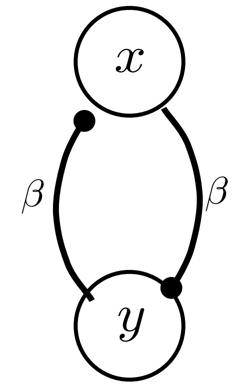
Non-linear dynamics



Mutual inhibition is a motif often seen in biology. For example, two genes that repress each other, or two pools of neurons that inhibit each other. In neuroscience, mutual inhibition is a very common model of decision-making.

(e.g., molecular biology: Mishra and Wigler, *Science* 200?; neuro: Wang, *Neuron* 2000; Machens et al., *Science* 2005)

We could make a linear model of mutual inhibition, and it would capture some of its important aspects; but it would miss two important things. (1) neither molecular concentrations nor firing rates of neurons can be less than zero. (2) Neither molecular concentrations nor firing rates of neurons can be infinitely large. These are *non-linearities*.

Let's assume that in the absence of y, we find x expressed at some constitutive level. We'll call this maximally uninhibited value "1".

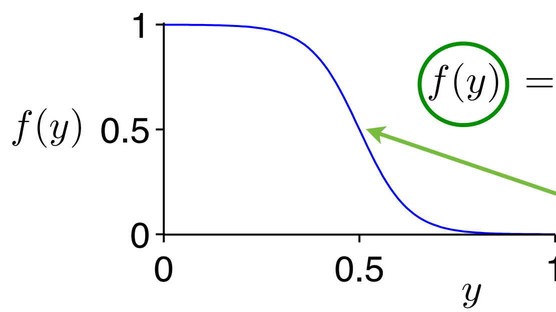
$$\text{If } y = 0, \text{ then } \dot{x} \approx 1 - x$$

Let's suppose that the inhibition is very strong ($\beta >> 0$): if there is a lot of y, then x should be totally inhibited.

$$\text{If } y = 1, \text{ then } \dot{x} \approx 0 - x$$

We want the equation for $\dot{x}$ to express the above two cases, as well as cases where $0 < y < 1$

$$\dot{x} = \underbrace{1/(1 + e^{4\beta * (y - 0.5)})}_{f(y)} - x$$



$$f(y) = 1/(1 + e^{4\beta * (y - 0.5)})$$

Parameter beta is slope at midpoint

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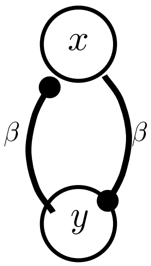
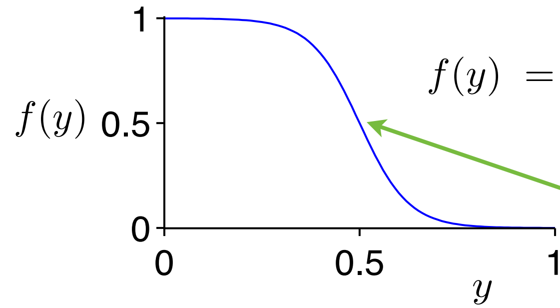


