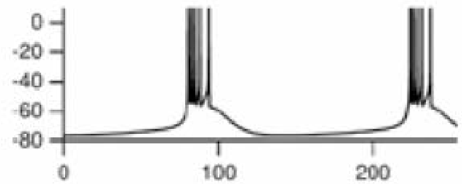
Dynamical System Analysis: Phase Plane Analysis

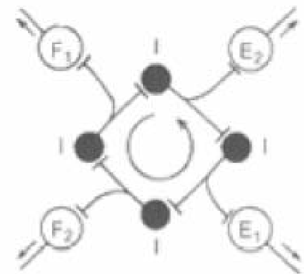
BME665/565

Central Pattern Generators

Pacemakers



Network Oscilators

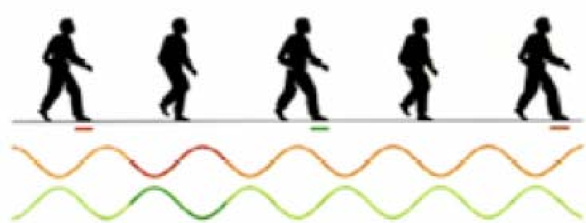


Sea Slugs

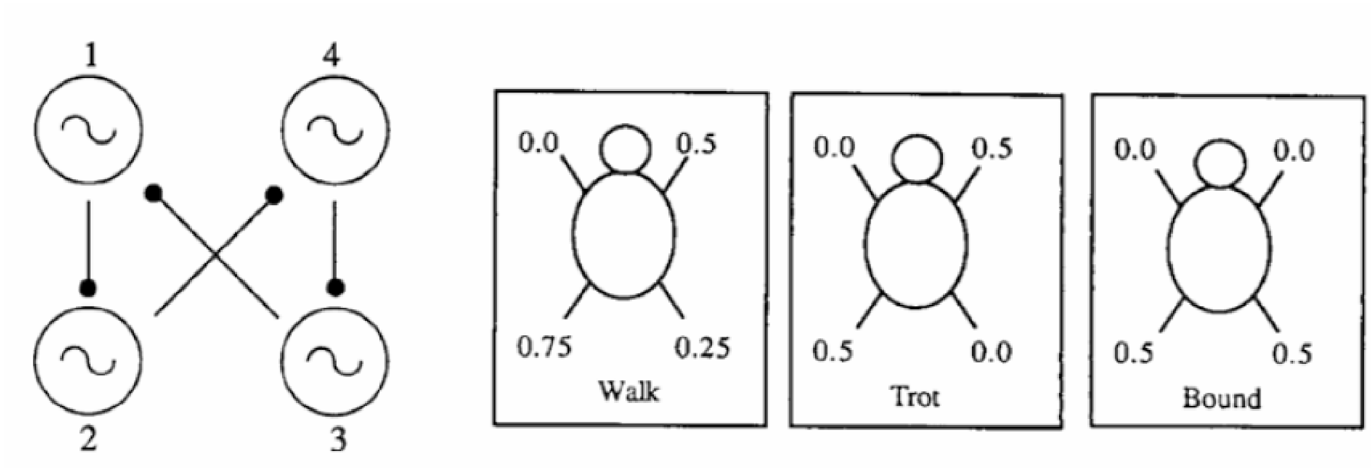
Lobsters

Lampreys

Animal Gaits



Dynamical system models

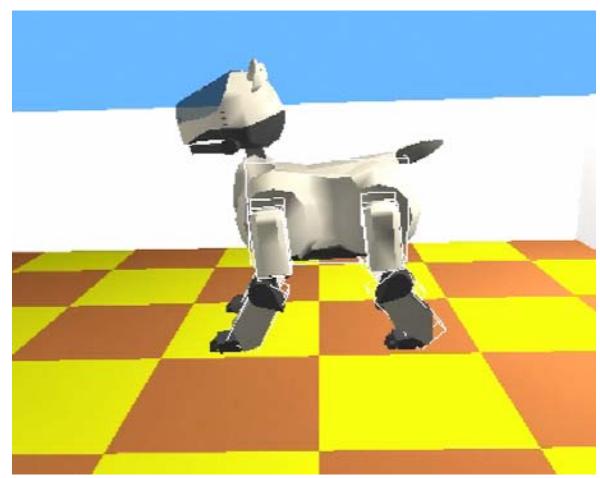


$$\dot{x}_i = a \cdot \left[-x_i + \frac{1}{1 + \exp(-f_{ci} - by_i + bz_i)} \right] \qquad \text{for } i = 1, 2, 3, 4$$

$$\dot{y}_i = x_i - py_i$$

$$\dot{z}_i = x_i - qz_i$$

$$f_{ci} = f \cdot \left[1 + k_1 \sin(k_2 t) + \sum_{j=1}^{4} \lambda_{ji} \cdot x_j \right]$$



2^{nd} Order (Linear) Dynamical Systems

$$\frac{dx}{dt} = a_1 x + a_2 y + b_1 \qquad \frac{dy}{dt} = a_3 x + a_4 y + b_2$$

- Can be written as:

$$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} a_1 & a_2 \\ a_3 & a_4 \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} b_1 \\ b_2 \end{pmatrix}$$

$$\frac{d\vec{X}}{dt} = \overleftrightarrow{A}\vec{X} + \vec{B}$$

2nd Order Dynamical Systems (cont.)

- Equilibrium points occur when the temporal derivative is 0, which defines equilibrium solutions $\vec{X}_{eq}$

$$\frac{d\vec{X}}{dt} = \overleftrightarrow{A}\vec{X} + \vec{B} = 0 \longrightarrow \vec{X}_{eq} = -\overleftrightarrow{A}^{-1}\vec{B}$$

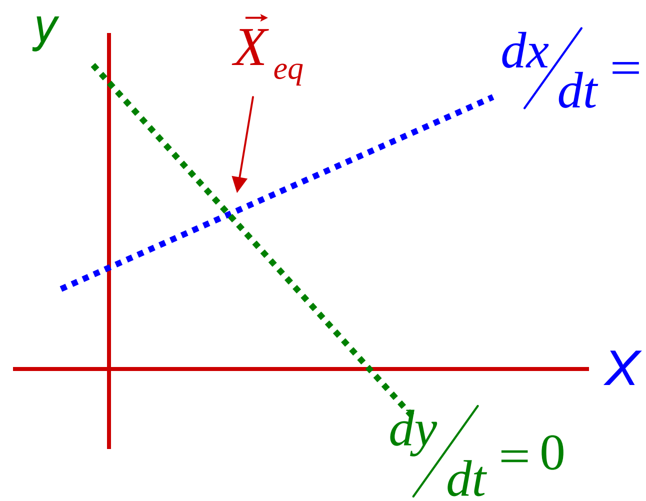
- A *trajectory* is the time course of the system given a particular set of initial conditions
- We can characterize a system by the behavior of its trajectories in the vicinity of the equilibrium points

Stability and state space

- We can plot trajectories in *state space* (also called the *phase plane*) in which the variables of our equations define the axis
- Then, the plots of *dx/dt=0* and *dy/dt=0* are called *nullclines*, and their intersection point represents the equilibrium state of the system

$$\frac{dx}{dt} = a_1 x + a_2 y + b_1$$

$$\frac{dy}{dt} = a_3 x + a_4 y + b_2$$



Stability and state space (cont.)

- The equilibrium point is *asymptotically stable* if all trajectories starting within a region containing the equilibrium point decay exponentially towards that point
- The equilibrium point is *unstable* if at least one trajectory beginning in a region containing the point leaves the region permanently
- The equilibrium is (neutrally) *stable* if trajectories remain nearby
- The behavior of trajectories can be determined by the eigenvalues of the system

2nd Order Dynamical Systems (cont.)

- But, how do we find the eigenvalues?

$$\Longrightarrow \qquad \frac{d\vec{X}}{dt} = \overleftrightarrow{A}\vec{X} + \vec{B} = 0$$

- We can transform the system steady state to the origin without changing the dynamics by setting

$$\vec{X}' = \vec{X} - \vec{X}_{eq}$$

- So that $\displaystyle \frac{d\vec{X}'}{dt} = \overleftrightarrow{A}\vec{X}'$

2nd Order Dynamical Systems (cont.)

