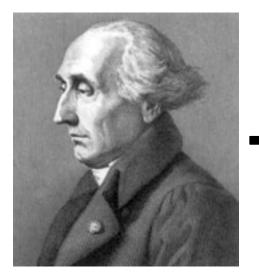
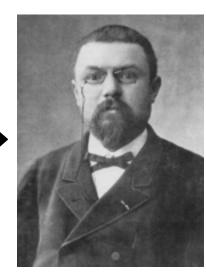
Lecture 98 Non-linear Dynamical Systems - Part 1

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# Qualitative analysis and principles of **non-linear** dynamical systems

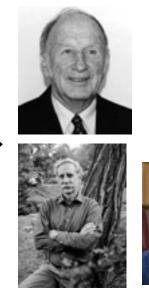


Joseph-Louis LaGrange 1736 - 1813



Henri Poincare 1854 - 1912

Edward Lorenz 1917-2008



Robert May 1936 -

Mitchell Feigenbaum 1944 -





Albert Libchaber 1934 -

So, today we explore the truly astounding emergent complexity inherent in even simple **non-linear dynamical systems**.

	n = 1	n = 2 or 3	n >> 1	continuum
Linear	exponential growth and decay single step conformational change fluorescence emission pseudo first order kinetics	second order reaction kinetics linear harmonic oscillators simple feedback control sequences of conformational change	electrical circuits molecular dynamics systems of coupled harmonic oscillators equilibrium thermodynamics diffraction, Fourier transforms	Diffusion Wave propagation quantum mechanics viscoelastic systems
Nonlinear	fixed points bifurcations, multi stability irreversible hysteresis overdamped oscillators	anharmomic oscillators relaxation oscillations predator-prey models van der Pol systems Chaotic systems	systems of non- linear oscillators non-equilibrium thermodynamics protein structure/ function neural networks the cell ecosystems	Nonlinear wave propagation Reaction-diffusion in dissipative systems Turbulent/chaotic flows

So, today:

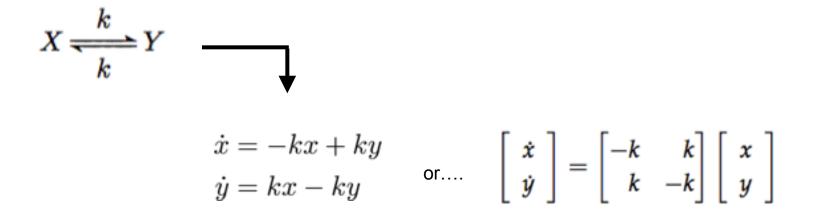
(1) A reminder of the **reducibility**, **simplicity**, and **predictability** of linear systems....we needed to understand what is not "complex" first!

(2) A case study of three small non-linear dynamical systems that exhibit remarkable **emergent** and **non-obvious** behaviors that linear systems cannot do. All relevant for biology...

We begin with a reminder of **linear systems**...

We begin with a reminder of **linear systems**...

Linearity implies a principle called superposition : If 
$$y_1(4)$$
 is the  
output of a system to imput  $y_1(4)$  and  $y_2(4)$  is the response to  
 $y_2(4)$ , then:  
(D)  $x_1(4) + y_2(4) \longrightarrow y_1(4) + y_2(4)$  [additivity]  
(2)  $a_1 \cdot x_1(4) \longrightarrow a_1 \cdot y_1(4)$  [scaling or homogonaty]  
Som if imput is  
 $x(4) = \sum_{k} a_k x_k(4) = a_1 \cdot x_1(4) + a_2 \cdot x_2(4) + \cdots$   
output will be:  
 $y(4) = \sum_{k} a_k y_k(4) = a_1 \cdot y_1(4) + a_2 \cdot y_2(4) + \cdots$   
This is superposition ... the output is a weighted sum of responses to  
independent imputs.



...a second-order biochemical reaction, for example

The general solution to second-order linear system...

$$\begin{split} \dot{x} &= ax + by \\ \dot{y} &= cx + dy \end{split} \longrightarrow \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} = \begin{bmatrix} a & b \\ c & d \end{bmatrix} \begin{bmatrix} x \\ y \end{bmatrix} \\ \dot{\mathbf{x}} &= A\mathbf{x} \quad \text{given } \mathbf{x_0} \quad \dots \text{a vector of initial conditions} \\ & \downarrow \\ \mathbf{x}(t) &= e^{\mathbf{A}t}\mathbf{x_0} \end{split}$$

....where **A** is the characteristic matrix. It's properties control all behaviors of the system

Properties of the characteristic matrix...

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \qquad \begin{aligned} \tau &= \operatorname{trace}(A) = a + d , \\ \Delta &= \det(A) = ad - bc . \end{aligned}$$

...the **trace** and **determinant** of the matrix

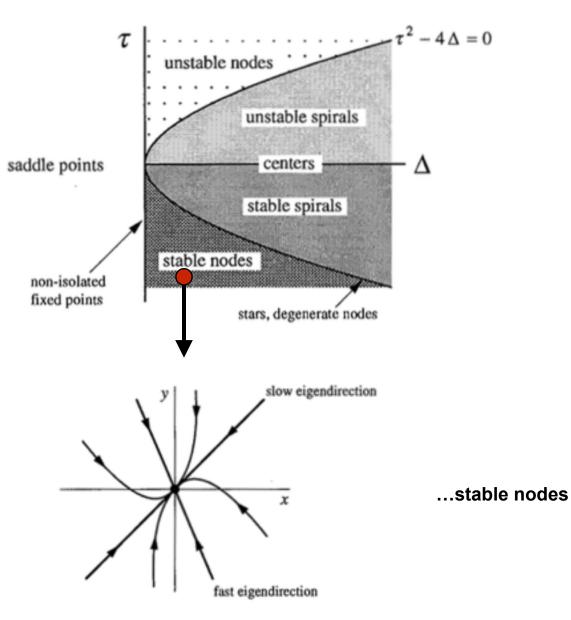
Properties of the characteristic matrix...

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \qquad \begin{array}{l} \tau = \operatorname{trace}(A) = a + d ,\\ \Delta = \det(A) = ad - bc . \end{array}$$
$$\lambda_{1,2} = \frac{1}{2} \left( \tau \pm \sqrt{\tau^2 - 4\Delta} \right)$$

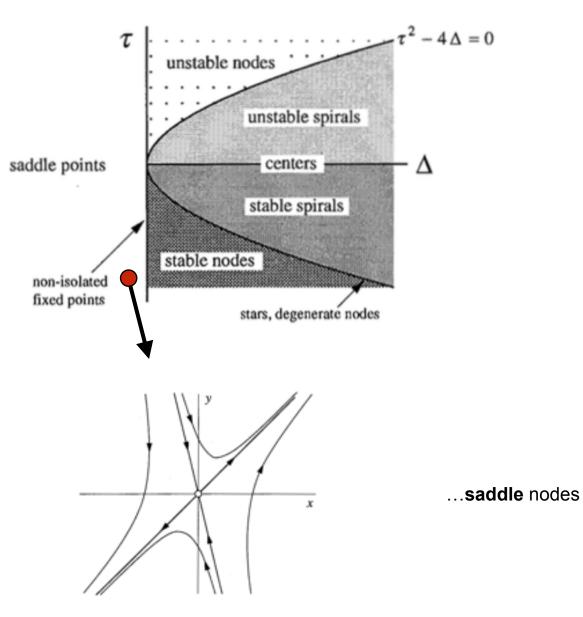
...the **eigenvalues** of **A** are completely determined by the **trace** and **determinant**...

