



Mathematical Foundations of Neuroscience - Lecture 7. Bifurcations II.

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Bifurcations

- On the last lecture we've met four bifurcations of equilibria:
 - saddle node,
 - saddle node on invariant circle,
 - supercritical Andronov-Hopf,
 - subcritical Andronow-Hopf
- We also met two bifurcations of cycles:
 - saddle homoclinic orbit
 - fold cycle
- All of these bifurcations are of codimension 1, that is they have one control parameter. In neural excitability it is usually the input current.



Bifurcations

- The above bifurcations are important from neuro-computational point of view, since they explain transitions from resting to spiking and back.
- Today we will study more complex bifurcations and their relations to neural activity.
- We will be interested in cases, when two or more bifurcations occur simultaneously, leading to bifurcations of higher codimension.
- First we will complete the list of codimension one bifurcations on the plane, and sketch the situations which might have happened in 3d.



Heteroclinic orbit bifurcation

- We have one more codimension one bifurcation in 2d left, namely heteroclinic orbit bifurcation
- In this case a heteroclinic trajectory changes its destination, hitting a saddle point
- This bifurcation is global, does not change the stability of any equilibria, does not create cycles.



Heteroclinic orbit bifurcation

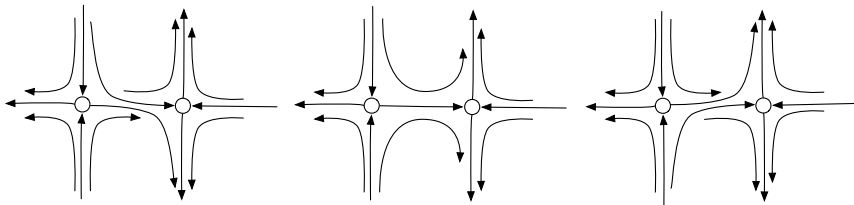


Figure: Heteroclinic orbit bifurcation



Summary - codimension 1 in 2d

We have therefore

- saddle node,
- saddle node on invariant circle,
- supercritical Andronov-Hopf,
- subcritical Andronow-Hopf
- supercritical saddle-homoclinic orbit
- subcritical saddle-homoclinic orbit
- heteroclinic orbit
- fold cycle

These are all codimension one bifurcations in 2d. But how do we know that?



Poincaré-Bendixon theorem

Theorem (Poincaré-Bendixon)

Given an autonomous ODE on the plane

$$\frac{dx}{dt} = F(x)$$

with continuous F , assume that solution $x(t)$ stays in a bounded region for all times. Then $x(t)$ converges as $t \rightarrow \infty$ to an equilibrium (with $F(x) = 0$) or to a single limit cycle.

Remark: the theorem rules out chaos in 2d.



Poincaré-Bendixon theorem - sketch proof

Definition

A curve γ is a **transverse** to a vector field F if at any point $\gamma(s)$ the vector tangent to γ is linearly independent of the field F . In other words γ is not tangent to field F at any point.

Definition

Omega limit set $\omega^+(x_0)$ of an orbit $x(t)$ passing through x_0 is the set of points x for which there exists a sequence of times t_n such that $x(t_n)$ converges to x . Formally

$$\omega^+(x_0) = \bigcap_{s>0} \overline{\{x(t), t > s\}}$$

where \overline{A} is a closure of set A .



Poincaré-Bendixon theorem - sketch proof

Lemma

The vector field F cannot change the direction along the transverse curve γ

Since F is continuous, changing direction would require (from Bolzano's intermediate value theorem), to have the component orthogonal to γ be equal zero, which would mean, that the field is tangent to γ .



Poincaré-Bendixon theorem - sketch proof

Lemma

Let γ be a transverse curve and $x(t)$ a trajectory. If $x(t)$ crosses γ in more than one point, successive crossing points form a monotonic sequence on the arc γ .

Let $\gamma(s_1) = x(t_1)$ and $\gamma(s_2) = x(t_2)$ be the crossing points. We can assume that $s_1 < s_2$ (otherwise the curve can be easily reparametrized). The union of two smooth curves $\{x(t), t_1 < t < t_2\}$ and $\{\gamma(s), s_1 < s < s_2\}$ forms a closed piecewise smooth curve, which by Jordan's curve theorem splits the plane into two regions. For $t > t_2$ $x(t)$ stays in one of those regions, for the next crossing we therefore have $s_3 > s_2$.



Poincaré-Bendixon theorem - sketch proof

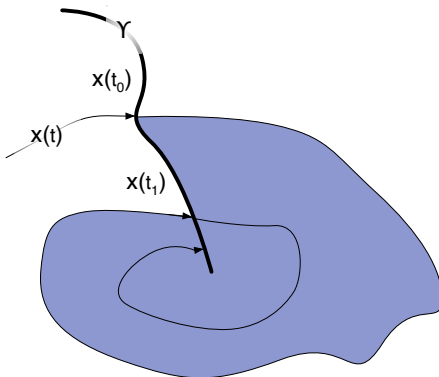


Figure: Intersections of a transverse γ and the trajectory $x(t)$ must form a monotonic sequence



Poincaré-Bendixon theorem - sketch proof

Lemma

Omega limit set $\omega^+(x_0)$ can only have one point in common with any transverse γ .

By definition $\omega^+(x_0)$ of an orbit $x(t)$ is the set of points x for which there exists a sequence of times t_n such that $x(t_n)$ converges to x . Assume there are two points of intersection with the transverse $x(t_1)$ and $x(t_2)$ which belong to $\omega^+(x_0)$. There exists a sequence of times $\tau_n > t_1$ for which $\lim x(\tau_n) = x(t_2)$. But there also exists sequence of times $\tau_m > t_2$ for which $\lim x(\tau_m) = x(t_1)$ (because $x(t_1)$ belongs to $\omega^+(x_0)$). But this contradicts the fact, that the sequence of crossings is monotonic on γ .