$$\dot{x} \;=\; f(y) - x$$

Similarly,

$$\dot{y} \;=\; f(x) - y$$



$$f(y) \;=\; 1/(1 + e^{4\beta*(y-0.5)})$$

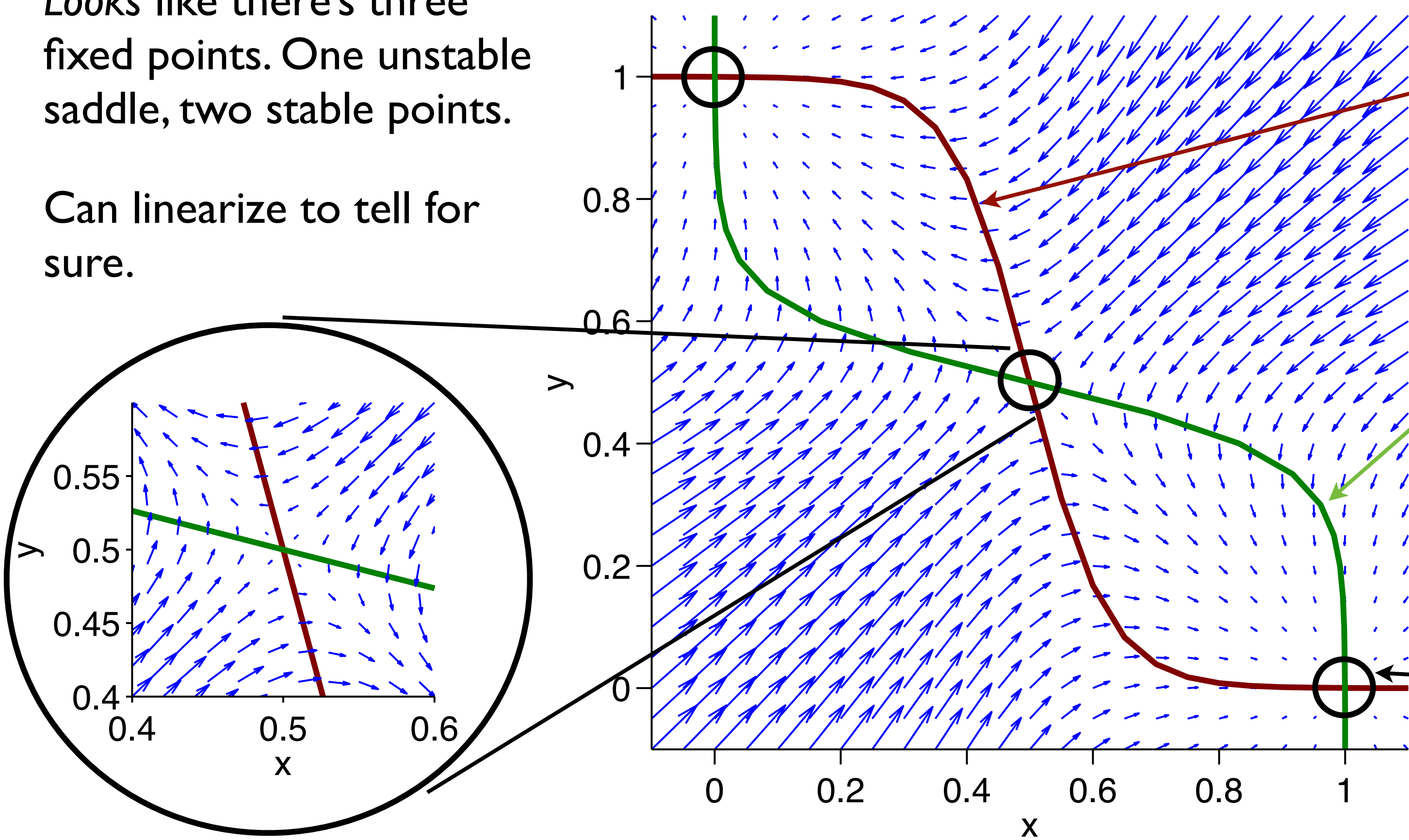
Parameter beta is slope at midpoint

In this plot we're using $\beta = 4$

Remember that the Euler integration rule still applies in N-dim: $\mathbf{x}(t + \Delta t) = \mathbf{x}(t) + \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t}\Delta t$

Looks like there's three fixed points. One unstable saddle, two stable points.

Can linearize to tell for sure.



y nullcline: $\dot{y} = 0$

(all arrows horizontal)

x nullcline: $\dot{x} = 0$

(all arrows vertical)

fixed points:

$\dot{x} = 0 \;\text{ and }\; \dot{y} = 0$

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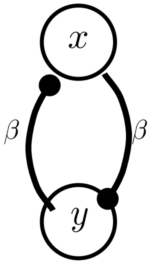
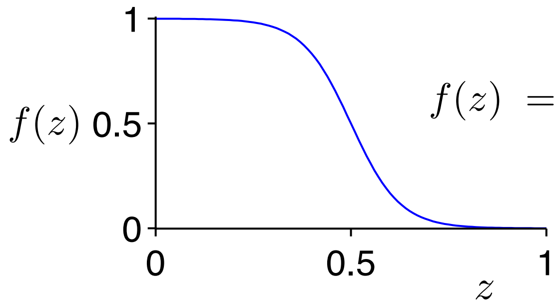
Back to the board for N-d Taylor expansions

Let's do this with our mutual inhibition example. We'll look at the fixed point at (0.5, 0.5)



$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} g(x,y) \\ h(x,y) \end{pmatrix} = \begin{pmatrix} f(y) - x \\ f(x) - y \end{pmatrix}$$



$$f(z) \;=\; 1/(1 + e^{4\beta*(z-0.5)})$$

$$\beta = 4$$

First we confirm that (0.5, 0.5) is a fixed point.

