

The Microscopic Brain

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Exponentials

We use the following shorthand for a time derivative

$$\dot{x} = \frac{dx}{dt}$$

The exponential function $x = \exp(t)$ is invariant to differentiation. Hence

$$\dot{x} = \exp(t)$$

and

$$\dot{x} = x$$

Hence $\exp(t)$ is the solution of the above differential equation.

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Initial Values and Fixed Points

An exponential increase ($a > 0$) or decrease ($a < 0$) from initial condition x_0

$$x = x_0 \exp(at)$$

has derivative

$$\dot{x} = ax_0 \exp(at)$$

The top equation is therefore the solution of the differential equation

$$\dot{x} = ax$$

with initial condition x_0 .

The values of x for which $\dot{x} = 0$ are referred to as Fixed Points (FPs). For the above the only fixed point is at $x = 0$.

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Matrix Exponential

If x is a vector whose evolution is governed by a system of linear differential equations we can write

$$\dot{x} = Ax$$

where A describes the linear dependencies.

The only fixed point is at $x = 0$.

For initial conditions x_0 the above system has solution

$$x_t = \exp(At)x_0$$

where $\exp(At)$ is the matrix exponential (written `expm` in matlab) (Moler and Van Loan, 2003).

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Eigendecomposition

The equation

$$\dot{x} = Ax$$

can be understood by representing A with an eigendecomposition, with eigenvalues λ_k and eigenvectors q_k that satisfy

$$Aq_k = \lambda_k q_k$$

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Eigendecomposition

If we put the eigenvectors into the columns of a matrix

$$Q = \begin{bmatrix} | & | & \cdot & | \\ q_1 & q_2 & \cdot & q_d \\ | & | & \cdot & | \end{bmatrix}$$

then, because, $Aq_k = \lambda_k q_k$, we have

$$AQ = \begin{bmatrix} | & | & \cdot & | \\ \lambda_1 q_1 & \lambda_2 q_2 & \cdot & \lambda_d q_d \\ | & | & \cdot & | \end{bmatrix}$$

Hence

$$AQ = Q\Lambda$$

where $\Lambda = \text{diag}(\lambda)$.

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Eigendecomposition

Given

$$AQ = Q\Lambda$$

we can post-multiply both sides by Q^{-1} to give

$$A = Q\Lambda Q^{-1}$$

This works as long as A has a full set of eigenvectors (Strang, p. 255).

We can then use the identity

$$\exp(A) = Q \exp(\Lambda) Q^{-1}$$

Because Λ is diagonal, the matrix exponential simplifies to a simple exponential function over each diagonal element.

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Dynamical Modes

This tells us that the original dynamics

$$\dot{x} = Ax$$

has a solution

$$x_t = \exp(At)$$

that can be represented as a linear sum of k independent dynamical modes

$$x_t = \sum_k q_k \exp(\lambda_k t)$$

where q_k and λ_k are the k th eigenvector and eigenvalue of A . For $\lambda_k > 0$ we have an unstable mode.

For $\lambda_k < 0$ we have a stable mode, and the magnitude of λ_k determines the time constant of decay to the fixed point.

The eigenvalues can also be complex. This gives rise to oscillations (see later).

Initial Conditions

With initial conditions x_0

$$\dot{x} = Ax$$

has the solution

$$x_t = \exp(At)x_0$$

The initial conditions are used to find a set of values c_k (each being a scalar) that satisfy

$$x_0 = \sum_k c_k q_k \exp(\lambda_k t_0)$$

We can then write

$$x_t = \sum_k c_k q_k \exp(\lambda_k t)$$

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Two Dimensional Node

This and the following examples are from (Wilson, 1999). They all have initial condition

$$\begin{bmatrix} x_1(0) \\ x_2(0) \end{bmatrix} = \begin{bmatrix} 1 \\ 1 \end{bmatrix}$$

If both eigenvalues are real and have the same sign we have a node. This gives a stable ($\lambda < 0$) or unstable ($\lambda > 0$) node. For example

$$\begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \end{bmatrix} = \begin{bmatrix} -2 & 4 \\ 0 & -3 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}$$

has $\lambda_1 = -2$, $\lambda_2 = -3$. Combined with information from initial conditions gives the solution

$$x_1(t) = 5 \exp(-2t) - 4 \exp(-3t)$$

$$x_2(t) = \exp(-3t)$$

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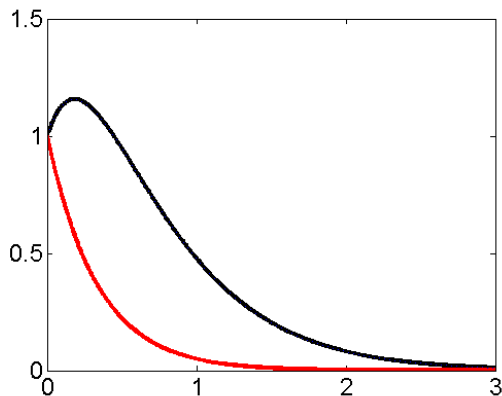
Two Dimensional Node

We plot time-series solutions

$$x_1(t) = 5 \exp(-2t) - 4 \exp(-3t)$$

$$x_2(t) = \exp(-3t)$$

for x_1 (black) and x_2 (red).