Poincaré-Bendixon theorem - sketch proof

Given $y_0 \in \omega^+(x_0)$ we have that $y(t)$ with $y(0) = y_0$ is defined for all times and stays in $\omega^+(x_0)$. Therefore either

- $\omega^+(x_0)$ contains a fixed point, in which case $\omega^+(x_0)$ simply is the fixed point.
- y_0 is a regular point, therefore there exists transverse γ passing it. $\omega^+(x_0) \cap \gamma$ has only one point. Since trajectory passing through y_0 converges arbitrarily close to y_0 (since it is contained in $\omega^+(x_0)$), orbit $y(t)$ through y_0 has to form a single limit cycle.

Q.E.D.



New bifurcations in 3d

- What can possibly happen in 3d?
- There can be no new bifurcations of equilibria (of codimension one), since 3×3 Jacobian matrix can have a simple zero eigenvalue or a pair of complex conjugate eigenvalues.
- There are however new bifurcations of cycles.
- As we will see the Poincaré-Bendixon theorem does not hold in 3d, and consequently there are some new types of attractors (including the so called *strange attractors*).



Saddle-focus homoclinic orbit

- Saddle-focus is a fixed point which is repelling in one direction, but in the orthogonal plane is an attracting focus (it can also be the other way round)
- Saddle-focus homoclinic orbit bifurcations occurs when a periodic orbit becomes homoclinic to the saddle-focus. The bifurcation is very similar to the saddle-homoclinic bifurcation, but here there are more degrees of freedom.
- The bifurcation occurs in two flavors - subcritical and supercritical.



Saddle-focus homoclinic orbit

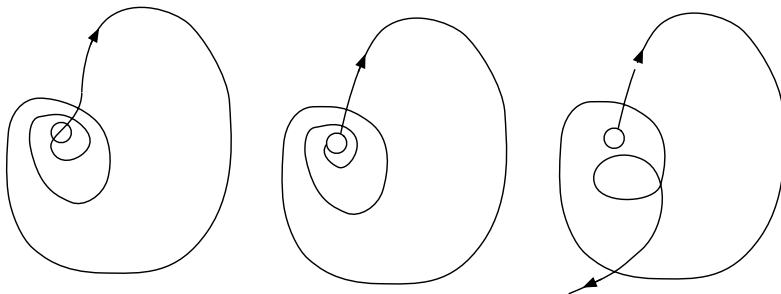


Figure: Supercritical saddle-focus homoclinic bifurcation



Flip

- Flip bifurcation occurs when two cycles of opposite stabilities collide. One of the cycles has to be of twice the period of the other one.
- The bifurcation (sometimes called period doubling bifurcation) looks as if there were three cycles (two say unstable on the inside and the outside and one say stable in the middle)
- The bifurcation actually appears in 2d, but the space has to have the Möbius strip topology
- There are two flavors - supercritical and subcritical.



Flip

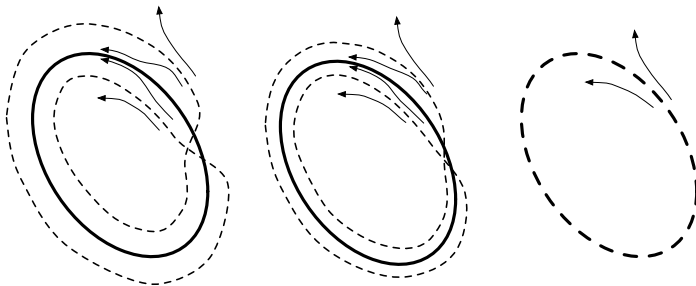


Figure: Subcritical flip bifurcation



Neimark-Sacker torus bifurcation

- When an unstable invariant torus (by the way - a new attractor - torus) shrinks into a stable cycle inside (or the other way round) we have the Neimark-Sacker torus bifurcation
- The cycle either loses or gains stability (depending on whether the bifurcation is supercritical or subcritical)
- This bifurcation is similar to the Andronov-Hopf bifurcation, and is sometimes referred as to *secondary Andronov-Hopf bifurcation*.



Neimark-Sacker torus bifurcation

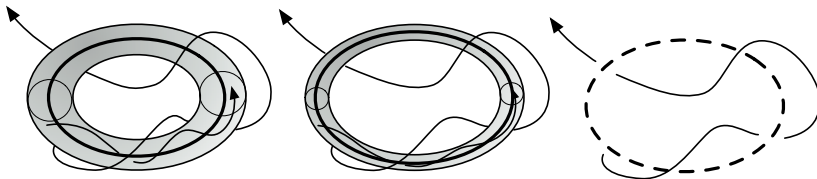


Figure: Subcritical Neimark-Sacker torus bifurcation



Blue Sky Catastrophe

- The Blue Sky Catastrophe (blue sky bifurcation) occurs when stable and unstable periodic orbits merge.
- At the critical bifurcation point there is a neutrally stable fold cycle, but trajectories departing from certain vicinity at the unstable side, come back arbitrarily near the cycle at the stable side, possibly making a long way in the mean time.
- Right when the cycle vanishes a large period, large amplitude periodic orbit emerges seemingly out of nowhere (out of the blue sky!)



Blue Sky Catastrophe

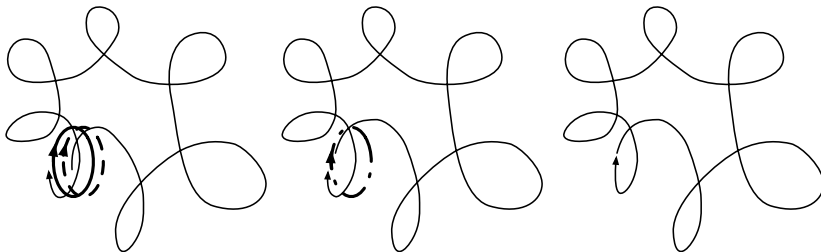


Figure: Blue sky bifurcation



Fold limit cycle on homoclinic torus

- Two cycle merge, forming a fold cycle, which turns out to lie in an invariant torus
- When the cycle vanishes, a quasi-periodic trajectory emerges, which always remains on the torus
- The bifurcation is similar to blue sky catastrophe, but in that case there was a periodic orbit. In this case it is quasi-periodic.



