left[\cos\frac{2\pi n}{N} - 1\right] + H'(-\psi_m)\left[\cos\frac{2\pi n}{N} - 1\right]$$

for H odd

$$\mathrm{Re}\,\lambda = 2H'(\psi_m)\left[\cos\frac{2\pi n}{N} - 1\right]$$

≤ 0 iff $H'(\psi_m) > 0$

Synchrony $\Leftrightarrow H'(0) > 0$

Two-d arrays

0	ξ	$\frac{\pi}{2}-\xi$	$\frac{\pi}{2}$
$-\xi$	0	$\frac{\pi}{2}$	$\frac{\pi}{2}+\xi$
$\frac{3\pi}{2}+\xi$	$\frac{3\pi}{2}$	π	$\pi-\xi$
$\frac{3\pi}{2}$	$\frac{3\pi}{2}-\xi$	$\pi+\xi$	π

$$\dot{\theta}_j = \omega + \sum_{k \in NN(j)} H(\theta_k - \theta_j)$$

PROVE For $H(\varphi) = \sin\varphi$ find $\xi \in (0, \pi/2)$

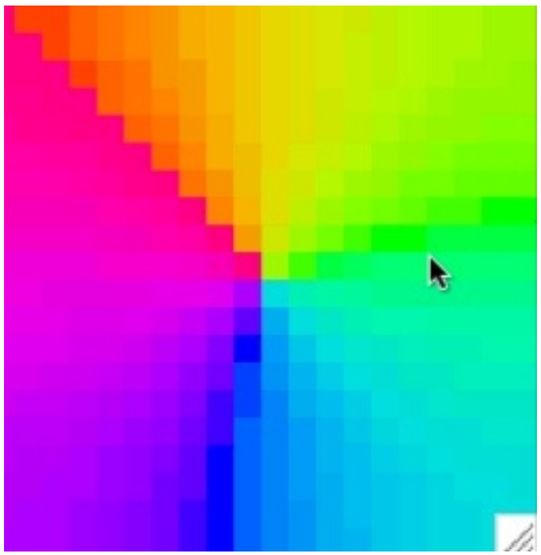
Prove Stable also!

Paullet proved if H is odd and $H'(\varphi) > 0$ for $-\frac{\pi}{2} < \varphi < \frac{\pi}{2}$
Then $\exists$ rotating wave for $2N \times 2N$ arrays

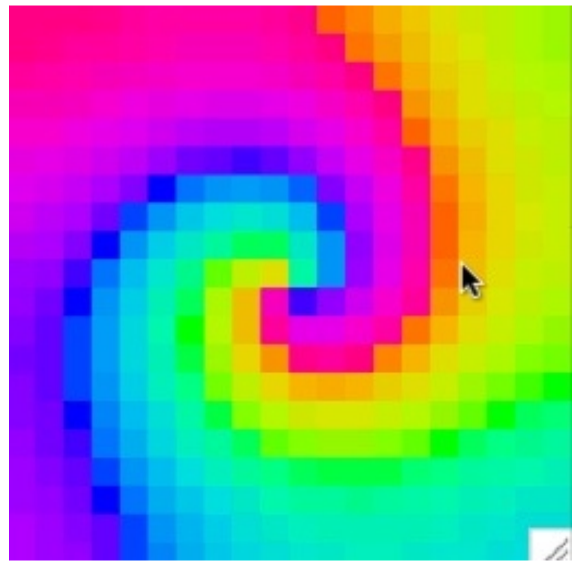
What happens when $H(\varphi)$ is not odd?

Wave with a twist!

$H(\phi) = \sin\phi + b(1-\cos\phi)$



20 x 20 $b=0$



20 x 20 $b=0.5$

Intuition: think of series of concentric rings
When $b=0$ no dependence of freq on ring size
but, for $b\neq0$, dispersion $\Rightarrow$ waves go @
diff freq, so get twisted

Waves with a twist (drift instability)

t1 t2 t3

$b = 0.85$

When freq diff is too big they cannot lock + get drift instability!

Noise + Oscillators

$$\frac{dX}{dt} = F(X) + \sigma \begin{pmatrix} 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix} \xi(t) \leftarrow \text{just put noise in voltage}$$

If σ is small, we can approximate this by studying the phase model:

$$\dot{\theta} = 1 + \sigma \Delta(\theta) \xi(t)$$

Caution: If $\xi(t)$ is white then, need other terms (but will be small)

Stochastic Synchrony

$$\dot\theta_1 = 1 + \sigma\xi(t)\Delta(\theta_1)$$
$$\dot\theta_2 = 1 + \sigma\xi(t)\Delta(\theta_2)$$

$\boxed{\text{Identical Noise}}$

$\phi = \theta_2 - \theta_1, \quad \theta_1$

$$\dot\theta_1 = 1 + \sigma\xi(t)\Delta(\theta_1)$$
$$\dot\phi = \sigma\xi(t)\left[\Delta(\theta_1+\phi) - \Delta(\theta_1)\right]$$
$$\approx \sigma\xi(t)\left[\Delta'(\theta_1)\phi\right]$$

$\xi(t)$ white, eg

Let $y = \ln(\phi)$ Apply ITÔ's Lemma

$$\frac{dy}{dt} = -\frac{\sigma^2}{2}\Delta'(\theta_1)^2 + \sigma\xi(t)\Delta'(\theta_1)$$

ASIDE: ITÔ'S Lemma

$dx = a\,dt + b\,dW$ (Change of variables)

$y = f(x)$ $\quad dy = f'(x)\,dx + \frac{f''(x)}{2}\,dx^2 + \cdots$

IMPORTANT THING ABOUT WHITE NOISE

"$(dW)^2 = dt$"

$$dy = f'(x)\left[a\,dt + b\,dW\right] + \underbrace{\frac{f''(x)}{2} b^2\,dt}_{\text{Extra term}}$$

Example $\quad y = \ln(x)$

$$dy = \frac{1}{x}\,dx - \frac{1}{2x^2}(dx)^2$$

Back to oscillators:

$$y = \ln(\varphi),$$

$$\frac{dy}{dt} = -\frac{\sigma^2}{2}\Delta'(\theta_1)^2 + \sigma\xi(t)\Delta'(\theta_1)$$

$$y \sim -\frac{\sigma^2}{2}\int \Delta'(\theta_1)^2\,dt + \text{Noise}$$

$$\langle y\rangle = \lim_{T\to\infty} -\frac{\sigma^2}{2}\int_0^T \Delta'(\theta_1(s))^2\,ds$$

$$-\frac{\sigma^2}{2}\int_0^{2\pi} \Delta'(\theta)^2 P(\theta)\,d\theta$$

For σ small, $\theta \sim$ uniform

$$\langle y\rangle \approx -\frac{\sigma^2}{2\cdot 2\pi}\int_0^{2\pi}\Delta'(\theta)^2\,d\theta$$

Liapunov exponent

$$\lambda = -\frac{\sigma^2}{2}\frac{1}{2\pi}\int_0^{2\pi} \Delta'(\theta)^2 d\theta$$

tells us how fast ϕ will converge to 0

λ is always negative for weak noise

General Results

$\Omega \equiv$ mean frequency of oscillator

$$D := \int_{-\infty}^{\infty} \langle [\dot{\phi}(t) - \langle \dot{\phi} \rangle (t)][\dot{\phi}(t+\tau) - \langle \dot{\phi} \rangle (t)] \rangle \, d\tau$$

phase diffusion (ISI variability)

For $\dot{x} = f(x,t)$

$$\dot{y} = f_x(x,t)\, y$$

$$\lambda = \lim_{T \to \infty} \frac{1}{T} \ln |y(t)|$$

Liapunov exponent

General Noise

$$C(\tau) = \langle \xi(t)\,\xi(t-\tau) \rangle$$

$$\Omega = 1 + O(\sigma^2) \quad \text{complicated}$$

$$D = \sigma^2 \left\langle \int_{-\infty}^{\infty} d\tau\, \Delta(\phi)\, \Delta(\phi+\tau)\, C(\tau) \right\rangle_\phi$$

$$\lambda = -\sigma^2 \left\langle \Delta'(\phi) \int_0^{\infty} \Delta'(\phi - s)\, C(s)\, ds \right\rangle_\phi$$

For example, we can ask what shape the oscillator's PRC should be to minimize λ for given $C(s)$

Slow Coupling

Example 1:

Some animals such as Pteroptyx malaccae, a South east Asian firefly

can not only shift phase, but also alter their ω!

