Dynamics of Neural Systems
Oscillations I: Mathematics

Martin A. Giese (including slides from C. Geisler)
Martin.giese@uni-tuebingen.de

Feb 3, 2025

Hertie-Institut
für klinische Hirnforschung

CIN
Werner Reichardt
Centre for Integrative
Neuroscience

Overview

- Relevance of oscillations in neuroscience
- Limit cycles

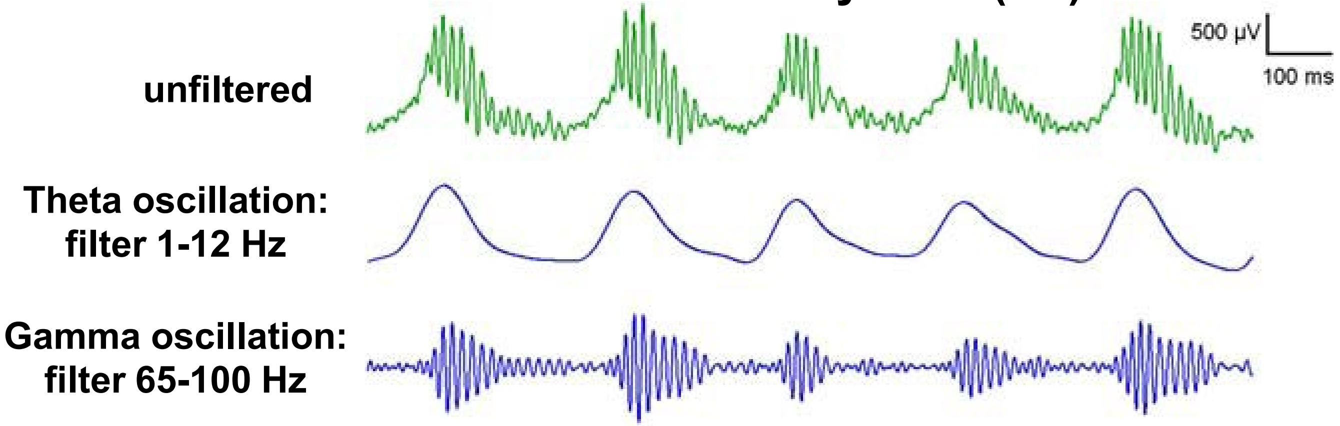
Overview

- Relevance of oscillations in neuroscience
- Limit cycles

Oscillations in the nervous system

- Oscillation ubiquitous in living organisms.
- Important role in other organs (circadian modulation, cardiac rhythm, breathing, locomotion, …).
- Important role also in the nervous system and in the function of individual neurons.
- Gamma oscillations of LFP in olfactory bulb (Adrian, 1942).

LFP olfactory bulb (rat)



Rojas-Libano & Key (2008)

Electroencephalogram (EEG)

Mirror galvano-meter

- First experiments in rabbits and monkeys with electrodes on surface of grey substance using galvanometer (Caton, 1875).

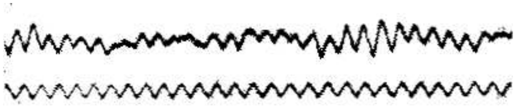
Electroencephalogram (EEG)

Mirror galvano-meter

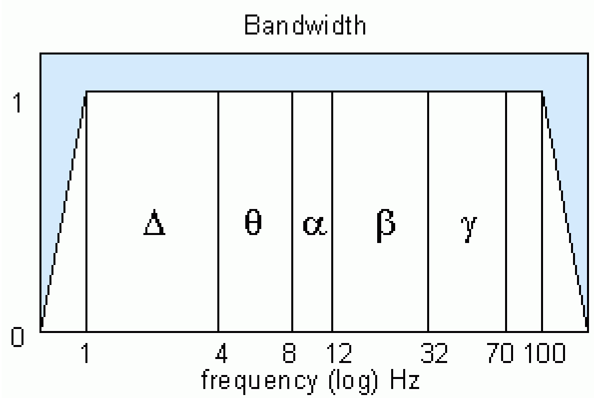
- First experiments in rabbits and monkeys with electrodes on surface of grey substance using galvanometer (Caton, 1875).
- First human EEG recorded in 1924 by Hans Berger (published 1929).
- Frequency bands related to modes of cortical function (e.g. sleep stages) and pathological states.

H. Berger

First recorded EEG

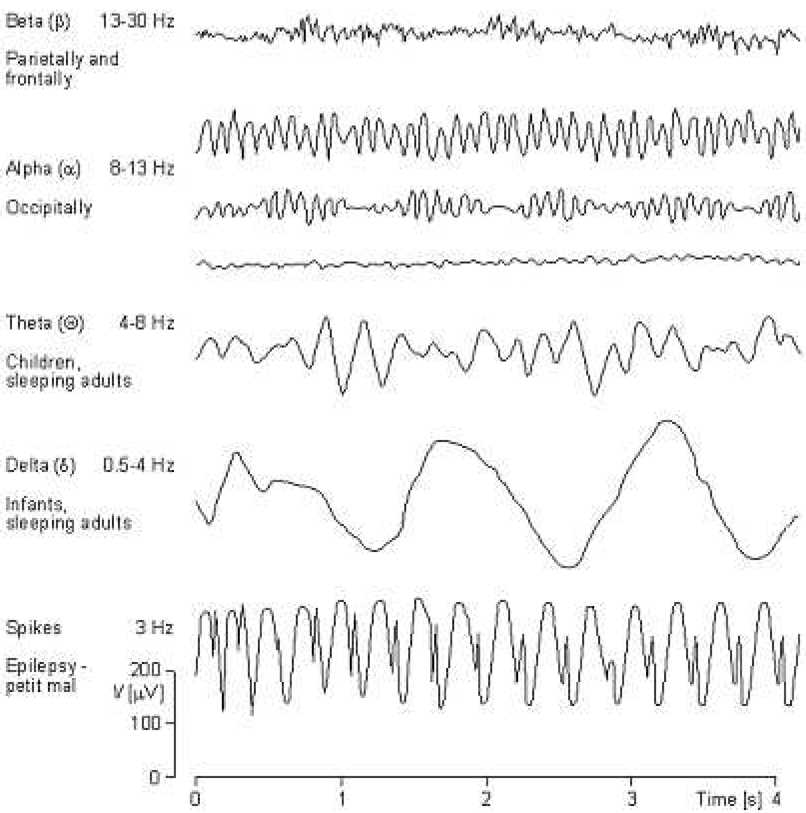


EEG frequency bands



Electroencephalogram (EEG)