Fold limit cycle on homoclinic torus

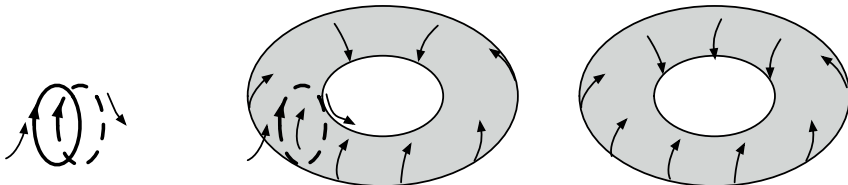


Figure: Fold limit cycle on homoclinic torus



Quasi-periodicity

Definition

A continuous differentiable function $f : \mathbb{R} \rightarrow \mathbb{R}^n$ is called **quasiperiodic** if $f(t) = g(\omega_1 t, \omega_2 t, \dots, \omega_n t)$ where g is a differentiable function 2π periodic in every component, and moreover frequencies ω_i are incommensurable, that is there are no such integers m_i with $\sum m_i^2 > 0$ for which $m_1 \omega_1 + m_2 \omega_2 + \dots + m_n \omega_n = 0$ holds.

If f is a quasiperiodic trajectory of an autonomous dynamical system, and $f(t_0) = y_0$, then for every $\varepsilon > 0$ there exists t such that $f(t) \in B(y_0, \varepsilon)$. That is quasiperiodic trajectory always comes back arbitrarily close to any of its previous values, but never hits exactly the same point.



Quasi periodic orbit

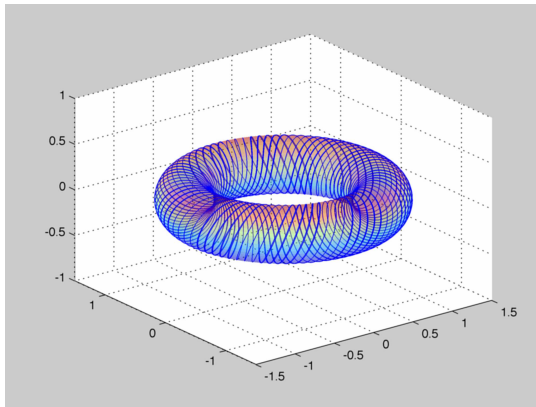


Figure: Quasi periodic orbit



Is Poincaré-Bendixon theorem valid in 3d?

- The proof of Poincaré-Bendixon theorem depends on Jordan's curve theorem, which fails even for certain 2d topologies (for example torus)
- It cannot hold in 3d as well, since torus can be submerged in 3d space.
- We have therefore new attractors like invariant torus and other manifolds etc.
- The orbits can be quasiperiodic (such an orbit will stay on an invariant manifold).
- But that is not the end. There can also be the so called strange attractors with chaotic orbits!



Chaos

- There is one dynamic regime which is neither stable cycle, neither quasiperiodic. The trajectories follow a strange pattern, in which they seem to be attracted by some strange manifold...
- Any attempts to track down the stable manifold fail, since in the end it seems to be infinitely complex spaghetti of trajectories
- In the chaotic regime the trajectory seems to behave randomly, even though the system is fully deterministic.
- Any tiny deviation in the initial conditions explodes exponentially with time, the system exhibits the so called butterfly effect (*the flap of a butterfly's wings in Brazil sets off a tornado in Texas*)



Lorenz Attractor

Chaos is easy to spot in discrete mappings based on function iteration (e.g. the logistic map). It has also been tracked down in differential dynamical systems by Edward Lorenz in 1972, in a seemingly simple set of differential equations in 3d originating in weather study:

$$\begin{aligned}\frac{dx}{dt} &= \sigma(y - x) \\ \frac{dy}{dt} &= x(\rho - z) - y \\ \frac{dz}{dt} &= xy - \beta z\end{aligned}$$

For parameters $\rho = 28, \sigma = 10, \beta = 8/3$ the systems behaves strangely, spinning randomly around two "fixed" points which seem to be neither attracting nor repelling.



Lorenz Attractor

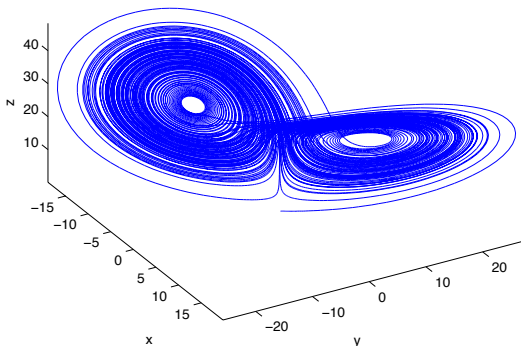


Figure: An orbit near Lorenz attractor switches "randomly" between spinning around two fixed points. The spaghetti like invariant set (the attractor) is hard to track, since it is a fractal set.



Chaos

For chaos to occur, the system has to

- be sensitive to initial conditions (butterfly effect)
- topologically mixing (for any two sets A and B there exists integer N such that for $t > N$, $\phi_t(A) \cap B \neq \emptyset$, where ϕ_t is the flow of the equation at time t)
- periodic orbits must be dense (set A is dense when the closure of A and the union of A and set of limits of sequences of elements from A are equal)

Chaotic systems are hard to analyze, but they are in the focus of interest of many contemporary mathematicians. Usually chaos occurs via an (infinite) cascade of period doubling bifurcations. Some chaotic behavior can also be present in the brain, nevertheless most neurons seem to exhibit rather simpler dynamics.



Chaos

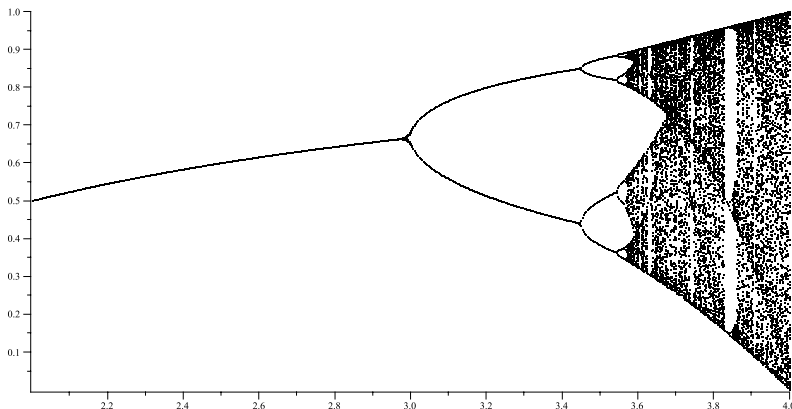


Figure: Period doubling cascade in the logistic map iteration. Poincaré maps of continuous systems look similarly. The diagram is known as the Feigenbaum diagram.