Eve Marder + colleagues have suggested a Homeostatic

Change in parameters gated by Calcium as a means of altering conductances

So to get started I will consider the following:

$$\dot{X}_j = F(X_j, \underbrace{I_j}_{\text{parameter}}) + \varepsilon\, G(X_k, X_j) \quad \leftarrow \text{Weak coupling}$$

$$\dot{I}_j = \varepsilon[\gamma(X_k) - \gamma(X_j)] + \varepsilon\,\eta\left[I_0 + \varepsilon\bar{\omega}_j - I_j\right] \quad \leftarrow \text{Slow coupling}$$

$$\varepsilon = 0, \quad I_j = I_0, \quad X_j(t) = X_0(t) \qquad \dot{X}_0 = F(X_0, I_0)$$

As usual $\exists$ T-periodic limit cycle, $X_0(t+T) = X_0(t)$

Let $\tau = \varepsilon t$ Write: $X_j(t) = X_0[t + \theta_j(\tau)] + \varepsilon Y_j[t;\tau] + O(\varepsilon^2)$

$I_j = I_0 + \varepsilon W_j + \varepsilon^2 V_j$

$$\theta_j' \dot{X}_0(t+\theta_j) + \dot{Y}_j = D_X F(X_0(t+\theta), I_0) + D_I(X_0, I_0) W_j + G(X_0(t+\theta_k), X_0(t+\theta_j))$$

$$\dot{W}_j = [\underbrace{\gamma(X_0(t+\theta_k)) - \gamma(X_0(t+\theta_j))}_{\text{integrates to 0 over } T}]$$

$$\Rightarrow W_j = \zeta(t+\theta_k) + \zeta(t+\theta_j) + q_j(\tau) \qquad \zeta(t) = \int_0^t \gamma(s)\,ds \qquad q_j \text{ is UNKNOWN!}$$

$$\dot{V}_j + q_j' = \underbrace{\gamma'(X_0(t+\theta_k))Y_k - \gamma'(X_0(t+\theta_j))Y_j}_{M(t+\theta_j,\, t+\theta_k)} + \eta[\omega_j - W_j]$$

V_j must be periodic in fast time, so:

$$\frac{dq_j}{d\tau} = \left[\frac{1}{T}\int_0^T M(t+\theta_j, t+\theta_k)\,dt + \eta\left[\omega_j - \frac{1}{T}\int_0^T W_j(t;\tau)\,dt\right]\right] \quad \bigstar$$

Almost There.

$$\dot{Y}_j = -\theta_j' \dot{X}_0 + \underbrace{D_X F(X_0(t+\theta_j), I_0)}_{A(t+\theta_j)} Y_j + G(X_0(t+\theta_k), X_0(t+\theta_j)) + D_I F(X_0(t+\theta_j), I_0) W_j$$

$\dot{Y}_j - A(t) Y_j \Leftarrow$ nontrivial nullspace

$$\Rightarrow \frac{1}{T}\int_0^T -X_0^*(t+\theta_j)\dot{X}_0(t+\theta_j)\,dt\,\frac{d\theta_j}{d\tau} + \underbrace{\frac{1}{T}\int_0^T X_0^*(t+\theta_j)\,G(X_0(t+\theta_k), X_0(t+\theta_j))\,dt}_{h_1} +$$

$$\underbrace{\frac{1}{T}\int_0^T X_0^*(t+\theta_j)\,D_I F(X_0(t+\theta_j), I_0)\,W_j(t,\tau)\,dt}_{h_2 + \beta} \equiv 0 \qquad (\star\star)$$

Lets unwrap it all

$$(\star\star) \Rightarrow \boxed{\frac{d\theta_j}{dt} = h_1(\theta_k - \theta_j) + h_2(\theta_k - \theta_j) + \beta\, q_j(\tau)} \Rightarrow$$

$$Y_j(t,\tau) = R_1(t+\theta_j)\frac{d\theta_j}{d\tau} + R_2(t+\theta_j, t+\theta_k) + R_3(t+\theta_j, t+\theta_k) + R_4(t+\theta_j)\, q_j$$

$$\frac{dq_j}{d\tau} = g_1(\theta_k - \theta_j) + \alpha(q_1 + q_2) + \eta[\omega_j - q_j] + \alpha_2\frac{d\theta_j}{dt} + \alpha_3\frac{d\theta_k}{dt}$$

This can be simplified to the following:

$$\frac{d\theta_j}{dt} = h(\theta_k - \theta_j) + \beta\, q_j \qquad \frac{dq_j}{dt} = \eta[\omega_j - q_j] + k[q_1 + q_2] + g(\theta_k - \theta_j)$$

Example with locking

Let $\phi = \theta_2 - \theta_1$ and $u = q_2 - q_1$

$$\frac{d\phi}{dt} = \underbrace{h(-\phi) - h(\phi)}_{-2h_0(\phi)} + \beta u \qquad \Delta = \omega_2 - \omega_1$$

$$\frac{du}{dt} = \eta\,[\Delta - u] + \underbrace{g(-\phi) - g(\phi)}_{-2g_0(\phi)}$$

Think of η as the "stiffness" of the frequencies

Infinite stiffness $\Rightarrow u \equiv \Delta$

$0 = -2h_0(\phi) + \beta\Delta \qquad \Delta \in \frac{1}{\beta}[-\mu, \mu] \qquad \mu = 2\max_{\phi} h_0(\phi)$

$\Rightarrow$ limited range in locking

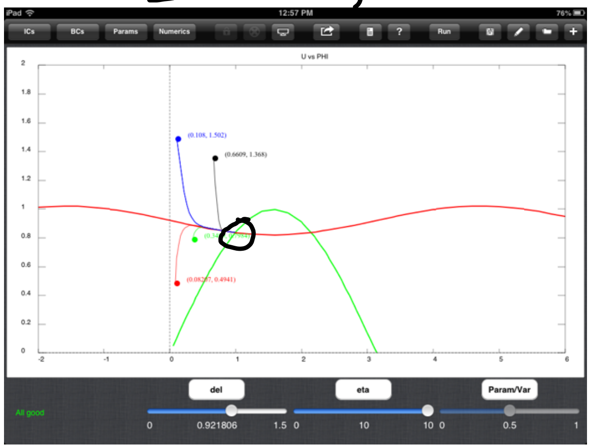
eg for $h = \frac{1}{2}\sin(\phi) = g \Rightarrow \mu \in (-1, 1)$

Take $\sin(\phi)$ as above, $\beta = 1$ (WLOG)

