

# Oscillations multimodales dans les équations différentielles stochastiques

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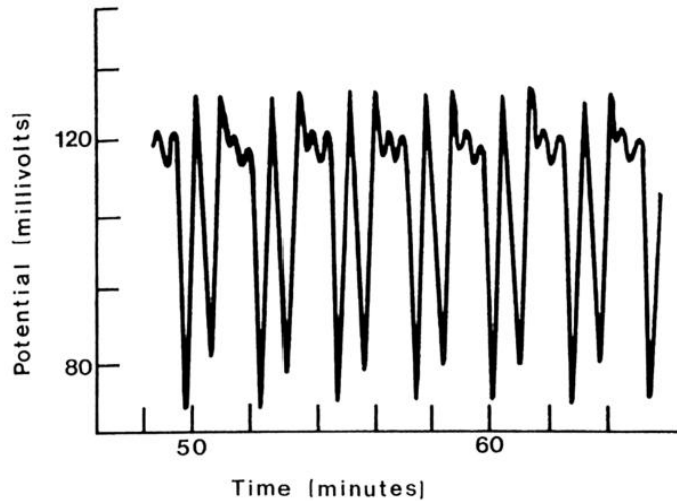
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Christian Kuehn, Max Planck Institute, Dresden

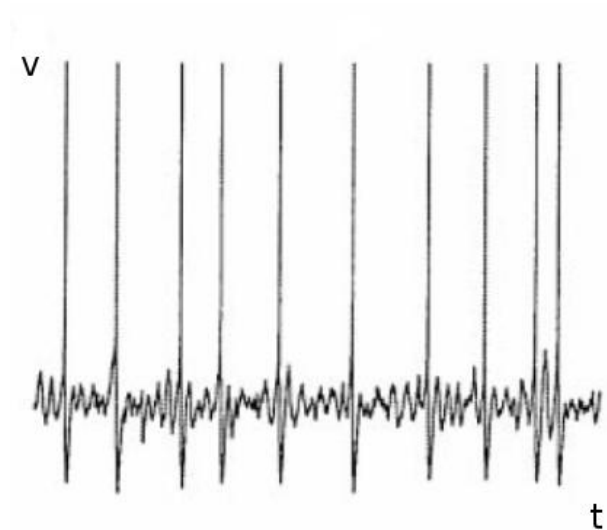
Projet ANR MANDy, Mathematical Analysis of Neuronal Dynamics

GdT Modélisation, LPMA, Paris, 5 mai 2011

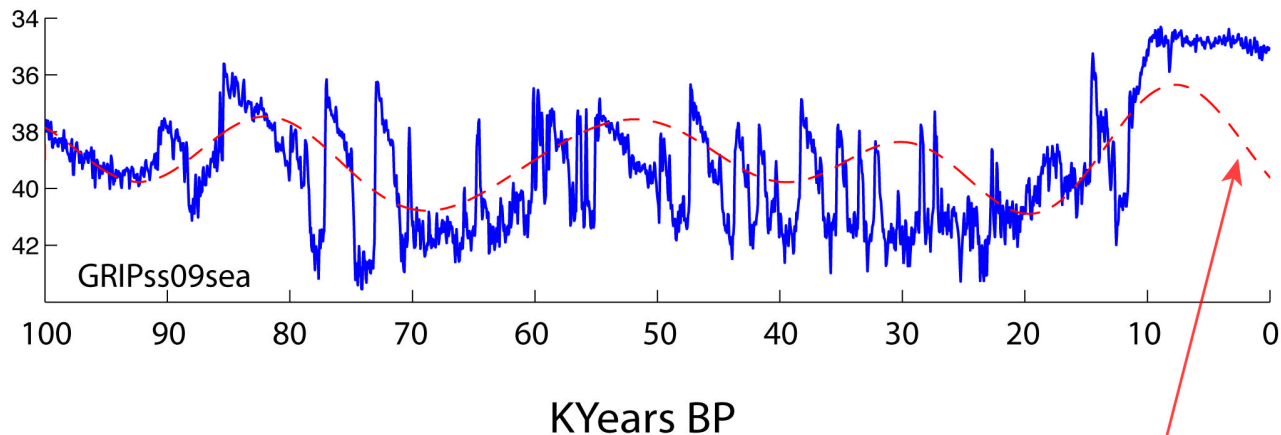
# Oscillations in natural systems



Belousov-Zhabotinsky reaction [Hudson 79]