Back to 2d

Lets get back to 2d, where hopefully Poincaré-Bendixon theorem works and neither chaos nor quasiperiodicity are possible.

- We've seen some bifurcations with one equality condition and certain inequality conditions imposed on the system.
- What happens when some of the inequalities are not satisfied? Usually still some bifurcation occurs, though more complex one.
- Recall that an equilibrium can be approximated via a linear system (Hartman-Grobman theorem). A system at a non degenerate bifurcation of an equilibrium (like the saddle node) can be approximated by the quadratic normal form.
- Similarly degenerate bifurcations can be approximated with higher order normal forms



Saddle-node homoclinic orbit

- Saddle-node homoclinic orbit bifurcation occurs, when saddle-node and saddle-homoclinic bifurcations occur simultaneously.
- The bifurcation occurs in the $I_{Na,p} - I_K$ model, with $\tau(V) = 0.17$ and $I = 4.51$. The bifurcation is very important for neural excitability, since it separates neurons which can have arbitrarily low spiking frequencies (those that start to spike via saddle node on invariant circle), from those which cannot exhibit frequency dependence (those that start to spike via a simple saddle-node bifurcation).

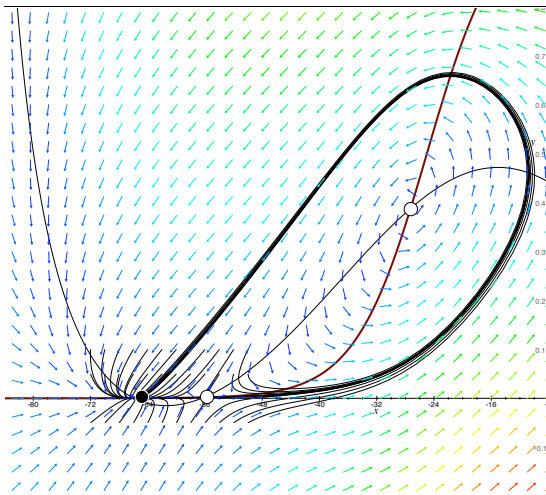


Figure: Saddle node homoclinic orbit.

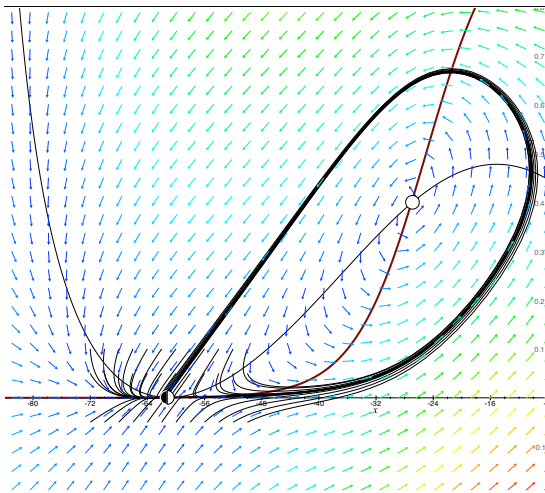


Figure: Saddle node homoclinic orbit.

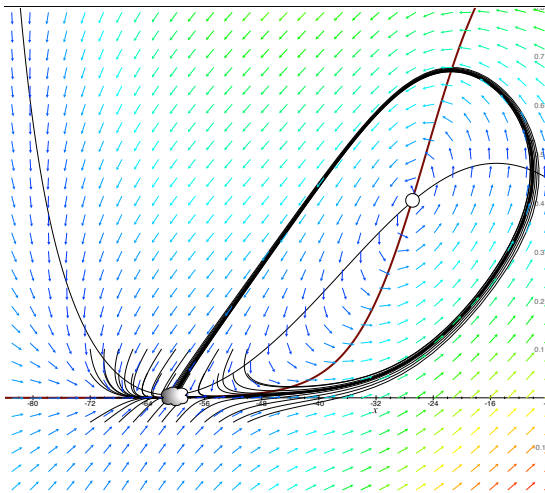


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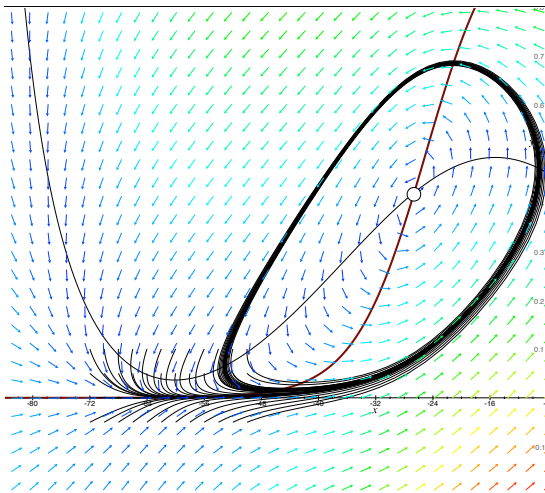


Figure: Saddle node homoclinic orbit.

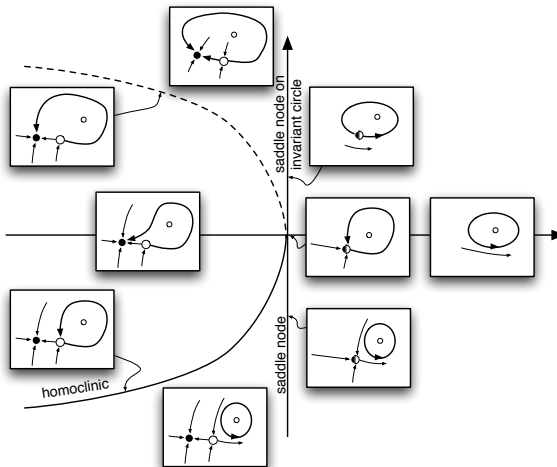


Figure: Saddle-node homoclinic bifurcation diagram.



