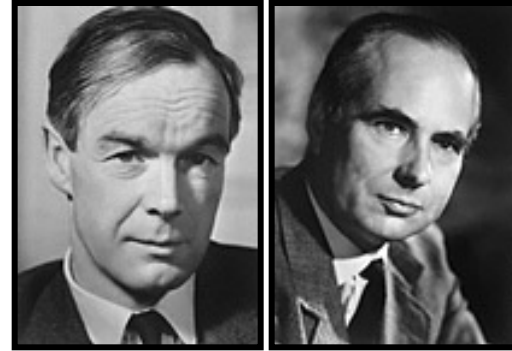
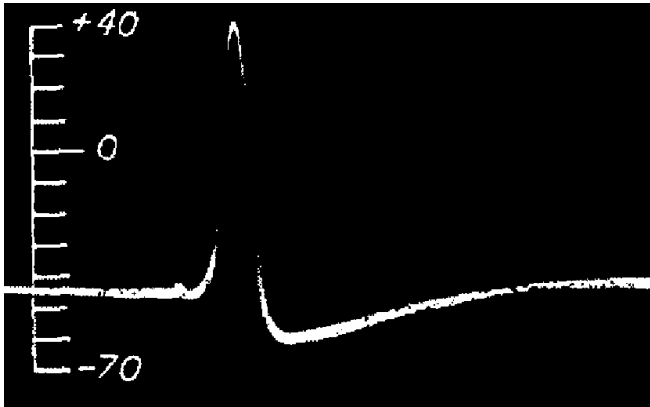
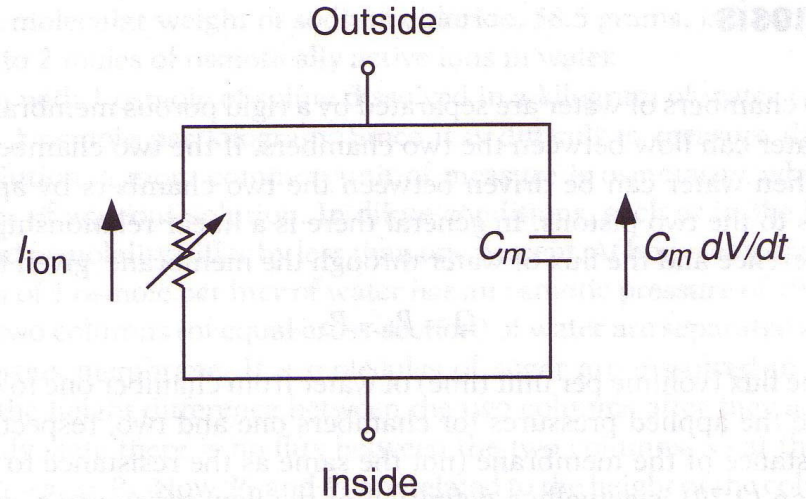
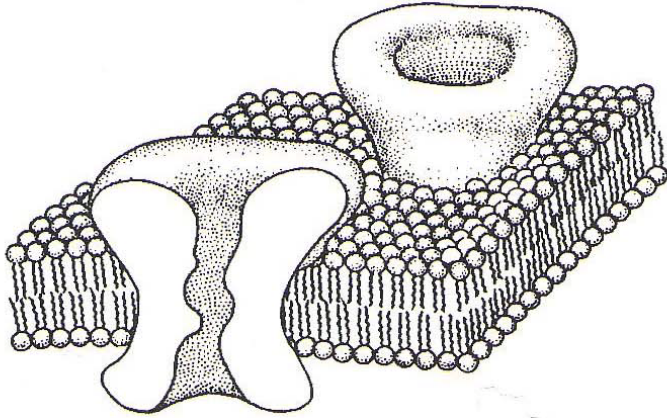


Hodgkin-Huxley model



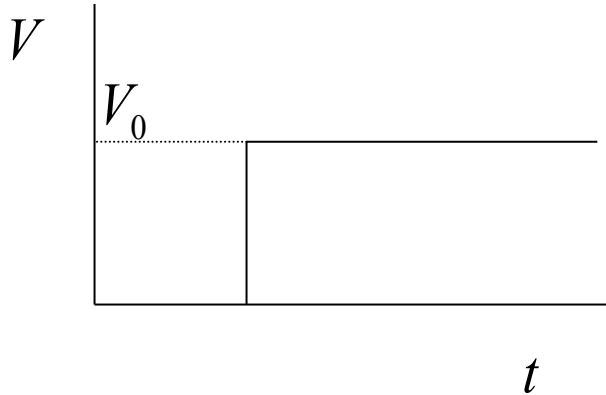
$$C_m \frac{dv}{dt} = -\bar{g}_K n^4 (v - v_K) - \bar{g}_{Na} m^3 h (v - v_{Na}) - \bar{g}_L (v - v_L) + I_{app},$$
$$\frac{dm}{dt} = \alpha_m (1 - m) - \beta_m m,$$
$$\frac{dn}{dt} = \alpha_n (1 - n) - \beta_n n,$$
$$\frac{dh}{dt} = \alpha_h (1 - h) - \beta_h h.$$

HH thought of neuronal membrane as a circuit

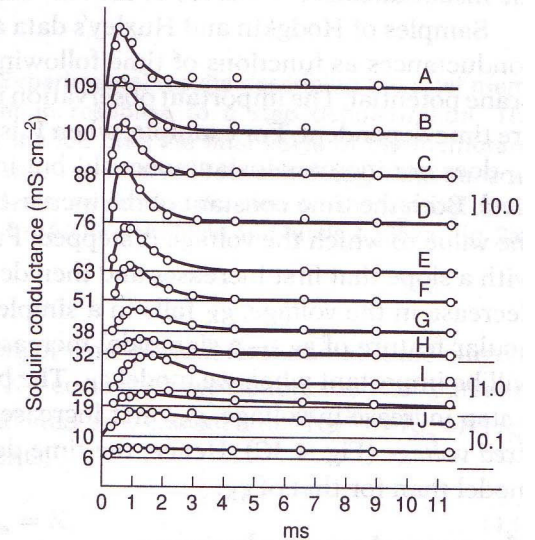
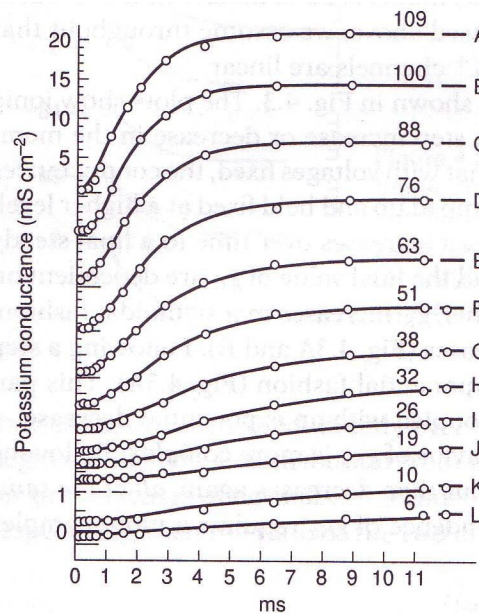
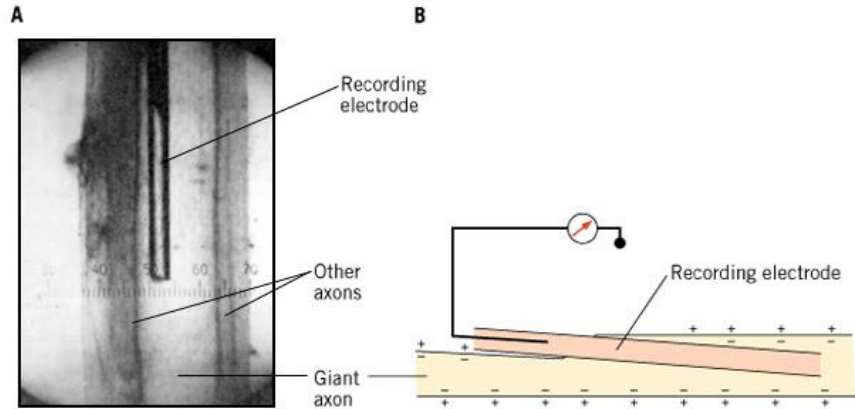


$$C_m \frac{dV}{dt} = -g_{Na^+} (V - V_{Na^+}) - g_{K^+} (V - V_{K^+})$$

Conductances depend on V and t (voltage-clamp experiments)



$$g_{K^+}(V_0, t) = \frac{V_0 - V_{K^+}}{I_{medido}(t)}$$



$$g_{K^+}(V, t)$$

HH could have assumed a differential equation like

$$\frac{dg_{K^+}}{dt} = f(V, t)$$

But they chose to assume the existence of channels with 'gates'

$$g_{K^+} = \bar{g}_{K^+} n^4 \quad ; \quad \frac{dn}{dt} = f(V, t)$$

What does this mean?

$$g_{K^+} = \bar{g}_{K^+} n^4 \quad ;$$

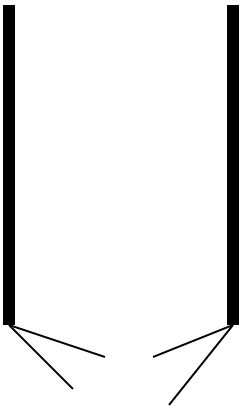
$$\frac{dn}{dt} = f(V, t)$$

Dynamics of probability that
a single gate is open
(depending on de voltage and time)

Maximum conductance

Probability that the four gates of the channel are
open

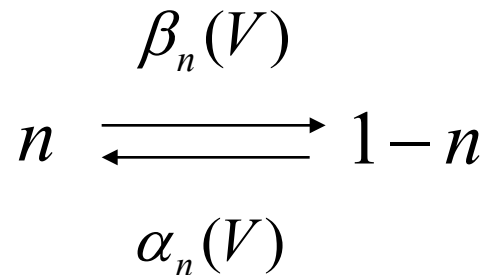
n : Probabilidad de que las 4 puertas del canal
estén abiertas al paso del ion



We assume a first-order kinetics for the gate

n : probability that a gate is open

$1 - n$: probability that a gate is closed



$$\frac{dn}{dt} = \alpha_n(V)(1 - n) - \beta_n(V)n$$

Rewriting the dynamics of gate opening

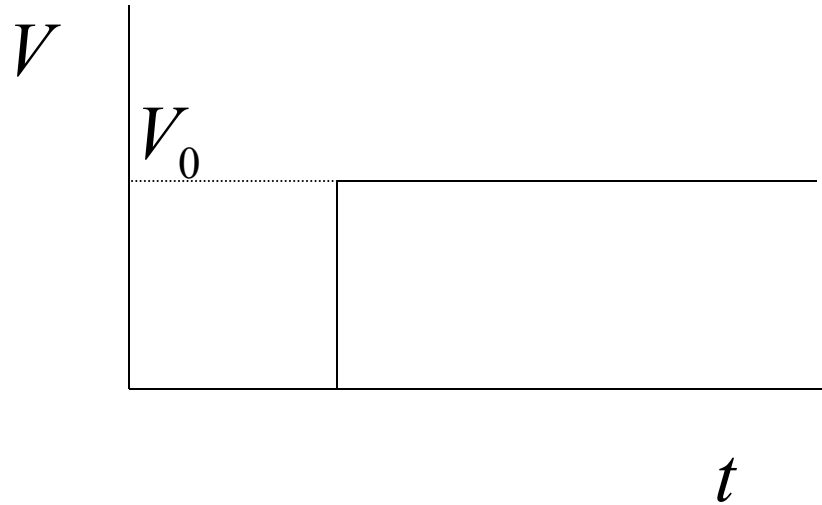
$$\frac{dn}{dt} = \alpha_n(V)(1-n) - \beta_n(V)n$$

$$n_\infty(V) \equiv \frac{\alpha_n(V)}{\alpha_n(V) + \beta_n(V)} \quad ; \quad \tau_n(V) \equiv \frac{1}{\alpha_n(V) + \beta_n(V)}$$

$$\frac{dn}{dt} = \frac{n_\infty(V) - n}{\tau_n(V)}$$

Dynamics of gate opening in voltage-clamp experiment

$$\frac{dn}{dt} = \frac{n_{\infty}(V) - n}{\tau_n(V)}$$

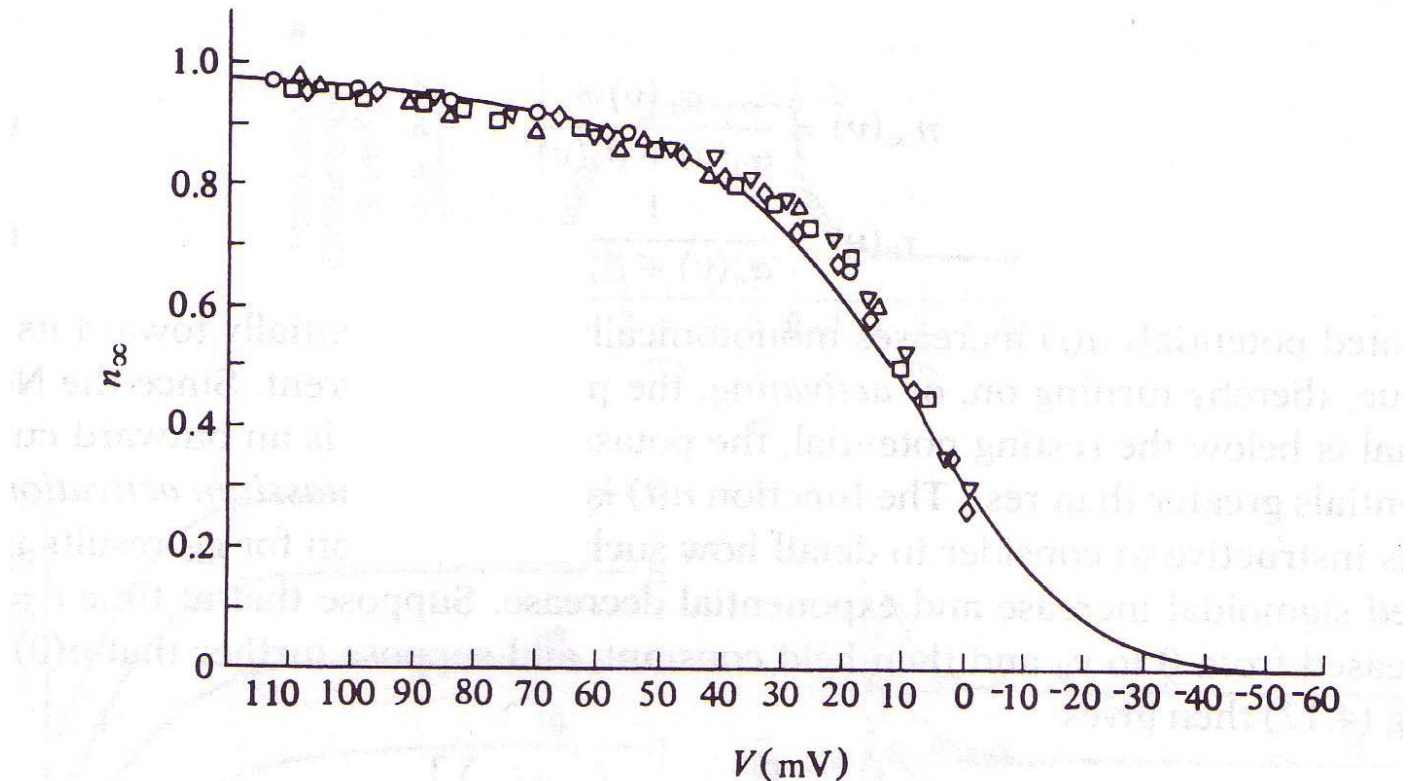


$$n(V_0, t) = n_{\infty}(V_0) \left[1 - \exp\left(-\frac{t}{\tau_n(V_0)}\right) \right]$$

Fit to experiments

$$n(V_0, t) = n_\infty(V_0) \left[1 - \exp\left(-\frac{t}{\tau_n(V_0)}\right) \right]$$

Fitting $n_\infty(V_0)$



The same for $\tau_n(V_0)$

We then obtain

$$\alpha_n = 0.01 \left(\frac{10 - V}{\exp\left(\frac{10 - V}{10}\right) - 1} \right) \quad \beta_n = 0.125 \left(\frac{-V}{80} \right)$$

$$\bar{g}_{K^+} = 36$$

$$V_{K^+} = -12$$

Really nice fit to voltage-clamp experiments

$$g_{K^+} = \bar{g}_{K^+} n^4$$

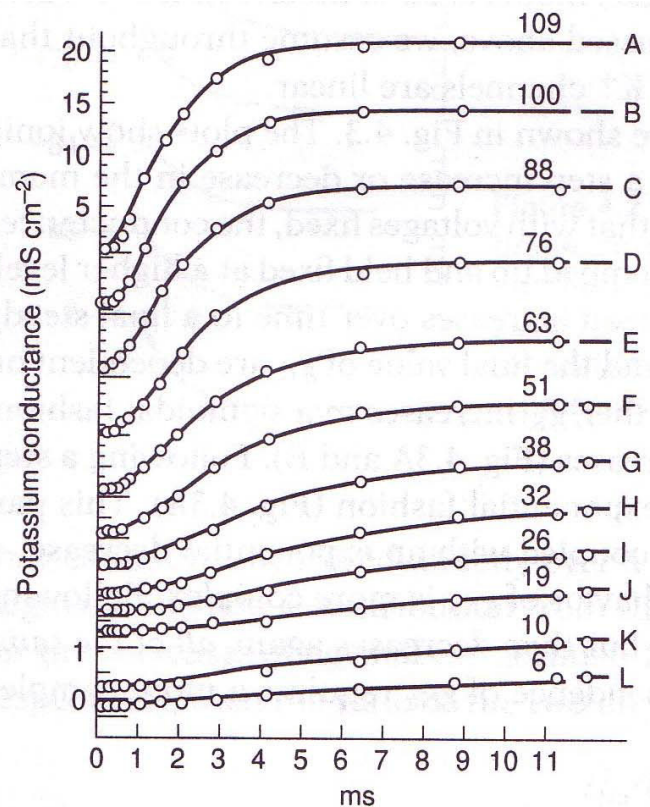
$$n(V_0, t) = \frac{\alpha_n(V)}{\alpha_n(V) + \beta_n(V)} \left[1 - \exp(-(\alpha_n(V) + \beta_n(V))t) \right]$$

$$\alpha_n = 0.01 \left(\frac{10 - V}{\exp\left(\frac{10 - V}{10}\right) - 1} \right)$$

$$\beta_n = 0.125 \left(\frac{-V}{80} \right)$$

$$\bar{g}_{K^+} = 36$$

$$V_{K^+} = -12$$



What do we have so far?

$$C_m \frac{dV}{dt} = -g_{Na^+} (V - V_{Na^+}) - g_{K^+} (V - V_{K^+})$$

$$C_m \frac{dV}{dt} = g_{Na^+} (V - V_{Na^+}) + \bar{g}_{K^+} n^4 (V - V_{K^+})$$

$$\frac{dn}{dt} = \alpha_n(V)(1-n) - \beta_n(V)n$$

$$\alpha_n = 0.01 \left(\frac{10-V}{\exp\left(\frac{10-V}{10}\right) - 1} \right) \quad \beta_n = 0.125 \left(\frac{-V}{80} \right)$$

$$\bar{g}_{K^+} = 36$$

$$V_{K^+} = -12$$

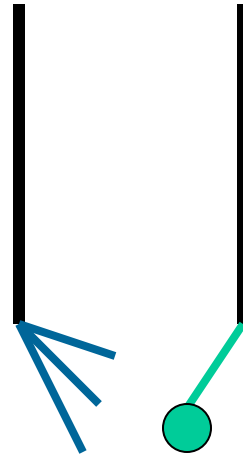
$$g_{Na^+}(V, t)$$

Fit to experiments assuming two types of gates

$$g_{Na^+} = \bar{g}_{Na^+} m^3 h$$

$$\frac{dm}{dt} = \alpha_m(V)(1-m) - \beta_m(V)m$$

$$\frac{dh}{dt} = \alpha_h(V)(1-h) - \beta_h(V)h$$



The complete model

$$C_m \frac{dV}{dt} = -\bar{g}_{Na^+} m^3 h (V - V_{Na^+}) - \bar{g}_{K^+} n^4 (V - V_{K^+}) - \bar{g}_L (V - V_L) + I_{ext}$$

$$\frac{dn}{dt} = \alpha_n(V)(1-n) - \beta_n(V)n$$

$$\frac{dm}{dt} = \alpha_m(V)(1-m) - \beta_m(V)m$$

$$\frac{dh}{dt} = \alpha_h(V)(1-h) - \beta_h(V)h$$

With functions (in (ms)⁻¹)

$$\alpha_m = 0.1 \left(\frac{25 - V}{\exp\left(\frac{25 - V}{10}\right) - 1} \right) \quad \alpha_h = 0.07 \exp\left(\frac{-V}{20}\right) \quad \alpha_n = 0.01 \left(\frac{10 - V}{\exp\left(\frac{10 - V}{10}\right) - 1} \right)$$

$$\beta_m = 4 \exp\left(\frac{-V}{18}\right) \quad \beta_h = \frac{1}{\exp\left(\frac{30 - V}{10}\right) + 1} \quad \beta_n = 0.125 \exp\left(\frac{-V}{80}\right)$$