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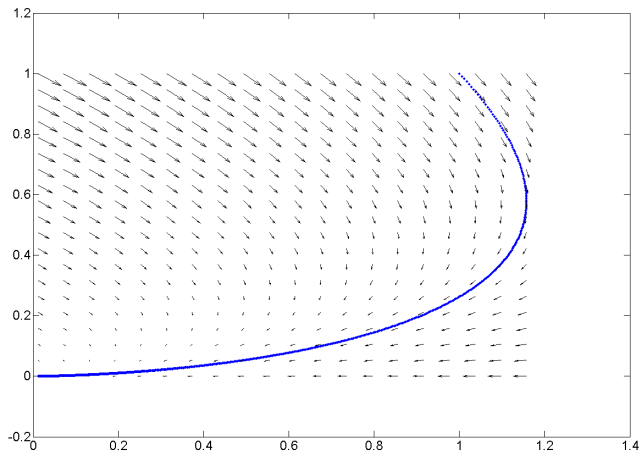
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State Space Representation

Plotting x_2 against x_1 gives a state-space representation, also known as phase space. The arrows depict the flow field \dot{x} .



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Two Dimensional Saddle

A saddle occurs if both eigenvalues are real and have different signs. For example

$$\begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \end{bmatrix} = \begin{bmatrix} 2 & -1 \\ 0 & -3 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}$$

has

$$\lambda_1 = 2$$

$$\lambda_2 = -3$$

giving solutions

$$x_1(t) = 0.8 \exp(2t) + 0.2 \exp(-3t)$$

$$x_2(t) = \exp(-3t)$$

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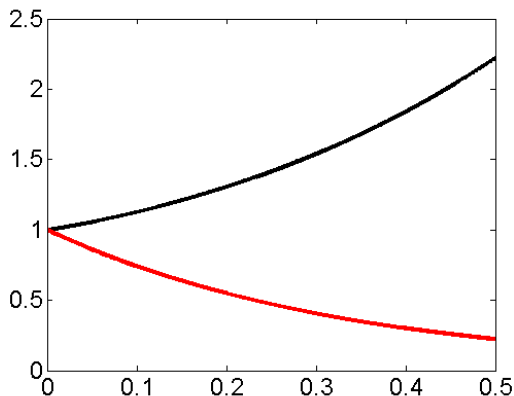
Two Dimensional Saddle

We plot time series solutions

$$x_1(t) = 0.8 \exp(2t) + 0.2 \exp(-3t)$$

$$x_2(t) = \exp(-3t)$$

for x_1 (black) and x_2 (red).



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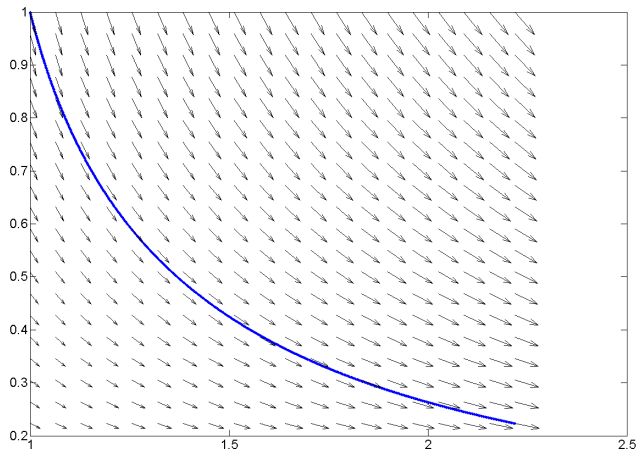
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Saddle State Space

Plotting x_2 against x_1 gives the state-space representation.



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Oscillations

We may also find pairs of complex eigenvalues (they always come in pairs). Each will be the conjugate of the other

$$\lambda_1 = a + bi$$

$$\lambda_2 = a - bi$$

where $i = \sqrt{-1}$. The dynamics corresponding to the sum of these two modes is given by

$$\begin{aligned} u_t &= \exp(\lambda_1 t) + \exp(\lambda_2 t) \\ &= \exp(at) [\exp(bit) + \exp(-bit)] \end{aligned}$$

From Euler's formula we have

$$\begin{aligned} \exp(bit) &= \cos bt + i \sin bt \\ \exp(-bit) &= \cos bt - i \sin bt \end{aligned}$$

Hence

$$u_t = 2 \exp(at) \cos(bt)$$

Hence the real part defines the damping constant and the imaginary part defines the frequency.

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Now consider an imaginary weighting of the two modes of the form

$$\begin{aligned}u_t &= i \exp(\lambda_1 t) - i \exp(\lambda_2 t) \\ &= \exp(at) [i \exp(bt) - i \exp(-bt)]\end{aligned}$$

From Euler's formula we have

$$\begin{aligned}i \exp(bt) &= i \cos bt + i^2 \sin bt \\ i \exp(-bt) &= i \cos bt - i^2 \sin bt\end{aligned}$$

Hence

$$u_t = -2 \exp(at) \sin(bt)$$

A complex weighting with both real and imaginary parts will give rise to both sin and cos components.