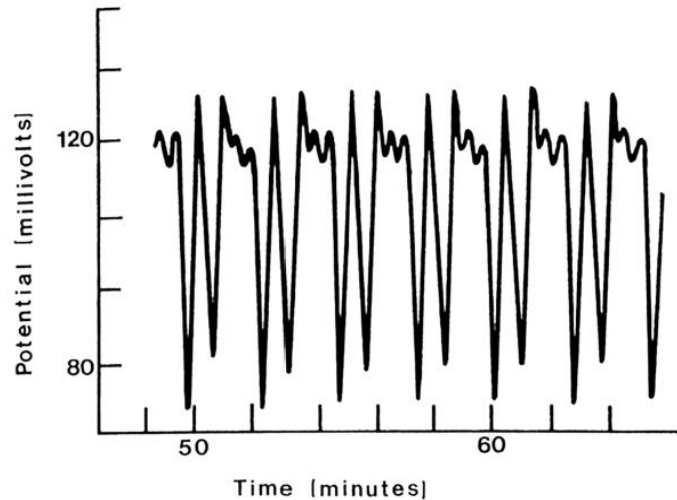


Stellate cells [Dickson 00]

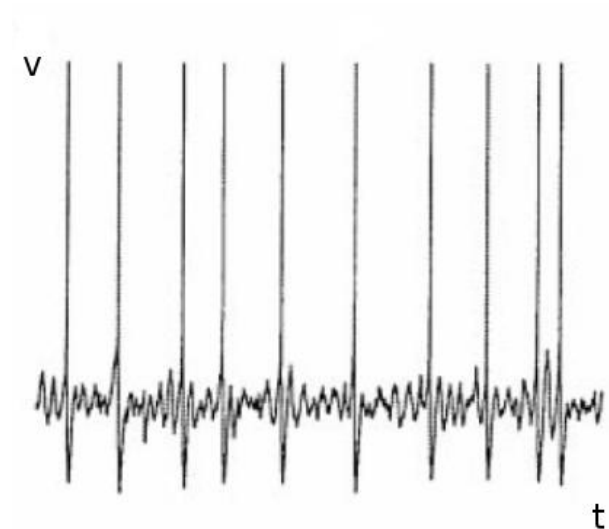


Mean temperature based on ice core measurements [Johnson et al 01]

## Oscillations in natural systems



Belousov-Zhabotinsky reaction [Hudson 79]



Stellate cells [Dickson 00]

- ▷ **Deterministic models** reproducing these oscillations exist and have been abundantly studied

They often involve **singular perturbation theory**

- ▷ We want to understand the effect of **noise** on oscillatory patterns

Noise may also induce oscillations not present in deterministic case

## Example: Van der Pol oscillator

$$x'' + \varepsilon^{-1/2}(x^2 - 1)x' + x = 0$$

$$\dot{x} = y + x - \frac{1}{3}x^3$$

$$\dot{y} = -\varepsilon x$$

$$t \mapsto \varepsilon t$$

$$\iff$$

$$\varepsilon \dot{x} = y + x - \frac{1}{3}x^3$$

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$$\Rightarrow \dot{x} = \frac{x}{1 - x^2}$$