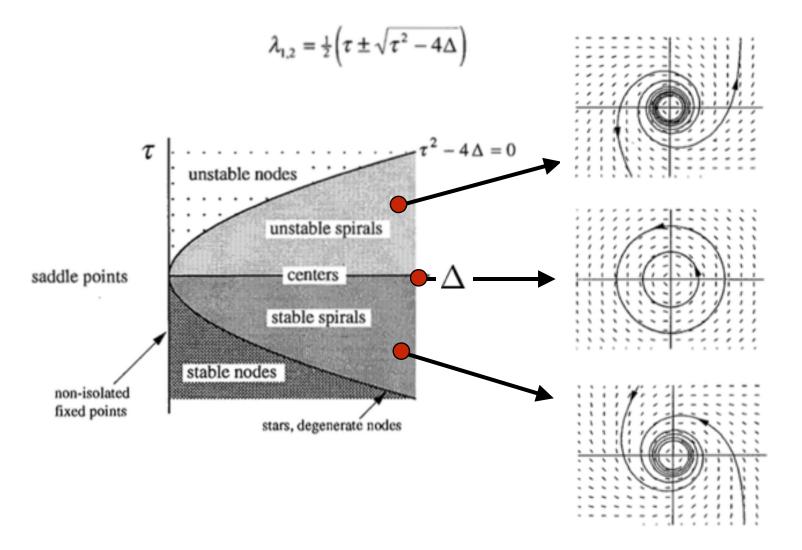
...the **zoo of all possible behaviors** for a linear, second-order system

$$\lambda_{1,2} = \frac{1}{2} \left( \tau \pm \sqrt{\tau^2 - 4\Delta} \right)$$

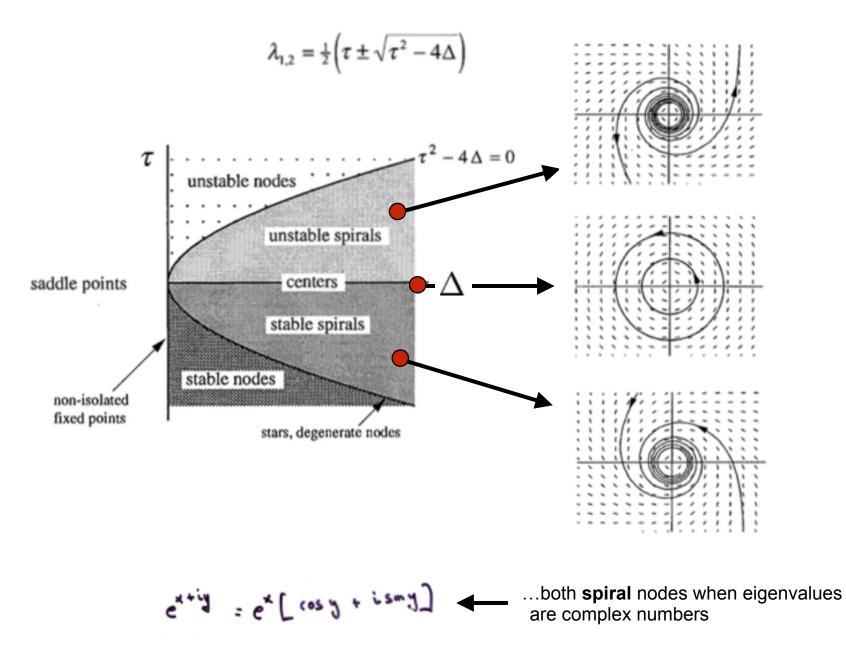


$$\lambda_{1,2} = \frac{1}{2} \left( \tau \pm \sqrt{\tau^2 - 4\Delta} \right)$$





...and **spiral** nodes when eigenvalues are complex numbers

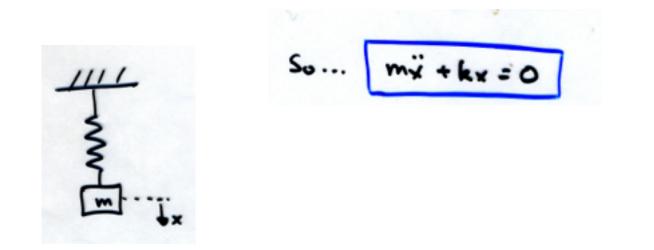


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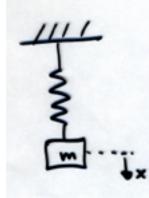
Often, it is hard to get analytic solutions. We need a way of "seeing" system behavior....

Now, the equation of motion is:  
F= ma, or...  
-kx = mix Remember that for  
a Hooke spring.  
F=-kx, and  

$$\dot{x} = \frac{dx}{dE} = v$$
  
 $\dot{x} = \frac{d^2x}{dE} = a$ 

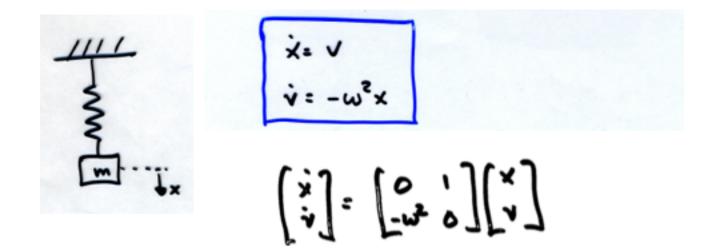


We can **re-write** this equation....

