Mathematical Foundations of Neuroscience - Lecture 6. Bifurcations in 2d systems.

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Bifurcation

Recall that a bifurcation is any qualitative change in the phase portrait (resulting portraits are not equivalent in topological sense) as some parameters of the system change. And 2d phase portraits can be very complex...

Nevertheless there are only four main ways of getting from resting to spiking (bifurcations of equilibria), and four ways of getting from spiking to resting (bifurcations of cycles).

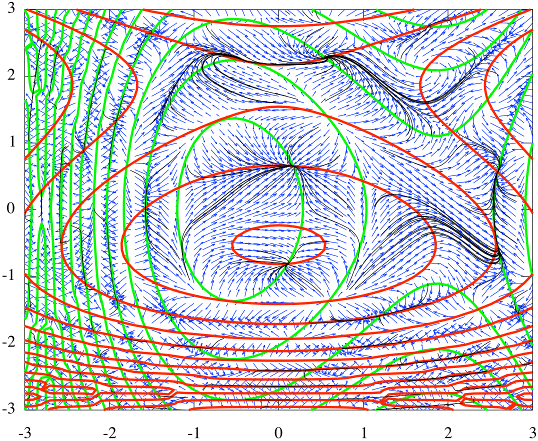


Figure: Some phase portrait in 2d. X nullclines in green, Y nullclines in red. See the lecture web page for a Matlab program that produces such figures.

Basic terminology

- Consider a bifurcation of some system with some parameter. Assume the parameter changes in such a direction that the number of stable elements (cycles, equilibria) increases as the parameter passes the bifurcation value.
- If stable elements appear, the bifurcation is said to be **supercritical**
- If unstable elements appear the bifurcation is said to be **subcritical**
- If the same number of stable and unstable elements appear, the bifurcation is **transcritical**

For the 2d system at a fixed point we have:

$$F(x,y) = a \cdot (x - x_0) + b \cdot (y - y_0) + HOT$$
$$G(x,y) = c \cdot (x - x_0) + d \cdot (y - y_0) + HOT$$

where $a = \frac{\partial F}{\partial x}(x_0, y_0)$, $b = \frac{\partial F}{\partial y}(x_0, y_0)$, $c = \frac{\partial G}{\partial x}(x_0, y_0)$, $d = \frac{\partial G}{\partial y}(x_0, y_0)$. Let

$$A = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$$

To determine stability, we have to find roots of the characteristic polynomial:

$$\det(A - I\lambda) = \det \begin{bmatrix} a - \lambda & b \\ c & d - \lambda \end{bmatrix} = (a - \lambda)(d - \lambda) - bc$$

We see that the characteristic polynomial:

$$\lambda^2 - (a+d)\lambda + ad - bc$$

can be written as

$$\lambda^2 - \tau\lambda + \Delta$$

where $\tau = \mathrm{tr} A = a + d$ (trace of the matrix A) and $\Delta = \det A = ad - bc$. The roots are then:

$$\lambda_1 = \frac{\tau + \sqrt{\tau^2 - 4\Delta}}{2}, \quad \lambda_2 = \frac{\tau - \sqrt{\tau^2 - 4\Delta}}{2}$$

They are real when $\tau^2 - 4\Delta > 0$, complex conjugate when $\tau^2 - 4\Delta < 0$ and real of multiplicity two when $\tau^2 - 4\Delta = 0$.

Possible bifurcations of equilibria

- When there are two real eigenvalues, and one of them is changing sign as the bifurcation parameter passes we have the saddle node bifurcation.
- When there are two complex conjugate eigenvalues, and their real parts change sign as as the bifurcation parameter passes we have Andronov-Hopf bifurcation, which as we will se can be subcritical and supercritical.
- When both eigenvalues become zero, the bifurcation degenerates, and we can no longer derive any useful information from the Jacobian matrix...

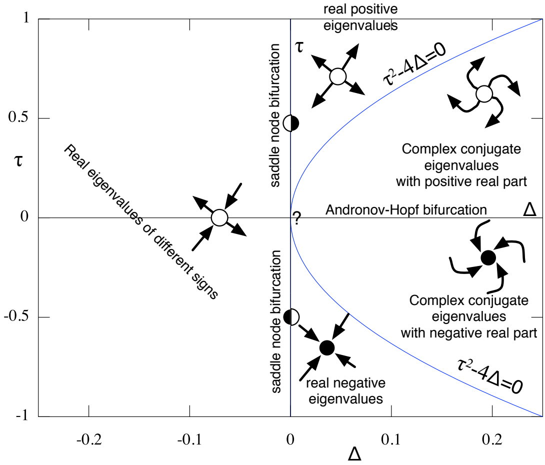


Figure: Equilibrium bifurcation diagram.

Saddle node bifurcation

- Recall that we've seen the saddle node bifurcation in 1d systems. It appears when the saddle and a stable node collide, which in turn gives birth to the semistable saddle-node.
- As the bifurcation parameter increases the saddle node disappears, leaving the ghost attractor that may slow down any passing nearby trajectory
- The necessary conditions for a system to undergo a saddle node bifurcation were: non-hyperbolicity, non-degeneracy and traversality. How to express these conditions with 2d systems?

Saddle node bifurcation

- Non-hyperbolicity in 2d means that the Jacobian matrix has exactly one zero eigenvalue.
- Determining non-degeneracy and traversality in general can be quite difficult, since it might require a reduction of the system to the center manifold (center manifold theorem)
- A center manifold is a manifold tangent to the eigenvector of the zero eigenvalue at the bifurcation point.
- Fortunately for (conductance based) neural models there is a workaround, since the saddle node bifurcation usually occurs where the n-nullcline is constant and the center manifold coincides with the n-nullcline in the vicinity of the saddle-node equilibrium.
- We can then reduce the system to 1d model, based on the I-V relations.

Saddle node bifurcation

We have

$$C_m \frac{dV}{dt} = -g_L(V - E_L) - g_{\mathrm{Na}} m_\infty(V)(V - E_{\mathrm{Na}}) - g_{\mathrm{K}} n(V - E_{\mathrm{K}})$$
$$\frac{dn}{dt} = (n_\infty(V) - n)/\tau_n(V)$$

but near the equilibrium $(V \approx -61mV)$ the n-nullcline

$$n = n_\infty(V) = \mathrm{const} \approx 0$$

We therefore reduce the system based on the steady state I-V relation:

$$C_m \frac{dV}{dt} = I - I_\infty(V) \Leftrightarrow \frac{dV}{dt} = \frac{I - I_\infty(V)}{C_m} = \mathbb{I}(V, I)$$

Saddle node bifurcation

- The equilibrium condition is that $\mathbb{I}(V, I) = 0$, therefore the bifurcation parameter $I_b = I_\infty(V)$. Non hyperbolicity implies the bifurcation can only occur on local maxima and minima of the I-V curve (therefore the necessary condition for the saddle-node bifurcation to occur is non-monotonic I-V relation).
- Non-degeneracy implies that the second order derivative of $\mathbb{I}(V, I_b) = 0$ with respect to V is non zero,

$$a = \frac{1}{2}\frac{\partial^2 \mathbb{I}(V, I_b)}{\partial V^2} \neq 0$$

Saddle node bifurcation

- Traversality implies

$$c = \frac{\partial \mathbb{I}(V_b, I)}{\partial I} \neq 0$$

- We can then expand the system in a normal form near the bifurcation as

$$\frac{dV}{dt} = c(I - I_b) + a(V - V_b)^2$$

- Lets consider the $I_{Na,p}$ - I_K model as defined on previous lecture. By solving the equations numerically we find that the bifurcation occurs for $I_b = 4.51$, $(V_b, n_b) = (-60.935, 0.0007)$. The Jacobian matrix

$$L = \begin{bmatrix} 0.0435 & -290 \\ 0.00015 & -1 \end{bmatrix}$$

Saddle node bifurcation

- Matrix L has two eigenvalues $\lambda_1 = 0$, $\lambda_2 = -0.9565$ with corresponding eigenvectors:

$$v_1 = \begin{bmatrix} 1 \\ 0.00015 \end{bmatrix}, v_2 = \begin{bmatrix} 1 \\ 0.0034 \end{bmatrix}$$

- The non-degeneracy and traversality conditions yield $a = 0.1887$ and $c = 1$ that is the topological normal form:

$$\frac{dV}{dt} = (I - 4.51) + 0.1887(V + 60.935)^2$$

- Note the normal form resembles quadratic integrate and fire neuron... The cycle is expanded out to infinity.

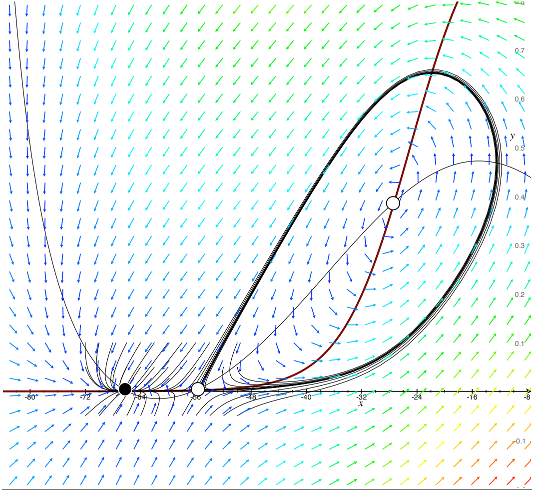
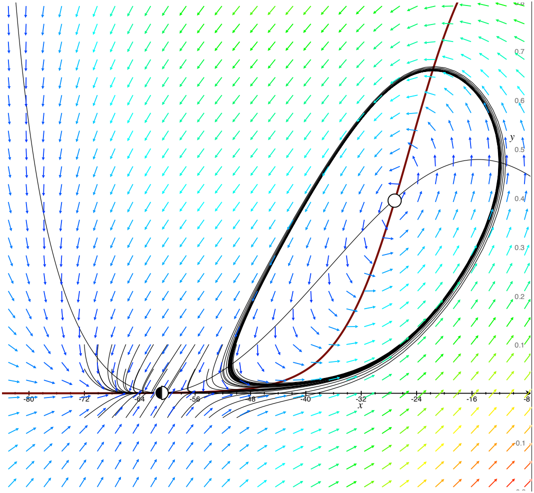


Figure: Saddle node in $I_{Na,p}$ - I_K model with fast K current ($\tau(V) = 0.152$).