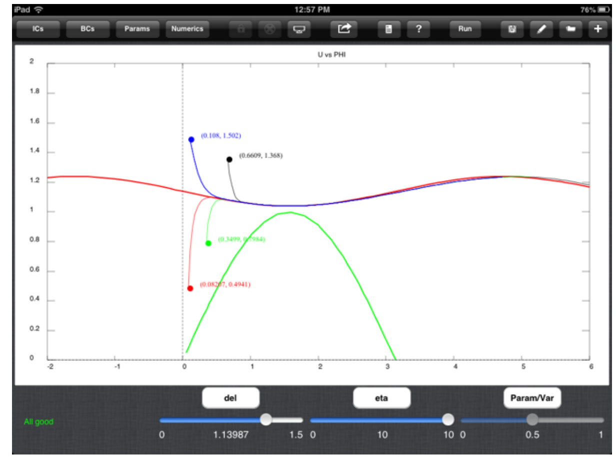
$0 = -\sin\phi + u, \quad 0 = -\sin\phi + \eta[\Delta - u] \Rightarrow u = \eta[\Delta - u]$

$$\Rightarrow u = \frac{\eta \Delta}{1+\eta} \Rightarrow \Delta \in \left(-\frac{1+\eta}{\eta}, \frac{1+\eta}{\eta}\right) \to (-\infty, \infty) \text{ as } \eta \to 0$$

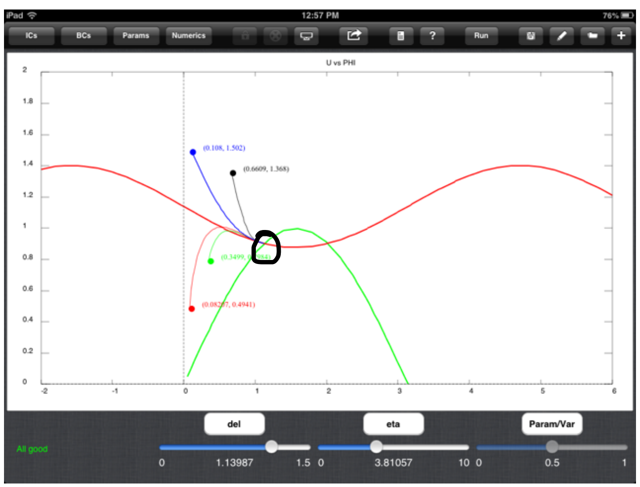
$\Delta = .98, \eta = 10$



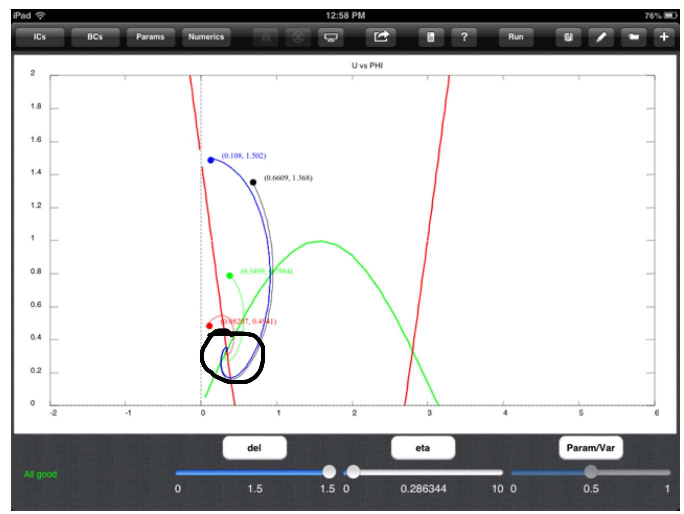
$\Delta = 1.1 \quad \eta = 10$



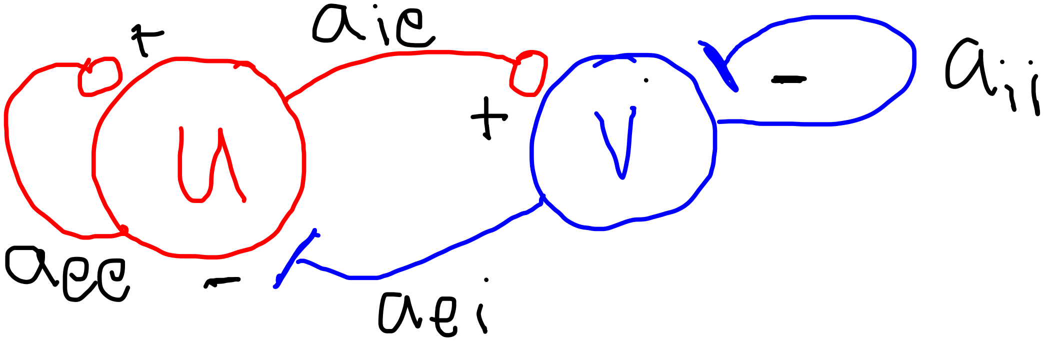
$\Delta = 1.3, \eta = 3$

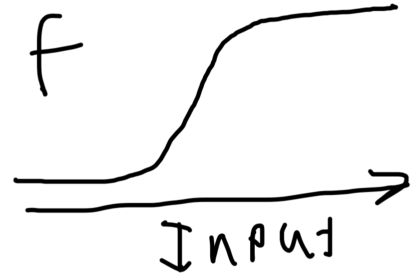


$\Delta = 1.5, \eta = 0.3$



Neural Field Models





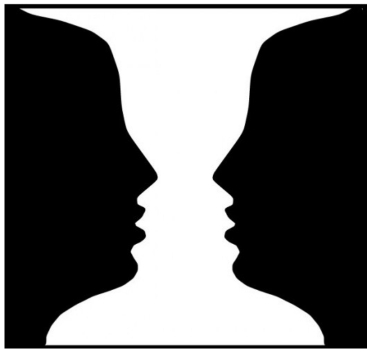
$$\tau_e \frac{du}{dt} + u = f(a_{ee}u - a_{ei}v + I_e)$$

$$\tau_i \frac{dv}{dt} + v = f(a_{ie}u - a_{ii}v + I_i)$$

These can be derived from a slow synapse assumption: Then $f(I)$ is the firing rate, eg

$$f(I) = \sqrt{[I]_+}\,/\,\pi \qquad \theta\text{-model}$$

Competition Circuit ("Rivalry")



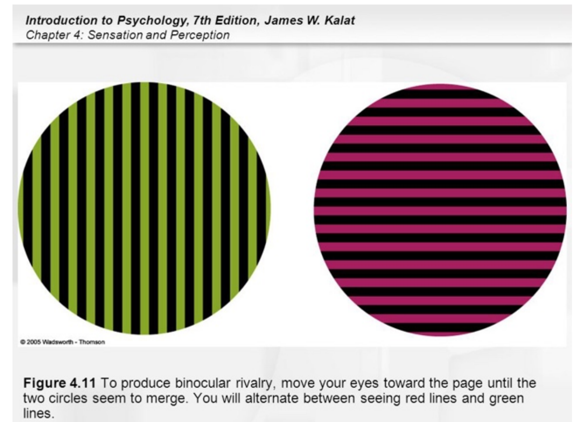


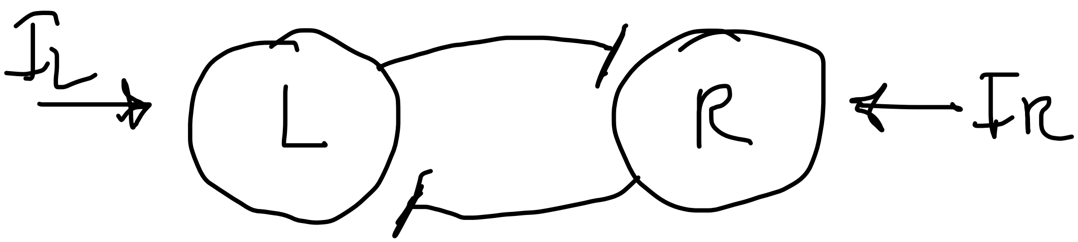
Figure 4.11 To produce binocular rivalry, move your eyes toward the page until the two circles seem to merge. You will alternate between seeing red lines and green lines.

