Dynamics of Neural Systems
Linear Dynamical Systems

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Overview

- Basic definitions
- Linear dynamical systems
- Stability of linear systems

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Dynamical systems in neuroscience

- The behavior of individual neurons is characterized by dynamical equations (differential equations (DEQs) describing functions of time) $\Leftarrow$ HH model.
- Many phenomena at the level of individual neurons, and neural networks can be understood better with methods from dynamical systems theory.
- Many of you might know something about **linear dynamical systems** (DS); unfortunately, most neural phenomena are described by nonlinear DS.
- Nonlinear dynamical systems often also discussed under the keyword ‘chaos theory’.

Dynamical systems (DS): definition

- Dynamical systems describe the behavior of a **state variable** $\mathbf{x}$ over time.
- Distinction:
  Discrete dynamical systems (map): t is an integer.

  $$\boxed{\mathbf{x}[t+1] = \mathbf{f}(\mathbf{x}[t], t)}$$

  (Iteration of a function; not treated extensively here.)

  Continuous dynamical systems: $t \in \mathrm{IR}$ is continuous.

  $$\boxed{\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = \mathbf{f}(\mathbf{x}(t), t)}$$ (differential equation in time)
- The function $\mathbf{x}(t)$ (or $\mathbf{x}[t]$) is called **trajectory** or **orbit** of the DS.

Autonomous dynamical systems

- Dynamical systems are called **autonomous** if the describing equation does not explicitly depend on time:

$$\boxed{\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = \mathbf{f}(\mathbf{x}(t))} \qquad \text{(respectively } \mathbf{x}[t+1] = \mathbf{f}(\mathbf{x}[t])\text{)}$$

- By introduction of a new dynamic variable non-autonomous dynamical systems can always be made autonomous, e.g.:

$$\boxed{\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = \mathbf{f}(\mathbf{x}(t), t) \quad \Leftrightarrow \quad \begin{array}{l} \dfrac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = \mathbf{f}(\mathbf{x}(t), y) \\ \dfrac{\mathrm{d}y}{\mathrm{d}t} = 1 \quad y(0) = 0 \end{array}}$$

Non-autonomous DS **Auxiliary autonomous DS**

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Linear dynamical systems I

- General form (for continuous dynamics):

$$\boxed{\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = \mathbf{A}\mathbf{x}(t) + \mathbf{u}(t)}$$

Matrix Driving term

- We analyze first the **homogenous equation**:

$$\boxed{\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = \mathbf{A}\mathbf{x}(t)}$$

- To compute the solution it is handy to define exponentials of matrices (linear operators).

Exponential of a matrix

- The exponential of a matrix can be defined as:

$$\boxed{e^{\mathbf{A}} = \sum_{n=0}^{\infty} \frac{1}{n!}\mathbf{A}^n}$$

  It can be shown that this series converges absolutely for any matrix $\mathbf{A}$.

- Like for the scalar case, we have:

$$\boxed{\begin{aligned} & e^{(a+b)\mathbf{A}} = e^{a\mathbf{A}} e^{b\mathbf{A}} \\ & e^{\mathbf{A}} e^{-\mathbf{A}} = \mathbf{I} \\ & e^{-\mathbf{A}} = (e^{\mathbf{A}})^{-1} \\ & e^{\mathbf{A}} e^{\mathbf{B}} = e^{\mathbf{A}+\mathbf{B}} \ \text{ if } \ \mathbf{AB} = \mathbf{BA} \end{aligned}}$$

- Remark: For non-singular $\mathbf{Q}$

$$\boxed{e^{\mathbf{QAQ}^{-1}} = \mathbf{Q} e^{\mathbf{A}} \mathbf{Q}^{-1}}$$

Exponential of a matrix

- Remark that for a diagonal matrix $\mathbf{\Lambda} = \mathrm{diag}(\lambda_1, \ldots, \lambda_N)$ because of $\mathbf{\Lambda}^k = \mathrm{diag}(\lambda_1^k, \ldots, \lambda_N^k)$ it follows:

$$\boxed{e^{\mathbf{\Lambda}} = \mathrm{diag}(\exp(\lambda_1), \ldots, \exp(\lambda_\mathrm{N}))}$$

Linear dynamical systems II

- From the definition of the series follows:

$$\frac{\mathrm{d}}{\mathrm{d}t}e^{t\mathbf{A}} = \lim_{h\to 0}\frac{e^{(t+h)\mathbf{A}} - e^{t\mathbf{A}}}{h} = e^{t\mathbf{A}}\lim_{h\to 0}\frac{e^{h\mathbf{A}} - \mathbf{I}}{h} = e^{t\mathbf{A}}\mathbf{A} = \mathbf{A}e^{t\mathbf{A}}$$

- This implies that the initial value problem

$$\boxed{\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = \mathbf{A}\mathbf{x}(t) \qquad \mathbf{x}(0) = \mathbf{x}_0}$$

‚Flow‘ of the DEQ

has the solution: $\boxed{\mathbf{x}(t) = e^{t\mathbf{A}}\mathbf{x}_0 = \boldsymbol{\varphi}(t, \mathbf{x}_0)}$

(It can be shown that no other solution exists.)