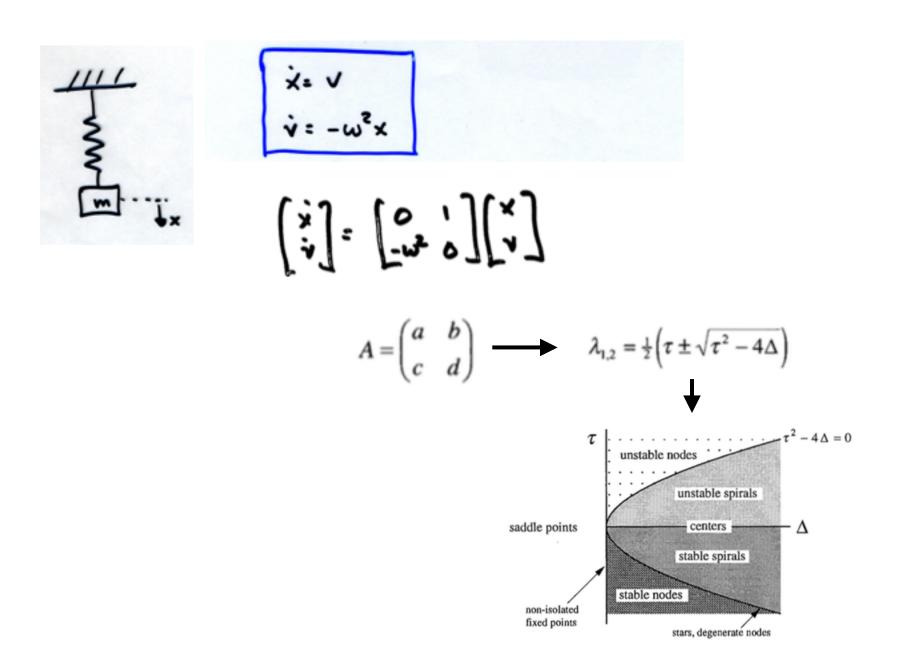


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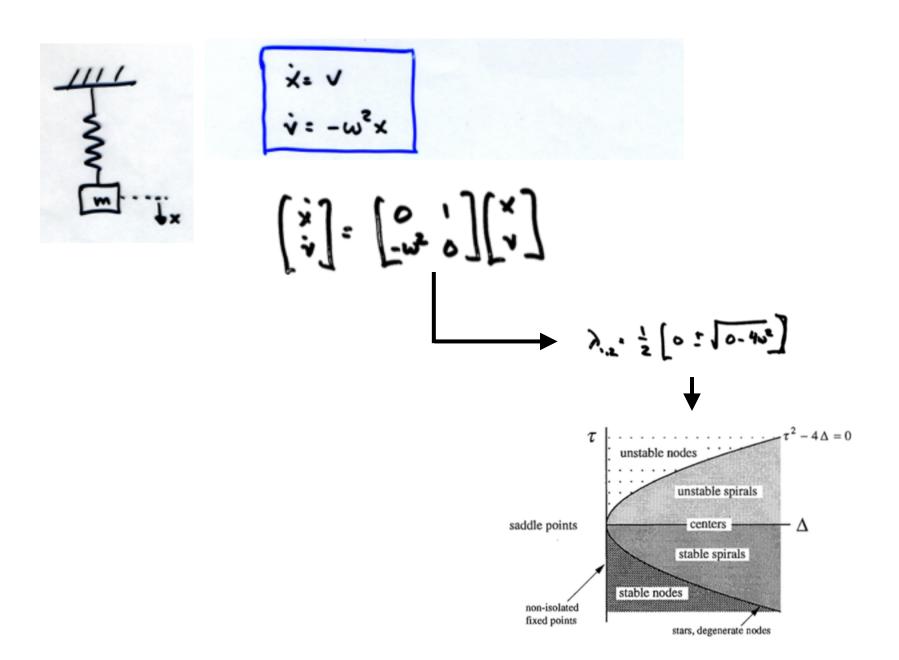
To simplify, we define 
$$\omega^2 = \frac{k}{m}$$
. So...  
 $\dot{x} = \sqrt{\frac{1}{v}} = -\omega^2 x$ 

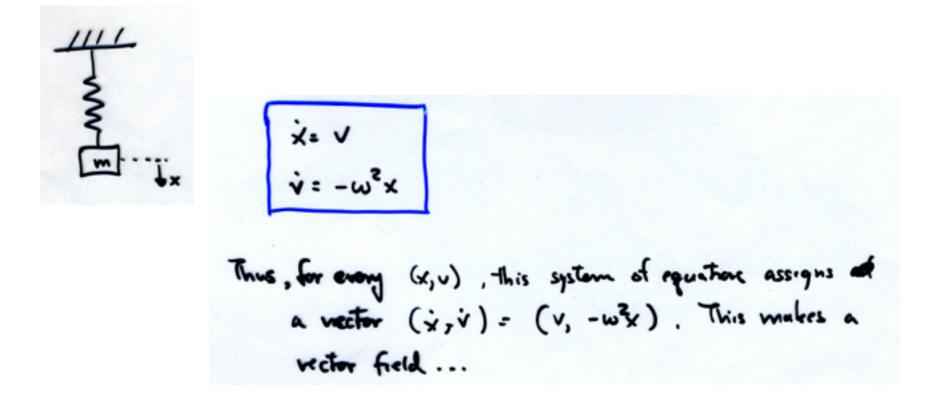


We know how to analyze the behavior, right?



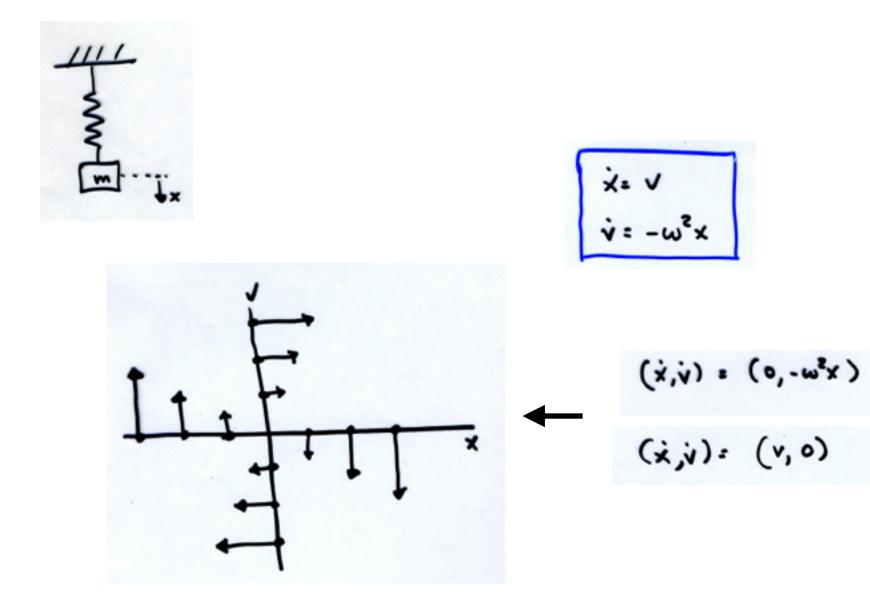
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....for this system, (x,v) represents a 2D "**phase space**" in which we can see the behavior of the system intuitively.

plot the system nullclines.... 
$$(\dot{x},\dot{v}) : (o, -\omega^{2}x)$$
$$(\dot{x},\dot{v}) : (v, o)$$



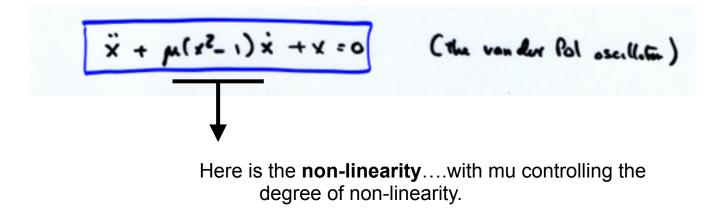
111 So ... you flow around the origin. (x, v) At the origin, all flave are zero, so you stay put ... a fixed point

This is called a "**phase portrait**"...a way of seeing system dynamics.

#### A summary....

Linear systems are:

- (1) **decomposable**, such that high-order systems are combinations of first-order systems. This is the concept that the behavior of the whole is predictable from knowledge of the behavior of the underlying parts.
- (2) **understandable**; their behavior can be mapped through a study of their so-called eigenfunctions. This is the concept that one can "understand" the properties of linear systems by sketching the behavior of these eigenfunctions.
- (3) **simple**; these systems show single fixed points...whether stable or unstable



$$\ddot{x} + \mu(x^2 - 1)\dot{x} + x = 0$$
 (the vandur Pol ascellation)

 for  $\mu >>1$ , this is the strongly non-linear limit. There is a position dependent damping terms  $\mu(x^2 - 1)\dot{x}$ . This acts like positive damping for  $|x| > 1$  to cause oscillations to decay, but acts like regative damping for  $|x| < 1$  to build oscillations up.

 It causes so-called "relaxation oscillations" ...

Lets unte the operation in the usual  $\dot{x}$  = ,  $\dot{y}$  = way to make a phone portrait ...

A little re-definition of variables ... note that

$$\ddot{x} + \mu(x^{2}-1)\dot{x} + x = 0$$
 (1)  
 $\ddot{x} + \mu(x^{2}-1)\dot{x} = \frac{d}{dt}(\dot{x} + \mu(\frac{1}{3}x^{3}-x))$  (2)

$$F(x) = \frac{1}{3}x^3 - x$$
 (3)  
 $w = x + \mu F(x)$  (4)

50 ....