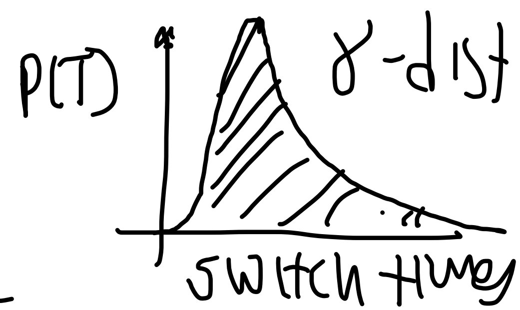
Perceptual Rivalry

Binocular Rivalry

Oscillate between two percepts

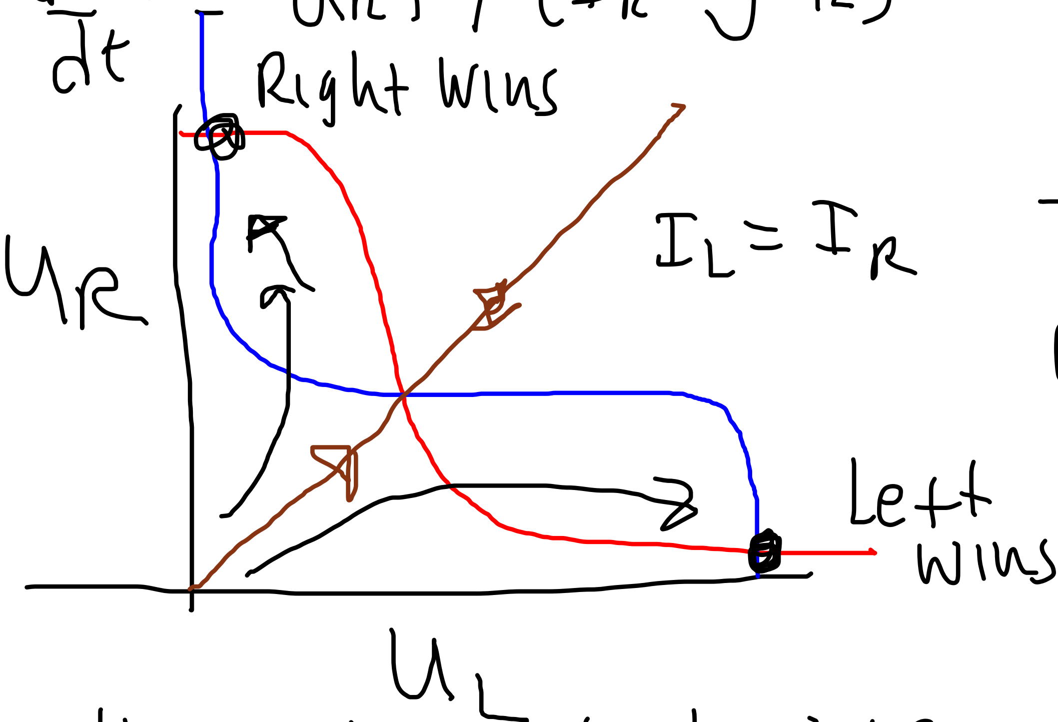
Simple model:

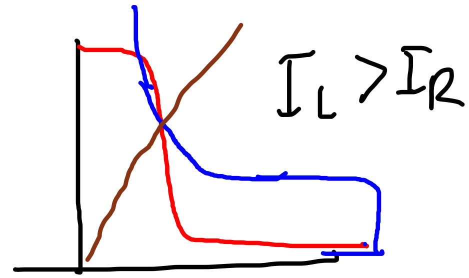


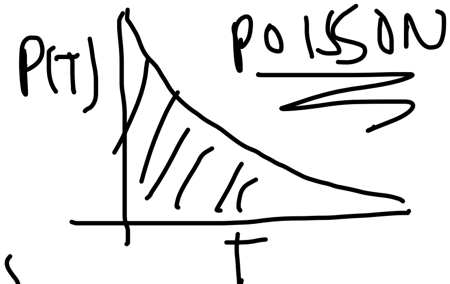


$$\tau \frac{du_L}{dt} = -u_L + F(I_L - g u_R)$$

$$\tau \frac{du_R}{dt} = -u_R + F(I_R - g u_L)$$







won't oscillate, but noise could cause switches, but They are expon. dist!

Add Adaptation:

$$\tau \frac{du_L}{dt} = -u_L + F(I - g u_R - \beta z_L)$$

$$\tau_A \frac{dz_L}{dt} = -z_L + u_L$$

When u_L is on for a while z_L builds up

Similar equ for u_R, z_R

Equilibrium: $u_L = u_R = z_L = z_R = \bar{u} = F(I-(g+\beta)\bar{u})$

Symmetric

Is it stable? $\gamma = F'(I-(\beta+g)\bar{u}) > 0$

$\tau = 1$ WLOG

$$M = \begin{pmatrix} -1 & -\gamma\beta & -\gamma g & 0 \\ \frac{1}{\tau_A} & -\frac{1}{\tau_A} & 0 & 0 \\ -\gamma g & 0 & -1 & -\gamma\beta \\ 0 & 0 & \frac{1}{\tau_a} & -\frac{1}{\tau_a} \end{pmatrix}$$

Symmetry Breaking

$\begin{pmatrix}1\\1\end{pmatrix}, \begin{pmatrix}1\\-1\end{pmatrix}$

$$\begin{bmatrix}\eta\\ \nu\\ \eta\\ \nu\end{bmatrix} \quad \begin{bmatrix}-1-\gamma g & -\gamma\beta \\ \frac{1}{\tau_a} & -\frac{1}{\tau_a}\end{bmatrix}$$

Symmetric pert

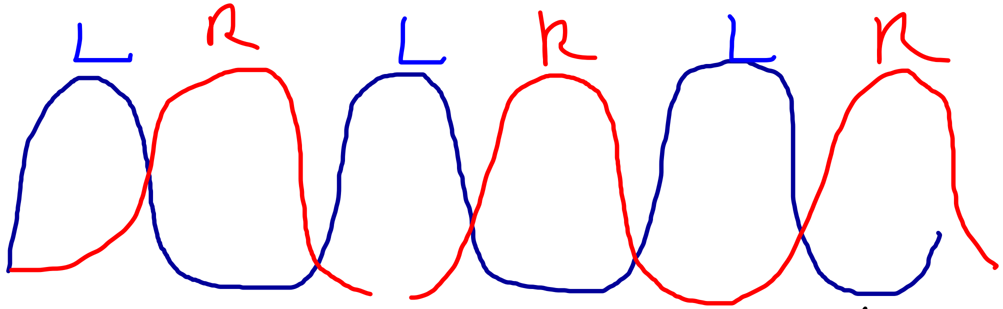
$Tr<0 \quad \det>0 \Rightarrow$ Stable

$$\begin{bmatrix}\eta\\ \nu\\ -\eta\\ -\nu\end{bmatrix} \rightarrow \begin{bmatrix}-1+\gamma g & -\gamma\beta \\ \frac{1}{\tau_a} & -\frac{1}{\tau_a}\end{bmatrix}$$

Antisymmetric pert

$\tau_a \ll 1 \Rightarrow$ det is negative at small γ W

$\tau_a \gg \;\Rightarrow Tr>0$ at small γ H



Nice switching – with noise γ-dist!