The cusp

- Saddle-node homoclinic orbit, though involving two bifurcations at a time is not degenerate, since one of the bifurcations is local, while the other global
- The simplest degenerate bifurcation in 1d is called the cusp bifurcation. Although it appears in 1d, it has codimension 2.
- Assume $\frac{\partial F}{\partial x} = 0$ and $\frac{\partial^2 F}{\partial x^2} = 0$ but $\frac{\partial^3 F}{\partial x^3} \neq 0$. In such case the system near the bifurcation can be approximated by the normal form:

$$\frac{dx}{dt} = c_1(b) + c_2(b)x + ax^3$$

where b is the bifurcation parameter, $c_1(b) = F(x_b, b)$,
 $c_2(b) = \frac{\partial F(x_b, b)}{\partial x}$, $a = \frac{\partial^3 F}{\partial x^3} / 6$



The cusp

- The bifurcation is of codimension 2, and there are more degrees of freedom of how the system can actually go through that bifurcation
- Think of $c_1(b)$ and $c_2(b)$ a parametric curves which determine the way through the bifurcation
- Since the system is at a bifurcation, c_1 and c_2 satisfy

$$c_1 + c_2x + ax^3 = 0$$

which is a surface in 3d, called the cusp surface.

- Moreover when $c_2 = \pm \frac{2}{\sqrt{a}}(c_1/3)^{3/2}$ the system undergoes the saddle node bifurcation.

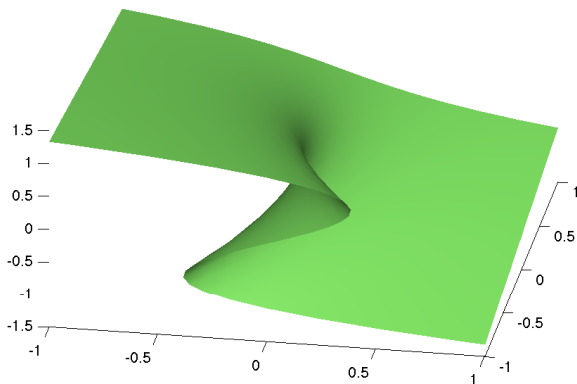


Figure: The cusp surface.



The cusp

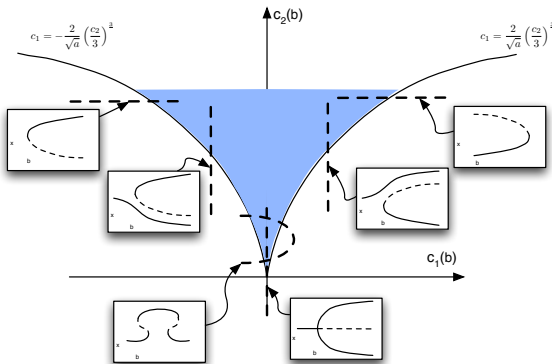


Figure: The cusp bifurcation diagram.



The pitchfork

- An important case of traversing the cusp is the situation in which $c_1 = 0$ and $c_2 = b$.
- The topological normal form is

$$\frac{dx}{dt} = bx + ax^3$$

- This bifurcation is called the pitchfork, and can either be subcritical or supercritical (depending on the sign of a)
- To some extent this bifurcation is 1d analog of the Andronov-Hopf bifurcation, though has infinite codimension, since equality condition involves all even order derivatives of F (unless there are some symmetry conditions imposed on the system).



The cusp

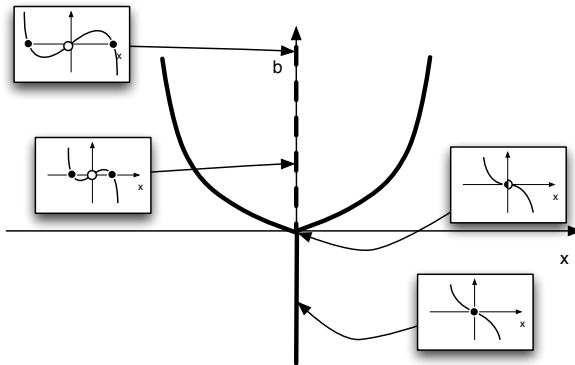


Figure: The supercritical pitchfork bifurcation diagram.



Bogdanov-Takens bifurcation

- What happens when the the Jacobian matrix has two zero eigenvalues?
- Depending on how the eigenvalues are crossing zero, it can have two saddle node bifurcations at a time, or saddle node and Andronov-Hopf bifurcation at a time,
- The bifurcation of codimension 2 is called Bogdanov-Takens bifurcation. As we will see soon, it is very important for neural excitability.
- Much like the cusp (which is a 1d example), there is no one way of traversing Bogdanov-Takens bifurcation.
- Surprisingly, not only saddle-node and Andronov-Hopf bifurcations occur near Bogdanov-Takens point - there is always saddle-homoclinic orbit bifurcation near by!



Bogdanov-Takens bifurcation

- The normal form for the bifurcation is:

$$\begin{aligned}\frac{dx}{dt} &= y \\ \frac{dy}{dt} &= c_1 + c_2x + x^2 + \sigma xy\end{aligned}$$

depending on the sign of σ the bifurcation is either subcritical or supercritical.