- Now, substitute a vector of exponentials for X with arbitrary (to be determined) coefficients c and d:

$$\vec{X}' = \begin{pmatrix} ce^{\lambda t} \\ de^{\lambda t} \end{pmatrix} = \vec{v}e^{\lambda t}$$

The $\boldsymbol{\lambda}$'s are the eigenvalues of the system, and the $\boldsymbol{v}$'s are the eigenvectors.

- So,

$$\frac{d\vec{X}'}{dt} = \underline{\overleftrightarrow{A}\vec{X}' = \lambda\vec{X}'} \longrightarrow \left\{\overleftrightarrow{A} - \lambda\overleftrightarrow{I}\right\}\vec{X}' = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

$$\frac{d\vec{X}'}{dt} = \overleftrightarrow{A}\vec{X}'$$

2^{nd} Order Dynamical Systems (cont.)

$$\left\{ \overleftrightarrow{A} - \lambda \overleftrightarrow{I} \right\} \vec{X}' = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

has a non-trivial solution only if $\left\{ \overleftrightarrow{A} - \lambda \overleftrightarrow{I} \right\}$

does not have an inverse – which means the determinant vanishes

$$\left| \overleftrightarrow{A} - \lambda \overleftrightarrow{I} \right| = 0$$

The determinant is simply a quadratic polynomial which is the *characteristic equation* of the system

$$\begin{pmatrix} a_1 - \lambda & a_2 \\ a_3 & a_4 - \lambda \end{pmatrix} = 0 \qquad remember\ this? \ \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

2^{nd} Order Dynamical Systems (cont.)

The solutions of the characteristic equation are called *eigenvalues* of *A*

If the eigenvalues are not equal ($\lambda_1 \neq \lambda_2$) then the solution of our original system

$$\frac{d\vec{X}}{dt} = \overleftrightarrow{A}\vec{X} + \vec{B}$$

is:

$$\vec{X} = \begin{pmatrix} c_1 e^{\lambda_1 t} \\ d_1 e^{\lambda_1 t} \end{pmatrix} + \begin{pmatrix} c_2 e^{\lambda_2 t} \\ d_2 e^{\lambda_2 t} \end{pmatrix} + \vec{X}_{eq}$$

So, we only need to determine the *c's* and *d's* (the eigenvectors) to determine the solution for the system of equations

2^{nd} Order Dynamical Systems (cont.)

To find the solution for X (i.e. find the *c's* and *d's*), we substitute in our eigenvalue(s)

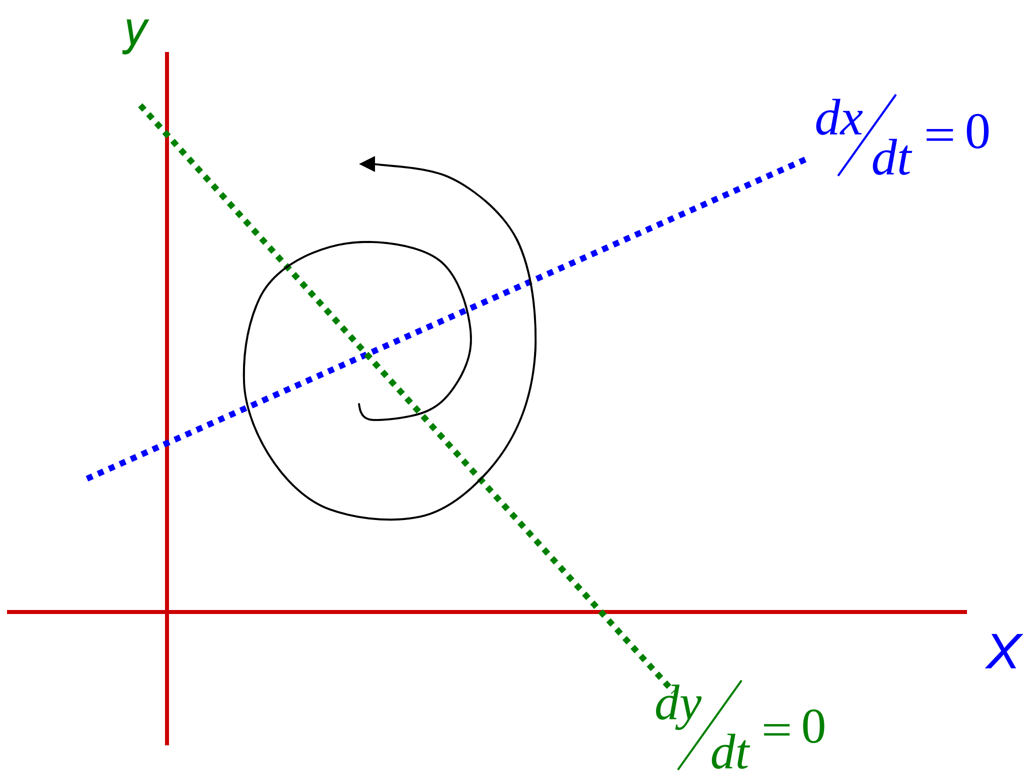
$$\lambda \vec{X}' = \overleftrightarrow{A} \vec{X}' \qquad \lambda_1 \begin{pmatrix} c_1 e^{\lambda_1 t} \\ d_1 e^{\lambda_1 t} \end{pmatrix} = \begin{pmatrix} a_1 & a_2 \\ a_3 & a_4 \end{pmatrix} \begin{pmatrix} c_1 e^{\lambda_1 t} \\ d_1 e^{\lambda_1 t} \end{pmatrix}$$

$$\lambda_2 \begin{pmatrix} c_2 e^{\lambda_2 t} \\ d_2 e^{\lambda_2 t} \end{pmatrix} = \begin{pmatrix} a_1 & a_2 \\ a_3 & a_4 \end{pmatrix} \begin{pmatrix} c_2 e^{\lambda_2 t} \\ d_2 e^{\lambda_2 t} \end{pmatrix}$$

Note: we must know the initial conditions to fully determine the *c's* and *d's*

Back to state space …

$$\begin{pmatrix} a_1-\lambda & a_2 \\ a_3 & a_4-\lambda \end{pmatrix} = 0$$



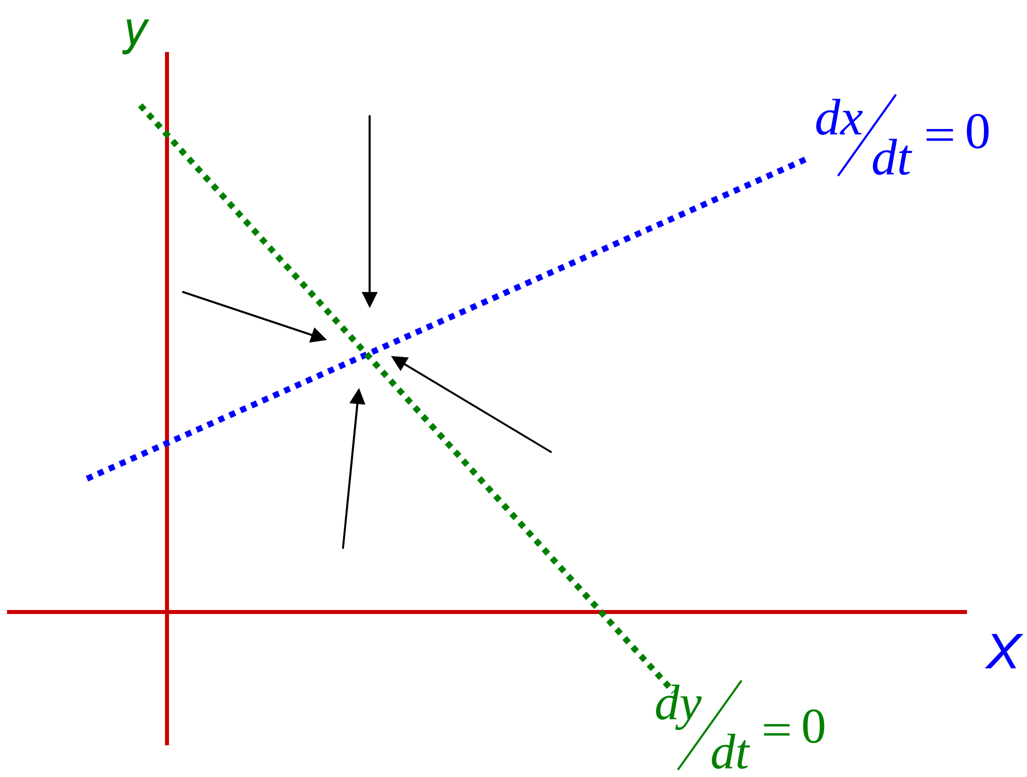
Eigenvalues are a complex conjugate pair: equilibrium point is a spiral point.