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Oscillations

The full solution is given by

$$x_t = \sum_k c_k q_k \exp(\lambda_k t)$$

If the eigenvalues are a complex conjugate pair

$$\lambda_1 = a + bi$$

$$\lambda_2 = a - bi$$

then so are the eigenvectors q_k . The weighting factors c_k are derived from the initial conditions

$$x_0 = \sum_k c_k q_k \exp(\lambda_k t_0)$$

and can also be complex. Thus, the weighting of each dynamic mode

$$w_k = c_k q_k$$

will also be complex

$$w_1 = \begin{bmatrix} c + di \\ e + fi \end{bmatrix}$$

and conjugate.

$$w_2 = \begin{bmatrix} c - di \\ e - fi \end{bmatrix}$$

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The full solution is therefore

$$x_t = \exp(at) \left(\begin{bmatrix} c + di \\ e + fi \end{bmatrix} \exp(bit) + \begin{bmatrix} c - di \\ e - fi \end{bmatrix} \exp(-bit) \right)$$

This complex weighting of each mode gives rise to both cos and sin components

$$x_1(t) = 2 \exp(at) [c \cos(bt) - d \sin(bt)]$$

$$x_2(t) = 2 \exp(at) [e \cos(bt) - f \sin(bt)]$$

See also Ch5 in Strang (1988).

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A spiral occurs when both eigenvalues are a complex conjugate pair. For example

$$\begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \end{bmatrix} = \begin{bmatrix} -2 & -16 \\ 4 & -2 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}$$

has

$$\lambda_1 = -2 + 8i$$

$$\lambda_2 = -2 - 8i$$

giving solutions

$$x_1(t) = \exp(-2t) [\cos(8t) - 2 \sin(8t)]$$

$$x_2(t) = \exp(-2t) [\cos(8t) + 0.5 \sin(8t)]$$

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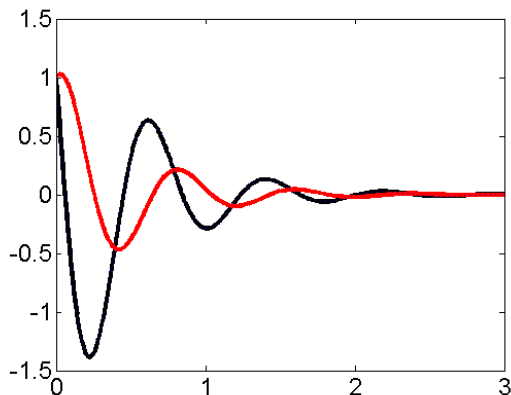
Spiral

We plot time series solutions

$$x_1(t) = \exp(-2t) (\cos(8t) - 2 \sin(8t))$$

$$x_2(t) = \exp(-2t) (\cos(8t) + 0.5 \sin(8t))$$

for x_1 (black) and x_2 (red).



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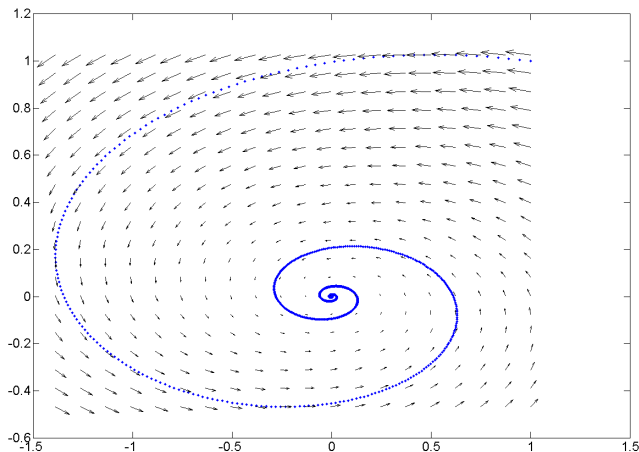
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Plotting x_2 against x_1 gives the state-space representation.



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A centre occurs when both eigenvalues are purely imaginary. That is the real part is zero. For example

$$\begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \end{bmatrix} = \begin{bmatrix} 1 & -2 \\ 5 & -1 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}$$

has

$$\lambda_1 = 3i$$

$$\lambda_2 = -3i$$

giving solutions

$$x_1(t) = \cos(3t) - 0.33 \sin(3t)$$

$$x_2(t) = \cos(3t) + 1.33 \sin(3t)$$

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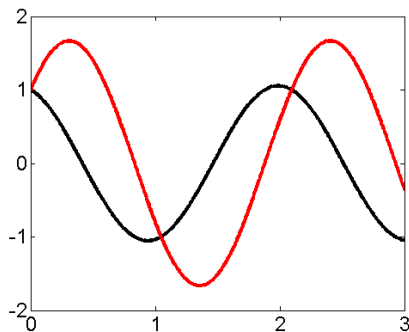
Centre

We plot time-series solutions

$$x_1(t) = \cos(3t) - 0.33 \sin(3t)$$

$$x_2(t) = \cos(3t) + 1.33 \sin(3t)$$

for x_1 (black) and x_2 (red).



The amplitude of the oscillation is determined entirely by the initial condition. If the initial values are twice as big so are the oscillations.