Example EEG patterns

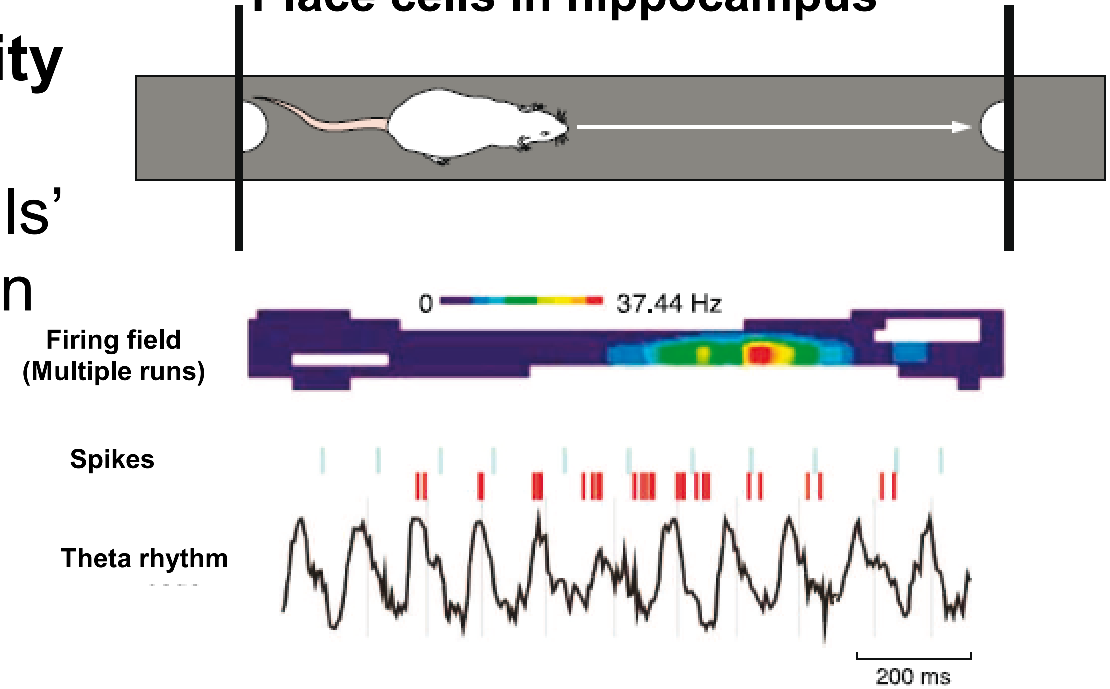


Comparison of EEG bands				
Band	**Frequency (Hz)**	**Location**	**Normally**	**Pathologically**
Delta	< 4	frontally in adults, posteriorly in children; high-amplitude waves	adult slow-wave sleep, in babies; continuous attention tasks	subcortical + midline lesions; hydrocephalus
Theta	4 – 7	Not task-related	high in young children, during drowsiness + idling	subcortical lesions, encephalopathy, midline disorders
Alpha	8 – 15	posterior regions of head, centrally at rest	relaxed, with closed eyes	coma
Beta	16 – 31	Frontally, both sides, low-amplitude waves	thinking, high alertness, anxiety	increased with benzodiazepines
Gamma	>32	Somatosensory cortex	Cross-modal perception , memory tasks	decreased gamma-band activity might correlate with cognitive decline
Mu	8 – 12	Sensorimotor cortex	Shows rest-state in motor taks	Mu suppression during activity of 'mirror neuron system', maybe reduced in autism

Oscillations of cortical neurons I

- Regular spike train corresponds to an oscillatory dynamics.
- Characteristic oscillatory states in specific subsystems; examples follow.
- **Theta** (7-8 Hz) **activity** in the rat: location encoded in 'place cells' by phase of oscillation when neurons fire.

Place cells in hippocampus

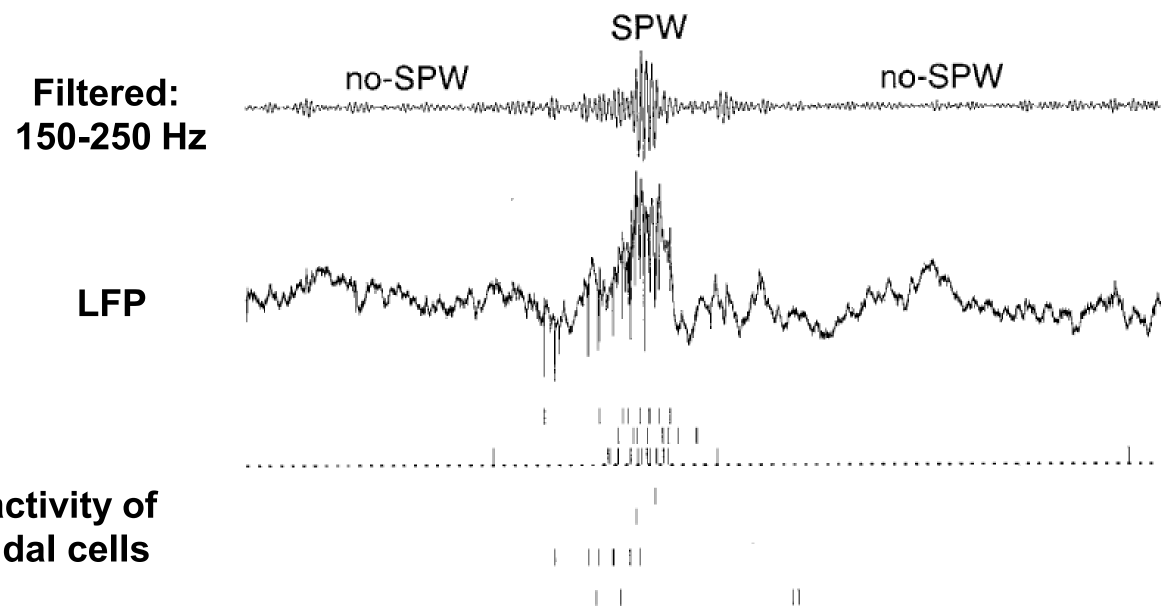


Buszaki & Draguhn (2004)

Oscillations of cortical neurons II

- **Sharp-wave ripples** during slow-wave sleep (> 150 Hz) in the rat hippo-campus; spiking prefe-rentially during the sharp-wave ripples (SPW).