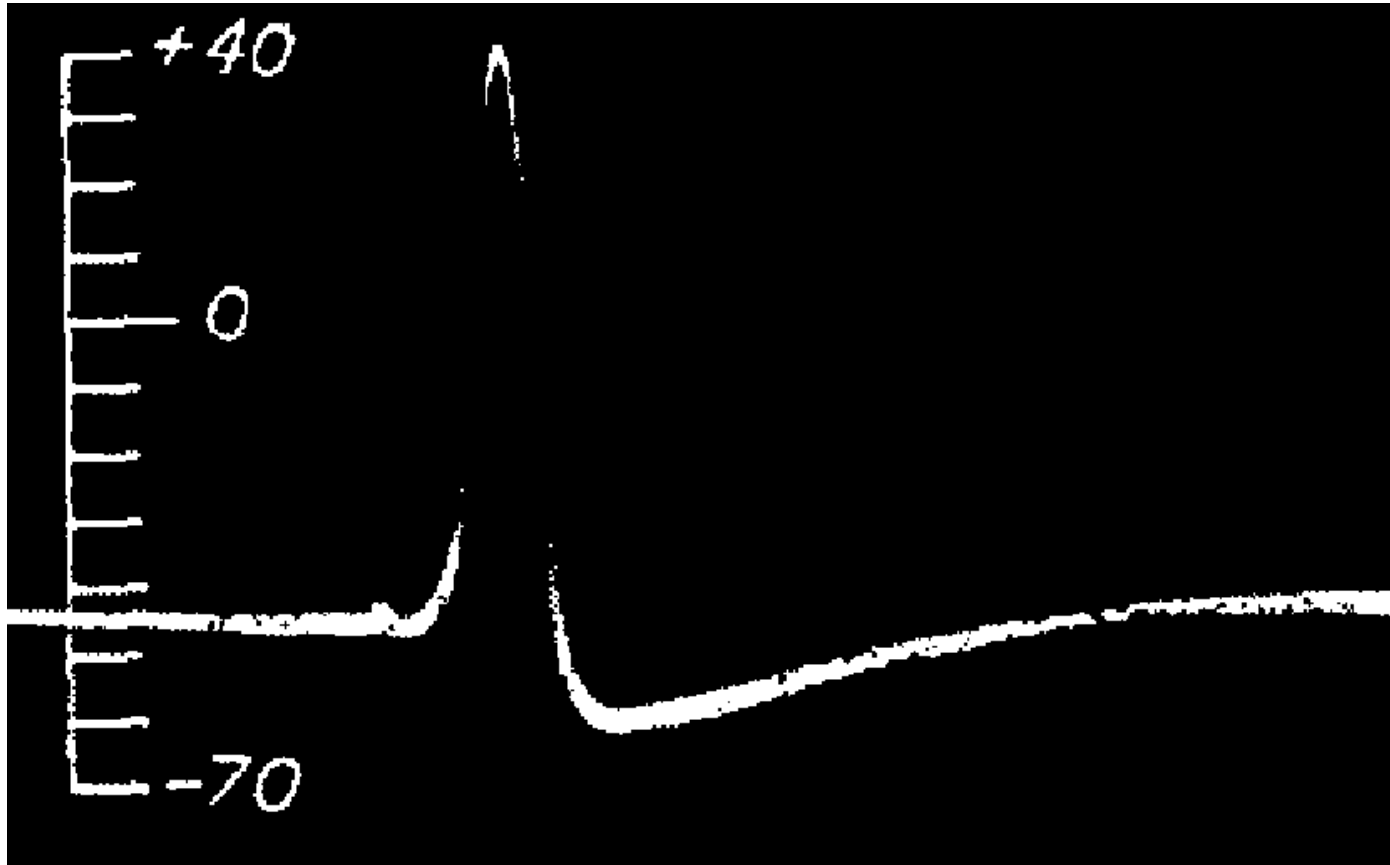
And constants

$$\bar{g}_{Na^+} = 120 \quad mS / cm^2 \quad \bar{g}_{K^+} = 36 \quad mS / cm^2 \quad \bar{g}_L = 0.3 \quad mS / cm^2$$

$$V_{Na^+} = 115 \quad mV \quad V_{K^+} = -12 \quad mV \quad V_L = 10.6 \quad mV$$

$$C_m = 1 \quad \mu F / cm^2$$

Does the HH model reproduce the action potential?




```

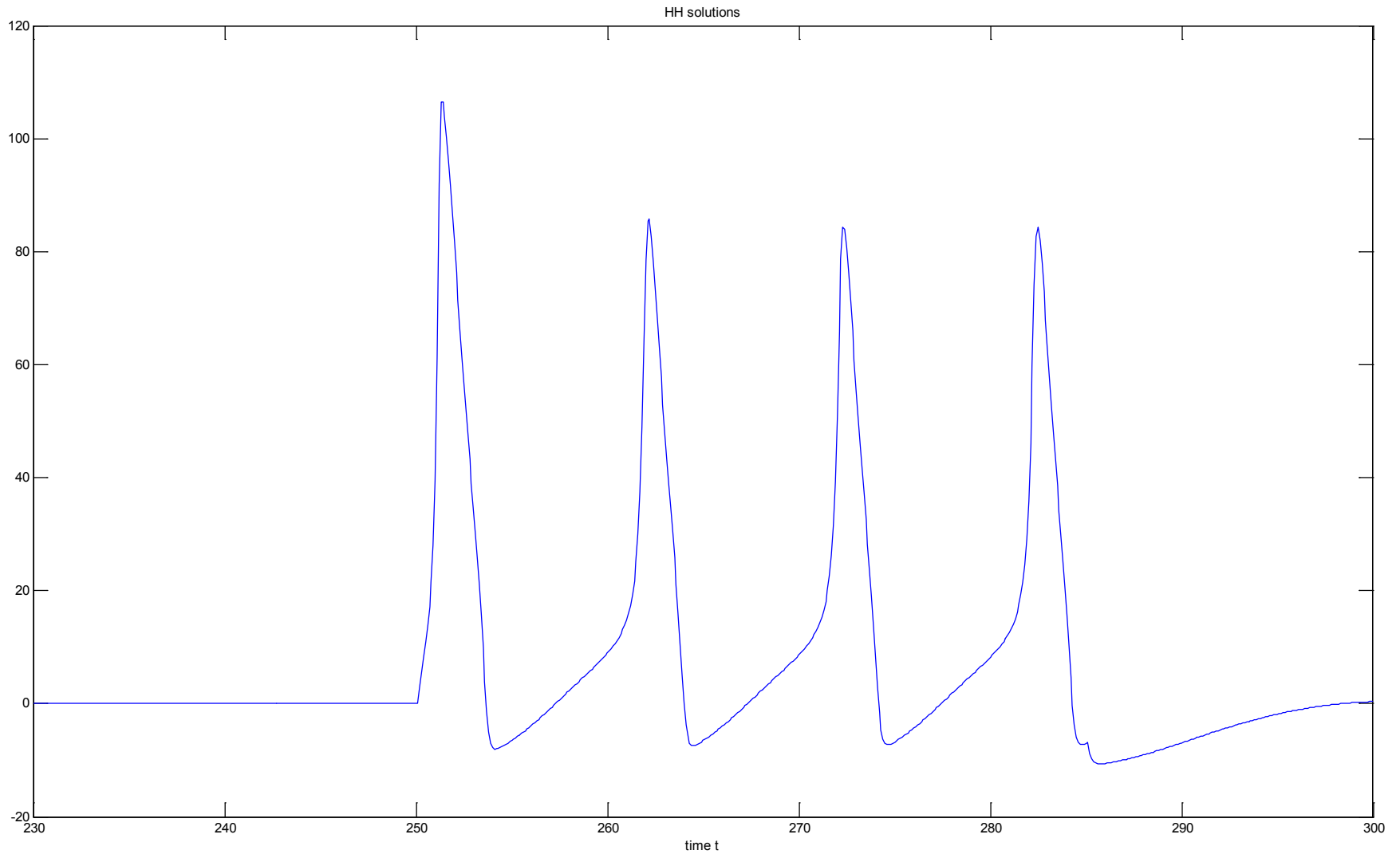
function hh
%
% Hodgkin-Huxley equations solved using ODE23s
%
clear all
time_length=500;           % duration of complete experiment in ms
time_resol=0.1;           % number of points in a ms
tspan = [0:time_resol:time_length]; % time points for solutions
%
% Initial values for voltage and conductances V0, n0, m0 and h0
%
yinit=[0;0.1;0.1;0.1];    % initial values for integration
%
% Call to integration routine
%
[t,y] = ode23(@hodgkinhuxley,tspan,yinit);
%
% Plotting
%
```

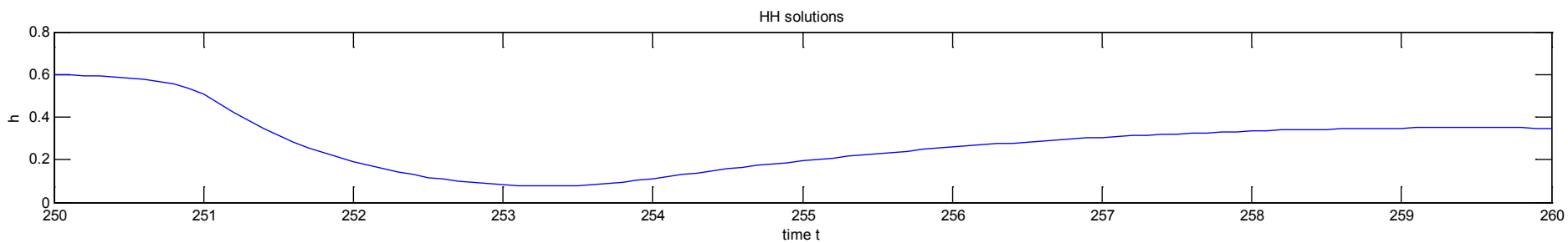
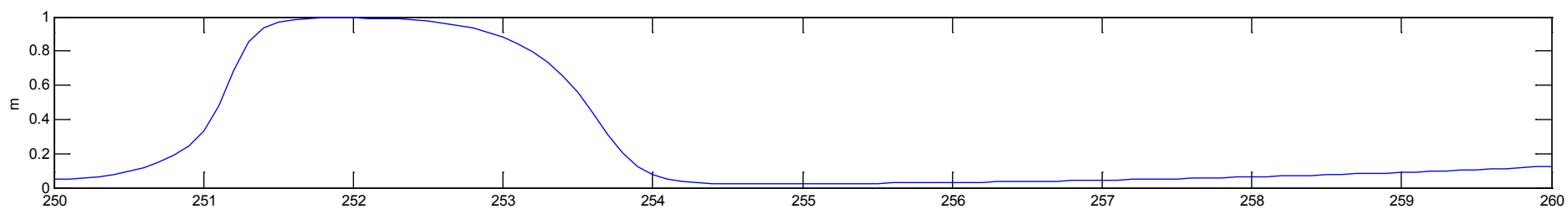
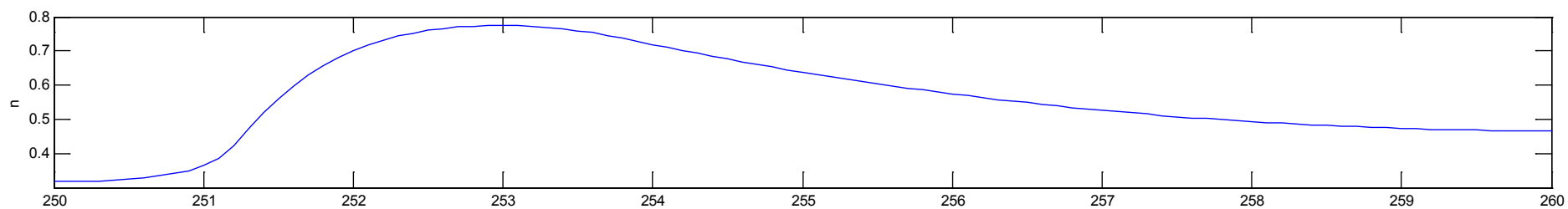
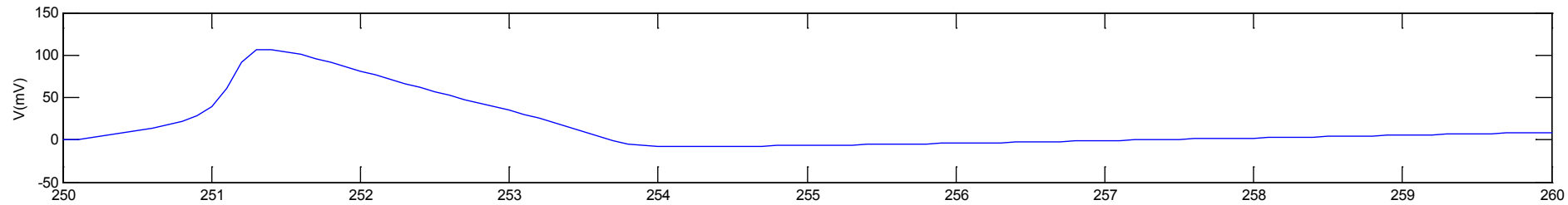
```
figure;  
plot([230:0.1:300],y(2300:3000,1));  
title(['HH solutions']);  
xlabel('time t');
```

```
function dydt = hodgkinhuxley(t,y)  
  
%  
% External current step I(t)  
%  
if t<250; I=0; elseif t>=250&t<285; I=30; else; I=0; end  
%  
% Parameters for the HH equations  
%  
cap=1; gK=36;gNa=120;gl=0.3;VK=-12;VNa=115;Vl=10.6;  
%  
% Functions for HH equations  
%  
alpha_n=(0.1-0.01*y(1))/(exp(1-0.1*y(1))-1);  
beta_n=0.125*exp(-y(1)/80);  
alpha_m=(2.5-0.1*y(1))/(exp(2.5-0.1*y(1))-1);  
beta_m=4*exp(-y(1)/18);  
alpha_h=0.07*exp(-y(1)/20);  
beta_h=1/( exp(3-0.1*y(1))+1 );
```

```
%  
% The HH equations  
%  
dydt = [      (I-gK*y(2)^4*(y(1)-VK)-gNa*y(3)^3*y(4)*(y(1)-VNa)-gl*(y(1)-Vl))/cap  
              alpha_n*(1-y(2))-beta_n*y(2)  
              alpha_m*(1-y(3))-beta_m*y(3)  
              alpha_h*(1-y(4))-beta_h*y(4)];
```

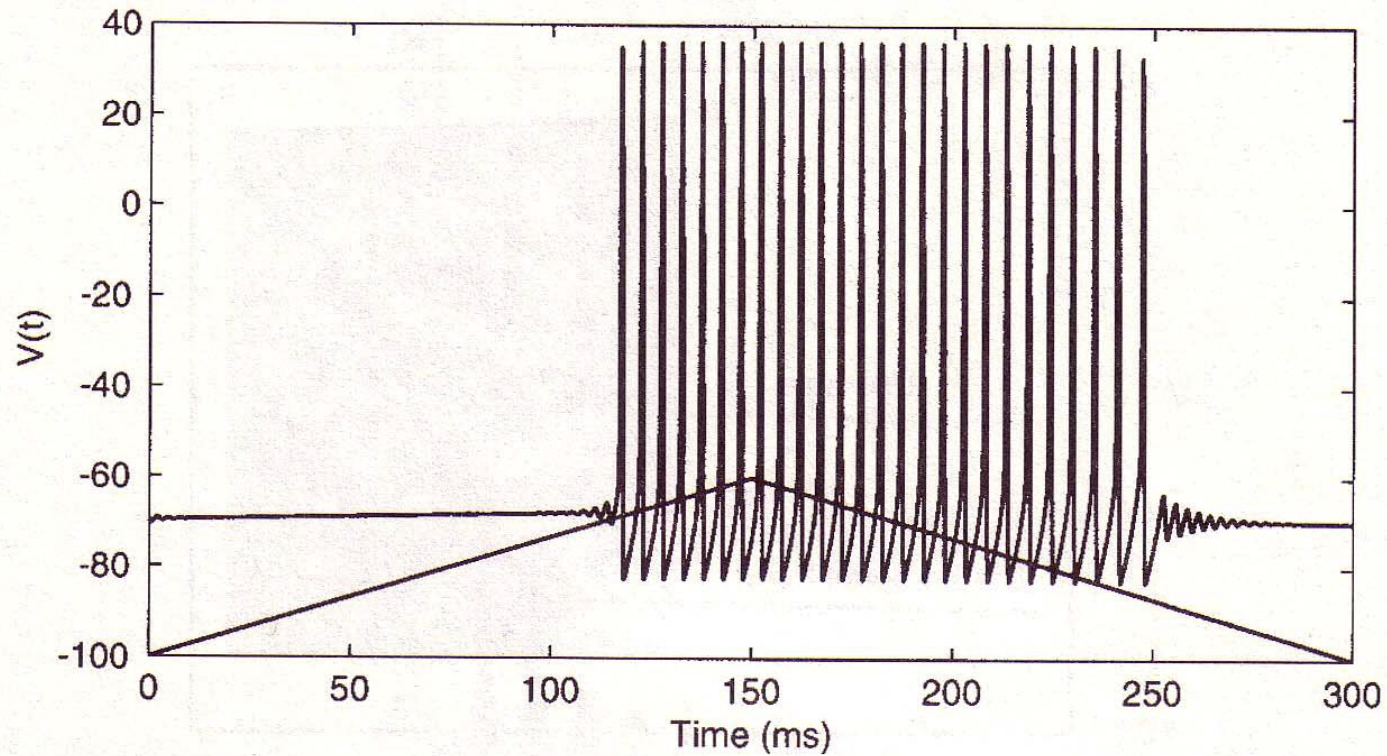
Response of model to injection of current step





1. HH model
2. Simplifications of HH model
 - 2.1. Rinzel model
 - 2.2. Wilson model
 - 2.3. FitzHugh-Nagumo model
3. Adaptation and bursts
4. Networks

How would you explain this?



Rinzel model

HH model (4 variables):

$$C_m \frac{dV}{dt} = -\bar{g}_{Na^+} m^3 h (V - V_{Na^+}) - \bar{g}_{K^+} n^4 (V - V_{K^+}) - \bar{g}_L (V - V_L) + I_{ext}$$

$$\frac{dn}{dt} = \alpha_n(V)(1-n) - \beta_n(V)n$$

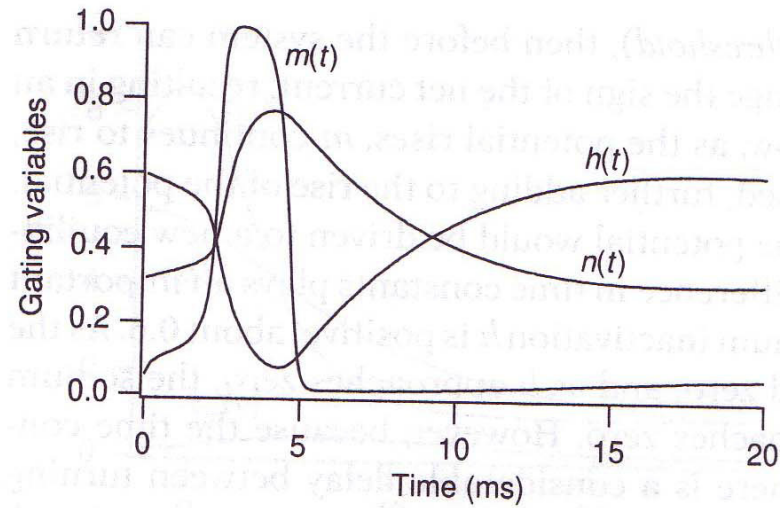
$$\frac{dm}{dt} = \alpha_m(V)(1-m) - \beta_m(V)m$$

$$\frac{dh}{dt} = \alpha_h(V)(1-h) - \beta_h(V)h$$

1. τ_m is small

$$m(V, t) = m_\infty(V) \left[1 - \exp\left(-\frac{t}{\tau_m(V)}\right) \right] \approx m_\infty(V)$$