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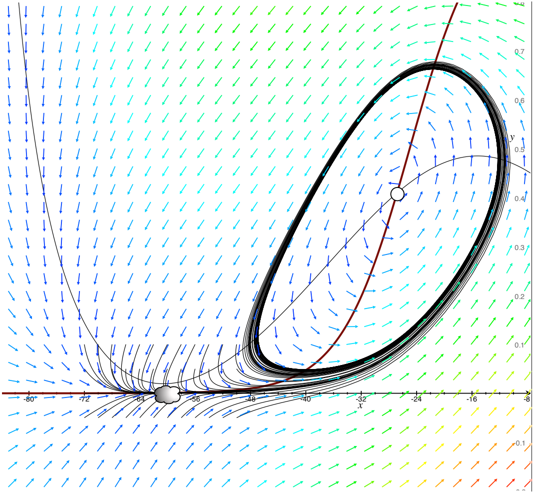

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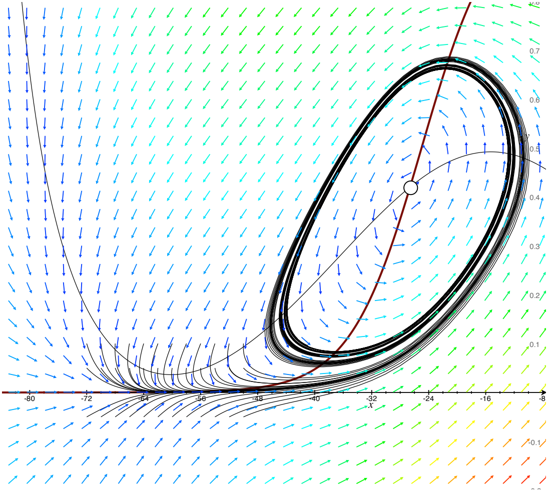

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Saddle node on invariant circle

- An important from the computational point of view is a special case of a saddle node bifurcation which appears on the invariant circle.
- Before the bifurcation there is a saddle and a node, connected by two heteroclinic orbits. These orbits form the invariant circle (it is invariant, since any trajectory departing from a point on the circle has to stay on it).
- When the bifurcation parameters crosses critical value, the invariant circle changes into a limit cycle.
- The trajectories while spinning at the cycle fly by the ghost attractor, resulting in a slow transition...

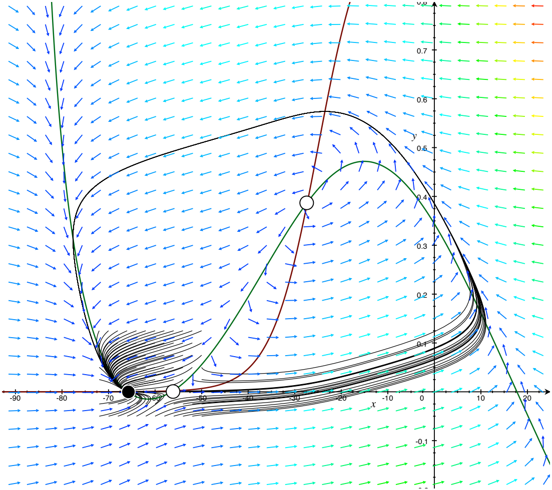
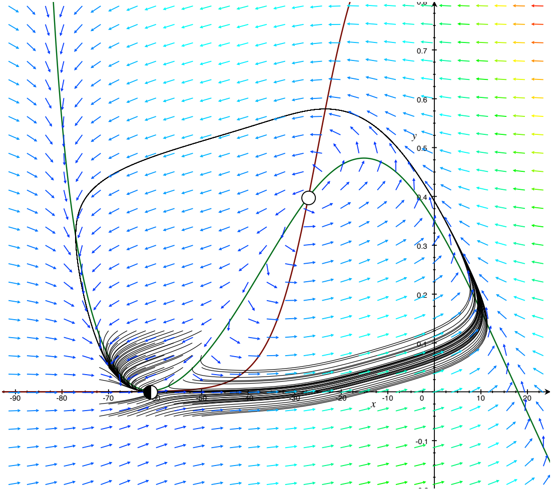


Figure: Phase plane of the $I_{Na,p}$ - I_K model I=0, I=5, I=10 and I=40.



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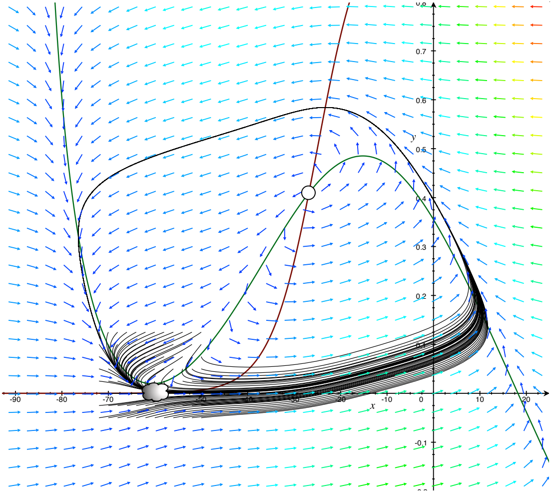

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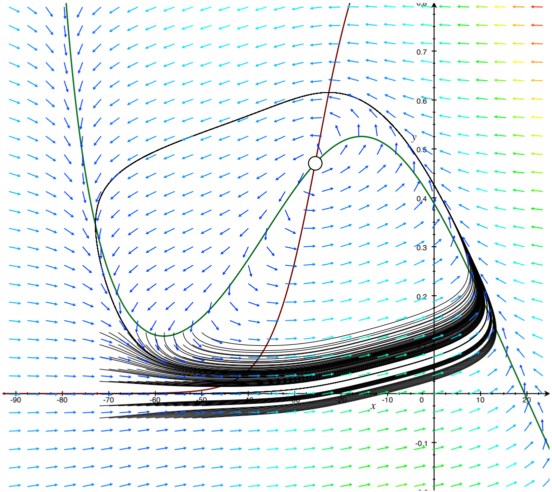

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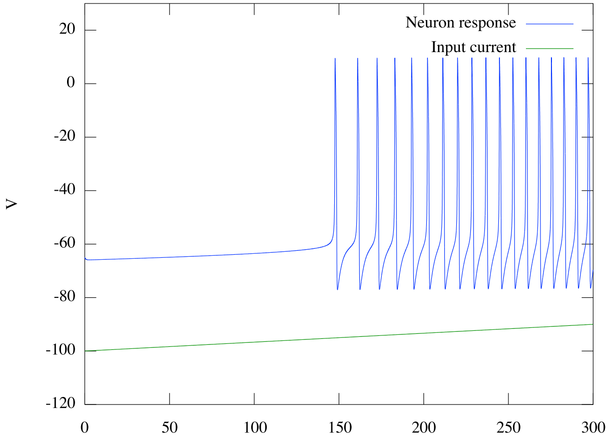


Figure: Saddle node on invariant circle bifurcation in $I_{Na,p}$ - I_K model (ramp current).

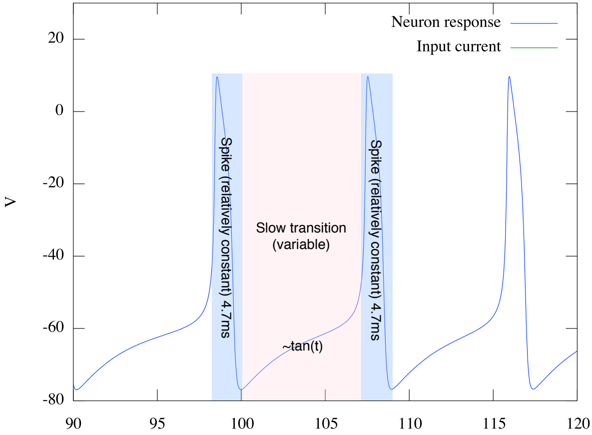


Figure: Saddle node on invariant circle bifurcation in $I_{Na,p}$ - I_K model (ramp current).

Saddle node on invariant circle - frequency

- Surprisingly the normal form at the bifurcation can be used to estimate the frequency of the response with respect to input current.
- Most of the time the system spends near the ghost equilibrium where it is approximated with the normal form

$$\frac{dV}{dt} = c(I - I_b) + a(V - V_b)^2$$

- Consider

$$V(t) = \frac{\sqrt{c(I - I_b)}}{\sqrt{a}} \tan(\sqrt{ac(I - I_b)}t)$$

note (by differentiating) that $V(t)$ is the solution of the normal form.

Recall that $\tan x' = 1 + \tan^2 x$, therefore

$$\frac{dV}{dt} = \frac{d}{dt}\frac{\sqrt{c(I-I_b)}}{\sqrt{a}}\tan(\sqrt{ac(I-I_b)}t) =$$
$$= \frac{\sqrt{c(I-I_b)}}{\sqrt{a}}\left(1+\tan^2(\sqrt{ac(I-I_b)}t)\right)\left(\sqrt{ac(I-I_b)}\right) =$$
$$= c(I-I_b)\left(1+\tan^2(\sqrt{ac(I-I_b)}t)\right) =$$
$$= c(I-I_b) + a\cdot\left(\frac{\sqrt{c(I-I_b)}}{\sqrt{a}}\tan(\sqrt{ac(I-I_b)}t)\right)^2 =$$
$$= c(I-I_b) + aV(t)^2$$

$\tan \pi/2 = -\infty$ and $\tan \pi/2 = \infty$, to it takes

$$T = \frac{\pi}{\sqrt{ac(I-I_b)}}$$

to get from $-\infty$ to ∞.