Re-writing the equations in a **more intuitive** way....

$$\ddot{x} + \mu(x^2 - 1)\dot{x} + x = 0$$

we can now rewrite the van dar Pologn (1) as ..  

$$\dot{X} = w - \mu FGr)$$
  
 $\ddot{w} = -X$ 

$$\ddot{x} + \mu(x^2 - 1)\dot{x} + x = 0$$

we can now rewrite the van day Pologn (1) as ...  

$$\dot{X} = w - \mu FGr)$$
  
 $\ddot{w} = -X$ 

One other convence ... set 
$$y = \frac{\omega}{\mu}$$
. Then ...  
 $\dot{x} = \mu \left[ y - F(x) \right]$   
 $\dot{y} = -\frac{1}{\mu} x$ 

$$\ddot{x} + \mu(x^2 - 1)\dot{x} + x = 0$$

we can now rewrite the van der Pologn (i) as ..  

$$\dot{X} = w - \mu FGr)$$
  
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$$y = \frac{\omega}{\mu}$$
. Then...  
 $\dot{x} = \mu [y - F(x)]$   
 $\dot{y} = -\frac{1}{\mu} x$   
Now, to see between of our system, we sketch the so-called  
"Mall climes" of the system ... The equations corresponding  
to  $\dot{x}=0$  and  $\dot{y}=0$ .

The van der Pol oscillator....

$$\ddot{x} + \mu(x^2 - 1)\dot{x} + x = 0$$

$$\dot{x} = \mu [y - fix]$$
  
 $\dot{y} = -\frac{1}{\mu} x$ 

$$y = F(x)$$
  
=  $\frac{1}{2}x^3 - x$  [a cabie function]

The van der Pol oscillator....

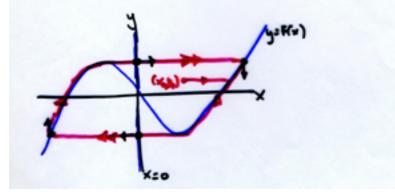
$$\ddot{x} + \mu(x^2 - 1)\dot{x} + x = 0$$

$$\dot{\mathbf{x}} = \mu [\mathbf{y} - \mathbf{f}_{\mathbf{x}})]$$
  
 $\dot{\mathbf{y}} = -\frac{1}{\mu} \mathbf{x}$ 

Nullchan me ....

y=F(x)=  $\frac{1}{2}x^3-x$  [a cabie function]





The van der Pol oscillator....

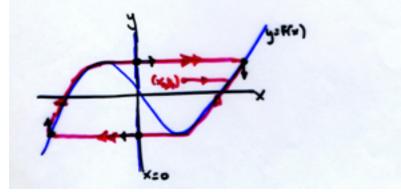
$$\ddot{x} + \mu(x^2 - i)\dot{x} + x = 0$$

$$\dot{x} = \mu [y - f(x)]$$
  
 $\dot{y} = -\frac{1}{\mu} \times$ 

Nullclimes and ....

$$y = F(x)$$
  
=  $\frac{1}{2}x^3 - x$  [a cubic function]

Plats ...



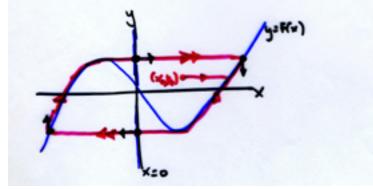
The van der Pol oscillator....

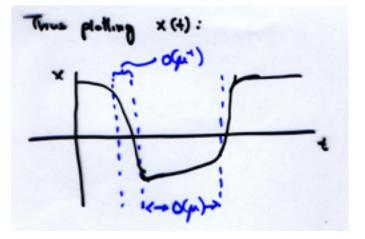
$$\ddot{x} + \mu(x^2 - i)\dot{x} + x = 0$$

$$\dot{\mathbf{x}} = \mu [\mathbf{y} - \mathbf{f}_{\mathbf{x}}]$$
  
 $\dot{\mathbf{y}} = -\frac{1}{\mu} \mathbf{x}$ 

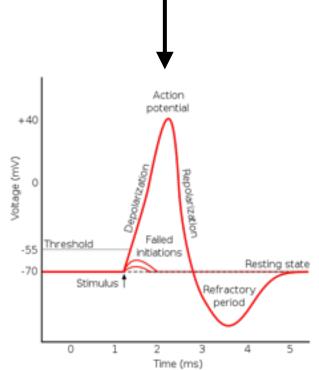
Nullclines are ....



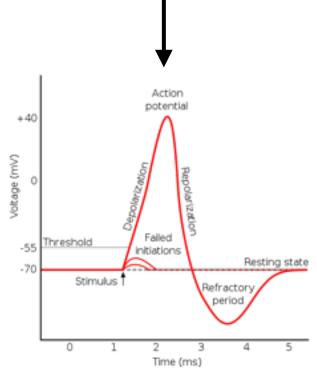




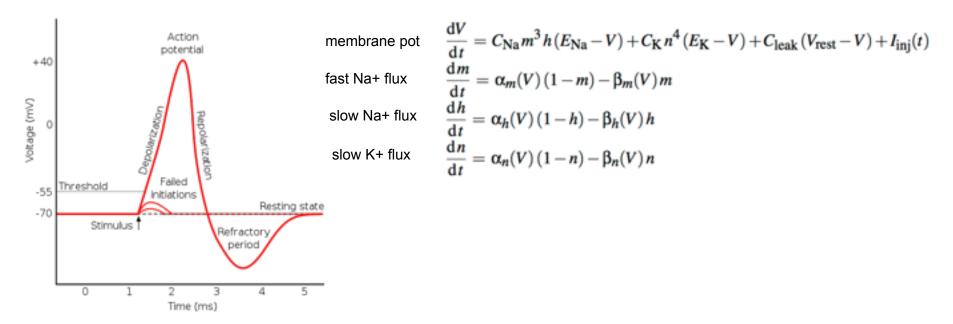
We will study the behavior of these systems in more detail next time, but as a preview, the basic model for the **neuronal action potential is** only a slight variation on the van der Pol oscillator...



We will study the behavior of these systems in more detail next time, but as a preview, the basic model for the **neuronal action potential is** only a slight variation on the van der Pol oscillator...



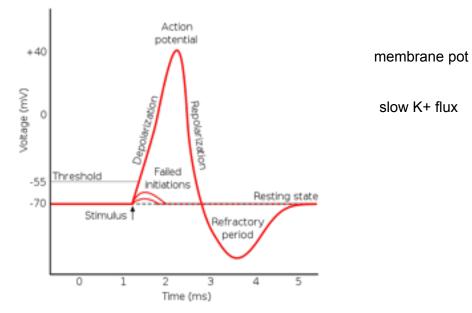
a regenerative, **non-linear activation** with a sharp **threshold**, an all-or-nothing character, and a **refractory period** afterwards...



Hodgkin-Huxley (1952)

but, **Fitzhugh and Nagumo** simplified this 4D set of equations....



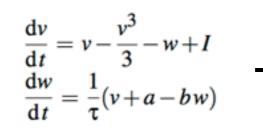


of  $\frac{\mathrm{d}v}{\mathrm{d}t} = v - \frac{v^3}{3} - w + I$  $\frac{\mathrm{d}w}{\mathrm{d}t} = \frac{1}{\tau}(v + a - bw)$ 

this is essentially the van der Pol oscillator, with **one difference**....

membrane pot

slow K+ flux



 $\dot{w}=0$ w v=0 0 -0,5 -2 0 -1 -3 1 ν Action potential +40Voltage (mV) 0 Failed Threshold -55 initiations Resting state -70 Stimulus 1 Refractory period 0 5 1 2 З 4 Time (ms)

2

0,5

the linear term to the w nullcline provides for **thresholded oscillation**....you will see next time A 1D discrete-time non-linear system

A seemingly innocuous thing....the so-called logistic equation

But led to principles have **broad application** in both basic and applied science....and art, social science, and the popular media.