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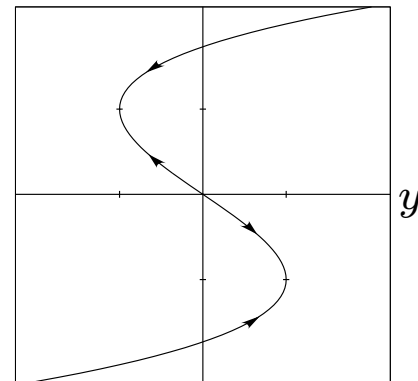
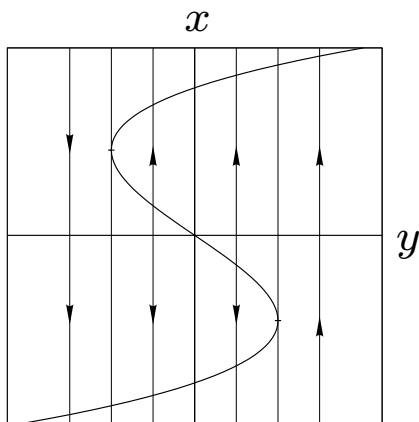
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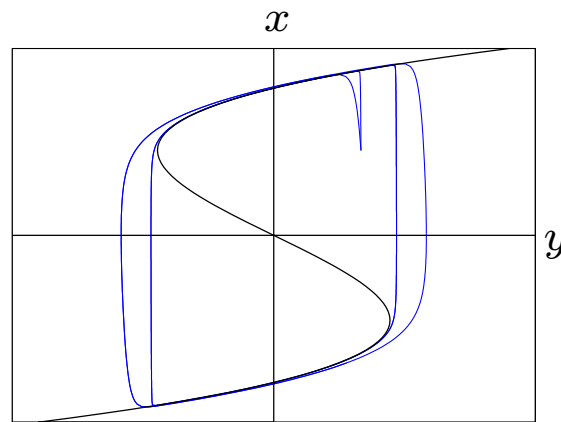


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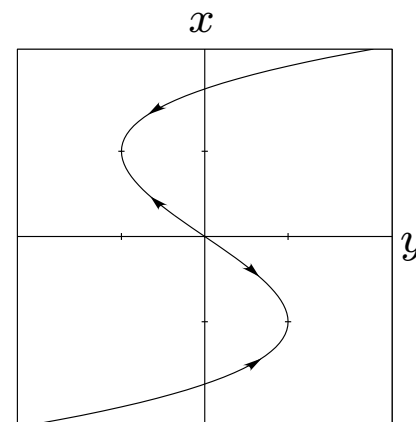
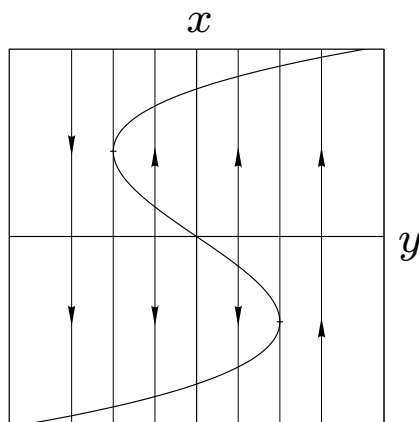
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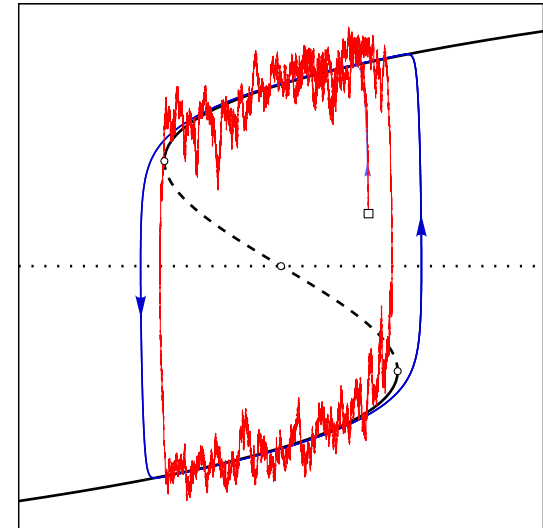