Classic Amari Model

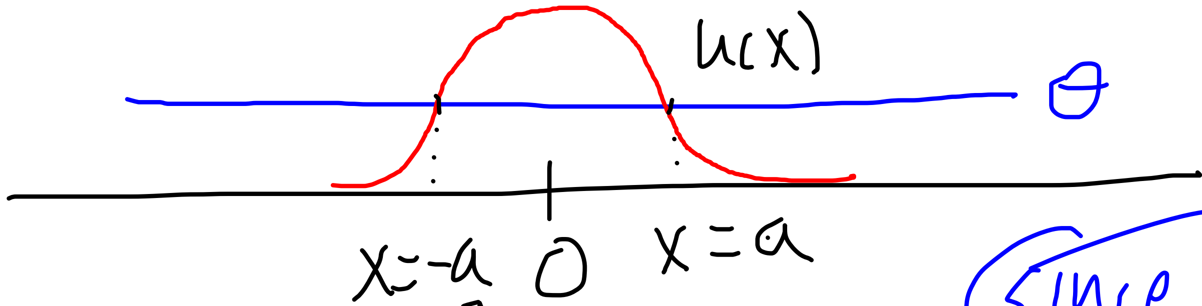
- working memory is thought to be a local attractor
- spatially located "bump" of activity encoding location of object in visual field
- Pre frontal ctx

Step function!

$$\frac{\partial u}{\partial t} = -u + \int_{-\infty}^{\infty} J(x-y)\, H(u(y,t)-\theta)\, dy$$

Spatially distributed network

$J(x)$ is symmetric



$$u(x) = \int_{-a}^{a} J(x-y)\,dy$$

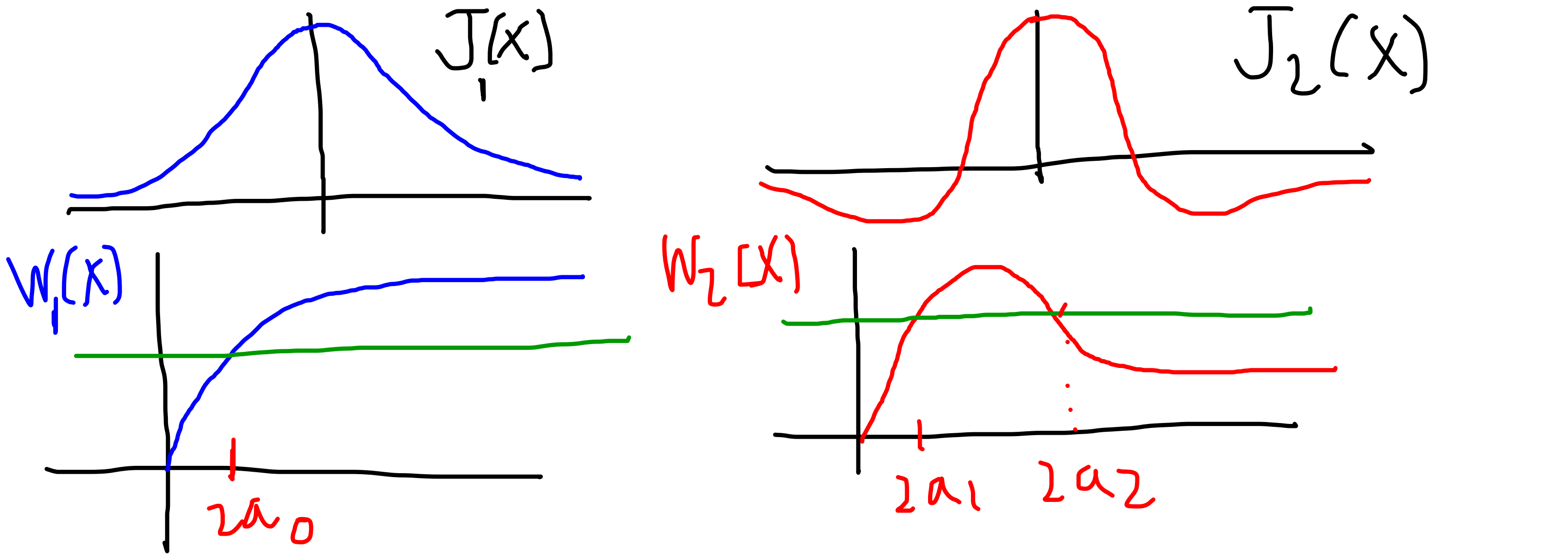
Since $H = 0$ for $u(x) < \theta$

Need $u(\pm a) = \theta$!

$$\theta = \int_{-a}^{a} J(a-y)\,dy = \int_{0}^{2a} J(y)\,dy$$

Let $W(x) = \int_{0}^{x} J(y)\,dy$

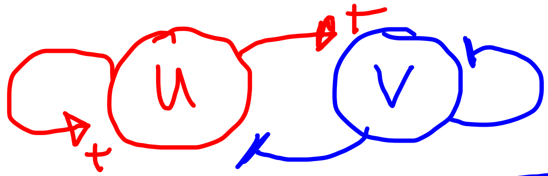
$$\theta = W(2a)$$

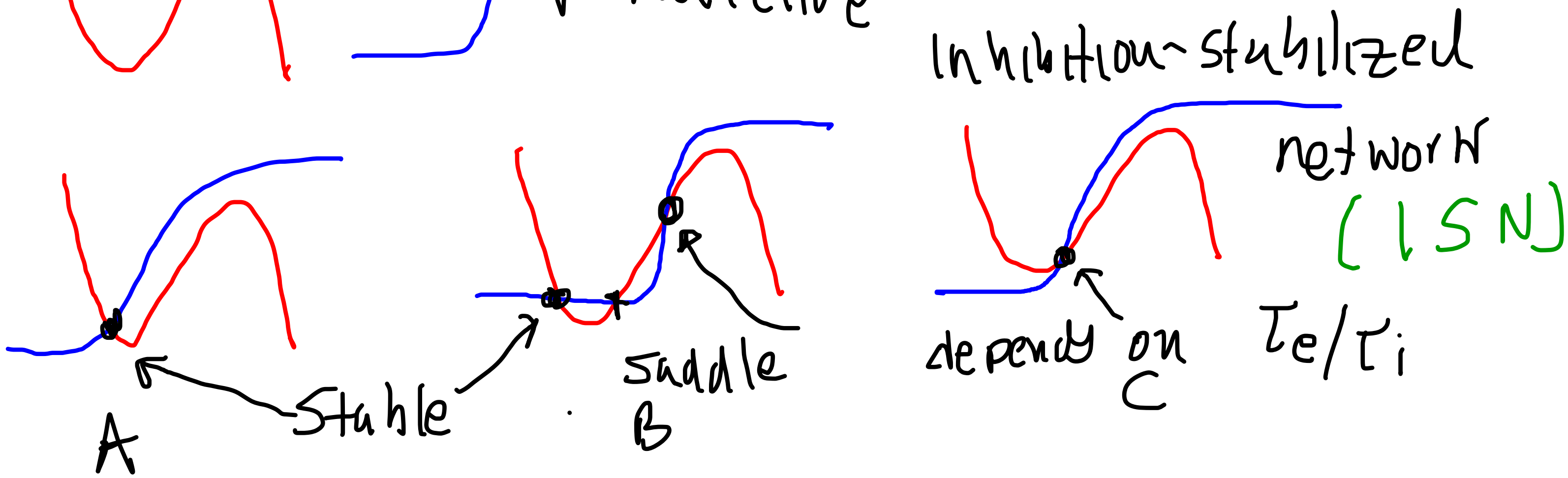


Exercise (Hard) Formally show that only a_2 is a stable bump width!