2. Symmetry between h and n

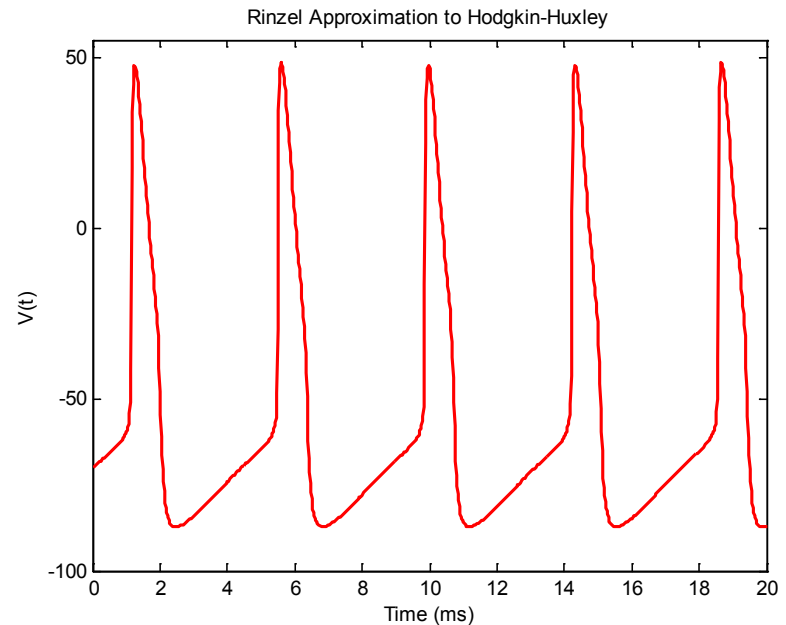
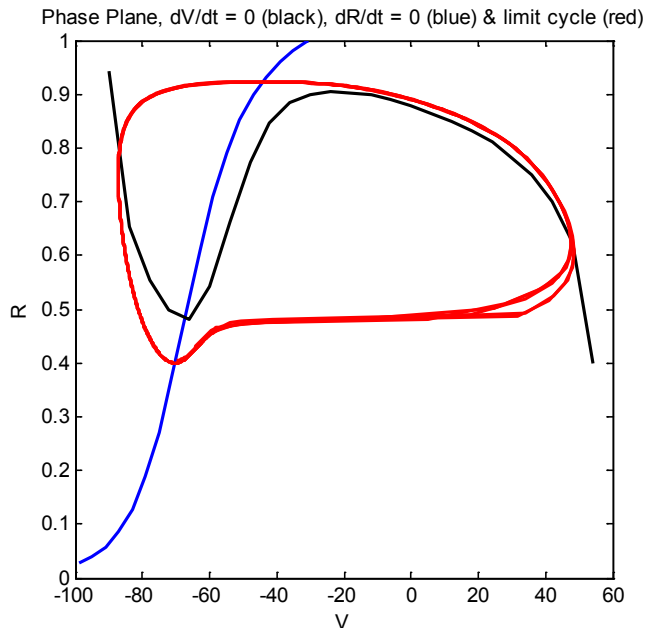


$$h(V, t) + n(V, t) \approx 1.0$$

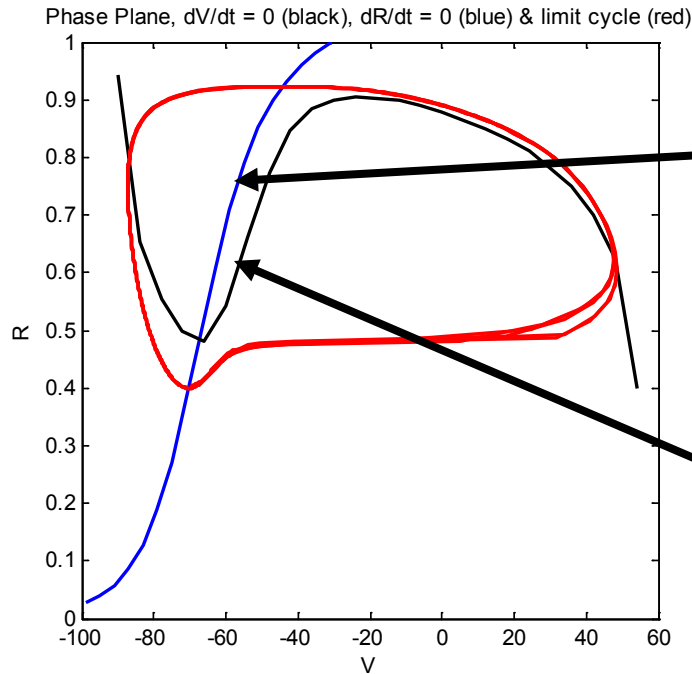
Rinzel model: approxs 1 & 2 on HH

$$C_m \frac{dV}{dt} = -\bar{g}_{Na^+} m_\infty^3 (1-R)(V - V_{Na^+}) - \bar{g}_{K^+} R^4 (V - V_{K^+}) - \bar{g}_L (V - V_L) + I_{ext}$$

$$\frac{dR}{dt} = \alpha_n(V)(1-R) - \beta_n(V)R$$



Wilson model simplifies Rinzel a bit more



1. $\frac{dR}{dt} = 0$

$$\frac{dR}{dt} = \frac{1}{\tau_R} (-R + G(V)); G(V) = 1.35V + 1.03$$

$$\frac{dR}{dt} = 0 \Rightarrow R = G(V) = 1.35V + 1.03$$

2. $\frac{dV}{dt} = 0$

$$C \frac{dV}{dt} = -g_{Na^+} (V - V_{Na^+}) - R(V - V_{K^+}) + I_{ext}$$

$$\frac{dV}{dt} = 0 \Rightarrow R = \frac{-g_{Na^+} (V - V_{Na^+}) + I_{ext}}{(V - V_{K^+})} ; g_{Na^+} = 17.81 + 47.71V + 32.63V^2$$

Wilson model simplifies Rinzel a bit more

$$0.8 \frac{dV}{dt} = -(17.81 + 47.71 V + 32.63 V^2)(V - 0.55) - 26.0 R(V + 0.92) + I_{ext}$$

$$\frac{dR}{dt} = \frac{1}{1.9} (-R + 1.35 V + 1.03)$$

V en decivoltios, I en $\mu A/100$ y t en ms

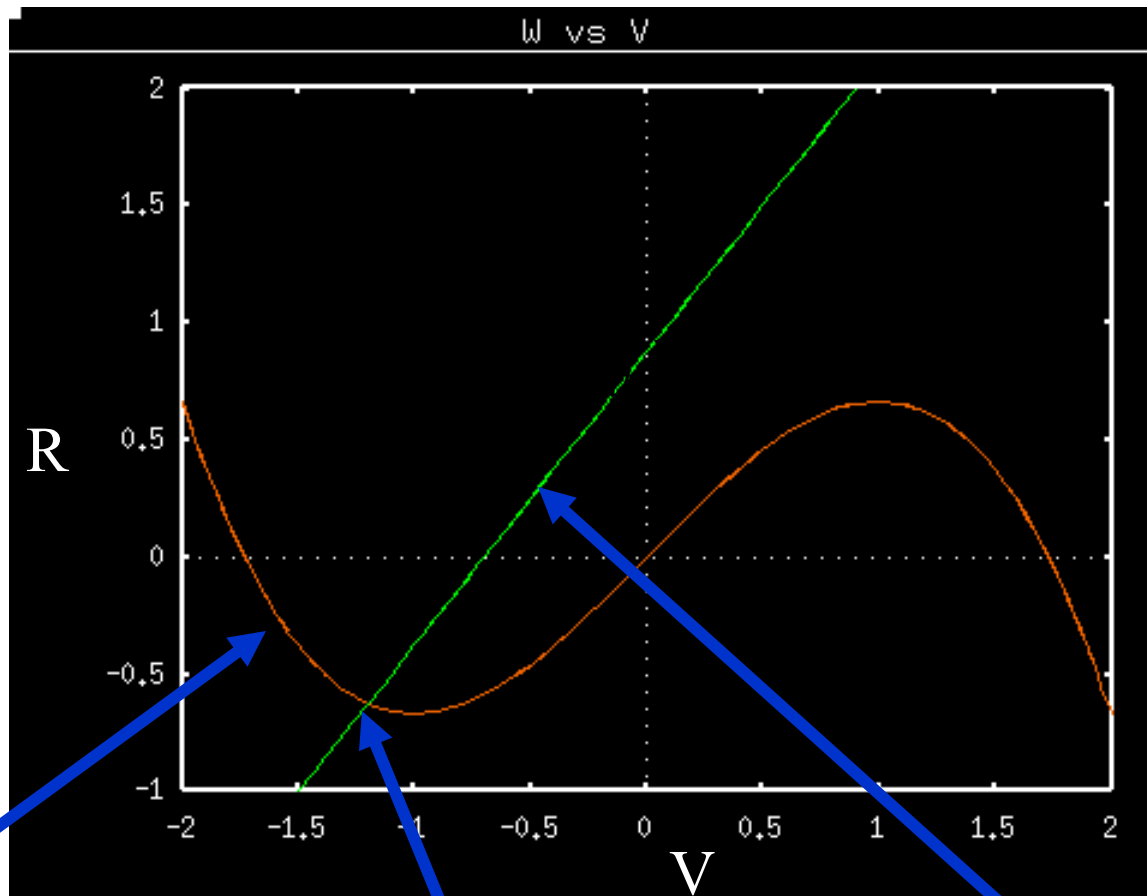
FitzHugh-Nagumo model

Skeleton version of Wilson

$$\frac{dV}{dt} = V - V^3 / 3 - R + I_{ext}$$

$$\frac{dR}{dt} = \phi(V + a - bR)$$

We will use $\phi = 0.08$; $a = 0.7$; $b = 0.8$



V nullcline

R nullcline

Equilibrium point

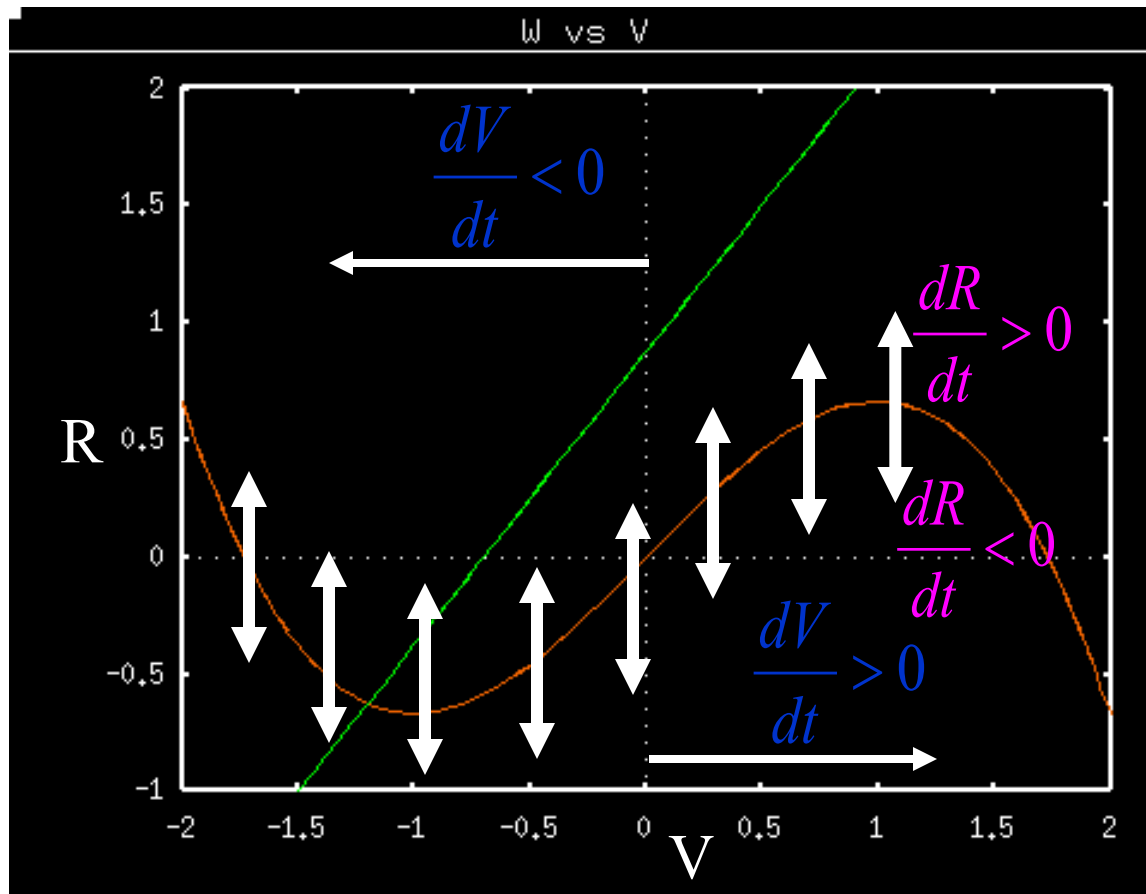
$$\frac{dV}{dt} = 0$$

$$\frac{dV}{dt} = \frac{dR}{dt} = 0$$

$$\frac{dR}{dt} = 0$$

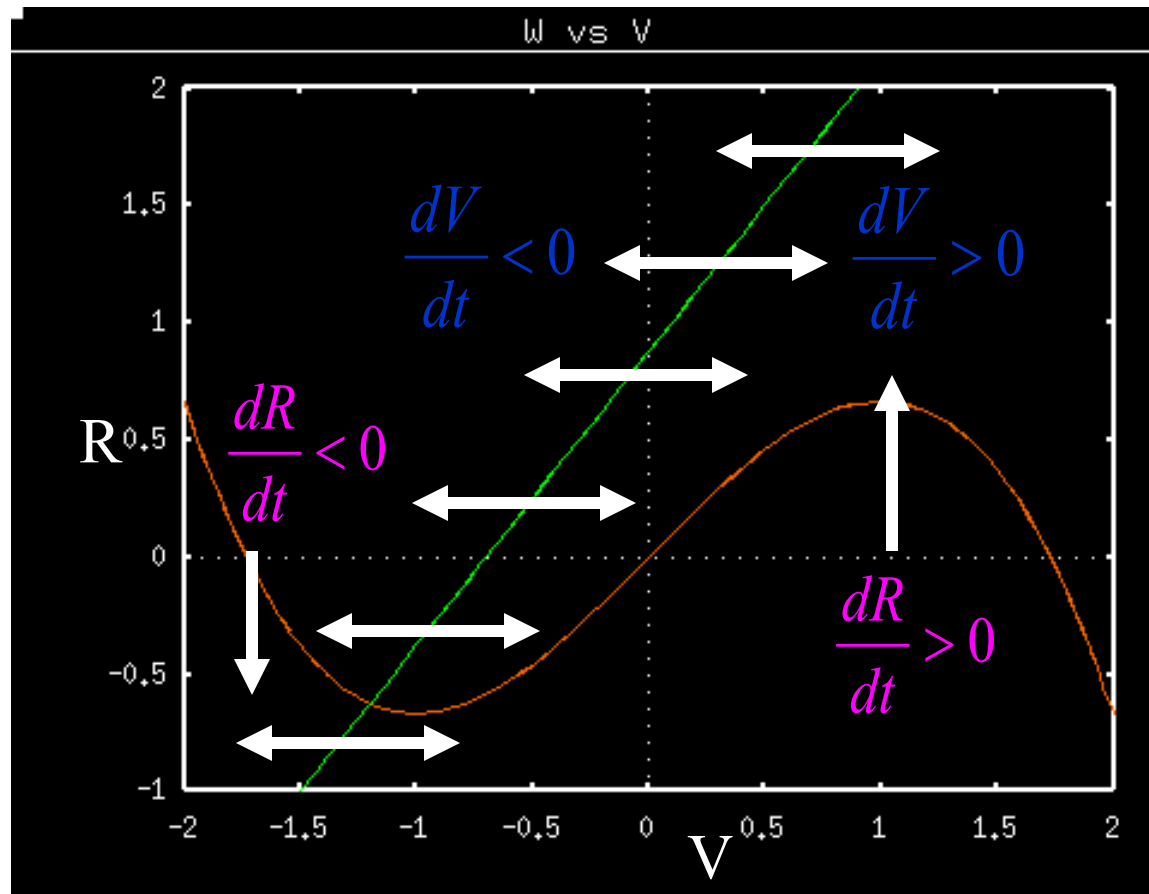
Flow implied by V nullcline (for $I_{ext}=0$)

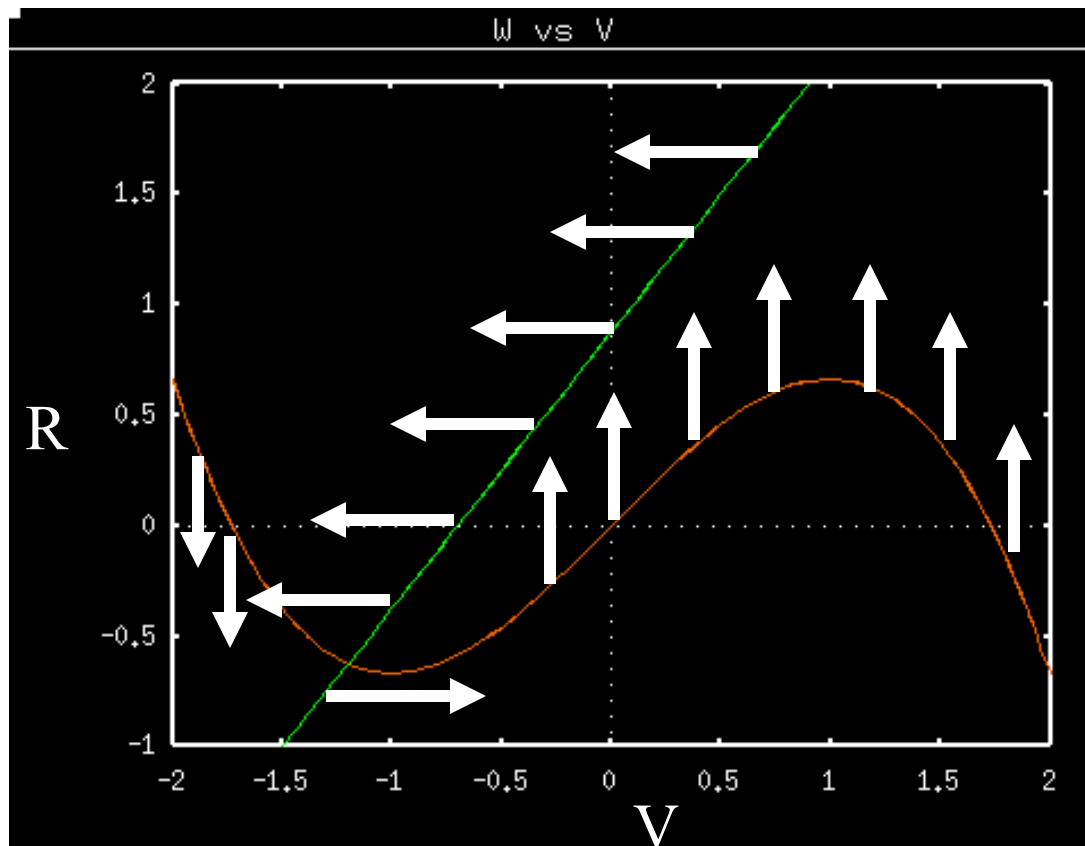
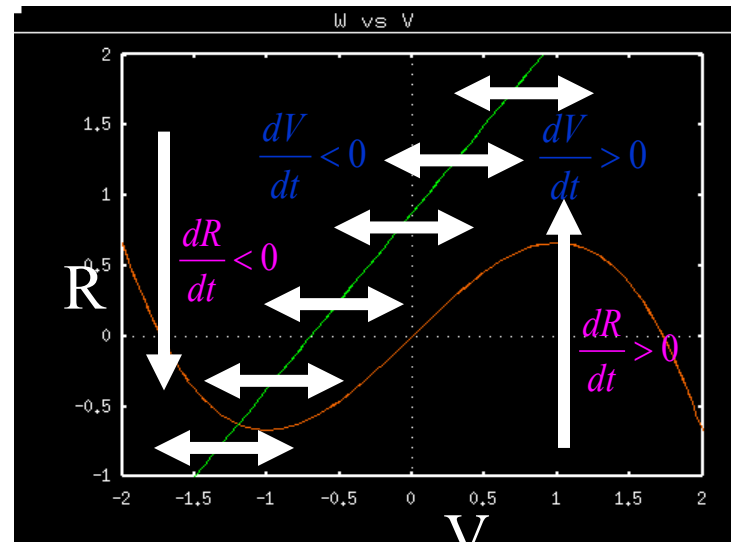
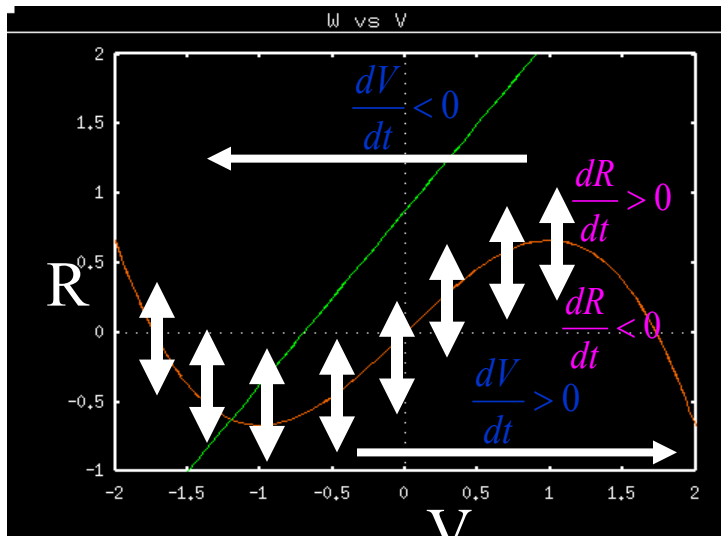
$$\frac{dV}{dt} = V - V^3/3 - R + I_{ext}$$

