Dynamics of Neural Systems
Local analysis of nonlinear systems I

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Overview

- Basic concepts
- Examples

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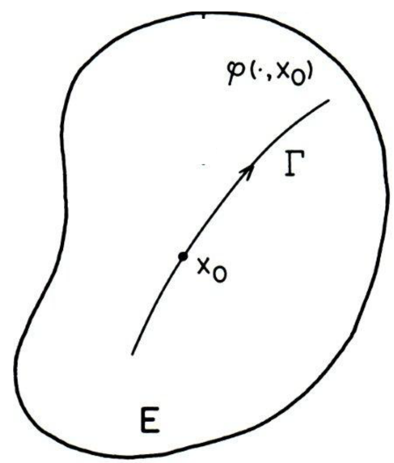
Nonlinear dynamical system

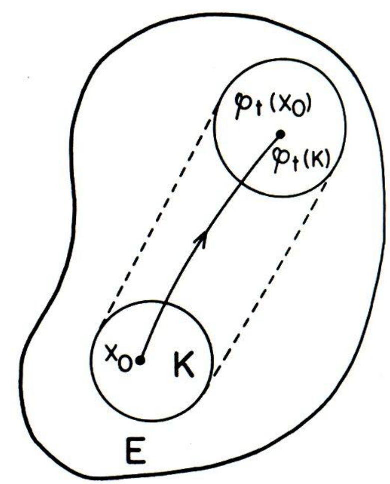
- In the following we regard (continuous) autonomous **nonlinear** dynamical systems: $\boxed{\dot{\mathbf{x}} = \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = \mathbf{f}(\mathbf{x}(t))}$
- It can be shown that if $\mathbf{f}$ is continuously differentiable ($\mathbf{f} \in C^1$) the corresponding initial value problem with $\mathbf{x}(0) = \mathbf{x}_0$ has a **unique solution** within an interval around $t = 0$ that depends continuously on the initial condition $\mathbf{x}_0$.

Flow of the differential equation I

- For linear dynamical systems we defined the flow:
  $$\boldsymbol{\varphi}_t : \mathbf{x}_0 \to \mathbf{x}(t) \quad \text{with} \quad \mathbf{x}(t) = e^{t\mathbf{A}}\mathbf{x}_0 =: \boldsymbol{\varphi}_t(\mathbf{x}_0)$$
- A similar definition can be made for nonlinear systems: The set of mappings of the form $\boldsymbol{\varphi}_t(\mathbf{x}_0) = \mathbf{x}(t)$ is called the **flow of the vector field** $\mathbf{f}(\mathbf{x})$.
- Analogy: Streaming fluid; trajectory describes the motion of individual particles.



Trajectory



Flow

Flow of the differential equation II

- Like for the linear case one can show the properties:

$$\boxed{\begin{aligned}&\boldsymbol{\varphi}_0(\mathbf{x}_0) = \mathbf{x}_0\\&\boldsymbol{\varphi}_{s+t}(\mathbf{x}_0) = \boldsymbol{\varphi}_s(\boldsymbol{\varphi}_t(\mathbf{x}_0))\\&\boldsymbol{\varphi}_{-t}(\boldsymbol{\varphi}_t(\mathbf{x})) = \mathbf{x} = \boldsymbol{\varphi}_t(\boldsymbol{\varphi}_{-t}(\mathbf{x}))\end{aligned}}$$

Flow of the differential equation III

- A set S is called **invariant** with respect to the flow if $\boldsymbol{\varphi}_t(S) \subset S$. (Implies: trajectories starting in S 'remain' in S.)
- If this condition is fulfilled for $t \geq 0$ ($t \leq 0$) the set is called **positively (negatively) invariant.**
- **Example:** For the nonlinear system

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}) = \begin{pmatrix} -x_1 \\ x_2 + x_1^2 \end{pmatrix}$$ one finds the solution:

$$\mathbf{x}(t) = \boldsymbol{\varphi}_t(\mathbf{x}_0) = \begin{pmatrix} x_{0,1}e^{-t} \\ x_{0,2}e^{t} + \dfrac{(x_{0,1})^2}{3}\left(e^{t} - e^{-2t}\right) \end{pmatrix}$$

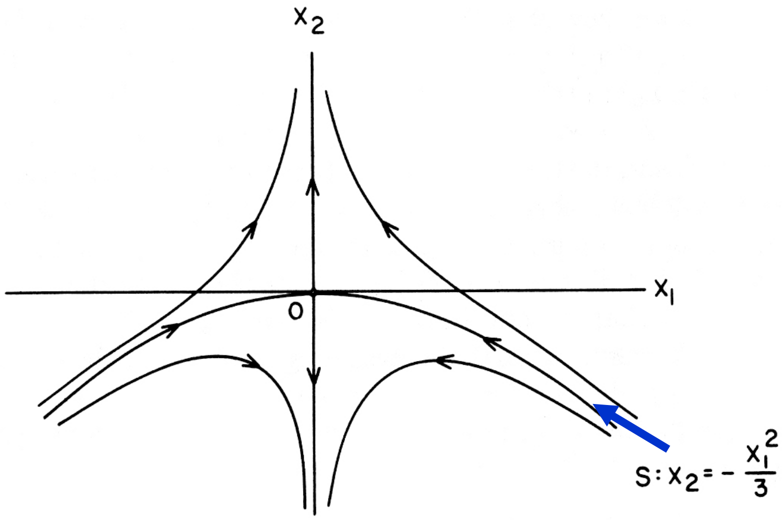
(Stable linear system for x_1 drives the unstable linear system for x_2 by nonlinear input term.)

Flow of the differential equation IV

- This implies that the set $S=\{\mathbf{x}\,|\,x_2=-x_1^2/3\}$ is invariant because then for the initial conditions

$$\mathbf{x}_0=\begin{pmatrix}x_{0,1}\\x_{0,2}\end{pmatrix}=\begin{pmatrix}x_{0,1}\\-x_{0,1}^2/3\end{pmatrix}\in S$$ follow the trajectories:

$$\boldsymbol{\varphi}_t(\mathbf{x}_0)=\begin{pmatrix}x_{0,1}e^{-t}\\-\frac{(x_{0,1})^2}{3}e^{t}+\frac{(x_{0,1})^2}{3}\left(e^{t}-e^{-2t}\right)\end{pmatrix}=\begin{pmatrix}x_{0,1}e^{-t}\\-\frac{(x_{0,1})^2}{3}e^{-2t}\end{pmatrix}\in S$$



(The trajectories starting in *S* therefore remain in *S*.)