(Hint: $$\int_{-\infty}^{\infty} \phi(x)\,\delta(u(x)-\theta)\,dx = \frac{\phi(a)+\phi(-a)}{|u'(a)|}$$)

Excitatory-Inhibit Nets





We will focus on $\boxed{\text{ISN}}$ spatially connected networks

$$\tau_E \frac{\partial u}{\partial t} = -u + f(a_{ee}\, k_e * u - a_{ei}\, k_i * v + I_e)$$

$$\tau_i \frac{\partial v}{\partial t} = -v + f(a_{ie}\, k_e * u - a_{ii}\, k_i * v + I_i)$$

$$K_e * u \equiv \int_\Omega K_e(x-y)\,u(y,t)\,dy, \quad \text{etc}$$

$$K_j(x) = \frac{K(x/\sigma_j)}{\sigma_j^{\,m}} \qquad m = \text{dimension of } \Omega \ (1 \text{ or } 2)$$

$$\text{eg} \quad K(x) = e^{-x^2}/\sqrt{\pi}^{\,m}, \quad e^{-|x|}/N, \ \text{etc}$$

Assume $(\bar{u}, \bar{v})$ is equilibrium in ISN

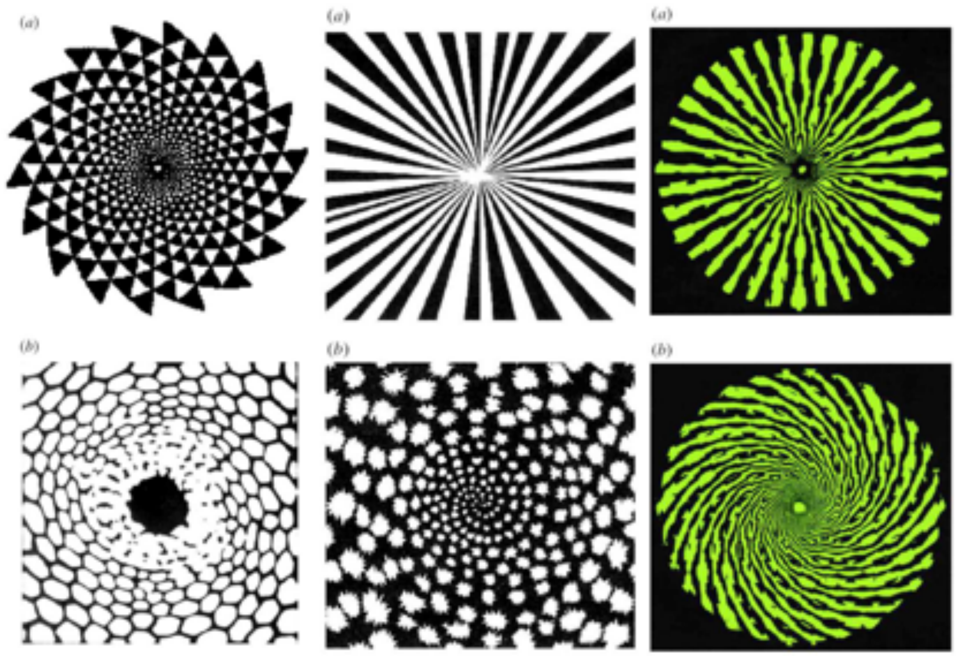
$$\Rightarrow \ -1 + f'(\sim)\,a_{ee} > 0 \qquad \begin{bmatrix} + & - \\ + & - \end{bmatrix} \Leftarrow \text{sign of Linearization}$$

TURING PATTERNS

VISUAL HALLUCINATIONS

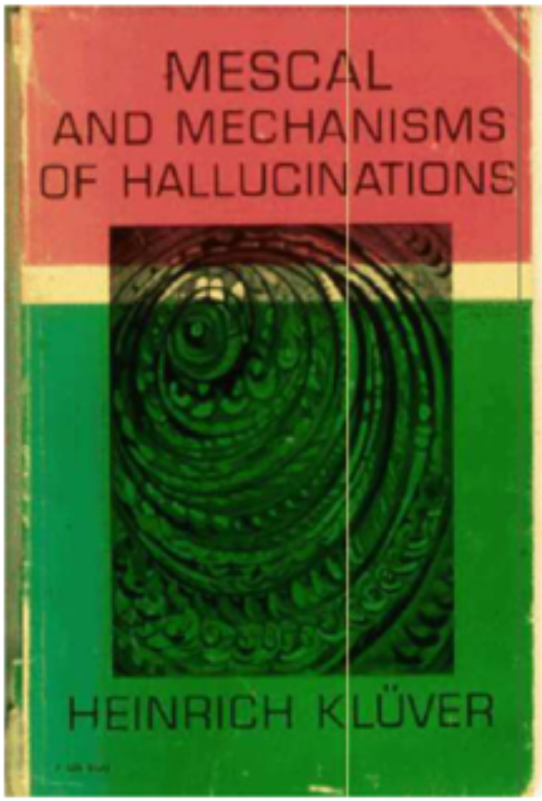
Classic patterns

Eye pressure, flicker, drugs!!



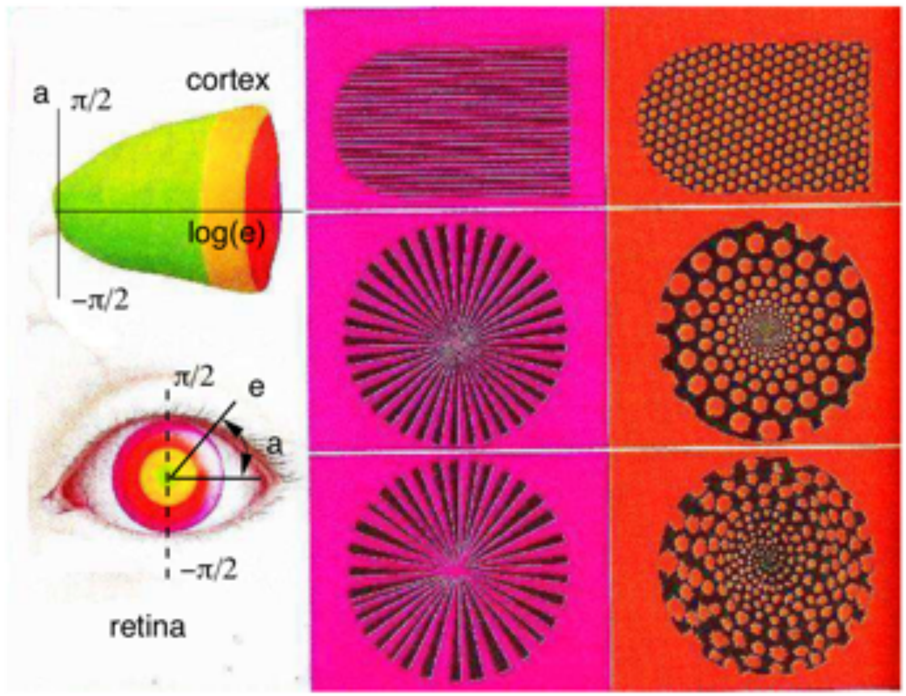
Bressloff et al

Form constants



- Spiral/vortex
- Funnel/tunnel
- Cobwebs/filigrees
- Exploding light rays
- Mosaics

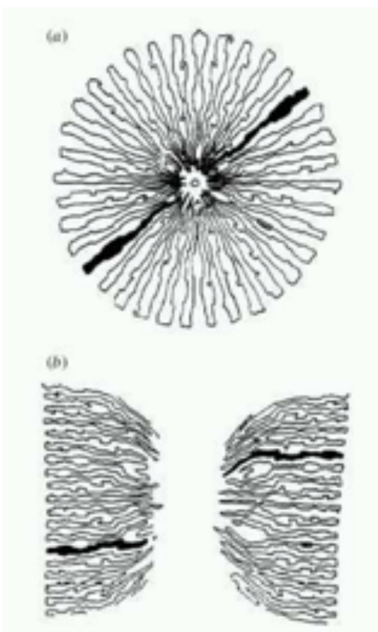
Retino-cortical transform

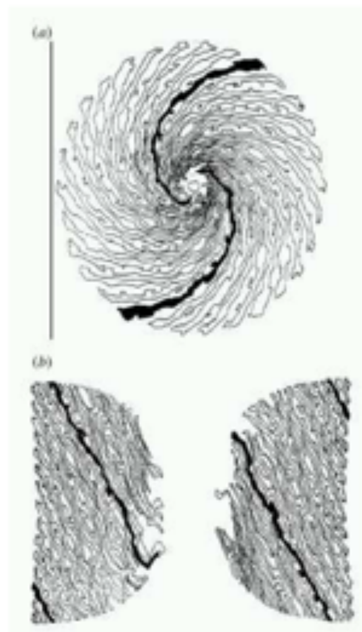


$$(e, a) \longrightarrow \left(\lambda \log(1 + e/e_0), -\lambda \frac{ea}{e_0 + e}\right)$$