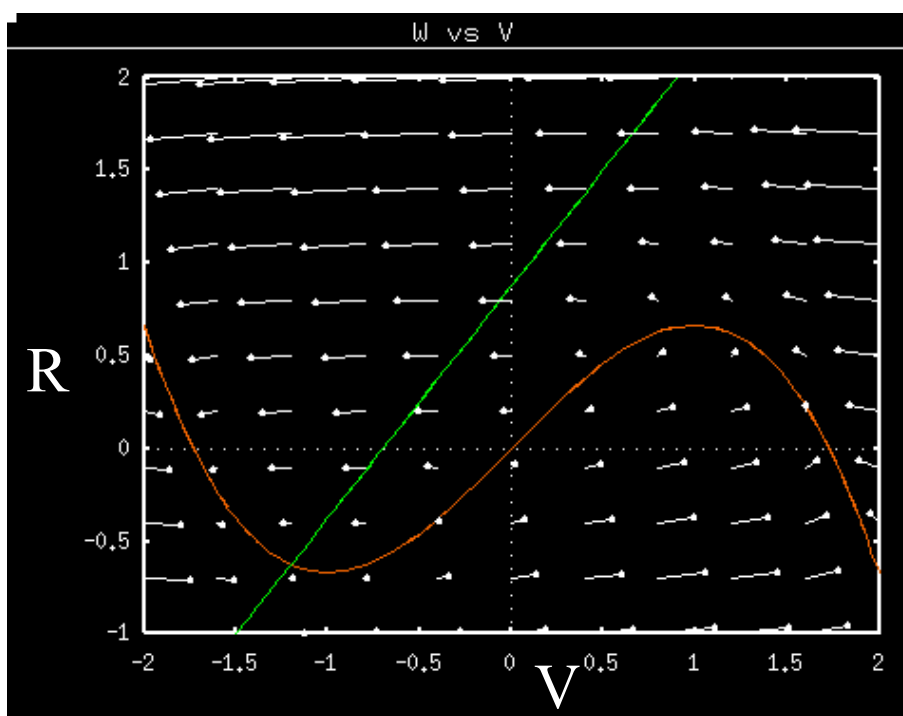
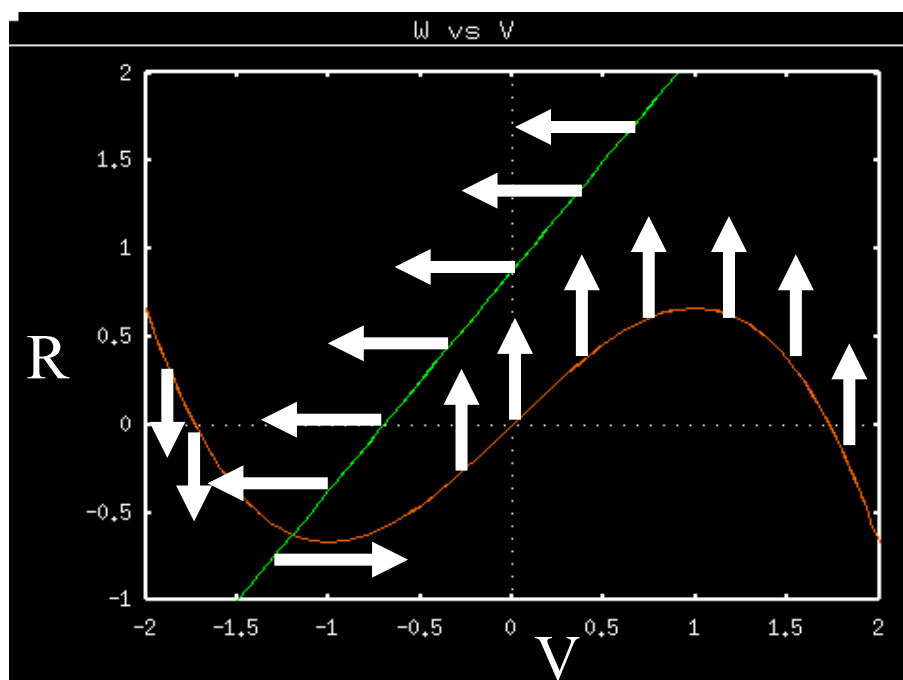


Flow implied by R nullcline

$$\frac{dR}{dt} = \phi(V + a - bR)$$

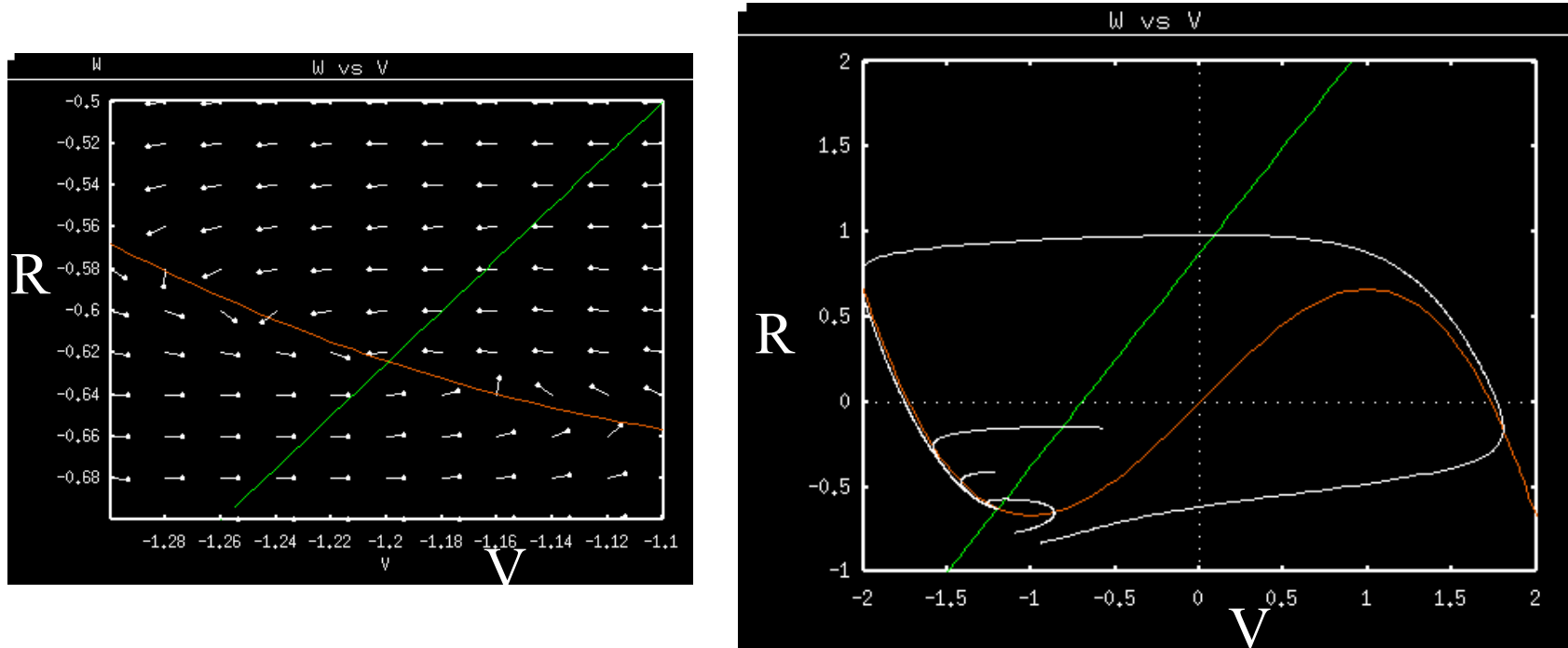






Stability of equilibrium point

For $l=0$, numerically we see:



But which types of equilibrium can we have?

Let us study the neighbourhood of equilibrium point (\bar{V}, \bar{R})

$$\dot{\bar{V}} + \delta \dot{V} = (\bar{V} + \delta V) - (\bar{V} + \delta V)^3 / 3 - (\bar{R} + \delta R) + I_{ext}$$

$$\dot{\bar{R}} + \delta \dot{R} = \phi((\bar{V} + \delta V) + a - b(\bar{R} + \delta R))$$

$$1. \quad \dot{\bar{V}} = 0 \Rightarrow \bar{V} - \bar{V}^3 / 3 - \bar{R} + I_{ext} = 0$$

$$(\bar{V}, \bar{R}) \text{ obeys: } 2. \quad \dot{\bar{R}} = 0 \Rightarrow \bar{V} + a - b\bar{R} = 0$$

$$3. \quad \dot{\bar{V}} = \dot{\bar{R}} = 0$$

Substituting conditions 1, 2 y 3 and taking linear terms only:

$$\delta \dot{V} = (1 - \bar{V}^2) \delta V - \delta R$$

$$\delta \dot{R} = \phi(\delta V - b \delta R)$$

In matrix form:

$$\begin{aligned}\delta \dot{V} &= (1 - \bar{V}^2) \delta V - \delta R \\ \delta \dot{R} &= \phi (\delta V - b \delta R)\end{aligned}\quad \begin{pmatrix} \delta \dot{V} \\ \delta \dot{R} \end{pmatrix} = \begin{pmatrix} 1 - \bar{V}^2 & -1 \\ \phi & -b\phi \end{pmatrix} \begin{pmatrix} \delta V \\ \delta R \end{pmatrix}$$

With solution: $\delta \bar{r}(t) = c_1 \bar{r}_1 \exp(\lambda_1 t) + c_2 \bar{r}_2 \exp(\lambda_2 t)$

with \bar{r}_1, \bar{r}_2 The eigenvectors, c_1, c_2 constants depending on i.c.
and λ_1, λ_2 the eigenvalues of the characteristic equation

$$(1 - \bar{V}^2 - \lambda)(-b\phi - \lambda) + \phi = 0$$

$$\lambda_{1,2} = \frac{1 - \bar{V}^2 - b\phi \pm \left((-1 + \bar{V}^2 + b\phi)^2 - 4b\phi(1 - \bar{V}^2) \right)^{1/2}}{2}$$

The type of solution depends on the eigenvalues

$$\delta \bar{r}(t) = c_1 \bar{r}_1 \exp(\lambda_1 t) + c_2 \bar{r}_2 \exp(\lambda_2 t)$$

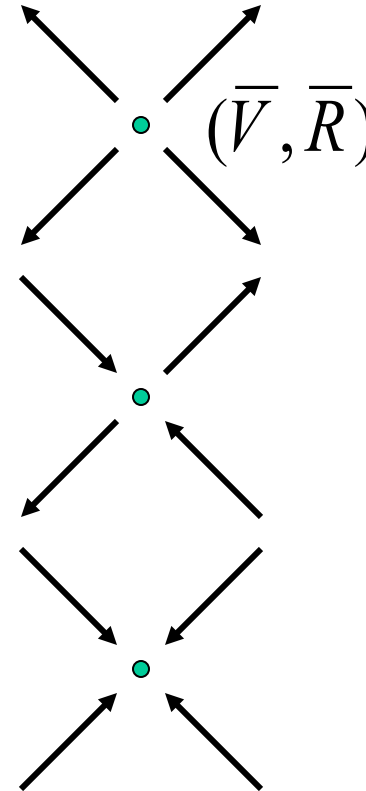
$$\lambda_{1,2} = \frac{1 - \bar{V}^2 - b\phi \pm \left((-1 + \bar{V}^2 + b\phi)^2 - 4b\phi(1 - \bar{V}^2) \right)^{1/2}}{2}$$

Types of solutions:

1. "Origin": $\lambda_1 > 0$ $\lambda_2 > 0$

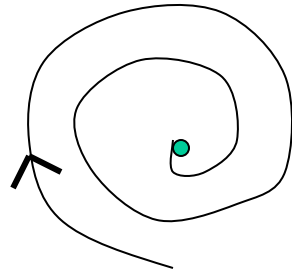
2. "Saddle": $\lambda_1 > 0$ $\lambda_2 < 0$

3. "Node": $\lambda_1 < 0$ $\lambda_2 < 0$



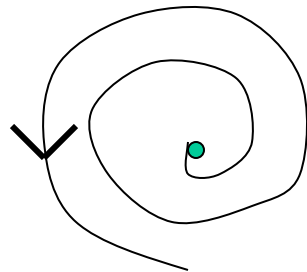
4. “Spiral” or “Attractor”:

$$\lambda_{1,2} = \alpha \pm i\omega \quad ; \quad \alpha < 0$$



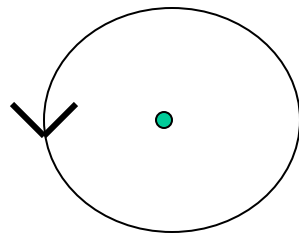
5. “Unstable spiral” or “focus”:

$$\lambda_{1,2} = \alpha \pm i\omega \quad ; \quad \alpha > 0$$



6. “Center”:

$$\lambda_{1,2} = \alpha \pm i\omega \quad ; \quad \alpha = 0$$

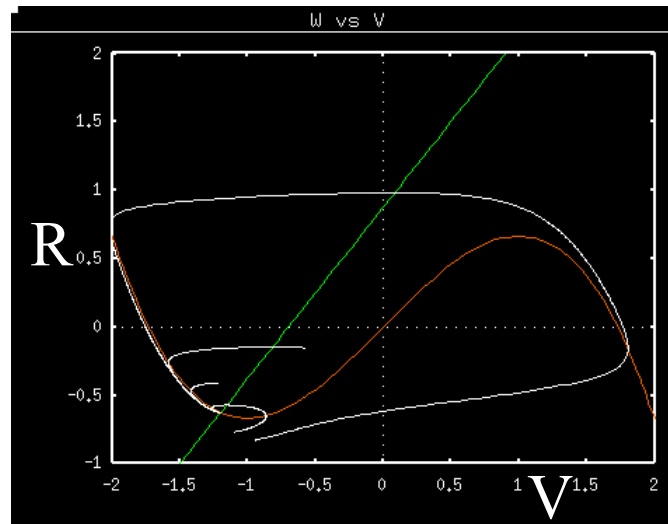
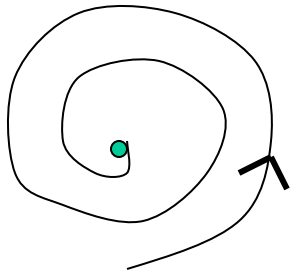


So what do we get in FitzHugh-Nagumo?

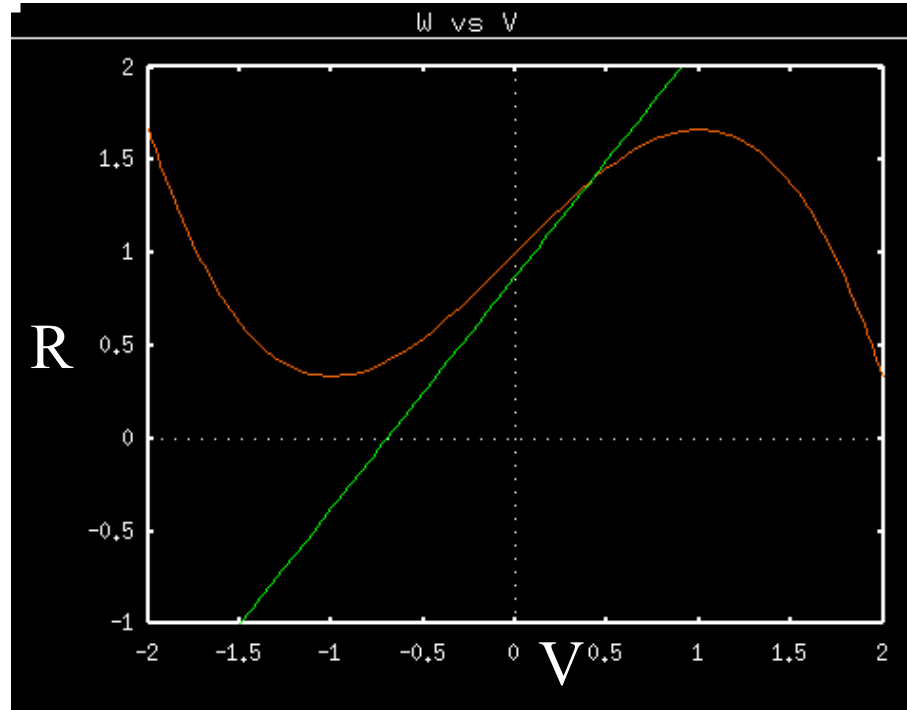
(a) $I_{\text{ext}}=0$

$$(\bar{V}, \bar{R}) = (-1.2, -0.625)$$

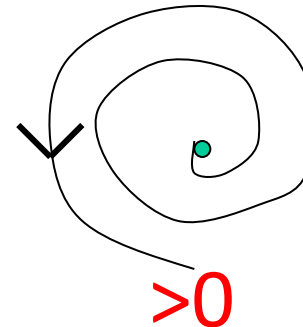
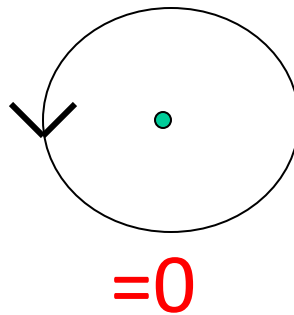
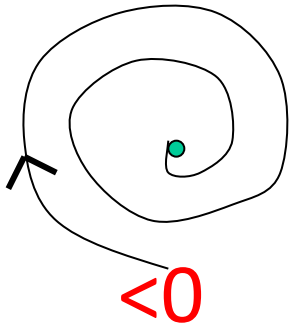
$$\lambda_{1,2} = \frac{1 - \bar{V}^2 - b\phi \pm \left((-1 + \bar{V}^2 + b\phi)^2 - 4b\phi(1 - \bar{V}^2) \right)^{1/2}}{2} = -0.5 \pm 0.42i$$



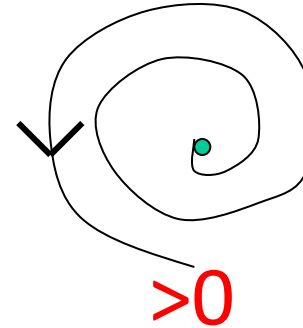
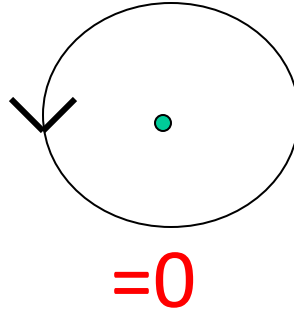
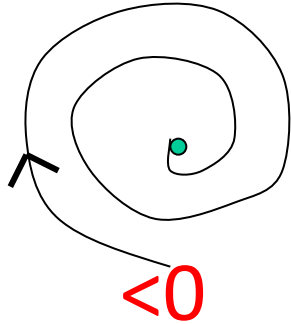
(b) $I_{\text{ext}} > 0$



$$\lambda_{1,2} = \frac{1 - \bar{V}^2 - b\phi \pm \left((-1 + \bar{V}^2 + b\phi)^2 - 4b\phi(1 - \bar{V}^2) \right)^{1/2}}{2}$$



$$\lambda_{1,2} = \frac{1 - \bar{V}^2 - b\phi \pm \left((-1 + \bar{V}^2 + b\phi)^2 - 4b\phi(1 - \bar{V}^2) \right)^{1/2}}{2}$$

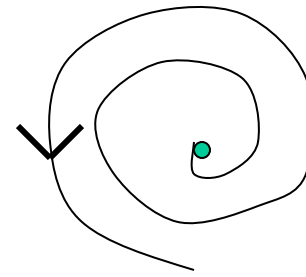
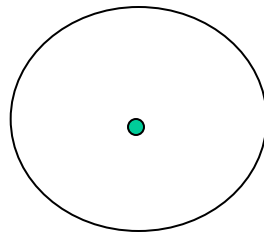
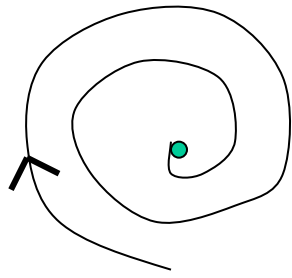


$$\bar{V}_{\pm} = \pm(1 - b\phi)^{1/2} = \pm 0.967$$

Sustituyendo en $\frac{dV}{dt} = 0 \Rightarrow R = V - V^3 / 3 + I_{ext}$

$$\frac{dR}{dt} = 0 \Rightarrow R = \frac{V + a}{b}$$

Obtenemos $I_- = 0.3313$ $I_+ = 1.42$



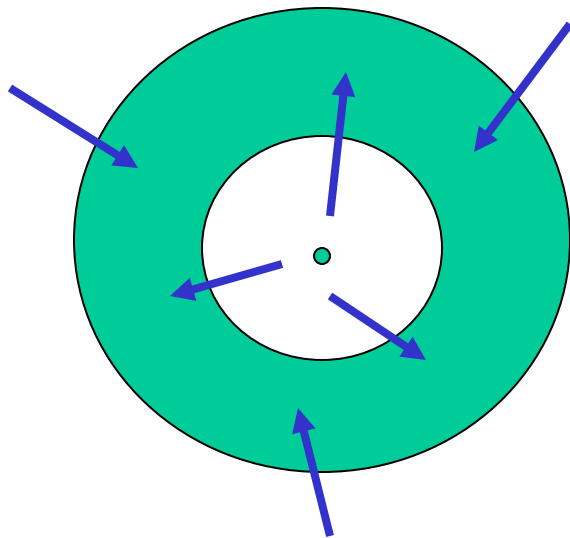
$l=0.3313$

l_{ext}

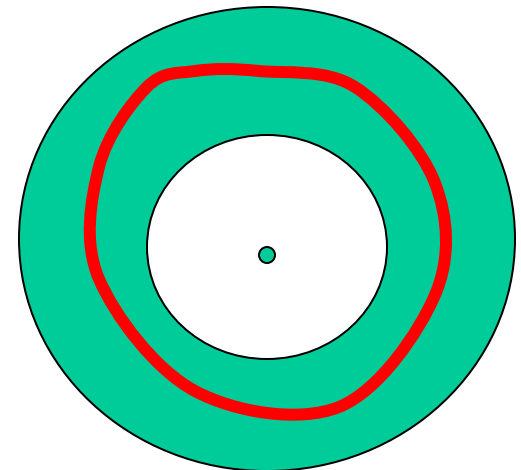
What type of solution for $l > 0.3313$?