A 1D discrete-time non-linear system

A seemingly innocuous thing....the so-called logistic equation

Lets see .... using a graphical method called an <u>iterative map</u>: This plats the value of a function against its previous value...

 $f(s) = F \{ f(s-s) \}$ 

An **iterative map** gives the current value of a system as a function of its previous value...

# $f(s) = F \{ f(s-s) \}$

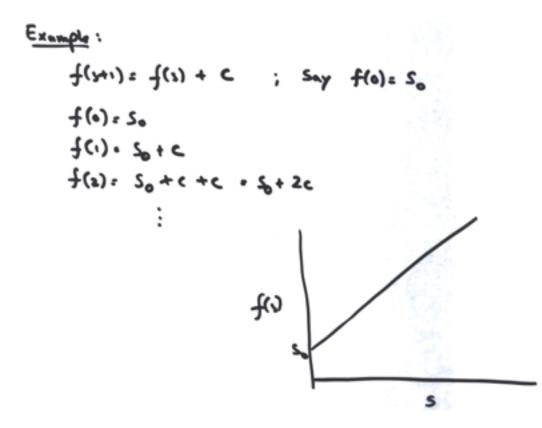
$$\frac{E_{xomple}:}{f(y+1) = f(y) + c}; S_{xy} f(0) = S_{0}$$

$$f(0) = S_{0}$$

$$f(1) = S_{0} + c$$

$$f(x) = S_{0} + c + c = S_{0} + 2c$$

 $f(s) = F \{ f(s-s) \}$ 



The equation for constant velocity motion....

Note that these maps are discrete time imposings! Also, we are now discussing just 1-0 maps. Why 10? Only one variable we are following:  

$$f(s) = F \{f(s-1)\}$$

Fixed points : Say a certain value of X satisfies the role that  $f(x) = x^*$ Then this value of x is called a fixed point, because the orbit stops at x" for all future values of x. Stability of the fixed point: To determine stubility, the idea is to course a small perhabation and ask whether the orbit is attracted back to X" or is reled.





stable steady state

unstable steady state

So consider ... x<sub>n</sub> = x\* + 7, T> perhabetion × ++ = x + + 2++ = f(x++2)  $= f(x^{*}) + f'(x^{*})\eta_{n} + O(\eta_{n}^{2})$ What is this?

So consider ... x\_= x\*+ 7\_ I perhurbation × ++ = x + + 2 ++ = f(x ++ 2)  $= f(x^{*}) + f'(x^{*})\eta_{n} + O(\eta_{n}^{2})$ 

What is this? Well, the **higher order stuff**, which we will conveniently ignore....

So consider ...  

$$X_{n} = \chi^{*} + \gamma_{n}$$

$$X_{n+1} = \chi^{*} + \gamma_{n+1} = f(\chi^{*} + \gamma_{n})$$

$$= f(\chi^{*}) + f'(\chi^{*})\gamma_{n} + O(\eta_{n}^{2})$$
But  $f(\chi^{*}) = \chi^{*}$ , so ...  

$$\gamma_{n+1} = f'(\chi^{*})\gamma_{n}$$
(all the "multipler" of the perhabation  $\lambda = f'(\chi^{*})$ . Then  

$$\gamma_{1} = \lambda \gamma_{0}$$

$$\gamma_{2} = \chi^{2} \gamma_{0}$$

$$\vdots$$

$$\gamma_{n} = \chi^{*} \gamma_{0}$$

So consider ...  

$$X_n = X^* + Z_n$$
  
 $T \rightarrow perturbation$ 

(all the "multiplier" of the perhabation 
$$\lambda = f'(x^*)$$
. Then  
 $\gamma_1 = \lambda \gamma_0$   
 $\gamma_2 = \lambda^2 \gamma_0$   
 $\vdots$   
 $\gamma_n = \lambda^n \gamma_0$ 

So... if 
$$|\lambda| < 1$$
, then  $\gamma_n \to 0$  as  $n \to \infty$  [shill fixed pt]  
if  $(\lambda) > 1$ , then  $\gamma_n \to \infty$  as  $n \to \infty$  [wish(6]]

**Fixed points**....a more formal treatment

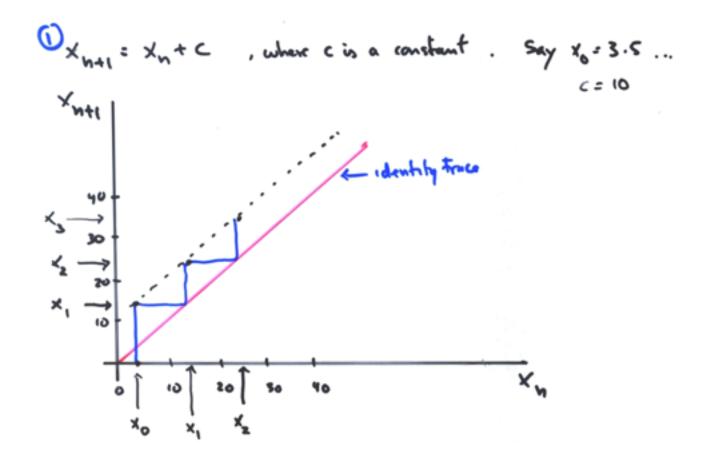
Example: Xnti = Xn Fixed points?

Example: 
$$x_{n+1} = x_n^2$$
  
Fixed points? 0 or 1.  
Shelig?  
 $\lambda = f'(x^*) = 2x^*$ 

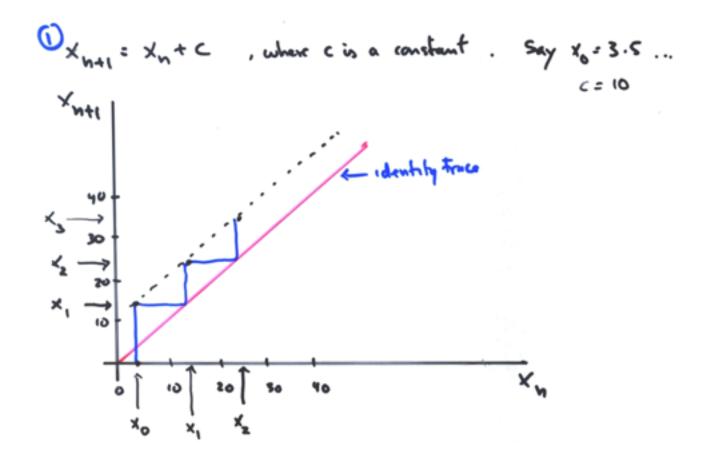
Example: 
$$x_{n_1} = x_n^2$$
  
Fixed points? 0 or 1.  
Shelig?  
 $\lambda = f'(x^*) = 2x^*$ 

So...the fixed point at zero is **stable**, and the one at 1 is **not**.

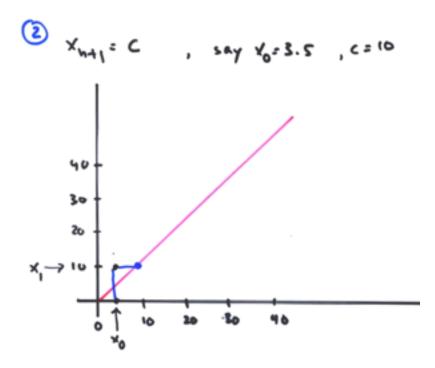
We will do a similar analysis for the logistic equation soon.