Linearization and fixed points

- For the system $\boxed{\dot{\mathbf{x}} = \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = \mathbf{f}(\mathbf{x}(t))}$ points with $\mathbf{f}(\mathbf{x}) = \mathbf{0}$

  are called **equilibrium** or **fixed points** (of the dynamics).
- These points are also fixed points of the flow since then $\varphi_t(\mathbf{x}_0) = \mathbf{x}_0$ for all t.
- The linear DS $\boxed{\dot{\mathbf{x}}(t) = \mathbf{A}\mathbf{x}(t)}$ with $\mathbf{A} = \frac{\partial \mathbf{f}(\mathbf{x}_0)}{\partial \mathbf{x}}$ is called **linearized dynamics** in the point $\mathbf{x}_0$.

  Jacobian in $\mathbf{x}_0$
- A fixed point is called **hyperbolic** if $\mathbf{A}$ has *no* eigen-values with zero real part.

Linearization and fixed points

- A hyperbolic fixed point is called:
  sink if all eigenvalues of $\mathbf{A}$ have *negative* real parts.
  source if all eigenvalues of $\mathbf{A}$ have *positive* real parts.

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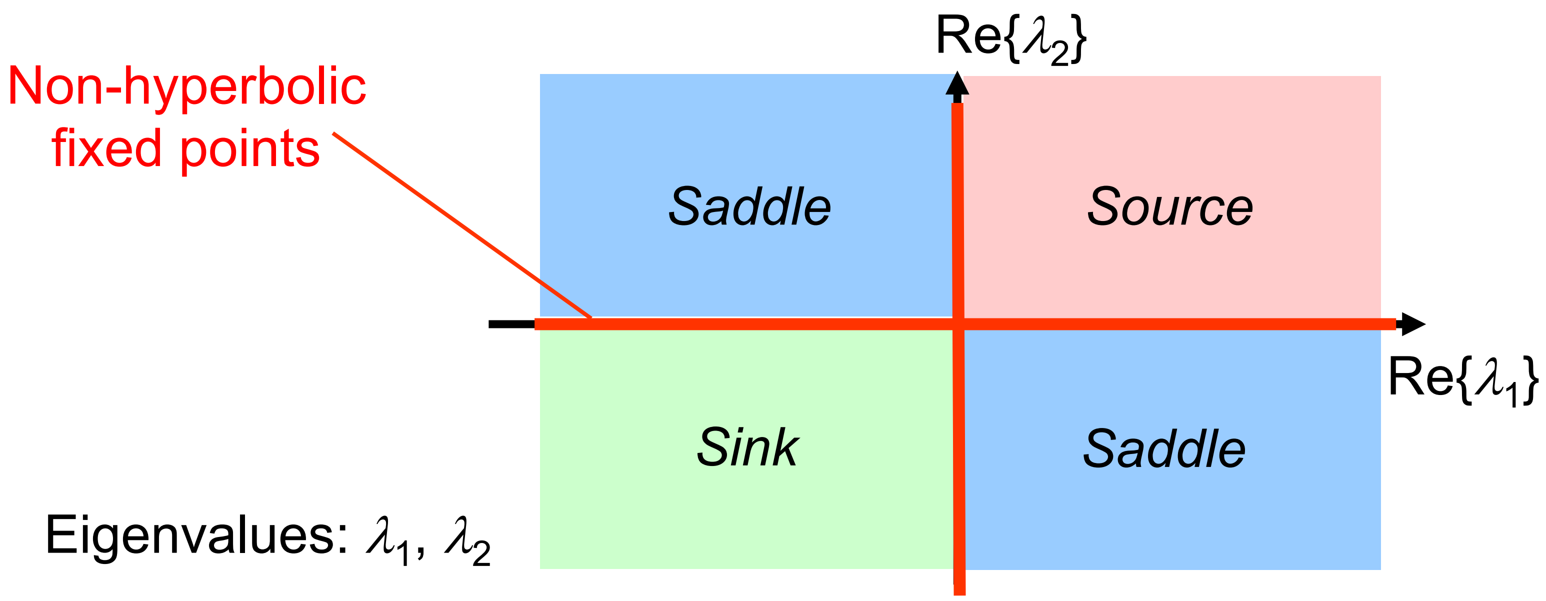
Example: 2D system



Overview

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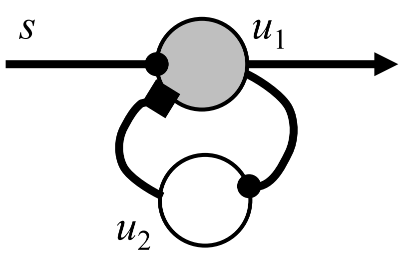
Example 1: divisive gain control I

- Network with feedback inhibition, originally as model for orientation-selective neurons in primary visual cortex (Wilson & Humanski, 1993); single stable fixed point.
- Differential equation:

Network



Output activity **Stimulus / input (≥ 0)**

$$\boxed{\begin{aligned} \tau_1 \frac{\mathrm{d}u_1}{\mathrm{d}t} &= -u_1(t) + \frac{s(t)}{1+u_2(t)} = f_1(u_1,u_2) \\ \tau_2 \frac{\mathrm{d}u_2}{\mathrm{d}t} &= -u_2(t) + 2u_1(t) \quad = f_2(u_1,u_2) \end{aligned}}$$

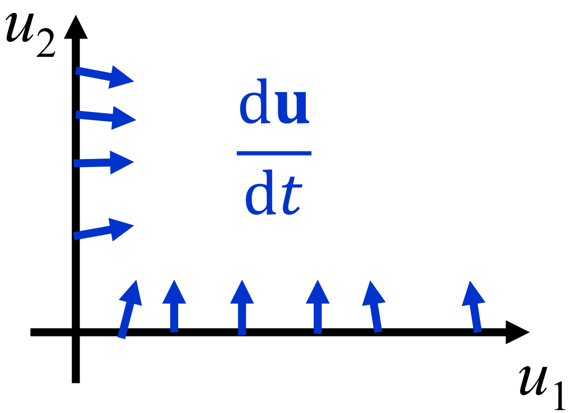
Activity of inhibitory neuron

Example 1: divisive gain control II

- It can be shown that for $u_1(0) \geq 0$ and $u_2(0) \geq 0$ implies $u_i(t) \geq 0$ for $t \geq 0$, i.e. solutions do not leave the first quadrant:

$$u_1 = 0 \Rightarrow \frac{\mathrm{d}u_1}{\mathrm{d}t} \geq 0 \text{ if } s \geq 0 \text{ and } -1 \leq u_2$$

$$u_2 = 0 \Rightarrow \frac{\mathrm{d}u_2}{\mathrm{d}t} \geq 0 \text{ if } u_1 \geq 0$$