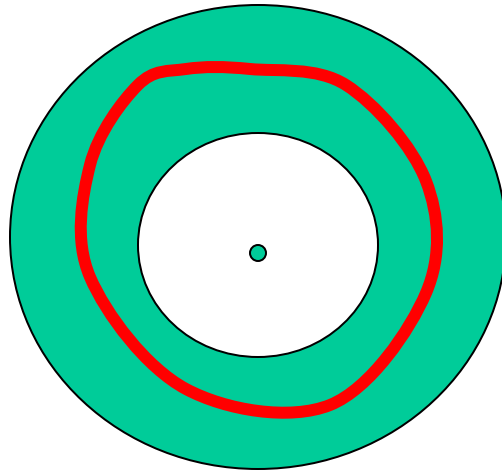
Poincaré-Bendixon theorem:

If

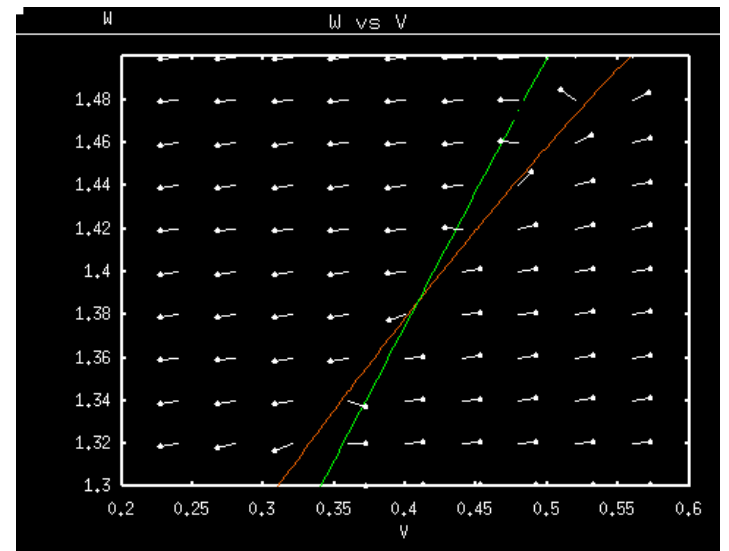
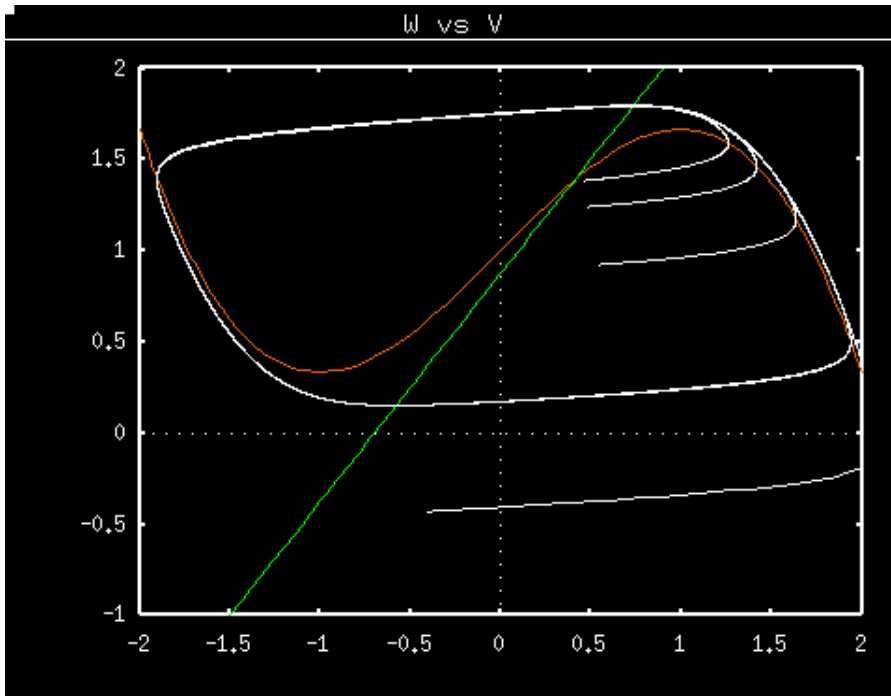


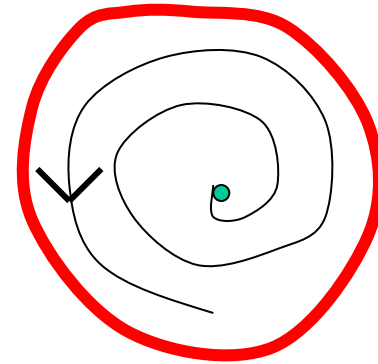
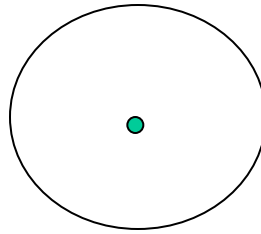
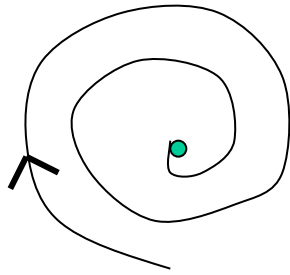
then





$l=1$



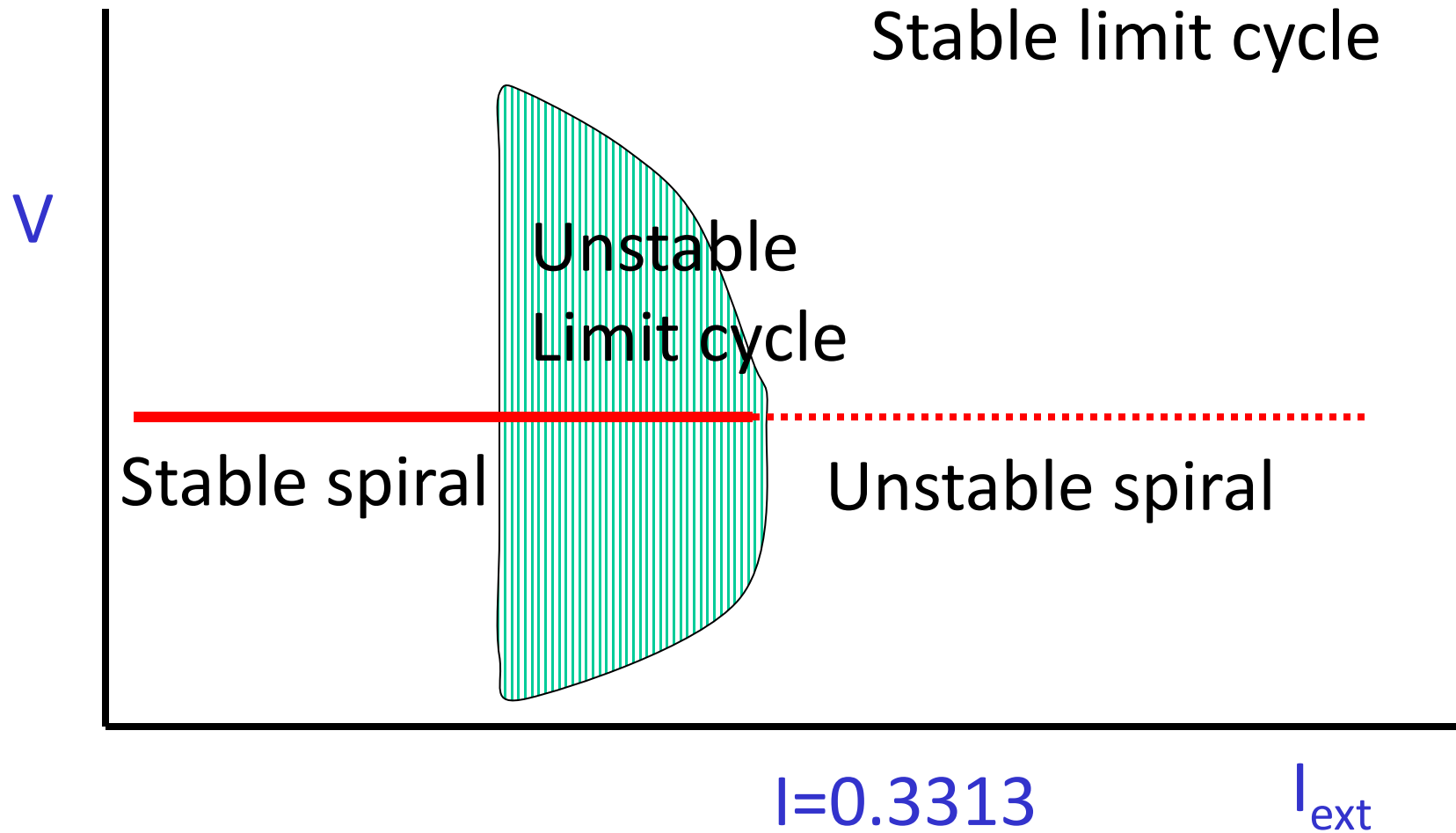


$I=0.3313$

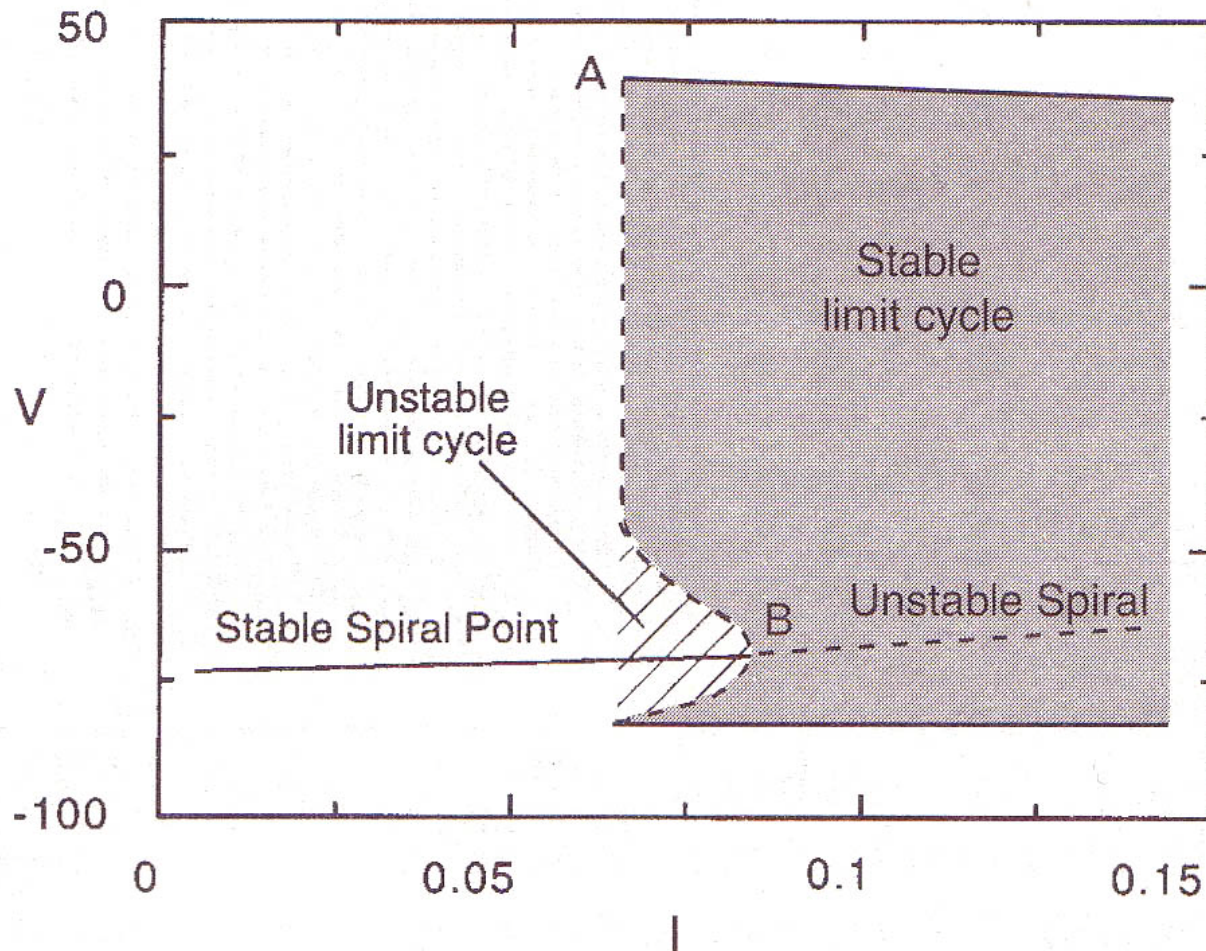
I_{ext}

Large oscillations (action potentials) suddenly appear at $I=0.3313$
→ Subcritical Hopf bifurcation

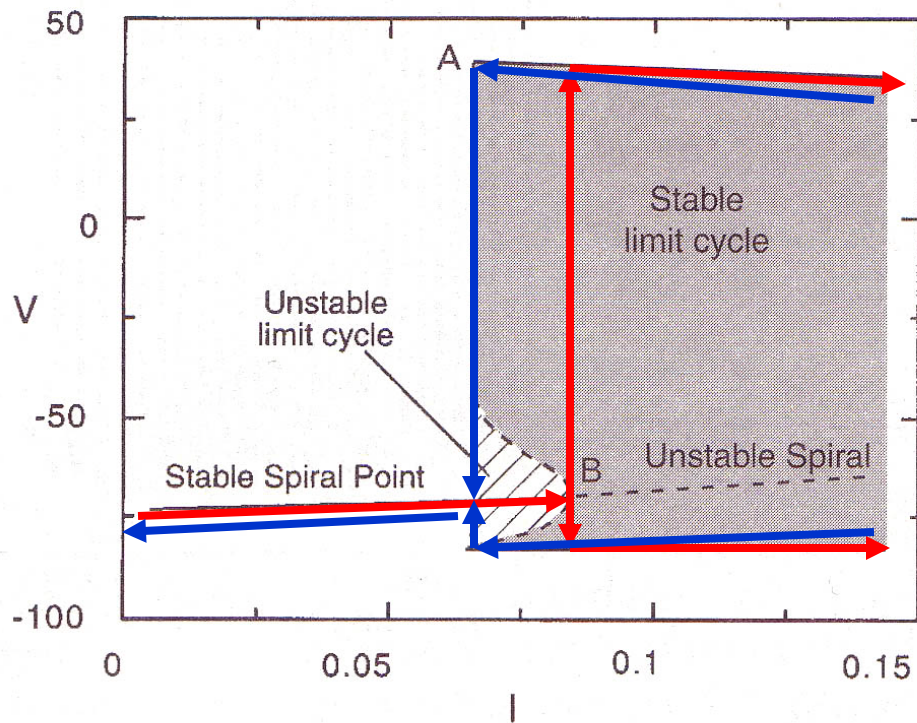
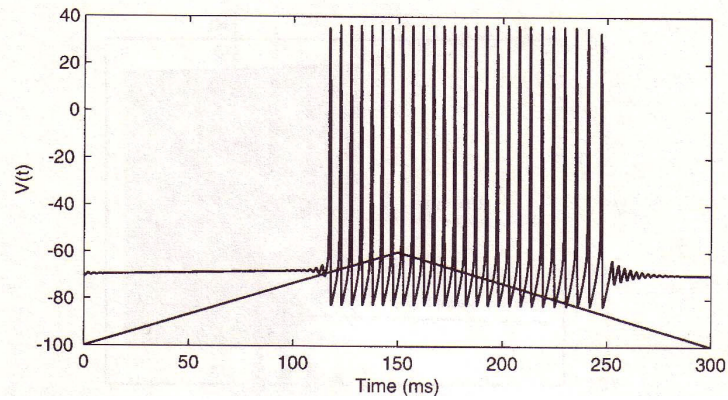
Subcritical Hopf bifurcation



Bifurcation diagram of Wilson model



Hysteresis in an axon



1. HH model
2. Simplifications of HH model
 - 2.1. Rinzel model
 - 2.2. Wilson model
 - 2.3. FitzHugh-Nagumo model
3. Adaptation and bursts
4. Networks

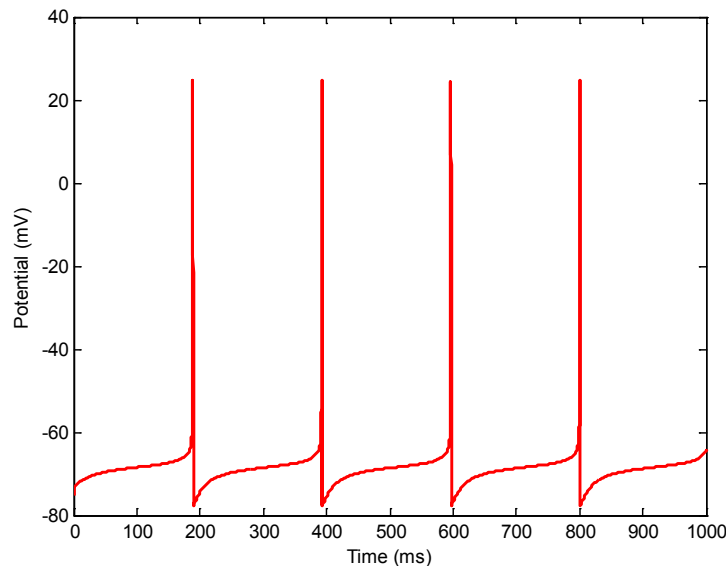
Low frequency firing (class I neuron)

Squid axon fires at 150-300 AP/sec.

Potassium current I_A allows for much lower firing rates

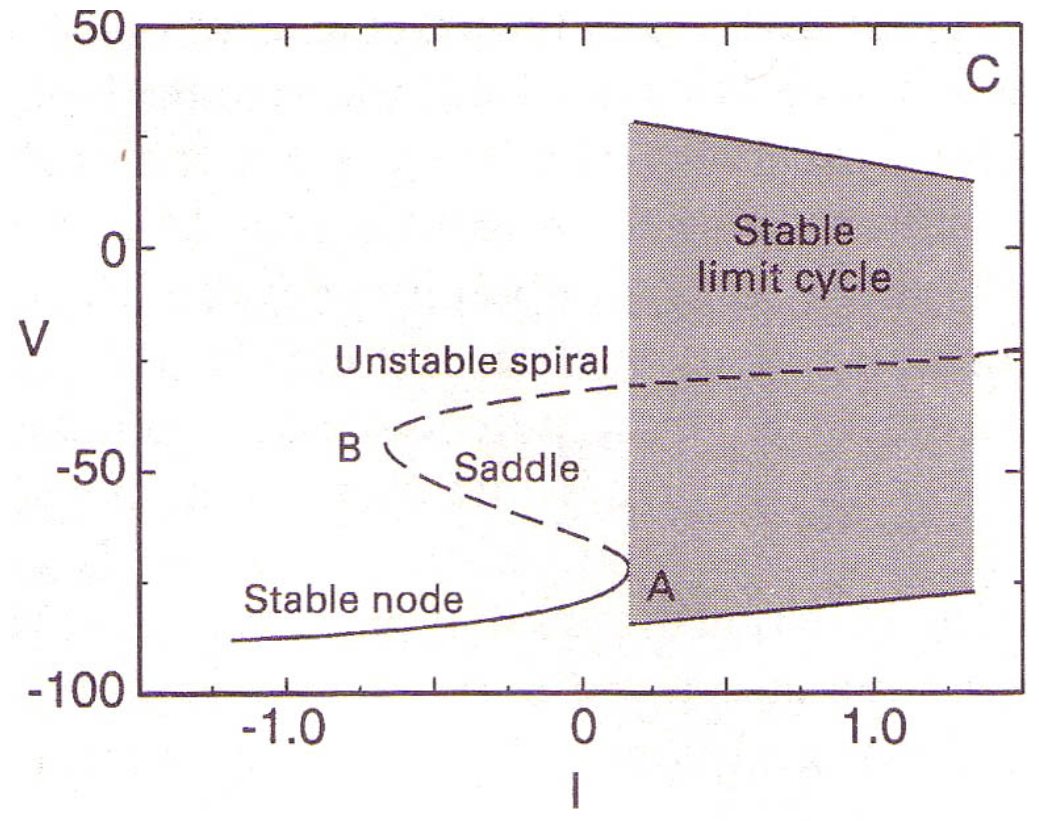
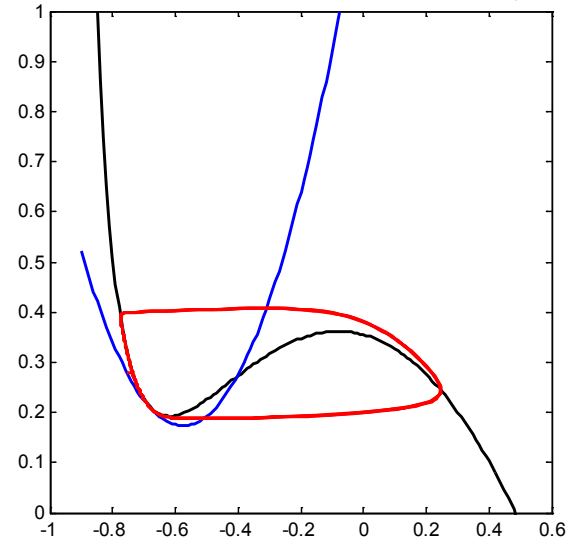
$$\frac{dV}{dt} = -(17.81 + 47.58V + 33.8V^2)(V - 0.48) - 26R(V + 0.95) + I_{ext}$$

$$\frac{dR}{dt} = \frac{1}{5.6} (-R + 1.29V + 0.79 + 3.3(V + 0.38)^2)$$



$$I = 0.25 \text{ nA}$$

$dV/dt = 0$ isocline (black), $dR/dt = 0$ isocline (blue) & limit cycle (red)



Adaptation of firing rates

Squid axon fires without adaptation.