Saddle node on invariant circle - frequency

- We have therefore, that the full period of the model is the sum $T = T_1 + T_2$, where T_1 is the fairly constant spike time (4.7ms) and

$$T_2 = \frac{\pi}{\sqrt{ac(I - I_b)}}$$

, which in our case gives

$$T_2 = \frac{\pi}{\sqrt{0.1887(I - 4.51)}}$$

- The analytical curve is then

$$\omega = \frac{1000Hz}{T_1 + T_2}$$

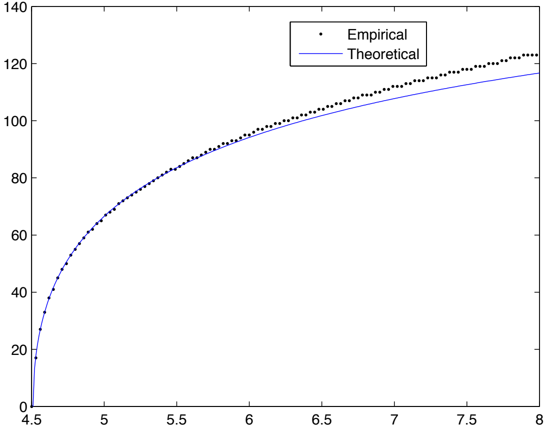


Figure: Frequency against input current in $I_{Na,p}$ - I_K model undergoing saddle node on invariant circle (SNIC) bifurcation. Comparison of the theoretical prediction and the numerical result.

Andronov-Hopf bifurcation

- When two complex conjugate eigenvalues become purely imaginary, we have the Andronov-Hopf bifurcation. It is a frequent bifurcation in neuronal models with monotonic I-V curve, since they cannot exhibit saddle node bifurcation (but have to get from resting to spiking somehow).
- In this case the equilibrium changes its stability, but also gives birth to either stable or unstable limit cycle.
- Consider the system

$$\frac{dv}{dt} = F(v, u, b)$$
$$\frac{du}{dt} = G(v, u, b)$$

Andronov-Hopf bifurcation

Assume the system has an equilibrium at the origin and bifurcation parameter $b = 0$. The system undegoes Andronov-Hopf bifurcation if the following conditions are satisfied:

- Non-hyperbolicity: Jacobian matrix

$$L = \begin{bmatrix} \frac{\partial F}{\partial v} & \frac{\partial F}{\partial u} \\ \frac{\partial G}{\partial v} & \frac{\partial G}{\partial u} \end{bmatrix}$$

  has a pair of purely imaginary eigenvalues $\pm i\omega \in \mathbb{C}$.
  $\mathrm{tr} L = \frac{\partial F}{\partial v} + \frac{\partial G}{\partial u} = 0$ and $\omega^2 = \det L = \frac{\partial F}{\partial v}\frac{\partial G}{\partial u} - \frac{\partial F}{\partial u}\frac{\partial G}{\partial v} > 0$

Andronov-Hopf bifurcation

Linear change of variables $v = x$ and $\frac{\partial F}{\partial u} u = \frac{\partial F}{\partial v} x - \omega y$ converts the system into:

$$\frac{dx}{dt} = -\omega y + f(x, y)$$
$$\frac{dy}{dt} = \omega x + g(x, y)$$

where $f(x, y) = F(v, u) + \omega y$ and $g(x, y) = -\left(\frac{\partial F}{\partial v} F(v, u) + \frac{\partial F}{\partial u} G(v, u)\right) / \omega - \omega x$. Now we are ready to state the next condition:

Andronov-Hopf bifurcation

- Non-degeneracy:

$$a = \frac{1}{16}\left(\frac{\partial^3 f}{\partial x^3} + \frac{\partial^3 f}{\partial x \partial y^2} + \frac{\partial^3 g}{\partial x^2 \partial y} + \frac{\partial^3 g}{\partial y^3}\right) +$$
$$+ \frac{1}{16\omega}\left(\frac{\partial^2 f}{\partial x \partial y}\left(\frac{\partial^2 f}{\partial x^2} + \frac{\partial^2 f}{\partial y^2}\right) - \frac{\partial^2 g}{\partial x \partial y}\left(\frac{\partial^2 g}{\partial x^2} + \frac{\partial^2 g}{\partial y^2}\right) +\right.$$
$$\left. - \frac{\partial^2 f}{\partial x^2}\frac{\partial^2 g}{\partial x^2} + \frac{\partial^2 f}{\partial y^2}\frac{\partial^2 g}{\partial y^2}\right) \neq 0$$

Andronov-Hopf bifurcation

- Transversality: Let $c(b) + i\omega(b)$ be the eignvalues of the Jacobian matrix near 0, with $c(0) = 0$ and $\omega(0) = \omega$. The real part of the eignvalues must not be degenerate, that is $c'(0) \neq 0$ (they truly cross the imaginary axis, not just touch it).

Since only one condition implies equality $\mathrm{tr}L = 0$, the codimension of the bifurcation is one. The sign of a determines the type of bifurcation:

- $a < 0$ - supercritical bifurcation, stable limit cycle emerges from stable equilibrium (which itself becomes unstable)
- $a > 0$ - subcritical bifurcation, unstable limit cycle emerges from unstable equilibrium (which itself becomes stable)

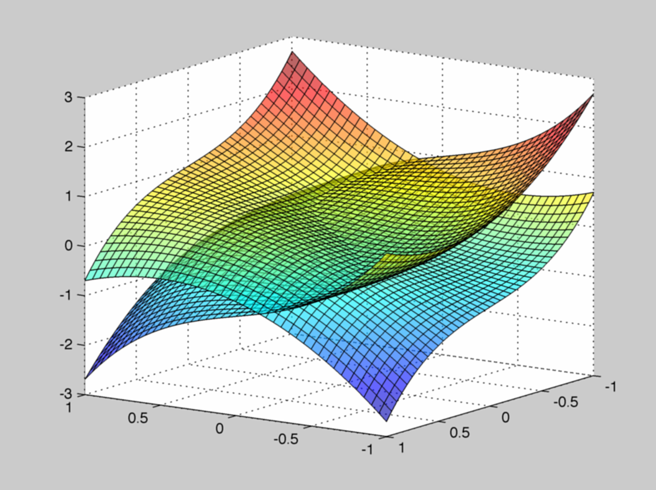


Figure: Vector field represented as a pair of surfaces near Andronov-Hopf bifurcation.

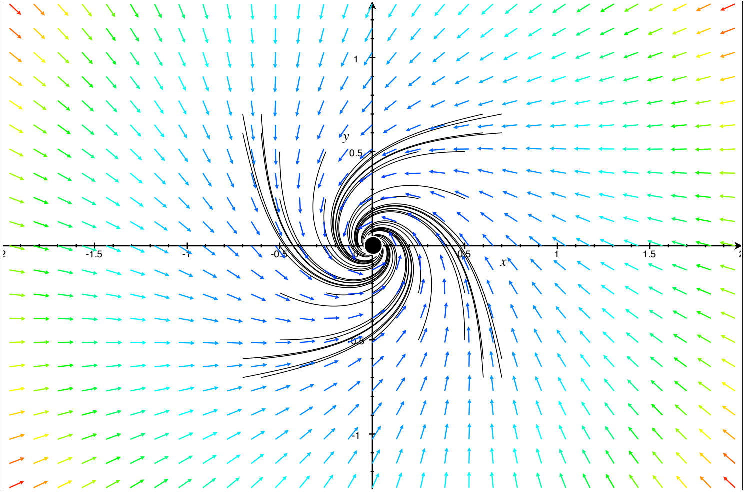
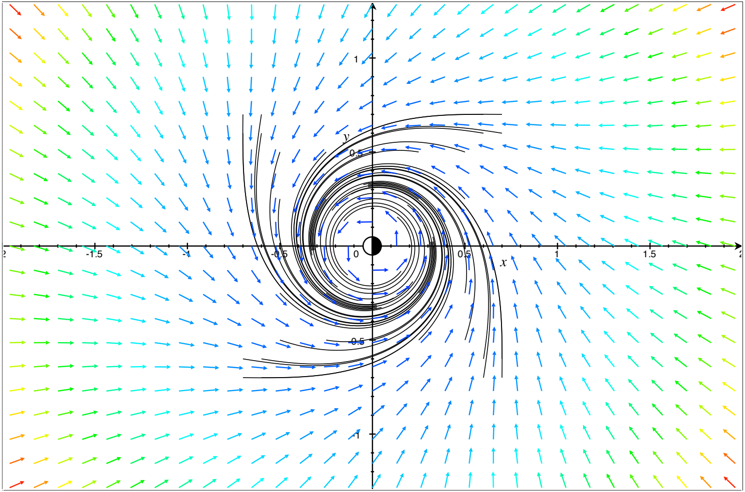


Figure: Supercritical Andronov-Hoph bifurcation.