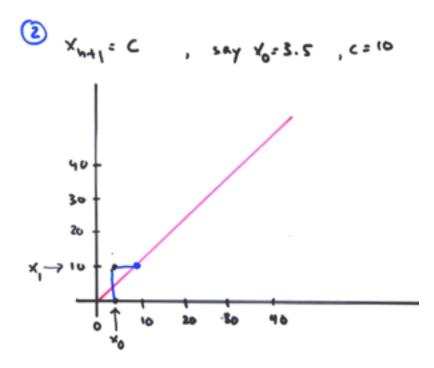
Just a way of plotting the "**orbit**"...or the behavior of the equation.



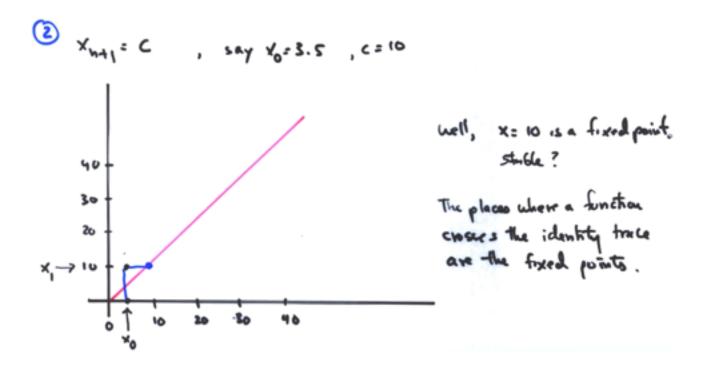
In this plot, what would a **fixed point** be? Are there any?



This is a **really boring** equation....



This is a **really boring** equation....but it does have a fixed point! What about stability of the fixed point?



3 So ... now for the so-called logistic equation  

$$X_{n+1} = r \times_n (1 - x_n)$$
  
 $\frac{x_{n+1}}{r}$ 

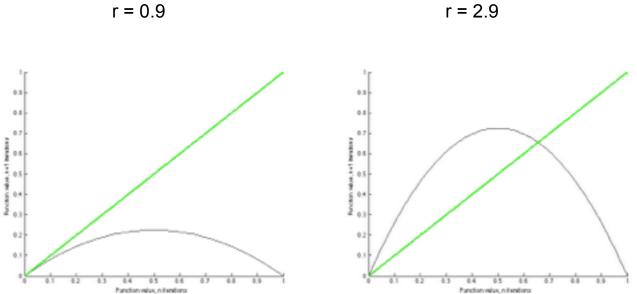
Ok.....but where is the **identity trace** relative to the curve?

3 So ... now for the so-called logistic equation  

$$X_{n+1} = r \times_n (1 - \chi_n)$$
  
 $\frac{\chi_{n+1}}{r}$ 

Ok.....but where is the identity trace relative to the curve? Well....it depends on **r**...

$$y(n+1) = ry(n)(1-y(n))$$



## $\mathsf{O}\mathsf{k}....\mathsf{n}\mathsf{o}\mathsf{w},\mathsf{w}\mathsf{h}\mathsf{e}\mathsf{r}\mathsf{e}\mathsf{ are the fixed points}$ and what about **stability**?

$$X_{n+1} = r Y_n (1 - X_n)$$
  $0 \le X_n \le 1$   
 $0 \le r \le 4$  ... the interesting rounge.

$$X_{n+1} = r Y_n (1 - X_n)$$
  $0 \le X_n \le 1$   
 $0 \le r \le 4$ 

() Find fixed points.  

$$X^{\#} = f(x^{\#}) = r x^{\#}(1-x^{\#})$$
, where is this true?

$$X_{n+1} = r Y_n (1 - X_n)$$
  $0 \le X_n \le 1$   
 $0 \le r \le 4$ 

() Find fixed points.  

$$X^{4} = -f(x^{4}) = r x^{4}(1-x^{4}) \qquad \text{where is this true}?$$

$$X^{4} = 0$$

$$x^{4} = 1 - \frac{1}{r}$$

$$X_{n+1} = r Y_n (1 - X_n)$$
  $0 \le X_n \le 1$   
 $0 \le r \le 4$ 

(2) Shelity  
well... 
$$\lambda = f'(x^{n}) = r - 2rx^{n}$$
  
For  $x^{n} = 0$ , the origin is stable for  $r < 1$  (since  $f'(x^{n}) = r$ )  
unstable for  $r > 1$ 

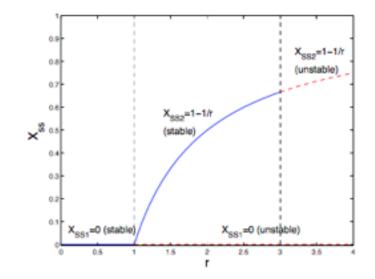
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unchall for  $r > 1$   
For  $x^{\alpha} = 1 - \frac{1}{r}$ ,  $f'(x^{\alpha}) = 2 - r$ . So ...  
shall for  $1 < r < 3$   
unshall for  $r > 3$ 

$$X_{n+1} = r Y_n (1 - X_n)$$
  $0 \le X_n \le 1$   
 $0 \le r \le 4$ 

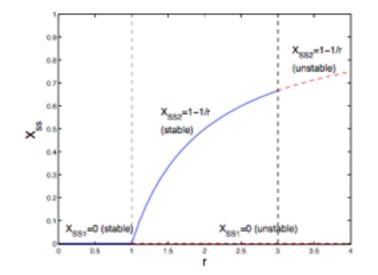
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unclude for  $r > 1$   
For  $x^{n} = 1 - \frac{1}{r}$ ,  $f'(x^{n}) = 2 - r$ . So ...  
shall for  $1 < r < 3$   
unshall for  $r > 3$   
 $x^{8} = 0$   
 $x^{$ 

$$X_{n+1} = r Y_n (1 - X_n)$$
  $0 \le X_n \le 1$   
 $0 \le r \le 4$ 



What happens for **r > 3**?

$$X_{n+1} = r Y_n (1 - X_n)$$
  $0 \le X_n \le 1$   
 $0 \le r \le 4$ 



What happens for **r > 3**?

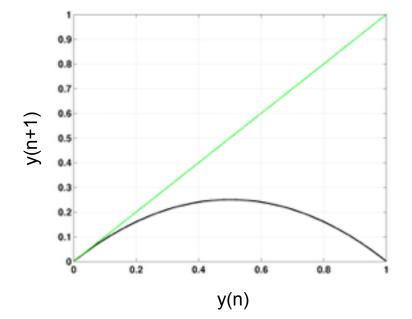
Nature 261 459-67 (1976)

## Simple mathematical models with very complicated dynamics

Robert M. May\*

Not only in research, but also in the everyday world of politics and economics, we would all be better off if more people realised that simple nonlinear systems do not necessarily possess simple dynamical properties.