Potassium current I_{AHP} (afterhyperpolarization):

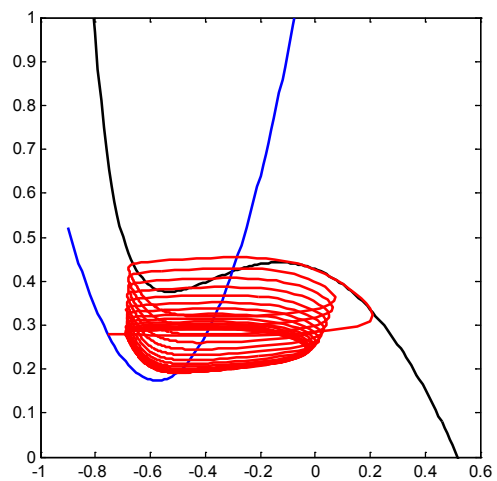
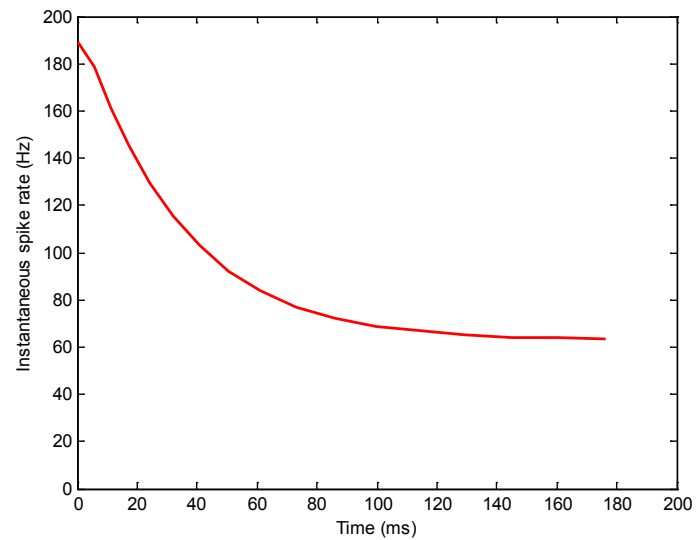
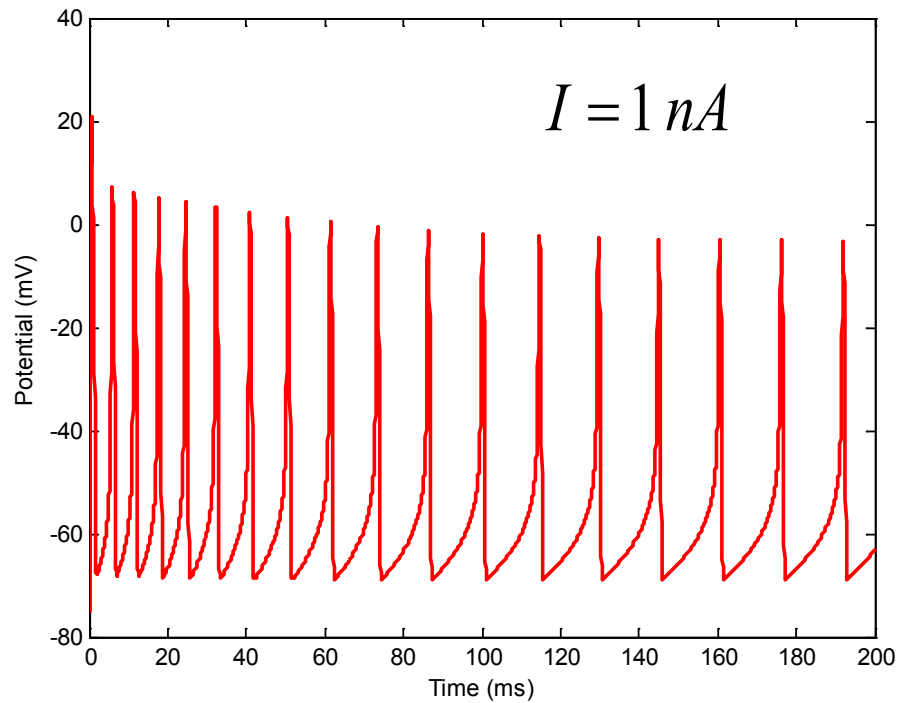
1. Slow: 99 ms (does not affect AP shape)
2. Acts only when the neuron is firing (zero at -0.754)
3. Its job is to eliminate the effect of I_{ext}

$$\frac{dV}{dt} = -(17.81 + 47.58V + 33.8V^2)(V - 0.48) - 26R(V + 0.95)$$

$$-13H(V + 0.95) + I_{\text{ext}}$$

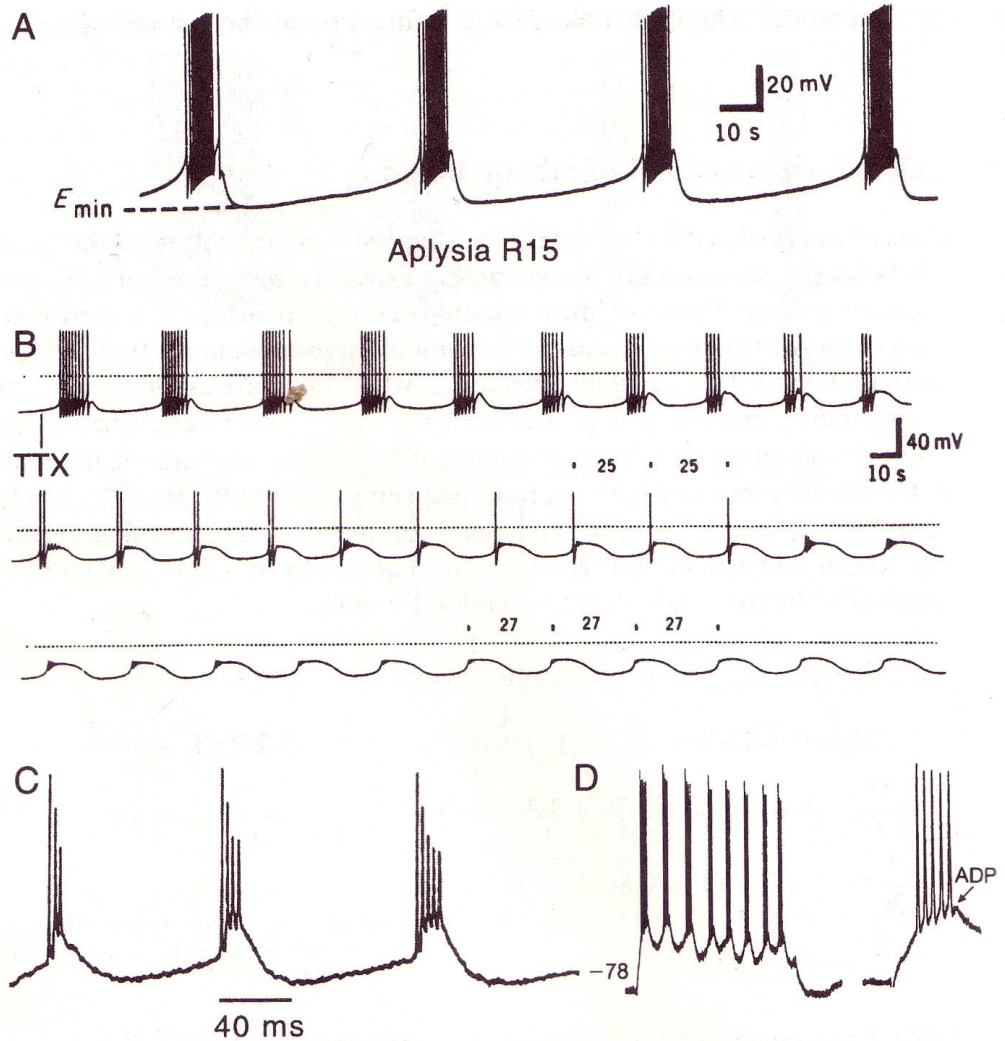
$$\frac{dR}{dt} = \frac{1}{5.6} (-R + 1.29V + 0.79 + 3.3(V + 0.38)^2)$$

$$\frac{dH}{dt} = \frac{1}{99} (-H + 11(V + 0.754)(V + 0.69))$$



Firing in burts

Examples



Neuron R15
in Aplysia

Applying
TTX to R15

Cortical neurons

Model for bursty neuron

2 currents:

Corriente de potasio I_{AHP} (afterhyperpolarization, dependiente de calcio)

Corriente de calcio I_{T} (depolarización)

$$\frac{dV}{dt} = -(17.81 + 47.58V + 33.8V^2)(V - 0.48) - 26R(V + 0.95) - 1.93X(1 - 0.5C)(V - 1.4) - 3.25C(V + 0.95)$$

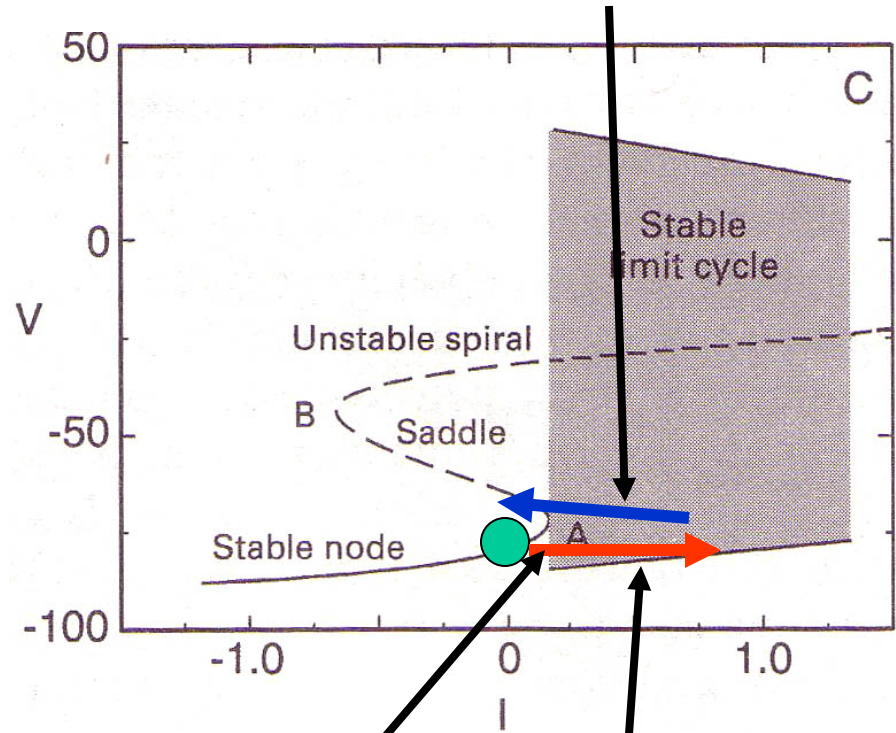
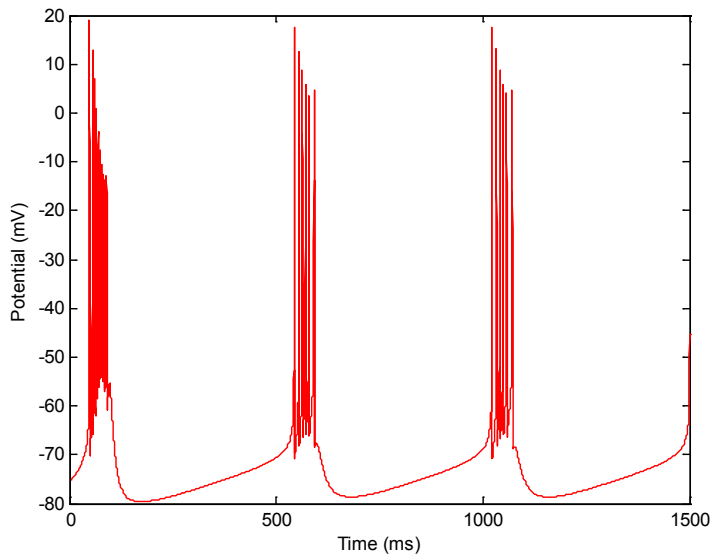
I_{T} I_{AHP}

$$\frac{dR}{dt} = \frac{1}{5.6}(-R + 1.29V + 0.79 + 3.3(V + 0.38)^2)$$

$$\frac{dX}{dt} = \frac{1}{30}(-X + 7.33(V + 0.86)(V + 0.84))$$

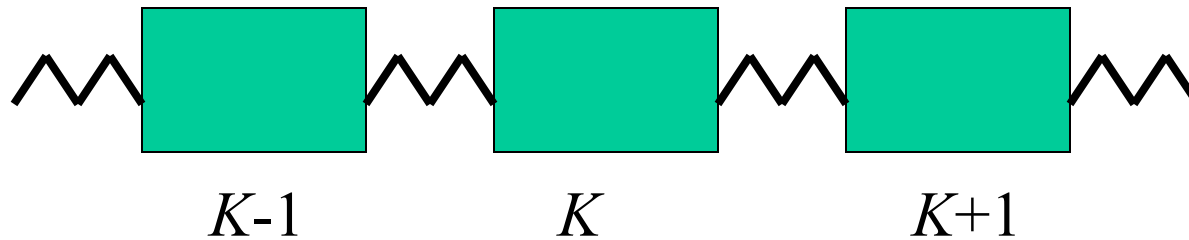
$$\frac{dC}{dt} = \frac{1}{100}(-C + 3X) \quad \text{Concentración de calcio}$$

C increases &
V decreases &
X inactivates



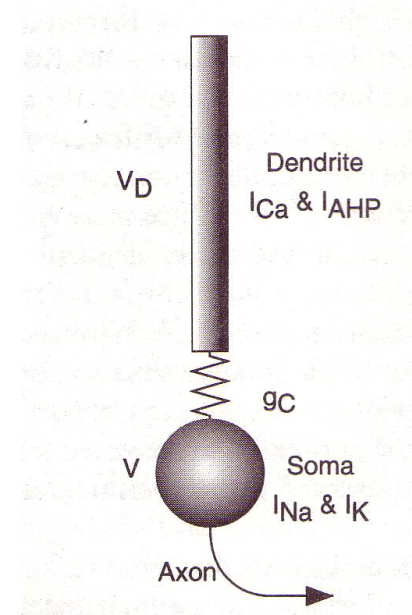
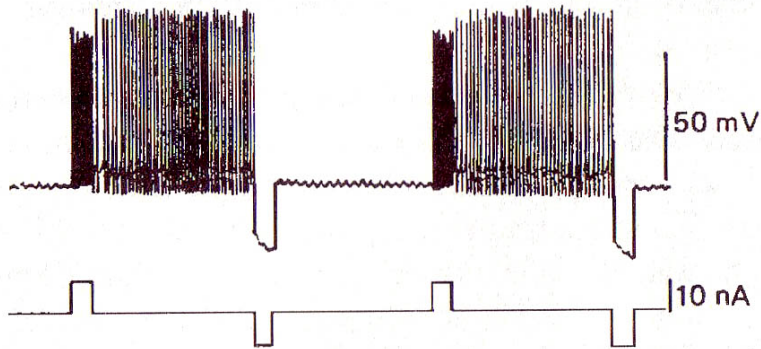
X increases V Firing

Compartments



$$C \frac{dV_K}{dt} = \sum_{j=1}^N I_j + g_{K-1,K} (V_{K-1} - V_K) + g_{K,K+1} (V_{K+1} - V_K)$$

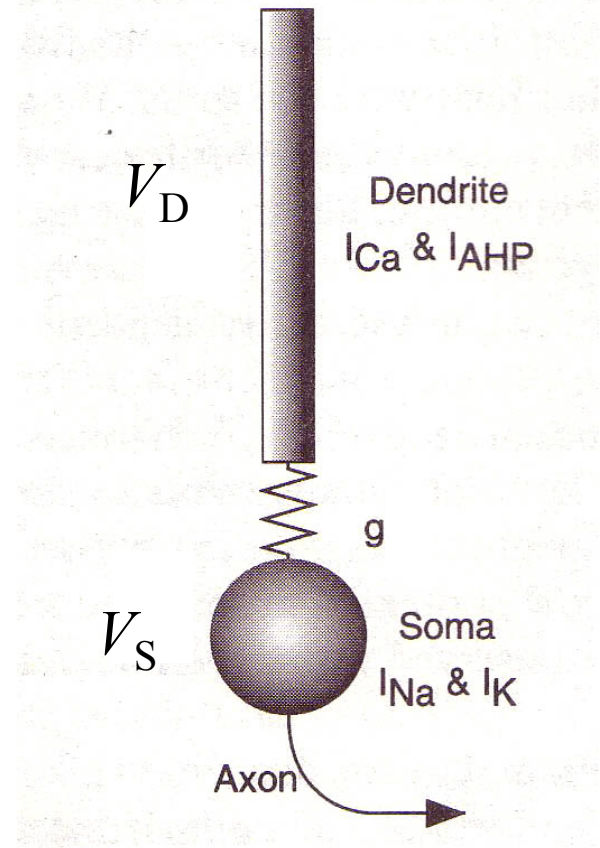
Example: dendrite+soma



$$C_S \frac{dV_S}{dt} = -I_{Na^+} - I_{K^+} + I_{ext} + \frac{g}{p} (V_D - V_S)$$

$$C_D \frac{dV_D}{dt} = -I_{Ca^{2+}} - I_{AHP} + \frac{g}{1-p} (V_S - V_D)$$

p : proporción de membrana en el soma



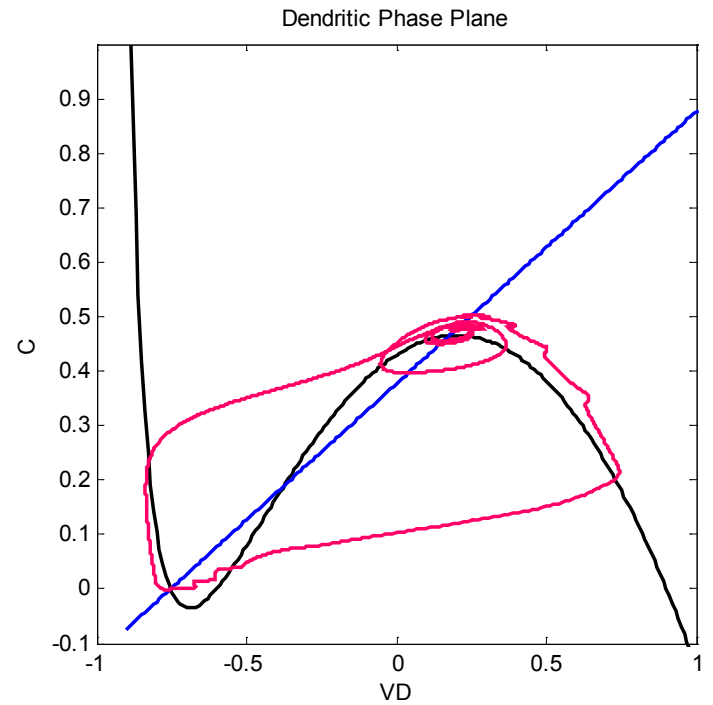
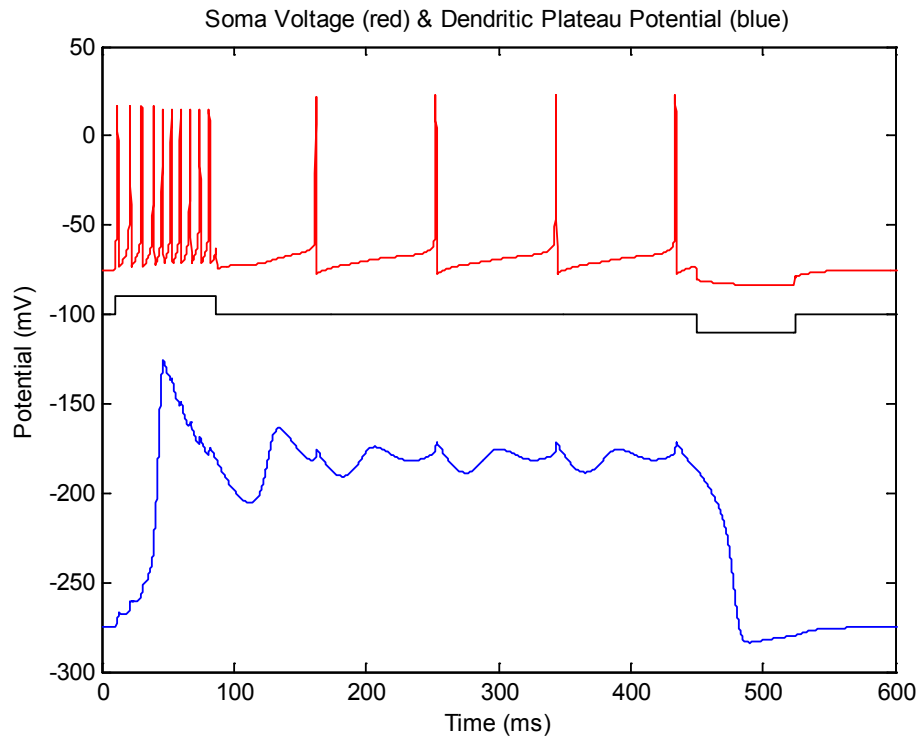
$$\frac{dV_S}{dt} = -(17.81 + 47.58 V_S + 33.8 V_S^2)(V_S - 0.48) - 26R(V_S + 0.95) + I_{ext} + \frac{g}{p}(V_D - V_S)$$

$$\frac{dR}{dt} = \frac{1}{5.6}(-R + 1.29 V_S + 0.79 + 3.3(V_S + 0.38)^2)$$

$$\frac{dV_D}{dt} = -(V_D + 0.754)(V_D + 0.7)(V_D - 1.0) - g_{AHP} C (V_D + 0.95) + \frac{g}{1-p}(V_S - V_D)$$

$$\frac{dC}{dt} = \frac{1}{20}(-C + 0.5(V_D + 0.754))$$

For $g_{\text{AHP}}=1.0$, $g=0.1$, $p=0.37$



A very simple model of a synapsis



$$C \frac{dV_{post}}{dt} = \sum_{j=1}^N I_j + k g_{syn} (V_{post} - E_{syn}) \quad ; \quad E_{syn} = \begin{cases} 0 & (exc) \\ -0.92 & (inh) \end{cases}$$