Relaxation oscillations



## Effect of noise on the Van der Pol oscillator

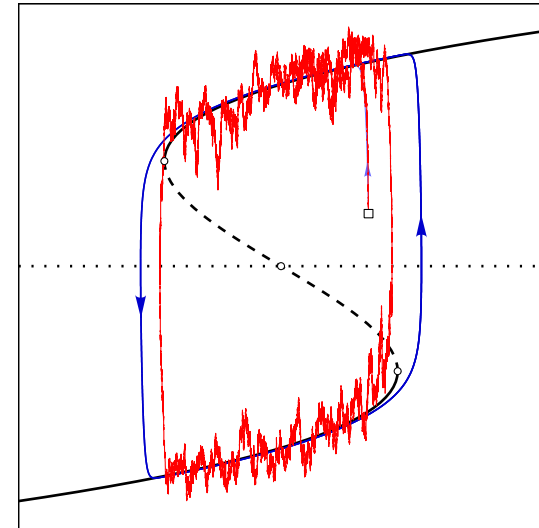
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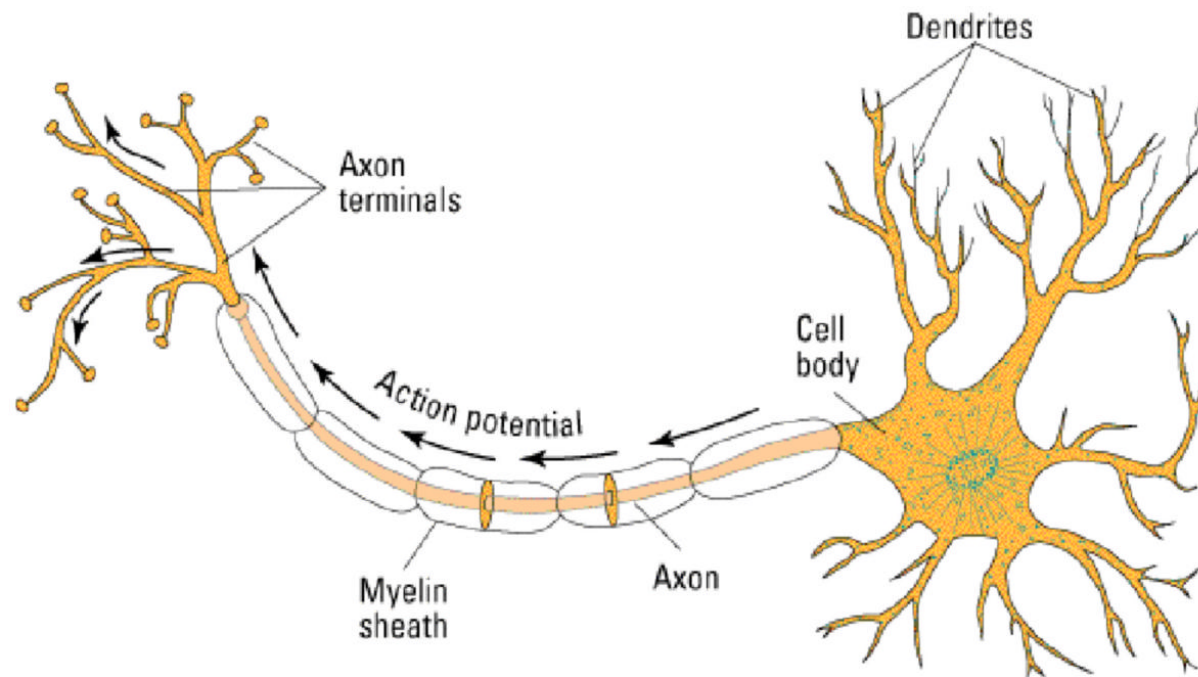
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### Theorem [B & Gentz 2006]

- $\sigma < \sqrt{\varepsilon}$  : Cycles comparable to deterministic ones with probability  $1 - \mathcal{O}(e^{-\varepsilon/\sigma^2})$
- $\sigma > \sqrt{\varepsilon}$  : Cycles are smaller, by  $\mathcal{O}(\sigma^{4/3})$ , than deterministic cycles, with probability  $1 - \mathcal{O}(e^{-\sigma^2/\varepsilon|\log \sigma|})$

# Neuron



- ▷ Single neuron communicates by generating action potential
- ▷ **Excitable**: small change in parameters yields spike generation
- ▷ May display **Mixed-Mode Oscillations (MMOs)** and **Relaxation Oscillations**

## Conductance-based models for membrane potential

### Hodgkin–Huxley model (1952)

$$C\dot{v} = - \sum_i \bar{g}_i \varphi_i^{\alpha_i} \chi_i^{\beta_i} (v - v_i^*)$$

voltage

$$\tau_{\varphi,i}(v)\dot{\varphi}_i = -(\varphi_i - \varphi_i^*(v))$$

activation

$$\tau_{\chi,i}(v)\dot{\chi}_i = -(\chi_i - \chi_i^*(v))$$

inactivation

- ▷  $i \in \{\text{Na}^+, \text{K}^+, \dots\}$  describes different types of ion channels
- ▷  $\varphi_i^*(v), \chi_i^*(v)$  sigmoidal functions, e.g.  $\tanh(av + b)$

