

Multidimensional dynamical systems

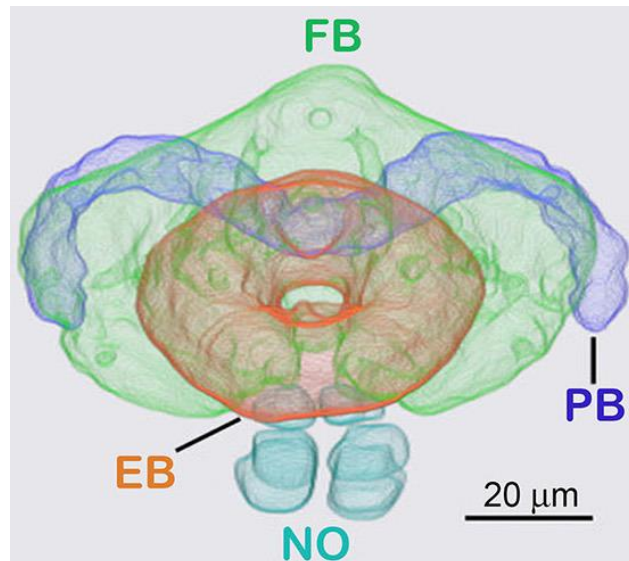
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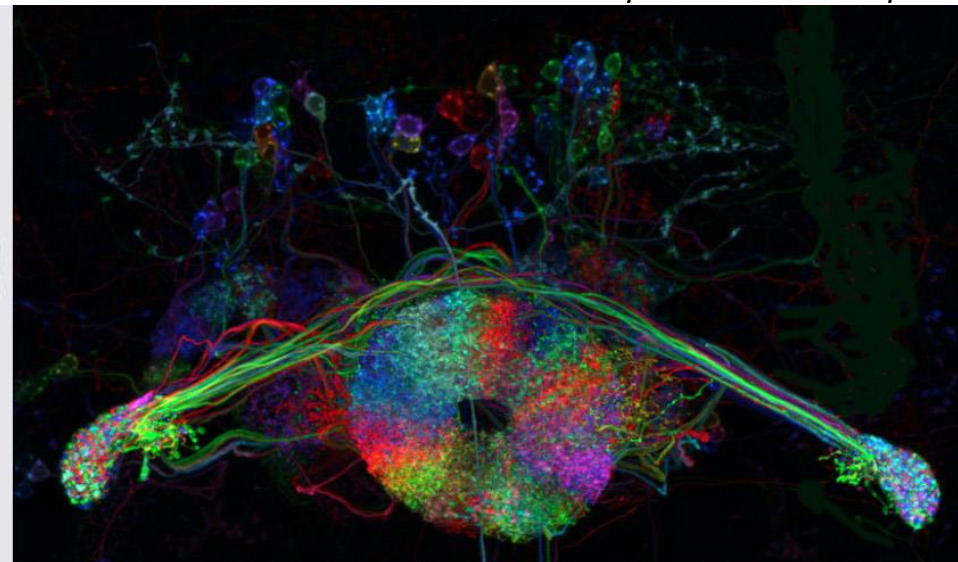
The Wilson-Cowan model: a simple model of neuron population firing rates

Wilson, H.R and Cowan, J.D. 1972, 1973 established a two-dimensional model of interacting populations of excitatory and inhibitory neurons.

“It is probably true that studies of primitive nervous systems should be focused on individual nerve cells and their precise, genetically determined interactions with other cells. Although such an approach may also be appropriate for many parts of the mammalian nervous system, it is not necessarily suited to an investigation of those parts which are associated with higher functions, such as sensory information processing and the attendant complexities of learning, memory storage, and pattern recognition.” – W&C 1972



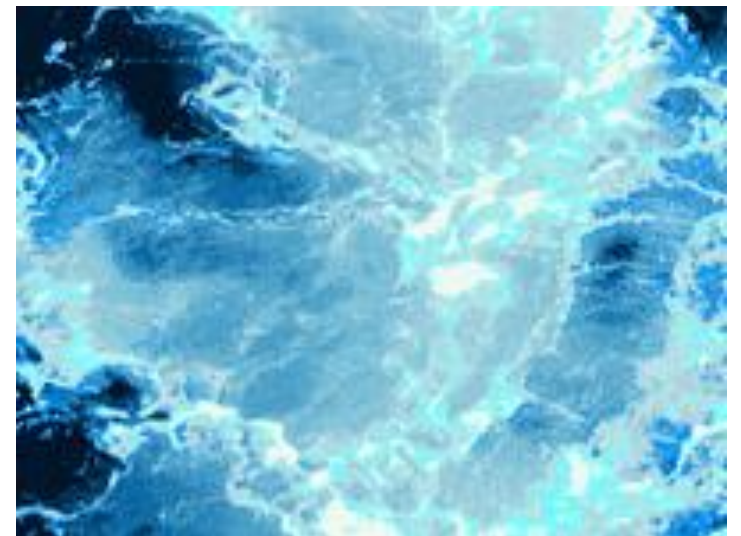
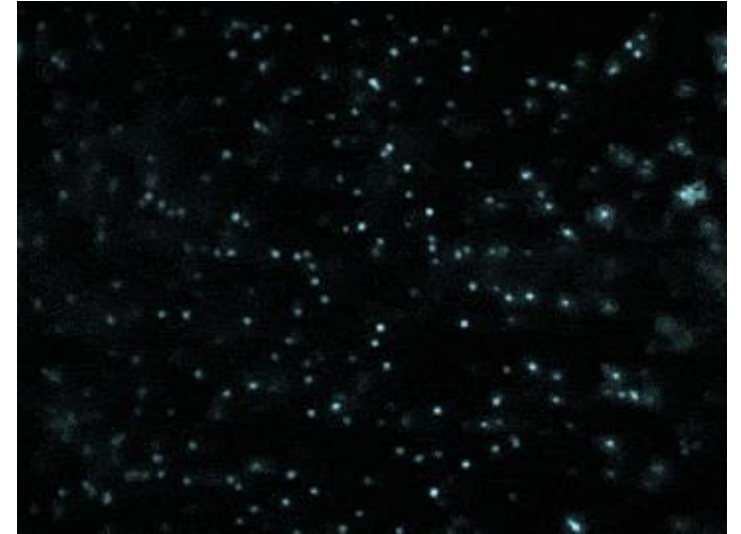
Drosophila central complex



The Wilson-Cowan model: a simple model of neuron population firing rates

Wilson, H.R and Cowan, J.D. 1972, 1973 established a two-dimensional model of interacting populations of excitatory and inhibitory neurons.

- We need a population modeling approach because simulating vast numbers of neurons individually is impractical.
- We hypothesize that **local interactions between neurons in regions like cortex are largely random**, but that this local randomness gives rise to precise macroscopic structure.
 - “If a fluid is observed at the molecular level, what is seen is **Brownian motion**, whereas the same fluid, viewed macroscopically, may be undergoing very **orderly streamlined flow**.”



For more history, read Wilson and Cowan 2021 “Evolution of the Wilson–Cowan equations”.

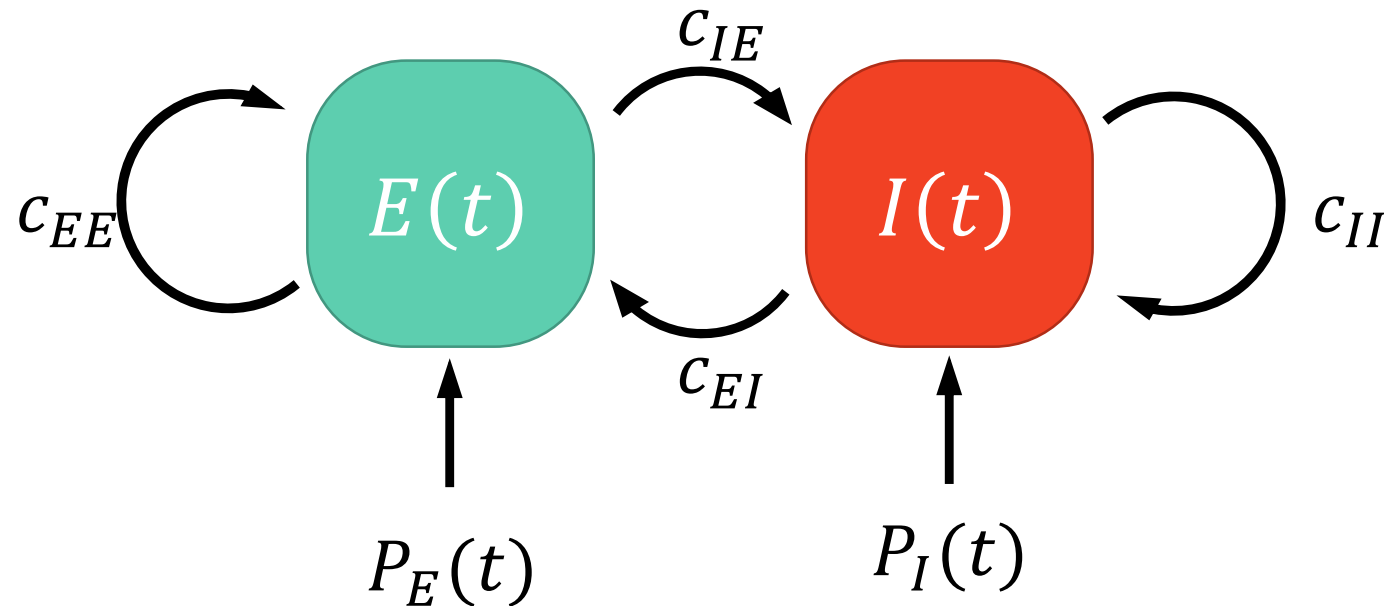
Or: <https://youtu.be/7Ht9k824nWA>

Or, drive down to U Chicago and ask Jack Cowan?

The Wilson-Cowan model: simulating a pair of interacting neural populations

Let's define:

- $E(t)$ = proportion of excitatory cells firing per unit time at the instant t .
- $I(t)$ = proportion of inhibitory cells firing per unit time at the instant t .



What fraction of each population spikes given this pattern of inputs?

The Wilson-Cowan model: defining the proportion of “excitable” neurons

If neurons are all independent of each other and the absolute refractory period of a neuron is r ms, then the **proportion of excitatory cells that are refractory** at any given time is

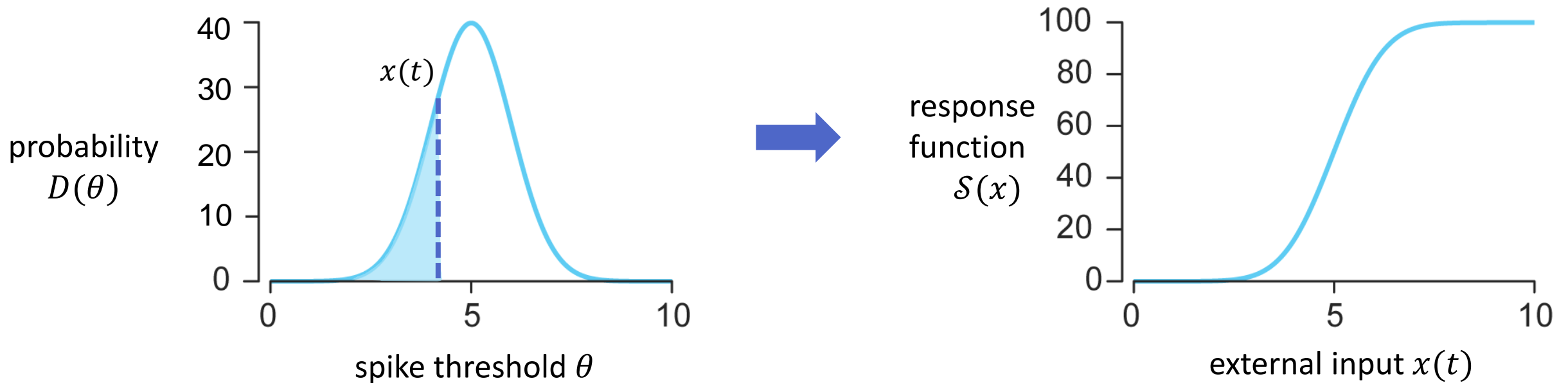
$$\int_{t-r}^t E(s) ds$$

Example: Say we’re sampling at 100 Hz, 20% of cells fire in a 10-ms window (one unit time), and r is 5 ms, then $\int_{t-(\frac{5}{10})}^t 20 ds = 10\%$ of cells are refractory in a 10-ms window.