- Interpretation: $\boldsymbol{\varphi}(t, \mathbf{x}_0)$ defines a **flow field** that maps the initial condition $\mathbf{x}_0$ onto $\mathbf{x}(t)$.

Linear dynamical systems III

- The solution for the inhomogeneous equation can be found by the technique of **variation of parameters**:
- Ansatz for the solution of the inhomogeneous system:

$$\mathbf{x}(t) = e^{t\mathbf{A}}\mathbf{k}(t)$$

  Determine $\mathbf{k}(t)$ as to match the requirements from inhomogeneous equation:

$$\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = \mathbf{A}e^{t\mathbf{A}}\mathbf{k}(t) + e^{t\mathbf{A}}\frac{\mathrm{d}\mathbf{k}}{\mathrm{d}t} = \mathbf{A}\mathbf{x}(t) + \mathbf{u}(t) = \mathbf{A}e^{t\mathbf{A}}\mathbf{k}(t) + \mathbf{u}(t)$$

$$\frac{\mathrm{d}\mathbf{k}}{\mathrm{d}t} = e^{-t\mathbf{A}}\mathbf{u}(t) \quad \Rightarrow \mathbf{k}(t) - \mathbf{k}_0 = \int_0^t e^{-t'\mathbf{A}}\mathbf{u}(t')\,\mathrm{d}t'$$

- This implies (because of $\mathbf{k}_0 = \mathbf{x}_0$) for the solution of the inhomogeneous equation:

$$\boxed{\mathbf{x}(t) = e^{t\mathbf{A}}\left(\mathbf{x}_0 + \int_0^t e^{-t'\mathbf{A}}\mathbf{u}(t')\,\mathrm{d}t'\right) = \underbrace{e^{t\mathbf{A}}\mathbf{x}_0}_{\text{General solution of homog. eq.}} + \underbrace{\int_0^t e^{(t-t')\mathbf{A}}\mathbf{u}(t')\,\mathrm{d}t'}_{\text{Particular solution}}}$$

Linear dynamical systems IV

- For the special case of a constant input $\mathbf{u}$ follows (for invertible $\mathbf{A}$):

$$\mathbf{x}(t) = e^{t\mathbf{A}}\left(\mathbf{x}_0 + \int_0^t e^{-t'\mathbf{A}}\,\mathrm{d}t'\,\mathbf{u}\right) = e^{t\mathbf{A}}\left(\mathbf{x}_0 + \left[-e^{-t'\mathbf{A}}\mathbf{A}^{-1}\right]_0^t \mathbf{u}\right) \Rightarrow$$

$$\boxed{\mathbf{x}(t) = e^{t\mathbf{A}}\mathbf{x}_0 - \left(\mathbf{I} - e^{t\mathbf{A}}\right)\mathbf{A}^{-1}\mathbf{u} = e^{t\mathbf{A}}\left(\mathbf{x}_0 + \mathbf{A}^{-1}\mathbf{u}\right) - \mathbf{A}^{-1}\mathbf{u}}$$

- We will see later that for stable systems and any $\mathbf{b}$ $\lim_{t\to\infty} e^{t\mathbf{A}}\mathbf{b} = \mathbf{0}$. This implies: $\boxed{\mathbf{x}(\infty) = -\mathbf{A}^{-1}\mathbf{u}}$
(The same follows for $\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = \mathbf{0}$ from the DEQ.)

Change of coordinates I

- Assuming that the matrix $\mathbf{A}$ can be diagonalized (for example if it has only distinct real **eigenvalues** λ_i), this implies: $\mathbf{A} = \mathbf{Q}\,\mathbf{\Lambda}\,\mathbf{Q}^{-1}$ where $\mathbf{\Lambda} = \mathrm{diag}(\lambda_1, \ \ldots, \lambda_N)$.
- Remark: The columns of $\mathbf{Q}$ are the eigenvectors of $\mathbf{A}$.
- We introduce new coordinates: $\mathbf{y} = \mathbf{Q}^{-1}\,\mathbf{x}$; in these new coordinates the homogenous DEQ has the form:

$$\boxed{\frac{\mathrm{d}\mathbf{y}}{\mathrm{d}t} = \mathbf{\Lambda}\mathbf{y}(t) \quad \Leftrightarrow \quad \frac{\mathrm{d}y_i}{\mathrm{d}t} = \lambda_i y_i(t)}$$