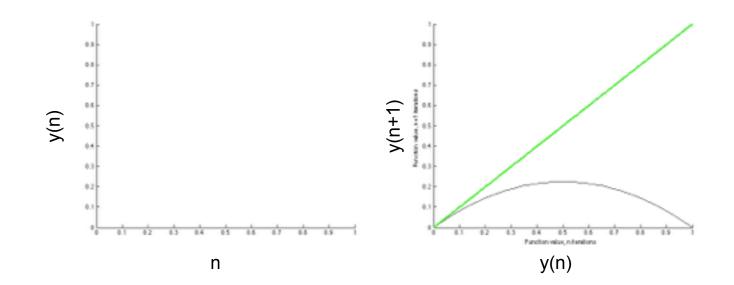
$$y(n+1) = ry(n)(1 - y(n))$$



Let's look at the dynamics of this equation. We will start with y(0)=0.9, and consider 100 iterations at various values of r. Remember that r is basically the feedback strength in our small positive feedback reaction scheme....

$$y(n+1) = ry(n)(1 - y(n))$$

y(0) = 0.9, r = 0.9

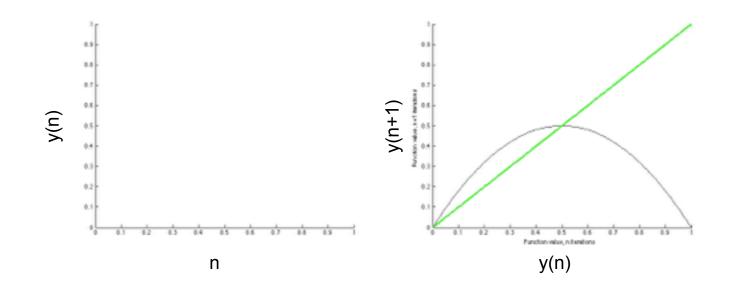


well... 
$$\lambda = f'(x^{n}) = r - 2rx^{n}$$
  
For  $x^{n} = 0$ , the origin is stable for  $r < 1$  (since  $f'(x^{n}) = r$ )  
unstable for  $r > 1$ 

R. May., Nature (1976) 261, 459-67

$$y(n+1) = ry(n)(1 - y(n))$$

y(0) = 0.9, r = 2.0

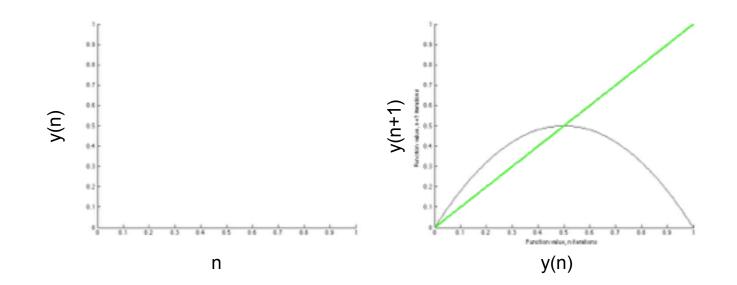


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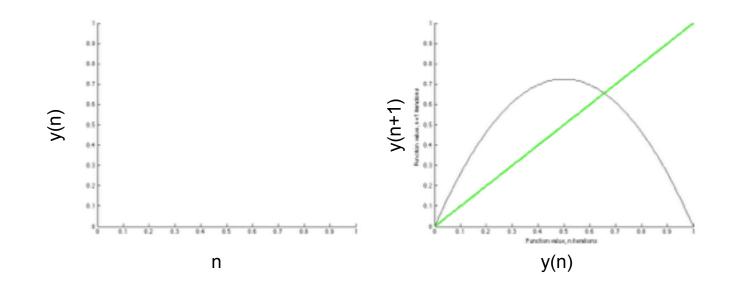
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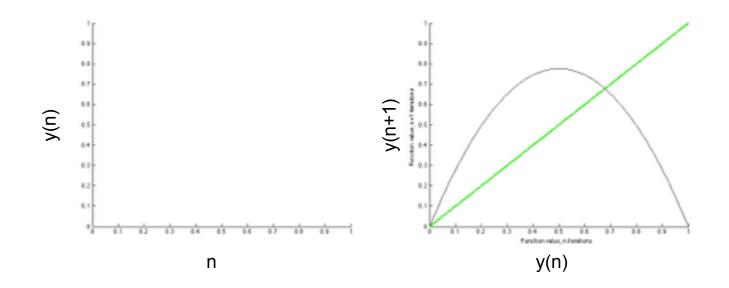
y(0) = 0.9, r = 2.9



For 
$$x^{*} = 1 - \frac{1}{r}$$
,  $f'(x^{*}) = 2 - r$ . So...  
shall for  $1 < r < 3$   
unstable for  $r > 3$ 

$$y(n+1) = ry(n)(1 - y(n))$$

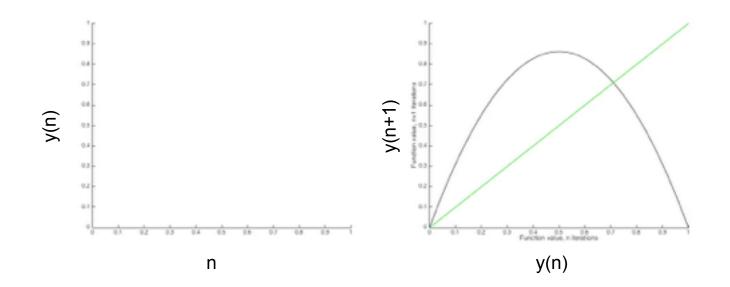
y(0) = 0.9, r = 3.1



So, this is called a **2-cycle**. That is, both fixed points have lost stability, and we have a system that is said to have **bifurcated**.

$$y(n+1) = ry(n)(1 - y(n))$$

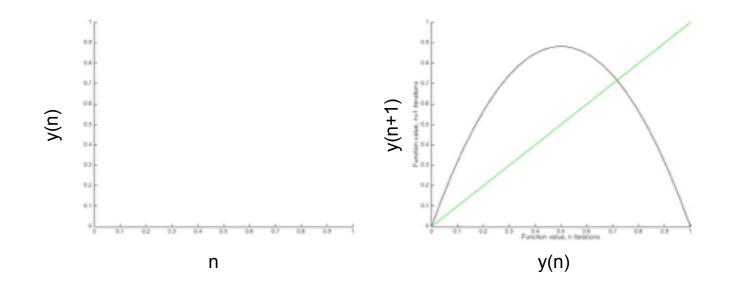
y(0) = 0.9, r = 3.45



Now...what happened? Even the two-cycle has lost stability! What do we have now?

$$y(n+1) = ry(n)(1 - y(n))$$

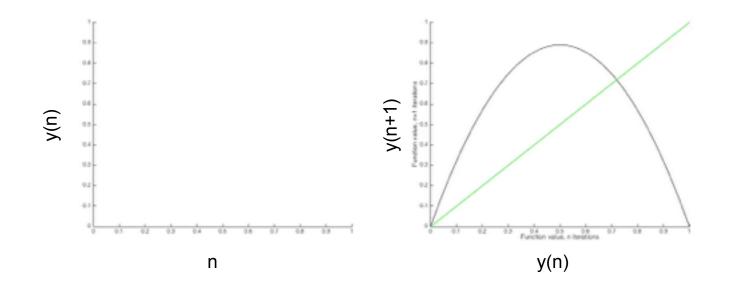
y(0) = 0.9, r = 3.53



So...a **4-cycle**. The system is said to have bifurcated again, or period doubling

$$y(n+1) = ry(n)(1 - y(n))$$

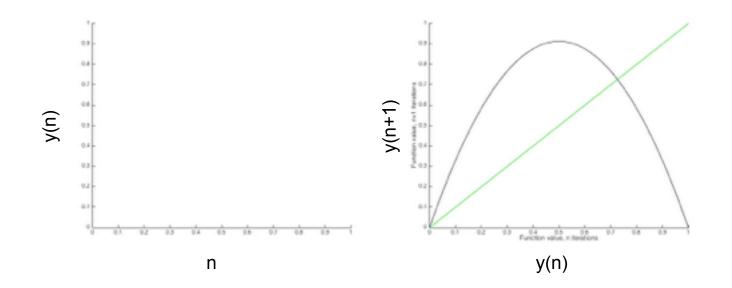
y(0) = 0.9, r = 3.56



And...a 8-cycle. Do you notice that the intervals over which our system bifurcates is getting smaller and smaller?