The Wilson-Cowan model: defining the population response function

If the **distribution of individual neuron spike thresholds is $D(\theta)$** and all cells get the same average excitation $x(t)$, then the fraction of neurons that get enough input to be active (the response function) is

$$\mathcal{S}(x) = \int_0^{x(t)} D(\theta) d\theta$$



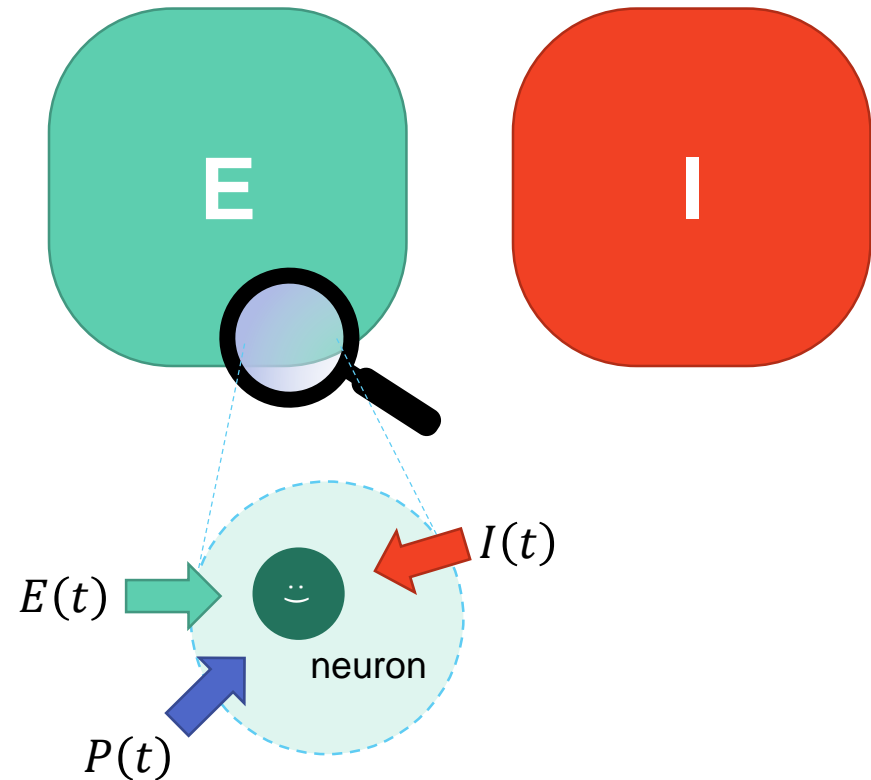
The Wilson-Cowan model: defining the input per neuron

Now we know how external input translates to the population response function. But how is input to the population processed by its neurons?

- Average cell gets c_E excitatory inputs
- Average cell gets c_I inhibitory inputs
- Average cell gets an external input $P(t)$
- Effect of stimulation decays with time course $\alpha(t)$ (akin to the membrane time constant)

Average
input
per cell:

$$\int_{-\infty}^t \alpha(t-s)(c_E E(s) - c_I I(s) + P(s)) ds$$



The Wilson-Cowan model: putting the terms together

- Effect of stimulation decays with time course $\alpha(t)$ (akin to the membrane time constant)
- Average cell gets c_E excitatory inputs
- Average cell gets c_I inhibitory inputs
- Average cell gets an external input $P(t)$

Average
input
per cell:

$$\int_{-\infty}^t \alpha(t-s)(c_E E(s) - c_I I(s) + P(s)) ds$$

- So: what fraction of the population spikes given this average input?
= (fraction of excitable cells) · (fraction of cells receiving sufficient excitation to spike)

Fraction of excitable cells:

$$1 - \int_{t-r}^t E(s) ds$$

Fraction of cells receiving enough input $x(t)$ to spike:

$$\mathcal{S}(x)$$

$$E(t + \Delta t) = \left(1 - \int_{t-r}^t E(s) ds \right) \cdot \mathcal{S}_E \left(\int_{-\infty}^t \alpha(t-s)(c_{EE} E(s) - c_{EI} I(s) + P_E(s)) ds \right)$$

$$I(t + \Delta t) = \left(1 - \int_{t-r}^t I(s) ds \right) \cdot \mathcal{S}_I \left(\int_{-\infty}^t \alpha(t-s)(c_{IE} E(s) - c_{II} I(s) + P_I(s)) ds \right)$$

The Wilson-Cowan model: coarse-graining to get rid of those integrals

To make the system easier to analyze, we will apply a physicist's trick called coarse-graining: replacing a variable (eg $E(t)$) by its moving average over time- ironing out the fastest fluctuations of the signal.

We are justified in doing so here because $E(t)$ and $I(t)$ already only appear as time-averaged values:

$$E(t + \Delta t) = \left(1 - \int_{t-r}^t E(s) ds \right) \cdot \mathcal{S}_E \left(\int_{-\infty}^t \alpha(t-s) (c_{EE} E(s) - c_{EI} I(s) + P(s)) ds \right)$$

So we will define:

$$\begin{aligned} \int_{t-r}^t E(s) ds &\rightarrow r \bar{E}(t) \\ \int_{-\infty}^t \alpha(t-s) E(s) ds &\rightarrow k \bar{E}(t) \end{aligned}$$

A first-order Taylor expansion $f(t + \tau) \sim f(t) + \frac{f'(t)}{1!} \tau$ giving us time coarse-grained differential equations:

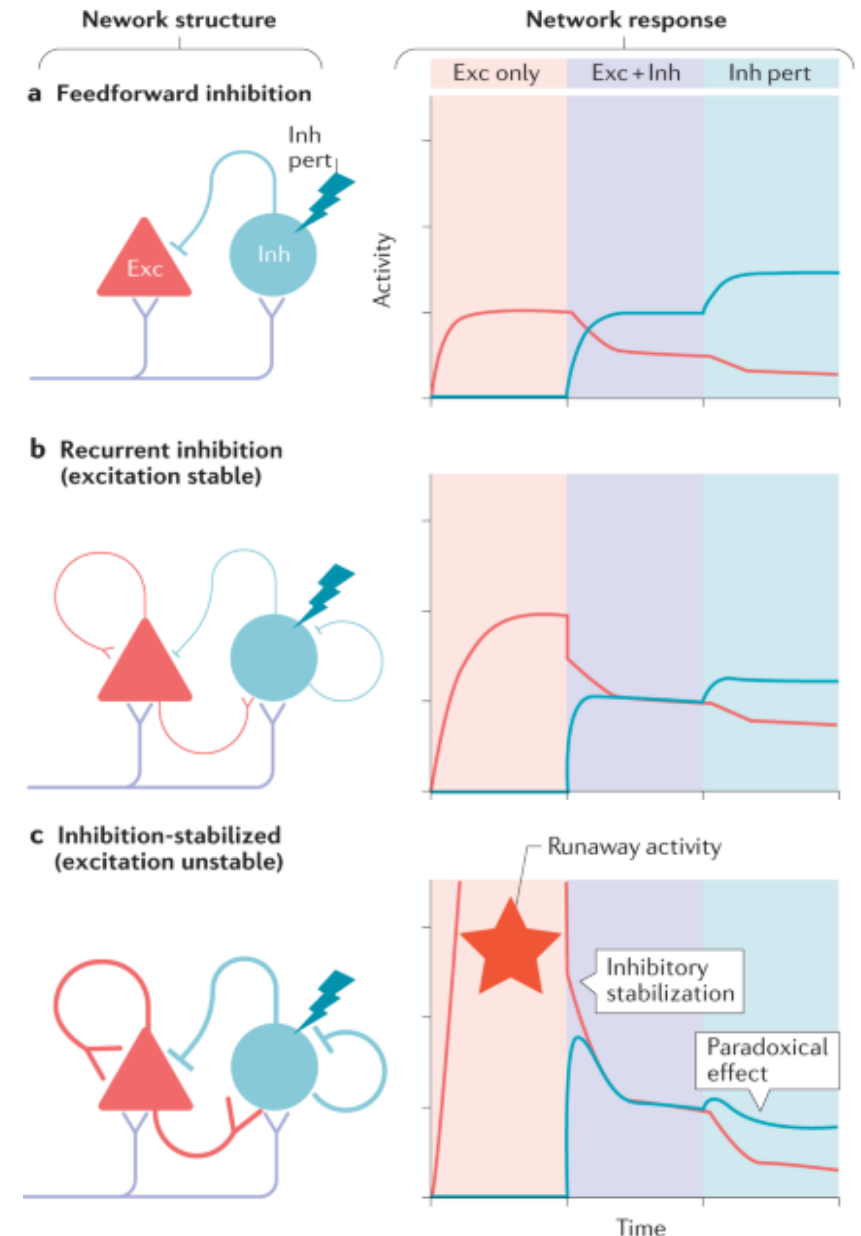
$$\tau_E \frac{d\bar{E}}{dt} = -\bar{E} + (1 - r\bar{E}) \cdot \mathcal{S}_E(kc_{EE}\bar{E} - kc_{EI}\bar{I} + kP_E(t))$$

$$\tau_I \frac{d\bar{I}}{dt} = -\bar{I} + (1 - r\bar{I}) \cdot \mathcal{S}_I(kc_{IE}\bar{E} - kc_{II}\bar{I} + kP_I(t))$$

Dynamics of Wilson-Cowan models

You can use Wilson-Cowan to study various configurations of E/I populations. One important concept that has emerged from the Wilson-Cowan model is the inhibitory-stabilized network (ISN) regime.

- Increasing the input to inhibitory interneurons sometimes causes a paradoxical decrease in their activity.
- ISNs can account for this, as introduced by Tsodyks, Skaggs, Sejnowski, and McNaughton 1997 in hippocampus.
- Also demonstrated to underly visual surround suppression in Ozeki et al 2009 (if you took Great Experiments.)
- Idea: excitatory neurons are unstable due to strong recurrent excitation, but this system is stabilized via reciprocal connection to an inhibitory population.