If the real part of the eigenvalues are negative, the point is asymptotically stable

Otherwise, it's unstable

Back to state space …

$$\begin{pmatrix} a_1 - \lambda & a_2 \\ a_3 & a_4 - \lambda \end{pmatrix} = 0$$



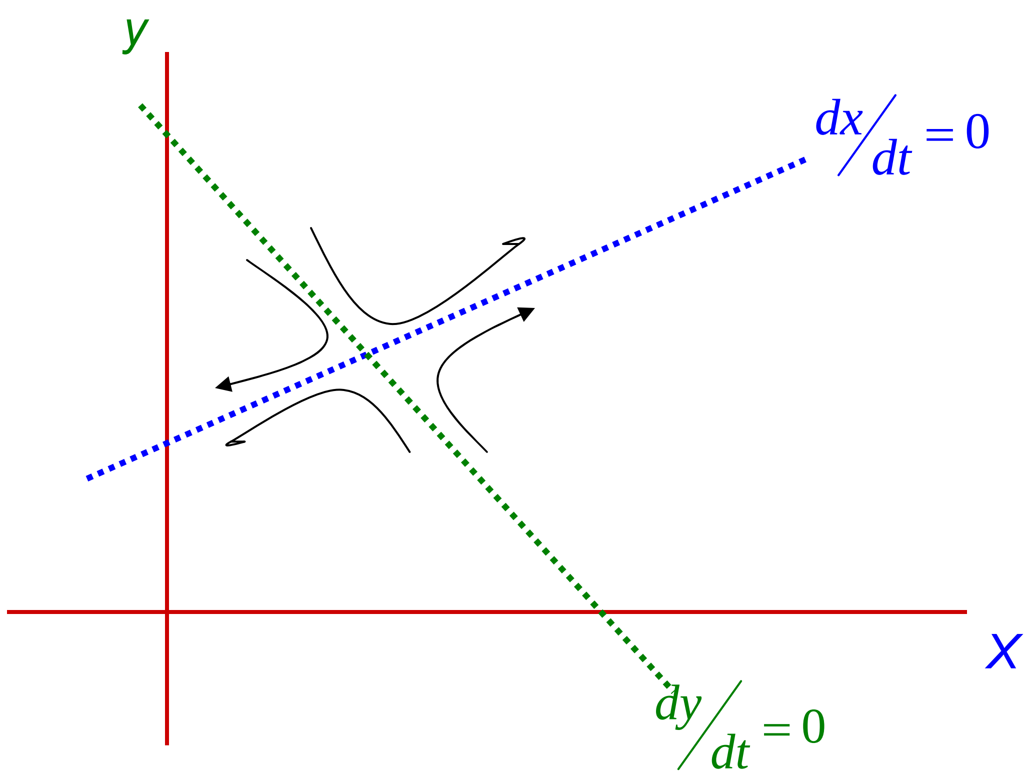
Eigenvalues are both real and have the same sign: equilibrium point is a node.

If the eigenvalues are negative, the point is asymptotically stable

Otherwise, it's unstable

Back to state space …

$$\begin{pmatrix} a_1-\lambda & a_2 \\ a_3 & a_4-\lambda \end{pmatrix} = 0$$

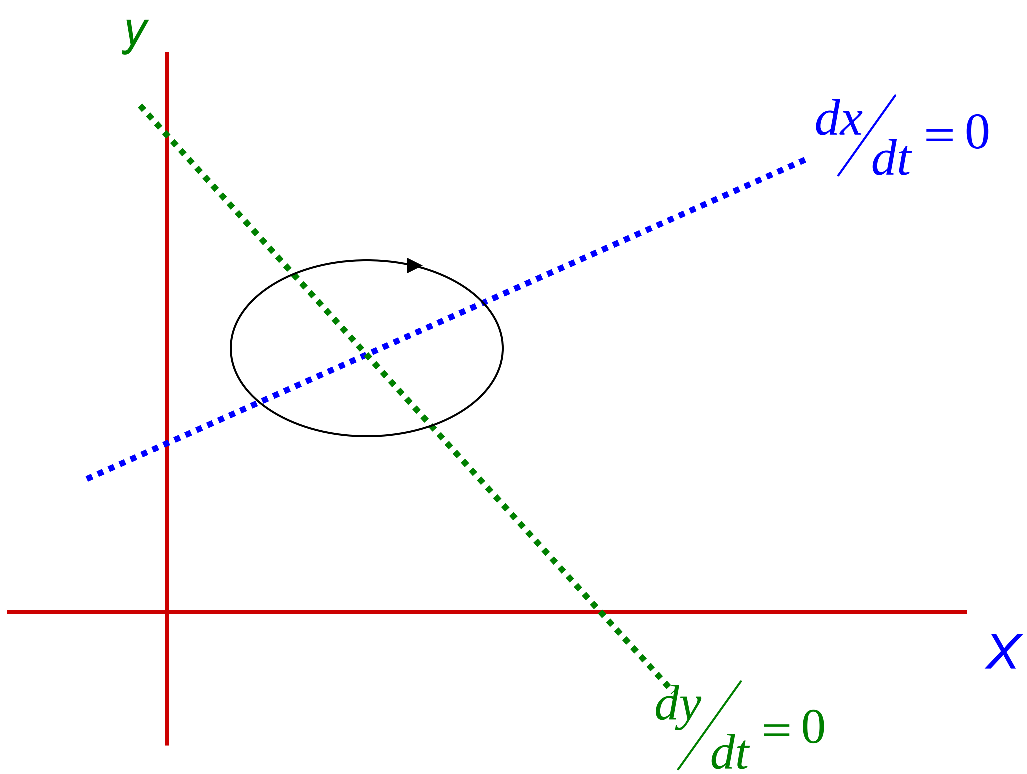


Eigenvalues are both real and have different signs: equilibrium point is a saddle point.