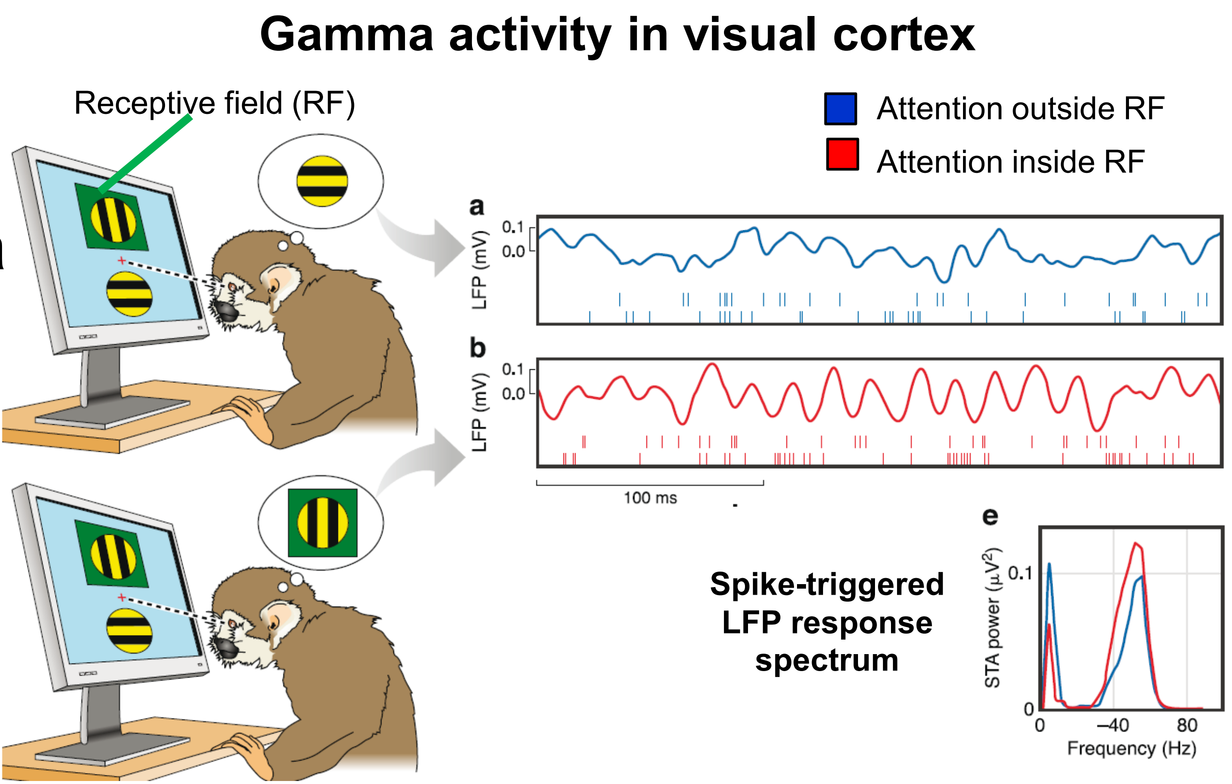
Activity of cells in rat hippocampus



Wang (2010)

Oscillations of cortical neurons III

- **Gamma activity** (50-80 Hz) in monkey primary visual cortex: for same stimulus covariation with attentional state; coexistence with theta rhythm; gamma activity higher and alpha activity lower in attentive state.
- Gamma syn-chronization involved in fea-ture binding (?)

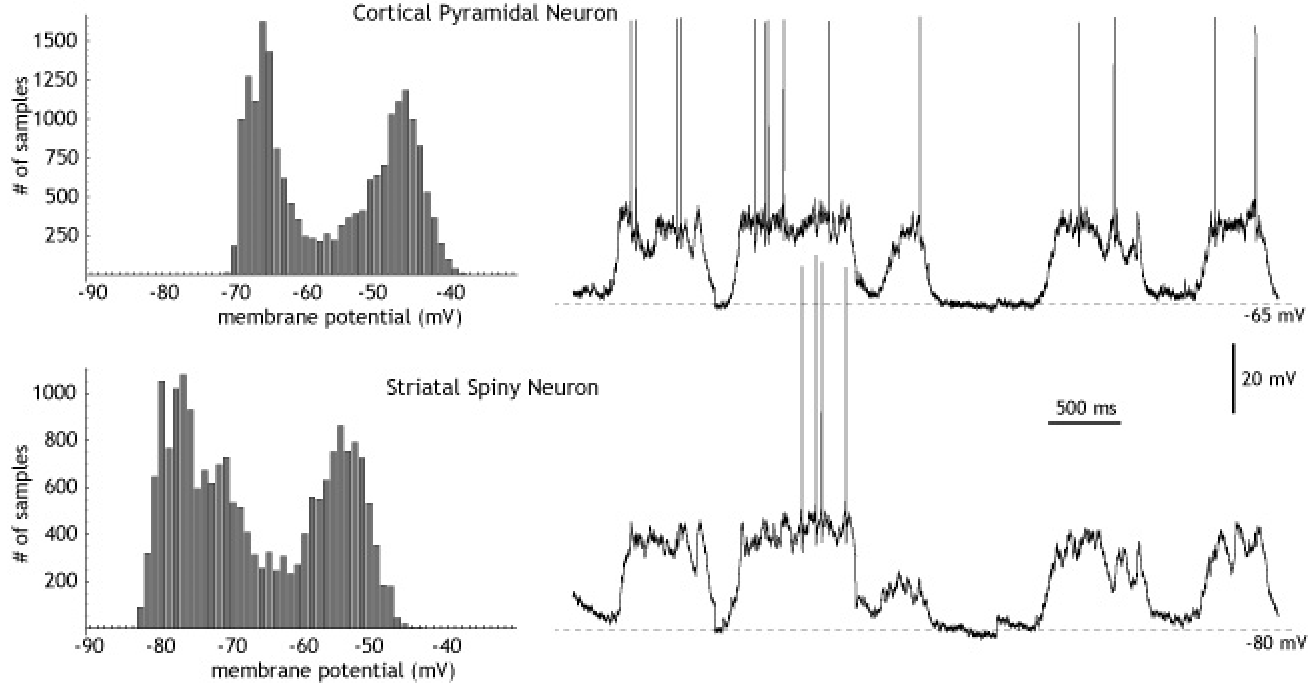


Wang (2010)

Oscillations of cortical neurons IV

- **Slow oscillations between up and down states** (about 1 Hz): two preferred plateau membrane potentials; bimodal histogram of membrane potentials; spiking preferentially in up-state; many cortical neurons show this bistability.