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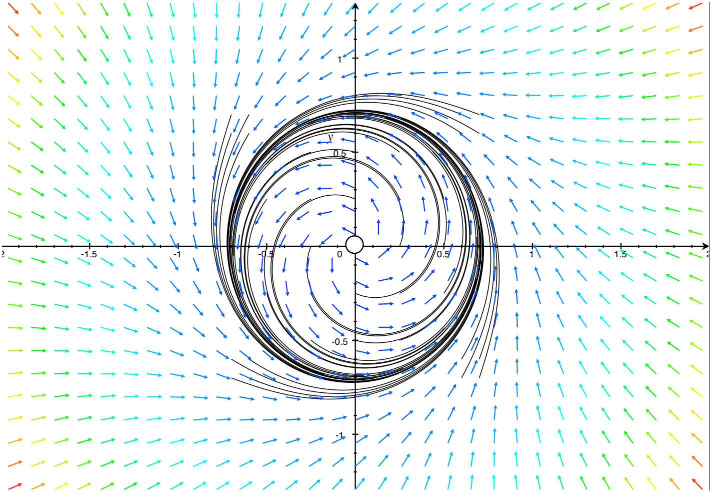

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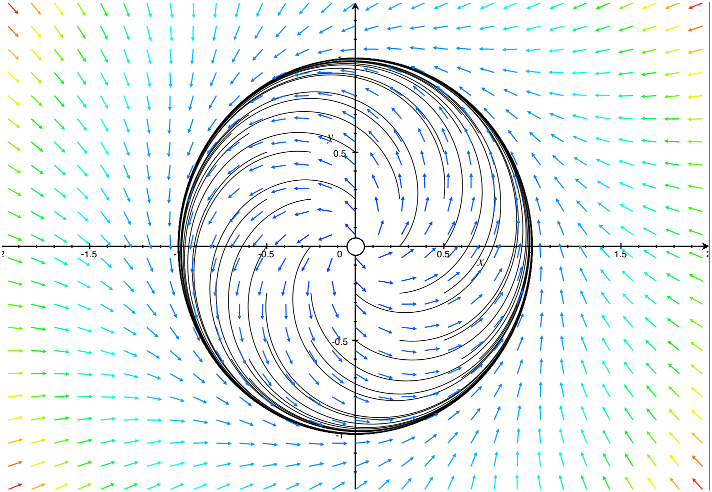

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Consider the $I_{Na,p}$ - I_K model

$$C_m \frac{dV}{dt} = -g_L(V - E_L) - g_{Na} m_\infty(V)(V - E_{Na}) - g_K n(V - E_K)$$
$$\frac{dn}{dt} = (n_\infty(V) - n)/\tau_n(V)$$

with $C_m = 1$, $E_L = -78$, $g_L = 8$, $E_{Na} = 60$, $g_{Na} = 20$, $E_K = -90$, $g_K = 10$, $m_\infty(V) = \frac{1}{1+\exp\left(\frac{-20-V}{15}\right)}$,$n_\infty(V) = \frac{1}{1+\exp\left(\frac{-45-V}{5}\right)}$, $\tau_n(V) = 1$, $I = 14.66$.

We will refer to that model as *low threshold* $K^{+}I_{Na,p}$ *-* I_K *model*. It has monotonic I-V relation, and exhibits supercritical Andronov-Hopf bifurcation at $I = 14.66$

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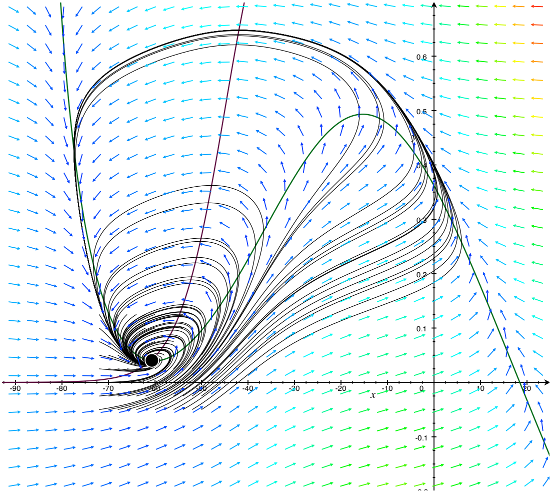
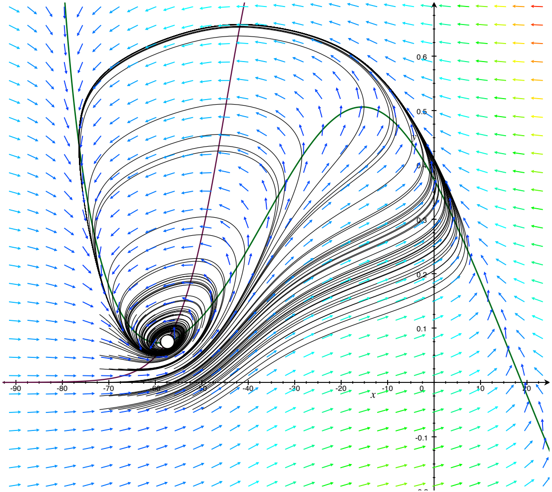


Figure: $I_{Na,p}$ - I_K model undergoing supercritical Andronov-Hoph bifurcation ($E_L = -78$, $n_\infty(V) = \frac{1}{1+\exp\left(\frac{-45-V}{5}\right)}$)



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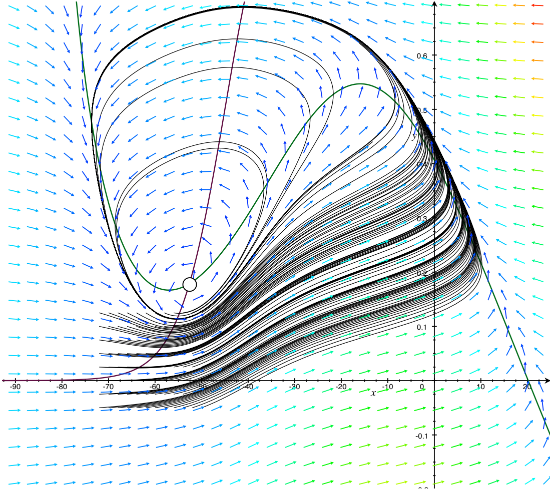

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- We can find via numeric simulation that the bifurcation occurs with $I = 14.66$ and $(V, n) = (-56, 0.09)$. The Jacobian matrix

$$L = \begin{bmatrix} 1 & -335 \\ 0.0166 & -1 \end{bmatrix}$$

has got a pair of complex conjugate eigenvalues $\pm 2.14i$, so the non-hyperbolicity condition is satisfied.

- We can further find numerically that eigenvalues near the equilibrium are approximatelly

$$c(I) + \omega(I)i \approx 0.03(I - 14.66) \pm (2.14 + 0.04(I - 14.66))i$$

The transversality condition is therefore also satisfied ($c'(14.66) \neq 0$).

- Either numerically or symbolically we find that $a = -0.0026$ so the non-degeneracy condition is satisfied.

It is worth emphasizing, that unlike the Saddle-node on invariant circle system, with Andronov-Hopf bifurcation the frequency of oscillations jumps abruptly from zero (resting state) to some fairly high frequency. The amplitude of oscillations however scales as $\sqrt{I}$.

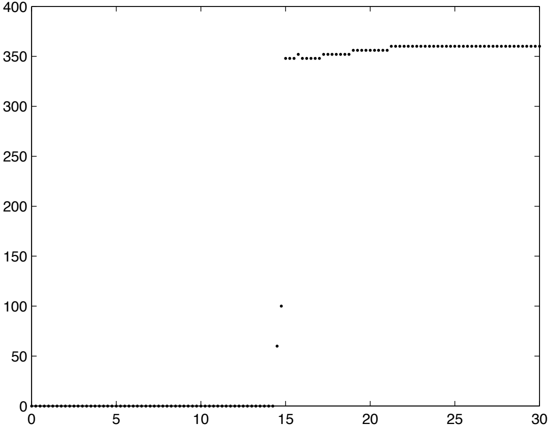

Figure: Frequency dependence on current in $I_{Na,p}$ - I_K model undergoing Andronov-Hoph bifurcation ($E_L = -78$, $n_\infty(V) = \frac{1}{1+\exp\left(\frac{-45-V}{5}\right)}$)

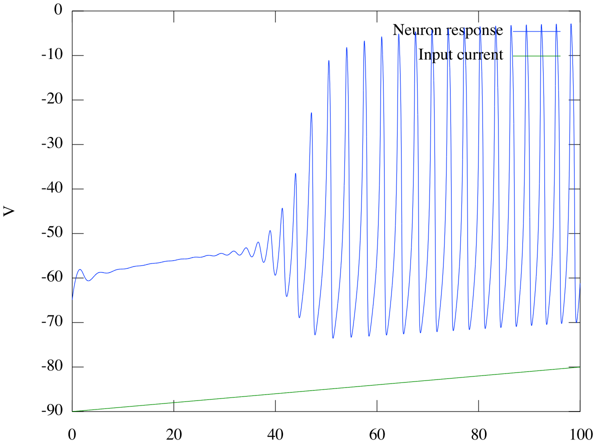

Figure: Supercritical Andronov-Hopf bifurcation in $I_{Na,p}$ - I_K model (ramp current).