Then we compute the derivative of f(z)

$$\frac{\mathrm{d}f}{\mathrm{d}z} = \frac{-4\beta e^{4\beta(z-0.5)}}{(1+e^{4\beta(z-0.5)})^2} \qquad \frac{\mathrm{d}f}{\mathrm{d}z}\Big|_{z=0.5} = -\beta$$

The approximate linearized dynamics around (0.5, 0.5) is given by:

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \\ \frac{\partial h}{\partial x} & \frac{\partial h}{\partial y} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} -1 & -4 \\ -4 & -1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

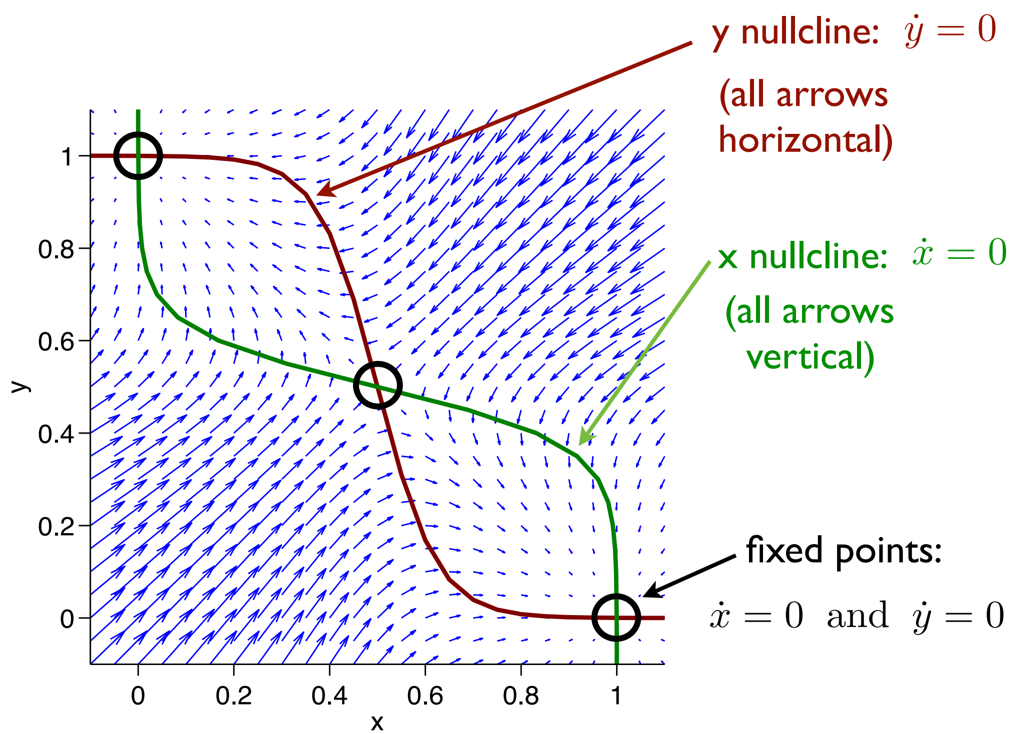
```
>> M = [-1 -4 ; -4 -1];  [V, D] = eig(M)

V =

    0.7071   -0.7071
    0.7071    0.7071


D =

    -5      0
     0      3
```



In-class exercise

Lotke-Volterra prey-predator equns

x is the prey;
y is the predator

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} \alpha x - \beta x y \\ \gamma x y - \delta y \end{pmatrix}$$