Example 1: divisive gain control III

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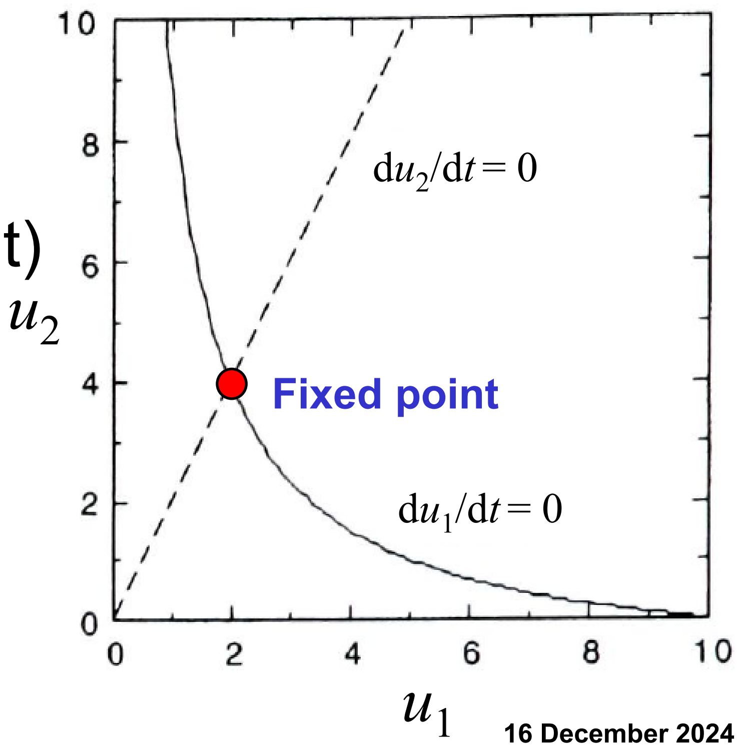
$$u_2 = 0 \Rightarrow \frac{\mathrm{d}u_2}{\mathrm{d}t} \geq 0 \text{ if } u_1 \geq 0$$

- **Fixed point $\mathbf{u}_0$** (in positive quadrant) from intersection of **isoclines** (curves with $\frac{\mathrm{d}u_i}{\mathrm{d}t} = 0$): $u_2 = 2u_1$

$$u_1 = \frac{s}{1+u_2} = \frac{s}{1+2u_1} \Leftrightarrow 2u_1^{\,2} + u_1 - s = 0$$

$$\Rightarrow u_{0,1} = \frac{-1+\sqrt{1+8s}}{4} \qquad u_{0,2} = 2u_{0,1}$$

Isoclines for $s = 10$

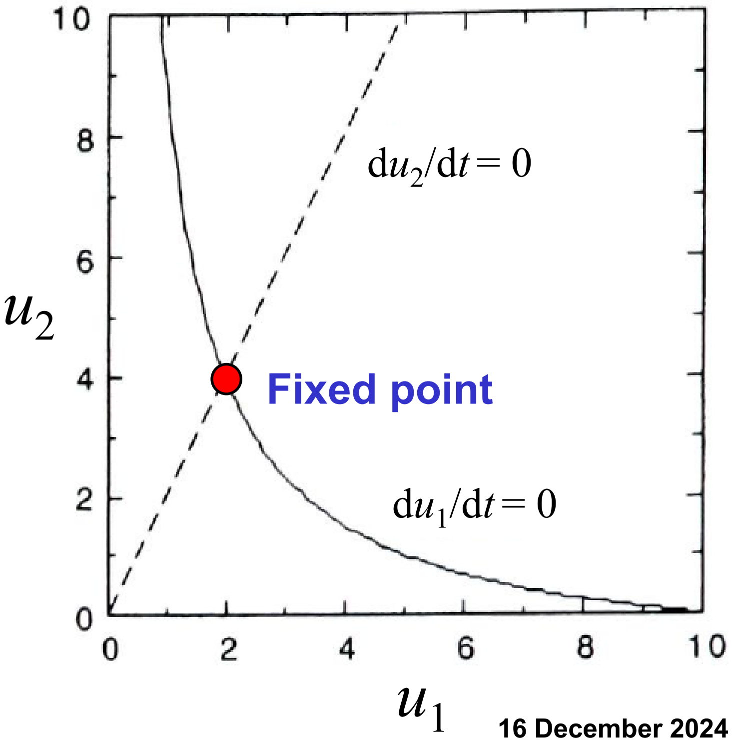


Example 1: divisive gain control IV

- Linearized dynamics $\dot{\mathbf{u}}(t) = \mathbf{A}\mathbf{u}(t)$ with:

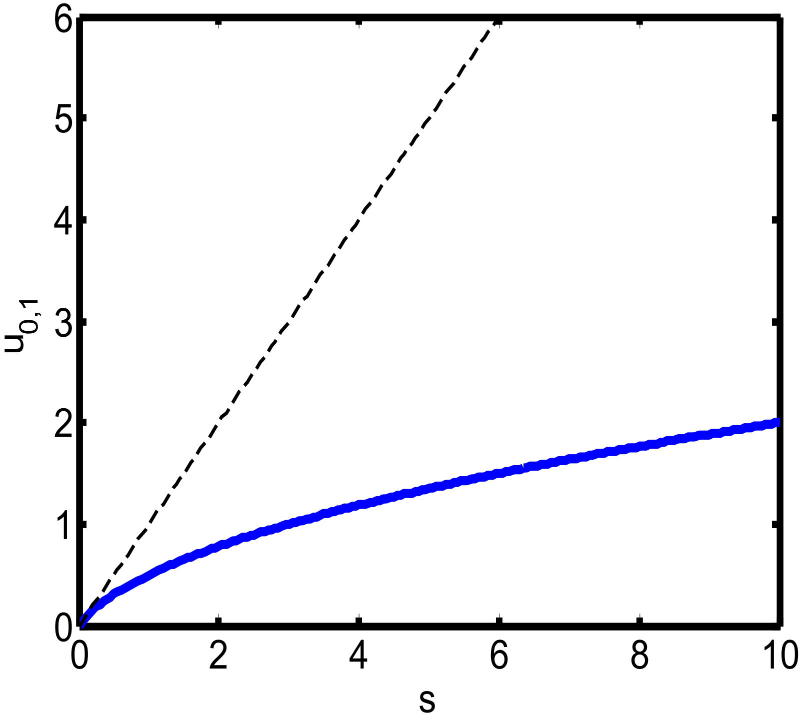
$$\mathbf{A} = \left.\frac{\partial \mathbf{f}}{\partial \mathbf{u}}\right|_{\mathbf{u}_0} = \begin{bmatrix} -\dfrac{1}{\tau_1} & -\dfrac{s}{\tau_1(1+u_2)^2} \\ \dfrac{2}{\tau_2} & -\dfrac{1}{\tau_2} \end{bmatrix}$$