Wilson and Cowan travel time and space

In their 1973 follow-up to the original paper, Wilson and Cowan extend their two-population model to include interactions of E and I populations across space, using a pair of partial differential equations:

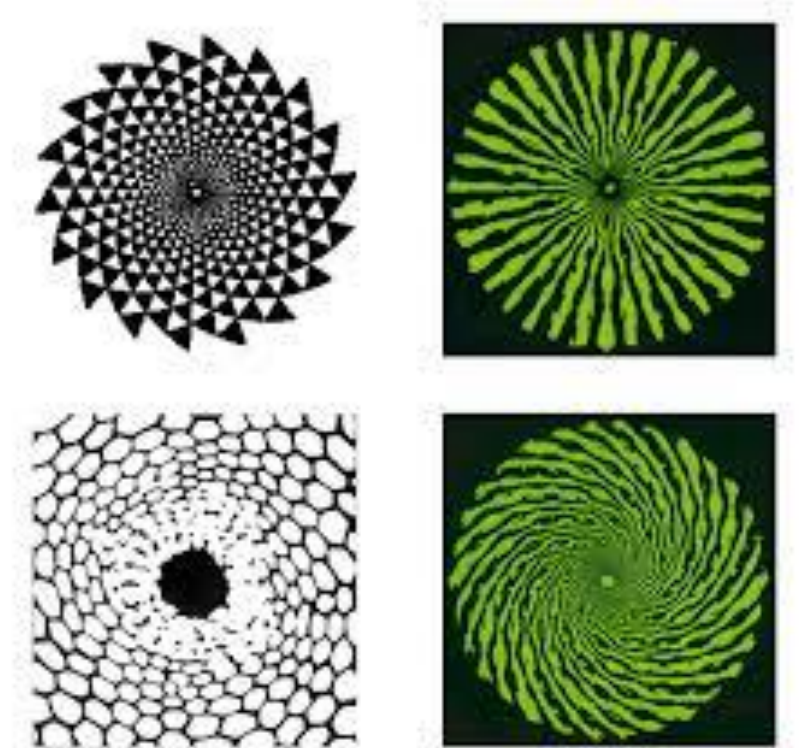
$$\tau_E \frac{\partial E}{\partial t} = -E + (1 - rE) \mathcal{S}_E(\beta_{EE}(x) * E - \beta_{EI}(x) * I + P_E(x, t))$$

$$\tau_I \frac{\partial I}{\partial t} = -I + (1 - rI) \mathcal{S}_I(\beta_{IE}(x) * E - \beta_{II}(x) * I + P_I(x, t))$$

Where $\beta_{EE}(x) * E$ is a convolution with a spatial filter:

$$\beta_{EE}(x) * E = \int_{-\infty}^{\infty} e^{-\frac{|x-x'|}{w_{EE}}} E(x') dx'$$

here an exponential, later more often Gaussian. By making the filter widths specific to the different projections (E-E, E-I, I-E, and I-I) a variety of effects can be produced. For example, traveling waves of activity in the 2D spatial model were proposed by Ermentrout and Cowan 1979 as a mechanism for visual hallucinations, inspired by observations from their U Chicago colleague Heinrich Klüver's self-experimentation with peyote.



How do we study the behavior of this 2D dynamical system?

First let's make life easier:

$$r = 1$$

$$k = 1$$

$$\tau_E \frac{d\bar{E}}{dt} = -\bar{E} + (1 - \cancel{r\bar{E}}) \cdot \mathcal{S}_E(\cancel{k}c_{EE}\bar{E} - \cancel{k}c_{EI}\bar{I} + \cancel{k}P_E(t))$$

$$\tau_I \frac{d\bar{I}}{dt} = -\bar{I} + (1 - \cancel{r\bar{I}}) \cdot \mathcal{S}_I(\cancel{k}c_{IE}\bar{E} - \cancel{k}c_{II}\bar{I} + \cancel{k}P_I(t))$$



$$\tau_E \frac{d\bar{E}}{dt} = -\bar{E} + (1 - \bar{E}) \cdot \mathcal{S}_E(c_{EE}\bar{E} - c_{EI}\bar{I} + P_E(t))$$

$$\tau_I \frac{d\bar{I}}{dt} = -\bar{I} + \underline{(1 - \bar{I})} \cdot \mathcal{S}_I(c_{IE}\bar{E} - c_{II}\bar{I} + P_I(t))$$



(A lot of more recent work just sets $r=0$ to remove these terms)

How do we study the behavior of this 2D dynamical system?

$$\tau_E \frac{d\bar{E}}{dt} = -\bar{E} + (1 - \bar{E}) \cdot \mathcal{S}_E(c_{EE}\bar{E} - c_{EI}\bar{I} + P_E(t))$$

$$\tau_I \frac{d\bar{I}}{dt} = -\bar{I} + (1 - \bar{I}) \cdot \mathcal{S}_I(c_{IE}\bar{E} - c_{II}\bar{I} + P_I(t))$$

Like we did on day 1, let's look for points where $\frac{d\bar{E}}{dt}$ and $\frac{d\bar{I}}{dt}$ are 0:

$$0 = -\bar{E} + (1 - \bar{E}) \cdot \mathcal{S}_E(c_{EE}\bar{E} - c_{EI}\bar{I} + P_E(t))$$

$$0 = -\bar{I} + (1 - \bar{I}) \cdot \mathcal{S}_I(c_{IE}\bar{E} - c_{II}\bar{I} + P_I(t))$$



The response function \mathcal{S} is always monotonic increasing, which means it's invertible:

$$\mathcal{S}_E^{-1}\left(\frac{\bar{E}}{1 - \bar{E}}\right) = c_{EE}\bar{E} - c_{EI}\bar{I} + P_E(t)$$

$$c_{EI}\bar{I} = c_{EE}\bar{E} - \mathcal{S}_E^{-1}\left(\frac{\bar{E}}{1 - \bar{E}}\right) + P_E(t)$$

Points where $\frac{d\bar{E}}{dt} = 0$

$$\mathcal{S}_I^{-1}\left(\frac{\bar{I}}{1 - \bar{I}}\right) = c_{IE}\bar{E} - c_{II}\bar{I} + P_I(t)$$

$$c_{IE}\bar{E} = c_{II}\bar{I} + \mathcal{S}_I^{-1}\left(\frac{\bar{I}}{1 - \bar{I}}\right) - P_I(t)$$

Points where $\frac{d\bar{I}}{dt} = 0$

How do we study the behavior of this 2D dynamical system?

$$c_{EI}\bar{I} = c_{EE}\bar{E} - \mathcal{S}_E^{-1}\left(\frac{\bar{E}}{1-\bar{E}}\right) + P_E(t) \quad \Rightarrow \quad \frac{d\bar{E}}{dt} = 0$$

$$c_{IE}\bar{E} = c_{II}\bar{I} + \mathcal{S}_I^{-1}\left(\frac{\bar{I}}{1-\bar{I}}\right) - P_I(t) \quad \Rightarrow \quad \frac{d\bar{I}}{dt} = 0$$

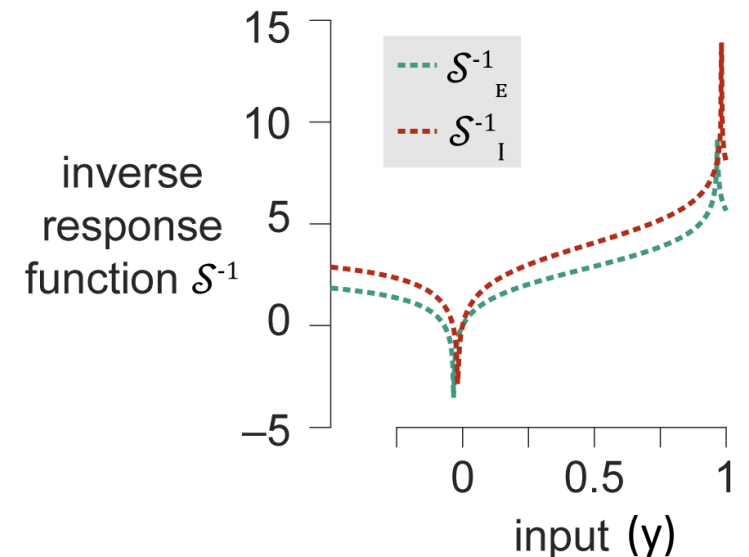
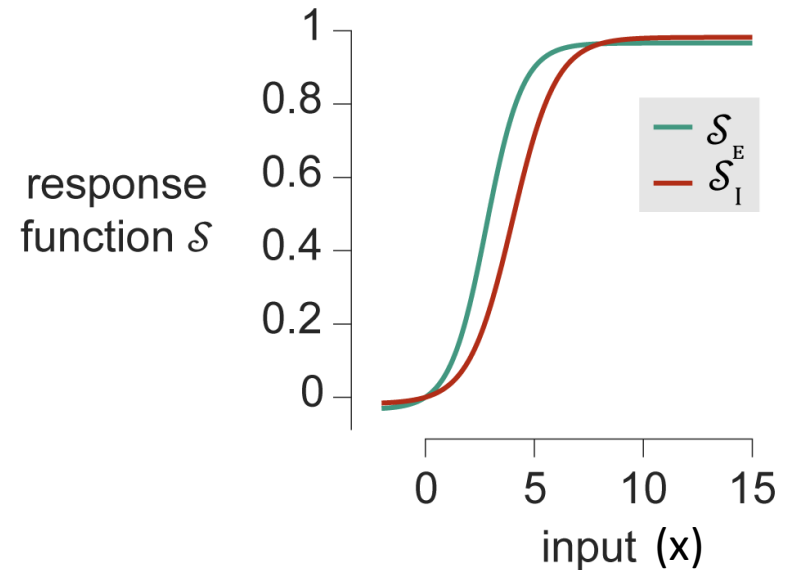
First, what is our response function \mathcal{S} ? Assuming a unimodal spike threshold distribution, \mathcal{S} should be sigmoidal (recall slide 4). W&C chose:

$$\mathcal{S}_n(x) = \frac{1}{1 + \exp(-a_n(x - \theta_n))} - \frac{1}{1 + \exp(a_n\theta_n)}$$

↓ after some fiddling

$$\mathcal{S}_n^{-1}(y) = -\frac{1}{a_n} \log\left(\frac{1 - y - y \exp(-a_n\theta_n)}{1 + y + \exp(a_n\theta_n)y}\right)$$

Plotted: $a_E = 1.2, \theta_E = 2.8, a_I = 1, \theta_I = 4$

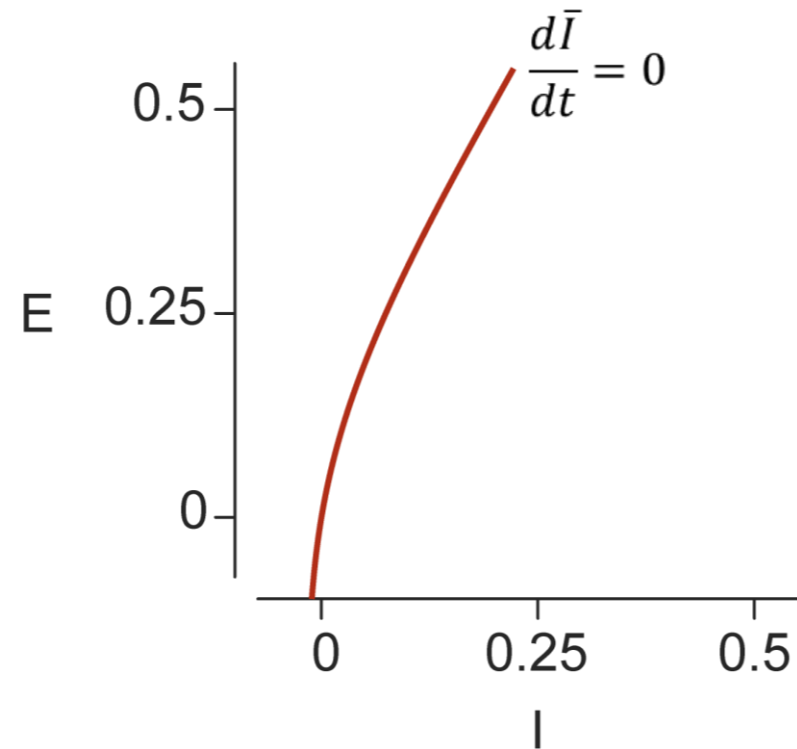
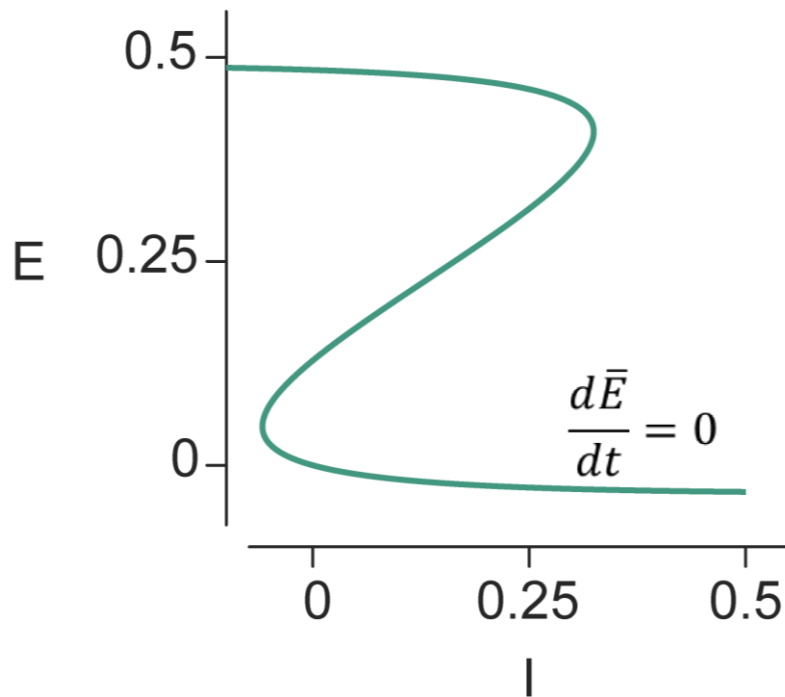