Like the complex logarithm

$$e\exp(ia) \to (\log e, a)$$





Hypothesis: Basic Hallucinations are symmetry breaking instabilities of the UNIFORM STATE

Linearization:

$$\tau_e u_t = -u + b_{ee} K_e(x) * u - b_{ei} K_i(x) * v$$

$$\tau_i v_t = -v + b_{ie} K_e(x) * u - b_{ii} K_i(x) * v$$

$$b_{ee} = a_{ee} f_e'(-), \quad b_{ei} = a_{ei} f_e'(-)$$

$$b_{ie} = a_{ie} f_i'(-), \quad b_{ii} = a_{ii} f_i'(-)$$

$$K(x) * e^{ik\cdot x} = \hat{K}(|k|^2)\, e^{ik\cdot x}$$

Thus
$$\begin{pmatrix} u(x,t) \\ v(x,t) \end{pmatrix} = \begin{pmatrix} \hat{u} \\ \hat{v} \end{pmatrix} e^{ik\cdot x} e^{\lambda t}$$

$$\lambda \begin{pmatrix} \hat{u} \\ \hat{v} \end{pmatrix} = \begin{bmatrix} \frac{1}{\tau_e}\left(-1 + b_{ee}\hat{K}_e\right) & -\frac{b_{ei}}{\tau_e}\hat{K}_i \\ \frac{b_{ie}}{\tau_i}\hat{K}_e & \frac{1}{\tau_i}\left(-1 - b_{ii}\hat{K}_i\right) \end{bmatrix} \begin{bmatrix} \hat{u} \\ \hat{v} \end{bmatrix}$$

Stability is easy: $Tr < 0$ + $\det > 0$

$$\det = \frac{1}{\tau_e}\frac{1}{\tau_i}\left[b_{ei} b_{ie} \hat{K}_e \hat{K}_i + (1 + b_{ii}\hat{K}_i)\underbrace{(1 - b_{ee}\hat{K}_e)}_{\text{could be negative or positive}} \right]$$

NB: $\hat{K}(|k|^2) \to 0$ as $|k| \to \infty$

$\det(k) \to 1/(\tau_e \tau_i)$ as $|k| \to \infty$

$$tr = (-(1 + b_{ee}\hat{K}_e)/\tau_e - (1 + b_{ii}\hat{K}_i)/\tau_i$$

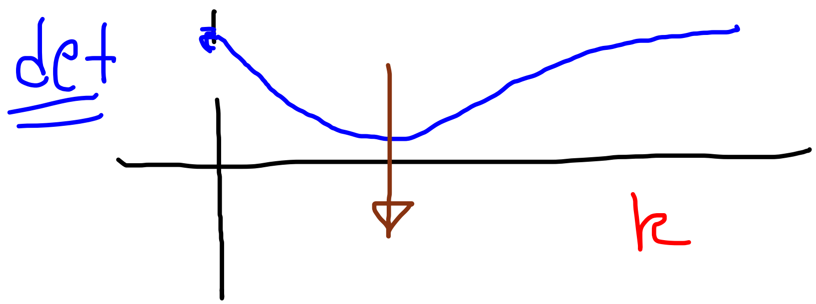
$tr(k) \to -\frac{1}{\tau_e} - \frac{1}{\tau_i}$ as $|k| \to \infty$

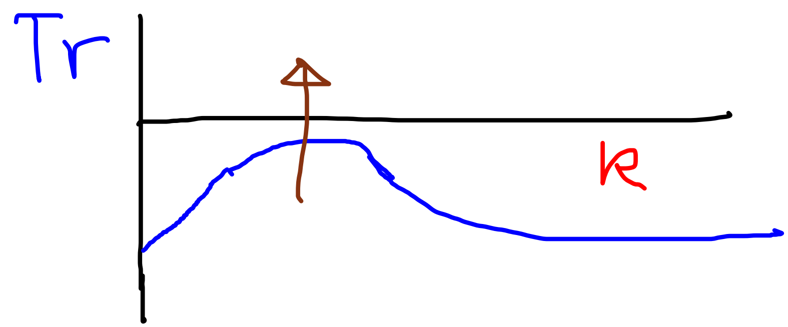
Assume $\det(0) > 0$, $\mathrm{Tr}(0) < 0$

Lateral inhibition $\sigma_e < \sigma_i$

inhibition has greater spread than excitation

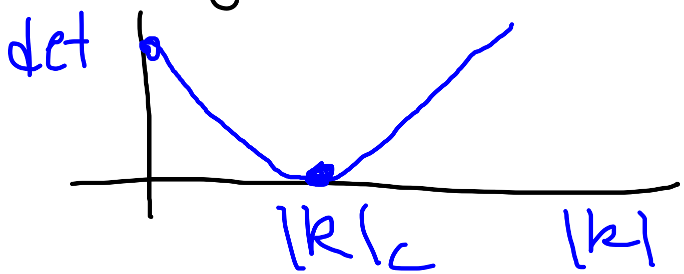
Consequence

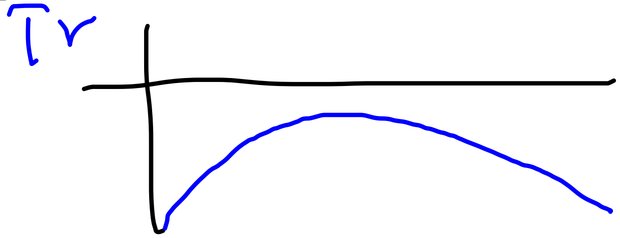




Manipulate, say a_{ee} or $f'(\cdots)$
can make $\downarrow$ det or $\uparrow$ tr

det goes negative while Tr stays neg





simplest case $\vec{k} = (\pm k_c, 0), (0, \pm k_c)$

$$z\, e^{ik_cx}, \; w e^{ik_cy} + c.c.$$

Bifurcation theory lets you compute amplitude equations

for z, w

$$\dot{z} = z(p - a|z|^2 - b|w|^2)$$
$$\dot{w} = w(p - a|w|^2 - b|z|^2)$$

p = parameter

a, b computed from Eqns

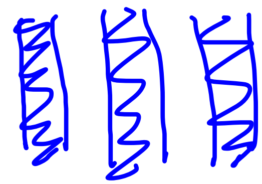
$$\dot{z} = z(p - a|z|^2 - b|w|^2)$$
$$\dot{w} = w(p - a|w|^2 - b|z|^2)$$

p is the bifurcation parameter

$p<0 \Rightarrow z,w=0 \Rightarrow$ No patterns

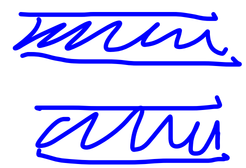
$p>0 \Rightarrow$ 3 solutions!