Saddle points are always unstable

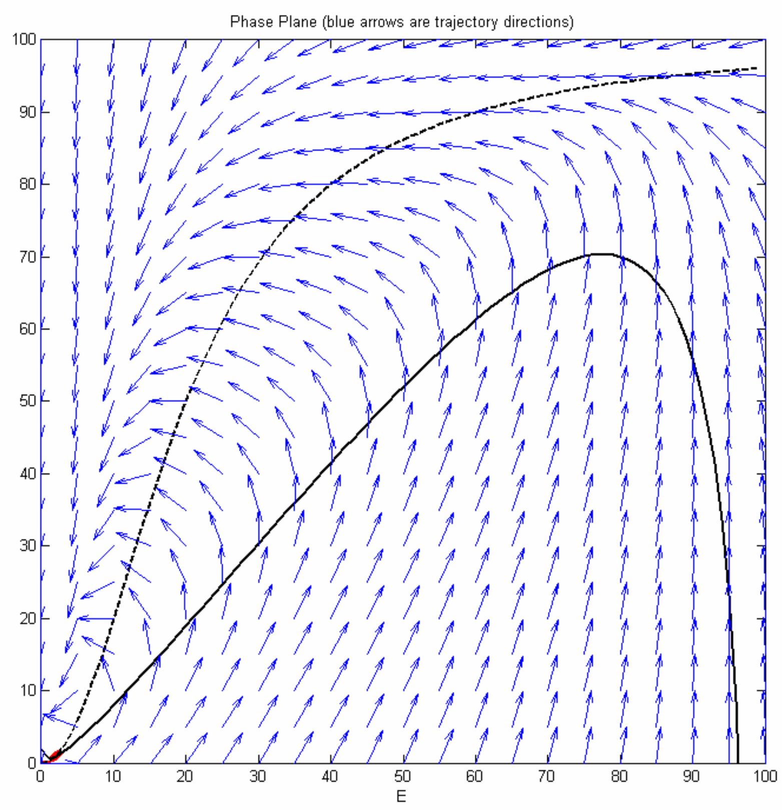
Back to state space …

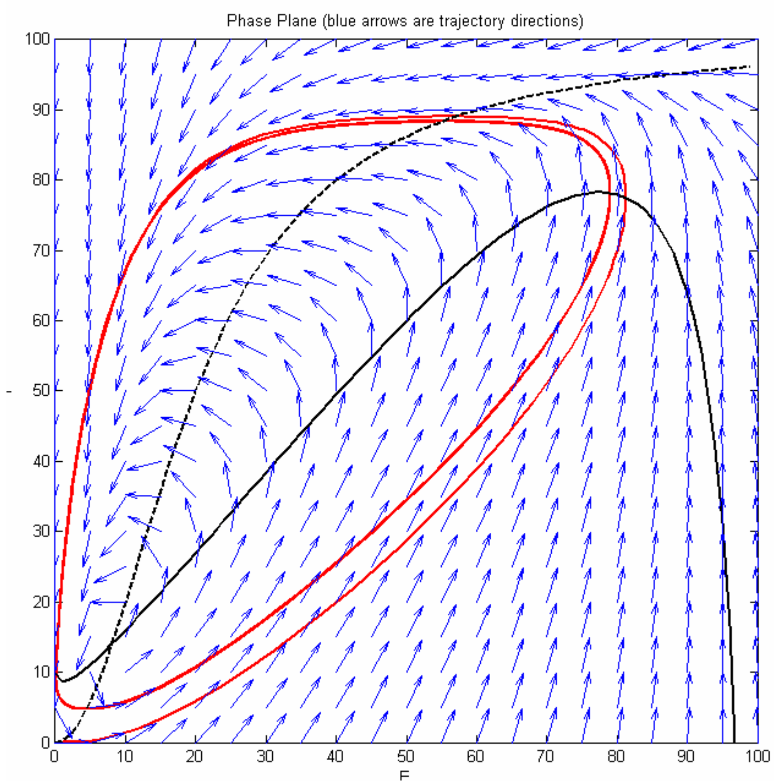
$$\begin{pmatrix} a_1-\lambda & a_2 \\ a_3 & a_4-\lambda \end{pmatrix} = 0$$



Eigenvalues are purely imaginary: equilibrium point is a center.

Centers are neutrally stable, and the trajectory around the equilibrium point will be strictly periodic oscillations


Phase Plane (blue arrows are trajectory directions)
E


Phase Plane (blue arrows are trajectory directions)

Non-linear Systems

- What about non-linear systems?
- We can solve for equilibrium points, but in this case we have non-linear functions, so how do we determine the eigenvalues?

…use the linear terms of the Taylor series expansion around the equilibrium points

$$\frac{d}{dt}\begin{pmatrix} u \\ w \end{pmatrix} = \begin{pmatrix} \left.\frac{\partial F}{\partial u}\right|_{eq} & \left.\frac{\partial F}{\partial w}\right|_{eq} \\ \left.\frac{\partial G}{\partial u}\right|_{eq} & \left.\frac{\partial G}{\partial w}\right|_{eq} \end{pmatrix} \begin{pmatrix} u \\ w \end{pmatrix}$$

$$\frac{du}{dt} = F(u,w) \qquad \frac{dw}{dt} = G(u,w)$$

Matrix of first derivatives:
Jacobian matrix

Example: Fitzhugh-Nugamo Model

- The FitzHugh-Nagumo model is a two-dimensional simplification of the Hodgkin-Huxley model of spike generation in squid giant axons
- The model captures the mathematical properties of excitation and propagation from the electrochemical properties of sodium and potassium ion flow
- It involves only three parameters, which allow it to be easily visualized using phase plane analysis:
  - ***V*** is a voltage-like variable having cubic nonlinearity that allows regenerative self-excitation via a positive feedback (membrane potential)
  - ***R*** is a recovery variable having a linear dynamics that provides a slower negative feedback
  - ***I*** is the magnitude of stimulus current

Fitzhugh-Nugamo Model

- The model is sometimes written in the abstract form

$$\dot{V} = \frac{1}{\tau}(f(V) - R + I)$$

$$\dot{R} = \frac{1}{\tau_R}(aV - bR + c)$$

where *F(V)* is a polynomial of third degree, and τ, τ_R, *a,b,c* are constant parameters

- One formulation for it is:

$$\dot{V} = \frac{1}{0.1}\left(V - {V^3}/{3} - R + I\right)$$

$$\dot{R} = \frac{1}{1.25}(1.25V - R + 1.5)$$

Solution for Fitzhugh-Nugamo

- Solve for equilibrium points
- Root of the equilibrium point are found (using Matlab *roots*) by solving:

$$R = V - V^3/3 + I$$
$$R = 1.25V + 1.5$$

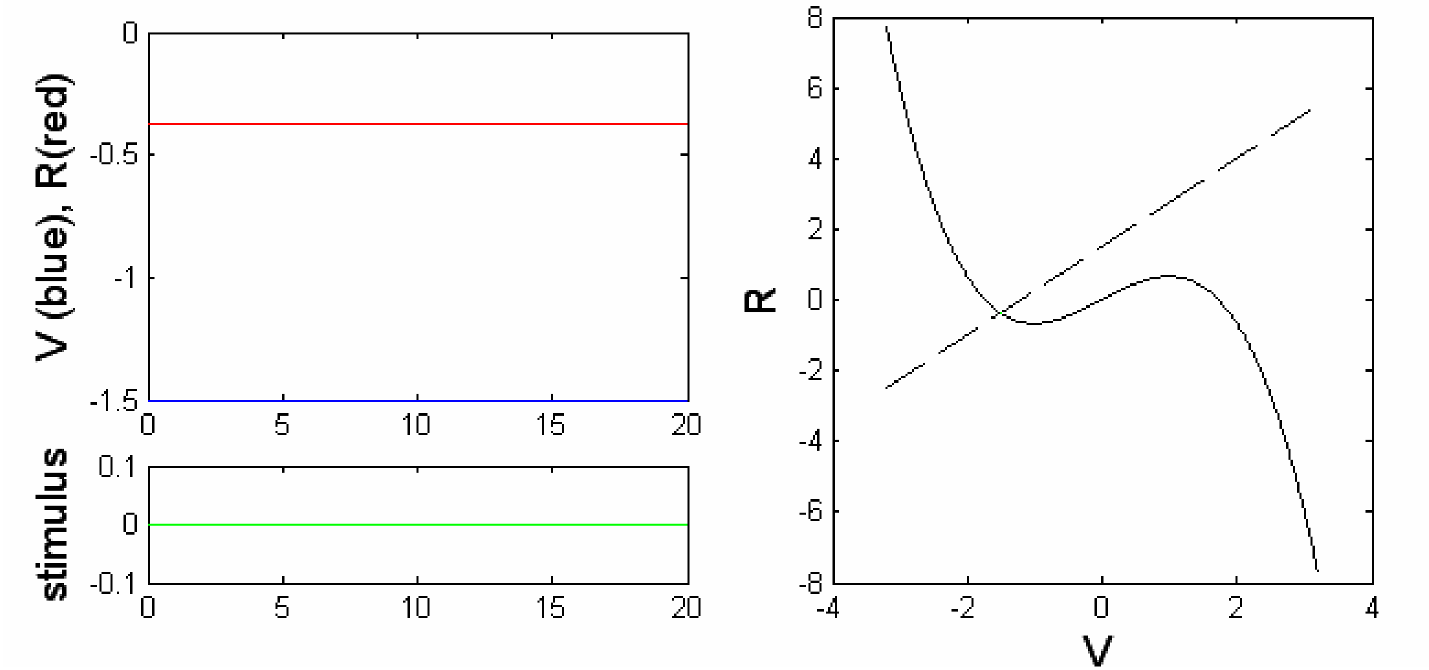
- For no input (*I=0*) we find V = -1.5, and therefore at R = -0.375
- These values can be substituted into our Jacobian to determine the eigenvalues:

$$\overleftrightarrow{A} = \begin{pmatrix} 10 - 10V^2 - \lambda & -10 \\ 2.5 & -2 - \lambda \end{pmatrix}$$

$$\boxed{\begin{aligned} \dot{V} &= \frac{1}{0.1}\left(V - V^3/3 - R + I\right) \\ \dot{R} &= \frac{1}{1.25}(1.25V - R + 1.5) \end{aligned}}$$

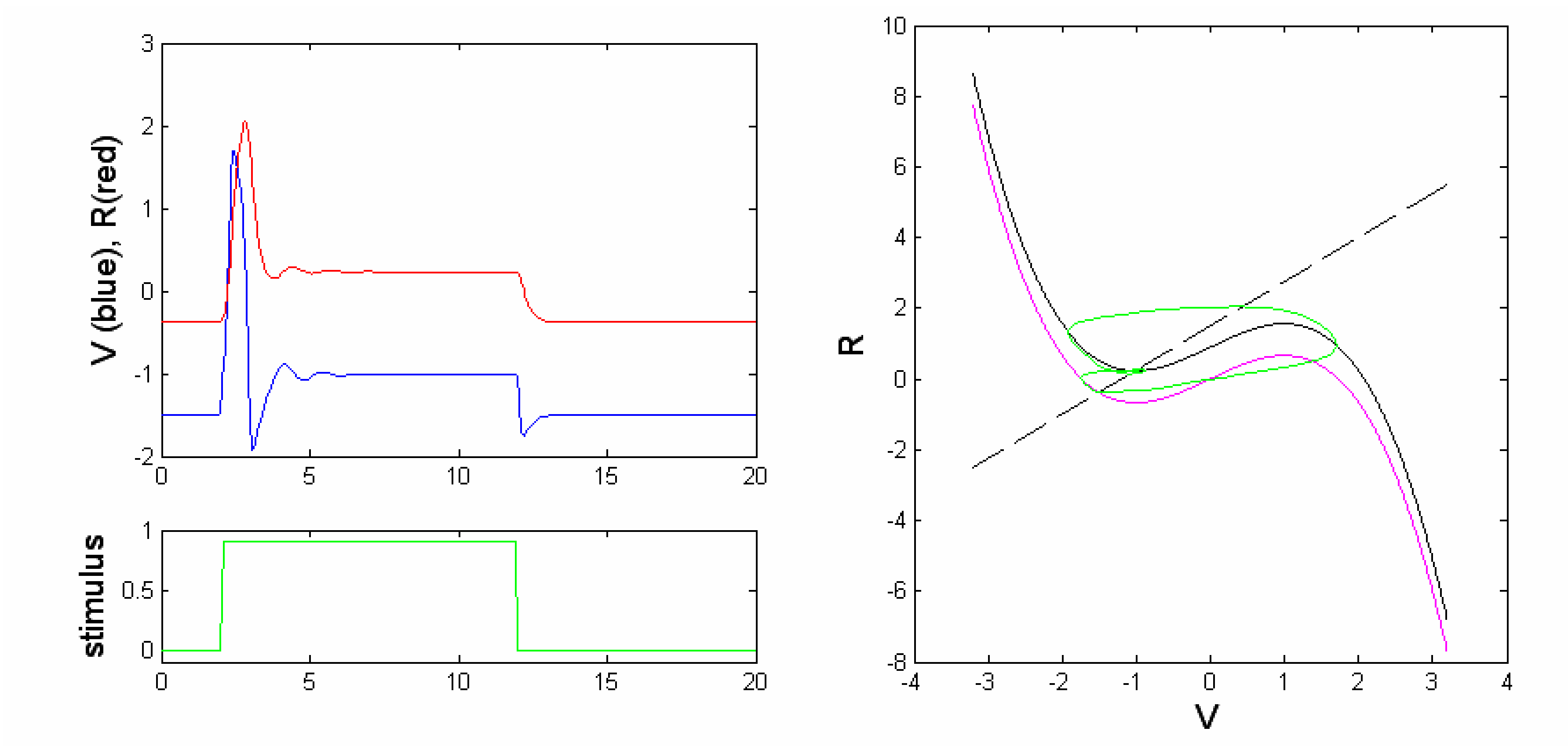
Stable equilibrium

Eigenvalues with 0 input are λ = -5.65, -8.85
➔ Stable node

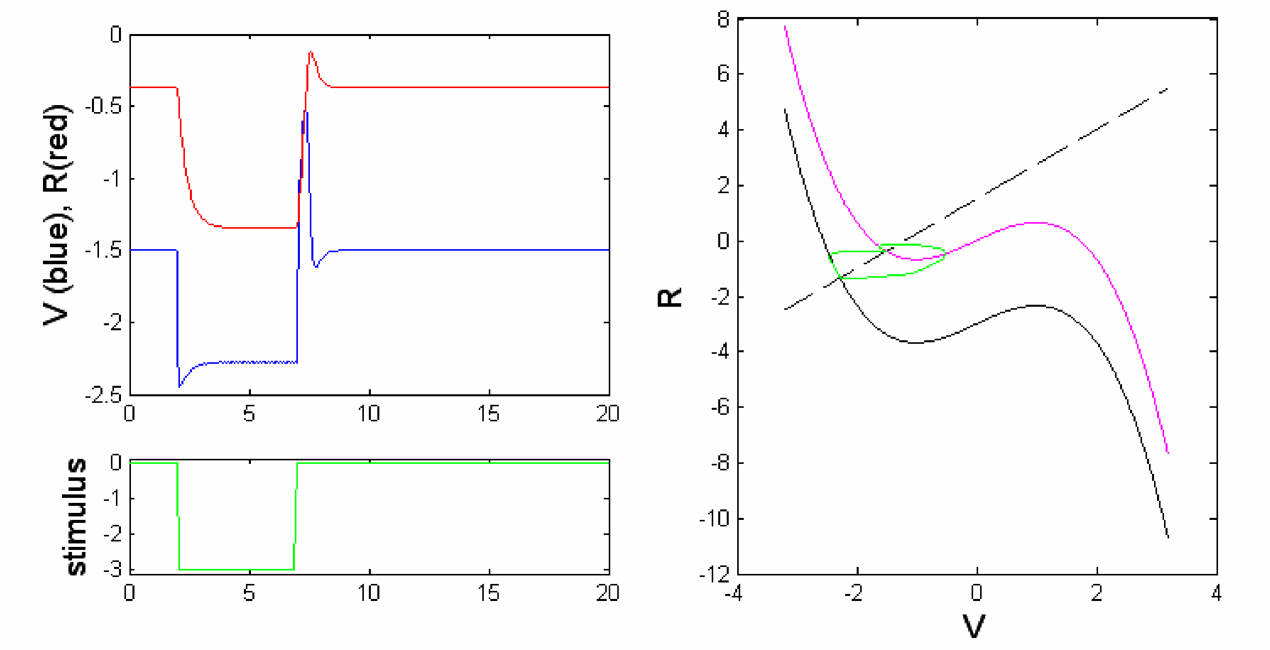


Spiking Behavior of Fitzhugh-Nagamo

Example: Input 0.9 for 10 msec



Post-inhibitory rebound



- As the stimulus becomes negative (hyperpolarization), the resting state shifts to the left
- When the system is released from hyperpolarization, the trajectory starts from a point far below the resting state, makes a large-amplitude excursion, i.e., fires a transient spike, and then returns to the resting state.