How do we study the behavior of this 2D dynamical system?

$$c_{EI}\bar{I} = c_{EE}\bar{E} - \mathcal{S}_E^{-1}\left(\frac{\bar{E}}{1-\bar{E}}\right) + P_E(t) \quad \Rightarrow \quad \frac{d\bar{E}}{dt} = 0$$

$$c_{IE}\bar{E} = c_{II}\bar{I} + \mathcal{S}_I^{-1}\left(\frac{\bar{I}}{1-\bar{I}}\right) - P_I(t) \quad \Rightarrow \quad \frac{d\bar{I}}{dt} = 0$$

Nullclines!



Plotted: $c_{EE} = 12, c_{EI} = 4, c_{EI} = 13, c_{II} = 11, a_E = 1.2, \theta_E = 2.8, a_I = 1, \theta_I = 4, P_E(t) = 0, P_i(t) = 0$

Studying dI/dt relative to the inhibitory nullcline

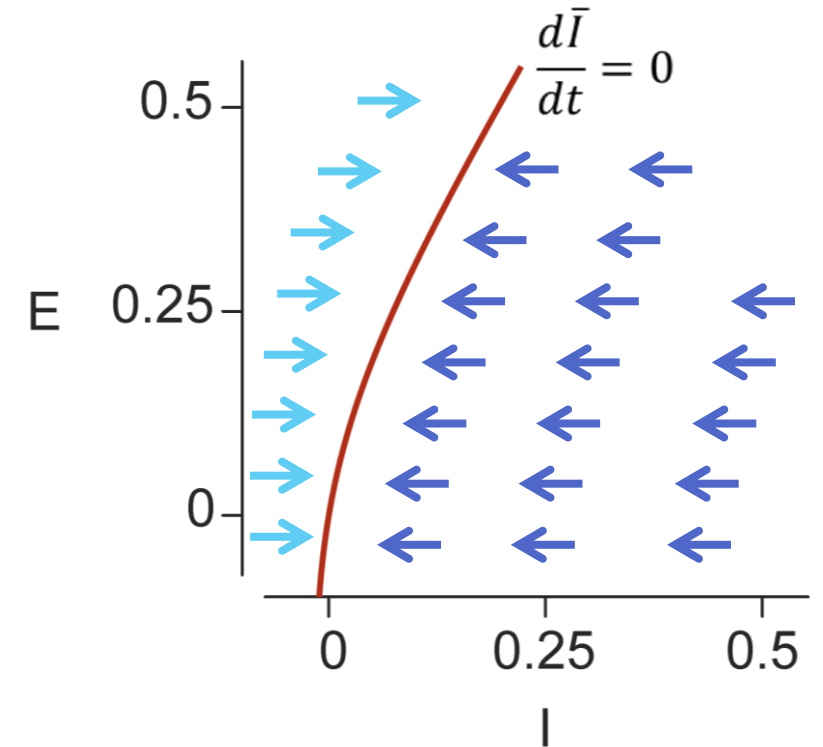
$$c_{IE}\bar{E} = c_{II}\bar{I} + S_I^{-1}\left(\frac{\bar{I}}{1-\bar{I}}\right) \quad \frac{d\bar{I}}{dt} = 0$$

This equation defines a line of values for which $\frac{d\bar{I}}{dt} = 0$. For any set of (\bar{E}, \bar{I}) values not on this line, \bar{I} will either increase or decrease over time.

Because $\frac{d\bar{I}}{dt}$ is a smooth, continuous function, it cannot jump from positive to negative values without crossing 0. Therefore, this nullcline forms a **boundary** between a region where $\frac{d\bar{I}}{dt} > 0$ and a region where $\frac{d\bar{I}}{dt} < 0$. But which is which? Check the equation:

$$\tau_I \frac{d\bar{I}}{dt} = -\bar{I} + (1 - \bar{I}) \cdot S_I(c_{IE}\bar{E} - c_{II}\bar{I})$$

- We know the point $(\bar{E} = 0, \bar{I} = 0)$ lies along the nullcline. (How?)
- For a small increase in \bar{E} , $(\bar{E} > 0, \bar{I} = 0)$, we see the right-hand side of this equation is positive; for a small decrease it's negative. (How?)
- Therefore $\frac{d\bar{I}}{dt} > 0$ for all points left of the nullcline, and $\frac{d\bar{I}}{dt} < 0$ for all points right of the nullcline.



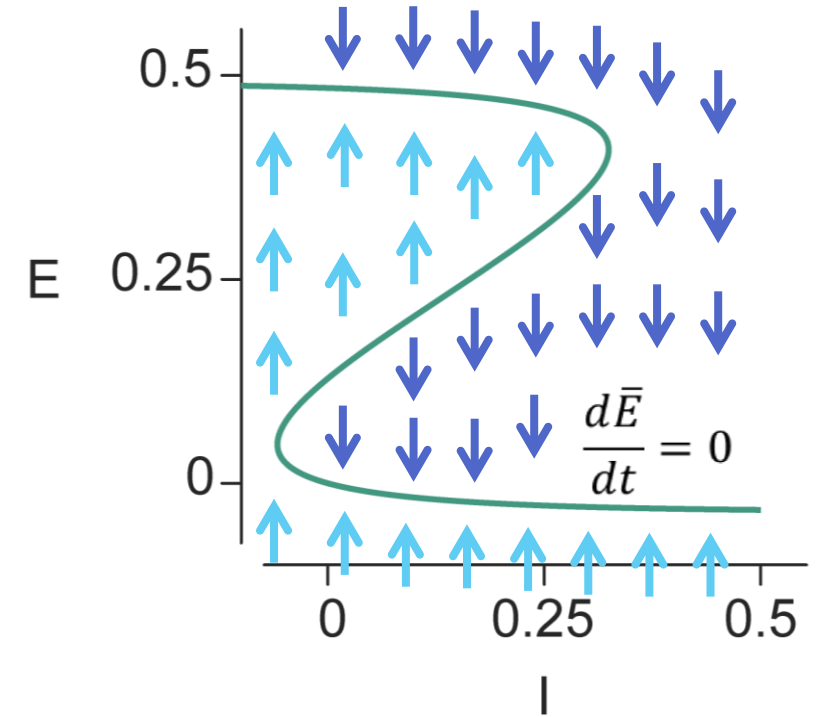
Studying dE/dt relative to the excitatory nullcline

$$c_{EI}\bar{I} = c_{EE}\bar{E} - \mathcal{S}_E^{-1}\left(\frac{\bar{E}}{1-\bar{E}}\right) \quad \frac{d\bar{E}}{dt} = 0$$

We can perform the same analysis to determine stability of regions delimited by the \bar{E} nullcline. Again, we check:

$$\tau_E \frac{d\bar{E}}{dt} = -\bar{E} + (1 - \bar{E}) \cdot \mathcal{S}_E(c_{EE}\bar{E} - c_{EI}\bar{I})$$

- Again, the point $(\bar{E} = 0, \bar{I} = 0)$ lies along the nullcline.
- For a small increase in \bar{I} , $(\bar{E} = 0, \bar{I} > 0)$, we see the right-hand side of this equation is negative; for a small decrease it's positive.
- Therefore $\frac{d\bar{E}}{dt} > 0$ for all points right + up from the nullcline, and $\frac{d\bar{E}}{dt} < 0$ for all points left + down from the nullcline.

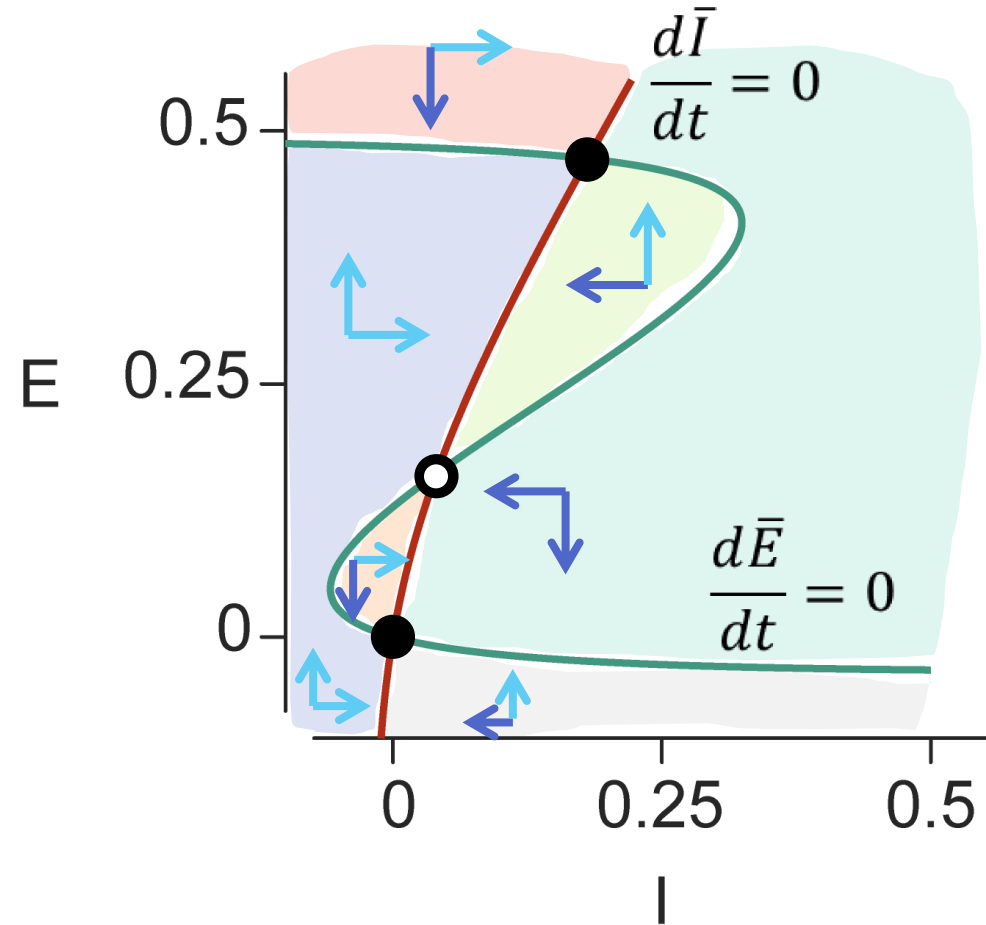


Combining the inhibitory and excitatory nullclines reveals the fixed points of the system