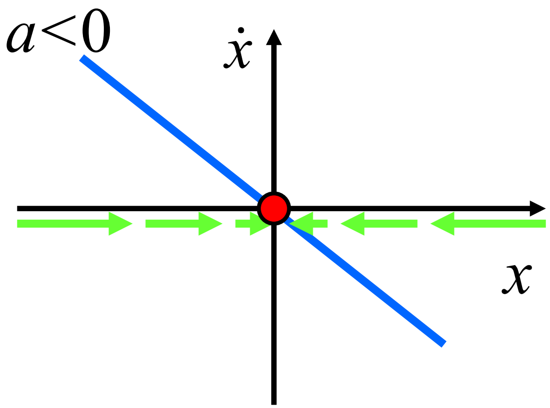
- This is a decoupled set of DEQ, where the individual equations can be easily solved: $y_i(t) = \exp(\lambda_i\, t)\, y_i(0)$.
- This implies: $\boxed{\mathbf{x}(t) = \mathbf{Q}\mathbf{y}(t) = \mathbf{Q}e^{t\mathbf{\Lambda}}\mathbf{y}(0) = \mathbf{Q}e^{t\mathbf{\Lambda}}\mathbf{Q}^{-1}\mathbf{x}(0)}$

Change of coordinates II

- The last point has important consequences:
  1. The solution is a linear combination of the basis functions $\exp(\lambda_i t)$.
  2. Each of these 'basis functions' is associated with its own linear subspace, which is given by the columns of $\mathbf{Q}$; the parts of the solutions with different dynamics are thus evolving in separate linear subspaces.
  3. Since $\mathbf{Q}$ can be shown to have full rank these subspaces are linearly independent.

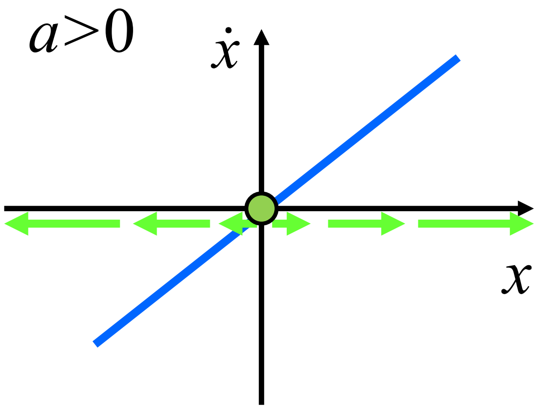
Phase portrait: 1D systems

- Simple graphical method to analyze how a DS behaves.
- First order equation: $\boxed{\dfrac{\mathrm{d}x}{\mathrm{d}t} = ax(t)}$
- Only three possible situations for **fixed points** with $\dfrac{\mathrm{d}x}{\mathrm{d}t} = 0$:



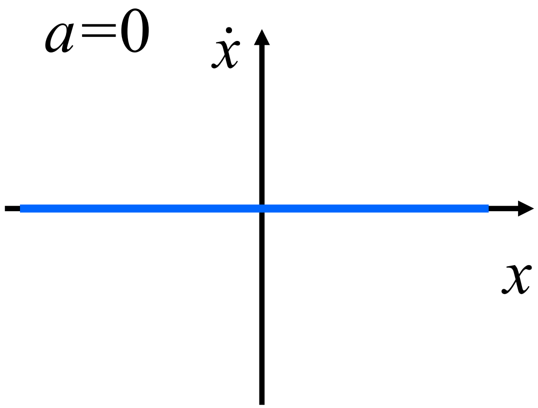
Stable fixed point / attractor for $x=0$

- Approached from any initial condition



Unstable fixed point / repellor for $x=0$

- Divergence from any initial condition, except for $x=0$

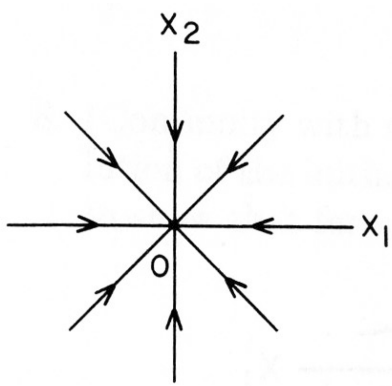


Marginally stable

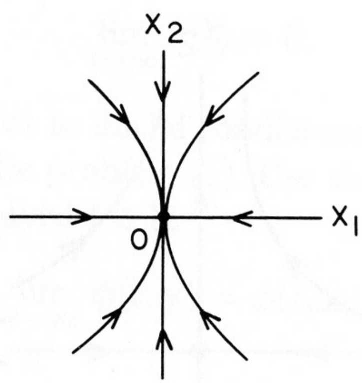
- Initial state persists; but no convergence

Phase portrait: 2D systems I

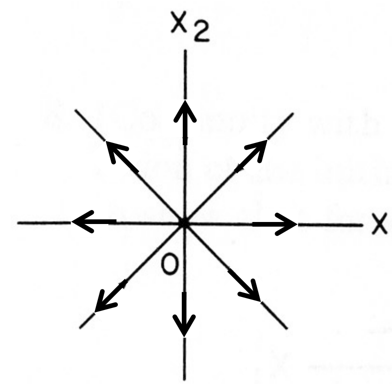
- More interesting / complex behavior for two dimensions.
- Transformed system has two distinct eigenvalues.
- Possible situations for real eigenvalues:



$\lambda_1 = \lambda_2 < 0$



$\lambda_1 < \lambda_2 < 0$

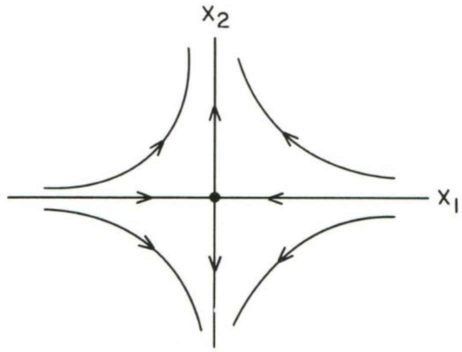


$\lambda_1, \lambda_2 > 0$

Stable knodes at $\mathbf{x}=0$

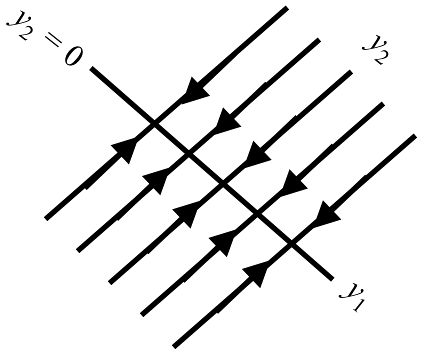
Unstable knode at $\mathbf{x}=0$

Phase portrait: 2D systems II



$\lambda_1 < 0 < \lambda_2$

Saddle point at $\mathbf{x}=0$



$\lambda_1 = 0, \ \lambda_2 < 0$

Marginally stable manifold $y_2 = 0$

- One stable and one unstable direction.

- Stable behavior in the direction of y_2.
- Marginally stable behavior in the direction of y_1.

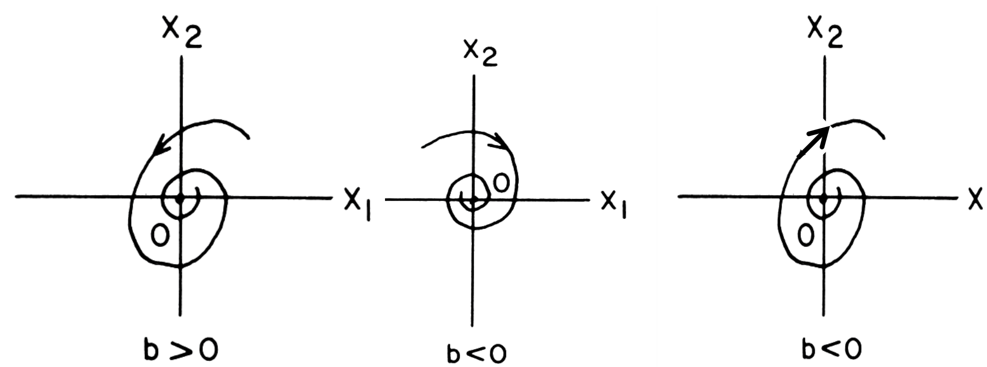
- Behavior results from the superposition of the behavior in different direction in linear independent subspaces.

Oscillatory components I

- The matrix $\boxed{\mathbf{A} = \begin{bmatrix} a & -b \\ b & a \end{bmatrix}}$ has the eigenvalues $\lambda_{1,2} = a \pm ib$.
- It can be shown: $e^{\mathbf{A}} = e^{a} \begin{bmatrix} \cos b & -\sin b \\ \sin b & \cos b \end{bmatrix}$

  (rotation by angle b and a stretching by the factor e^{a}).
- This implies for the solution of the corresponding DEQ:

$$\boxed{\begin{aligned} \mathbf{x}(t) &= e^{\mathbf{A}t}\mathbf{x}_0 \\ &= \underbrace{e^{at}}_{\text{Scaling factor}} \underbrace{\begin{bmatrix} \cos bt & -\sin bt \\ \sin bt & \cos bt \end{bmatrix}}_{\text{Rotation matrix}} \mathbf{x}_0 \end{aligned}}$$



$\lambda_{1,2} = a \pm ib, a < 0$

Stable spirals

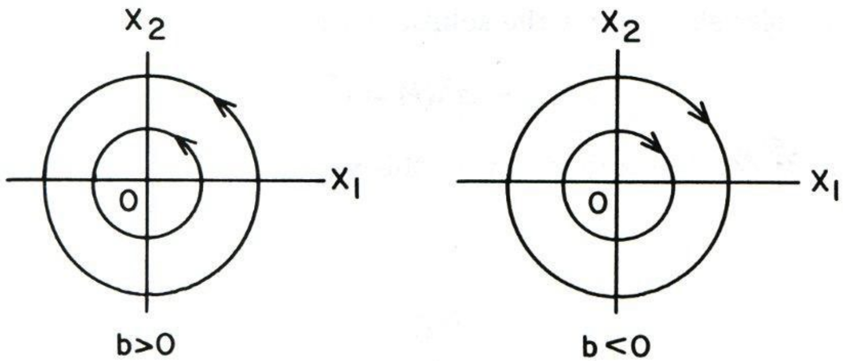
$\lambda_{1,2} = a \pm ib, a > 0$

Unstable spiral

- These are **spirals** towards or away from the origin.