Isoclines for $s = 10$

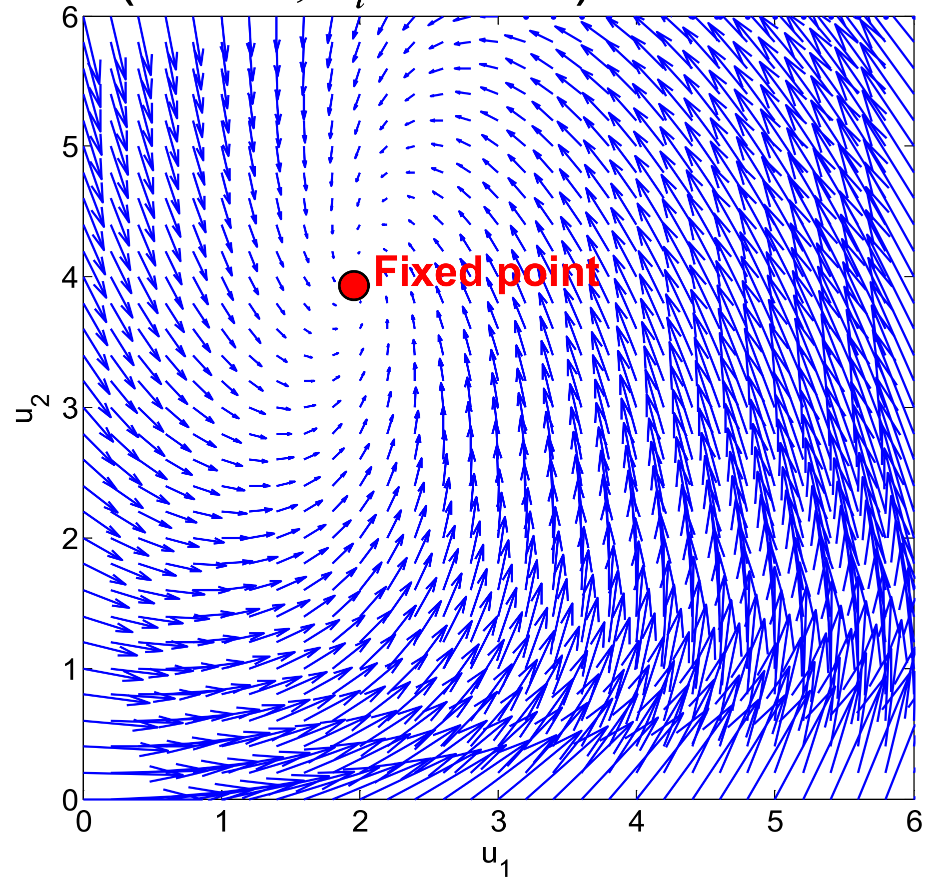


Example 1: divisive gain control V

- Contrast differences of s are 'compressed' by the divisive gain control.



- Plot of the vector field: $\frac{\mathrm{d}\mathbf{u}}{\mathrm{d}t}$ $(s = 10;\ \tau_i = 10\mathrm{ms})$

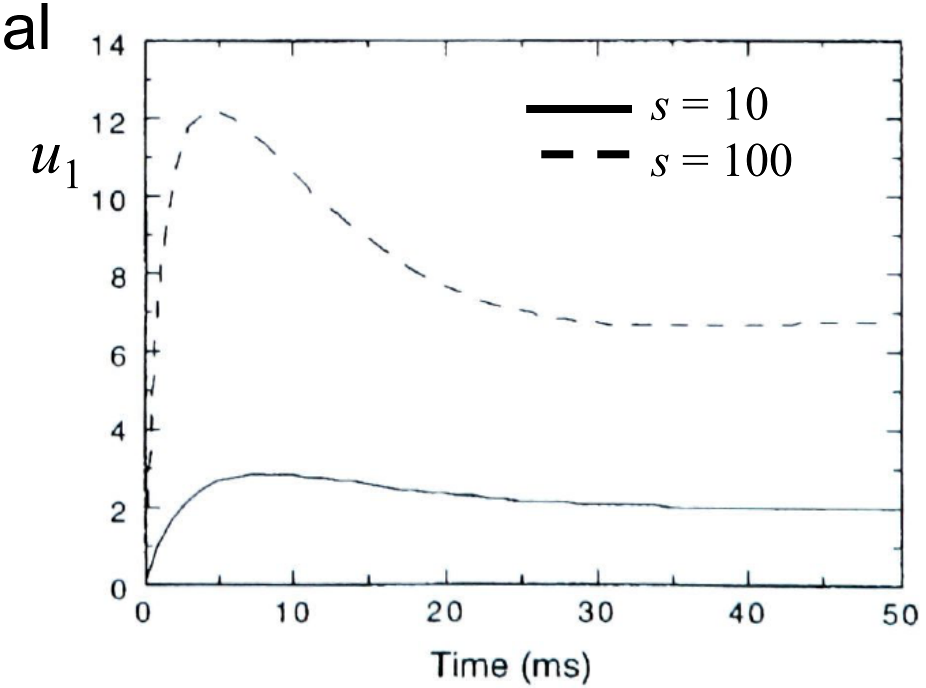


Example 1: divisive gain control VI

- Example parameters: $s = 10$ and $\tau_i = 10\text{ms} \Rightarrow$

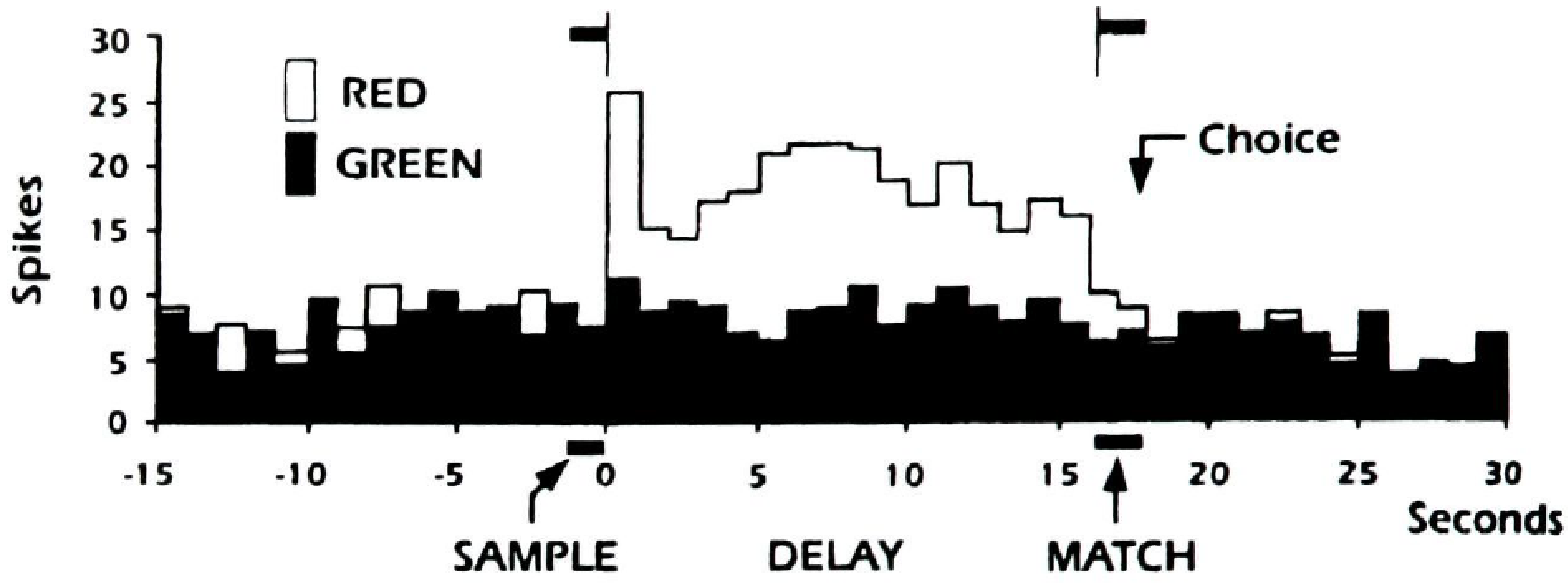
$$\mathbf{u}_0 = \begin{pmatrix} 2 \\ 4 \end{pmatrix} \qquad \mathbf{A} = \begin{bmatrix} -100 & -40 \\ 200 & -100 \end{bmatrix}$$