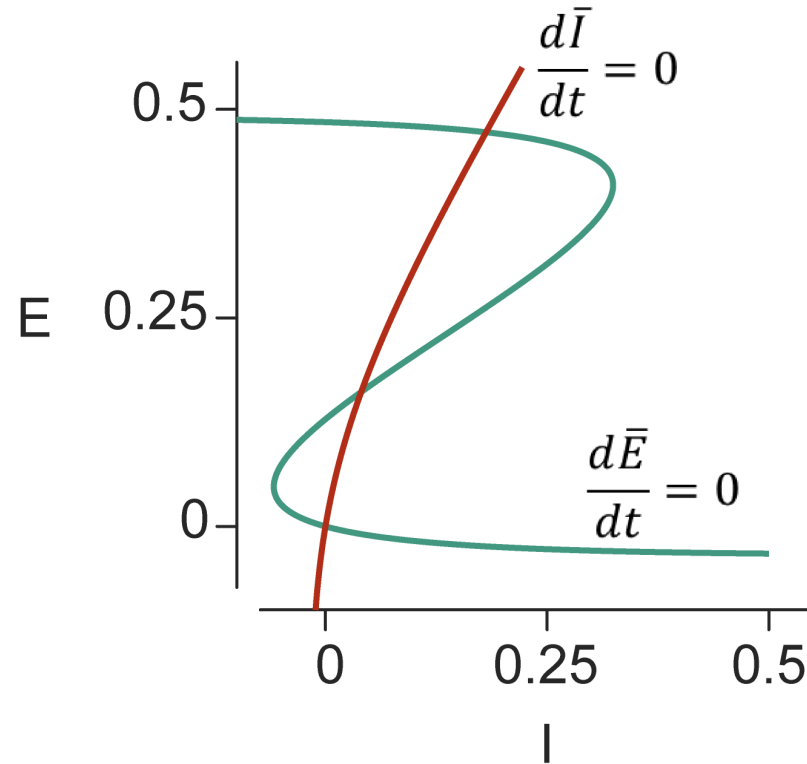
$$c_{EI}\bar{I} = c_{EE}\bar{E} - \mathcal{S}_E^{-1}\left(\frac{\bar{E}}{1-\bar{E}}\right) \quad \frac{d\bar{E}}{dt} = 0$$

$$c_{IE}\bar{E} = c_{II}\bar{I} + \mathcal{S}_I^{-1}\left(\frac{\bar{I}}{1-\bar{I}}\right) \quad \frac{d\bar{I}}{dt} = 0$$

- Putting our two nullclines together, we see they cross at three points, each of which is a fixed point of the system, often written (\bar{E}^*, \bar{I}^*) .
- Each region delimited by the two nullclines will show a characteristic direction of flow, from which we can sometimes guess the stability or instability of fixed points.



Plotting some system trajectories



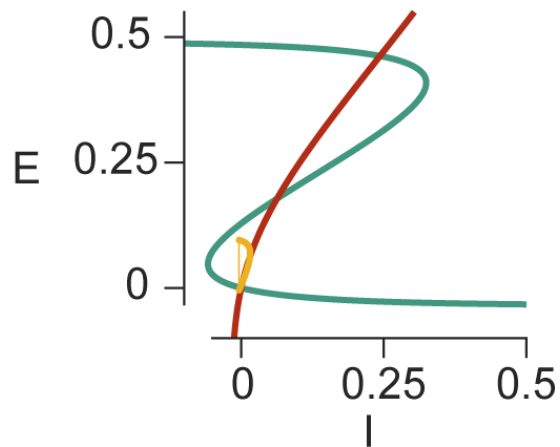
Recurrent weights: $\begin{bmatrix} c_{EE} & c_{EI} \\ c_{IE} & c_{II} \end{bmatrix} = \begin{bmatrix} 12 & 4 \\ 13 & 11 \end{bmatrix}$

External input: $\begin{bmatrix} P_E \\ P_I \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$

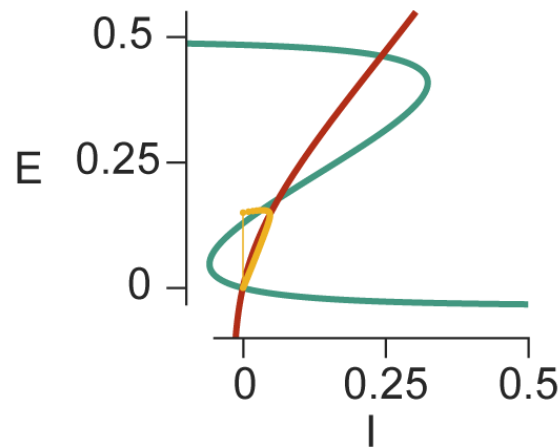
Response function: $\begin{bmatrix} a_E \\ a_I \end{bmatrix} = \begin{bmatrix} 1.2 \\ 1 \end{bmatrix}; \begin{bmatrix} \theta_E \\ \theta_I \end{bmatrix} = \begin{bmatrix} 2.8 \\ 4 \end{bmatrix}$

Plotting some system trajectories

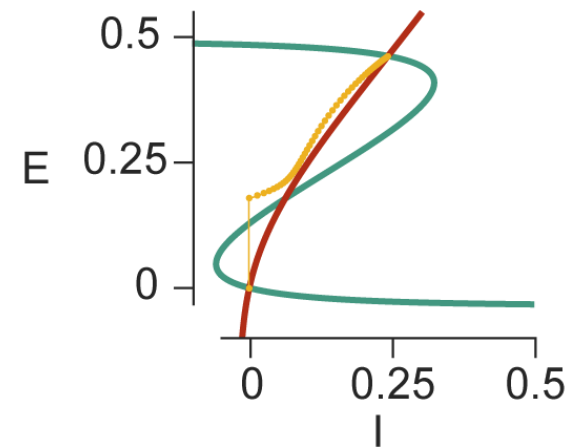
“kick” at step 500: $\begin{bmatrix} \Delta_E \\ \Delta_I \end{bmatrix} = \begin{bmatrix} 0.1 \\ 0 \end{bmatrix}$



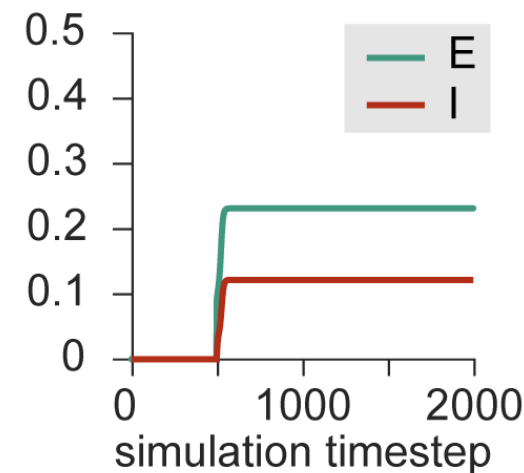
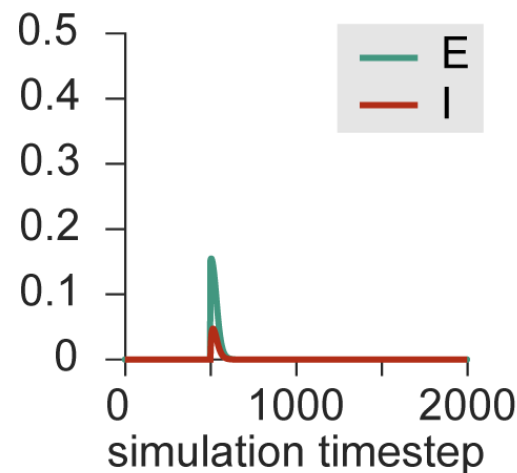
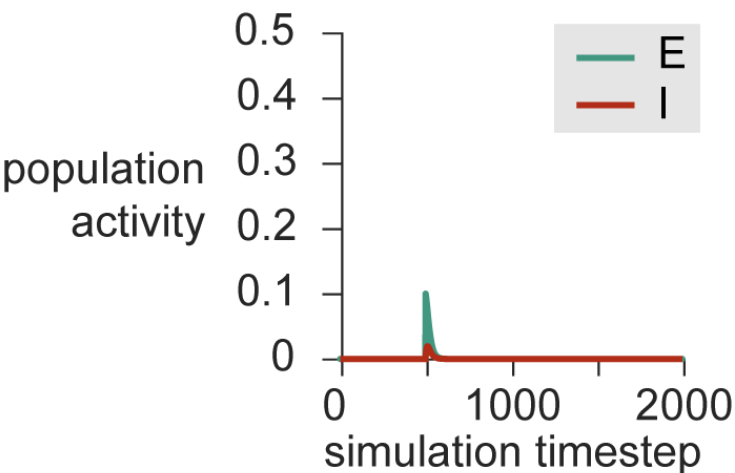
$\begin{bmatrix} \Delta_E \\ \Delta_I \end{bmatrix} = \begin{bmatrix} 0.15 \\ 0 \end{bmatrix}$



$\begin{bmatrix} \Delta_E \\ \Delta_I \end{bmatrix} = \begin{bmatrix} 0.18 \\ 0 \end{bmatrix}$

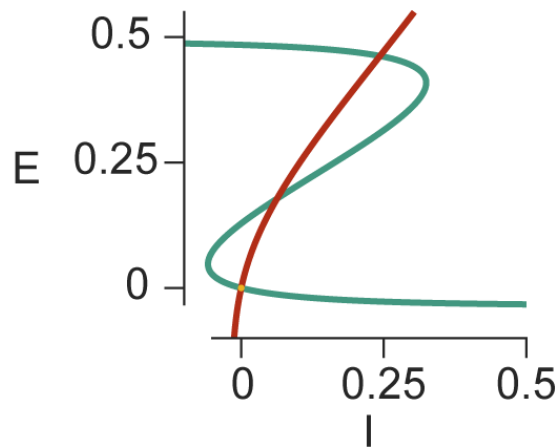


Bistability
== working
memory

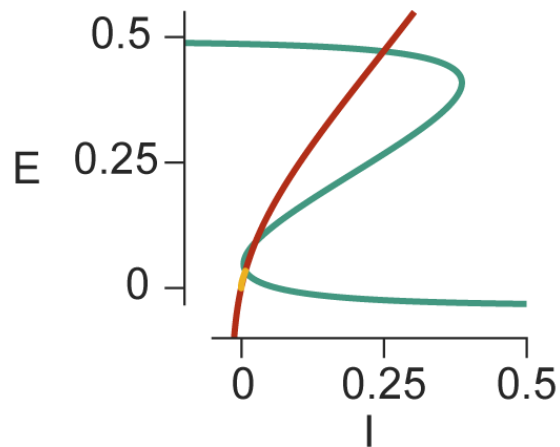


Plotting some system trajectories

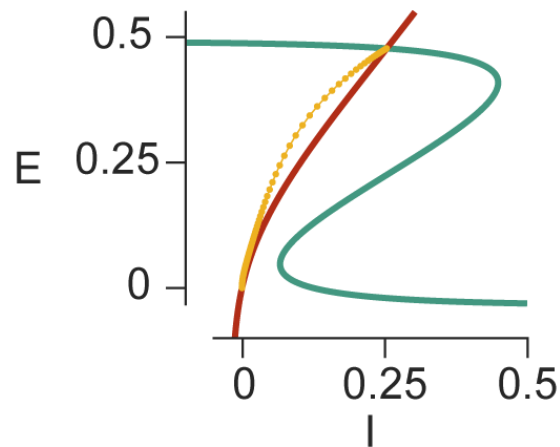
External input: $\begin{bmatrix} P_E \\ P_I \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$



