Noise-induced collective behavior
in globally coupled excitable systems:

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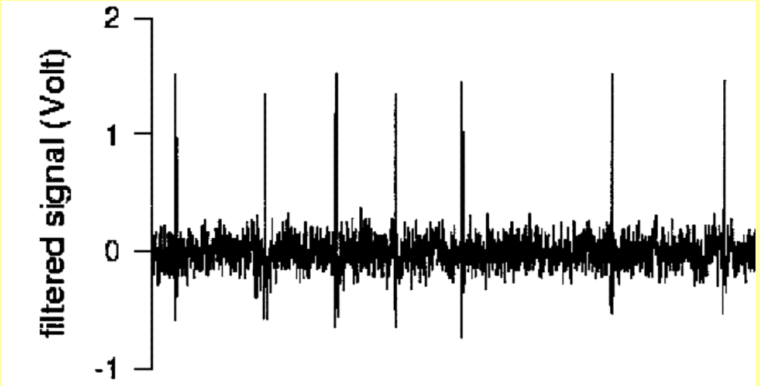
Outline

- *Excitability in simplistic models of neurons*
- *Direct simulation for large ensembles*
  - *onset of irregular small-scale oscillations of the mean field*
  - *different spiking regimes*
- *Gaussian approximation: low-dimensional dynamics for cumulants*
  - *slow and fast motions*
  - *onset of chaotic subthreshold oscillations*
  - *transition to chaos: "canard" explosion in the chaotic attractor ?*
- *Finite-state model: non-Markovian description*

Preamble: excitability in models of neurons



Ingredients: sharp peaks of potential (spikes)
nearly quiescent intervals (refractory time)
subthreshold oscillations

Theoretical models

Hodgkin-Huxley equations (∼1950): 4 variables

FitzHugh-Nagumo equations (∼1960): 2 variables

Separation of timescales:

fast variable x: (*action potential*, *"activator"*)
slow variable y: (*gating variable*, *"inhibitor"*)

$$\varepsilon \frac{dx}{dt} = x - \frac{x^3}{3} - y$$

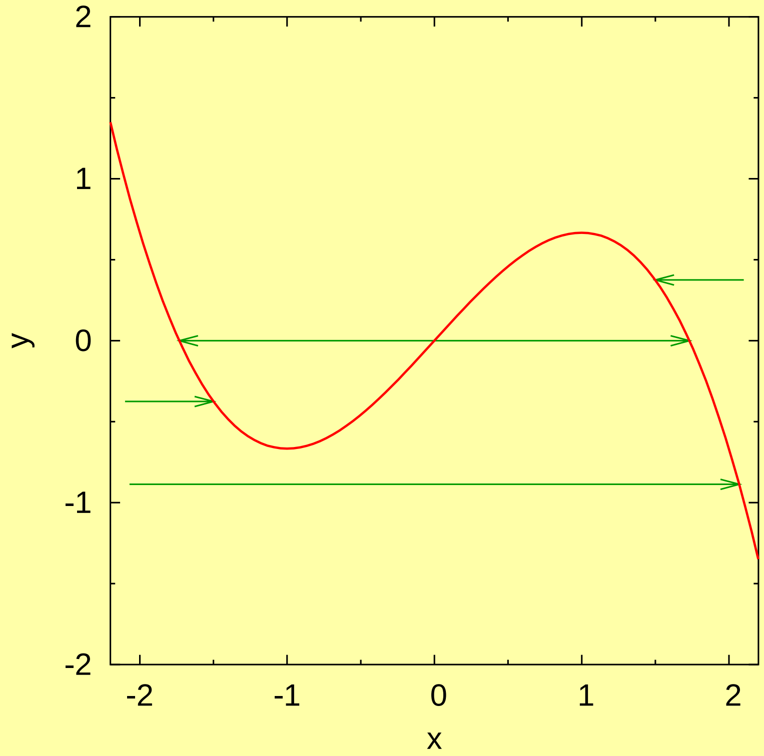
$$\frac{dy}{dt} = x + a$$

$\varepsilon \ll 1$: timescale separation

a : "excitability parameter"

$\varepsilon \to 0$: Slow manifold and stability of the equilibrium state

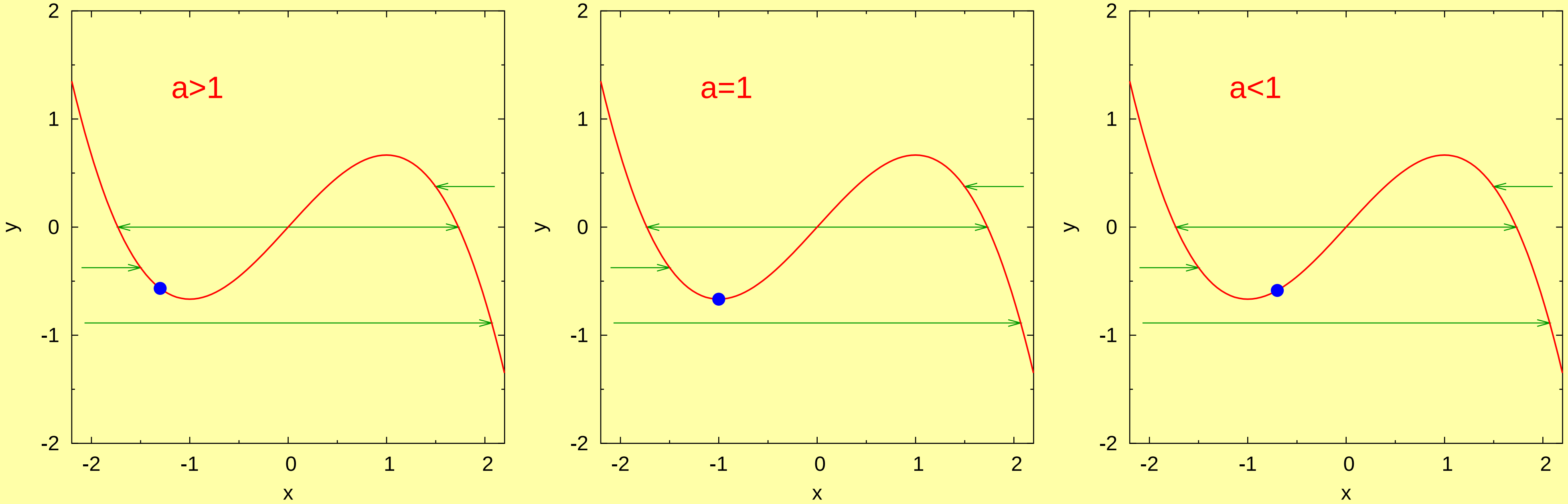
$$y = f(x) = x - \frac{x^3}{3}$$



Equilibrium: $x = -a \quad y = f(x)$

$\varepsilon \to 0$: Slow manifold and stability of the equilibrium state

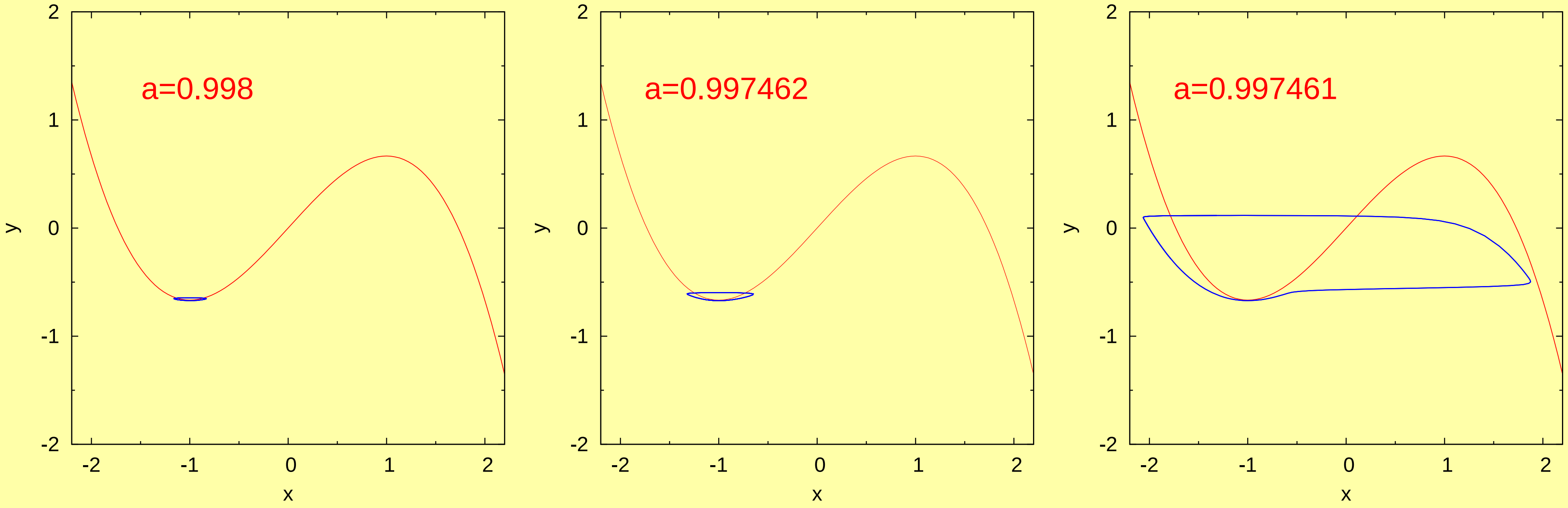
$$y = f(x) = x - \frac{x^3}{3}$$



$a > 1$: *equilibrium is stable:* *excitability*

$a < 1$: *equilibrium is unstable:* *oscillatory state*

$\varepsilon \to 0$: Slow manifold and size of the limit cycle



"canard explosion"

Part 1: Globally coupled FitzHugh-Nagumo systems

$$\begin{aligned} \epsilon \dot{x}_i &= x_i - \frac{x_i^3}{3} - y_i + \gamma\,(\bar{x} - x_i), \\ \dot{y}_i &= x_i + a + \sqrt{2T}\,\xi_i(t), \qquad i = 1, \ldots, N \end{aligned}$$

γ: coupling strength

$\xi_i(t)$: white Gaussian noise

$\epsilon \ll 1$: separation of timescales $(\epsilon = 0.01)$

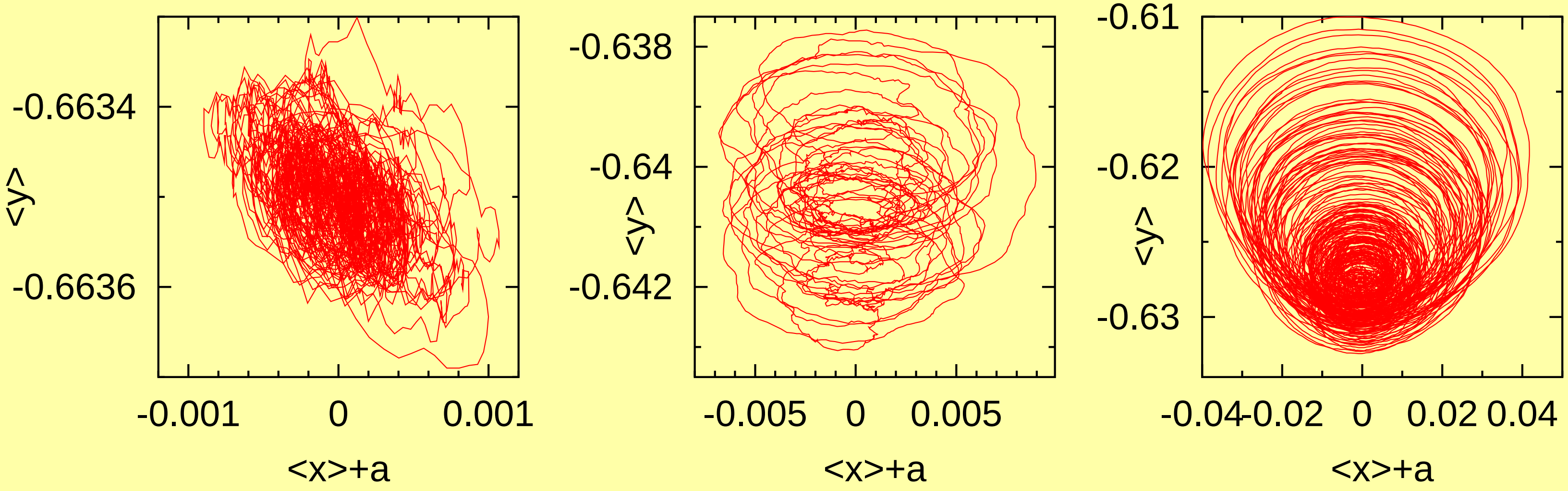
$T = 0$: equilibrium $(\,x_i = -a, \;\; y_i = a^3/3 - a\,)$ is stable for $a^2 > \max(1, 1-\gamma)$.