Subcritical Andronov-Hopf bifurcation

- A subcritical Andronov-Hopf bifurcation occurs when an unstable cycle shrinks into stable equilibrium causing it to loose stability.
- Since such a bifurcation may lead to destruction of a stable equilibrium it may lead from resting to spiking.
- The bifurcation occurs in $\mathrm{I_{Na,p}}$ - $\mathrm{I_K}$ with parameters $C_m = 1$, $E_L = -78$, $g_L = 1$, $E_{\mathrm{Na}} = 60$, $g_{\mathrm{Na}} = 4$, $E_{\mathrm{K}} = -90$, $g_{\mathrm{K}} = 4$, $m_\infty(V) = \frac{1}{1+\exp\left(\frac{-30-V}{7}\right)}$, $n_\infty(V) = \frac{1}{1+\exp\left(\frac{-45-V}{5}\right)}$, $\tau_n(V) = 1$, $I = 48.75$

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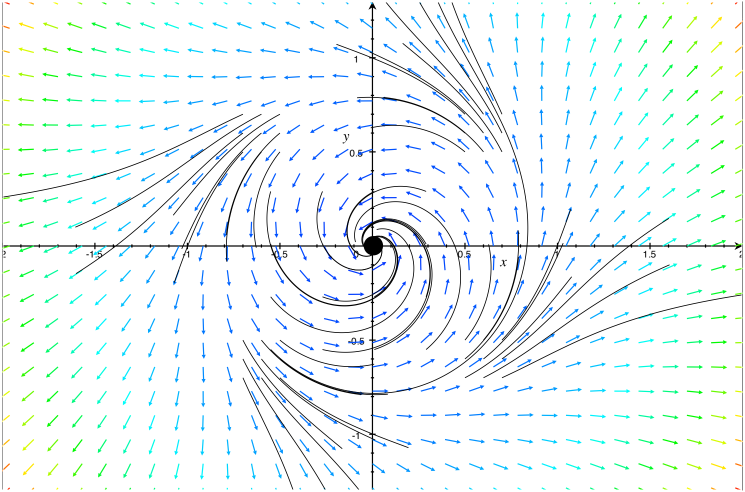
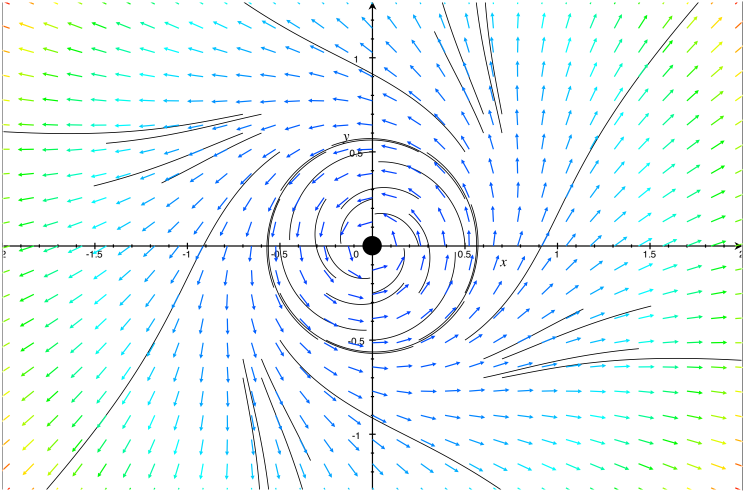


Figure: Subcritical Andronov-Hopf bifurcation.



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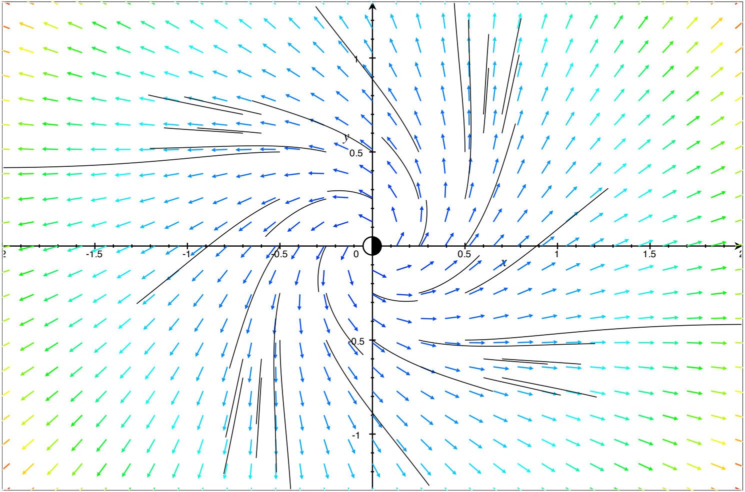

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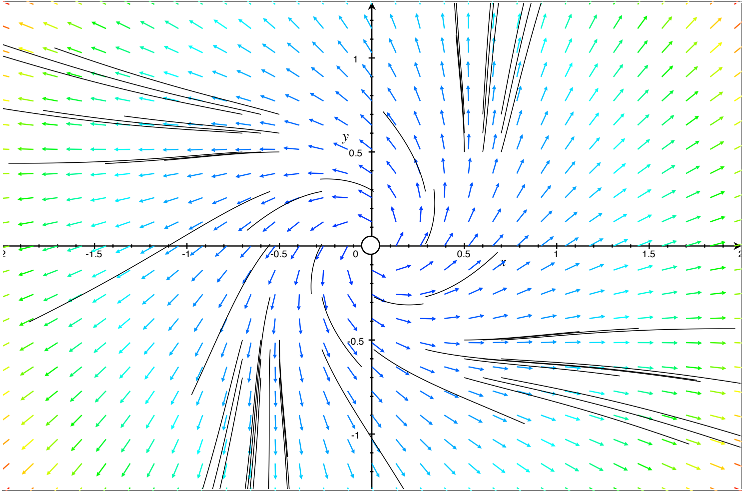


Figure: Subcritical Andronov-Hopf bifurcation.

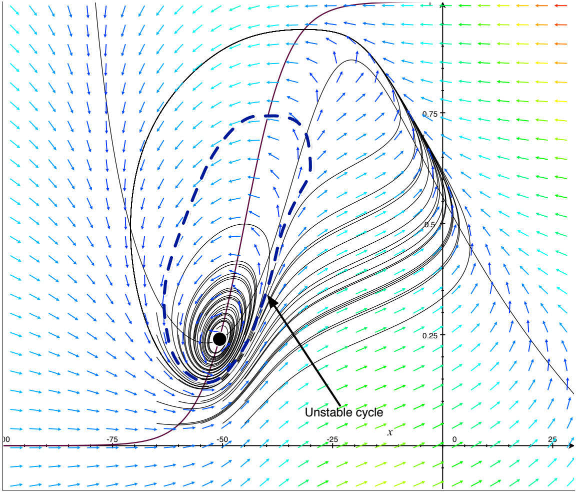


Figure: Subcritical Andronov-Hopf bifurcation in $I_{Na,p}$ - I_K as above.

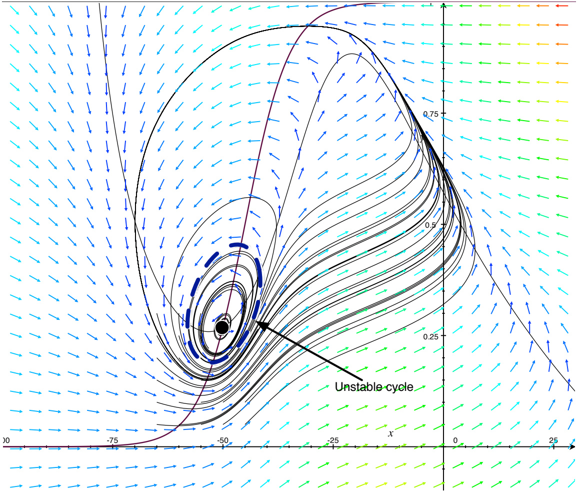


Figure: Subcritical Andronov-Hopf bifurcation in $I_{Na,p}$ - I_K as above.

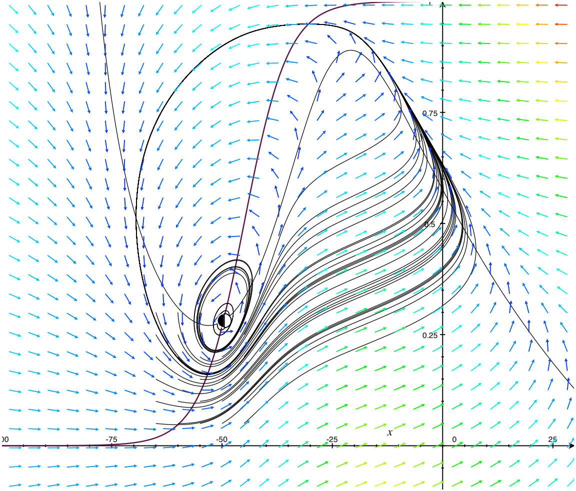


Figure: Subcritical Andronov-Hopf bifurcation in $I_{Na,p}$ - I_K as above.

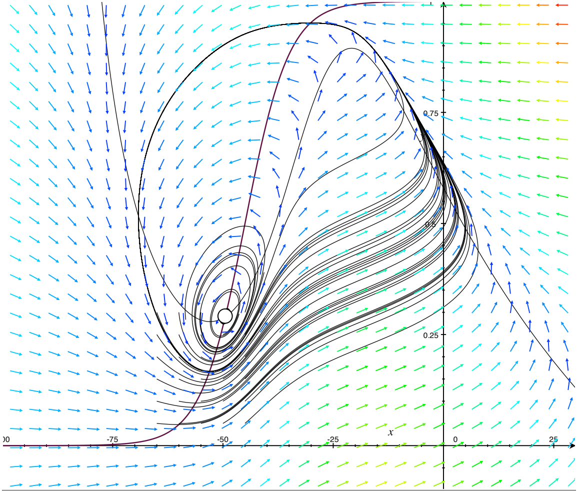


Figure: Subcritical Andronov-Hopf bifurcation in $I_{Na,p}$ - I_K as above.

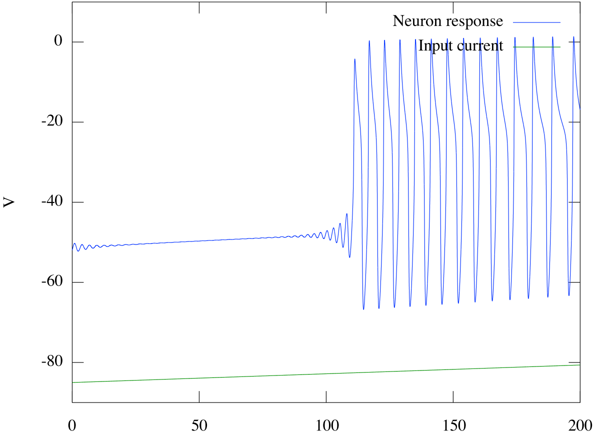


Figure: Subcritical Andronov-Hopf bifurcation in $I_{Na,p}$ - I_K model as above (ramp current).