- The eigenvalues of $\mathbf{A}$ are: $\lambda_{1,2} = -100 \pm 89.44\, i$; this implies an stable spiral solution for the linearized system.
- The fixed point of the original system is thus hyperbolic and a **sink**.
- The oscillatory nature is evident in the simulation (overshoot).



Example 2: short term memory I

- Neurons, for example in area IT or prefrontal cortex show **delay activity**: Their firing rate remains increased after presentation of a target stimulus (e.g. color pattern) until a behavioral response has to be given by the animal. The activity has thus to be maintained in absence of the stimulus.

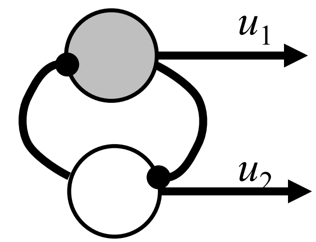


Example 2: short term memory II

- Simple model: two neurons with excitatory coupling.
- Model equation: $(w > 0)$

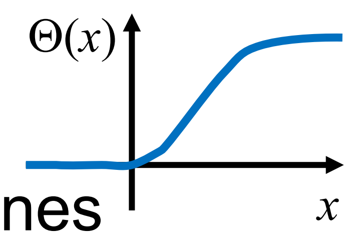
$$\boxed{\begin{aligned}\tau \frac{\mathrm{d}u_1}{\mathrm{d}t} &= -u_1(t) + w\Theta(u_2(t)) \\ \tau \frac{\mathrm{d}u_2}{\mathrm{d}t} &= -u_2(t) + w\Theta(u_1(t))\end{aligned}}$$

Network

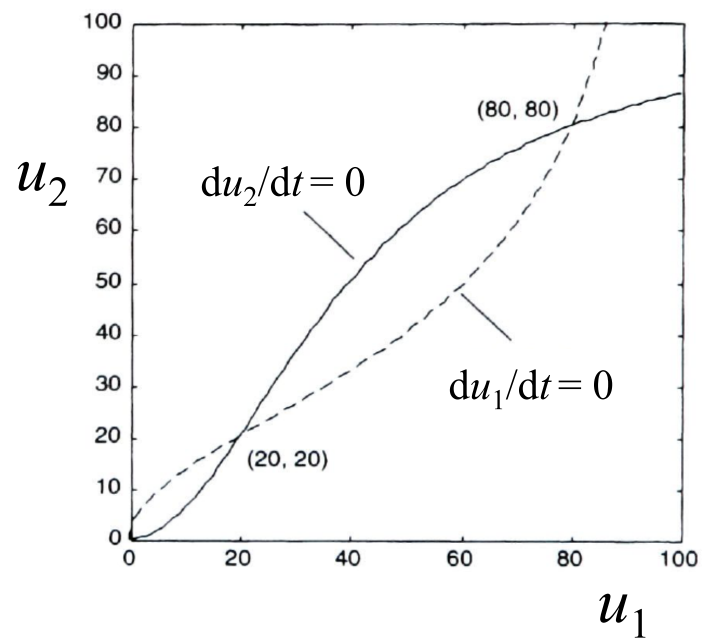


where the sigmoidal nonlinear threshold function is given by the Naka-Rushton function:

$$\Theta(x) = \begin{cases} \dfrac{(3x)^2}{k^2 + (3x)^2} & \text{for} \quad x \geq 0 \\ 0 & \text{otherwise} \end{cases}$$