Up and down states in cortical neurons

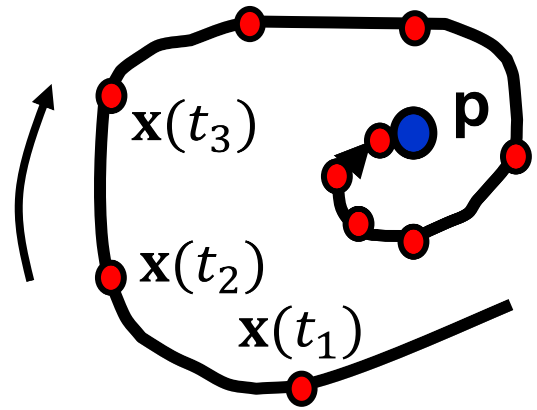


Overview

- Relevance of oscillations in neuroscience
- Limit cycles

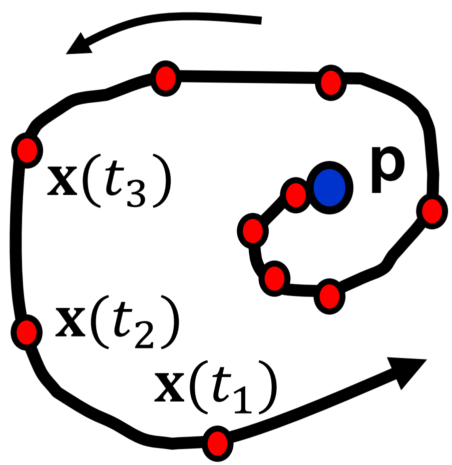
Limit sets of dynamical systems

- Stable oscillations in nonlinear systems 'attract' neighbor-ing trajectories (⇔ linear systems: oscillations marginally stable; small perturbation results in different oscillation amplitude); we thus need to define 'attraction'.
- For the dynamical system $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$ points $\mathbf{p}$ for which there exists a sequence $t_n \to \infty$ with $\lim_{n\to\infty} \phi(t_n, \mathbf{x}) = \mathbf{p}$ are called **ω-limit points** of the trajectory (assuming $\mathbf{x}$ is part of the trajectory).



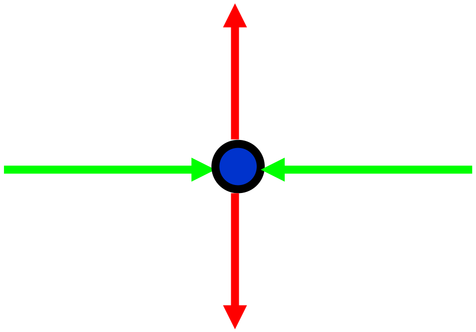
Limit sets of dynamical systems

- For the dynamical system $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$ points $\mathbf{p}$ for which there exists a sequence $t_n \to -\infty$ with $\lim_{n\to\infty} \phi(t_n, \mathbf{x}) = \mathbf{p}$ are called **α-limit points** of the trajectory (assuming $\mathbf{x}$ is part of the trajectory).
- The sets of all limit points are called the **ω-limit set** (**α-limit set**) of the trajectory.
  They can be shown to be invariant under the flow mapping ϕ.



Attractors

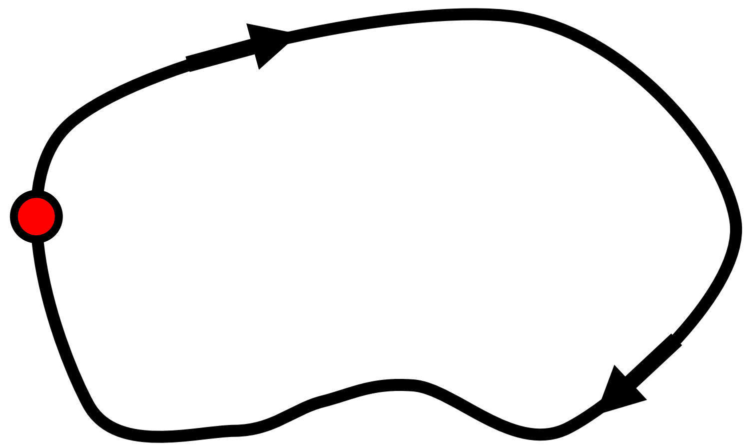
- **Def.:** An invariant set A (in state space) is an **attractor** if for a neigborhood U of A each $\mathbf{x} \in \mathrm{U}$ fulfills: $\phi_t(\mathbf{x}) \in U$ for $t \geq 0$ and $\mathbf{x}(t) \rightarrow A$ for $t \rightarrow \infty$, and if A contains a dense orbit.
- Dense orbit condition excludes unions of separated small attracting sets.
- An isolated fixed point with $\phi(t, \mathbf{x}_0) = \mathbf{x}_0$ is its own ω– or α-limit set; a stable isolated fixed point is an attractor.
- A saddle point is also ω–limit set for certain trajectories, but not for others in the neighborhood of the fixed point. It is thus no attractor.