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For  $C/\bar{g}_i \ll \tau_{x,i}$ : **slow–fast** systems of the form

$$\varepsilon\dot{v} = f(v, w)$$

$$\dot{w}_i = g_i(v, w)$$

## Conductance-based models for membrane potential

Fitzhugh–Nagumo model (1962)

$$\varepsilon \dot{x} = x - x^3 + y$$

$$\dot{y} = \alpha - \beta x - \gamma y$$

# Conductance-based models for membrane potential

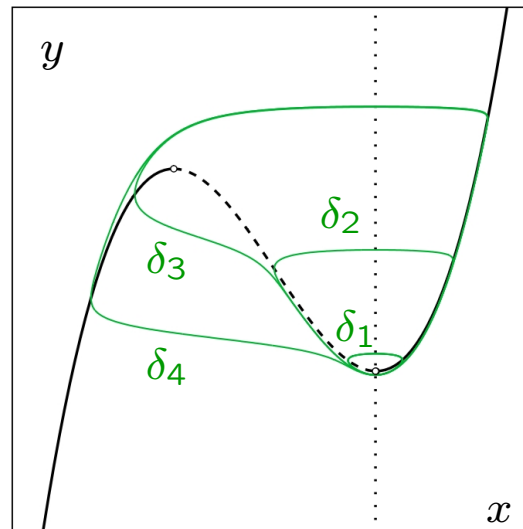
## Fitzhugh–Nagumo model (1962)

$$\begin{aligned}\varepsilon \dot{x} &= x - x^3 + y \\ \dot{y} &= \alpha - \beta x - \gamma y \\ &= \frac{1}{\sqrt{3}} + \delta - x\end{aligned}$$

## The canard (french duck) phenomenon

[J.-L. Callot, F. Diener, M. Diener (1978), E. Benoît (1981), ...]

$$\begin{aligned}\varepsilon &= 0.05 \\ \alpha &= \frac{1}{\sqrt{3}} + \delta \\ \beta &= 1 \\ \gamma &= 0 \\ \delta_1 &= -0.003 \\ \delta_2 &= -0.003765458 \\ \delta_3 &= -0.003765459 \\ \delta_4 &= -0.005\end{aligned}$$



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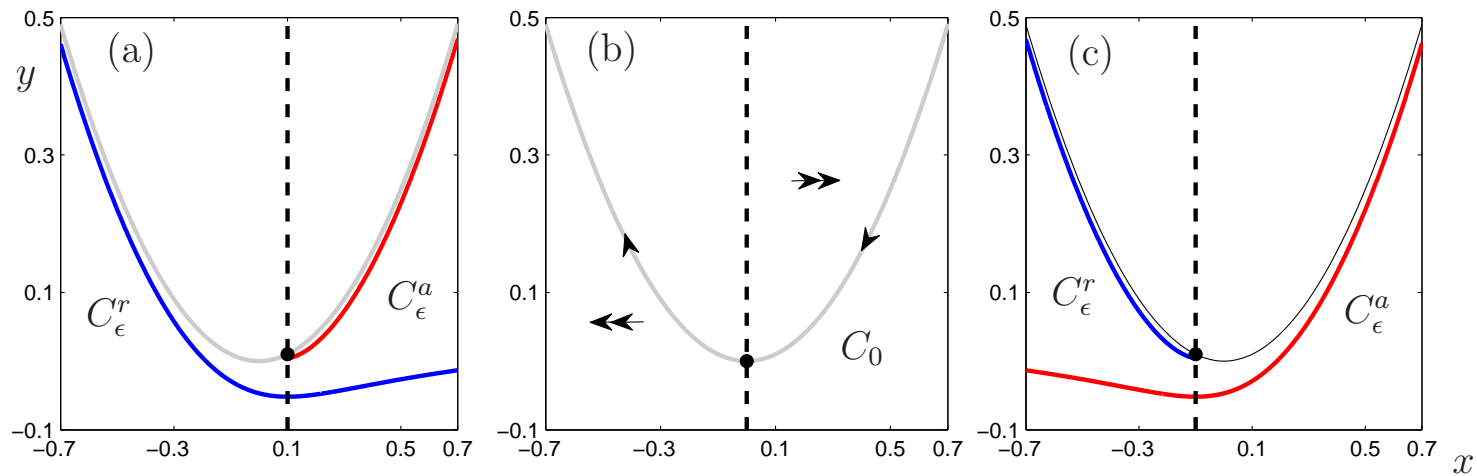
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# The canard (french duck) phenomenon