- The bifurcation occurs when $c_1 = c_2 = 0$. Again c_1 and c_2 can be interpreted as functions of some parameter which determine the way through the bifurcation. In particular $c_1(\alpha)$ and $c_2(\alpha)$ can form a closed loop around the bifurcation point, which is useful to study "nearby" bifurcations

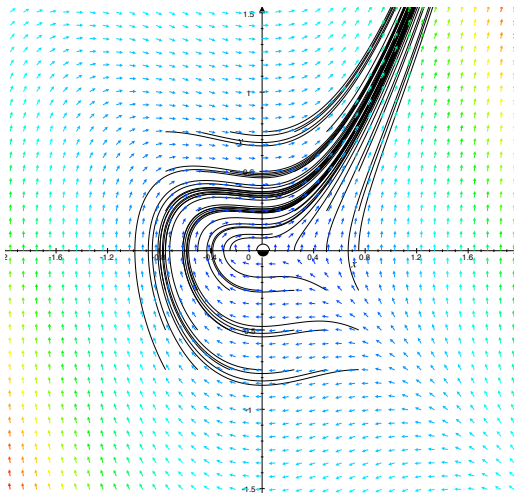


Figure: Bogdanov-Takens bifurcation

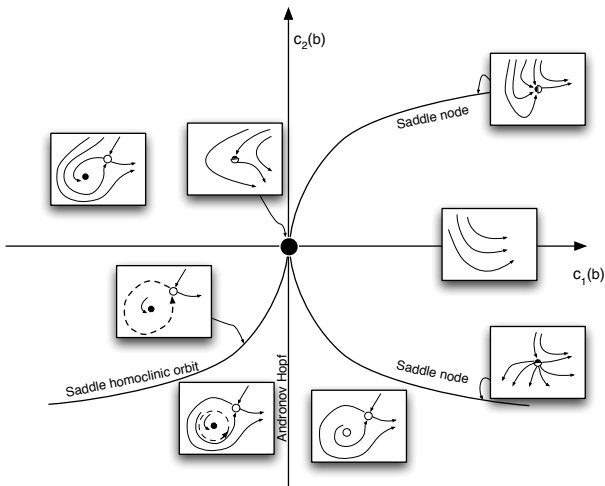


Figure: Bogdanov-Takens bifurcation diagram

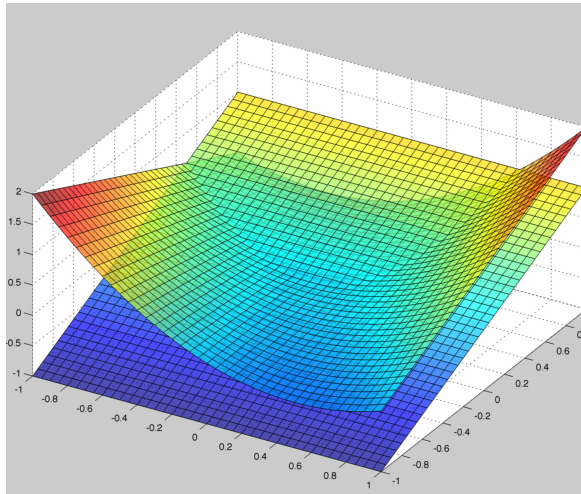


Figure: Vector field as two surfaces at Bogdanov-Takens bifurcation

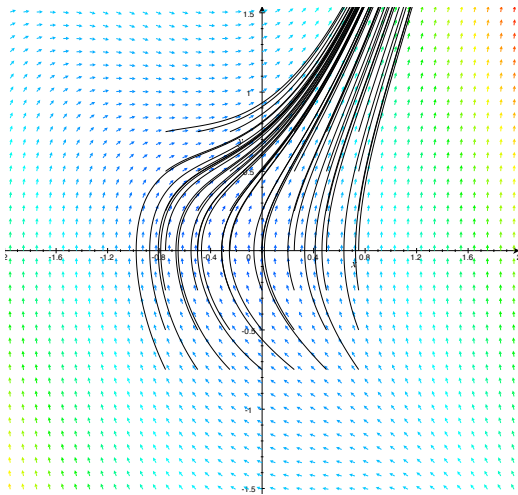


Figure: Dynamic regimes near Bogdanov-Takens bifurcation

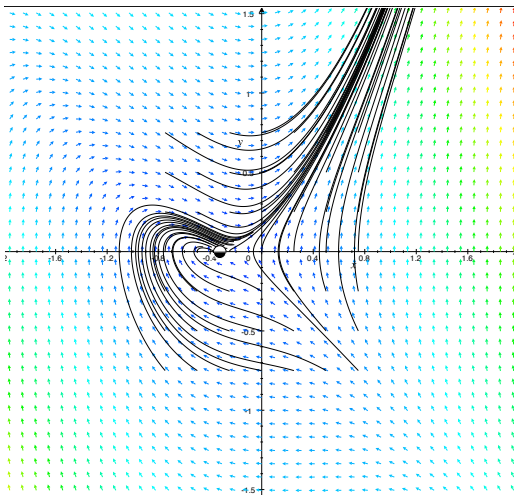


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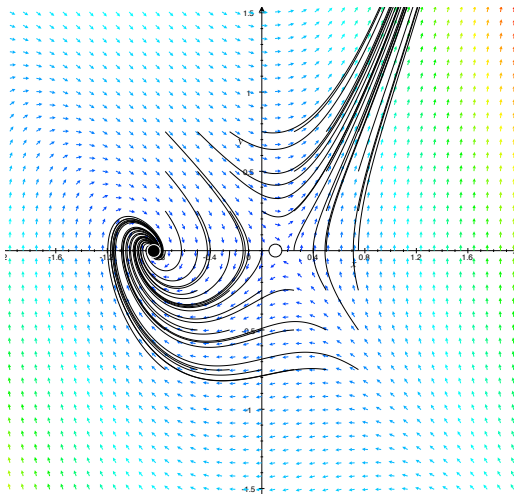


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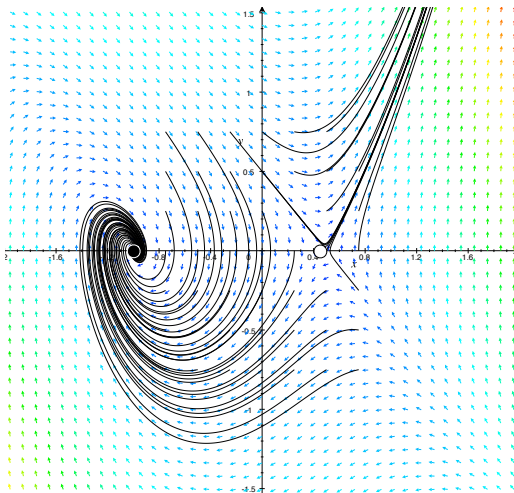