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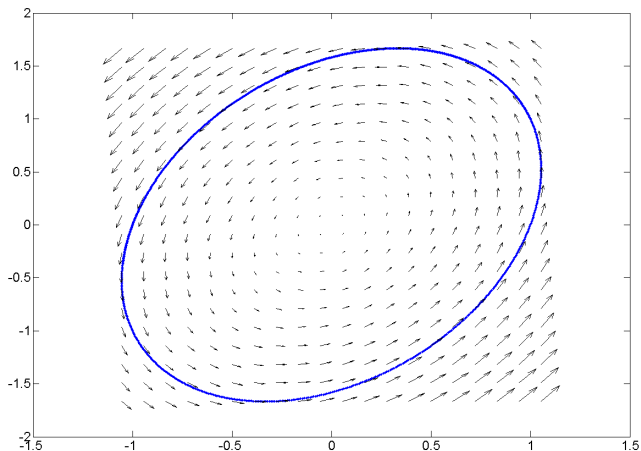
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Centre State Space

Plotting x_2 against x_1 gives the state-space representation.



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Offsets

For the more general linear differential equation with an offset

$$\dot{x} = Ax + b$$

the fixed point is given by

$$x_{FP} = -A^{-1}b$$

These systems are analysed in a new coordinate system centred around x_{FP} . That is

$$\tilde{x} = x - x_{FP}$$

$$\tilde{x}_0 = x_0 - x_{FP}$$

The new system

$$\dot{\tilde{x}} = A\tilde{x}$$

can then be analysed in the old way. The new dynamics are then found by adding x_{FP} onto the solution for \tilde{x}_t .

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Retinal Circuit

Wilson (1999) reviews a simple feedback circuit in the retina describing activity of cones, c , and horizontal cells, h

$$\begin{bmatrix} \tau_c \dot{c} \\ \tau_h \dot{h} \end{bmatrix} = \begin{bmatrix} -1 & -k \\ 1 & -1 \end{bmatrix} \begin{bmatrix} c \\ h \end{bmatrix} + \begin{bmatrix} L \\ 0 \end{bmatrix}$$

They have time constants $\tau_c = 25\text{ms}$ and $\tau_h = 80\text{ms}$.

Fixed point $x_{FP} = -A^{-1}b$ can also be worked out from intersection of nullclines. These are the points for which

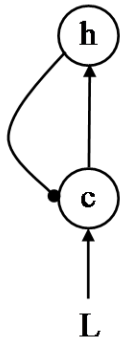
$$\dot{c} = 0$$

$$\dot{h} = 0$$

This gives

$$h = -\frac{1}{k}c + \frac{L}{k}$$

$$h = c$$



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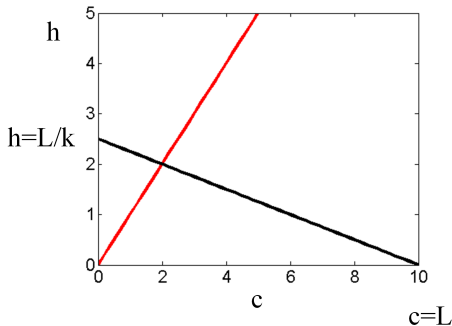
References

Nullclines

Figure shows nullcline for $\dot{c} = 0$ (black) and $\dot{h} = 0$ (red). The nullclines intersect at the fixed point $c = h = L/(k + 1)$ which for $L = 10$, $k = 4$ is

$$\begin{bmatrix} c \\ h \end{bmatrix} = \begin{bmatrix} 2 \\ 2 \end{bmatrix}$$

Increasing input L changes the fixed point.



For linear differential equations there is only ever one fixed point.

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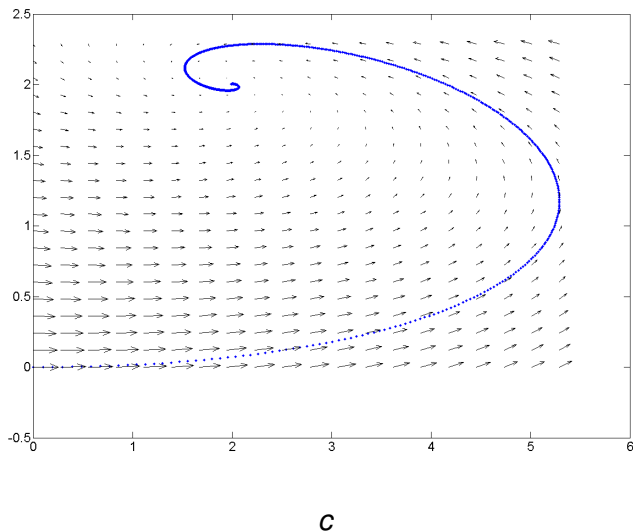
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Retinal State Space

Plotting h against c gives the state-space representation.



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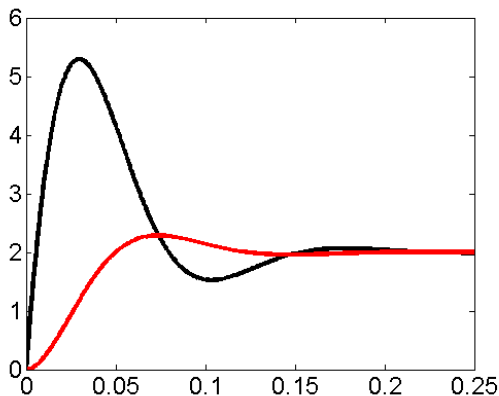
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Retinal solution

We plot time series solutions for cones, c , (black) and horizontal cells, h , (red).