$$(z,w) = \left(\sqrt{\frac{p}{a}},\ 0\right)$$



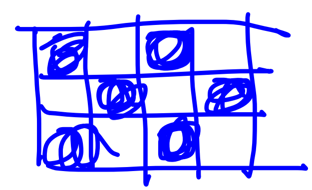
vertical stripes

$$(z,w) = \left(0,\ \sqrt{\frac{p}{a}}\right)$$

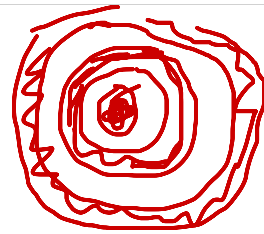
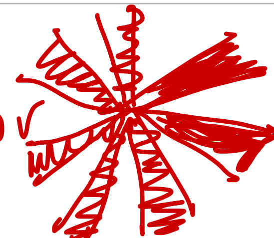


Horz. stripes

$$(z,w) = \left(\sqrt{\frac{p}{a+b}},\ \sqrt{\frac{p}{a+b}}\right)$$



checks

stripes $\Rightarrow$  or 

vert horz

STABLE IFF $a < b$

Checks $\Rightarrow$ 

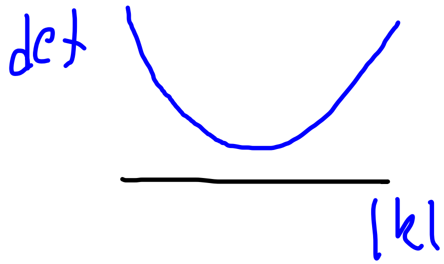
STABLE IFF $a > b$

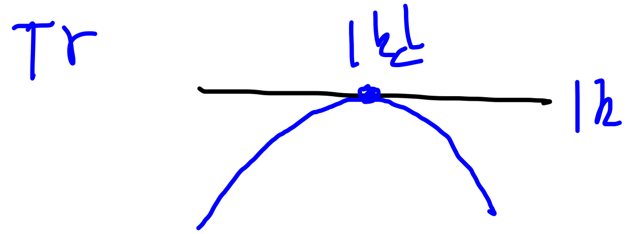
Patterns depend on the non linear term in the model

SUMMARY Lateral inhibition coupled with fast inhibition & some form of enhanced excitation $\Rightarrow$ spontaneous patterns in cortical network that resemble

EARLY VISUAL HALLUCINATIONS

What about the second case:





TURING-HOPF Bifurcation

High-dimensional Null space!

E.F. $\exp(i\, U_n)$

$$U = k_c x \pm \omega t, \quad k_c y \pm \omega t \Big\} \text{ 4-dimensional in } \mathbb{C}$$

z_1, z_2, w_1, w_2

many different patterns

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math.uh.edu

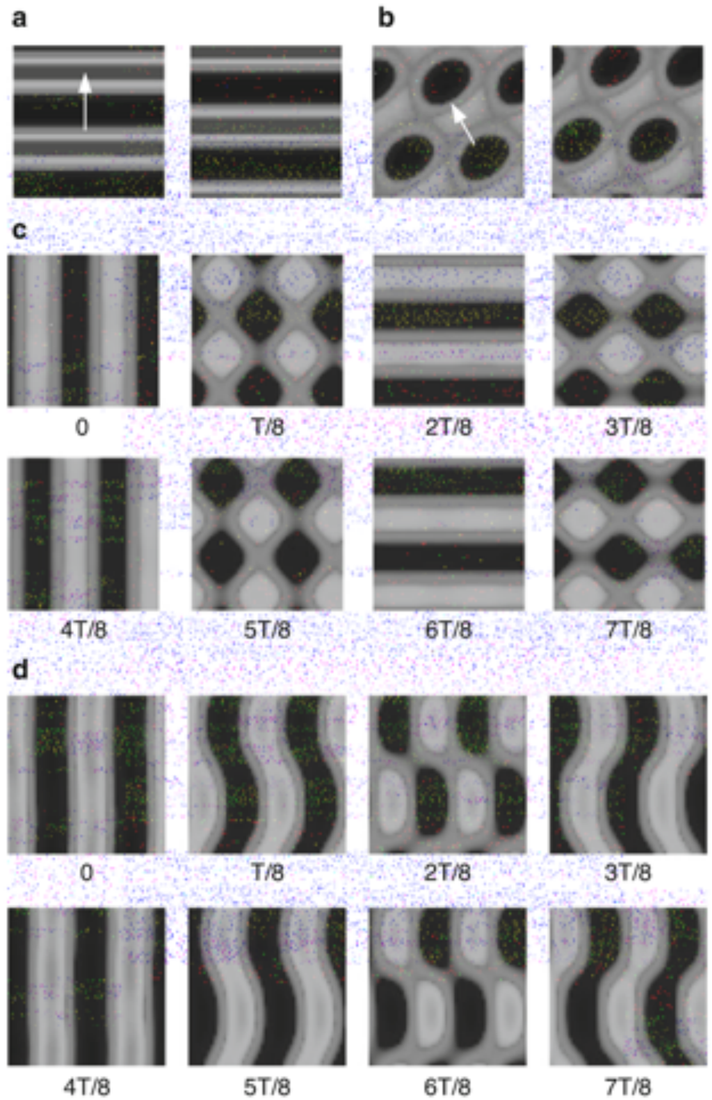
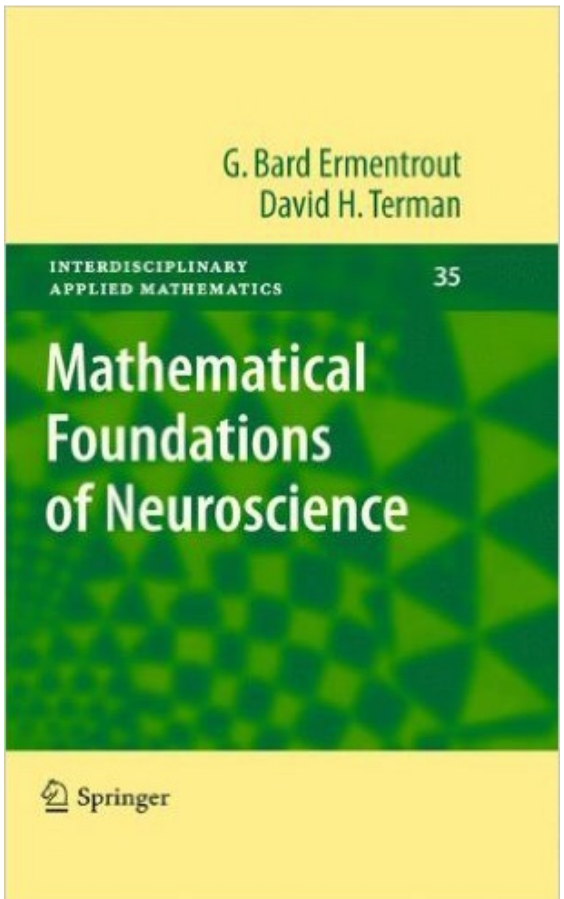


Fig. 4.3 Two-dimensional time-periodic patterns with period T in (4.1) for $\beta = 0.25, \alpha = 0.1$: (**a**) $k = 0.1, r = 3, u_{th} = 0$; (**b**) $k = 0.09, r = 5, u_{th} = 0.3$; (**c**) $k = 0.085, r = 3, u_{th} = 0$; (**d**) $k = 0.09, r = 3, u_{th} = 0$

and $z_2 = z_4 \neq 0$ are also standing rolls.) Traveling squares or spots correspond to $z_1 = z_2 \neq 0$ and $z_3 = z_3 = 0$. Standing squares (a blinking checkerboard pattern) correspond to $z_1 = z_2 = z_3 = z_4 \neq 0$. A very interesting pattern that we see is the

We have only touched on a few of the topics in MATH NEUROSCIENCE

For many more examples & more details



ALSO:

Journal of Math Neuro

Journal of Comp Neuro

SIAM J. Appl. Dyn Syst