Limit cycle I

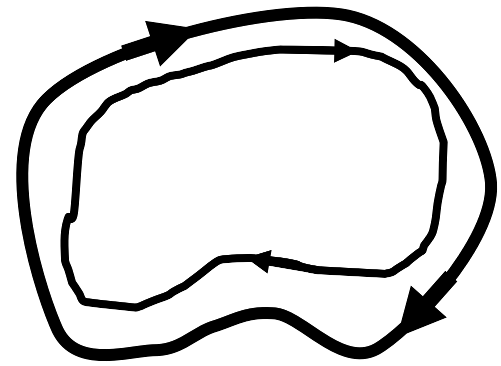
- A trajectory (orbit) of the dynamical system is **periodic** if it fulfills $\phi(t, \mathbf{x}_0) = \phi(t+T, \mathbf{x}_0)$ for some $T > 0$. The minimal T is called the **period** of the oscillation.
- This implies $\phi(t, \mathbf{x}_0) = \phi(t+nT, \mathbf{x}_0)$ for $n \in \mathrm{I\!N}$.
- The frequency of the oscillation is thus $f = 1 / T$.

$$\mathbf{x}(t) = \mathbf{x}(t+nT)$$

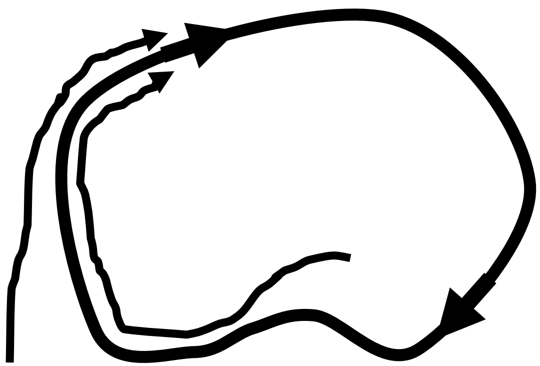


Limit cycle I

- A periodic orbit Γ is **stable** if all trajectories that are closer than ε to Γ remain at a distance of less then ε to Γ. Otherwise, the orbit is called unstable.

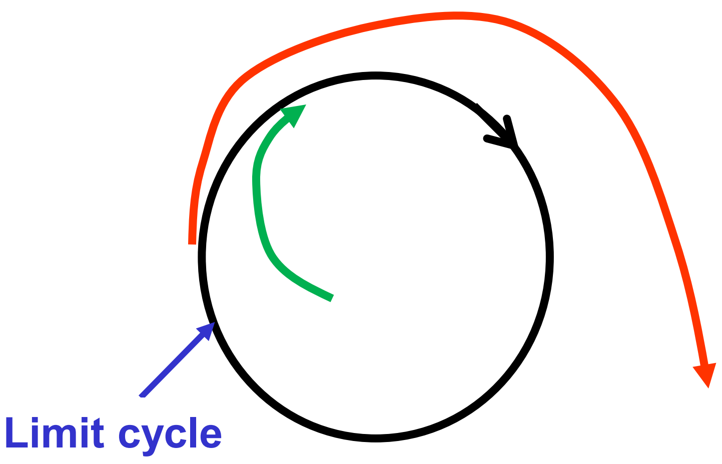


- The periodic orbit is called **asymptotically stable** if the distance between trajectories in the neighborhood and Γ converges to zero for $t \to \infty$.
  (See Lyapunov stability!)



Limit cycle II

- A periodic orbit that is an ω– (or α-)limit set of all trajectories in the neighborhood is called **stable (unstable) limit cycle**.
- In general, a periodic orbit can also be the ω–limit set of trajectories coming from some side, and the α–limit set for trajectories coming from other directions (analogously to a saddle).



Example: Andronov-Hopf oscillator I

- Two dimensional dynamical system ($\omega_0 \neq 0, A > 0$):

$$\boxed{\begin{aligned} \dot{x} &= -\omega_0 y + \alpha x(A - x^2 - y^2) \\ \dot{y} &= \omega_0 x + \alpha y(A - x^2 - y^2) \end{aligned}}$$

- Dynamics easier to understand if we use polar coordinates:

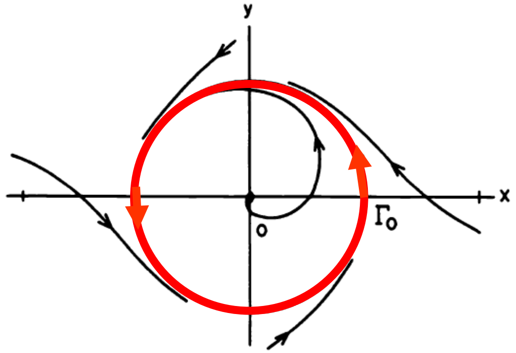
$$x = r\cos\theta \quad y = r\sin\theta \quad \Leftrightarrow \quad r = \sqrt{x^2 + y^2} \quad \theta = \arctan(y/x)$$

resulting in the equivalent dynamics:

$$\boxed{\begin{aligned} \dot{r} &= \alpha\, r(A - r^2) \\ \dot{\theta} &= \omega_0 \end{aligned}}$$

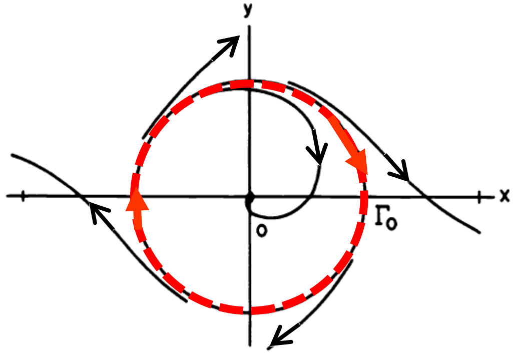
Example: Andronov-Hopf oscillator II

- Interpretation of stationary solution in polar coordinates: Phase θ increases linearly in time with constant rate ω_0, defining oscillation with fixed frequency.
  For $\alpha > 0$: Unstable fixed point in $r = 0$, stable one in $r = \sqrt{A}$.



$\rightarrow$ Oscillation with stable amplitude; asymptotically stable limit cycle (ω–limit set); attracts neighboring trajectories.

For $\alpha < 0$: Stable fixed point in $r = 0$, unstable one in $r = \sqrt{A}$.



$\rightarrow$ Stable fixed point for $\mathbf{x} = \mathbf{0}$; unstable limit cycle (α–limit set); repels neighboring trajectories.

Example: Andronov-Hopf oscillator III

- Remark that there is a fixed point inside the limit cycle; reflects general property that is formulated by Poincaré-Bendixon theorem (s.b.).
- Remark that the unstable limit cycle separates two regions in state space; the basin of attraction of the fixed point and a region where trajectories diverge from the limit cycle to infinity.