Short summary

Bifurcation of an equilibrium	Amplitude of spikes	Frequency of spikes
Saddle node	nonzero	nonzero
Saddle node on invariant circle	nonzero	$\approx \sqrt{I - I_b}$
Supercritical Andronov-Hopf	$\approx \sqrt{I - I_b}$	nonzero
Subcritical Andronov-Hopf	nonzero	nonzero

From spiking to resting

- We've seen how a neuron can get from resting state to spiking, via four bifurcations. We will now study the ways of getting back from a cycle to a resting state.
- Again we have four main bifurcations to study - two of them are ones we already met, but with bifurcation parameter (current) reversed. These are saddle node on invariant circle, and supercritical Andronov-Hopf.
- There are two new bifurcations, fold cycle and saddle homoclinic orbit.

Saddle node on invariant circle

- Exactly like in the case of increasing current, the decreasing current can reverse the saddle node bifurcation.
- In this case the amplitude of the spikes remains constant until the last spike is fired, while the frequency grows, as described a couple of slides earlier.
- This case is not particularly interesting due to full symmetry...

Saddle homoclinic orbit

- The bifurcation gives birth to stable (or unstable) limit cycle.
- One of the heteroclinic trajectories departing from the saddle (via unstable manifold) becomes homoclinic as the bifurcation parameter changes. Therefore the orbit becomes a limit cycle, though the period of the cycle is infinite at the bifurcation point (transition through the saddle takes infinite amount of time)
- As the bifurcation parameter progresses, the homoclinic orbit becomes a full blown limit cycle flying somewhat neat the saddle...
- Depending on the saddle quantity (sum of eigenvalues at the saddle point), the bifurcation can be either subcritical or supercritical. In neural model we will only see the supercritical case.

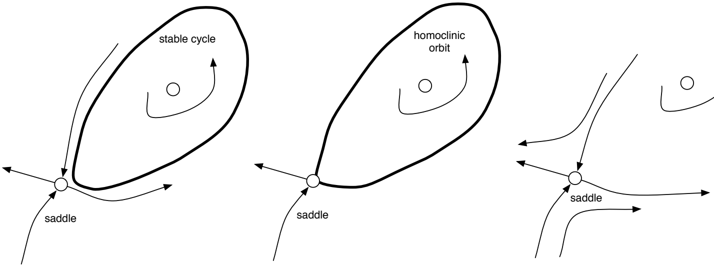


Figure: Supercritical saddle-homoclinic-orbit bifurcation

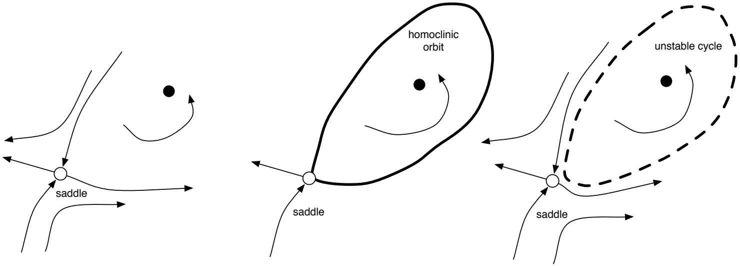


Figure: Subcritical saddle-homoclinic-orbit bifurcation

Saddle homoclinic orbit

- The bifurcation appears in $I_{Na,p}$ - I_K with fast K^+ current, for example with $\tau(V) = 0.16$ and $I = 3.08$
- It gives birth to the limit cycle, but is not responsible for spiking since the stable resting node remains intact.
- However if the system was in the spiking regime, and the current was dropping, the bifurcation cuts the cycle, ale allows the system to get back to steady equilibrium.
- Since the period of the homoclinic orbit becomes infinite, the it may be the case that again the spike frequency can become arbitrarily low?

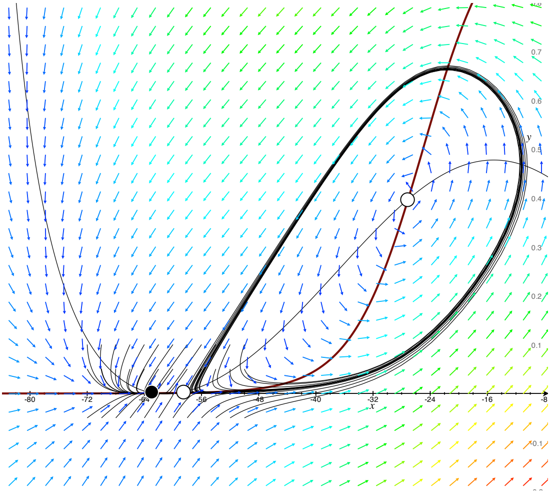


Figure: Saddle homoclinic orbit bifurcation in $I_{Na,p}$ - I_K with fast K^+ current.

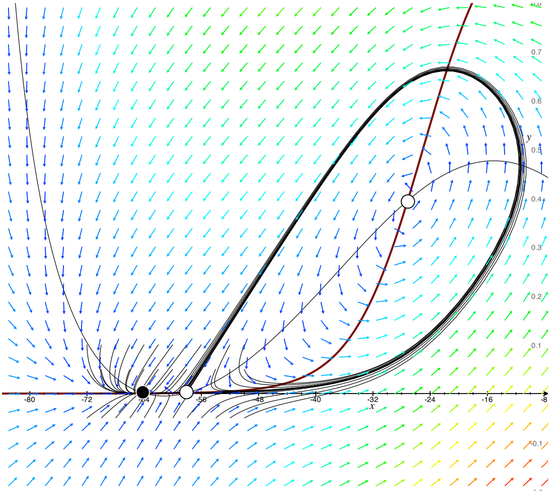


Figure: Saddle homoclinic orbit bifurcation in $I_{Na,p}$ - I_K with fast K^+ current.

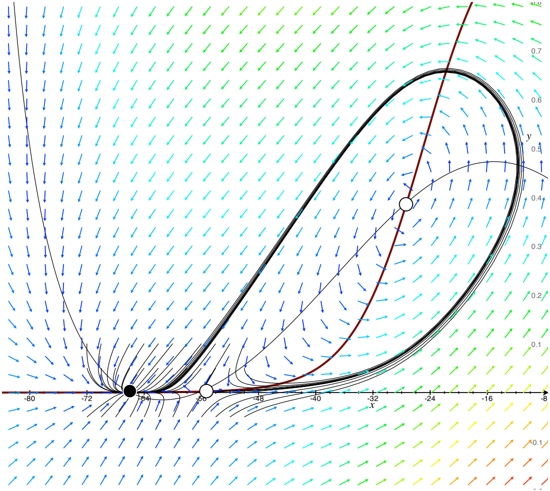


Figure: Saddle homoclinic orbit bifurcation in $I_{Na,p}$ - I_K with fast K^+ current.

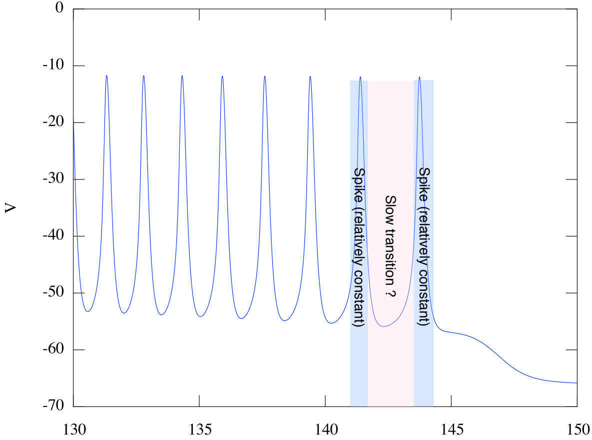


Figure: Is there a slow transition with the saddle-homoclinic orbit bifurcation?

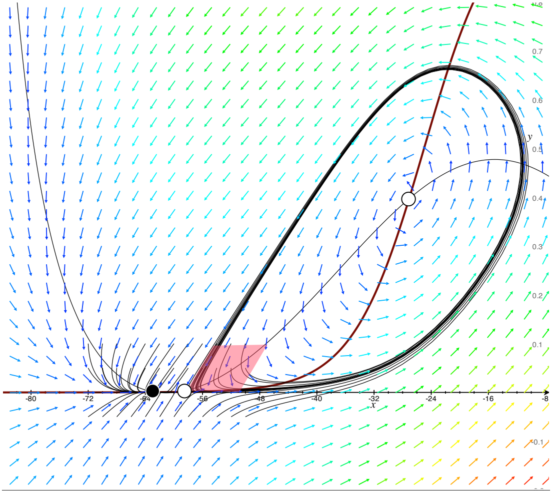
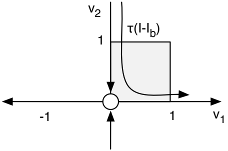


Figure: How long will the trajectory spend in the shaded region?

- We can estimate the frequency via linearization. Consider the diagram:



- How long will the trajectory need to leave the square? The projection of the system on v_1 axis is given by $\frac{dx}{dt} = \lambda_1 x$, $x(0) = \tau(I - I_b)$.
- The trajectory will leave the square when $x(t) = \tau(I - I_b)e^{\lambda_1 t} = 1$, that is:

$$t = -\frac{1}{\lambda_1}\ln(\tau(I - I_b))$$

- For the $I_{Na,p}$ - I_K model with fast K^+, $\tau(V) = 0.16$ and $I = 3.08$ we can estimate $\tau = 0.2$ (if the period and the eigenvalue λ_1 are known for at least one value of I).
- The frequency curve will also depend on the $\lambda(I) \approx 0.87\sqrt{4.51 - I}$ which accounts for the changes in positive eigenvalue of the saddle as I progresses.
- Eventually we have

$$\omega(I) = \frac{1000Hz\lambda(I)}{-\ln(0.2 \cdot (I - 3.014))}$$

- Exercise: check if this prediction is in agreement with numerical data!