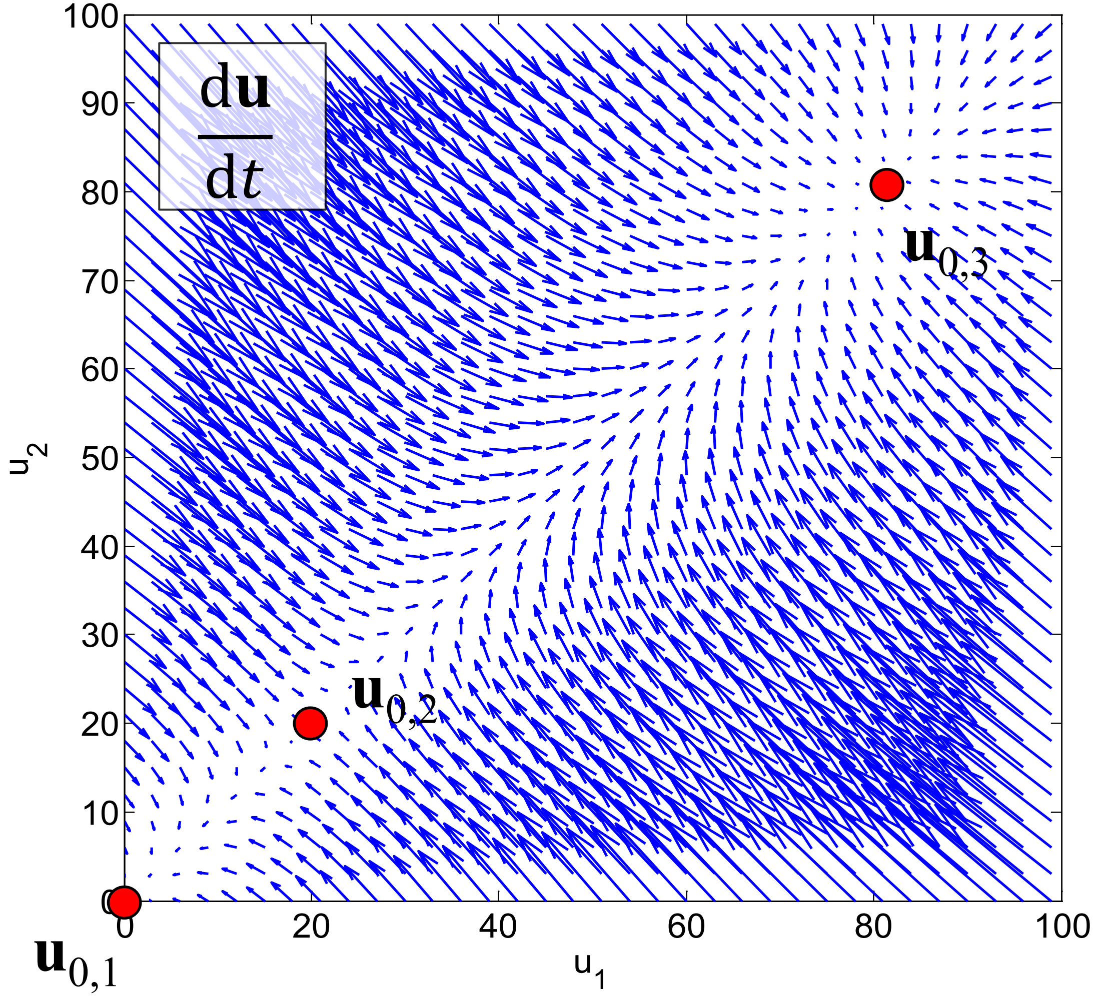


- In this case the isoclines intersect at three points with $u_1 = u_2$.



Example 2: short term memory III

- Phase portrait:



Example 2: short term memory IV

- Fixed points: One is $\mathbf{u}_0 = \mathbf{0}$; the others follow from solving $u_{0,1} = w\Theta(u_{0,2})$ and $u_{0,2} = w\Theta(u_{0,1})$ resulting in the equation $u_{0,i}{}^3 - wu_{0,i}{}^2 + \left(\frac{k}{3}\right)^2 u_{0,i} = 0$, $i = 1,2$, with the additional two solutions:

$$u_{0,i} = \frac{w}{2} \pm \sqrt{\left(\frac{w}{2}\right)^2 - \left(\frac{k}{3}\right)^2}$$

- The system matrix of the linearized system is $\mathbf{A} = \frac{1}{\tau}\begin{bmatrix} -1 & w\Theta'(u_{0,2}) \\ w\Theta'(u_{0,1}) & -1 \end{bmatrix}$ which can be computed using the derivative: $\Theta'(u) = \frac{18\,k^2 u}{(k^2 + 9u^2)^2} 1(u)$

- For the parameters: $k = 120$, $w = 100$, and $\tau = 20\text{ms}$ one finds the following fixed points and stabilities:

Example 2: short term memory V

$$\mathbf{u}_{0,1} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}: \quad \mathbf{A} = \begin{bmatrix} -50 & 0 \\ 0 & -50 \end{bmatrix} \Rightarrow \quad \lambda_1 = \lambda_2 = -50 \qquad \text{(sink)}$$

$$\mathbf{u}_{0,2} = \begin{pmatrix} 20 \\ 20 \end{pmatrix}: \quad \mathbf{A} = \begin{bmatrix} -50 & 80 \\ 80 & -50 \end{bmatrix} \Rightarrow \quad \lambda_1 = -130, \lambda_2 = 30 \qquad \text{(saddle)}$$

$$\mathbf{u}_{0,3} = \begin{pmatrix} 80 \\ 80 \end{pmatrix}: \quad \mathbf{A} = \begin{bmatrix} -50 & 20 \\ 20 & -50 \end{bmatrix} \Rightarrow \quad \lambda_1 = -70, \lambda_2 = -50 \qquad \text{(sink)}$$

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- The two stable fixed points $\mathbf{u}_{0,1} = \mathbf{0}$ and $\mathbf{u}_{0,3}$ model the two stable states of the neurons that encode memorized information: memory activity remains present / not present (in spite of the absence of an external input).

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- The two stable fixed points $\mathbf{u}_{0,1} = \mathbf{0}$ and $\mathbf{u}_{0,3}$ model the two stable states of the neurons that encode memorized information: memory activity remains present / not present (in spite of the absence of an external input).
- The system is **bistable**: It has two stable states.

Example 2: short term memory VI

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- As example, we extend our model by an input signal s. How much excitatory / inhibitory input is required in order to store or delete the memory activity?

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- As example, we extend our model by an input signal s. How much excitatory / inhibitory input is required in order to store or delete the memory activity?
- Extended model:

$$\boxed{\begin{aligned}\tau\frac{\mathrm{d}u_1}{\mathrm{d}t} &= -u_1(t) + w\Theta(u_2(t)+s)\\ \tau\frac{\mathrm{d}u_2}{\mathrm{d}t} &= -u_2(t) + w\Theta(u_1(t)+s)\end{aligned}}$$

Example 2: short term memory VI

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- For very strong inputs s the neurons are forced into the active state, and the state with both neurons off becomes unstable.

Example 2: short term memory VII

- For very low inputs the neurons cannot activate each other; and the attractor with both neurons ‘on’ becomes unstable.

Example 2: short term memory VII

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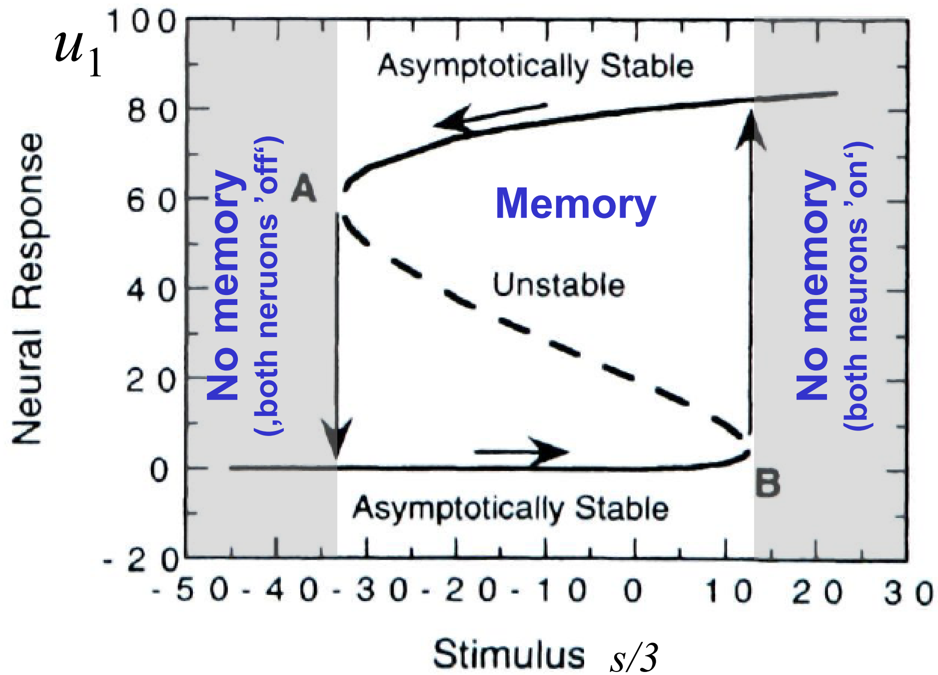
- The stationary neural response can be plotted against the stimulus strength, resulting in a **hysteresis plot**; all 3 fixed points exist only in limited range of the parameter s.