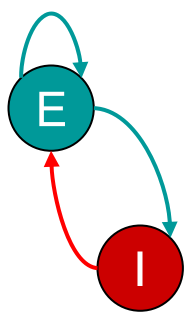
Another example: Wilson-Cowan equations

- The Wilson-Cowan equations describe the interaction between excitatory and inhibitory neurons:

$$\tau \frac{dE(x)}{dt} = -E(x) + g_E\left[I^{ext} + w_{EE}E(x) - w_{IE}I(x)\right]$$

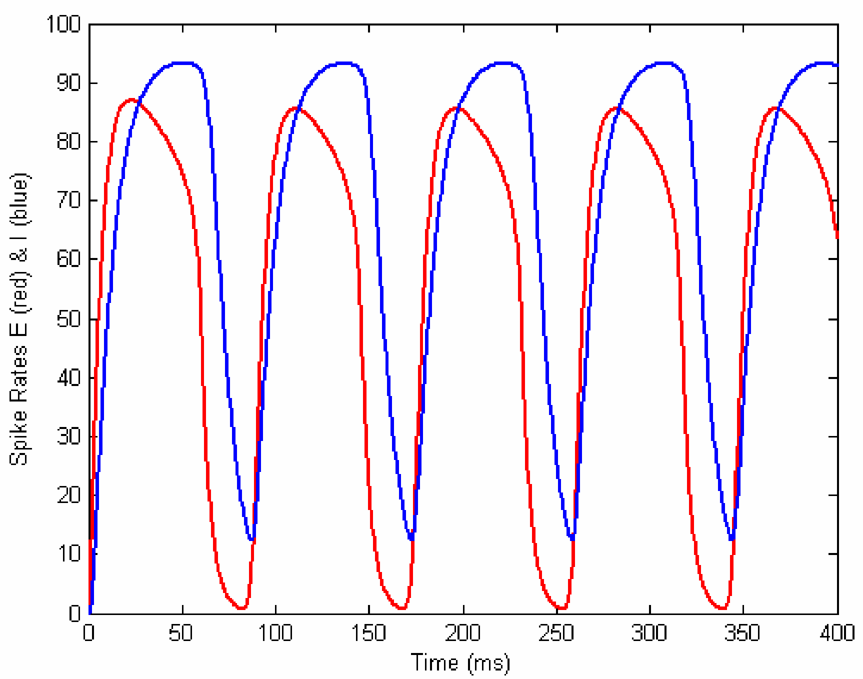
$$\tau \frac{dI(x)}{dt} = -I(x) + g_I\left[w_{EI}E(x)\right]$$

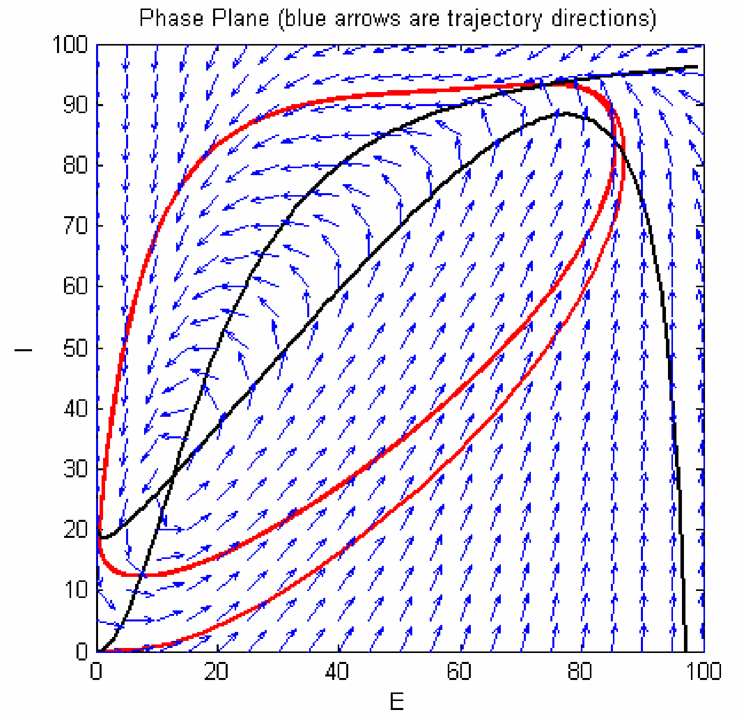
$$g(P) = \begin{cases} \dfrac{100P^2}{30^2 + P^2} & for\ \ P \geq 0 \\ 0 & for\ \ P < 0 \end{cases}$$



Wilson-Cowan example (cont.)