Normal form near fold point

$$\begin{aligned}\varepsilon \dot{x} &= y - x^2 \\ \dot{y} &= \delta - x\end{aligned}\quad (+ \text{ higher-order terms})$$





## Folded node singularity

Normal form [Benoît, Lobry '82, Szmolyan, Wechselberger '01]:

$$\begin{aligned}\epsilon \dot{x} &= y - x^2 \\ \dot{y} &= -(\mu + 1)x - z && (+ \text{ higher-order terms}) \\ \dot{z} &= \frac{\mu}{2}\end{aligned}$$

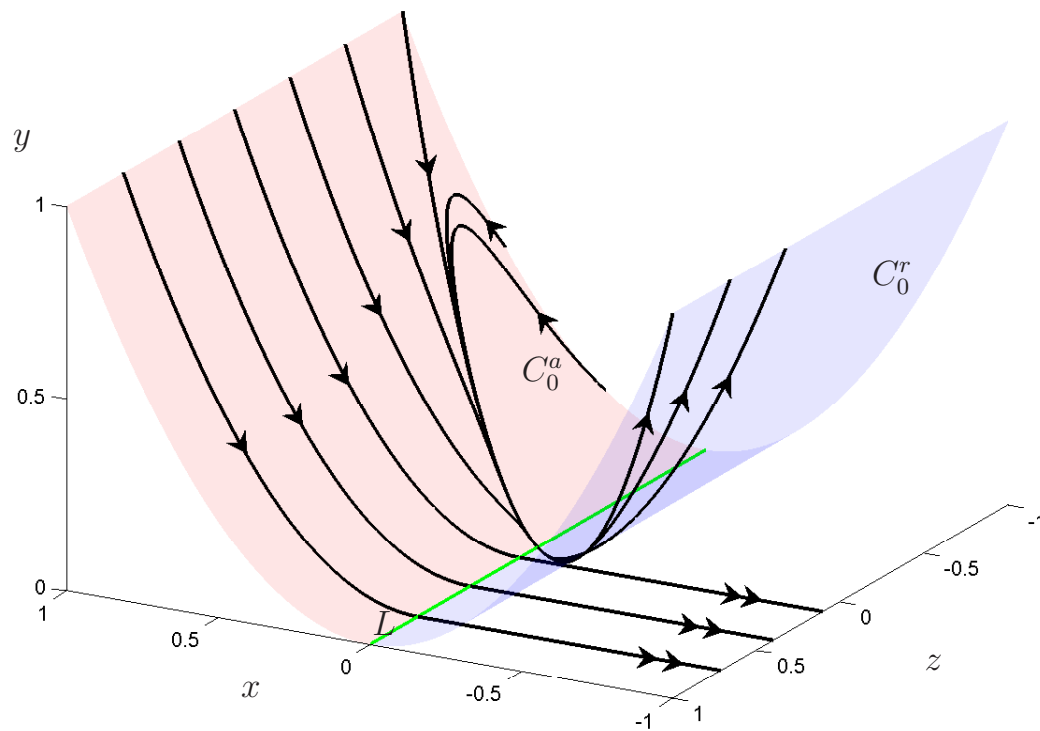
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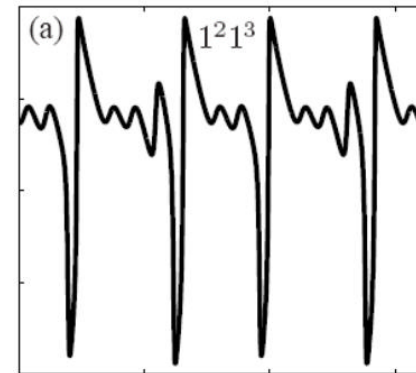
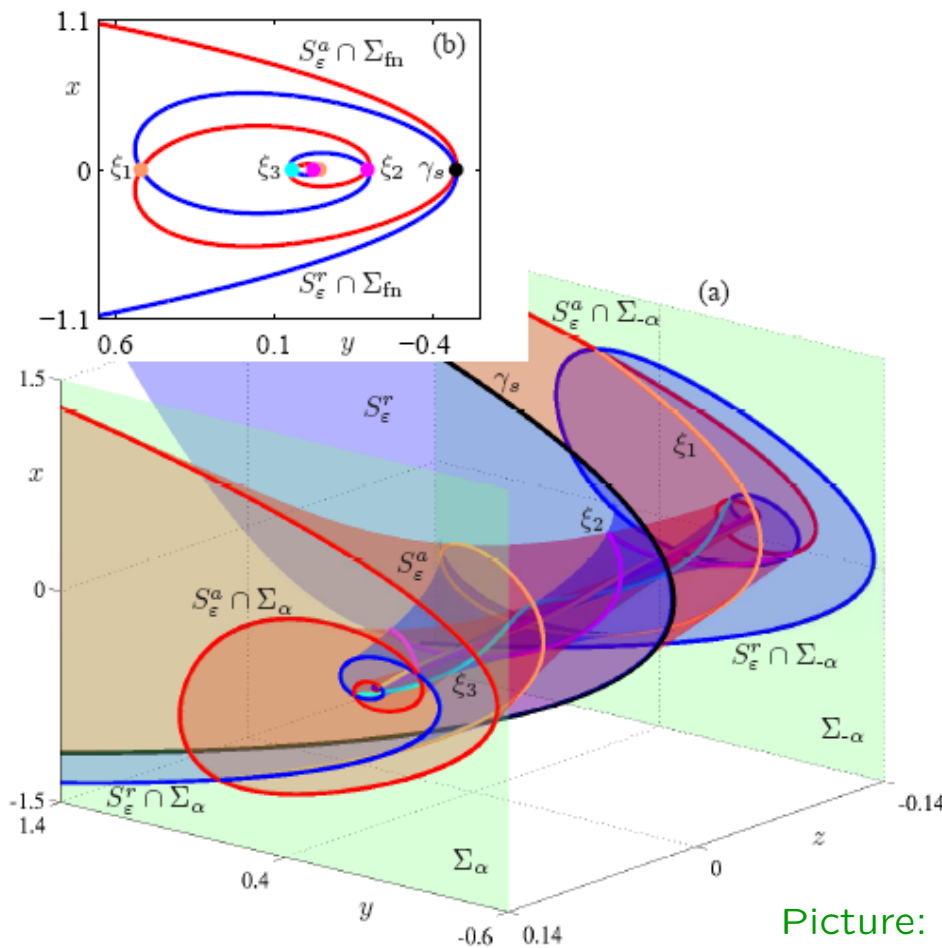