Direct numerical simulation

$$a = 1.05, \quad \gamma = 0.1, \quad \epsilon = 0.01, \quad N = 10^5$$

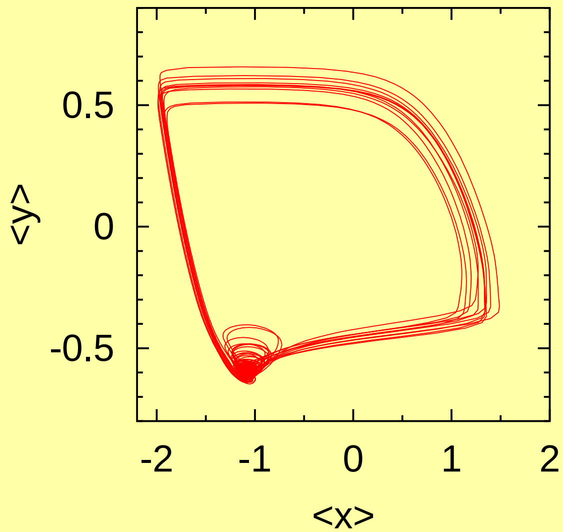
Phase portraits for subthreshold states

$T = 10^{-4}$ $\qquad$ $T = 2.4 \times 10^{-4}$ $\qquad$ $T = 2.7 \times 10^{-4}$

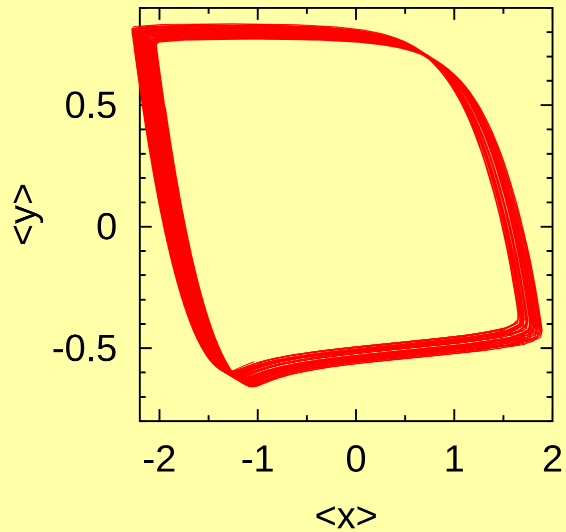


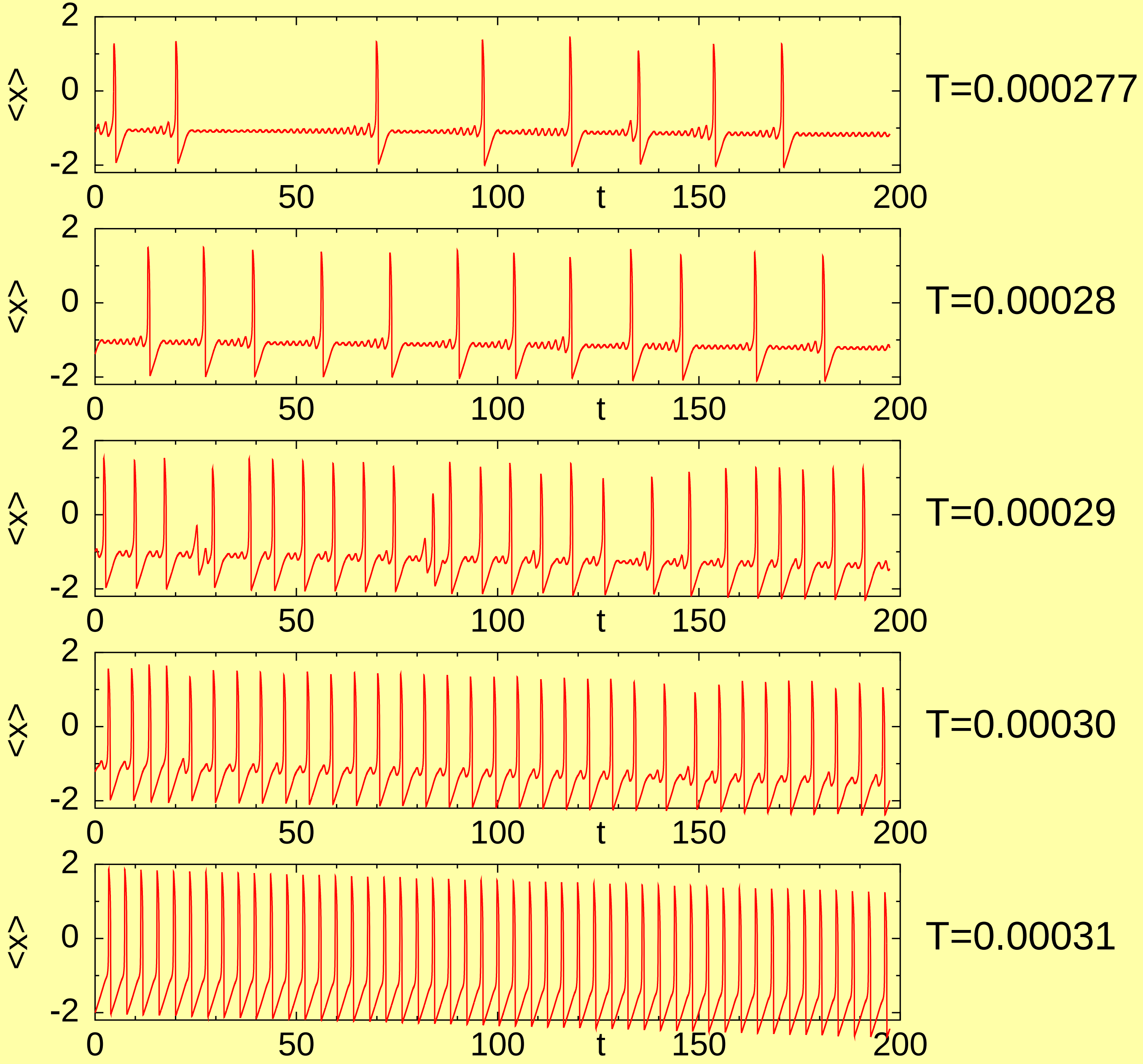
Onset of spiking

$T = 2.77 \times 10^{-4}$



$T = 3.1 \times 10^{-4}$





<x>
2
0
-2
0
50
100
t
150
200
T=0.000277
T=0.00028
T=0.00029
T=0.00030
T=0.00031

Part 2: dynamics of cumulants

$$\begin{aligned} \epsilon\,\dot{x}_i &= x_i - \frac{x_i^3}{3} - y_i + \gamma\,(\bar{x} - x_i), \\ \dot{y}_i &= x_i + a + \sqrt{2T}\,\xi_i(t), \qquad i = 1, \ldots, N \end{aligned}$$

Description in terms of probability distributions for $N \to \infty$.

Hypothesis of "molecular chaos" $\Rightarrow$ decoupling of correlations

$$P_N(x_1, y_1, x_2, y_2, \ldots, x_N, y_N, t) \,=\, P(x_1, y_1, t)\, P(x_2, y_2, t)\, \ldots\, P(x_N, y_N, t)$$

Fokker-Planck equation for one-particle density $P(x, y, t)$

$$\frac{\partial P}{\partial t} \,=\, -\frac{1}{\epsilon}\frac{\partial}{\partial x}\left(x(1-\gamma) - \frac{x^3}{3} - y + \gamma \int x' P(x', y', t) dx' dy'\right) P - (x+a)\,\frac{\partial P}{\partial y} + T\,\frac{\partial^2 P}{\partial y^2}$$

Description in terms of probability distributions: infinite hierarchy of moments

Approximation (closure): instantaneous Gaussian distribution of both x and y.

$$P(x,y,t) = \frac{1}{2\pi\sqrt{D_xD_y - D_{xy}^2}} \exp\left[-\frac{D_xD_y}{2(D_xD_y - D_{xy}^2)}\left(\frac{(x-m_x)^2}{D_x} + \frac{(y-m_y)^2}{D_y} - \frac{2D_{xy}}{\sqrt{D_xD_Y}}(x-m_x)(y-m_y)\right)\right]$$

Cumulants:

mean fields $m_x(t) = \langle x_i(t)\rangle$ and $m_y(t) = \langle y_i(t)\rangle$,

variances $D_x(t) = \langle x_i^2(t)\rangle - \langle x_i(t)\rangle^2$ and $D_y(t) = \langle y_i^2(t)\rangle - \langle y_i(t)\rangle^2$,

covariance $D_{xy}(t) = \langle x_i(t)y_i(t)\rangle - \langle x_i(t)\rangle\langle y_i(t)\rangle$.

$$D_x \geq 0,\ \ D_y \geq 0,\ \ D_xD_y \geq D_{xy}^2.$$

Deterministic equations for cumulants:

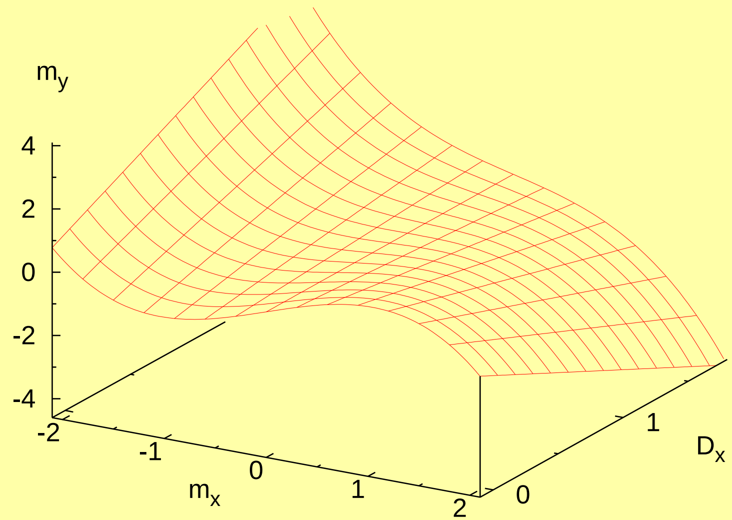
$$
\begin{aligned}
\epsilon \frac{d}{dt} m_x &= m_x - \frac{m_x^3}{3} - m_y - m_x D_x \\
\frac{d}{dt} m_y &= m_x + a \\
\epsilon \frac{d}{dt} D_x &= 2D_x(1 - D_x - m_x^2 - \gamma) - 2D_{xy} \\
\frac{d}{dt} D_y &= 2(D_{xy} + T) \\
\epsilon \frac{d}{dt} D_{xy} &= D_{xy}(1 - D_x - m_x^2 - \gamma) - D_y + \epsilon D_x
\end{aligned}
$$

Three "fast" equations and two "slow" ones.