$I_{ext} = 20$

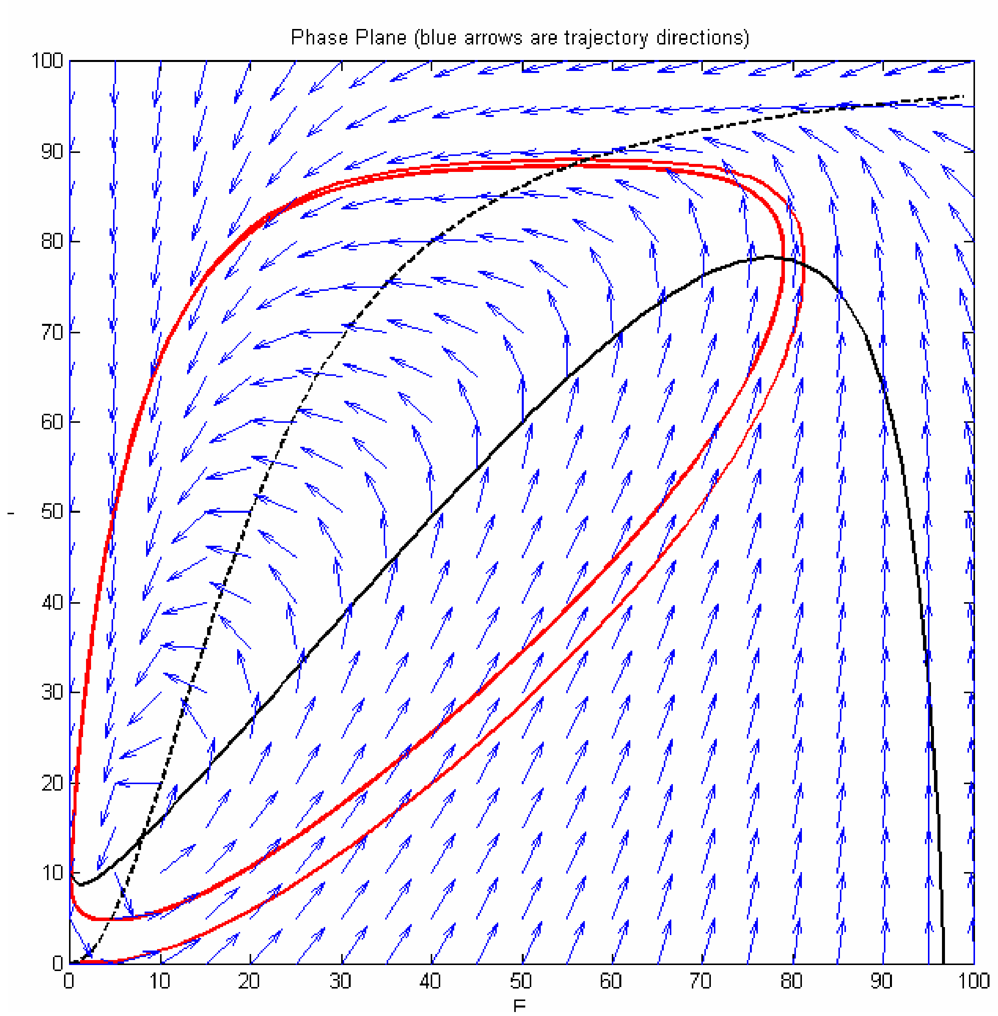




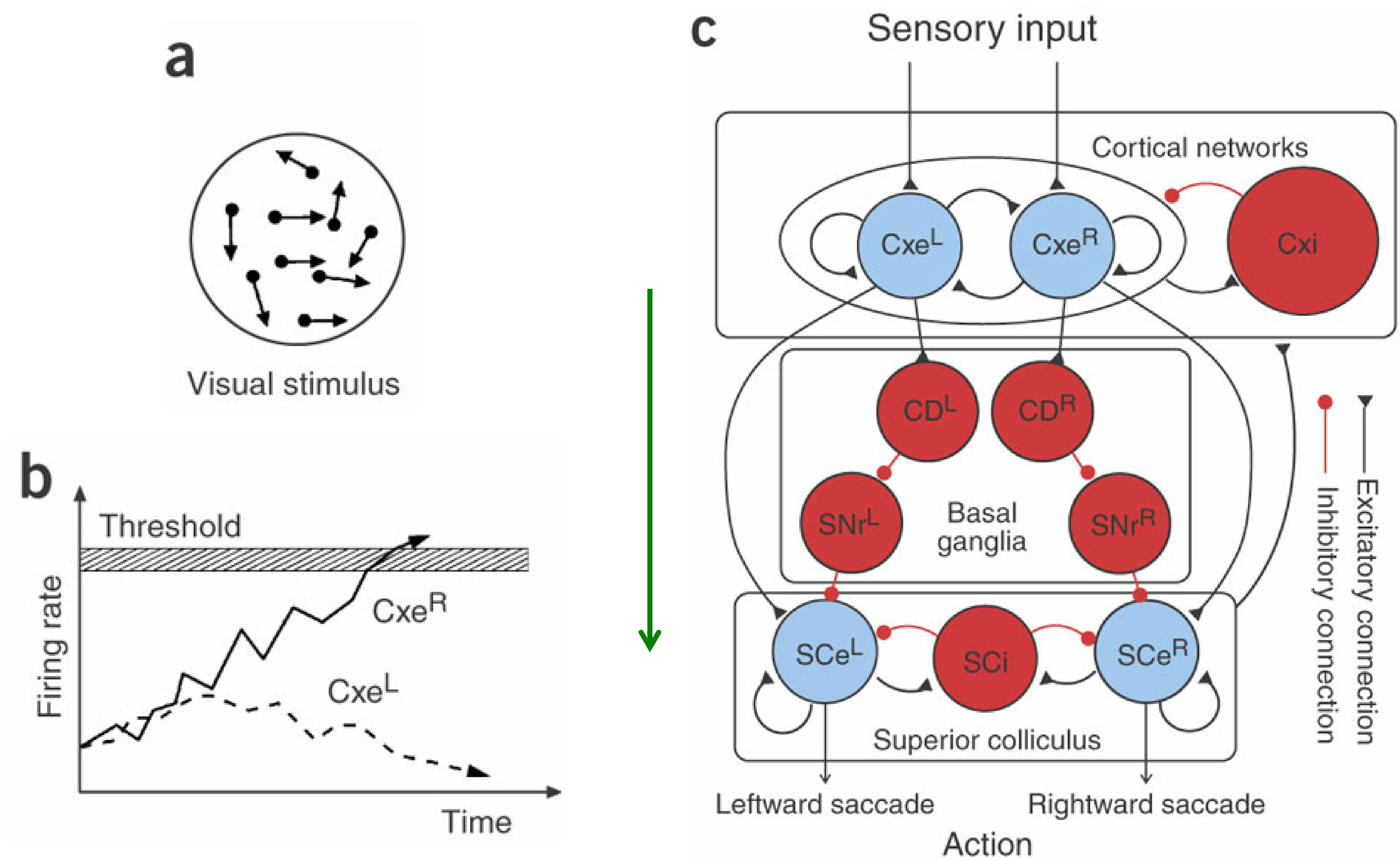
Limit cycles

- An oscillatory trajectory is a *limit cycle* if all trajectories within a small region enclosing the oscillatory trajectory are spirals
  - If neighboring trajectories spiral towards the oscillatory trajectory, then the limit cycle is asymptotically stable
  - If they spiral away, the limit cycle is unstable
- Poincaré-Bendixon theorem:
  - Suppose there is an annular region that contains no equilibrium points and for which all trajectories that cross the boundary of the annulus enter it
  - Then, the annulus must contain at least one asymptotically stable limit cycle

Wilson-Cowan example (revisited)

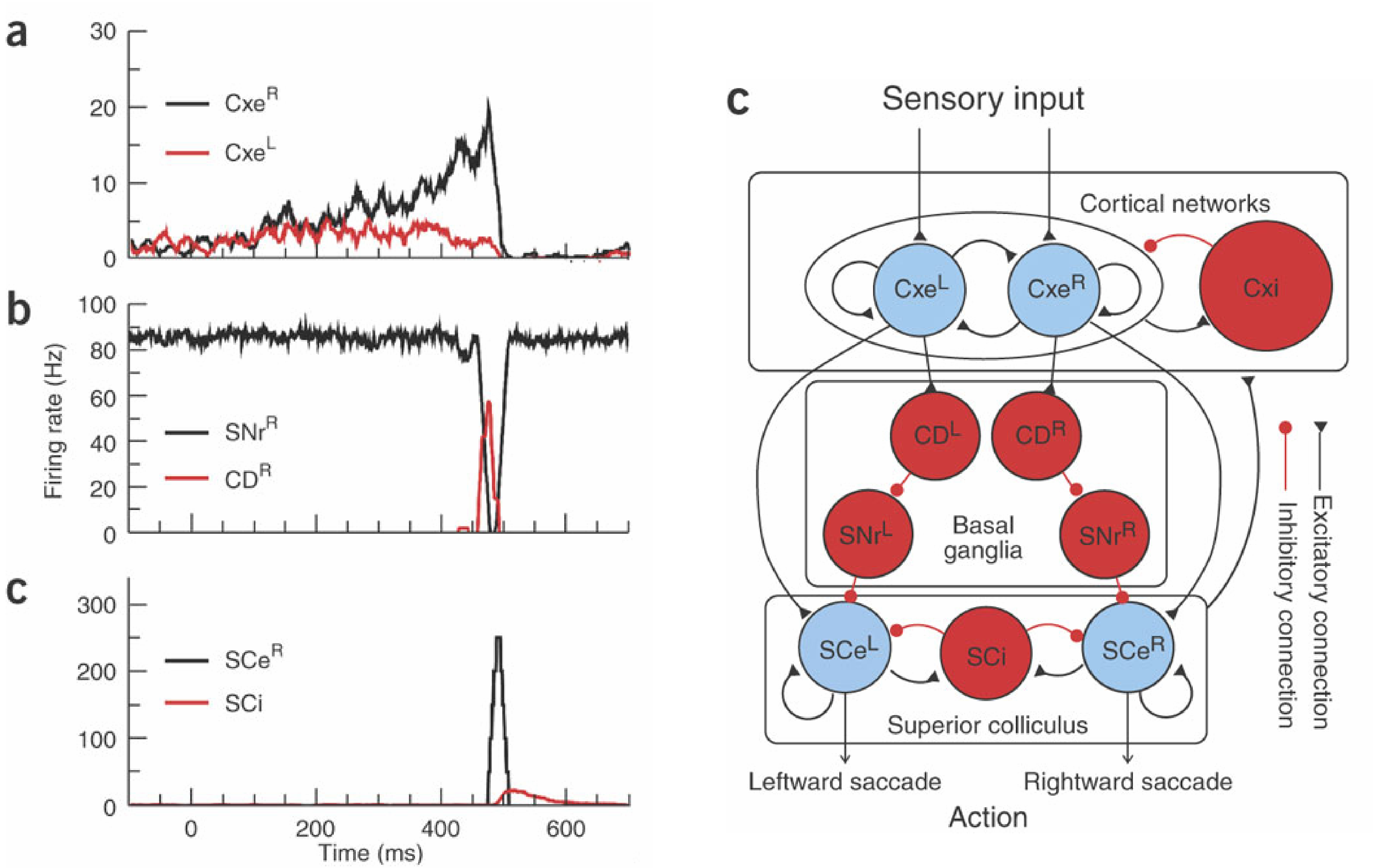


Phase Plane analysis for systems: Decision response in the visual system



Lo and Wang, ***Nature Neuroscience*** 9, 956 - 963 (2006)