First let's find the fixed points:

$$\begin{pmatrix} 0 \\ 0 \end{pmatrix} = \begin{pmatrix} \alpha x - \beta x y \\ \gamma x y - \delta y \end{pmatrix} \Rightarrow \begin{pmatrix} x = 0 \\ y = 0 \end{pmatrix} \text{ or } \begin{pmatrix} x = \delta/\gamma \\ y = \alpha/\beta \end{pmatrix}$$

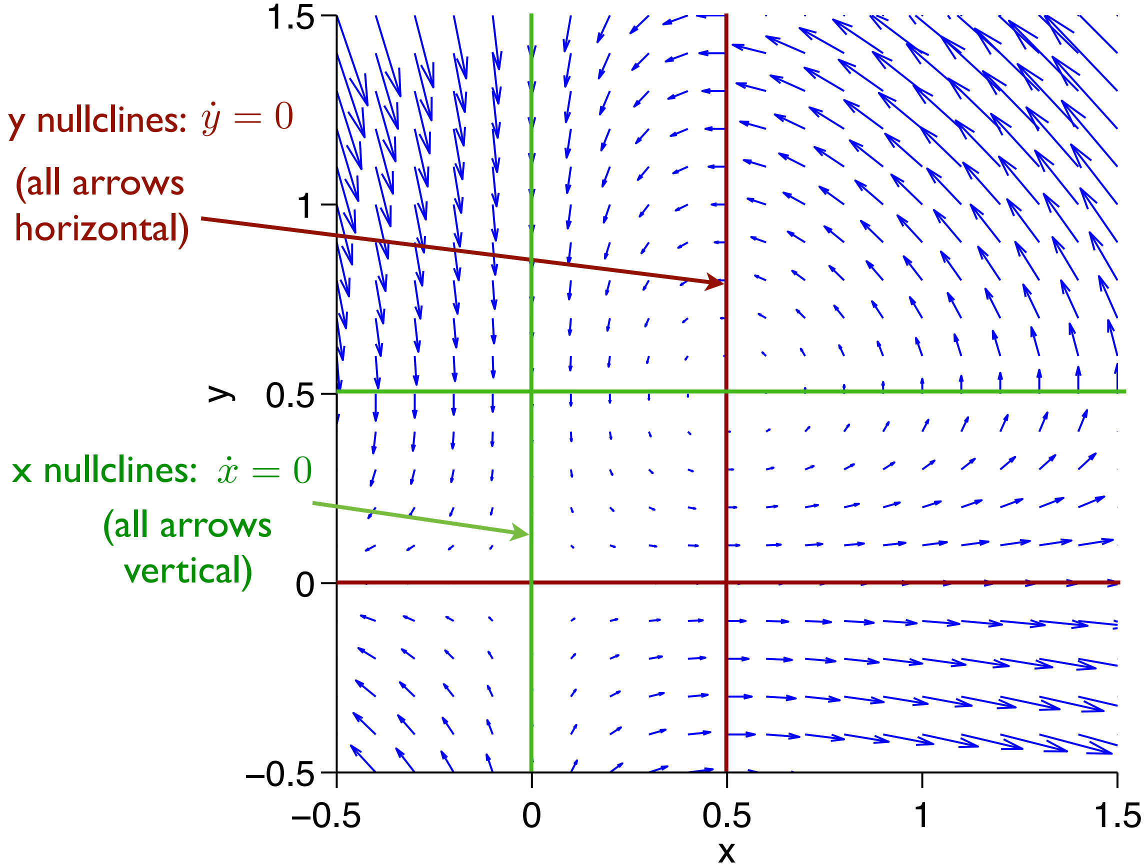
And let's draw a quiver plot:

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} \alpha x - \beta xy \\ \gamma xy - \delta y \end{pmatrix}$$

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \\ \frac{\partial h}{\partial x} & \frac{\partial h}{\partial y} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

$$= \begin{pmatrix} \alpha - \beta y & -\beta x \\ \gamma y & \gamma x - \delta \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

$\alpha = 1,\ \beta = 2,\ \gamma = 2,\ \delta = 1$ (as in K & G)