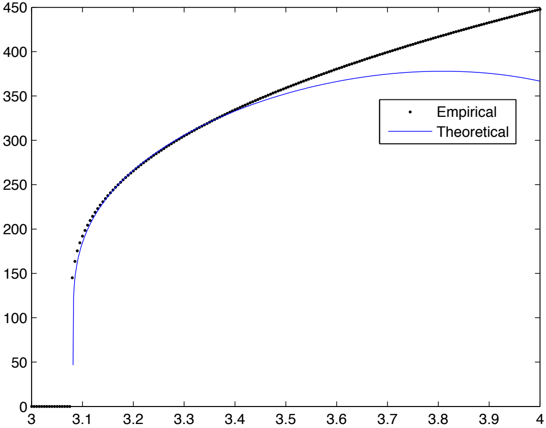


Figure: Frequency/current relation in $I_{Na,p}$ - I_K model with fast K^+ ($\tau(V) = 0.16$). Althought the curve is continuously approaching 0, the slope becomes infinite... Therefore in numerical experiments the drop will show up as discontinuous.

Supercritical Andronov-Hopf

- Recall that with the supercritical Andronov-Hopf bifurcation a stable limit cycle emerges from stable equilibrium
- This process can also reverse itself, that is a stable cycle eventually shrinks into an equilibrium
- Much like with the saddle node on invariant circle, this case is not particularly interesting due to symmetry

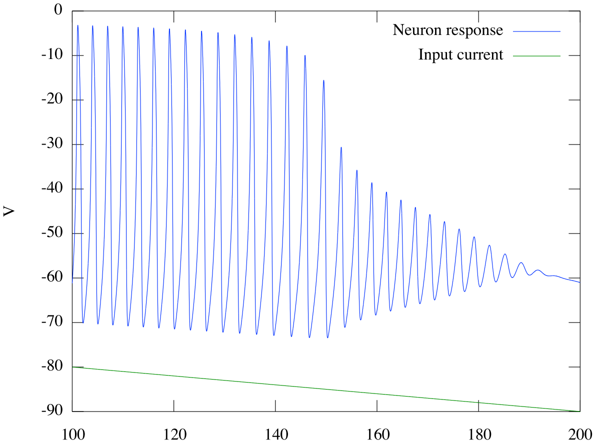


Figure: Supercritical Andronov-Hopf bifurcation in $I_{Na,p}$ - I_K model (ramp current).

Fold limit cycle bifurcation

- Recall that with subcritical Andronov-Hopf bifurcation an unstable limit cycle shrinks into a stable equilibrium which eventually looses stability. The state of the system can then fall onto a large stable cycle (spiking)
- If we reverse that process however, even though the unstable cycle emerges and the equilibrium becomes stable, the state of the system can still follow the stable cycle. We have a bistable neuron!
- Nevertheless if we drop the current even more in $I_{Na,p}$ - I_K model which exhibits subcritical AH bifurcation, at some point the spiking stops and the neuron gets back to the rest state... Something else has to be going on...

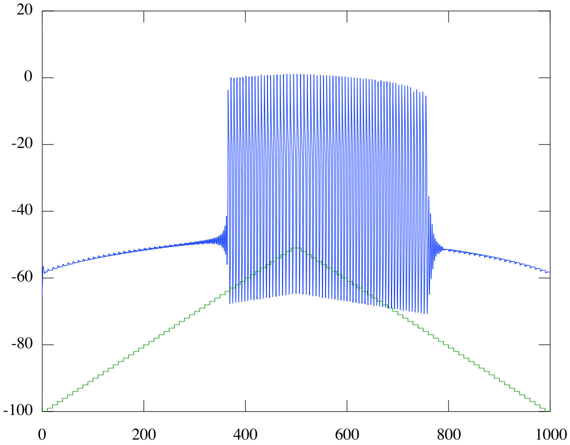


Figure: $I_{Na,p}$ - I_K exhibiting subcritical AH bifurcation from resting to spiking, once excited continues to spike at low currents...

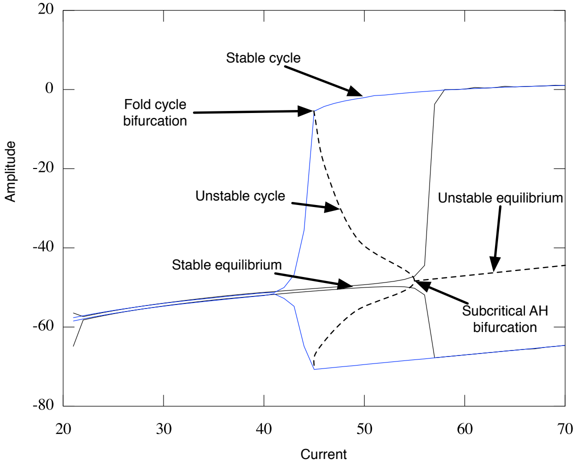


Figure: Amplitude of the spikes from previous figure folded in the middle and reflected reveals the place where another bifurcation takes place.

Fold limit cycle bifurcation

- The mysterious bifurcation that is taking place is called a fold limit cycle bifurcation.
- In this case a stable cycle collides with an unstable one, forming the neutrally stable fold cycle
- The bifurcation resembles the saddle node, but in this case instead of equilibria we have cycles...
- We can actually spot the unstable cycles by simulating models backwards (with time reversed).

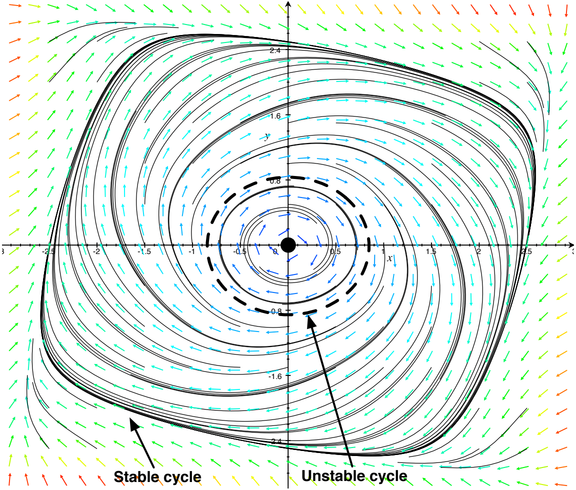
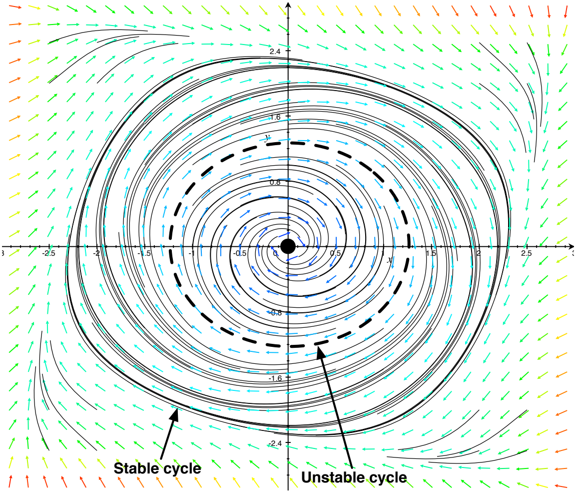


Figure: Fold limit cycle bifurcation.



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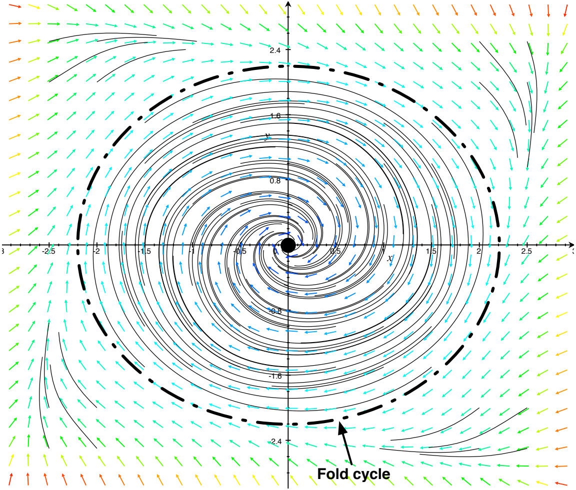

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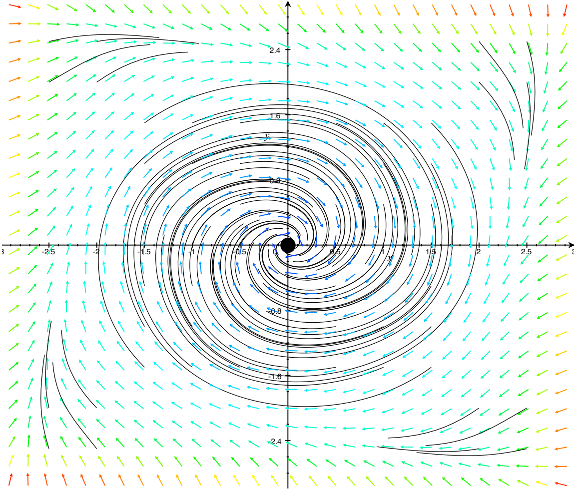

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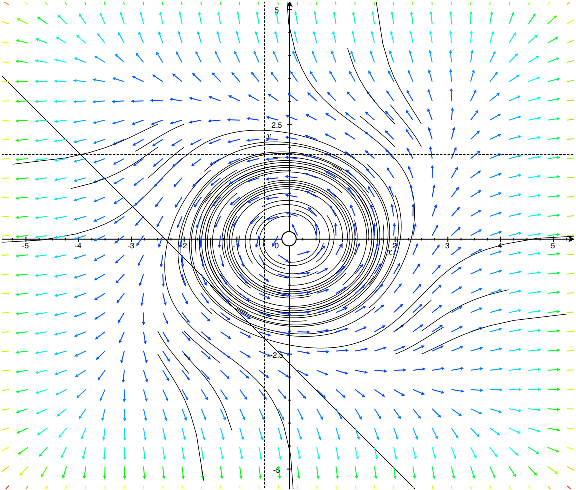
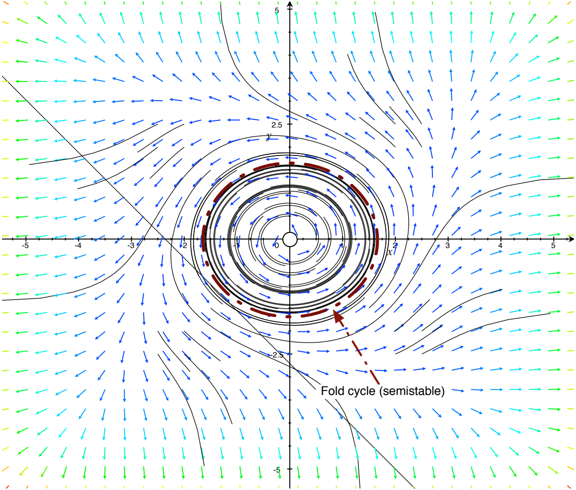


Figure: Another example of fold limit cycle bifurcation.