$$y(n+1) = ry(n)(1 - y(n))$$

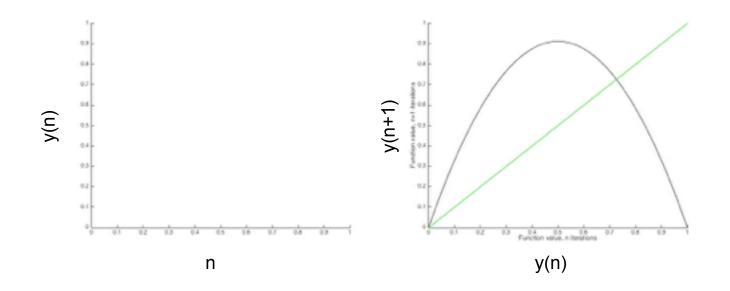
y(0) = 0.9, r = 3.6



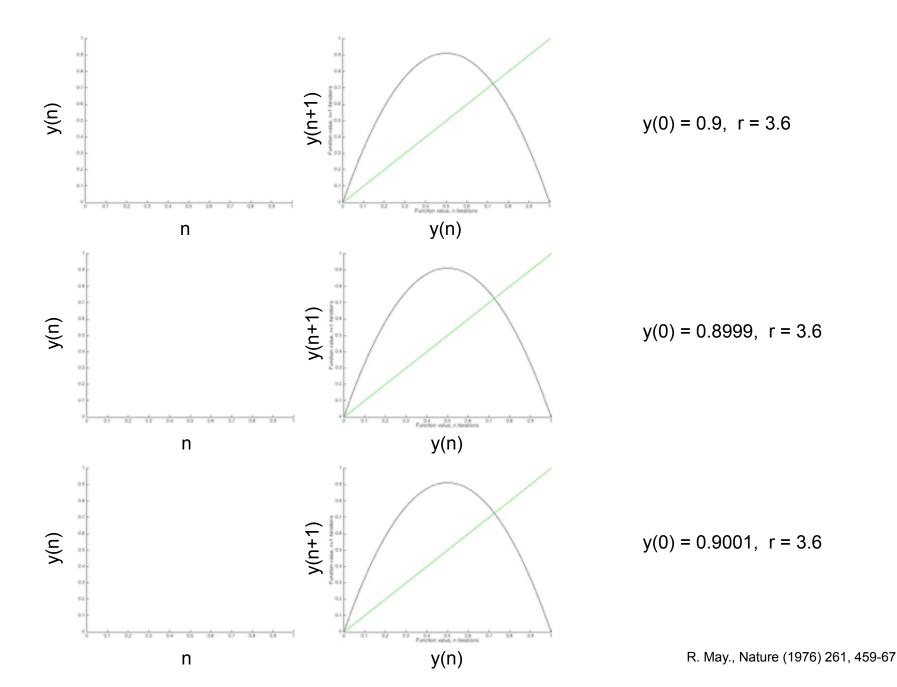
And then we come to this....a regime of so-called **deterministic chaos.** 

$$y(n+1) = ry(n)(1 - y(n))$$

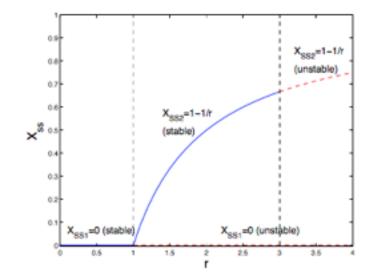
y(0) = 0.9, r = 3.6



And then we come to this....a regime of so-called **deterministic chaos.** This is characterized by two things: (1) a large number of seemingly constantly changing states, and (2) extreme sensitivity to initial conditions. Deterministic chaos: sensitivity to initial conditions.... (the "butterfly effect")

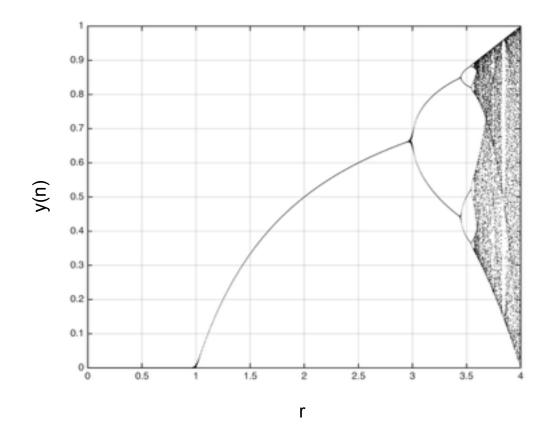


$$y(n+1) = ry(n)(1 - y(n))$$



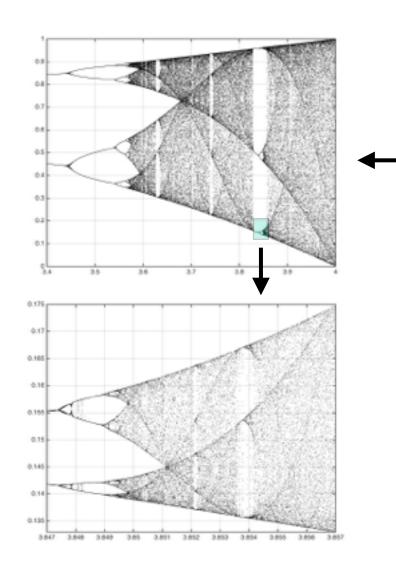
So...what does happen for **r > 3**?

y(n+1) = ry(n)(1 - y(n))

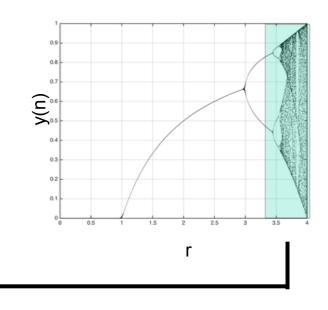


The famous diagram of **period doublings**....

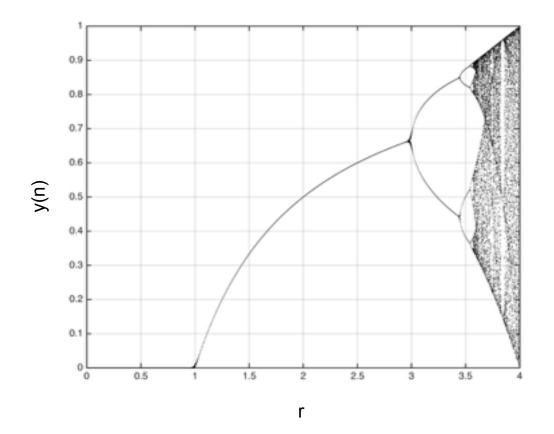
y(n+1) = ry(n)(1 - y(n))



The notions of **self-similarity** and **scale invariance**....



y(n+1) = ry(n)(1 - y(n))



The famous diagram of **period doublings**....can we mathematically understand every doubling point and the entrance into the regime of chaos? Next, we will further analyze the simple non-linear oscillator systems...

	n = 1	n = 2 or 3	n >> 1	continuum
Linear	exponential growth and decay single step conformational change fluorescence emission pseudo first order kinetics	second order reaction kinetics linear harmonic oscillators simple feedback control sequences of conformational change	electrical circuits molecular dynamics systems of coupled harmonic oscillators equilibrium thermodynamics diffraction, Fourier transforms	Diffusion Wave propagation quantum mechanics viscoelastic systems
Nonlinear	fixed points bifurcations, multi stability irreversible hysteresis overdamped oscillators	anharmomic oscillators relaxation oscillations predator-prey models van der Pol systems Chaotic systems	systems of non- linear oscillators non-equilibrium thermodynamics protein structure/ function neural networks the cell ecosystems	Nonlinear wave propagation Reaction-diffusion in dissipative systems Turbulent/chaotic flows