Slow surface in the phase space at $\epsilon \to 0$

Parameterization in terms of m_x and D_x:

$$\begin{aligned} m_y &= m_x - m_x^3/3 - m_x D_x \\ D_{xy} &= D_x\,(1 - D_x - m_x^2 - \gamma) \\ D_y &= D_x\,(1 - D_x - m_x^2 - \gamma)^2 \end{aligned}$$



Slow surface in the phase space at $\epsilon \to 0$

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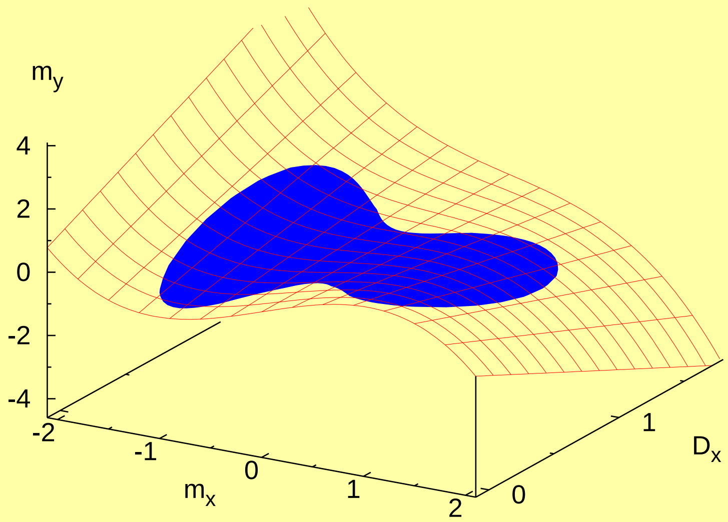
\end{aligned}
$$

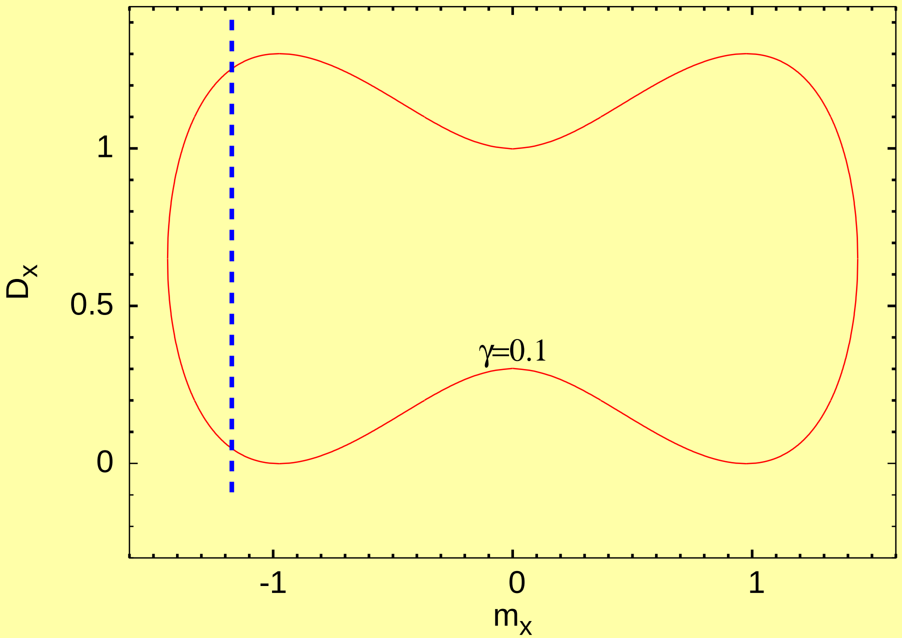


Repelling region: $(m_x^2 - 1)^2 + D_x\,(3D_x - 4) \;<\; \gamma\,(1 - m_x^2 - D_x)$

(position depends only on γ)

Steady equilibrium:

$$m_x = -a, \quad D_x = \frac{1 - a^2 - \gamma + \sqrt{(1 - a^2 - \gamma)^2 + 4T}}{2}, \quad \ldots$$



D_x is a monotonically growing function of T. $D_x\,(T = 0)\, = 0.$

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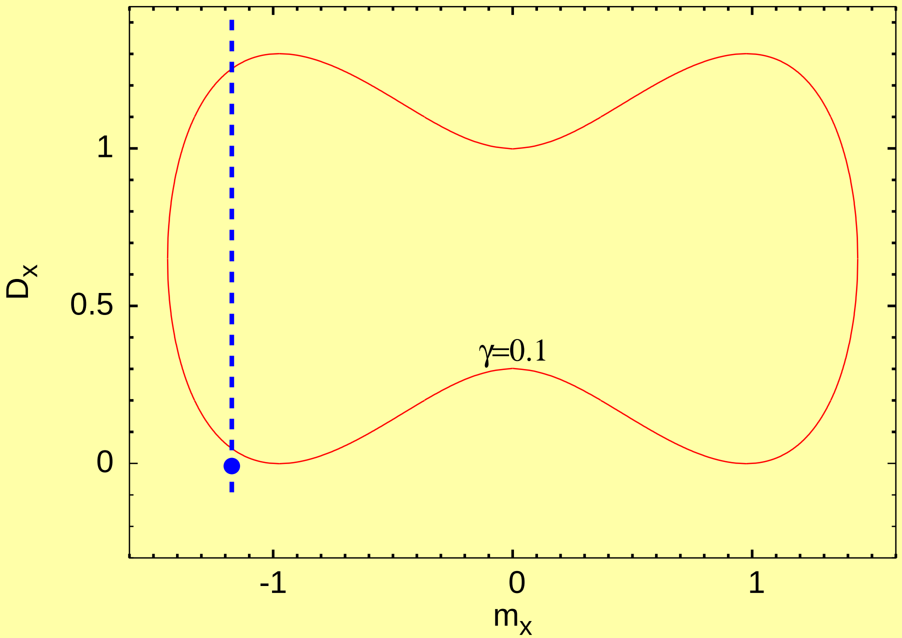

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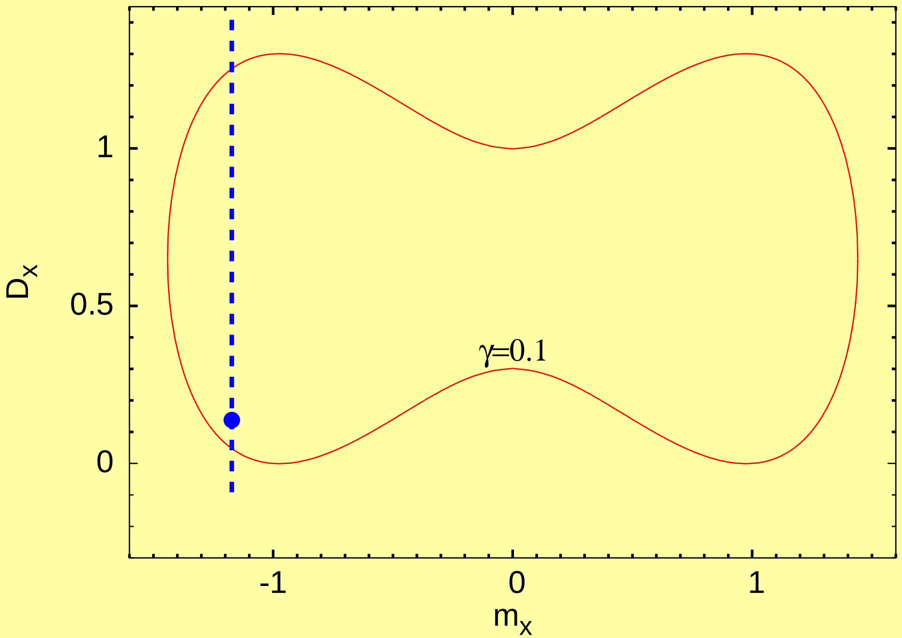

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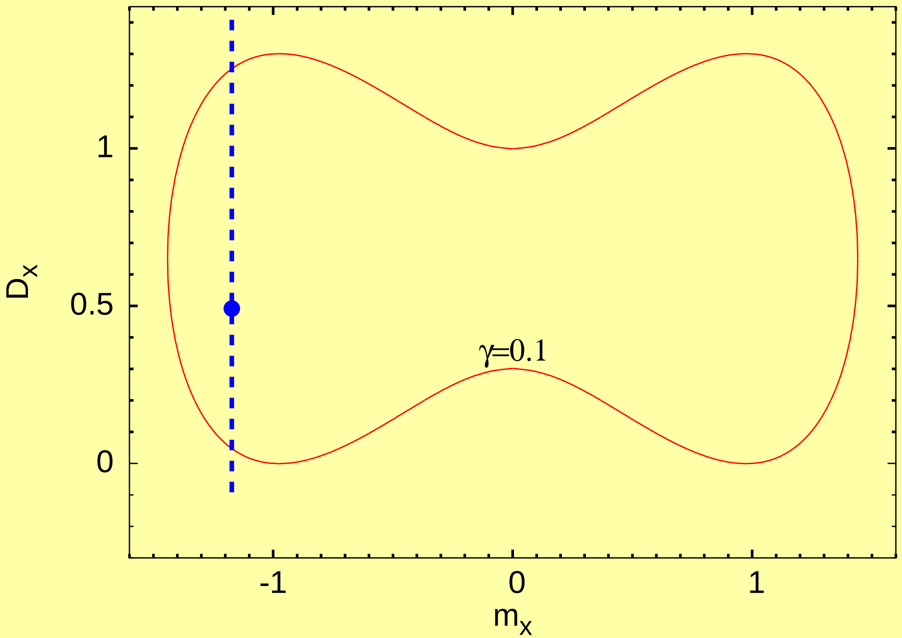

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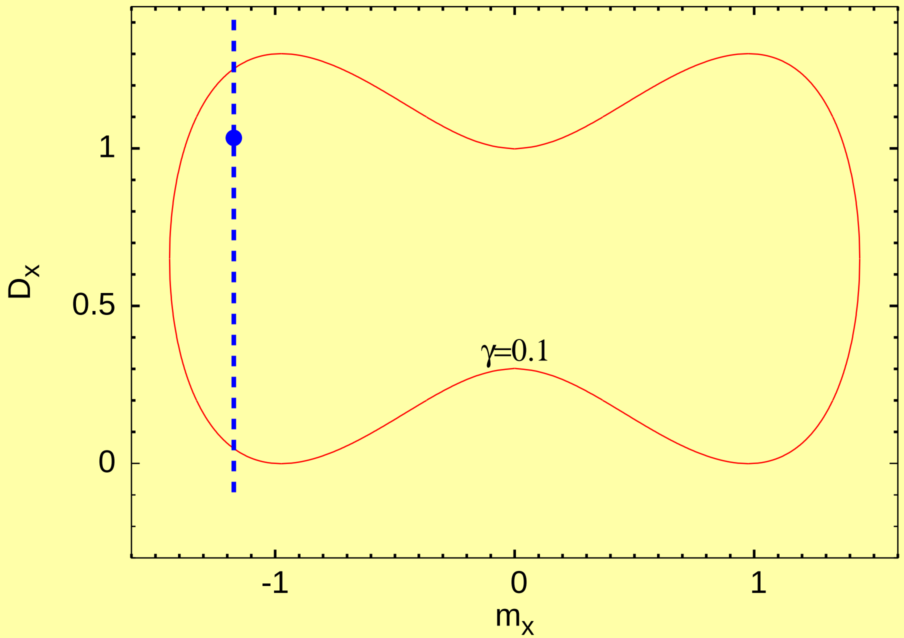

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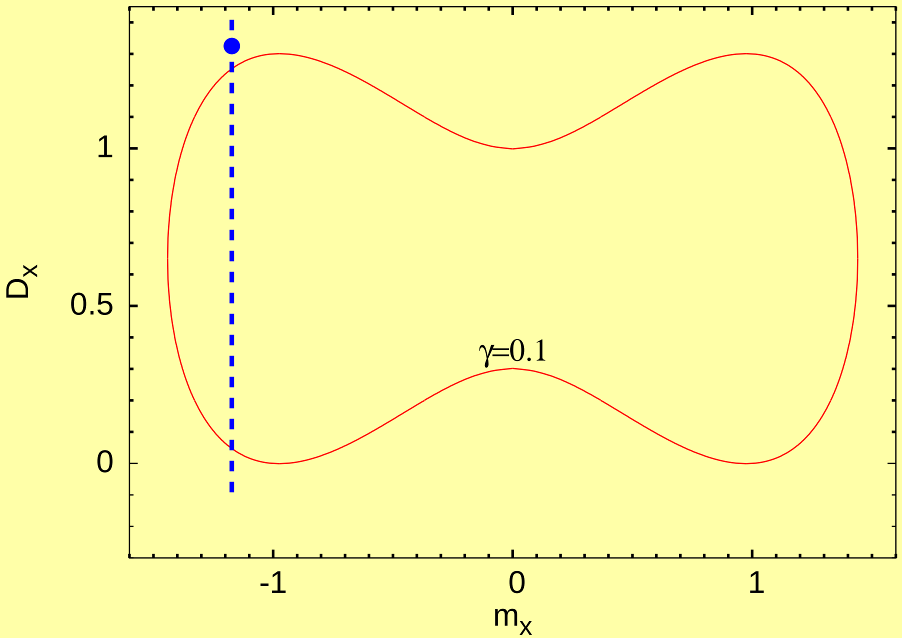
Steady equilibrium:

$$m_x = -a, \quad D_x = \frac{1 - a^2 - \gamma + \sqrt{(1 - a^2 - \gamma)^2 + 4T}}{2}, \quad \dots$$



D_x is a monotonically growing function of T. $D_x\,(T = 0)\, = 0.$

$\Rightarrow$ With growth of T the equilibrium enters the repelling region and leaves it again.