At the fixed point $y = 0;\ \ x = 0$

$$= \begin{pmatrix} \alpha & 0 \\ 0 & -\delta \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

eigenvalues are? $\lambda = \alpha,\ \ -\delta$

Saddle point

At the fixed point $y = \alpha/\beta;\ \ x = \delta/\gamma$

$$= \begin{pmatrix} 0 & -\beta\delta/\gamma \\ \alpha\gamma/\beta & 0 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

eigenvalues are? $\lambda\ =\ \pm\, i\, \alpha\delta$

Oscillations

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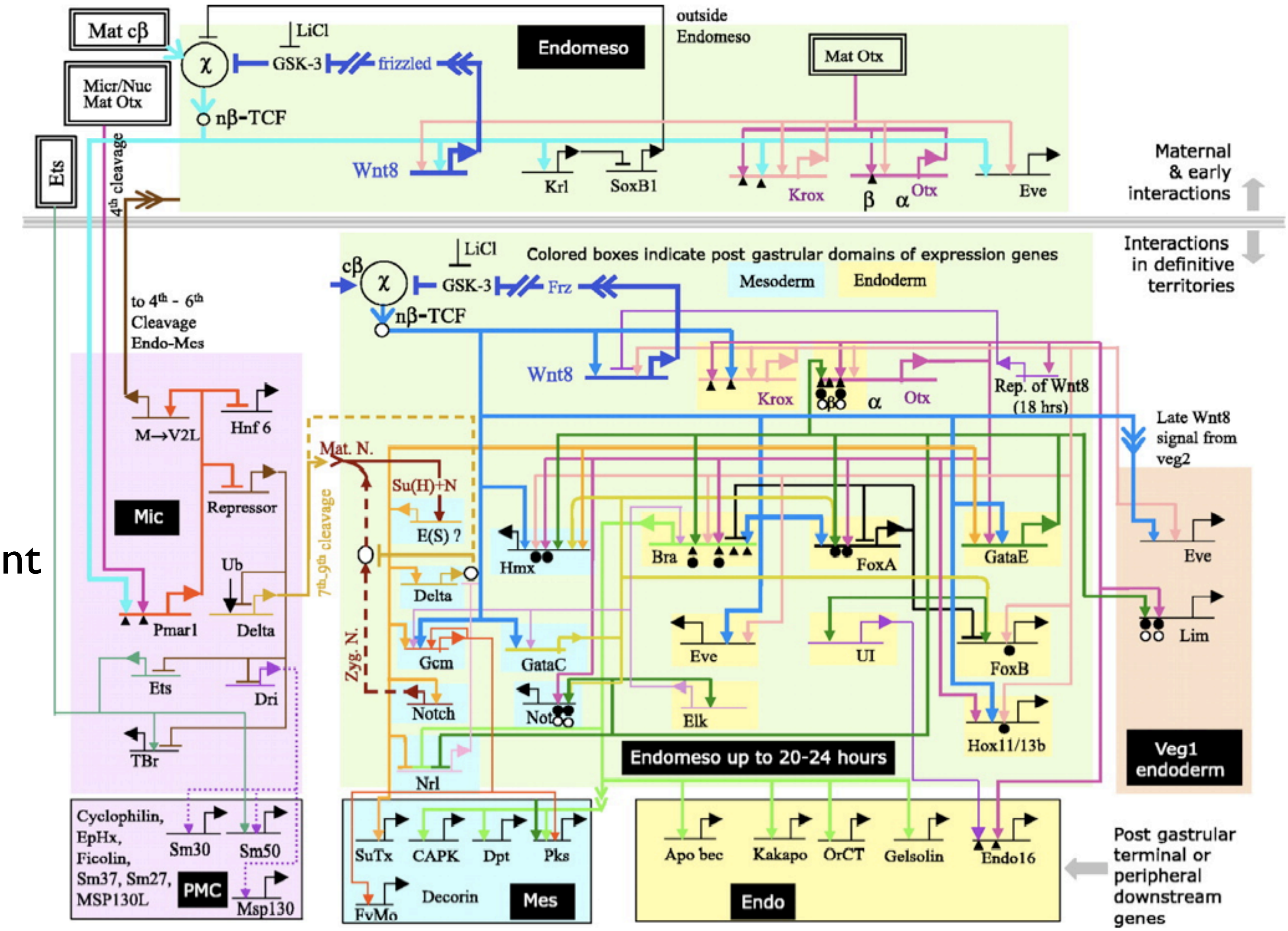
In two dimensions, we can draw the quiver plot. But in high number of dimensions? We turn to linearizing and eigenvalue analysis.