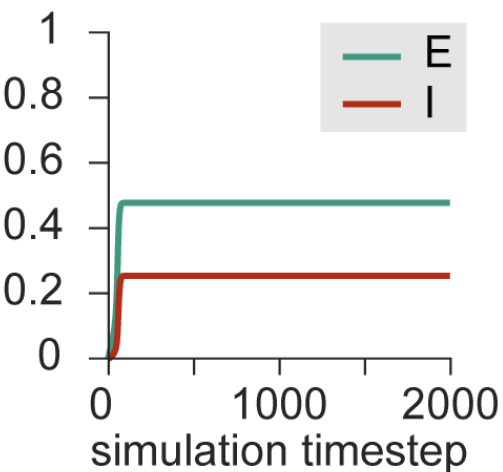
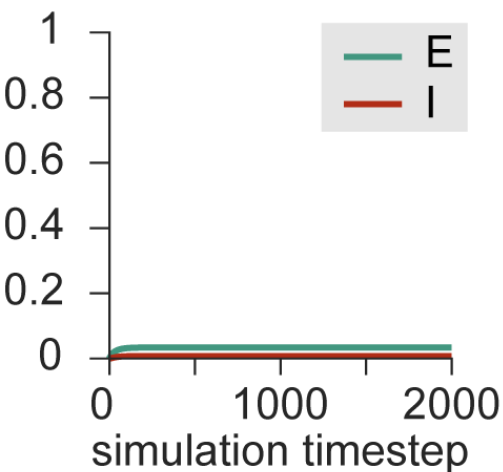
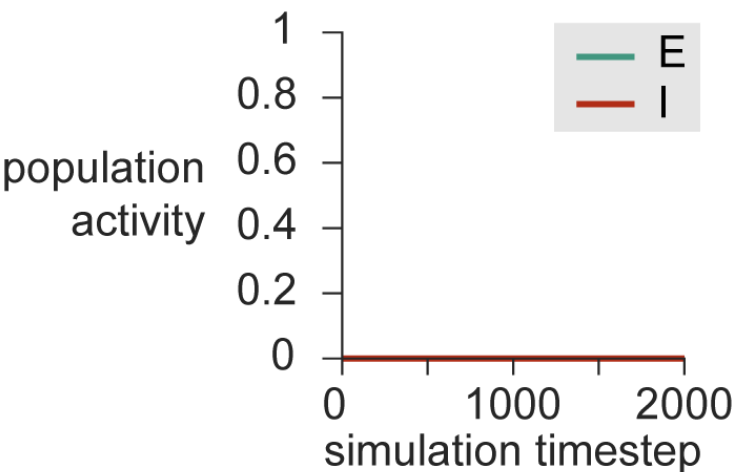
$\begin{bmatrix} P_E \\ P_I \end{bmatrix} = \begin{bmatrix} 0.25 \\ 0 \end{bmatrix}$



$\begin{bmatrix} P_E \\ P_I \end{bmatrix} = \begin{bmatrix} 0.5 \\ 0 \end{bmatrix}$



Saddle node
bifurcation



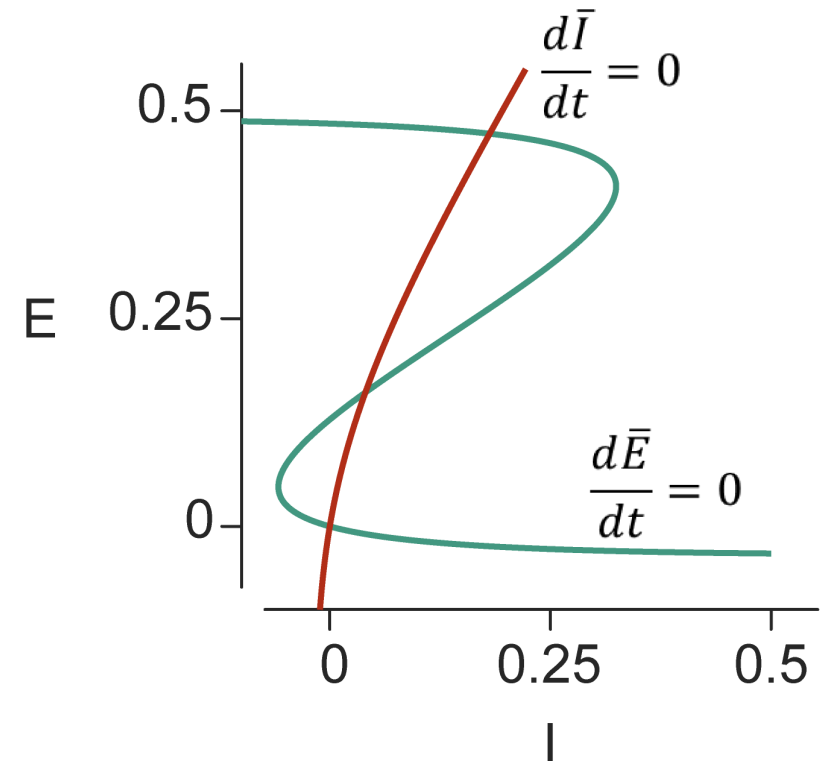
How do we find the fixed points of the system?

$$\begin{aligned} c_{EI}\bar{I} &= c_{EE}\bar{E} - \mathcal{S}_E^{-1}\left(\frac{\bar{E}}{1-\bar{E}}\right) & \frac{d\bar{E}}{dt} &= 0 \\ c_{IE}\bar{E} &= c_{II}\bar{I} + \mathcal{S}_I^{-1}\left(\frac{\bar{I}}{1-\bar{I}}\right) & \frac{d\bar{I}}{dt} &= 0 \end{aligned}$$

Fixed points occur where both nullclines are 0. Solving for the zeros of the above equations is messy, but we can find them numerically using a root-finder:

```
scipy.optimize.root(myWC, (e_init, i_init))
```

Where `myWC` is a python function we must write that returns $\left(\frac{d\bar{E}}{dt}, \frac{d\bar{I}}{dt}\right)$ evaluated at some point (\bar{E}, \bar{I}) , and (e_init, i_init) is an initial guess of the root's location. Only the nearest root will be found, so we call this function 3 times with 3 initial conditions close to where the two lines intersect.



Evaluating stability of fixed points

While we got an intuition of fixed point stability from the phase portrait, we can also determine the stability and nature of a fixed point by linearizing the dynamics of the system around that point. We do this by computing the Jacobian matrix at that fixed point:

$$J = \begin{bmatrix} \frac{\partial}{\partial \bar{E}} \left(\frac{d\bar{E}}{dt}(\bar{E}^*, \bar{I}^*) \right) & \frac{\partial}{\partial \bar{I}} \left(\frac{d\bar{E}}{dt}(\bar{E}^*, \bar{I}^*) \right) \\ \frac{\partial}{\partial \bar{E}} \left(\frac{d\bar{I}}{dt}(\bar{E}^*, \bar{I}^*) \right) & \frac{\partial}{\partial \bar{I}} \left(\frac{d\bar{I}}{dt}(\bar{E}^*, \bar{I}^*) \right) \end{bmatrix}$$

The linearized system is defined as $\frac{dx}{dt} = Jx$ where J is our Jacobian.

We can decompose J into its eigenvectors and eigenvalues: $J = UVU^\dagger$ where V is a diagonal matrix of eigenvalues.

This gives us an equivalent system of independent eigenmodes, $\frac{du_i}{dt} = \lambda_i u_i$, where $u = U^\dagger x$ and u_i is a column of u .

Each eigenmode is stable if $\lambda_i < 0$. The whole system is stable if all eigenmodes are stable!

Evaluating stability of fixed points

So, to determine stability of a fixed point, we find the eigenvalues of the Jacobian matrix at that fixed point. For a 2d matrix $\begin{bmatrix} a & b \\ c & d \end{bmatrix}$ this comes down to finding the roots of the quadratic equation $\lambda^2 + (a + d)\lambda + (ad - bc) = 0$, which gives us a pair of solutions:

$$\lambda = \frac{(a + d)}{2} \pm \sqrt{\frac{(a + d)^2}{4} - ad + bc}$$

Remember from linear algebra that $a + d$ is called the Trace of a matrix and $ad - bc$ is called the Determinant, thus we could also write:

$$\lambda = \frac{\text{Tr}}{2} \pm \sqrt{\frac{\text{Tr}^2}{4} - \text{Det}}$$

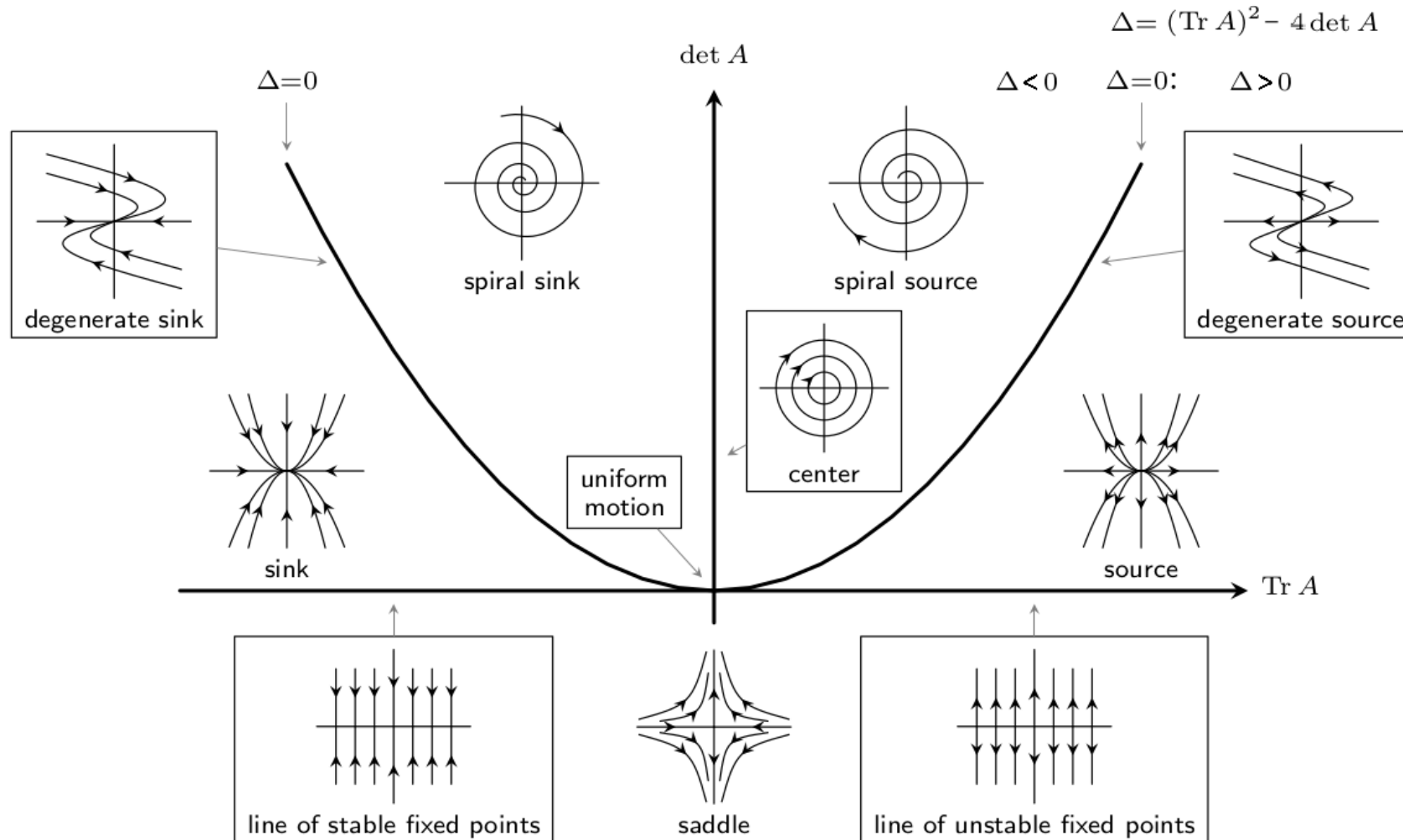
Evaluating stability of fixed points

The eigenvalues $\lambda = \frac{\text{Tr}}{2} \pm \sqrt{\frac{\text{Tr}^2}{4} - \text{Det}}$ thus tell us how the system will behave in the neighborhood of the fixed point.