... loses stability and regains it.

Destabilization of equilibrium:

Stability crisis (Andronov-Hopf bifurcation) at

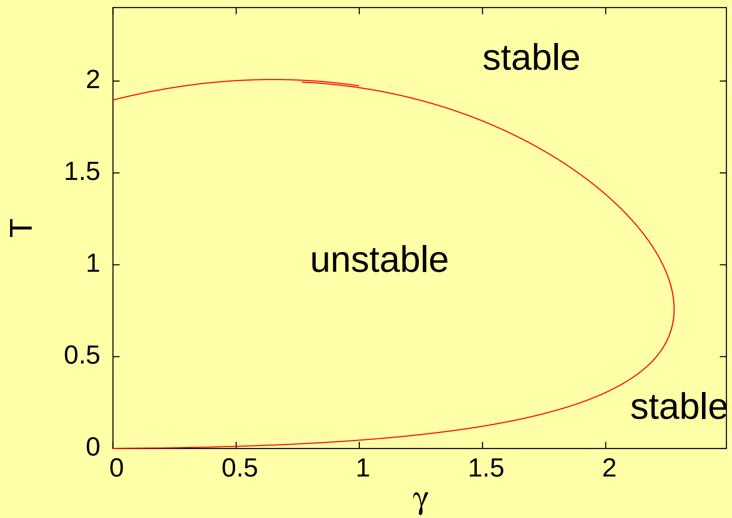
$$9T^2 + T(16b^2 - 16 - 12b - 4\gamma + 9b\gamma + 2\gamma^2) + 2b(b+\gamma)^2(2 + 2b + \gamma) \;=\; 0$$

$$(\, b \equiv a^2 - 1\,)$$

Necessary condition for the bifurcation: $\gamma \le \gamma_0 = 2\,(3a^2 - 1 - 2a\sqrt{3a^2 - 3}\,)$.

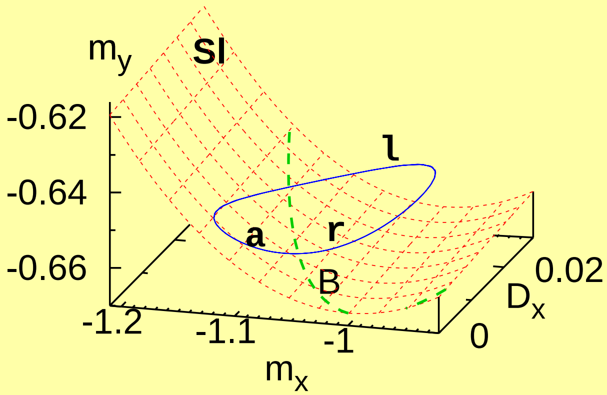
For $\gamma \;>\; \gamma_0$ coupling prevails over noise irrespective of T.

For $a > a_0 = \sqrt{1 + \sqrt{4/3}} \approx 1.467$ the steady state is stable irrespective of γ and T.

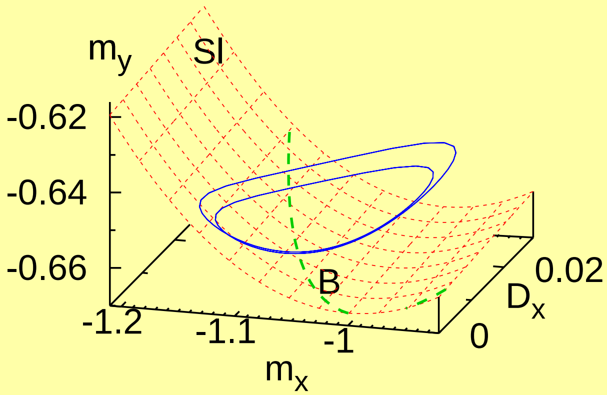


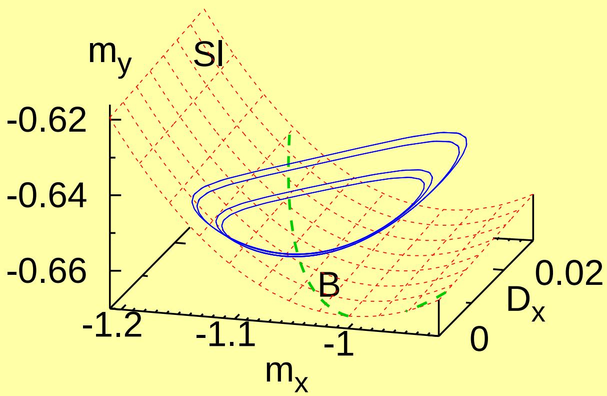
Subthreshold oscillations at $a = 1.05$, $\gamma = 0.1$, $\epsilon = 0.01$

$T = 0.00157$

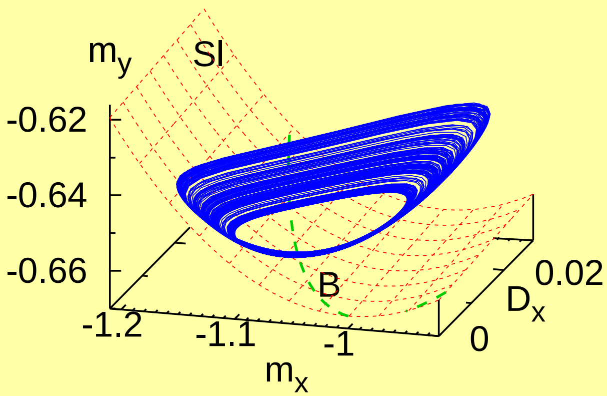


$T = 0.00158$





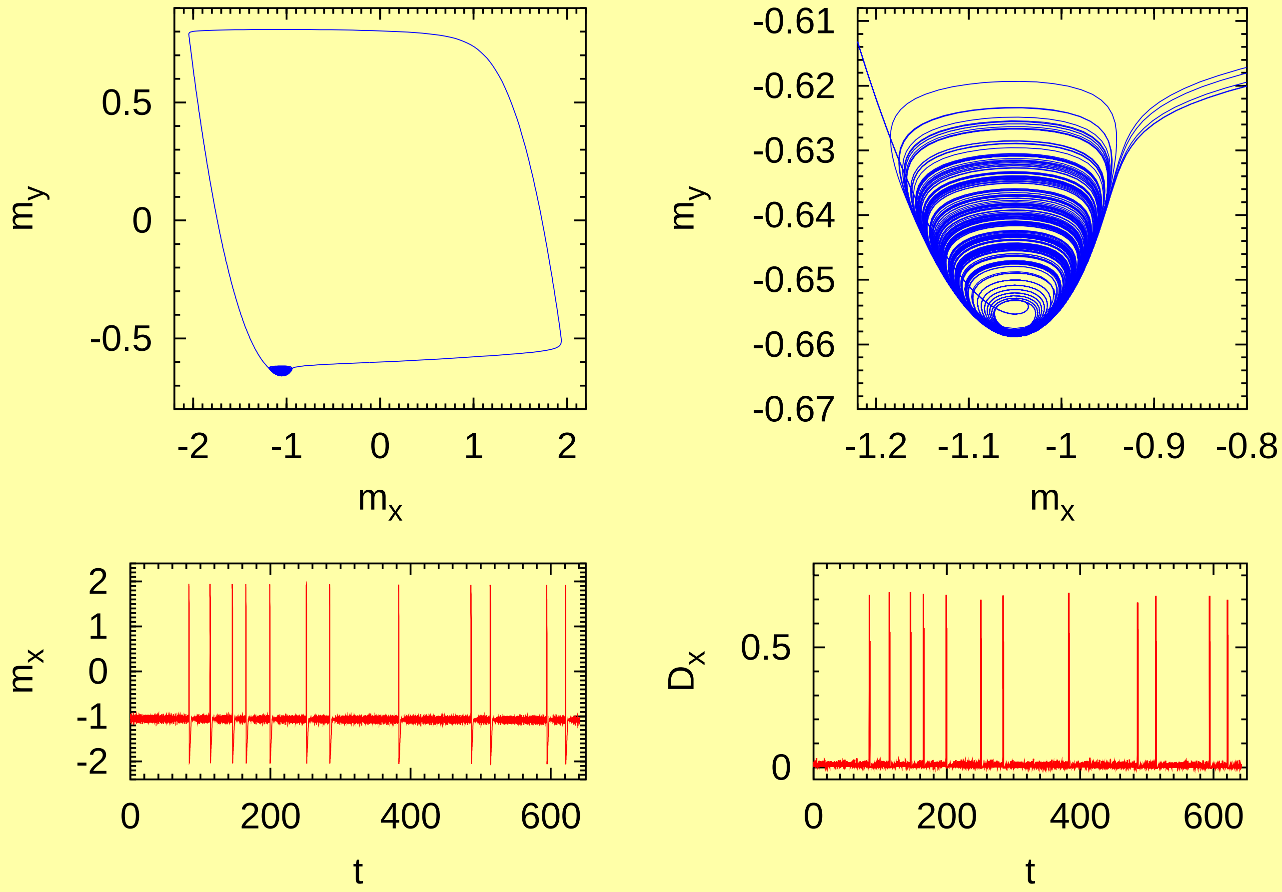
$T = 0.0015826$



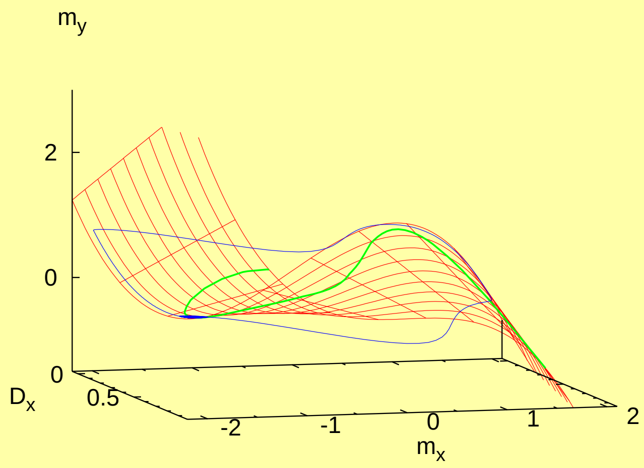
$T = 0.001585$

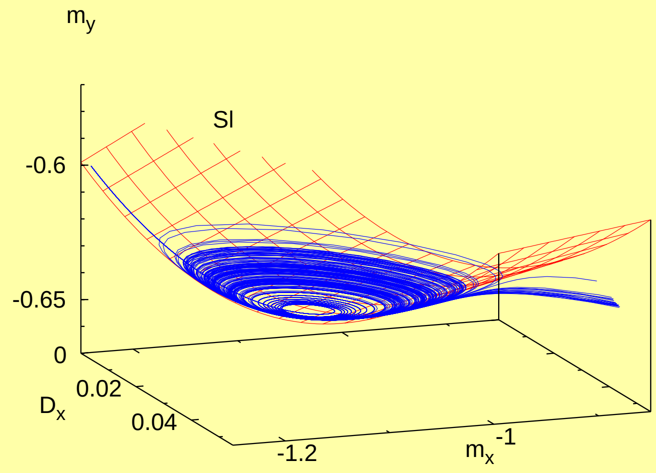
Onset of spiking regime

$$T = 0.001586$$



Attractor and the slow surface





$\Rightarrow$ canard explosion for the whole chaotic attractor ?