Pathway response to stimulus



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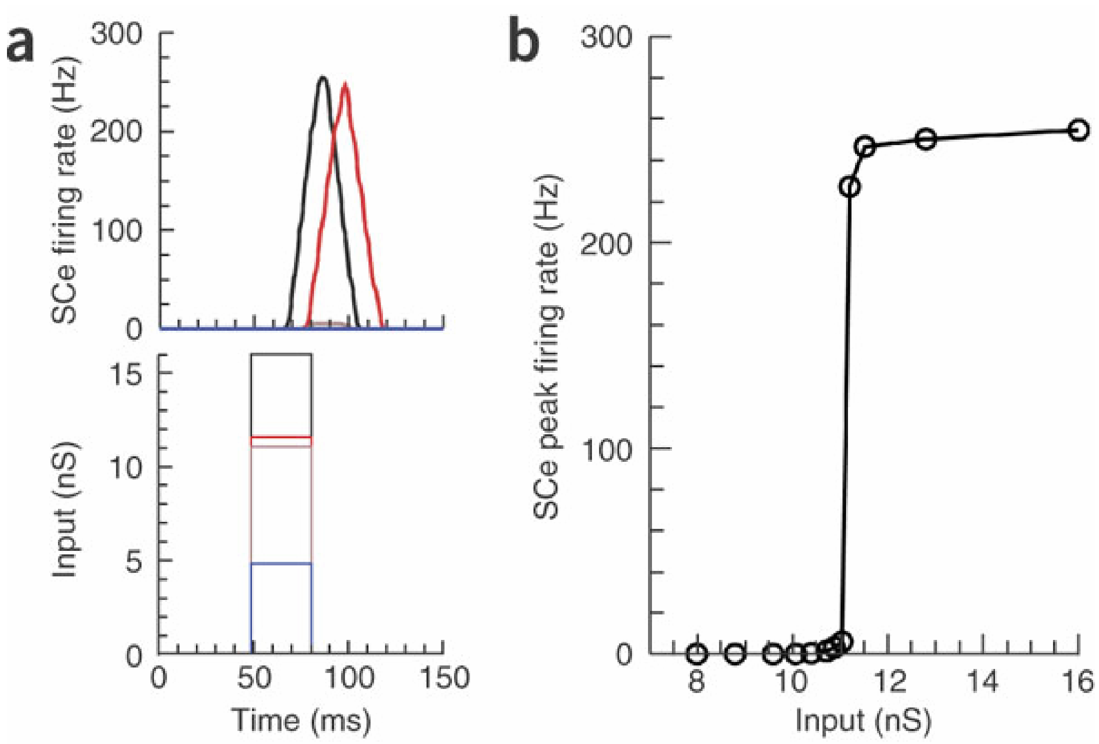
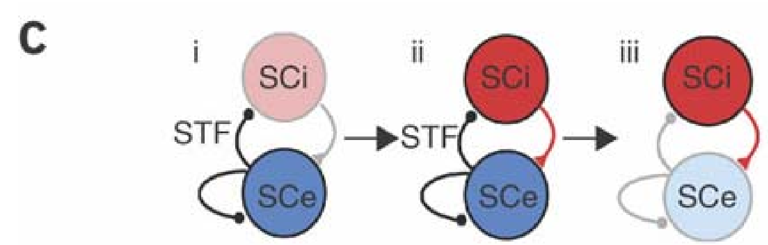
Superior colliculus: thresholded response to input



Interactions between excitatory and inhibitory neurons in the superior colliculus lead to thresholded burst generation.



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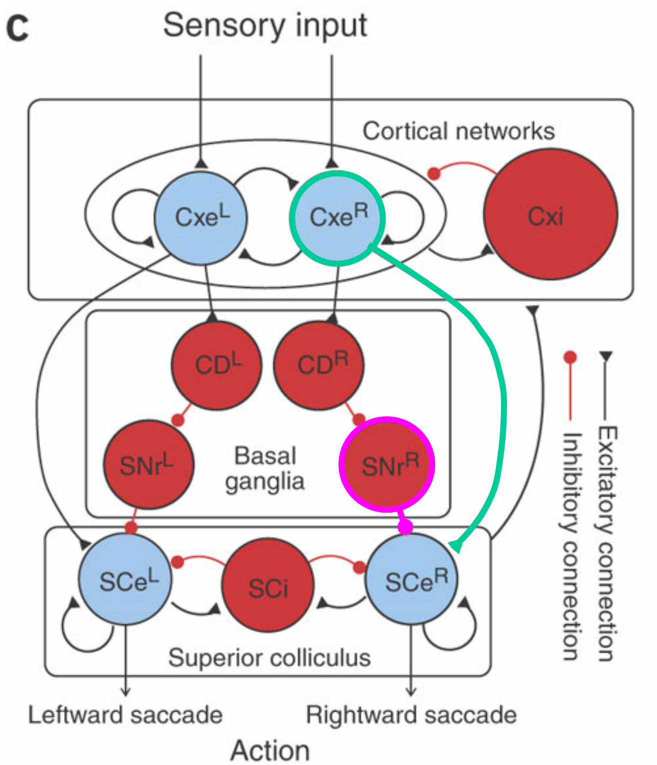
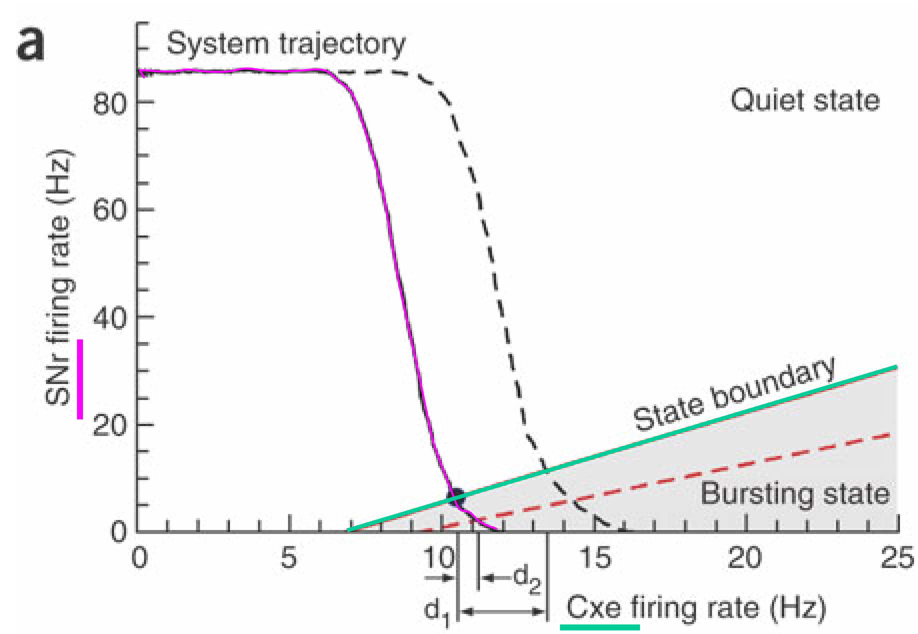
Contributions to the threshold mechanism: Cxe-SC or Cxe-CD





- An increase in the efficacy of the Cxe-SC synapses results in only a small increase in the threshold for firing
- However, an increase in the efficacy of the SNr-SC synapses leads to a large change in the threshold

  → implies that the Cxe→basal ganglia→SC pathway is better able to tune this threshold

Lo and Wang, ***Nature Neuroscience*** 9, 956 - 963 (2006)