Evaluating stability of fixed points

The eigenvalues $\lambda = \frac{\text{Tr}}{2} \pm \sqrt{\frac{\text{Tr}^2}{4} - \text{Det}}$ tell us how the system will behave in the neighborhood of the fixed point:

Poincaré Diagram: Classification of Phase Portraits in the $(\det A, \text{Tr } A)$ -plane



Evaluating stability of fixed points

While we got an intuition of fixed point stability from the phase portrait, we can also determine the stability and nature of a fixed point by linearizing the dynamics of the system around that point. We do this by computing the Jacobian matrix at that fixed point:

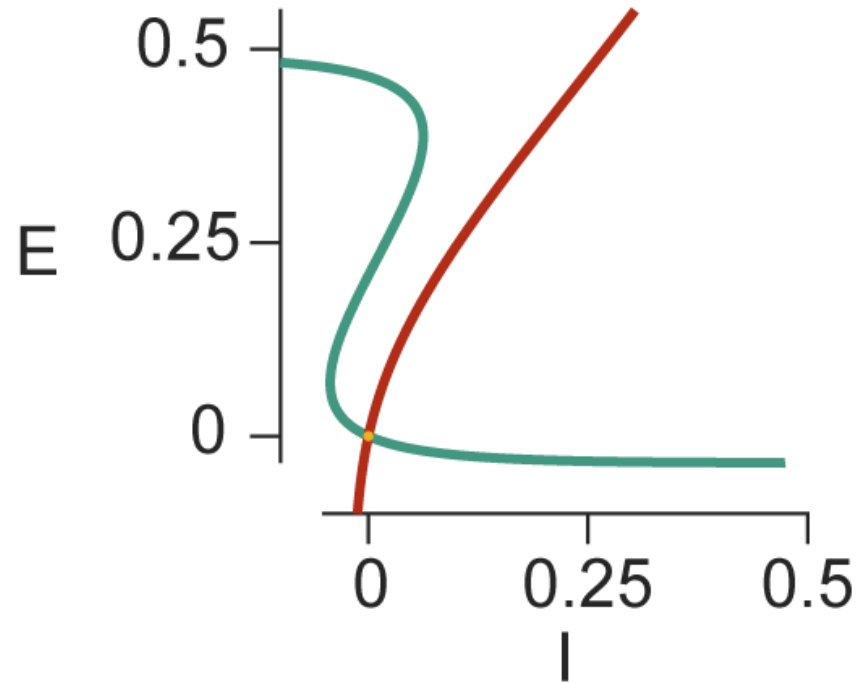
$$J = \begin{bmatrix} \frac{\partial}{\partial \bar{E}} \left(\frac{d\bar{E}}{dt}(\bar{E}^*, \bar{I}^*) \right) & \frac{\partial}{\partial \bar{I}} \left(\frac{d\bar{E}}{dt}(\bar{E}^*, \bar{I}^*) \right) \\ \frac{\partial}{\partial \bar{E}} \left(\frac{d\bar{I}}{dt}(\bar{E}^*, \bar{I}^*) \right) & \frac{\partial}{\partial \bar{I}} \left(\frac{d\bar{I}}{dt}(\bar{E}^*, \bar{I}^*) \right) \end{bmatrix}$$

Computing partial derivatives of $\frac{d\bar{E}}{dt} = \frac{1}{\tau_E} (-\bar{E} + (1 - \bar{E}) \cdot \mathcal{S}_E(c_{EE}\bar{E} - c_{EI}\bar{I}))$ (we can do the same for $\frac{d\bar{I}}{dt}$):

$$\begin{aligned} \frac{\partial}{\partial \bar{E}} \frac{d\bar{E}}{dt} &= -\frac{1}{\tau_E} (1 - \mathcal{S}_E(c_{EE}\bar{E} - c_{EI}\bar{I}) + (1 - \bar{E})c_{EE}\mathcal{S}_E'(c_{EE}\bar{E} - c_{EI}\bar{I})) \\ \frac{\partial}{\partial \bar{I}} \frac{d\bar{E}}{dt} &= -\frac{1}{\tau_E} (1 - \bar{E})c_{EI}\mathcal{S}_E'(c_{EE}\bar{E} - c_{EI}\bar{I}) \end{aligned}$$

Recall that $\mathcal{S}_n(x) = \frac{1}{1+\exp(-a_n(x-\theta_n))} - \frac{1}{1+\exp(a_n\theta_n)}$, so we can compute $\mathcal{S}'_E(x) = \frac{a_E \exp(-a_E(x-\theta_E))}{(1+\exp(-a_n(x-\theta_n)))^2}$

Some more simulations



Recurrent weights: $\begin{bmatrix} c_{EE} & c_{EI} \\ c_{IE} & c_{II} \end{bmatrix} = \begin{bmatrix} \mathbf{10} & \mathbf{8} \\ 13 & 11 \end{bmatrix}$

External input: $\begin{bmatrix} P_E \\ P_I \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$

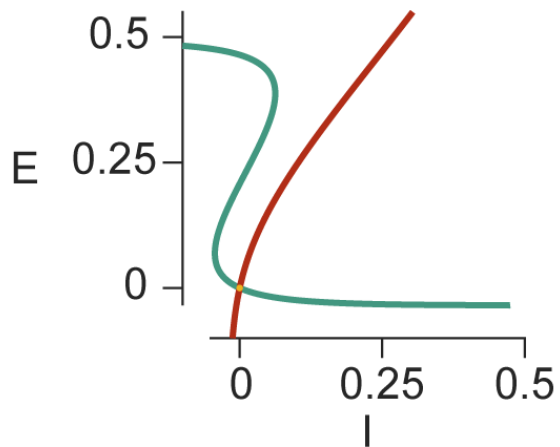
This system has a single fixed point.

It is a stable, spiral node.

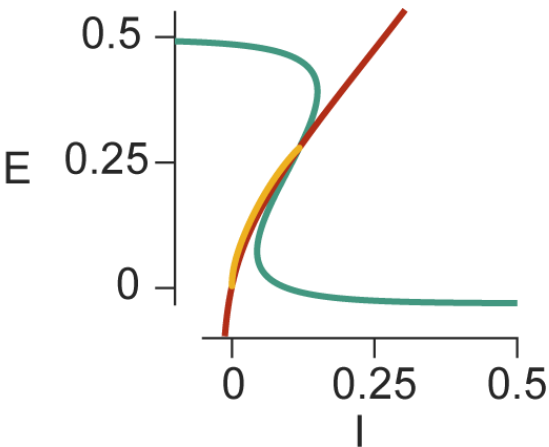
(compute the trace and determinant of the Jacobian at (0,0) to convince yourself of this.)

Plotting some system trajectories

External input: $\begin{bmatrix} P_E \\ P_I \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$

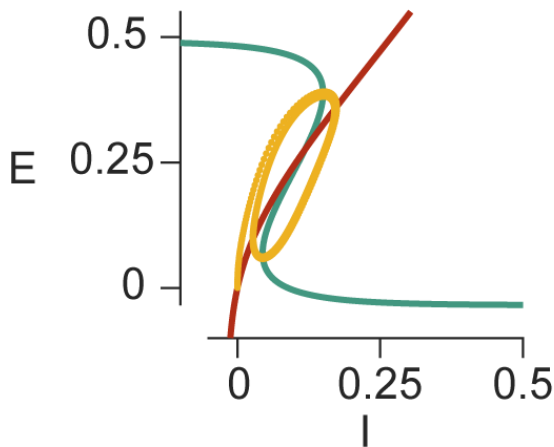


$\begin{bmatrix} P_E \\ P_I \end{bmatrix} = \begin{bmatrix} 0.7 \\ 0 \end{bmatrix}$

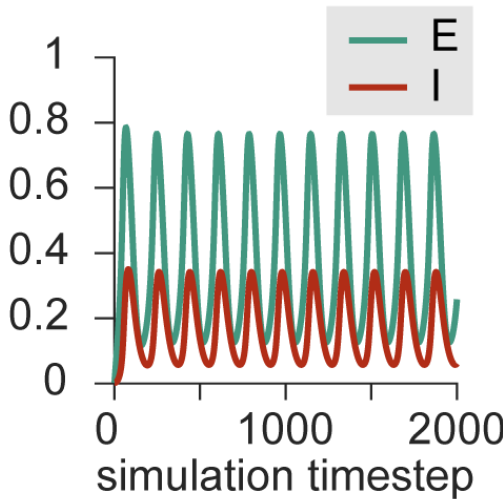
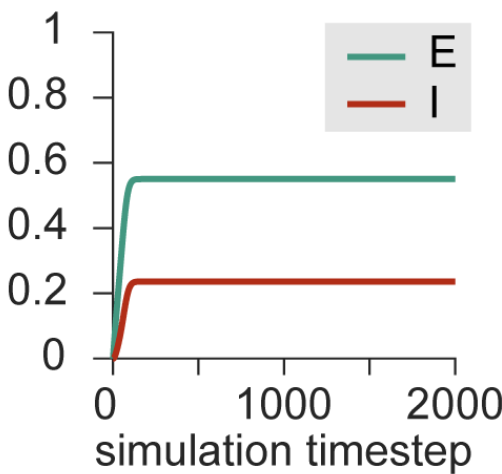
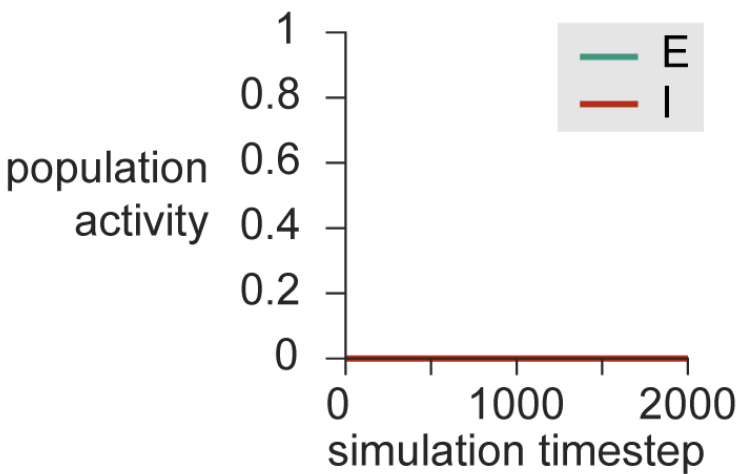


$\begin{bmatrix} \tau_E \\ \tau_I \end{bmatrix} = \begin{bmatrix} 10 \\ 40 \end{bmatrix}$

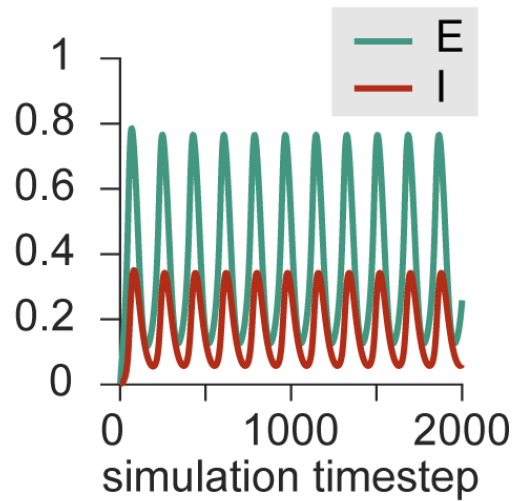
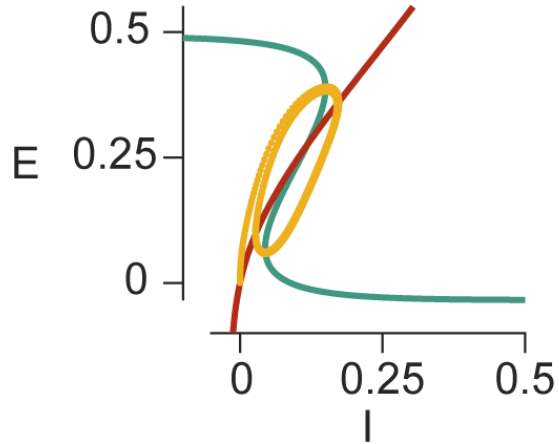
$\begin{bmatrix} P_E \\ P_I \end{bmatrix} = \begin{bmatrix} 0.7 \\ 0 \end{bmatrix}$



Oscillations!