The gene regulatory network for development in the sea urchin.



Davidson et al. *Science* 2002

With linear dynamics there's only one fixed point, and we know how to understand it.

With *non*linear dynamics, we can linearize to see *locally* whether a fixed point is stable or unstable. But what happens as further away from the fixed point? We're in the dark?!?!

Understanding the topological structure of the dynamics can be very helpful. This is what makes *bifurcations* important.

But if we're very lucky, we can find a *Lyapunov function* for the dynamics. The mutual inhibition circuit we've been looking at has a Lyapunov function. Let's see how it can help us.

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} f(y) - x \\ f(x) - y \end{pmatrix} \qquad f(z) = 1/(1 + e^{4\beta * (z - 0.5)})$$

Define the following scalar function of the state of the system:

$$L(x,y) = f(x)\,f(y) - \int_0^{f(x)} f^{-1}(z)\mathrm{d}z - \int_0^{f(y)} f^{-1}(z)\mathrm{d}z$$

(I know, this equn seemed to just come out of nowhere.) (Hopfield, PNAS, 1984)

$$\frac{\mathrm{d}L}{\mathrm{d}t} = f'(x)\,f(y)\,\dot{x} + f(x)\,f'(y)\,\dot{y} - x\,f'(x)\,\dot{x} - y\,f'(y)\,\dot{y}$$

(you need to know that $\frac{\mathrm{d}}{\mathrm{d}x}\int_0^x f(z)\mathrm{d}z = f(x)$)

$$= f'(x)\,\dot{x}(f(y) - x) \;\; + f'(y)\,\dot{y}(f'(x) - y)$$

$$= f'(x)\,\dot{x}^2 \;\; + f'(y)\,\dot{y}^2 \qquad \boxed{\Longrightarrow \frac{\mathrm{d}L}{\mathrm{d}t} \leq 0}$$

$(\; f'(x) > 0, \;\; f'(y) > 0 \;)$

A *Lyapunov function* is a scalar function of the state of the system whose time derivative is always less than or equal to zero, and is zero only at fixed points.

Thus, if a Lyapunov function exists, the dynamics always goes downhill in it.