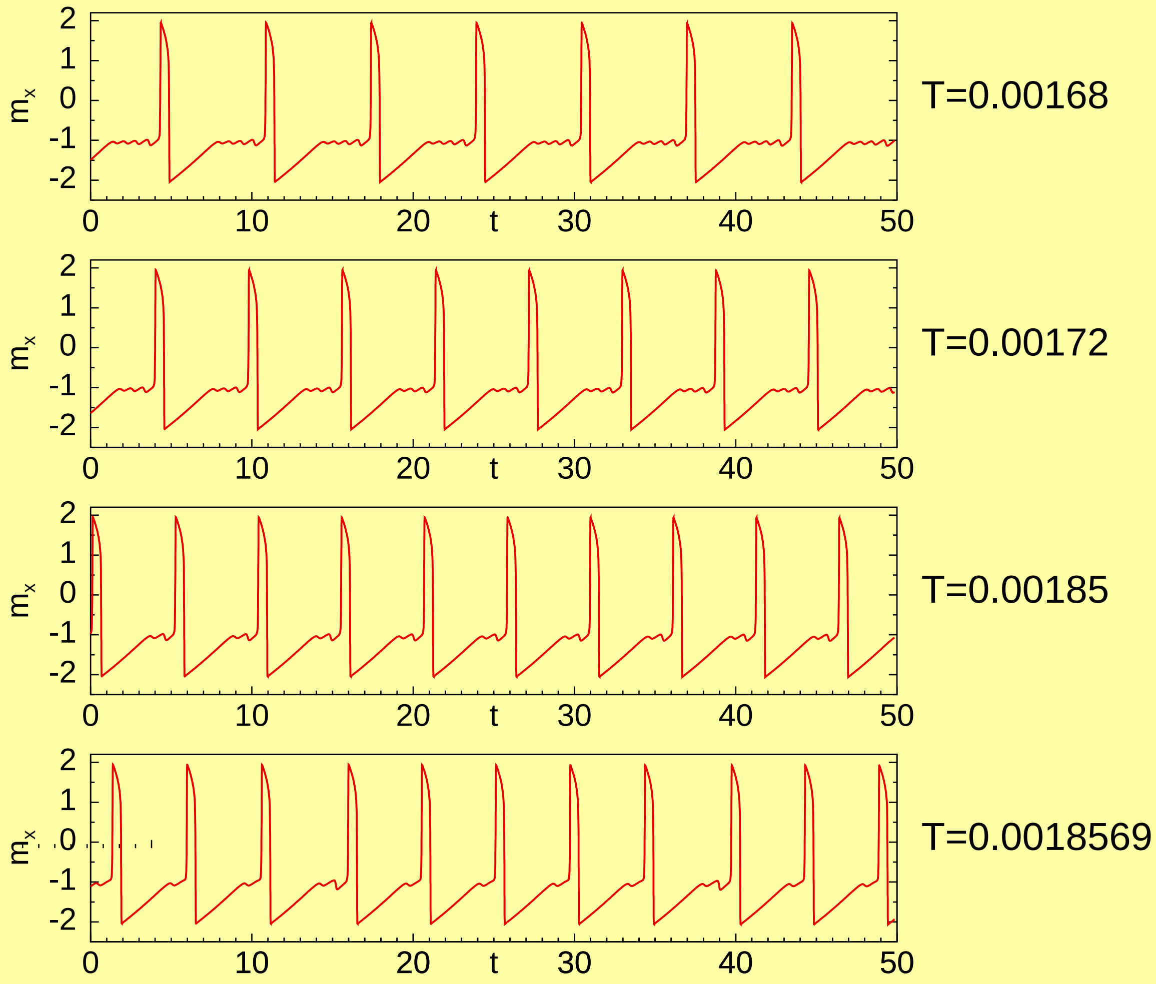
Canards in flows with 2 slow variables: Szmolyan, Guckenheimer, Wechselberger, Krupa…

mixed-mode oscillations (MMO)

No transitions from the small-scale chaotic attractor have been reported.

From chaotic to regular spiking:

inverse period-adding sequence



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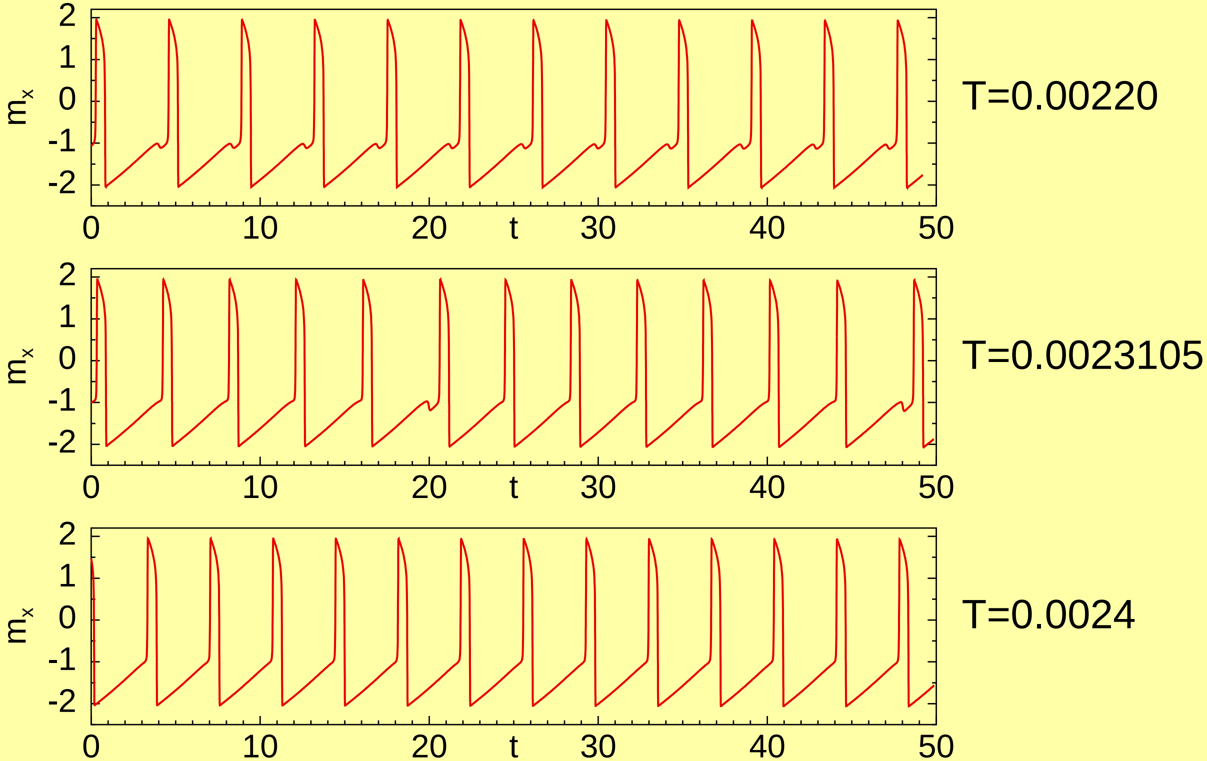
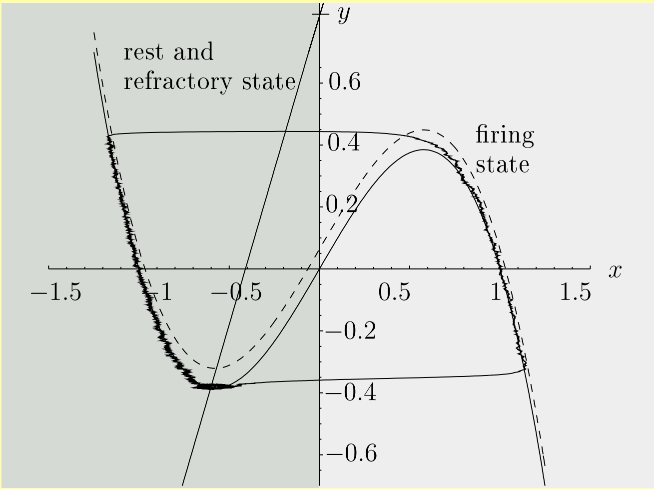


Part 3:   Three-state description



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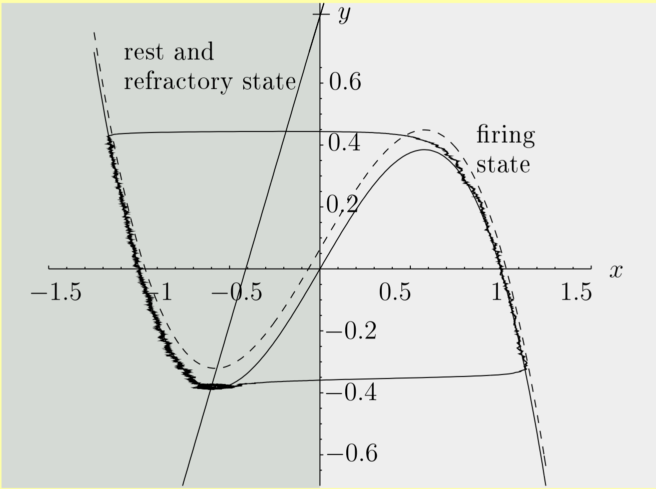
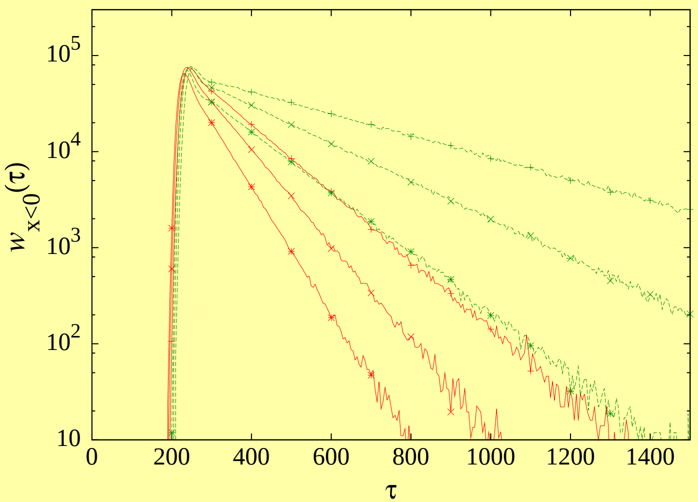
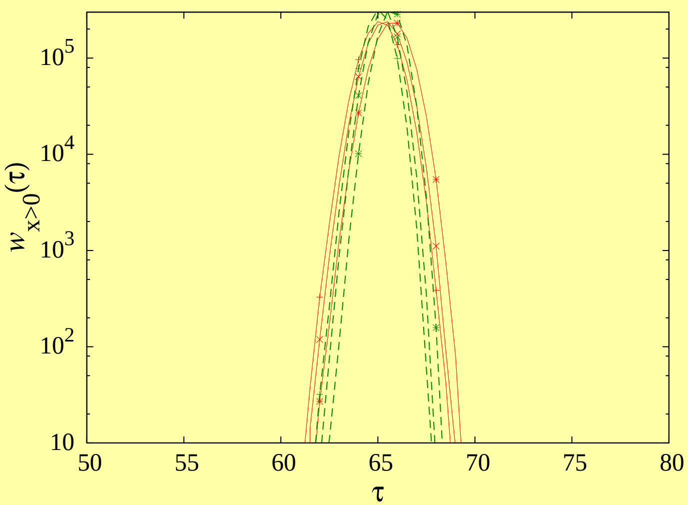


Residence (waiting) times:



(in $x < 0$)



(in $x > 0$)

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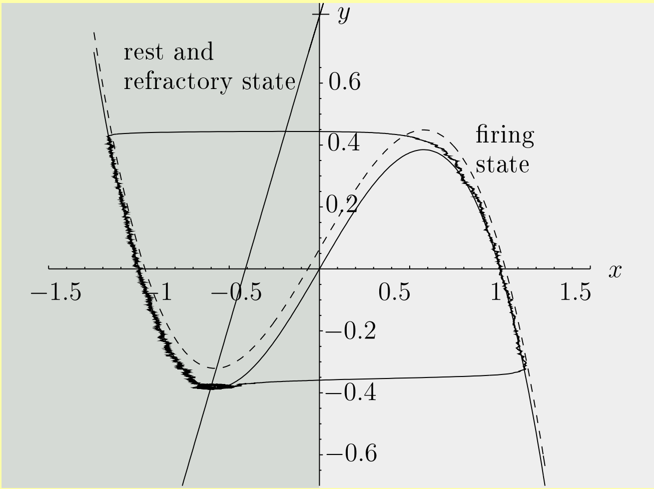