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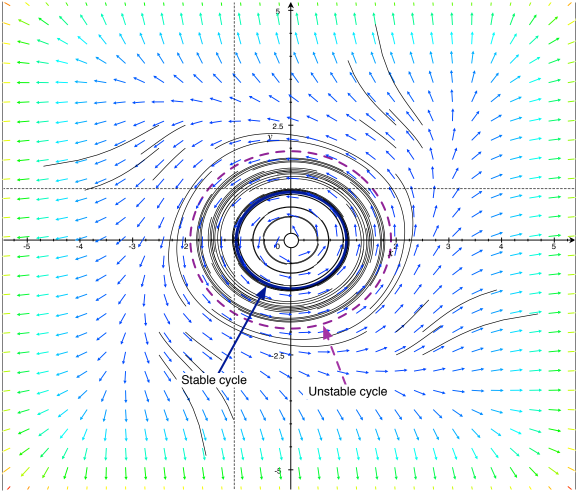

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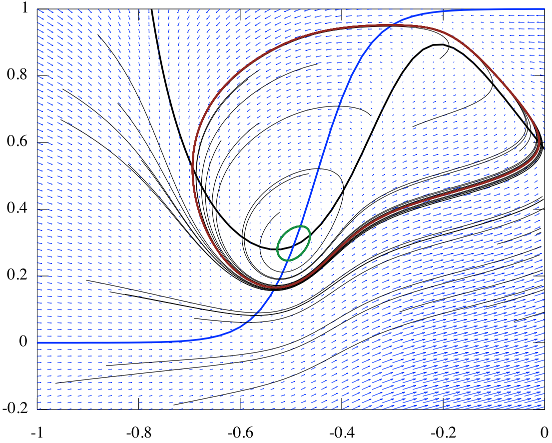
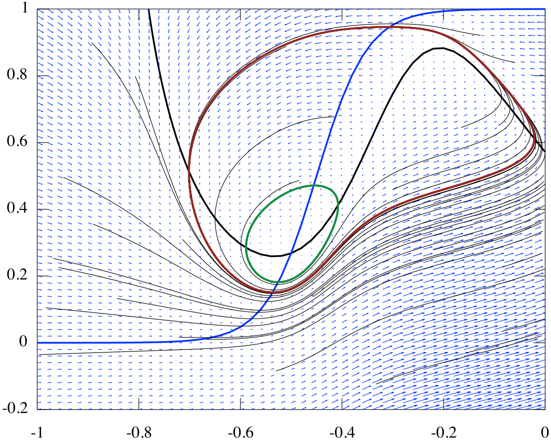


Figure: Fold cycle bifurcation in $I_{Na,p}$ - I_K model. Stable cycle marked red, while the unstable green.



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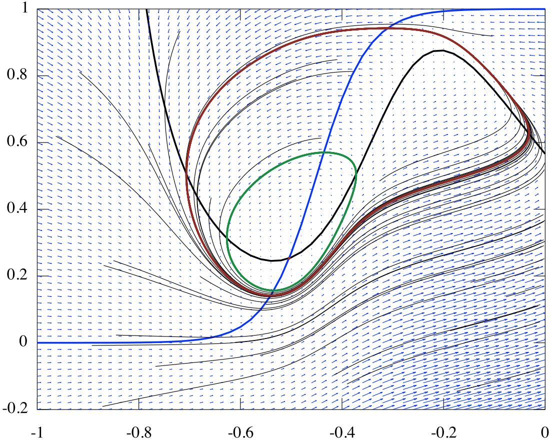

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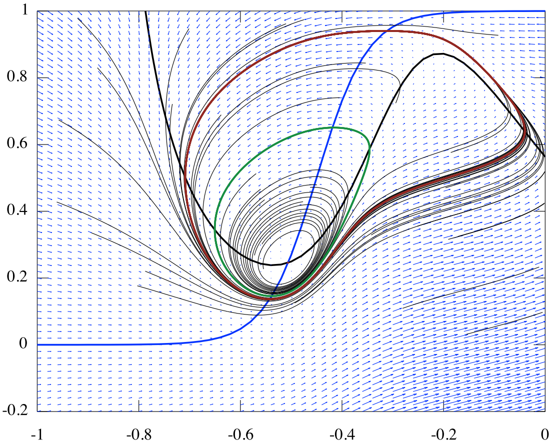

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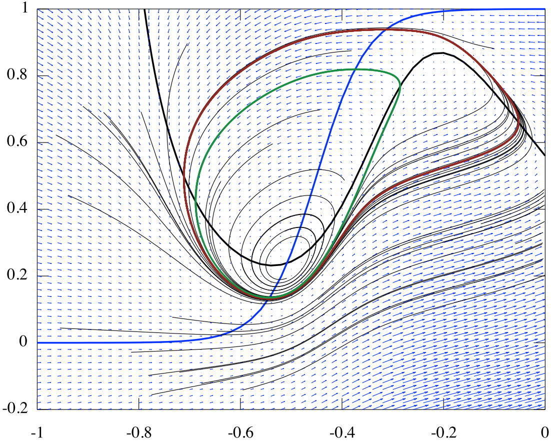

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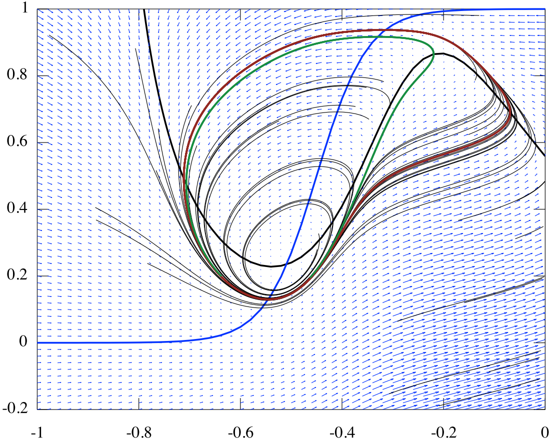

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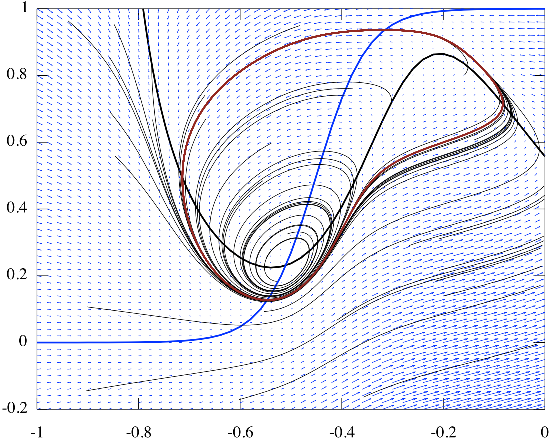

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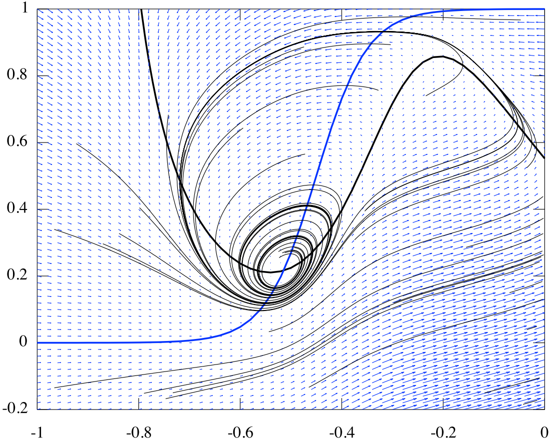

Figure: Fold cycle bifurcation in $I_{Na,p}$ - I_K model. Stable cycle marked red, while the unstable green.

Short summary

Bifurcation of a limit cycle	**Amplitude of spikes**	**Frequency of spikes**
Saddle node on invariant circle	nonzero	$\approx \sqrt{I - I_b}$
Supercritical Andronov-Hopf	$\approx \sqrt{I - I_b}$	nonzero
Fold limit cycle	nonzero	nonzero
Saddle homoclinic orbit	nonzero	$\approx \frac{-1}{\ln(I - I_b)}$

Recapitulation

- The phase portrait in 2d can be very complex, nevertheless the number of possible bifurcations (expecially those of codimension one) is very limited.
- It turns out that only four bifurcations of equilibria are responsible for getting from resting to spiking, and other four (partially overlapping) are responsible for getting from spiking back to rest
- Different bifurcations exhibit different neurocomputational properties, some modulate frequency of spikes, some modulate the amplitude.
- All of these cases can be studied with $I_{Na,p}$ - I_K model by varying some of its parameters!