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High Dimensional Systems and Stability

The nature of a fixed point in a high dimensional system is determined by all of the eigenvalues.

Some modes will decay faster than others. The longer-term characteristics of the system will depend on the more slowly decaying modes.

Consider a region R near a fixed point (FP) x_{eq} .

A FP is *asymptotically stable* if all trajectories in R decay to x_{eq} exponentially as $t \rightarrow \infty$.

A FP is unstable if at least one trajectory in R leaves R permanently.

A FP is stable if points in R remain in R , but do not approach x_{eq} asymptotically eg. a centre.

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Fitzhugh-Nagumo

This describes the trajectory of a voltage across the cell membrane v which is driven by an input current I and a recovery variable r

$$\begin{aligned}\tau_v \dot{v} &= [v - \frac{1}{3}v^3 - r + I] \\ \tau_r \dot{r} &= [-r + 1.25v + 1.5]\end{aligned}$$

with ms time unit.

The recovery variable may be thought of primarily as outwards flow of K^+ current that causes hyperpolarization after each spike.

The time scales of spiking and recovery are $\tau_v = 0.1$ ms and $\tau_r = 12.5$ ms. The nullclines are given by

$$\begin{aligned}r &= v - \frac{1}{3}v^3 + I \\ r &= 1.25v + 1.5\end{aligned}$$

Voltage variable has a cubic nonlinearity and recovery variable is linear.

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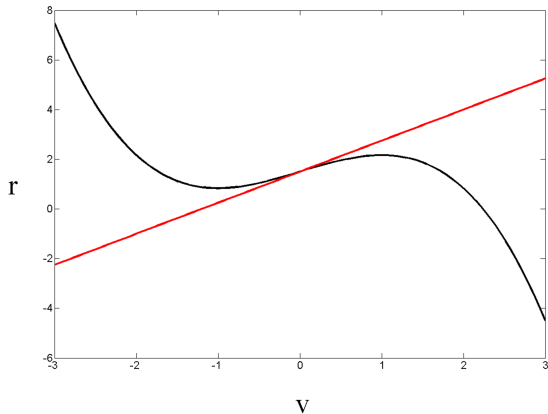
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Nonlinear Dynamics

Figure shows nullcline for $\dot{v} = 0$ (black) and $\dot{r} = 0$ (red). Intersection of nullclines defines FPs.

Can have many FPs for nonlinear systems $\dot{x} = f(x)$. They are generally found numerically from the roots of the equation $f(x) = 0$.



Here, for $I = 1.5$ we have a single FP given by $v = 0, r = 1.5$.

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Linearization

The nature of FPs is determined by a local linearisation about each FP.

$$\dot{x} = f(x)$$

Using a first order Taylor series we have

$$f(x) = f(x_{eq}) + \frac{df(x)}{dx}(x - x_{eq}) + \dots$$

In local coordinates $\tilde{x} = (x - x_{eq})$ we have

$$\dot{\tilde{x}} = J\tilde{x}$$

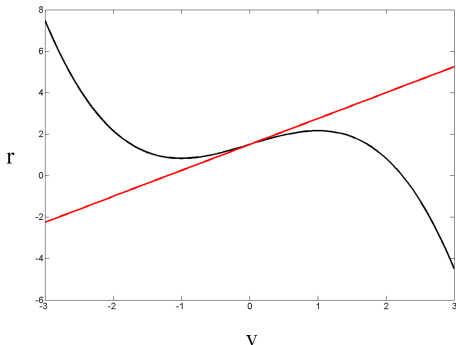
where J is the Jacobian having entries

$$J_{ij} = \frac{df_i(x)}{dx_j}$$

The eigenvalues of J then determine the dynamics around the fixed point.

Nonlinear Oscillation

Here, we have a single FP given by $v = 0, r = 1.5$. It is an unstable node (not a centre). The dynamics around this node form a nonlinear oscillation (limit cycle). This can be explored via numerical integration of the differential equation.



A limit cycle is given by $x(t + T) = x(t)$ for some period T . It is asymptotically stable if enclosed by trajectories which spiral towards it. Otherwise its unstable. A limit cycle must surround one or more FPs.

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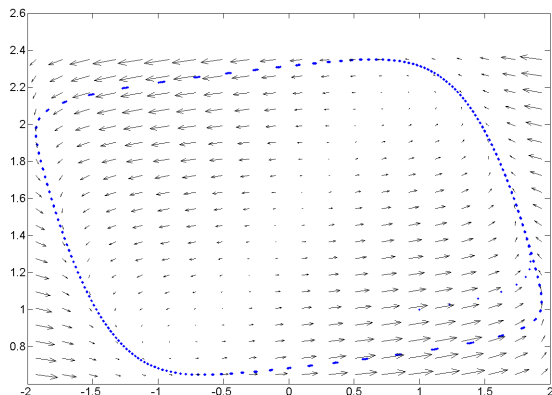
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Nonlinear Oscillation

The amplitude of a nonlinear oscillation is not determined by the initial conditions. It is therefore robust to noise.