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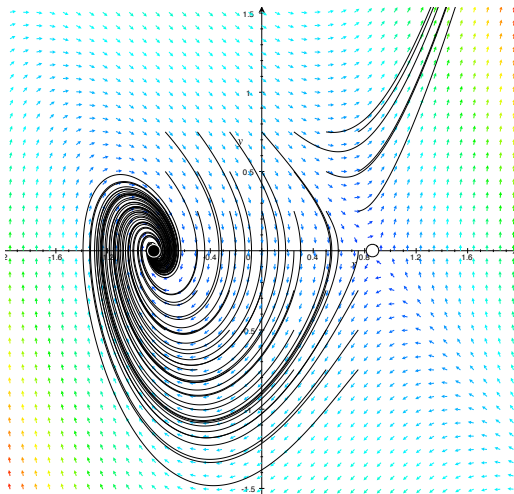


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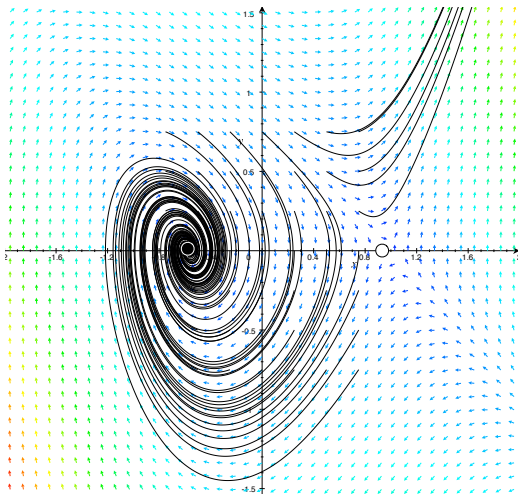


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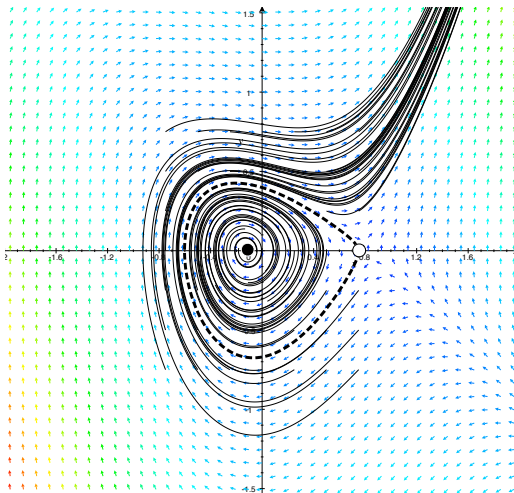


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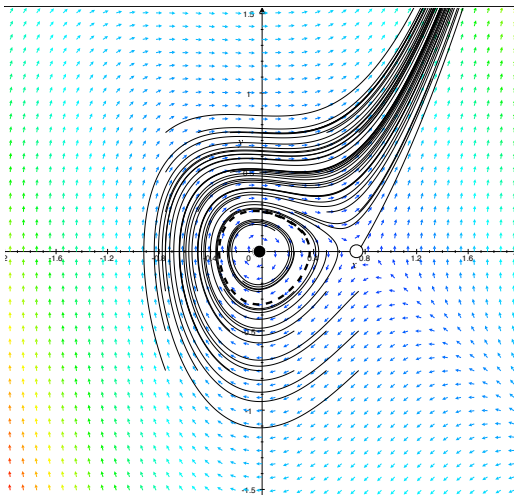


Figure: Dynamic regimes near Bogdanov-Takens bifurcation

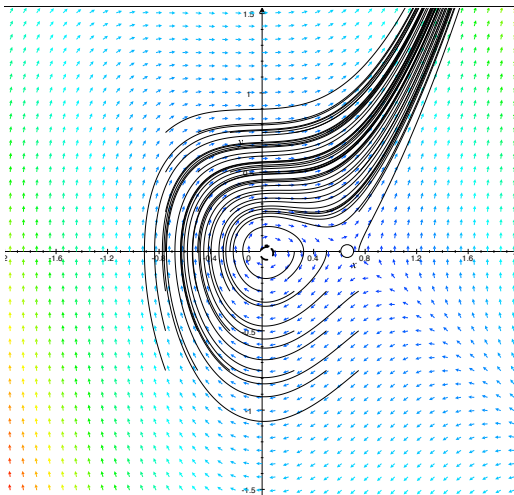


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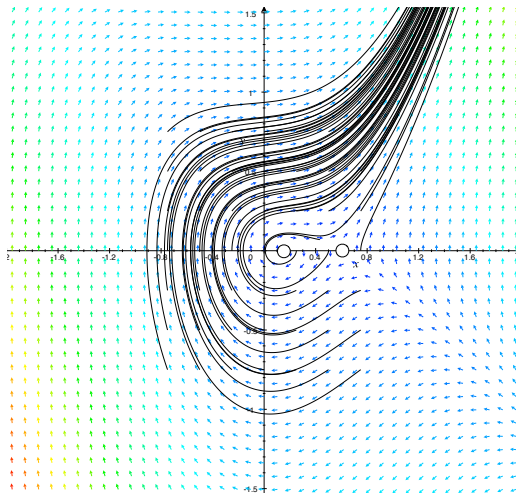