Example 2: short term memory VII

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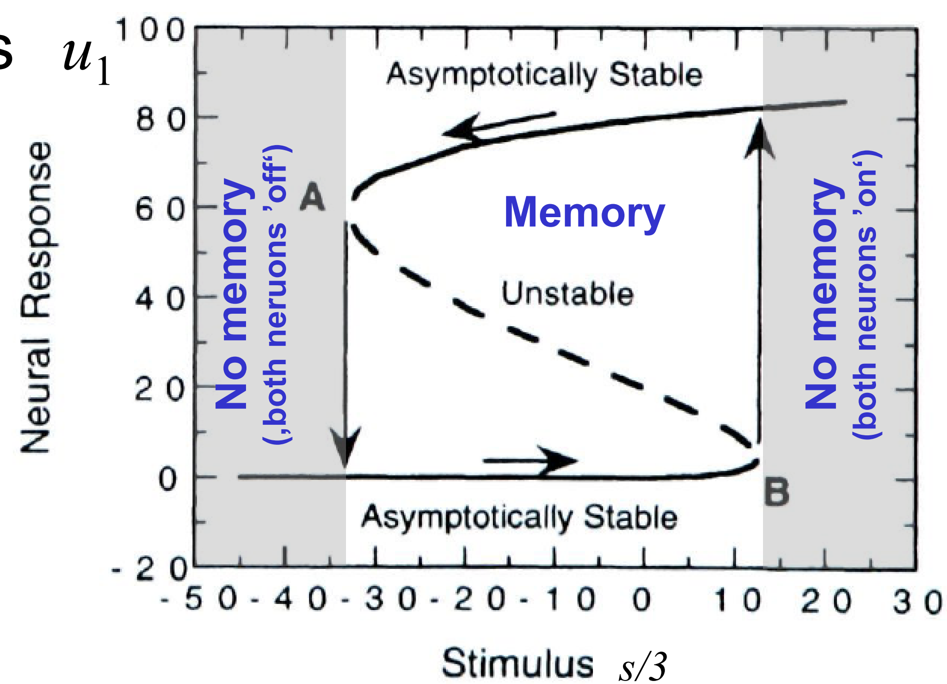
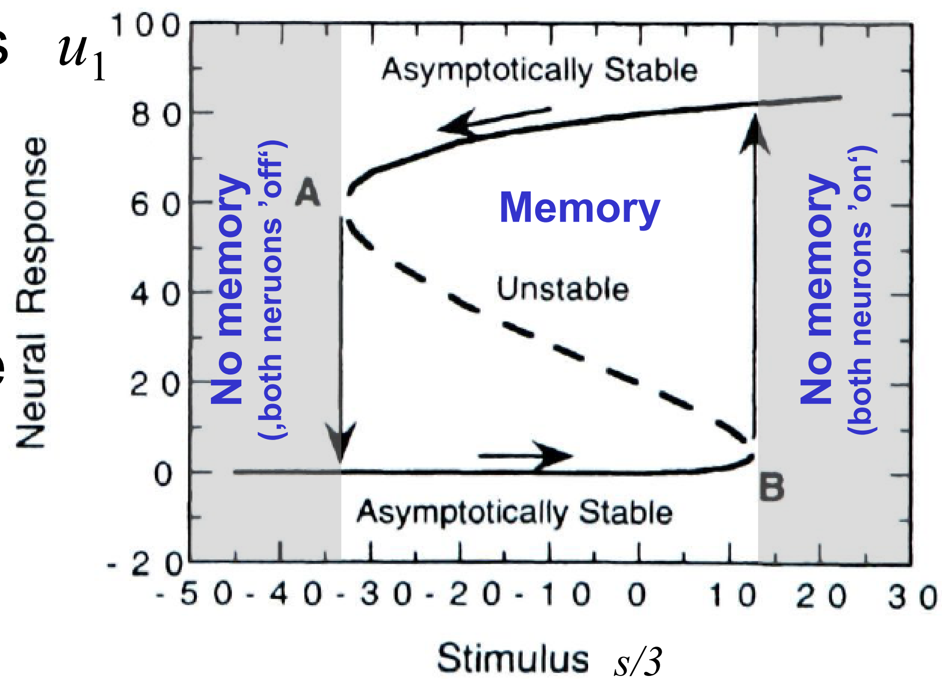
- The stationary neural response can be plotted against the stimulus strength, resulting in a **hysteresis plot**; all 3 fixed points exist only in limited range of the parameter s.
- If the stimulus parameter is changed the neurons tend to remain in the previous activation state.