Homoclinic orbits

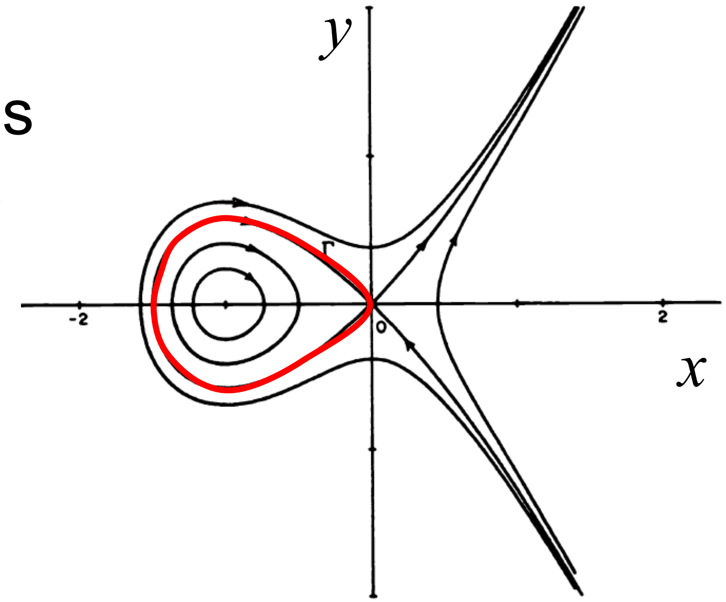
- Circular orbit that starts and ends in the same fixed point is called **homoclinic cycle**;
  Example: conservative system:

$$\boxed{\begin{aligned}\dot{x} &= y \\ \dot{y} &= x + x^2\end{aligned}}$$

  Solutions fulfill:

$$E(x,y) = y^2 - x^2 - \frac{2}{3}x^3 = C$$

- Remark: Homoclinic cycle separates region with marginally stable cycles and region with unstable solutions.
- The closed curve that results from the union of the homoclinic cycle and the fixed point is called **separatrix cycle.**

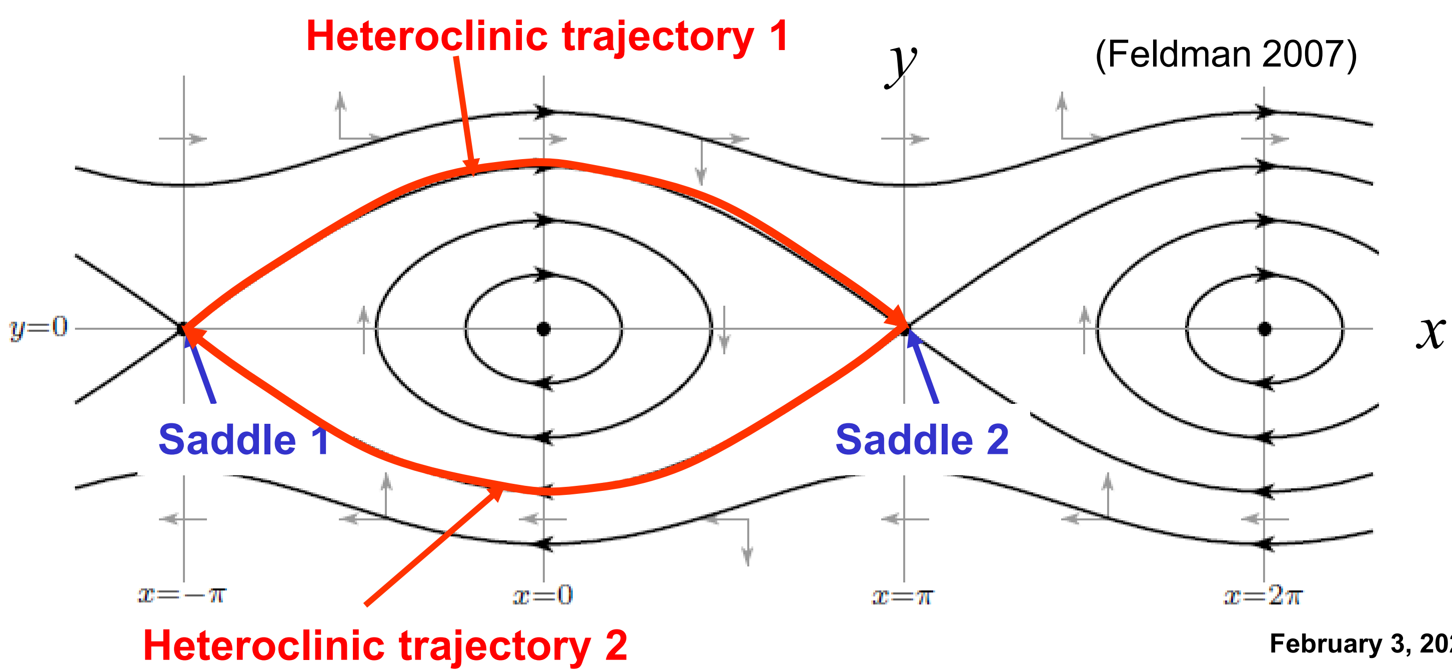


Heteroclinic orbits

- Orbits that link different ω– and α-limit sets (e.g. saddle points) are called **heteroclinic orbits**. Example: nonlinear pendulum:

$$\boxed{\begin{aligned}\dot{x} &= y \\ \dot{y} &= -\sin x\end{aligned}}$$

- Union of compatibly oriented heteroclinic cycle forms a (compound) **separatrix cycle.**