The instantaneous frequency of a nonlinear oscillation is not constant. Here, the initial conditions were $v = r = 1$.

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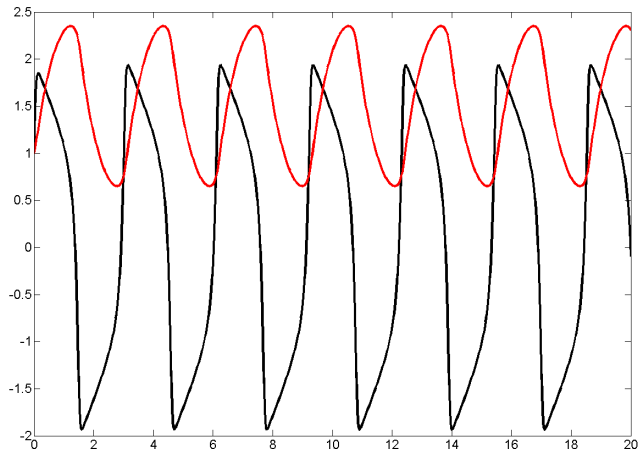
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Nonlinear Oscillation

For input $I = 1.5$ we have the solution for v (black) and r (red).



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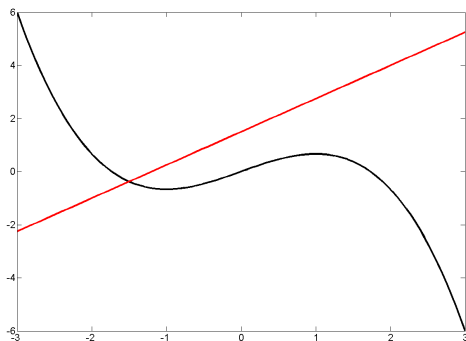
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Zero Input

For input $I = 0$ the fixed point is given by $v = -1.5$,
 $r = -3/8$. It is a stable node.



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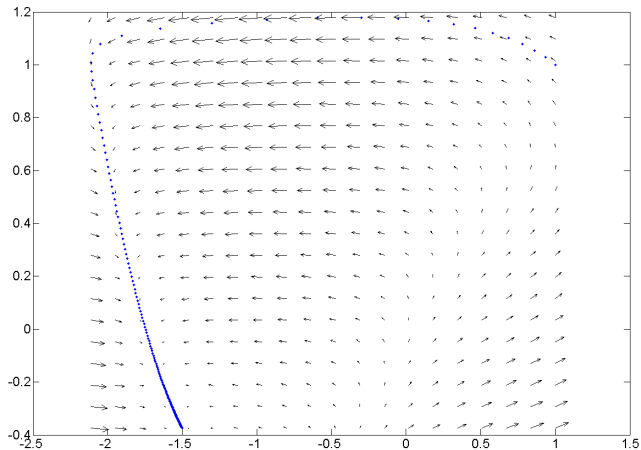
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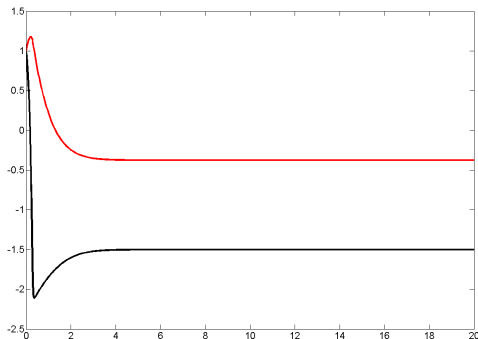
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Excitable Systems

A dynamical system such as a spiking neuron which produces a stable node in the absence of input, and a limit cycle with input is said to be excitable. For input $I = 0$ we have the solution for v (black) and r (red).



With FN neurons, increasing input causes a Hopf Bifurcation (Ch4, Bard Ermentrout and Terman, 2010).

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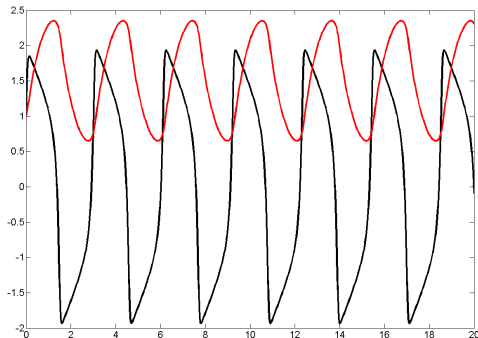
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Hopf Bifurcation Theorem

In dynamical systems, a bifurcation means that the system undergoes a qualitative change in behaviour. For an N -dimensional dynamical system with $N \geq 2$

$$\dot{x} = f(x, \beta)$$

with fixed points x_{FP} and Jacobian $J(\beta)$. A Hopf bifurcation will occur given the following conditions. For $\beta < \alpha$, x_{FP} is asymptotically stable. For $\beta = \alpha$, J has one pair of purely imaginary eigenvalues defining a linear oscillation (centre). For $\beta > \alpha$, x_{FP} is unstable.

There are then two types of Hopf bifurcation.

- ▶ Subcritical: an unstable limit cycle for $\beta < \alpha$.
- ▶ Supercritical: an asymptotically stable limit cycle for $\beta > \alpha$

For $\beta = \alpha$ the oscillation will be of frequency f and will emerge with infinitesimally small amplitude.