What just happened?



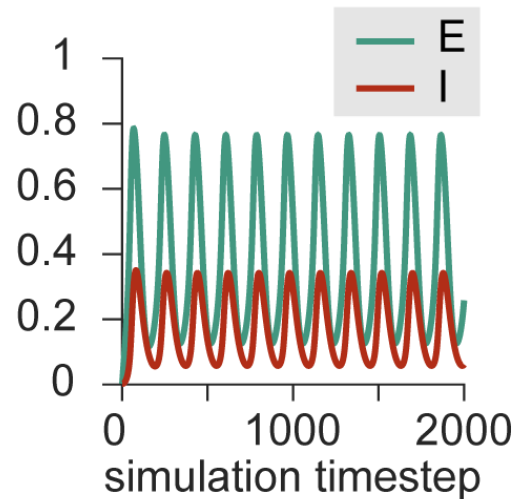
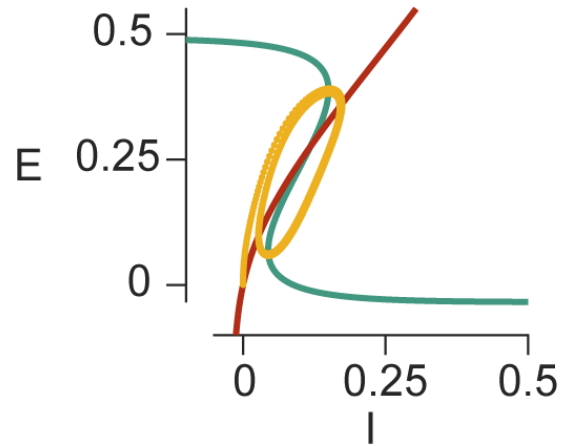
Increasing the time constant of the inhibitory population doesn't move the fixed point of the system, BUT it can cause it to become unstable.

- You can compute the trace of the Jacobian to convince yourself of this.

The system has a single unstable fixed point, but its state doesn't "blow up" to $\pm\infty$. (Why not?)

Instead, it converges to a periodic solution known as a limit cycle.

Detecting limit cycles: the Poincaré-Bendixon theorem



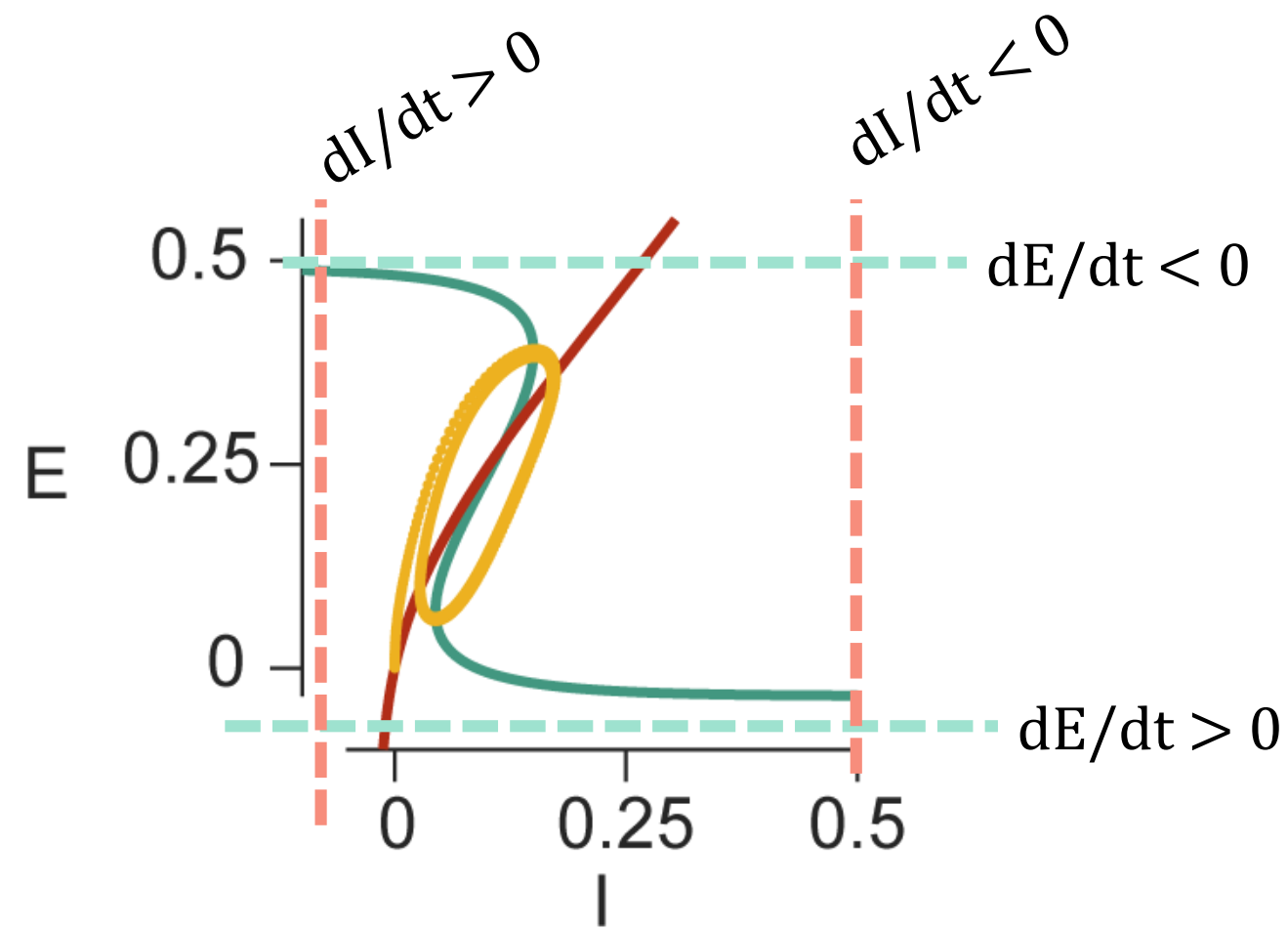
Definition: a forward-invariant region is one that is bounded: once the state of an autonomous system enters it, it will never leave.

Poincaré-Bendixon theorem: If you can draw a region in the phase portrait of a 2D autonomous system such that that region is forward-invariant, the system within that region will either:

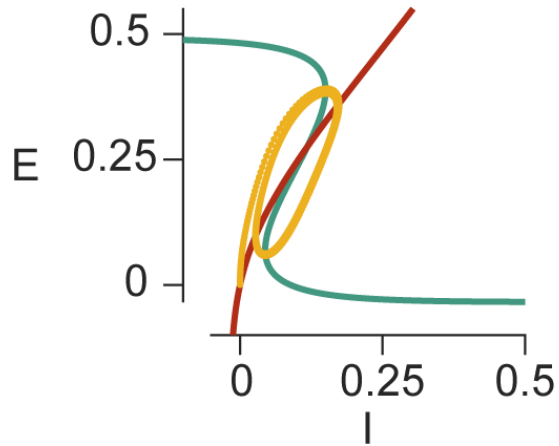
- a) Approach a fixed point
- b) Approach a limit cycle

Our Wilson-Cowan system has only an unstable fixed point, so if we can show that its state is bounded, we know that it has a limit cycle. A region over which the state is bounded is sometimes called the trapping region.

Finding the trapping region



Bonus slide: finding the trapping region



$$\tau_E \frac{d\bar{E}}{dt} = -\bar{E} + (1 - \bar{E}) \cdot \mathcal{S}_E(c_{EE}\bar{E} - c_{EI}\bar{I} + P_E(t))$$

Let's look at the excitatory population. When $E = 0.5$:

$$\tau_E \frac{d\bar{E}}{dt} = -0.5 + 0.5 \cdot \mathcal{S}_E(\dots)$$

We know \mathcal{S}_E is bounded by 1, so the system will never grow above $E = 0.5$ (similarly for $I = 0.5$).

Recurrent weights: $\begin{bmatrix} c_{EE} & c_{EI} \\ c_{IE} & c_{II} \end{bmatrix} = \begin{bmatrix} 10 & 8 \\ 13 & 11 \end{bmatrix}$

External input: $\begin{bmatrix} P_E \\ P_I \end{bmatrix} = \begin{bmatrix} 0.7 \\ 0 \end{bmatrix}$

Response function: $\begin{bmatrix} a_E \\ a_I \end{bmatrix} = \begin{bmatrix} 1.2 \\ 1 \end{bmatrix}; \begin{bmatrix} \theta_E \\ \theta_I \end{bmatrix} = \begin{bmatrix} 2.8 \\ 4 \end{bmatrix}$

Time constants: $\begin{bmatrix} \tau_E \\ \tau_I \end{bmatrix} = \begin{bmatrix} 10 \\ 40 \end{bmatrix}$

$$\mathcal{S}_n(x) = \frac{1}{1 + \exp(-a_n(x - \theta_n))} - \frac{1}{1 + \exp(a_n\theta_n)}$$

For $E < 0$, the terms $-\bar{E}$ and $(1 - \bar{E})$ will both be positive, and $\frac{d\bar{E}}{dt}$ becomes positive when

$$-\bar{E} > (1 - \bar{E}) \cdot \mathcal{S}_E(c_{EE}\bar{E} - c_{EI}\bar{I} + P_E(t))$$

\mathcal{S}_E is bounded below by $B = -\frac{1}{1 + \exp(a_E\theta_E)}$, so we can plug in this value to get

$$-\frac{\bar{E}}{(1 - \bar{E})} > B$$

Which has the solution $\bar{E} = \frac{B}{(1+B)} = -0.0347$ for our current parameters. So the system will never drop below $E = -0.0347$ (and we can find a similar value for I).

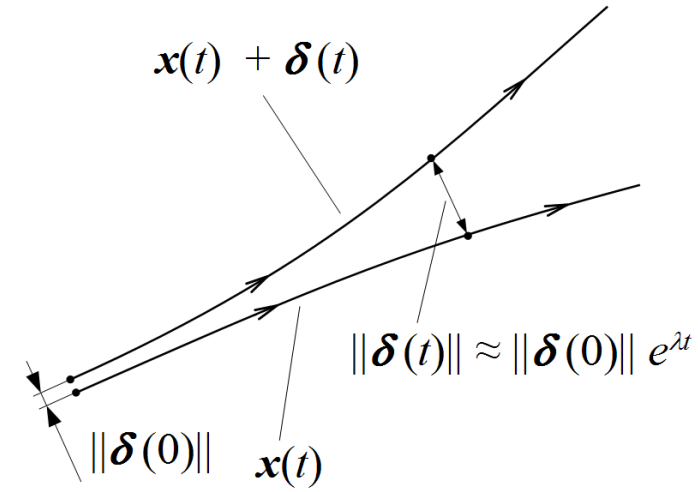
Next time: journeying into higher dimensions

1D dynamical systems: fixed points

2D dynamical systems: limit cycles

3D dynamical systems: chaos!

On Monday, we'll learn about models of large neural populations, their dynamics, and how we can leverage them to compute interesting things.



A chaotic system is one in which points originating in neighboring conditions diverge arbitrarily in the future.