Post-synaptic factor

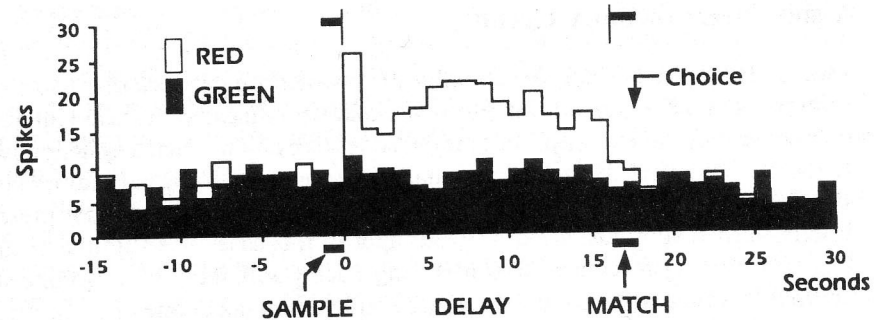
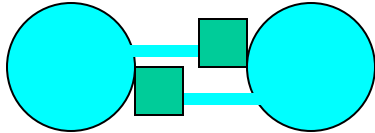
Synaptic conductance

$$\frac{dg_{syn}}{dt} = \frac{1}{\tau_{syn}} (-g_{syn} + f)$$

$$\frac{df}{dt} = \frac{1}{\tau_{syn}} (-f + H(V_{pre} - \Theta)) \quad ; \quad H(X) = \begin{cases} 0 & X \leq 0 \\ 1 & X > 0 \end{cases}$$

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 - 2.2. Wilson model
 - 2.3. FitzHugh-Nagumo model
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Simple memory circuit



$$\dot{E}_1 = \frac{1}{\tau} (-E_1 + S(3E_2; 100, 2, 120))$$

τ : 20ms

$$\dot{E}_2 = \frac{1}{\tau} (-E_2 + S(3E_1; 100, 2, 120))$$

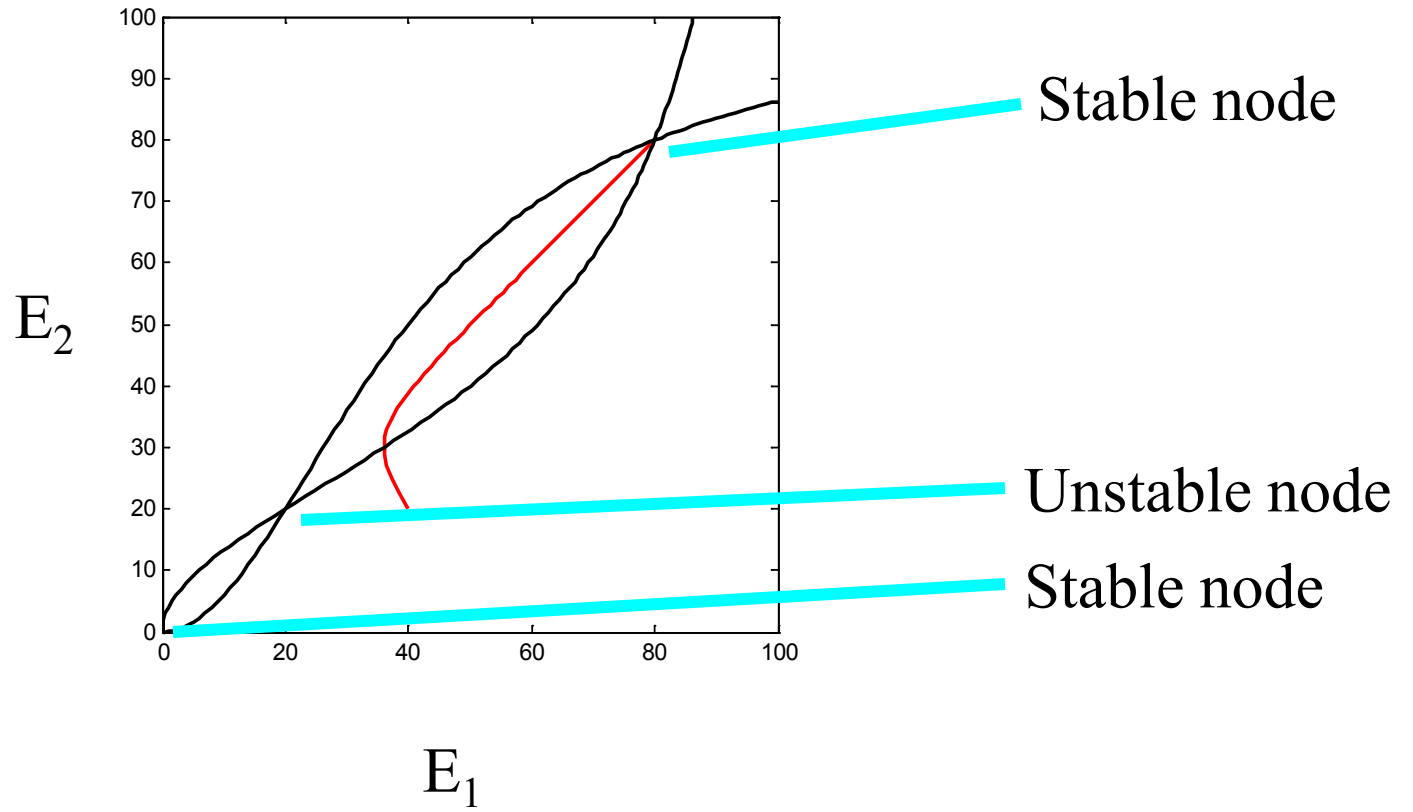
Synaptic weight: 3

$$S(P; M, N, \sigma) = \frac{MP^N}{\sigma^N + P^N}$$

M: maximum firing rate

N: determines maximum slope

σ : point with $S(P)/2$

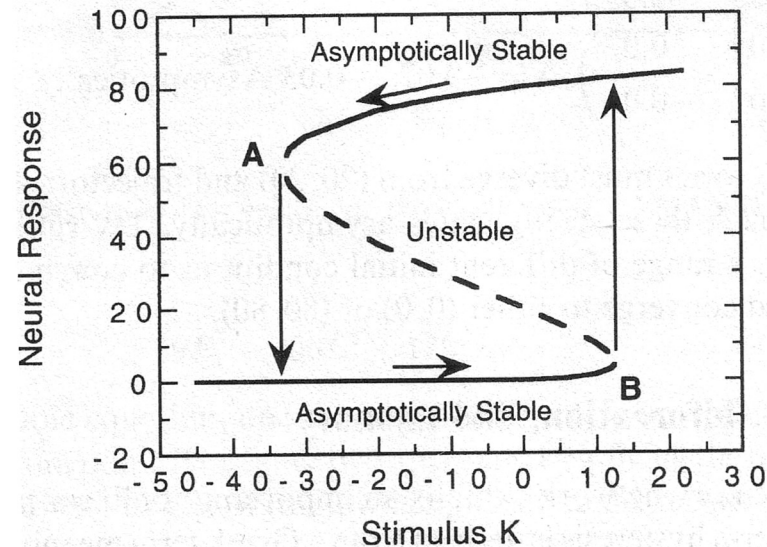


Memory and hysteresis

$$\dot{E}_1 = \frac{1}{\tau} \left(-E_1 + S(3E_2 + K; 100, 2, 120) \right)$$

$$\dot{E}_2 = \frac{1}{\tau} \left(-E_2 + S(3E_1 + K; 100, 2, 120) \right)$$

K : stimulus



Memory decay by adaptation

Adaptation thorough an increase of σ

$$\dot{E}_1 = \frac{1}{\tau} (-E_1 + S(3E_2; 100, 2, 120 + A_1))$$

τ : 20ms

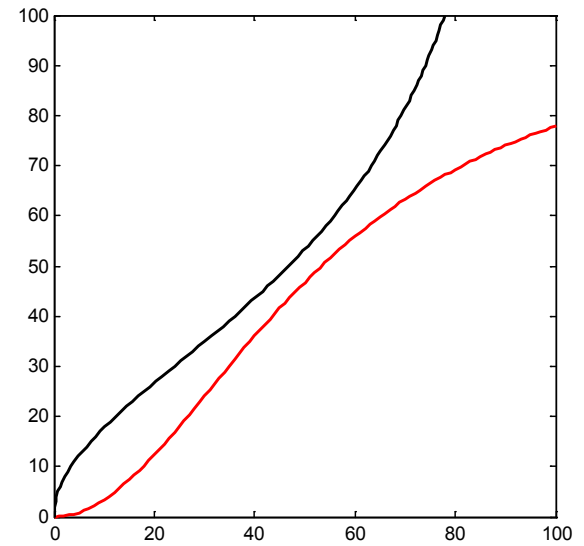
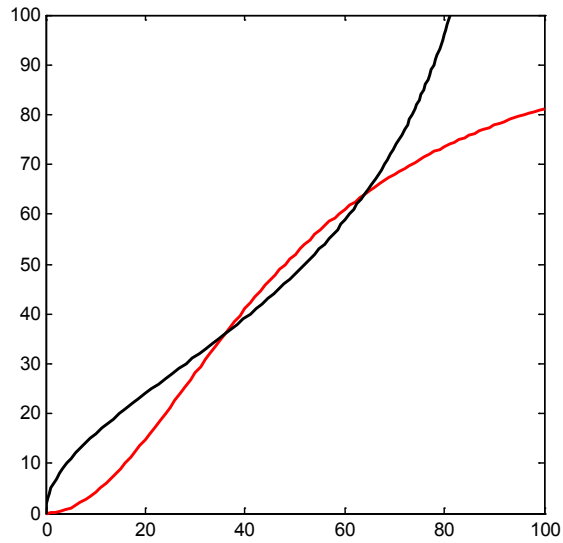
$$\dot{E}_2 = \frac{1}{\tau} (-E_2 + S(3E_1; 100, 2, 120 + A_2))$$

τ_a : 4000ms

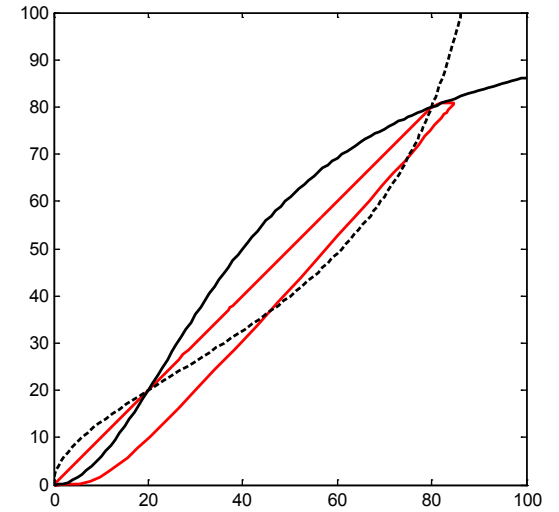
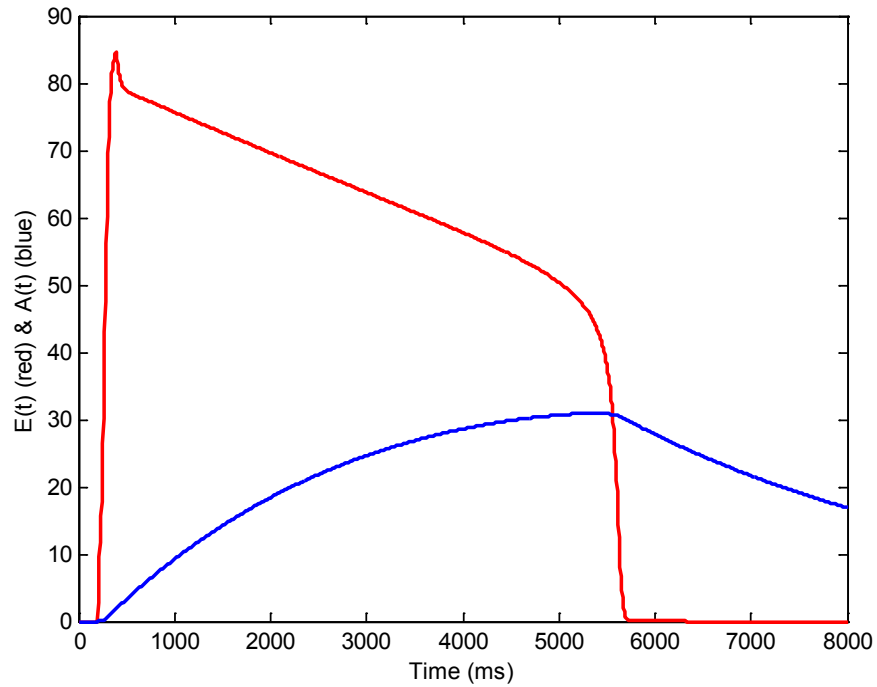
$$\dot{A}_1 = \frac{1}{\tau_a} (-A_1 + 0.7E_1)$$

$$\dot{A}_2 = \frac{1}{\tau_a} (-A_2 + 0.7E_2)$$

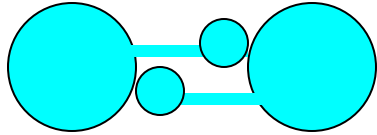
Adaptation affects nullclines



$K=50$ for 200ms and then $K=0$



Competition and decisions by neurons

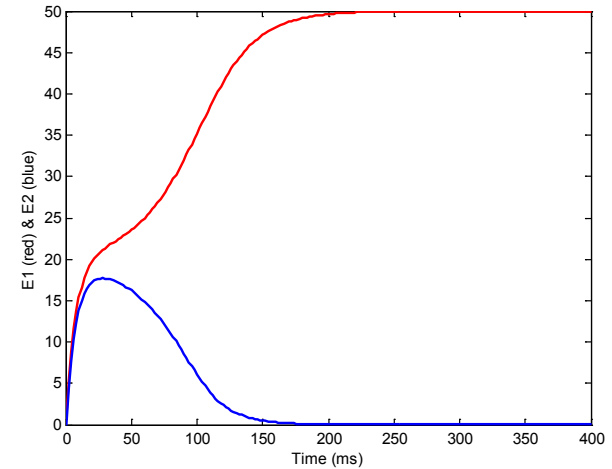
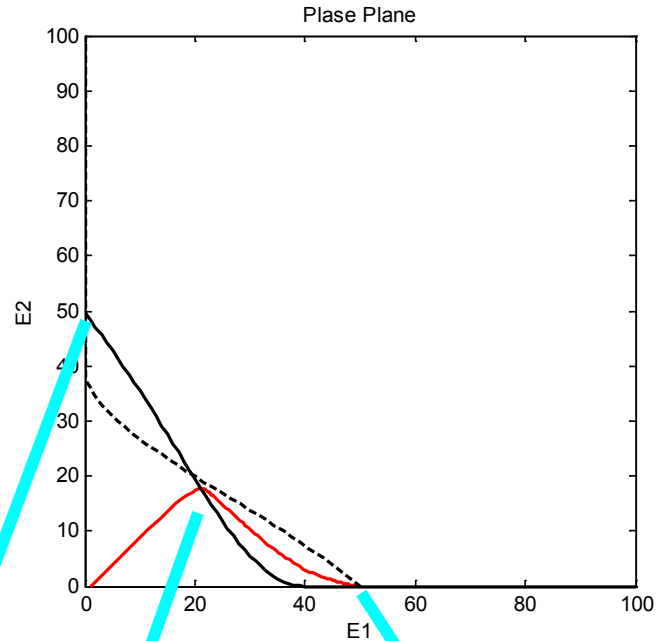


$$\dot{E}_1 = \frac{1}{\tau} (-E_1 + S(K_1 - 3E_2; 100, 2, 120))$$

$$\dot{E}_2 = \frac{1}{\tau} (-E_2 + S(K_2 - 3E_1; 100, 2, 120))$$

$$S(P; M, N, \sigma) = \frac{MP^N}{\sigma^N + P^N}$$

Wins the neuron receiving more stimulation (WTA)

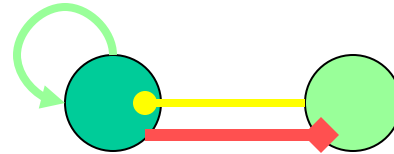
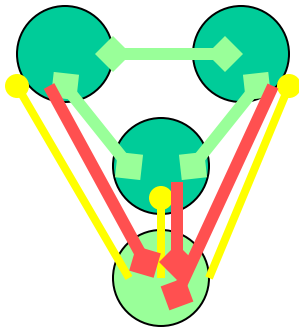


Stable node

Saddle (unstable)

Stable node

Oscillatory network (Wilson-Cowan)

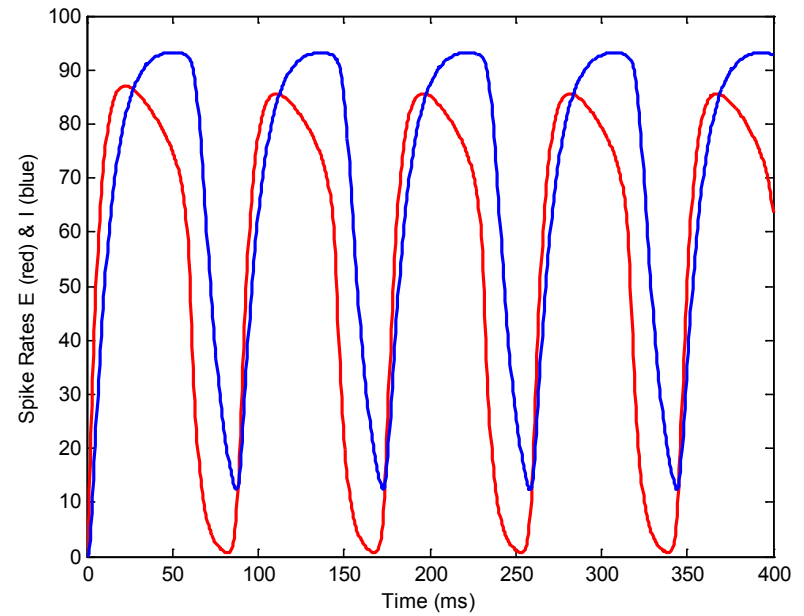
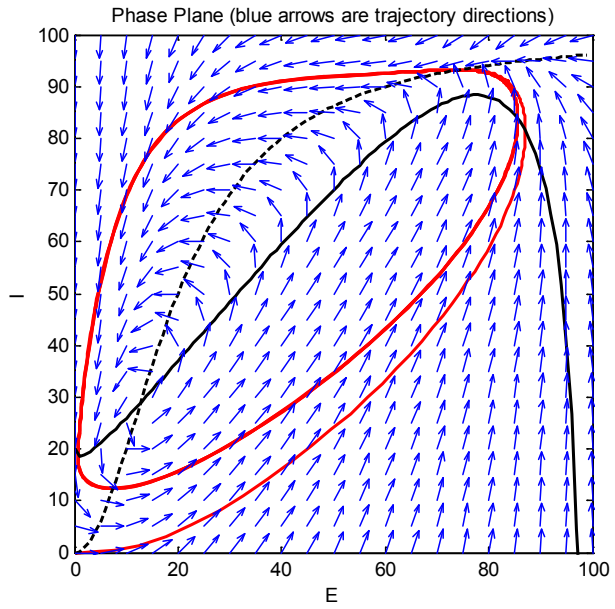


Reduced system doing the same when
Excitatory neurons receive and send with same
weights

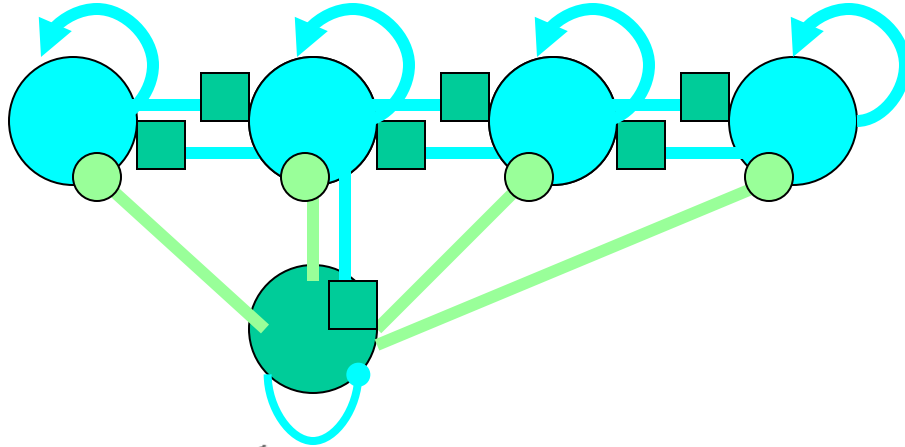
$$\dot{E} = \frac{1}{5}(-E + S(1.6E - I + K; 100, 2, 30))$$

$$\dot{I} = \frac{1}{10}(-I + S(1.5E; 100, 2, 30))$$

$K=20$



Cortical dynamics of Wilson-Cowan type



$$\dot{E}(x) = \frac{1}{\tau} \left(-E(x) + S \left(\sum_x w_{EE} E(x) - \sum_x w_{IE} I(x) + P(x); 100, 2, \sigma_E \right) \right)$$

$$\dot{I}(x) = \frac{1}{\tau} \left(-I(x) + S \left(\sum_x w_{EI} E(x) - \sum_x w_{II} I(x) + Q(x); 100, 2, \sigma_I \right) \right)$$

$$w_{ij} = b_{ij} \exp(-|x - x'| / \sigma_{ij})$$

$$\sigma_{EE} = 40 \mu\text{m}; \sigma_{IE} = \sigma_{EI} = 60 \mu\text{m}; \sigma_{II} = 30 \mu\text{m};$$