Oscillatory components II

- Special case: $a = 0$: imaginary eigenvalues; marginally stable oscillation with constant amplitude (**center** at the origin).



$$\lambda_{1,2} = a \pm ib, a = 0$$

Center at origin

Oscillatory components III

- General result: Matrices with N distinct complex eigenvalues (appearing in conjugate pairs) can be **(block-)diagonalized** in the form: $\mathbf{A} = \mathbf{Q}\,\mathbf{\Lambda}\,\mathbf{Q}^{-1}$ with

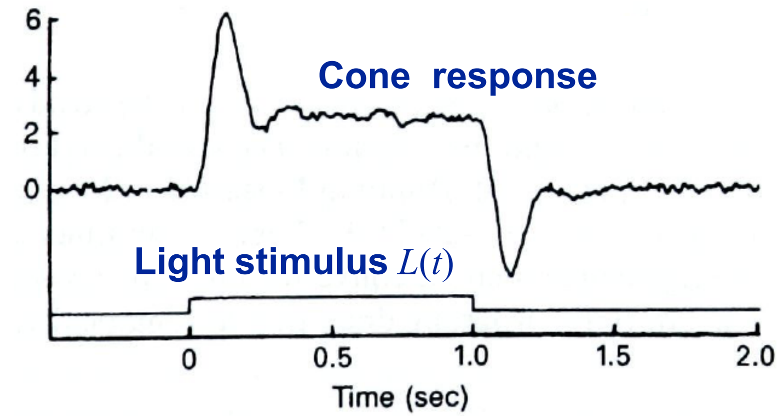
$$\mathbf{\Lambda} = \begin{bmatrix} \mathbf{\Lambda}_1 & & \mathbf{0} \\ & \ddots & \\ \mathbf{0} & & \mathbf{\Lambda}_N \end{bmatrix} \text{ and } \mathbf{\Lambda}_k = \begin{bmatrix} a_k & -b_k \\ b_k & a_k \end{bmatrix} \quad \text{with} \quad \begin{matrix} \lambda_{k,1} = a_k + ib_k \\ \lambda_{k,2} = a_k - ib_k \end{matrix}$$

- The matrix $\mathbf{Q}$ consists of the real and imaginary parts of the complex eigenvectors of $\mathbf{A}$.
- This implies oscillatory solutions in the corresponding linear subspaces if $b_i \neq 0$.

Example: negative feedback in retina I

- Horizontal cells provide negative feedback signals for cones in the retina.
- Recording results for stimulation with rectangular light pulse.
- Oscillatory overshoot.
- Simple model (Wilson book):

Response of cone



Light intensity

Cone activity:

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = \frac{1}{\tau_{\mathrm{C}}}\left(-x_1(t) - kx_2(t) + L(t)\right)$$

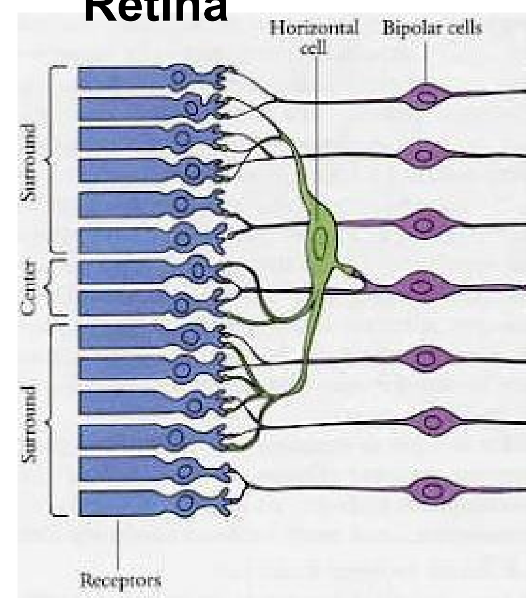
Horizontal cell activity:

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = \frac{1}{\tau_{\mathrm{H}}}\left(-x_2(t) + x_1(t)\right)$$

with $\tau_{\mathrm{C}} = 25\mathrm{ms}, \tau_{\mathrm{H}} = 80\mathrm{ms}$, and $k = 4$

Strength of inhibition

Retina



Example: negative feedback in retina II

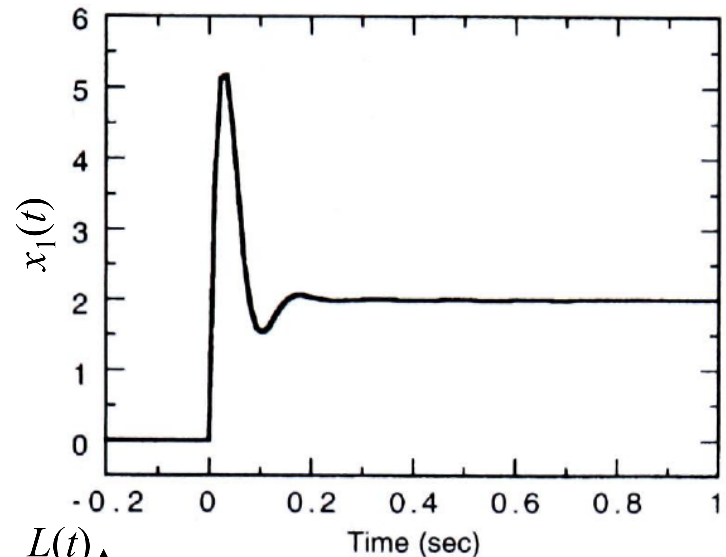
- The system matrix is given by:

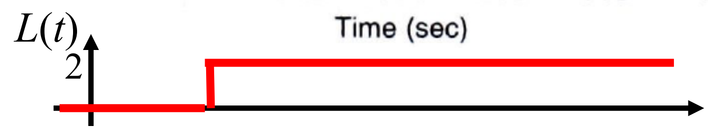
$$\mathbf{A} = \begin{bmatrix} -40 & -160 \\ 12.5 & -12.5 \end{bmatrix}$$

(dropping the units)

- The eigenvalues are: $\lambda_{1,2} = -26.25 \pm 42.56i$
- This defines a stable spiral.
- Stationary solution for step input with $L(t) = 10$ for $t > 0$ from $\mathrm{d}/\mathrm{d}t = 0$: $x_1(\infty) = x_2(\infty) = 2$

Model response





- Explicit solution for non-autonomous system:

$$x_1(t) = \left(-2e^{-t/25\mathrm{ms}} \cos(42.56\,\mathrm{Hz}\,t) + 8.17e^{-t/25\mathrm{ms}} \sin(42.56\,\mathrm{Hz}\,t) + 2\right) \cdot 1(t)$$
$$x_2(t) = \left(-2e^{-t/25\mathrm{ms}} \cos(42.56\,\mathrm{Hz}\,t) - 1.23e^{-t/25\mathrm{ms}} \sin(42.56\,\mathrm{Hz}\,t) + 2\right) \cdot 1(t)$$

Overview

- Basic definitions
- Linear dynamical systems
- Stability of linear systems

Dynamical stability

- The linear dynamical system is called **asymptotically stable** if its solution converges against a single point for $t \to \infty$.
- The system is **unstable** if there is at least one solution that diverges from the stability region permanently for $t \to \infty$.
- The system is **(neutrally) stable** or stable if nearby trajectories remain nearby for $t \to \infty$.
- Obviously, these properties depend on the eigenvalues of the matrix $\mathbf{A}$.

Stable and unstable subspaces I

- We have shown that individual eigenvalues (and thus dynamical 'modes') of the system are associated with independent linear subspaces.
- Let $\mathbf{w}_j = \mathbf{u}_j + i\,\mathbf{v}_j$ be the generalized complex eigenvector of the (real) matrix $\mathbf{A}$ belonging to eigenvalue $\lambda_j = a_j + ib_j$.
- We define the following linear subspaces:

stable subspace: $E^{\mathrm{s}} = \mathrm{Span}\left\{\mathbf{u}_{\mathrm{j}}, \mathbf{v}_{\mathrm{j}} \mid a_j < 0\right\}$

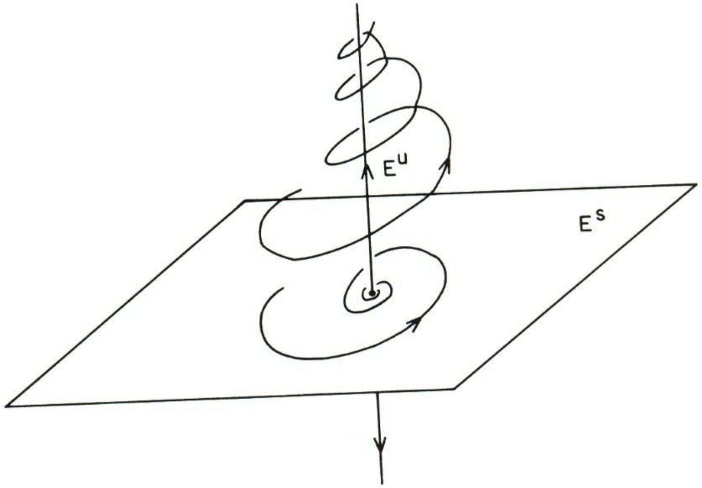
center subspace: $E^{\mathrm{c}} = \mathrm{Span}\left\{\mathbf{u}_{\mathrm{j}}, \mathbf{v}_{\mathrm{j}} \mid a_j = 0\right\}$

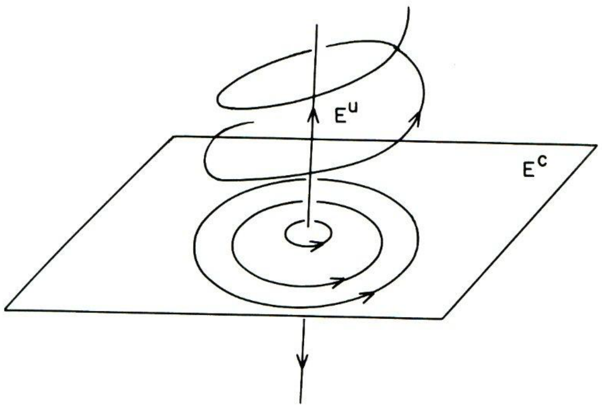
unstable subspace: $E^{\mathrm{u}} = \mathrm{Span}\left\{\mathbf{u}_{\mathrm{j}}, \mathbf{v}_{\mathrm{j}} \mid a_j > 0\right\}$

The stable / unstable / neutrally stable modes of the solution evolve separately in these subspaces.