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Hodgkin-Huxley

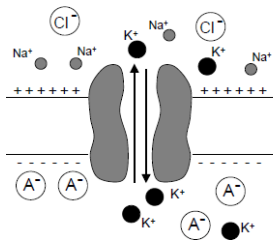
The Hodgkin-Huxley equations describe the change in membrane potential as a function of sodium, I_{Na} , potassium, I_K , leak I_L and input I currents

$$C\dot{v} = -I_{Na} - I_K - I_L + I_{in}$$

with membrane capacitance C where each current obeys Ohms Law

$$I = g(v - E)$$

with conductance g and equilibrium potential E .



Hodgkin-Huxley

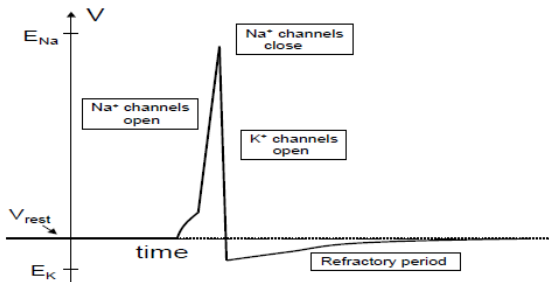


Figure 2.7. *The action potential. During the upstroke, sodium channels open and the membrane potential approaches the sodium Nernst potential. During the downstroke, sodium channels are closed, potassium channels are open and the membrane potential approaches the potassium Nernst potential.*

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The Hodgkin-Huxley equations can be written

$$\begin{aligned}C\dot{v} &= -g_{Na}m^3h(v - E_{Na}) - g_Kn^4(v - E_K) - g_L(v - E_L) + I_{in} \\ \tau_m(v)\dot{m} &= -m + M(v) \\ \tau_h(v)\dot{h} &= -h + H(v) \\ \tau_n(v)\dot{n} &= -n + N(v)\end{aligned}$$

where m is the Na activation rate and n is the K activation rate.

Na channels have a second process which can deactivate them. The term h captures this deactivation (Ch5, Dayan and Abbot, 2001).

The mathematical forms of the v -dependent functions were chosen to provide a good fit to data from the giant squid axon (Ch 9, Wilson 1999).

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Rinzel Approximation

Rinzel (1985) noted that the Na activation dynamics were sufficiently fast that $m = M(v)$ is a good approximation. This eliminates the second equation.

Second, the time series for h and n and their equilibrium values were sufficiently similar that $h = 1 - n$ is a good approximation. This means the rate of Na channel closing is assumed equal and opposite to the rate of K channel opening. This eliminates the third equation.

The resulting Rinzel approximation to HH therefore has two state variables and its state space is readily visualised (Wilson, 1999).

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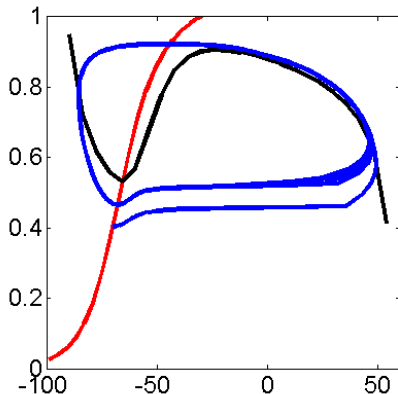
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Rinzel Approximation

Interestingly the nullcline for v is cubic, as in the Fitzhugh-Nagumo model. But Rinzel retains an explicit description in terms of K channel.



The nullcline for r is sigmoidal but rather linear in the range of the fixed points.

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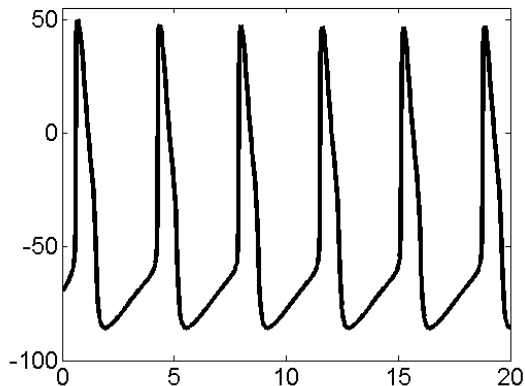
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Rinzel Approximation

Rinzel Spike Dynamics, v .



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The squid giant axon is unusual for having only one Na and one K current. As a result it cannot fire at rates below about 175Hz. Human cortical neurons, however, can fire over a much broader range of frequencies. This is because they have a rapid, transient K current (Wilson, 1999). This is referred to as the I_A current. The HH model has been augmented to include this.