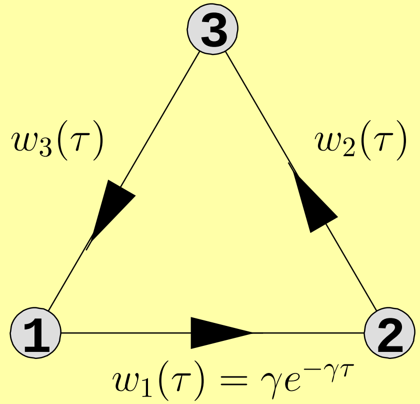

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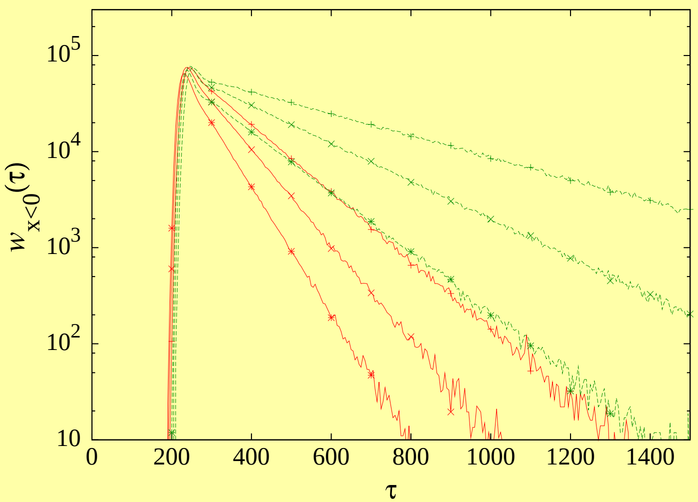
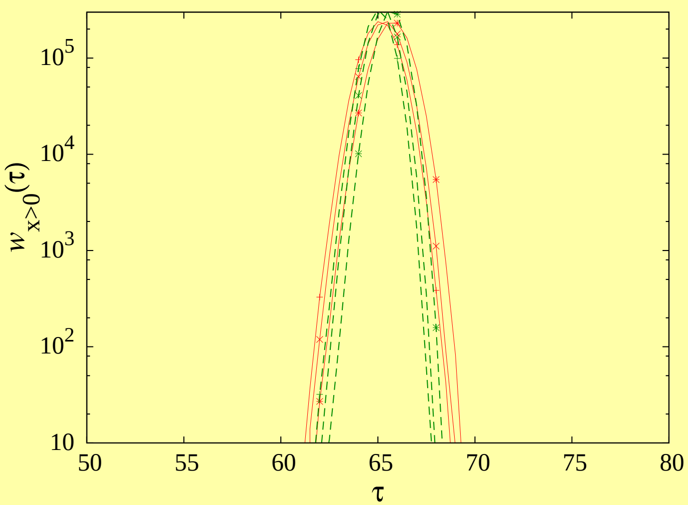


(in $x < 0$)



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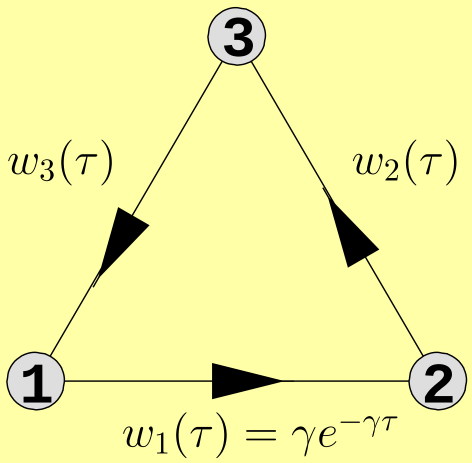


$w_1(\tau)$: Markovian escape from state of rest with rate γ;

$w_2(\tau)$, $w_3(\tau)$: Γ-densities

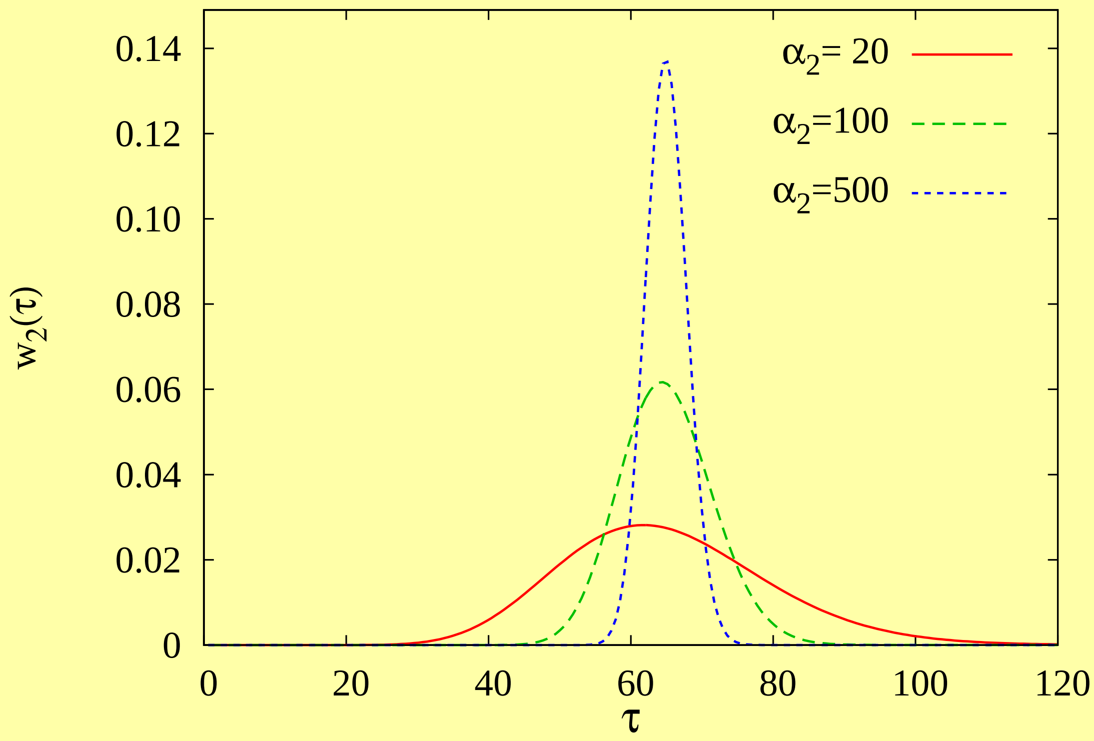
$$w_2(\tau)) = \frac{\alpha_2}{\tau_2\,\Gamma(\alpha_2)}\left(\frac{\alpha_2\tau}{\tau_2}\right)^{\alpha_2-1}\exp\left(-\frac{\alpha_2\tau}{\tau_2}\right)$$

$$w_3(\tau)) = \frac{\alpha_3}{\tau_3\,\Gamma(\alpha_3)}\left(\frac{\alpha_3\tau}{\tau_3}\right)^{\alpha_3-1}\exp\left(-\frac{\alpha_3\tau}{\tau_3}\right)$$

$\tau_{2,3}$ – mean values of waiting times.

$\dfrac{\tau_{2,3}^2}{\alpha_{2,3}}$ – variances of waiting times.

Shapes of Γ-density function



$$\tau_2 \; = \; 65$$

$\alpha_{2,3}$ characterize sharpness of transitions. $\alpha = 1$: exponential distribution of waiting times.
$\alpha \to \infty$: δ-distributed waiting times.

(Integer values of α: Erlang distributions)

Balance equations for probabilities

$$\frac{d}{dt}P_1(t) = -J_{1\to 2}(t) + J_{3\to 1}(t)$$
$$\frac{d}{dt}P_2(t) = -J_{2\to 3}(t) + J_{1\to 2}(t)$$
$$\frac{d}{dt}P_3(t) = -J_{3\to 1}(t) + J_{2\to 3}(t)$$

Integral equations:

$$P_2(t) = \int_0^\infty d\tau \gamma P_1(t-\tau) z_2(\tau)$$
$$P_3(t) = \int_0^\infty d\tau \int_0^\infty d\tau' \gamma P_1(t-\tau-\tau') w_2(\tau) z_3(\tau')$$
$$P_1(t) = 1 - P_2(t) - P_3(t)$$

$z_2(\tau) = \int_\tau^\infty d\tau' w_2(\tau')$ and $z_3(\tau) = \int_\tau^\infty d\tau' w_3(\tau')$:

probabilities to survive longer than τ in the states 2 and 3.

Ensembles of coupled elements

$n_1(t)/N$, $n_2(t)/N$, $n_3(t)/N$ – relative occupation numbers in respective states.

Transition rate γ depends on the number of units in the firing state:

$$\gamma(t) = \gamma\left(\frac{n_2(t)}{N}\right)$$

In the limit $N \to \infty$ the values $n_i(t)/N$ converge to $P_i(t)$

in the sense of $\lim_{N\to\infty} \sum_{n_1=0}^{N} \sum_{n_2=0}^{N-n_1} p(n_1, n_2, N-n_1-n_2, t) f(\frac{n_1}{N}, \frac{n_2}{N}, \frac{N-n_1-n_2}{N}) = f(P_1(t), P_2(t), P_3(t))$.

Mean-field integral equations

$$\begin{aligned} P_1(t) &= 1 - P_2(t) - P_3(t) \\ P_2(t) &= \int_0^\infty d\tau \gamma\left(P_2\left(t-\tau\right)\right) P_1\left(t-\tau\right) z_2(\tau) \\ P_3(t) &= \int_0^\infty d\tau \int_0^\infty d\tau' \gamma\left(P_2\left(t-\tau-\tau'\right)\right) P_1\left(t-\tau-\tau'\right) z_3(\tau) w_2\left(\tau'\right) \end{aligned}$$

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$$\begin{aligned}
P_1(t) &= 1 - P_2(t) - P_3(t) \\
P_2(t) &= \int_0^\infty d\tau \gamma\left(P_2\left(t-\tau\right)\right) P_1\left(t-\tau\right) z_2(\tau) \\
P_3(t) &= \int_0^\infty d\tau \int_0^\infty d\tau' \gamma\left(P_2\left(t-\tau-\tau'\right)\right) P_1\left(t-\tau-\tau'\right) z_3(\tau) w_2\left(\tau'\right)
\end{aligned}$$

For integer α_2 and α_3: set of $(\alpha_2 + \alpha_3)$ ODEs.

Stationary states

$$\begin{aligned} P_2^* &= \frac{\tau_2}{\tau_2 + \tau_3 + 1/\gamma(P_2^*)} \\ P_3^* &= \frac{\tau_3}{\tau_2} P_2^*, \\ P_1^* &= 1 - P_2^* - P_3^* \end{aligned}$$

Equations are $\alpha_{2,3}$-independent, $\Rightarrow$ number of solutions depends only on $\tau_{2,3}$ and function $\gamma(P)$.

Artificial "parameters": $r = \gamma(P_2^*)$ and $s = P_1^* \gamma'(P_2^*)$.

Characteristic equation:

$$\lambda + \left[s \left(1 + \frac{\tau_2 \lambda}{\alpha_2}\right)^{-\alpha_2} - s + r - r \left(1 + \frac{\tau_2 \lambda}{\alpha_2}\right)^{-\alpha_2} \left(1 + \frac{\tau_3 \lambda}{\alpha_3}\right)^{-\alpha_3} \right] = 0$$

Bifurcations of stationary states

Characteristic equation:

$$\lambda + \left[s \left(1 + \frac{\tau_2 \lambda}{\alpha_2} \right)^{-\alpha_2} - s + r - r \left(1 + \frac{\tau_2 \lambda}{\alpha_2} \right)^{-\alpha_2} \left(1 + \frac{\tau_3 \lambda}{\alpha_3} \right)^{-\alpha_3} \right] = 0$$

Saddle-node bifurcation: $$s = \frac{r\,(\tau_2 + \tau_3) + 1}{\tau_2}$$

Hopf bifurcation (in parametric form):