Stable and unstable subspaces II

- Examples:





$$A = \begin{bmatrix} -2 & -1 & 0 \\ 1 & -2 & 0 \\ 0 & 0 & 3 \end{bmatrix}$$

$$w_{1,2} = \begin{bmatrix} 0 \\ 1 \\ 0 \end{bmatrix} \pm i \begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix} \quad \text{belonging to } \lambda_{1,2} = -2 \pm i$$

$$w_3 = \begin{bmatrix} 0 \\ 0 \\ 1 \end{bmatrix} \quad \text{belonging to } \lambda_3 = 3$$

$$A = \begin{bmatrix} 0 & -1 & 0 \\ 1 & 0 & 0 \\ 0 & 0 & 2 \end{bmatrix}$$

$$w_{1,2} = \begin{bmatrix} 0 \\ 1 \\ 0 \end{bmatrix} \pm i \begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix} \quad \text{belonging to } \lambda_{1,2} = \pm i$$

$$w_3 = \begin{bmatrix} 0 \\ 0 \\ 1 \end{bmatrix} \quad \text{belonging to } \lambda_3 = 2$$

Invariance of the subspaces

- It can be shown that these subspaces are invariant under the flow $\boldsymbol{\varphi}(t, \mathbf{x}_0) = e^{t\mathbf{A}}\mathbf{x}_0$; this means a solution that starts in a subspace E^i remains in this space forever.
- In addition, for an n x n matrix $\mathbf{A}$ the subspaces span the whole IR^n:

$$\boxed{\mathrm{IR}^n = E^s \oplus E^c \oplus E^u}$$

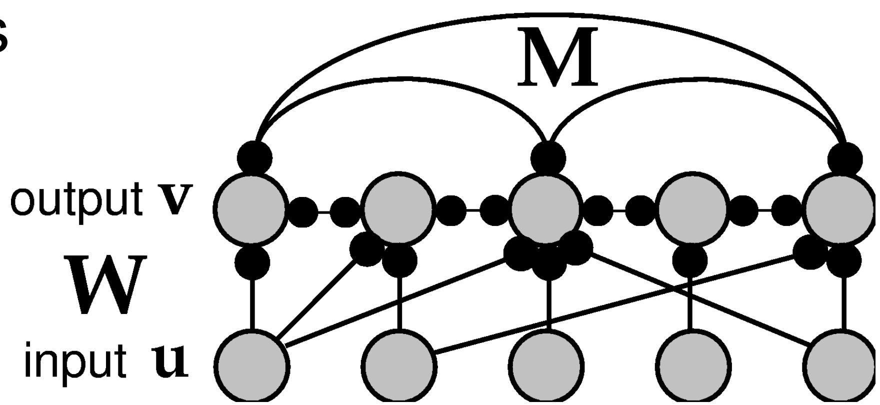
Example: linear recurrent network I

Recurent weights Feed-forward weights

- Mean firing rate approximation results in the DEQ:

  $\boxed{\tau \dot{\mathbf{v}} = -\mathbf{v} + \mathbf{M}\mathbf{v} + \mathbf{s}}$ with $\mathbf{s} = \mathbf{W}\mathbf{u}$.
- The system matrix $\mathbf{A} = \mathbf{M}\text{-}\mathbf{I}$ can be diagonalized; we assume that $\mathbf{M}$ is symmetric, implying that $\mathbf{M} = \mathbf{Q}\,\mathbf{\Lambda}\,\mathbf{Q}^{\mathrm{T}}$ with $\mathbf{\Lambda} = \mathrm{diag}(\lambda_1, \ldots, \lambda_N)$ and $\mathbf{Q}\mathbf{Q}^{\mathrm{T}} = \mathbf{I}$.
- Transforming the system to new coordinates $\mathbf{z}(t) = \mathbf{Q}^{\mathrm{T}}\mathbf{v}(t)$ we obtain the system: $\boxed{\tau \dot{\mathbf{z}} = -\mathbf{z} + \mathbf{\Lambda}\mathbf{z} + \mathbf{Q}^T\mathbf{s}}$
- When $\mathbf{q}_n$ signifies the columns of $\mathbf{Q}$ this implies the decoupled set of equations:

$$\tau \dot{z}_n = -z_n + \lambda_n z_n + \mathbf{q}_n{}^T \mathbf{s}$$



Example: linear recurrent network II

- The solution of these DEQs is:

$$z_n(t) = \frac{\mathbf{q}_n{}^T \mathbf{s}}{1-\lambda_n}\left(1-\exp\left(-\frac{1-\lambda_n}{\tau}t\right)\right) + z_n(0)\exp\left(-\frac{1-\lambda_n}{\tau}t\right)$$