Rose and Hindmarsh (1989) have shown that properties of the I_A current can be implemented by making the recovery variable quadratic.

$$\begin{aligned}\dot{v} &= -(17.8 + 47.8v + 33.8v^2)(v - 0.48) - 26r(v + 0.95) + I \\ \dot{r} &= \frac{1}{\tau_r} [-r + 1.29v + 0.79 + 0.33(v + 0.38)^2]\end{aligned}$$

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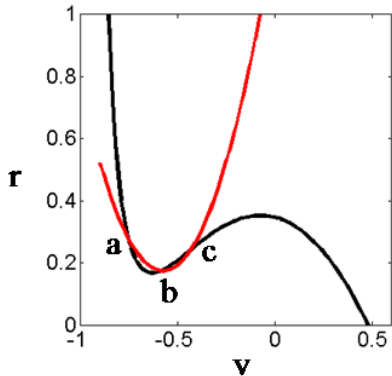
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- Rose-Hindmarsh**
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- Type 1 and 2 Cells

References

Rose-Hindmarsh

For zero input current $I = 0$ there are three fixed points

- ▶ (a) Stable node
- ▶ (b) Saddle point
- ▶ (c) Unstable spiral



Black curve shows $\dot{v} = 0$, red curve $\dot{r} = 0$.

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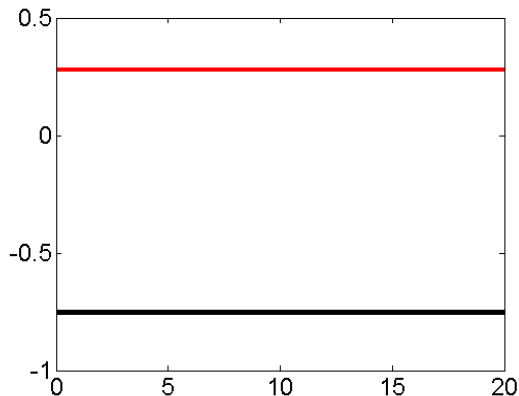
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Rose-Hindmarsh

With zero input $I = 0$ and initial point at (a) we get flat time series.



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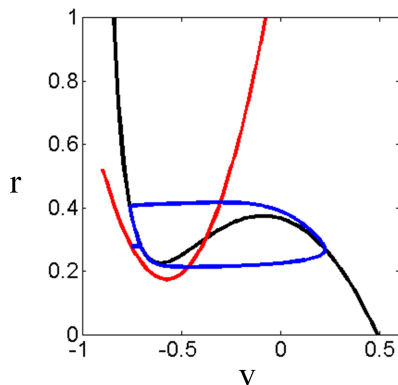
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Saddle-Node Bifurcation

Increasing input to $I = 0.5$ makes (a) and (b) coalesce, then disappear. This leaves only (c). A limit cycle then forms around (c). This is known as a Saddle-Node Bifurcation.



The limit cycle that emerges has non-zero amplitude at inception (because it originates around a pre-existing FP, unlike Hopf). This corresponds to a sharp spike threshold. Not all saddle-node bifurcations produce limit cycles (Guckenheimer and Holmes, 2003).

Linear Dynamics

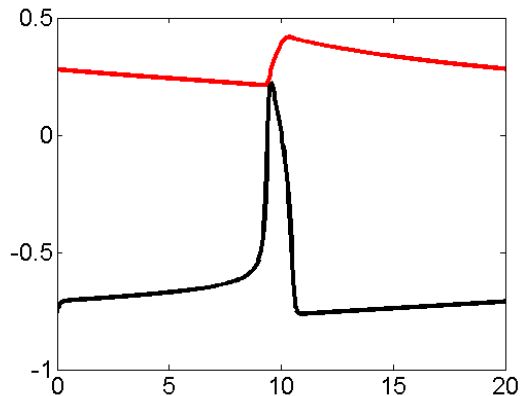
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With input $I = 0.5$ and initial point at (a) we now get slow spiking.



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Type 1 and 2 Cells

Hodgkin classified two types of spiking cells

- ▶ Type 1 cells have sharp thresholds and can fire at arbitrarily low frequencies
- ▶ Type 2 cells have variable thresholds and a positive minimal frequency

These correspond to Saddle-Node and Hopf bifurcations (Bard Ermentrout and Terman, 2010).

Can use normal form models of each bifurcation type, instead of ones with specific biophysical parameters (Guckenheimer and Holmes, 1983).

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Type 1 and 2 Cells

(Tateno et al. 2004) found that regular spiking (RS) cortical pyramidal cells have type 1 dynamics whereas fast spiking (FS) inhibitory interneurons have type 2 dynamics.

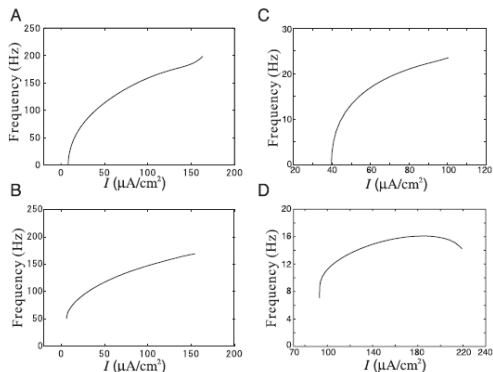


FIG. 10. f - I curves for simple models of type 1 and type 2 behavior. *A*: 6-variable Connor et al. model of molluscan neuron, incorporating A-type K^+ conductance, showing type 1 behavior (Connor et al. 1977). *B*: 4-variable Hodgkin-Huxley model of the squid giant axon membrane patch, showing type 2 behavior (Hodgkin and Huxley 1952). *C*: 2-variable Morris-Lecar model with type 1 parameters (Morris and Lecar 1981). *D*: Morris-Lecar model with type 2 parameters.

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References

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