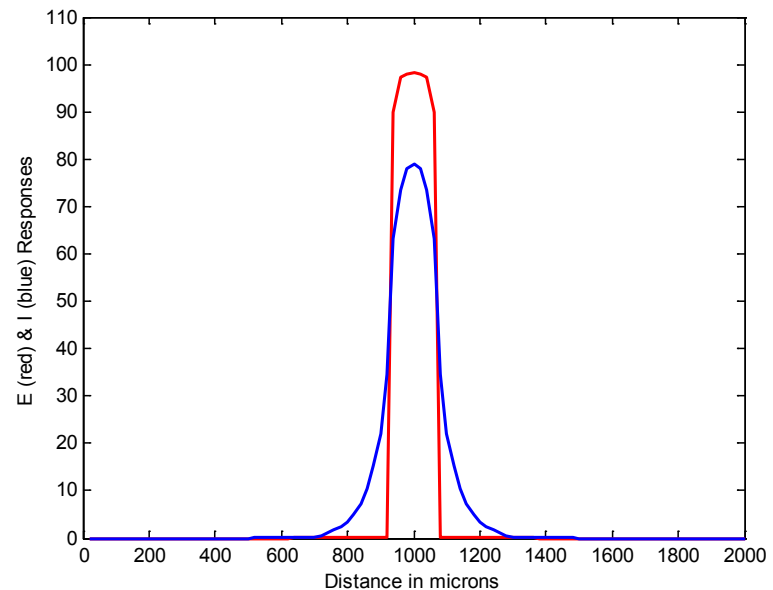
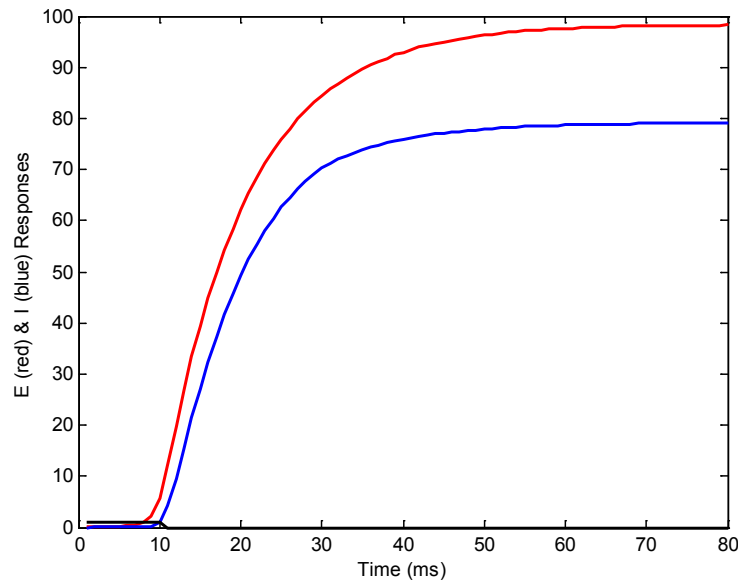
$$\sigma_E = 20; \sigma_I = 40;$$

$$b_{EI} = b_{IE}$$

Memory mode of Wilson-Cowan model

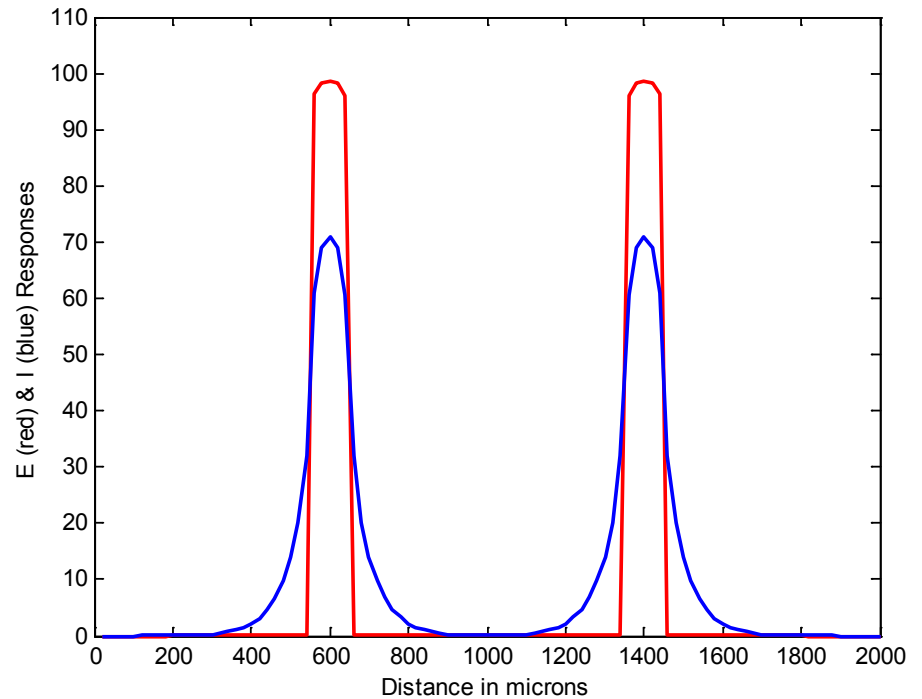
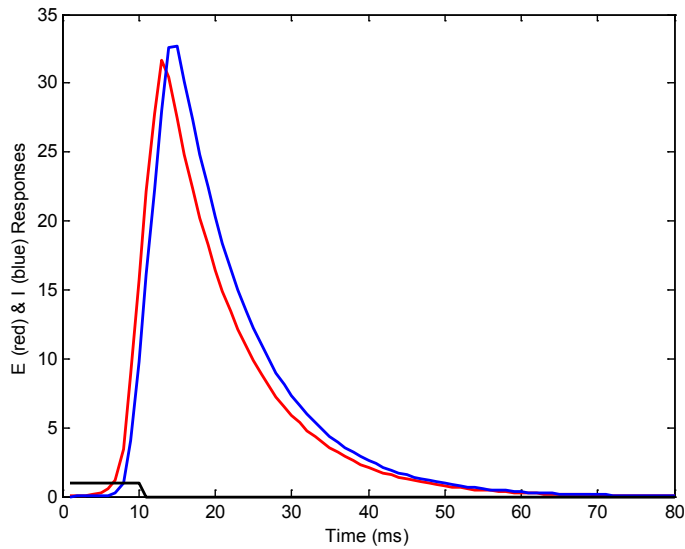
$$b_{EE} = 1.95, b_{EI} = 1.4, b_{II} = 2.2$$

Stimulus of value $P=1$ for 10ms and affecting $100\mu\text{m}$



$$b_{EE} = 1.95, b_{EI} = 1.4, b_{II} = 2.2$$

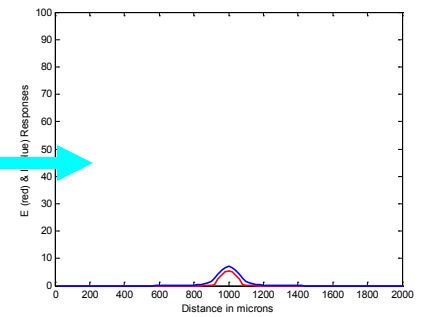
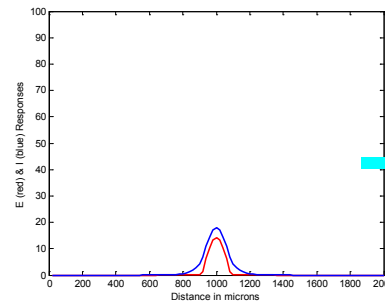
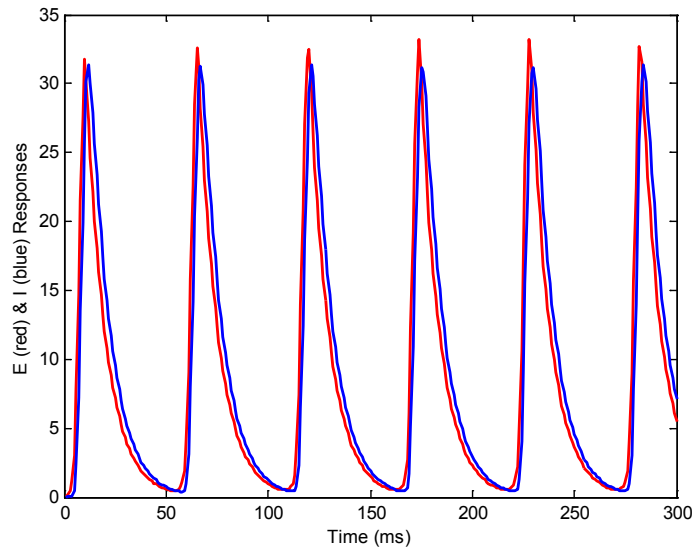
Stimulus of value $P=1$ for 10ms and affecting $1000\mu\text{m}$



Oscillations in a localized region

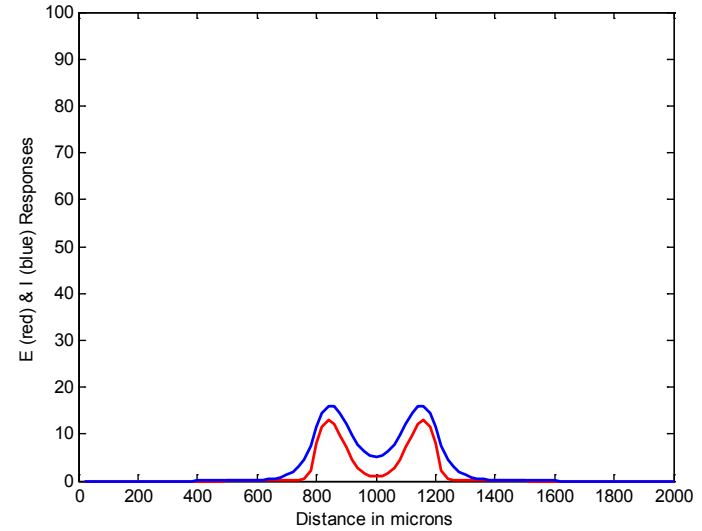
$$b_{EE} = 1.9, b_{EI} = 1.5, b_{II} = 1.5$$

Intensity of stimulus of $P=1$ for 5ms and a width of $100\mu\text{m}$



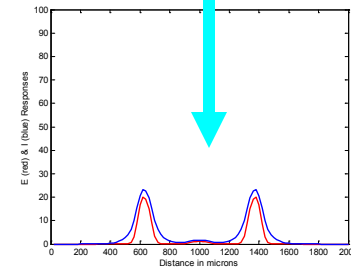
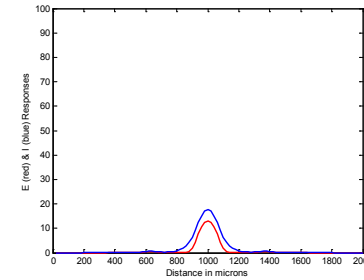
$$b_{EE} = 1.9, b_{EI} = 1.5, b_{II} = 1.5$$

Stimulus of intensity $P=1$
for 5ms and a width of $400\mu\text{m}$



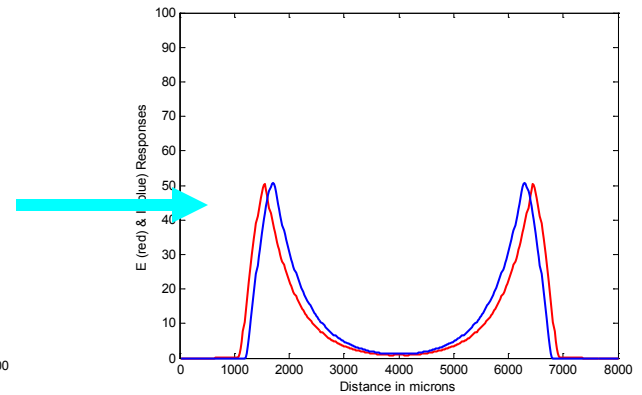
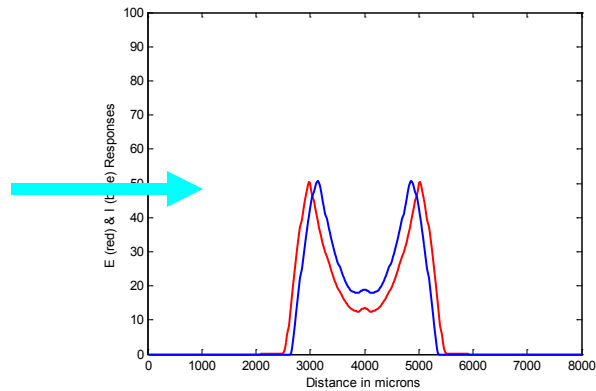
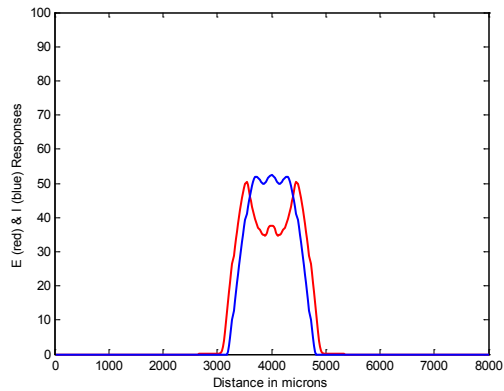
$$b_{EE} = 1.9, b_{EI} = 1.5, b_{II} = 1.5$$

Stimulus of intensity $P=1$
for 5ms and a width of $800\mu\text{m}$



Travelling waves mode (epilepsia)

As in oscillatory mode but with $Q=-90$ (inhibition gets reduced)



Visual hallucinations

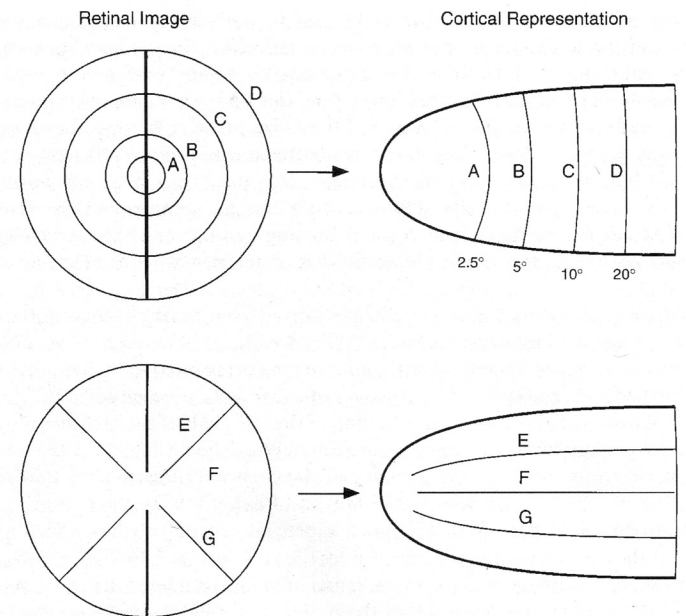
Extension of WC to 2D with more weight among excitatory neurons

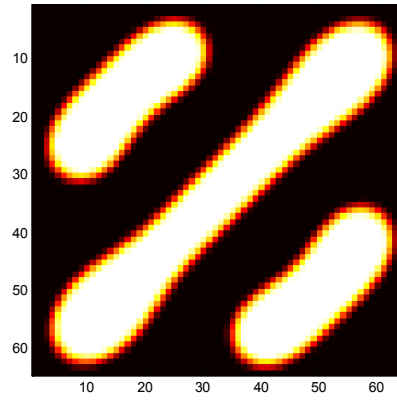
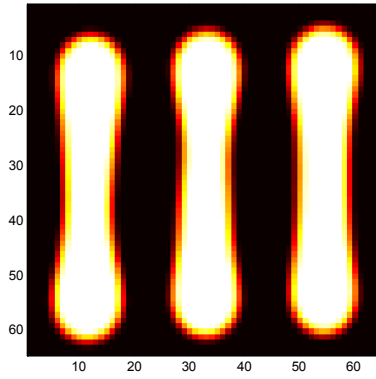
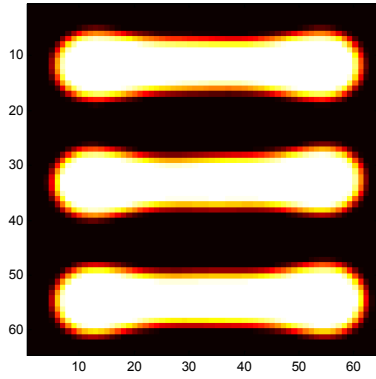
Remember that polar coordinates in retina (R, θ) are transformed to cortical coordinates $(1+R)$ and θ

This means that concentric circles in retina transform to vertical lines in cortex

and

Radial excitation in retina into horizontal lines in cortex





Learning in networks

Hebb's rule

If neurons i and j fire simultaneously at frequencies E_i y E_j , respectively, the synaptic weight between them is

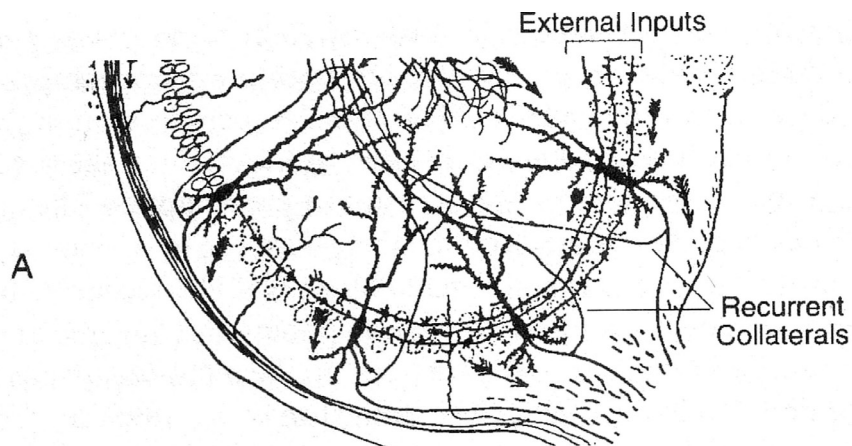
$$w_{ij} = kE_iE_j$$

A more practical rule is

$$w_{ij} = kH(E_i - 0.5M)H(E_j - 0.5M); \quad H(x) = \begin{cases} 1 & x > 0 \\ 0 & x \leq 0 \end{cases}$$

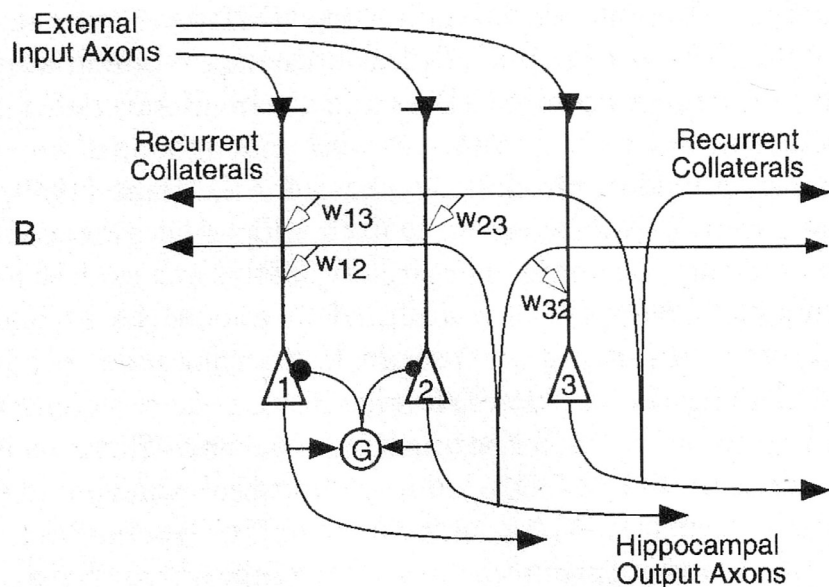
A synapse goes from value 0 to value k only when neurons i and j fire at more than half their maximum firing frequency M

Modelización de la red CA3 del hipocampo



256 excitatory neurons
(16x16 matrix):

Each of them has a Webb
synapse with the other 255



1 inhibitory neuron gets excited
by excitatory neurons and
inhibits them

Model

$$\dot{E}_i = \frac{1}{10} \left(-E_i + S \left(\sum_{j=1}^{255} w_{ij} E_j - 0.1I; 100, 2, 10 \right) \right)$$

$$\dot{I} = \frac{1}{10} \left(-I + 0.076 \sum_{i=1}^{256} E_i \right)$$

$$w_{ij} = kH(E_i - 0.5M)H(E_j - 0.5M); \quad H(x) = \begin{cases} 1 & x > 0 \\ 0 & x \leq 0 \end{cases}$$

1. Training phase

4 patterns get chosen as stimuli (32 pixel images en in a 16x16 matrix)

Each pattern excites 32 excitatory neurons . The rest of neurons are not excited initially.

We run the model and synapses change accordingly

2. Recognition phase

Show to the network an image made up of 1/3 of the pixels of one of the trained images and 2/3 of random pixels