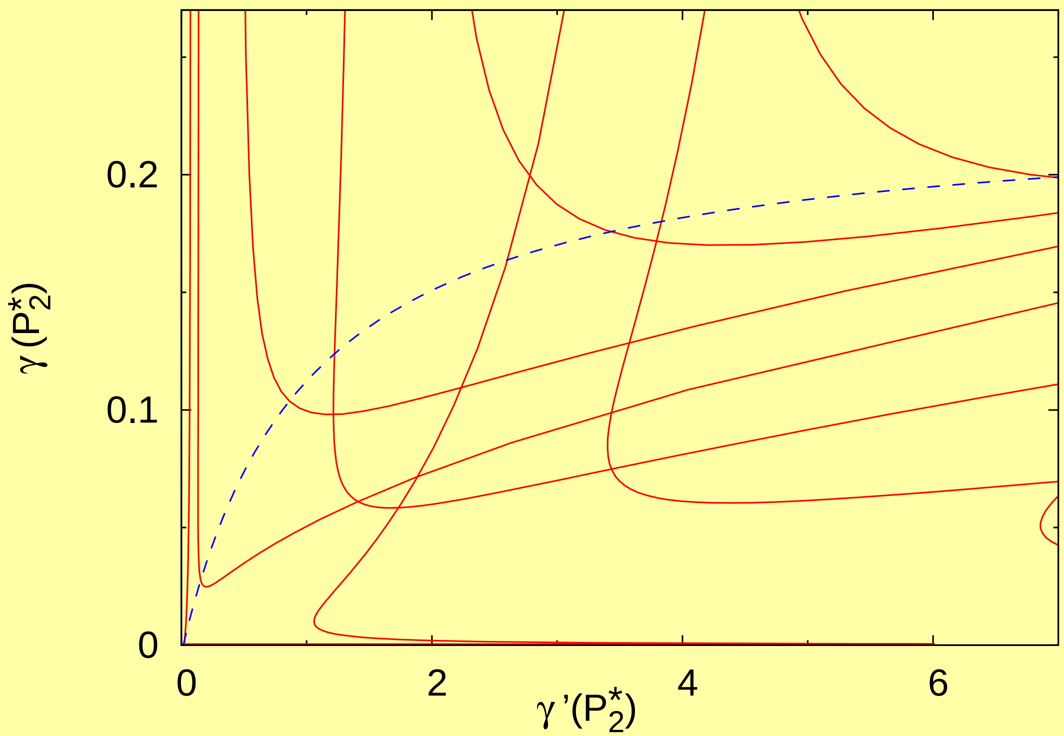
$$\begin{aligned} r_{\text{Hopf}}(\omega) &= \omega \frac{I_{23}(I_3 - I_{23}) + R_{23}(R_3 - R_{23})}{I_{23} - I_{23}R_3 - I_3 + I_3 R_{23}} \\ s_{\text{Hopf}}(\omega) &= -\,\omega \frac{I_{23}^2 + R_{23}(R_{23} - 1)}{I_{23} - I_{23}R_3 - I_3 + I_3 R_{23}} \end{aligned}$$

$$R_2 = \text{Re}\Big((1 + i\omega\tau_2/\alpha_2)^{\alpha_2}\Big), \quad I_2 = \text{Im}\Big((1 + \mathrm{i}\omega\tau_2/\alpha_2)^{\alpha_2}\Big), \text{ etc.}$$

At $\omega = 0$ Takens-Bogdanov point (double zero eigenvalue):

$$r_{\text{TB}} = \frac{\tau_2 \alpha_3 (\alpha_2 + 1)}{\tau_2 \tau_3 \alpha_3 (\alpha_2 - 1) + \alpha_2 (\alpha_3 + 1) \tau_3^2}$$

Example 1: bifurcation diagram for $\alpha_2 \to \infty$, $\alpha_3 \to \infty$
(fixed waiting times: $\tau_2 = 65$, $\tau_3 = 220$)

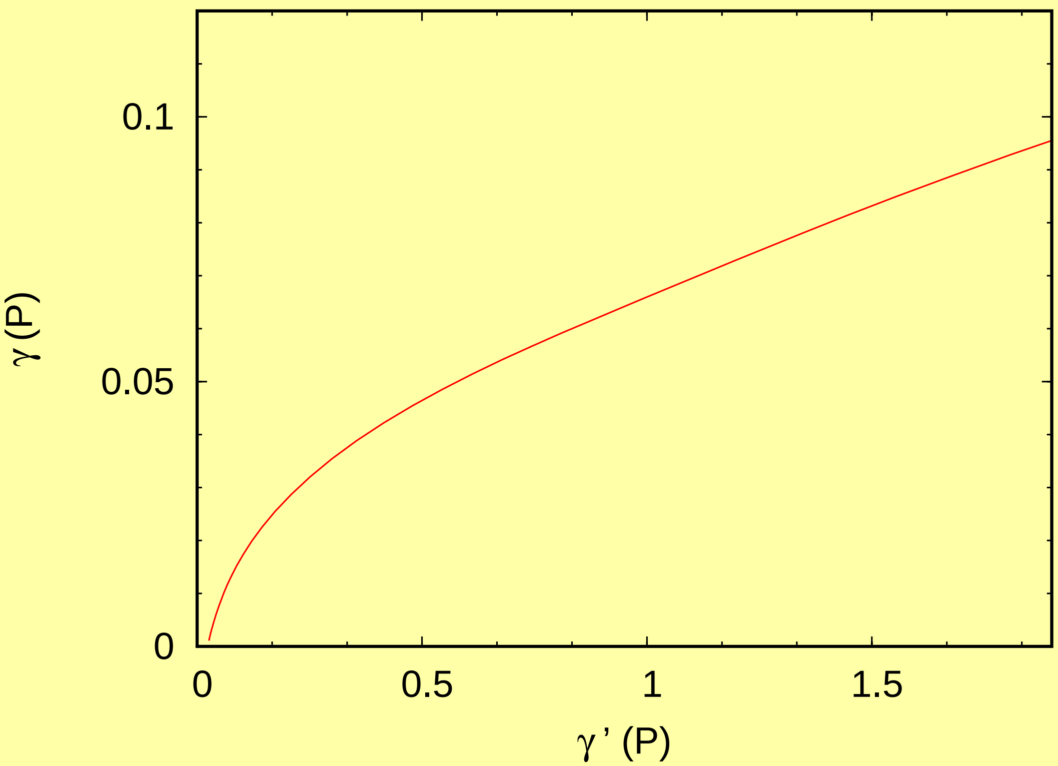


Dashed line: saddle-node bifurcation.
Solid lines: Hopf bifurcation

Codimension-2 points.

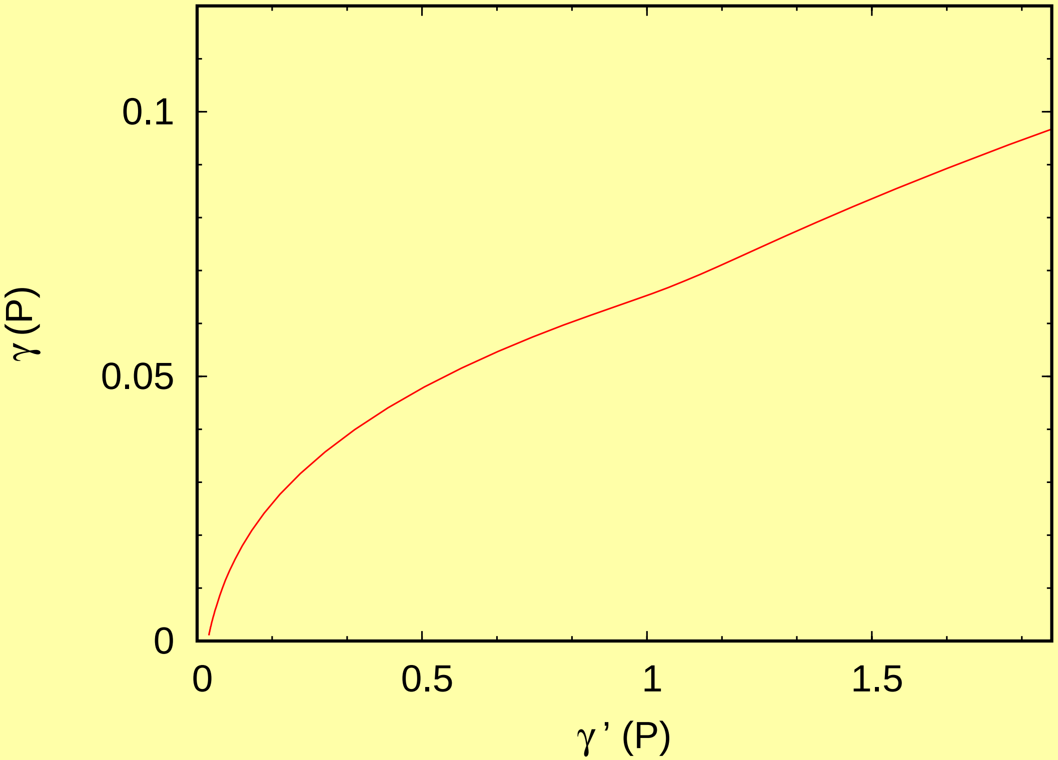
Example 2: Hopf bifurcation for $\tau_2 = 65, \ \tau_3 = 220$

$\alpha_2 = \alpha_3 = 10$



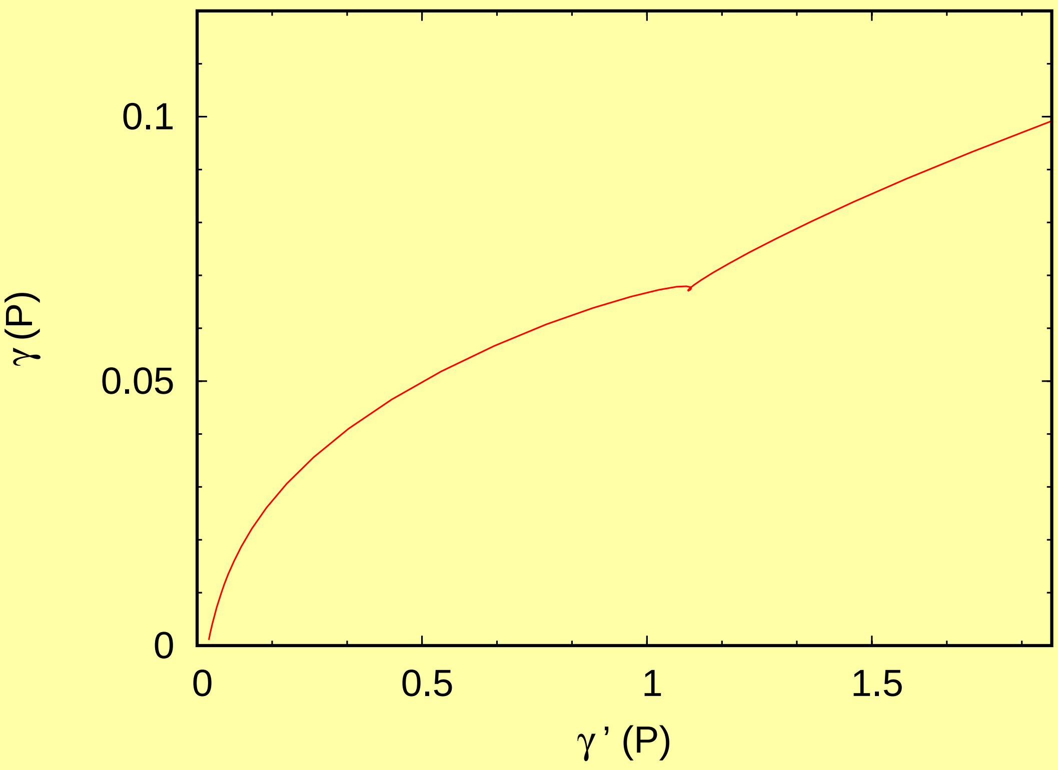
Example 2: Hopf bifurcation for $\tau_2 = 65, \ \tau_3 = 220$