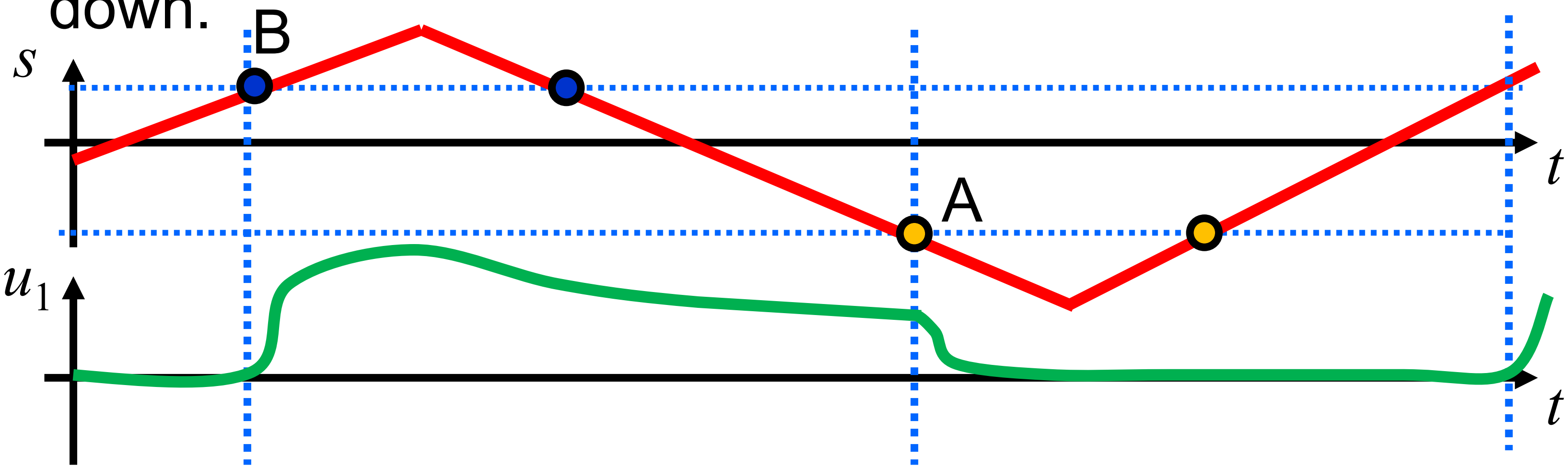
Example 2: short term memory VII

- For very low inputs the neurons cannot activate each other; and the attractor with both neurons ‘on’ becomes unstable.
- The stationary neural response can be plotted against the stimulus strength, resulting in a **hysteresis plot**; all 3 fixed points exist only in limited range of the parameter s.
- If the stimulus parameter is changed the neurons tend to remain in the previous activation state.
- A switch to the other stable state occurs if initial fixed point becomes unstable.



Example 2: short term memory VIII

- This tendency explains the hysteresis loop that is measured if s is changed continuously and slowly up and down.



- At the points A and B the number and type of fixed points changes; these points are called **bifurcation points** of the dynamics. (Much more about this topic later.)

Example 2: short term memory IX

- The discussed model does not account for **forgetting**.
- Simple model: add adaptation of the memory neurons.
- Data suggests that adaptation changes the threshold parameter k in the threshold function.
- With the new threshold function $\Theta(x,k) = \left[\frac{x^2}{k^2 + x^2} \right]$

  a dynamics with threshold adaptation can be easily derived:

$$\boxed{\begin{aligned}
\tau \frac{\mathrm{d}u_1}{\mathrm{d}t} &= -u_1(t) + w\Theta(u_2(t) + s, k_0 + a_1(t)) \\
\tau \frac{\mathrm{d}u_2}{\mathrm{d}t} &= -u_2(t) + w\Theta(u_1(t) + s, k_0 + a_2(t)) \\
\tau_a \frac{\mathrm{d}a_1}{\mathrm{d}t} &= -a_1(t) + cu_1(t) \\
\tau_a \frac{\mathrm{d}a_2}{\mathrm{d}t} &= -a_2(t) + cu_2(t)
\end{aligned}}$$

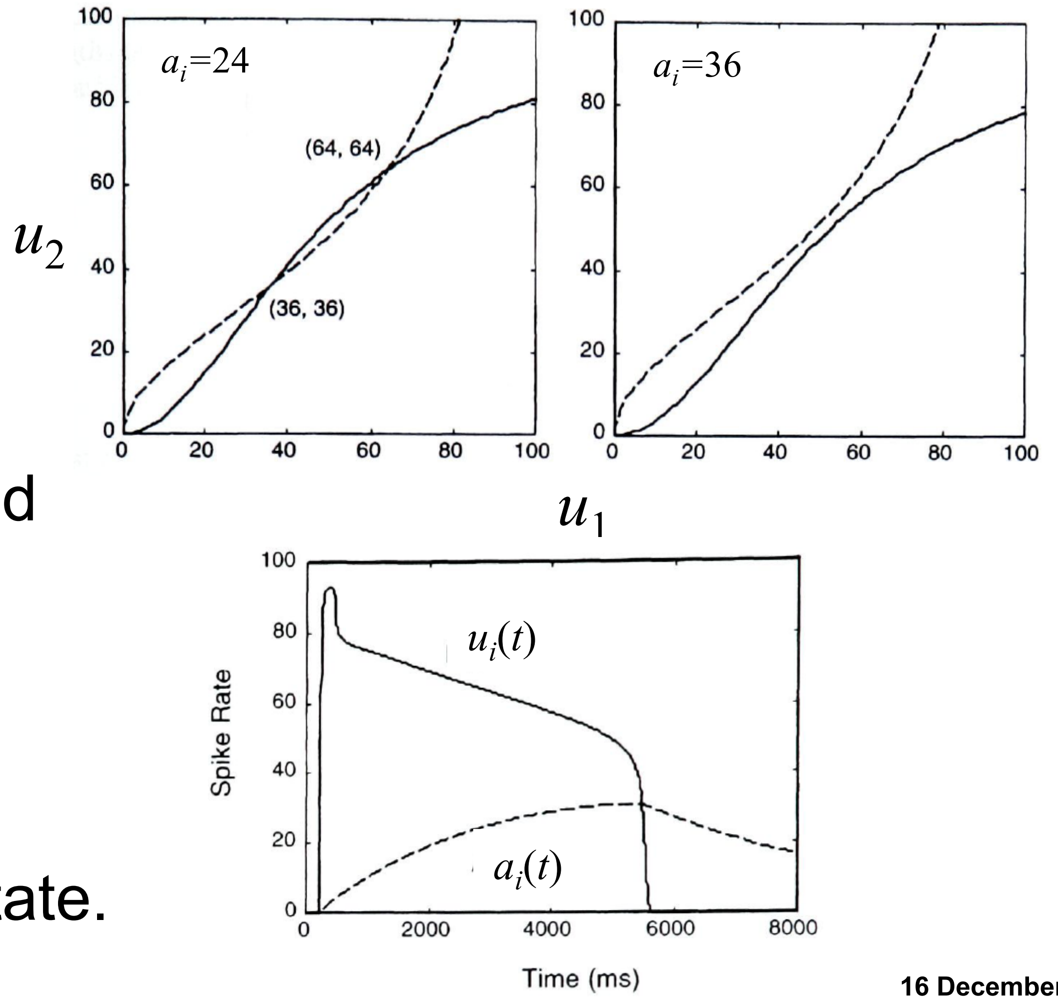
Adaptation dynamics

Assumption:

$$\boxed{\tau_a >> \tau}$$

Example 2: short term memory X

- For larger values of the adaptation variable a_i the attractor with nonzero activity disappears.
- Adaptation dynamics much slower than memory dynamics ($\tau_a >> \tau$); forgetting (instability of activated state after many seconds).
- Results in slow oscillation between the active and inactive state.



Things to remember

- Flow of the differential equation $\rightarrow$ 2)
- Positively / negatively invariant sets $\rightarrow$ 2)
- Fixed point $\rightarrow$ 2)
- Linearized dynamics $\rightarrow$ 2)
- Hyperbolic fixed point $\rightarrow$ 2)
- Analysis using isoclines $\rightarrow$ 3)
- Multi-stability, bifurcation, and hysteresis $\rightarrow$ 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 2.

3) Wilson, H.R. (1999) *Spikes, Decisions, and Actions.* Oxford University Press, UK. Chapters 6 and 14.