Figure: Dynamic regimes near Bogdanov-Takens bifurcation

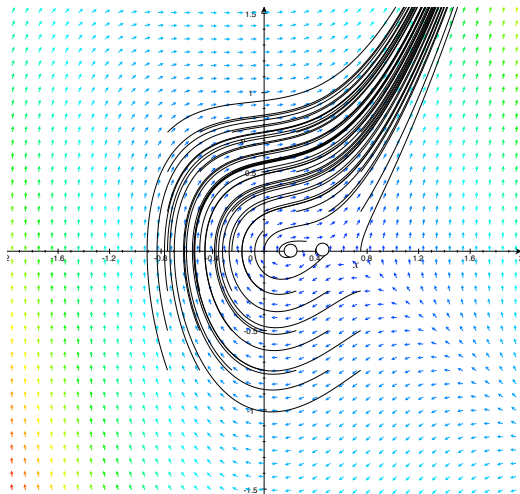


Figure: Dynamic regimes near Bogdanov-Takens bifurcation

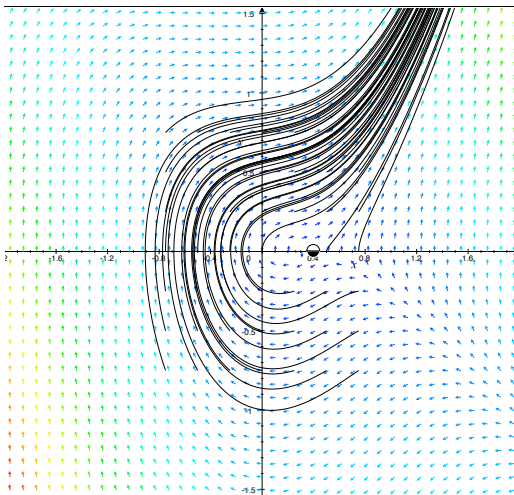


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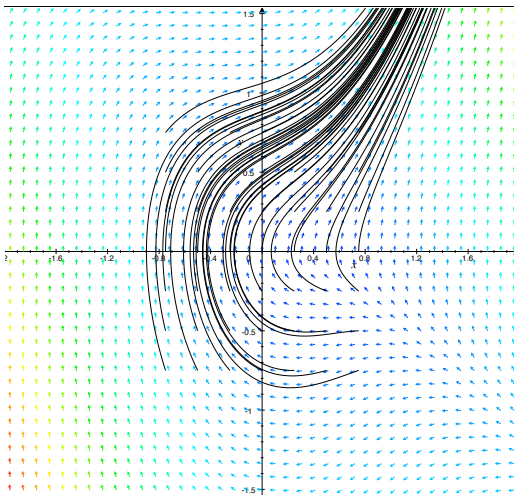


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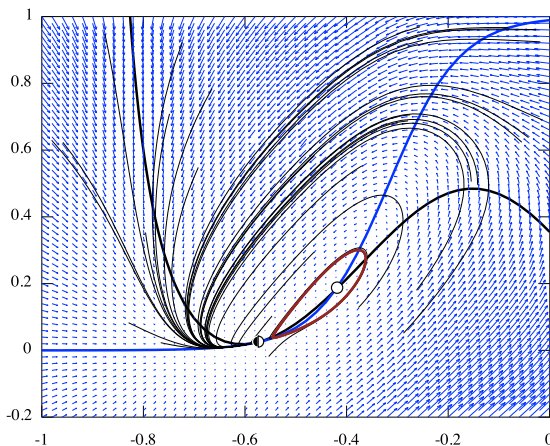


Figure: Bogdanov-Takens bifurcation in $I_{Na,p} - I_K$ model with $E_L = -79.42$,
 $I = 5$, $n_\infty(V) = 1/(1 + e^{((-31.64 - V)/7)})$



Bautin bifurcation

- What happens when the Andronov-Hopf bifurcation switches from supercritical to subcritical?
- That is:

$$a = \frac{1}{16} \left(\frac{\partial^3 f}{\partial x^3} + \frac{\partial^3 f}{\partial x \partial y^2} + \frac{\partial^3 g}{\partial x^2 \partial y} + \frac{\partial^3 g}{\partial y^3} \right) +$$

$$+ \frac{1}{16\omega} \left(\frac{\partial^2 f}{\partial x \partial y} \left(\frac{\partial^2 f}{\partial x^2} + \frac{\partial^2 f}{\partial y^2} \right) - \frac{\partial^2 g}{\partial x \partial y} \left(\frac{\partial^2 g}{\partial x^2} + \frac{\partial^2 g}{\partial y^2} \right) + \right.$$

$$\left. - \frac{\partial^2 f}{\partial x^2} \frac{\partial^2 g}{\partial x^2} + \frac{\partial^2 f}{\partial y^2} \frac{\partial^2 g}{\partial y^2} \right)$$

changes sign?

- At that point the stability of cycles change as well as stability of equilibria...



Bautin bifurcation

- It turns out that near the bifurcation from subcritical AH to supercritical AH (called Bautin bifurcation), there is always fold cycle bifurcation near by
- The normal form (in terms of complex variable) is:

$$\frac{dz}{dt} = (c + i\omega)z + az|z|^2 + a_2z|z|^4$$

where a and a_2 are often called Lyapunov coefficients. Bautin bifurcation occurs, when $a = c = 0$ and $a_2 \neq 0$, hence is of codimension 2.

- The normal form undergoes fold cycle bifurcation when $a^2 - 4ca_2 = 0$.

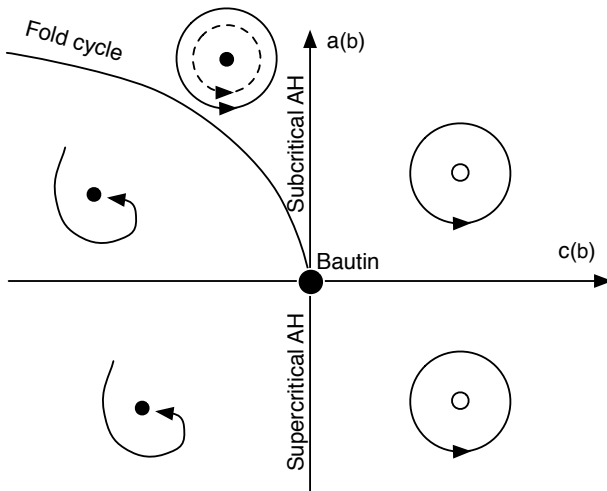


Figure: Bautin bifurcation diagram



Recapitulation

- Attractor sets in 2d are either cycles or equilibria, due to Poincaré-Bendixon theorem
- The theorem relies on Jordan's curve theorem which fails on some 2d topologies like torus or Möbius strip
- In 3d things are much more complex, orbits can be quasiperiodic or chaotic
- Saddle-node homoclinic orbit, Bogdanov-Takens and Bautin's are codimension 2 bifurcations in 2d which separate certain dynamical regimes, important from neurocomputational point of view.