$\alpha_2 = \alpha_3 = 12$



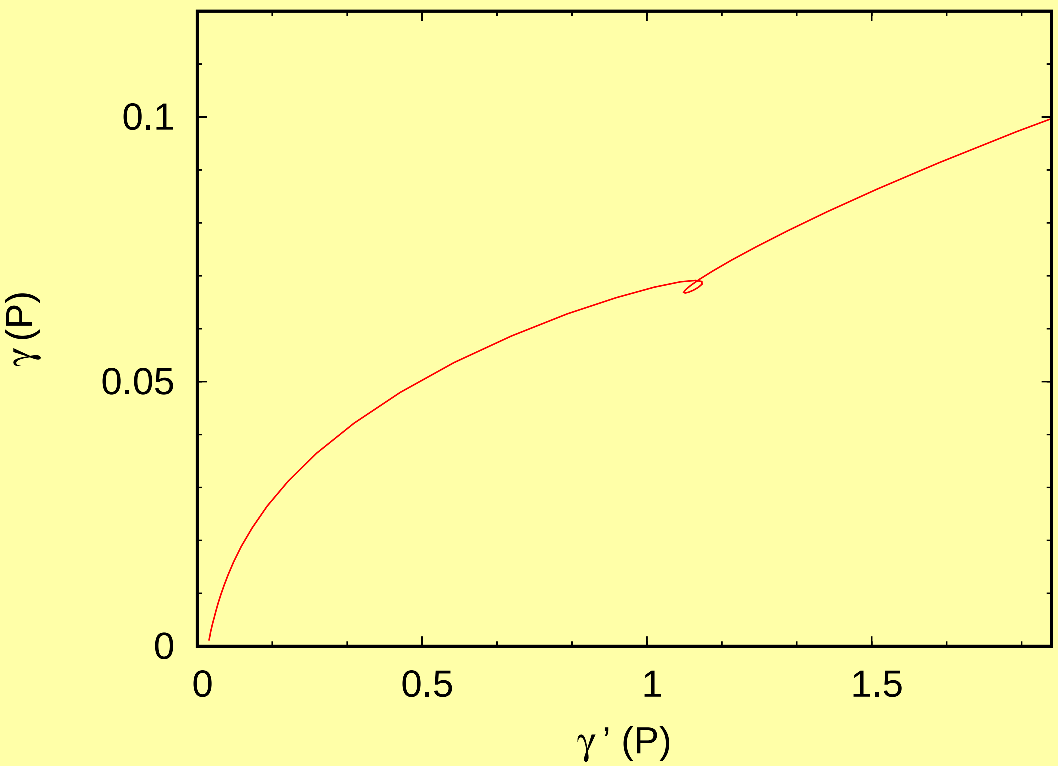
Example 2: Hopf bifurcation for $\tau_2 = 65, \ \tau_3 = 220$

$$\alpha_2 = \alpha_3 = 14.5$$



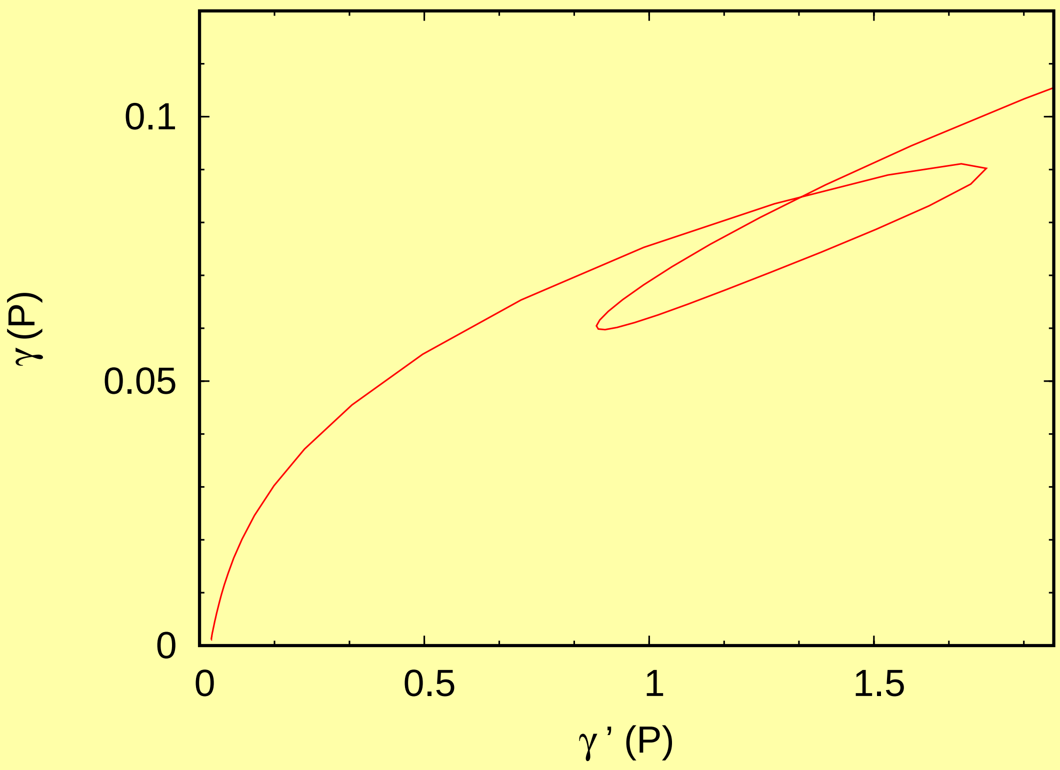
Example 2: Hopf bifurcation for $\tau_2 = 65, \ \tau_3 = 220$

$\alpha_2 = \alpha_3 = 15$



Example 2: Hopf bifurcation for $\tau_2 = 65, \ \tau_3 = 220$

$$\alpha_2 = \alpha_3 = 20$$



Formation of the loop upon the bifurcation curve.
Jump of the critical frequency.

Application: Arrhenius-type excitatory coupling

$$\text{Firing rate:} \quad \gamma(P_2) = \gamma_0 \exp\left(-\frac{\Delta U(P_2)}{D}\right)$$

Simplistic dependence: $\Delta U(P_2) = \Delta U_0(1 - \sigma P_2)$

ΔU_0: barrier of an individual unit, σ : coupling strength

Prescription:

1. For each pair $\left(\gamma(P_2^*), \gamma'(P_2^*)\right)$ calculate the pair (σ, D) through

$$\sigma = \frac{\gamma'(P_2^*)T}{\gamma'(P_2^*)\tau_2 + \gamma(P_2^*)T\log(\frac{\gamma_0}{\gamma(P_2^*)})},$$

$$D = \frac{T\Delta U_0 \gamma(P_2^*)}{\gamma'(P_2^*)\tau_2 + \gamma(P_2^*)T\log(\frac{\gamma_0}{\gamma(P_2^*)})}$$

$T = \tau_2 + \tau_3 + 1/\gamma(P_2^*)$: mean duration of a cycle

2. Solve for P_2^*:

$$P_2^* = \frac{\tau_2}{\tau_2 + \tau_3 + \frac{1}{\gamma_0}\exp\left(\frac{\Delta U_0(1-\sigma P_2^*)}{D}\right)}$$

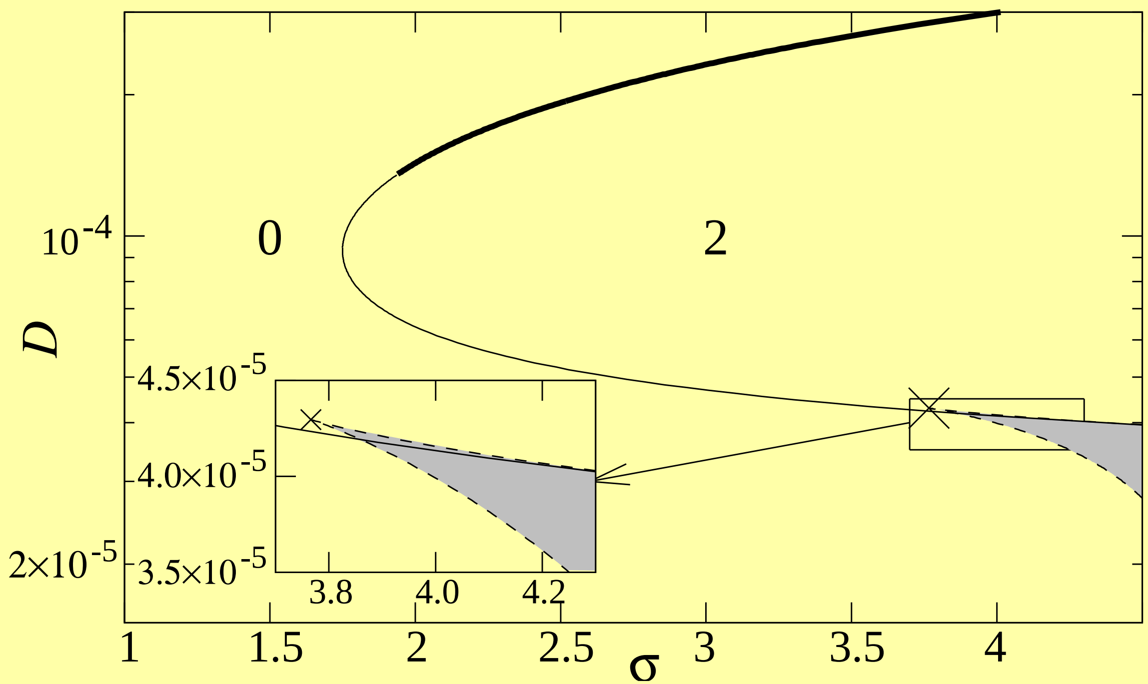
3. Replot bifurcation curves in new coordinates

Arrhenius-type rate

$$\gamma(P_2) = \gamma_0 \exp\left(-\frac{\Delta U(P_2)}{D}\right)$$

$$\Delta U(P_2) = \Delta U_0(1 - \sigma P_2), \quad \Delta U_0 = 0.0002,\ \gamma_0 = 0.05$$

Bifurcation diagram



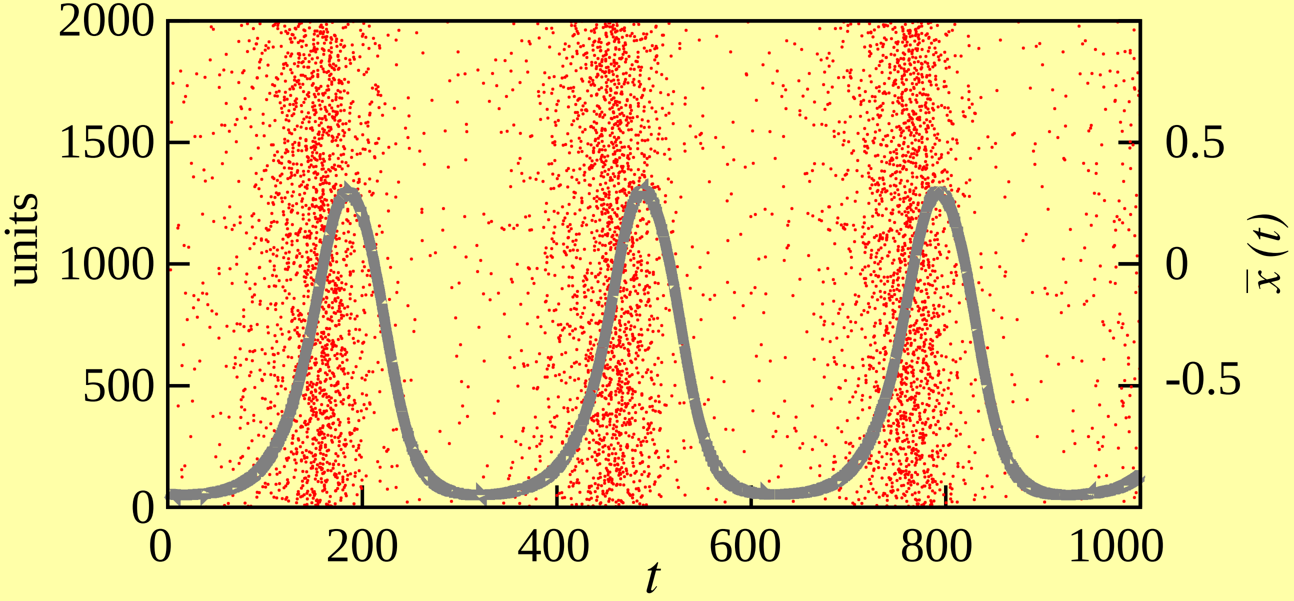
Hopf bifurcation: supercritical or subcritical

Arrhenius-type rate

$$\gamma(P_2) = \gamma_0 \exp\left(-\frac{\Delta U(P_2)}{D}\right)$$

$$\Delta U(P_2) \;=\; \Delta U_0(1-\sigma P_2), \quad \Delta U_0 = 0.0002,\; \gamma_0 = 0.05,\; D = 0.0002,\; \sigma = 3$$

Temporal evolution for 10^5 coupled three-state units



Red dots: transitions from state 1 to state 2

Conclusions

- Additive noise can play an ordering role: drive the ensemble
  to regime of synchronized spiking.
- Stochastic behavior is reasonably well captured by deterministic description
- Subthreshold oscillations become chaotic *before* transition to spiking
- In the phase space, transition to spiking is a canard explosion of the chaotic attractor
- ensemble of non-Markovian three-state units provides a good qualitative description for an ensemble of globally coupled excitable elements