- The stationary solution in original coordinates is thus:

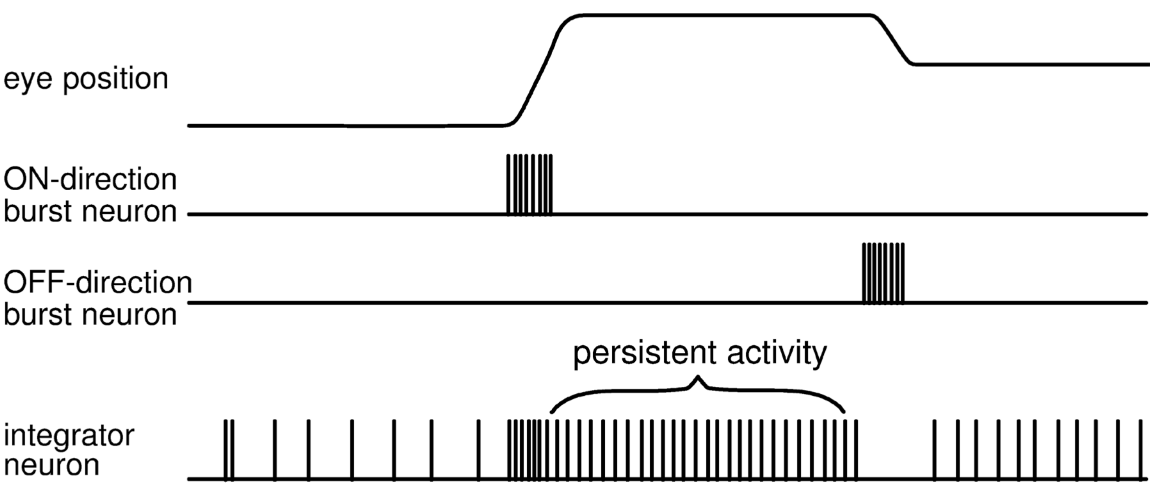
$$\boxed{\mathbf{v}(\infty) = \mathbf{Q}\mathbf{z}(\infty) = \sum_{n=1}^{N} \frac{\mathbf{q}_n{}^T \mathbf{s}}{1-\lambda_n}\mathbf{q}_n}$$

(assuming $\lambda_n < 1$)

- Dynamics defined by linear combination of independent ‘modes’, driven by projections of input signal onto the eigenvectors of $\mathbf{M}$.
- If one eigenvalue is close to one, and not the others, the corresponding eigenmode is selectively amplified: $\mathbf{v}(\infty) \approx \frac{\mathbf{q}_1{}^T \mathbf{s}}{1-\lambda_1}\mathbf{q}_1$. Similarly, multiple eigencomponents can be amplified.

Example: linear recurrent network III

- If $\lambda_1 = 1$ and $\lambda_n << 1$ for $n > 1$, the network can act as an **integrator** since then holds: $\tau \dot{z}_1 = \mathbf{q}_1{}^T \mathbf{s}$
  Solution (even for time-dependent input):
  $$z_1(t) = z_1(0) + \frac{1}{\tau} \int_0^t \mathbf{q}_1{}^T \mathbf{s}(t')\,\mathrm{d}t'$$
  With $\lambda_1 >> \lambda_n$ follows: $\boxed{\mathbf{v}(t) \approx \frac{\mathbf{q}_1}{\tau} \int_0^t \mathbf{q}_1{}^T \mathbf{s}(t')\,\mathrm{d}t'}$ (for sufficiently large times, so that the modes for the $\lambda_n << 1$ modes have decayed to zero)
- Neurons with such integrator charac-teristics have been found in the brain stem in networks that control eye position.



Things to remember

- Continuous vs. discrete DS $\rightarrow$ 2)
- Autonomous DS $\rightarrow$ 2)
- Linear DS $\rightarrow$ 2)
- Exponential of a matrix $\rightarrow$ 2)
- Phase portrait $\rightarrow$ 2)
- General form of the solution for linear autonomous DS $\rightarrow$ 2)
- Stability-related subspaces $\rightarrow$ 2)
- Neural network applications $\rightarrow$ 1,3)

Literature (for this lecture)

1) Dayan, P. & Abbott, L.F. (2001 / 2005) *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems.* MIT Press, Cambridge MA, USA. Chapter 7.

2) Perko, L. (1998) *Differential Equations and Dynamical Systems.* Springer-Verlag, Berlin. Chapter 1.

3) Wilson, H.R. (1999) *Spikes, Decisions, and Actions.* Oxford University Press, UK. Chapters 2-4. (Can be downloaded from Hugh Wilson's homepage !)