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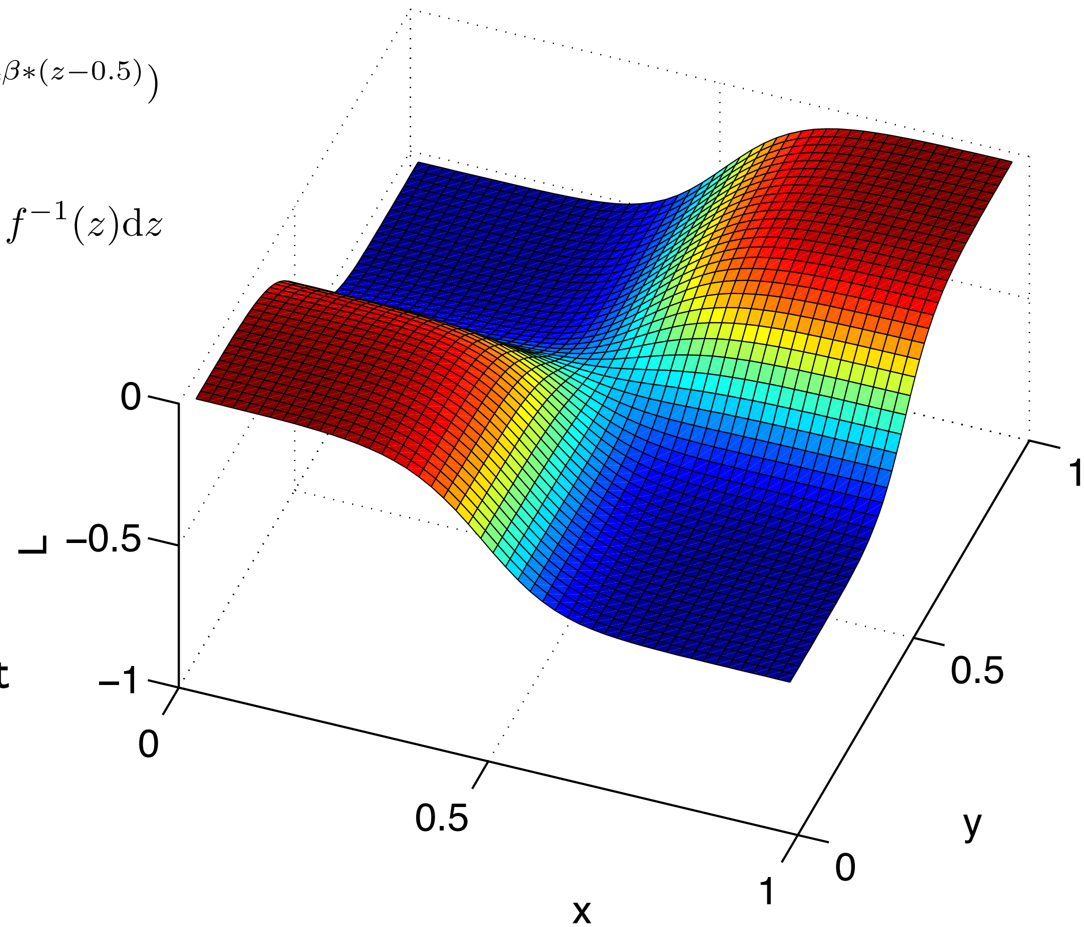
$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} f(y) - x \\ f(x) - y \end{pmatrix} \qquad f(z) = 1/(1 + e^{4\beta*(z-0.5)})$$

$$L(x,y) = f(x)\,f(y) - \int_0^{f(x)} f^{-1}(z)\mathrm{d}z - \int_0^{f(y)} f^{-1}(z)\mathrm{d}z$$