I.O. Bendixon

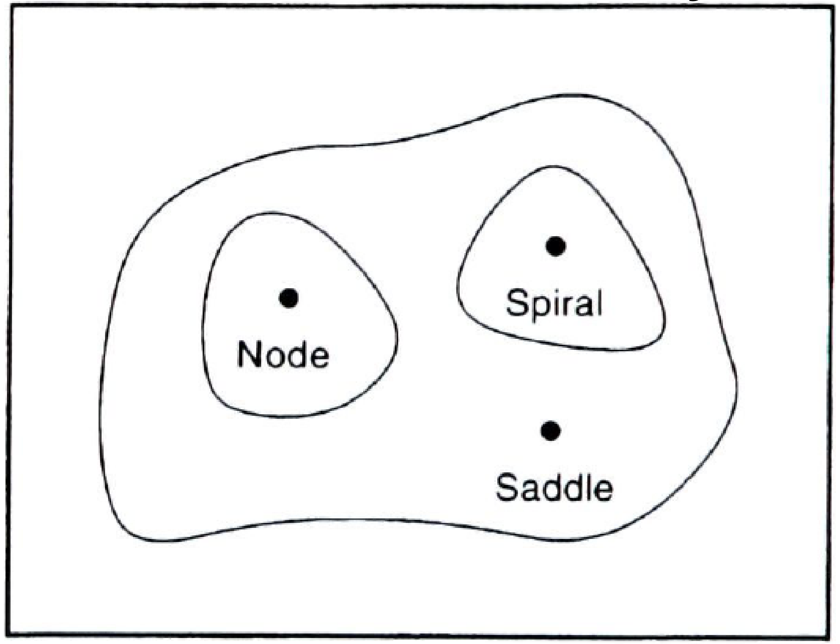
Poincaré-Bendixon Theorem I

- **(Planar) systems** with two-dimensional state space have particularly simple ω– and α-limit sets; thus they are particularly important as tractable models for neurons.
- **Poincaré-Bendixon Theorem:** Systems with $\mathbf{x} \in \mathrm{IR}^2$ with a finite number of isolated critical points have (within open compact regions) as ω–limit set either a critical point, a limit cycle, or (homoclinic or heteroclinic) orbits that link the critical points.
- It can be shown (Poincaré) that for autonomous planar systems limit cycles always must surround at least one critical point; if surrounds multiple critical points the number of nodes, foci and centers N and the number of saddle points S must fulfill the equation: $N - S = 1$.

Poincaré-Bendixon Theorem II

- Intuitively, the last proposition follows from the fact that in the two-dimensional space trajectories of the system can not cross; thus no trajectory can cross the limit cycle; all trajectories starting or ending in the limit cycle must end or originate somewhere (either in a fixed point or in another limit cycle that can't be crossed).
- Last theorems do not give sufficient conditions for the existence of a limit cycle.

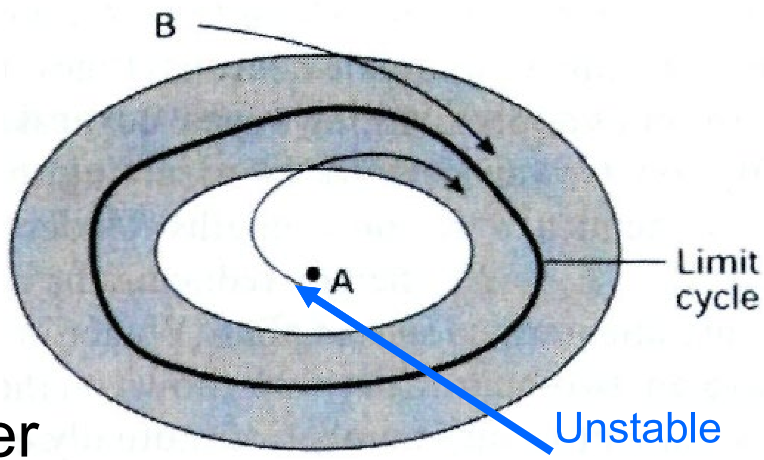
Possible locations for limit cycles

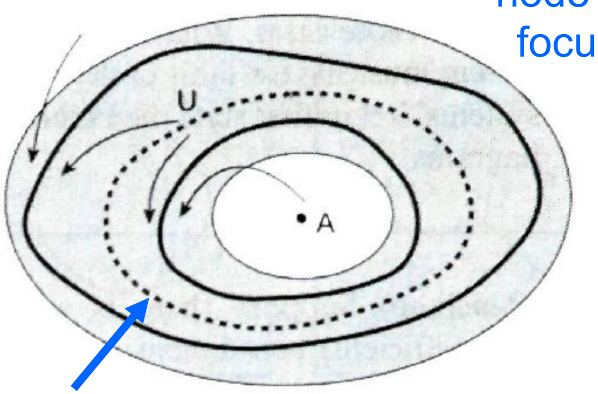


Critical points and linearized dynamics:
Node: source or sink; real eigenvalues with same sign
Focus (spiral): conjugate complex eigen values
Saddle: real eigenvalues with opposite signs

Poincaré-Bendixon Theorem III

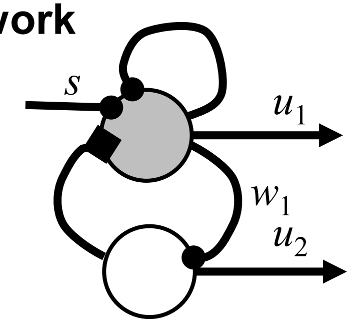
- A sufficient criterion for existence of a limit cycle can be given for planar systems; difficult for higher dimensions.
- If for such a system all trajectories enter an annular region that contains no critical points this annulus must contain a limit cycle.
- It also can contain an odd number of limit cycles; then stable and unstable limit cycles must alternate.
- The limit cycles tile the state space in different basins of attraction.





Example: Wilson-Cowan oscillator

Network



- Like single point in Wilson-Cowan field model; dynamic interaction between excitatory and inhibitory population.
- Differential equation ($w_1 = 1.6;\ w_2 = 1.5;\ \tau_1 = 5;\ \tau_1 = 10$):

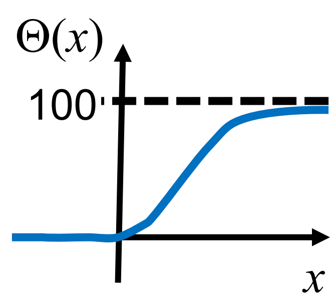
Excit.

$$\tau_1 \frac{\mathrm{d}u_1}{\mathrm{d}t} = -u_1(t) + \Theta(w_1 u_1(t) - u_2(t) + s)$$

Inhib.

$$\tau_2 \frac{\mathrm{d}u_2}{\mathrm{d}t} = -u_2(t) + \Theta(w_2 u_1(t))$$

$$\Theta(x) = \begin{cases} \dfrac{100(x)^2}{30^2 + (x)^2} & \text{for} \quad x \geq 0 \\ 0 & \text{otherwise} \end{cases}$$