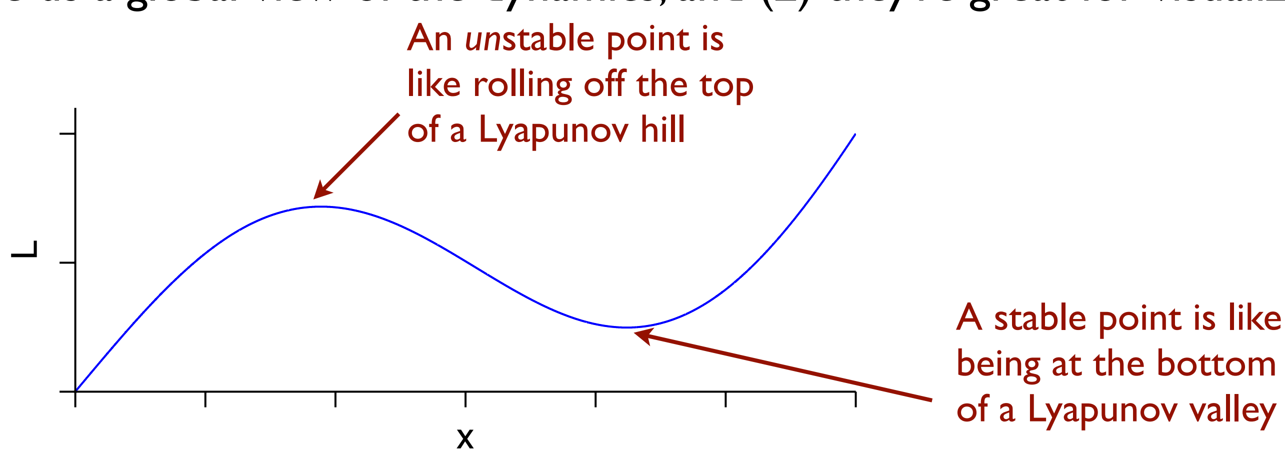


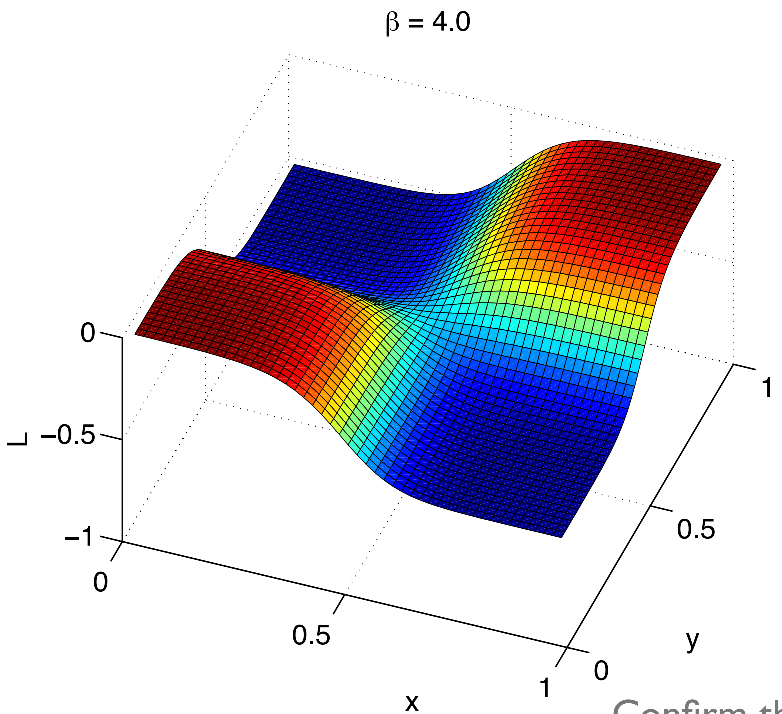
Unfortunately finding a Lyapunov function is a bit of a black art.

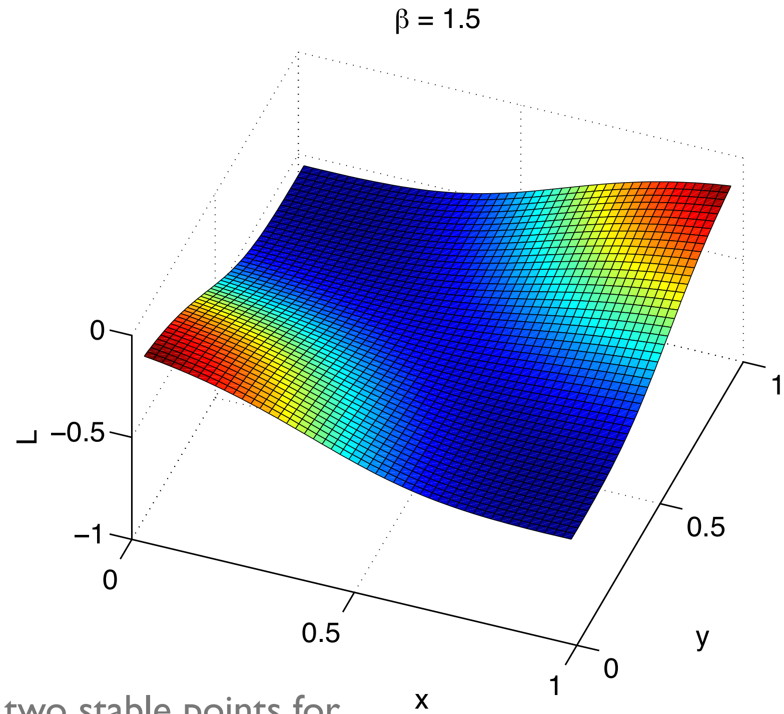
In physical systems with conserved energy, the energy is a Lyapunov function. But life isn't about *conserving* energy: it's about *spending* it! (That's why we eat.) Energy isn't always a Lyapunov function for our system.

Side note: $\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} \neq \begin{pmatrix} \partial L/\partial x \\ \partial L/\partial y \end{pmatrix}$!!!

What makes Lyapunov functions useful is that (1) they're defined over the entire state space, so they give us a global view of the dynamics; and (2) they're great for visualization!







Confirm that we go from two stable points for beta>1 to a single stable point for beta<1 using linearization around (0.5, 0.5)