Example: Wilson-Cowan oscillator

- For $s \equiv 0$ the only fixed point is $\mathbf{u} \equiv \mathbf{0}$; stable FP:
- For larger s oscillatory solutions emerge; example: $s \equiv 20$.
- Isoclines from: (solve numerically)

$$u_1 = \Theta(w_1 u_1 - u_2 + s) \quad \Rightarrow \Theta(w_1 u_1 - \Theta(w_2 u_1) + s) - u_1 = 0$$

$$u_2 = \Theta(w_2 u_1) \quad \Rightarrow \mathbf{u}^* = [12.77,\, 28.96]^T$$

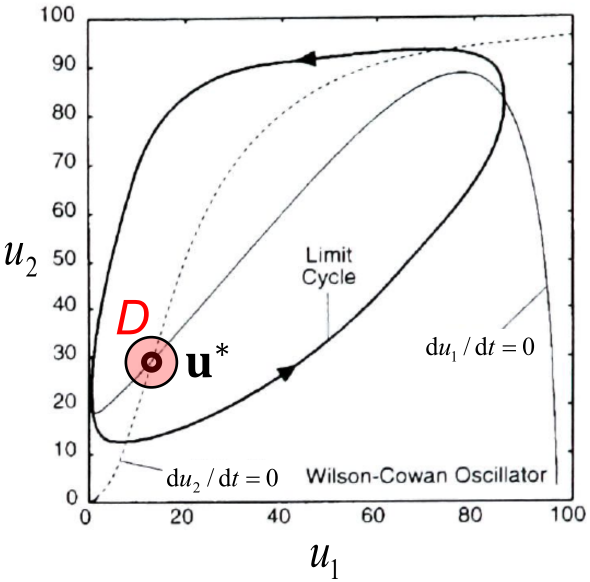
- System matrix of linearized dynamics at fixed point: $\mathbf{A} = \left.\frac{\partial \mathbf{f}}{\partial \mathbf{u}}\right|_{\mathbf{u}^*} = \begin{bmatrix} 0.42 & -0.39 \\ 0.32 & -0.1 \end{bmatrix}$

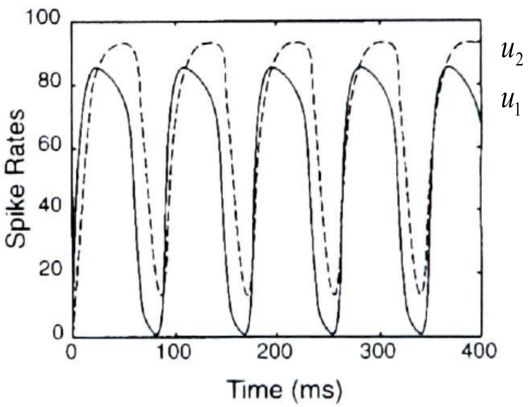
Eigenvalues: $\lambda_{1,\,2} = 0.16 \pm 0.24\, i$

$\Rightarrow$ unstable spiral!

Example: Wilson-Cowan oscillator

- Because Θ is bounded for $0 \leq s \leq 100$ the trajectories cannot leave the box interval $0 \leq u_{1,2} \leq 100$; (proof like in lecture 7; see Wilson book).
- Since the spiral is unstable, trajectories always leave the disk *D* into the region around it.
- Define an annular region as area outside this disk and inside the box; the Poincaré-Bendixon Theorem implies the existence of a limit cycle in this region.



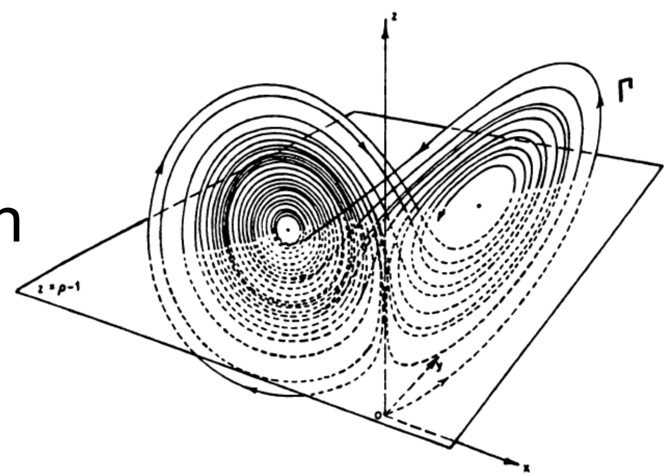


Chaos I

- Unfortunately, for systems with more than two dimensions the structure of the limit sets can be substantially more complex, and much less is known about the conditions that guarantee simple structures of the limit sets.
- A famous example is the **Lorenz system** (Lorenz, 1963): The simple three-dimensional dynamics:

$$\boxed{\begin{aligned}\dot{x} &= \sigma(y-x)\\ \dot{y} &= \rho x - y - xz\\ \dot{z} &= -\beta z + xy\end{aligned}}$$

  has a (so-called) **strange attractor** (e.g. for $\sigma = 10$, $\rho = 28$, $\beta = 8/3$).
- Attracting set consists of an infinite number of branched surfaces that intersect, while trajectories of the system do not intersect; within each cycle the trajectory samples another one of those surfaces.



Chaos II

- It can be proven that this invariant set contains a countable set of periodic orbits with arbitrarily large period, an uncountable set of non-periodic motions, and a dense orbit.
- More details about chaotic dynamical systems can be found in the books by Perko and Wilson.
- Extensive discussions whether **brain dynamics** is based on **chaotic attractors** (e.g. Skarda & Freeman, 1987); today's hypothesis is that brain operates at the 'edge of chaos' (e.g. Kitzbichler et al. 2009).
- Idea: simple attractors do not support interesting information processing / representation of complex patterns; fully chaotic attractors make system almost impossible to control.

Things to remember

- Relevance of oscillations in neuroscience $\rightarrow$ 1,2)
- Limit sets, attractors, homoclinic / heteroclinic orbits $\rightarrow$ 3)
- Limit cycle $\rightarrow$ 3,4)
- Poincaré-Bendixon theorem $\rightarrow$ 3,4)
- Chaos $\rightarrow$ 3,4)

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 6.

2) Izhikevich, E.M. (2007) *Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting.* MIT Press, Cambridge MA, USA. Chapters 5, 6.

3) Perko, L. (1998) *Differential Equations and Dynamical Systems.* Springer-Verlag, Berlin. Chapters 3 + 4.

4) Wilson, H.R. (1999) *Spikes, Decisions, and Actions.* Oxford University Press, UK. Chapter 8+9.