## Folded node singularity

**Theorem** [Benoît, Lobry '82, Szmolyan, Wechselberger '01]:

For  $2k + 1 < \mu^{-1} < 2k + 3$ , the system admits  $k$  canard solutions

The  $j^{\text{th}}$  canard makes  $(2j + 1)/2$  oscillations



Mixed-mode oscillations (MMOs)

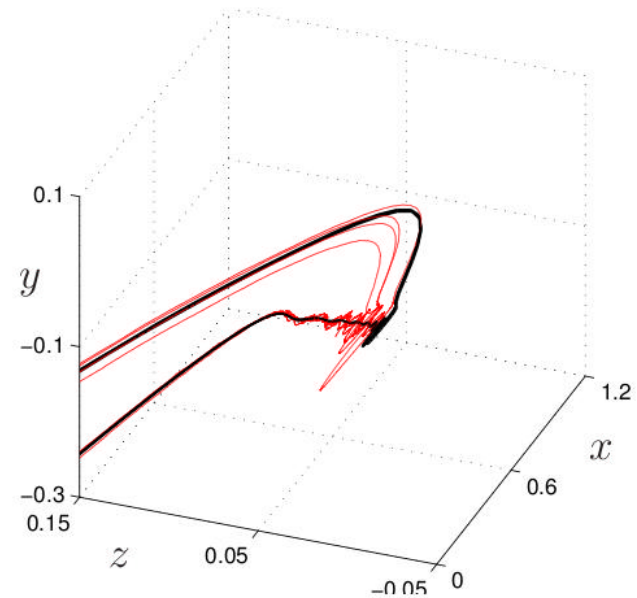
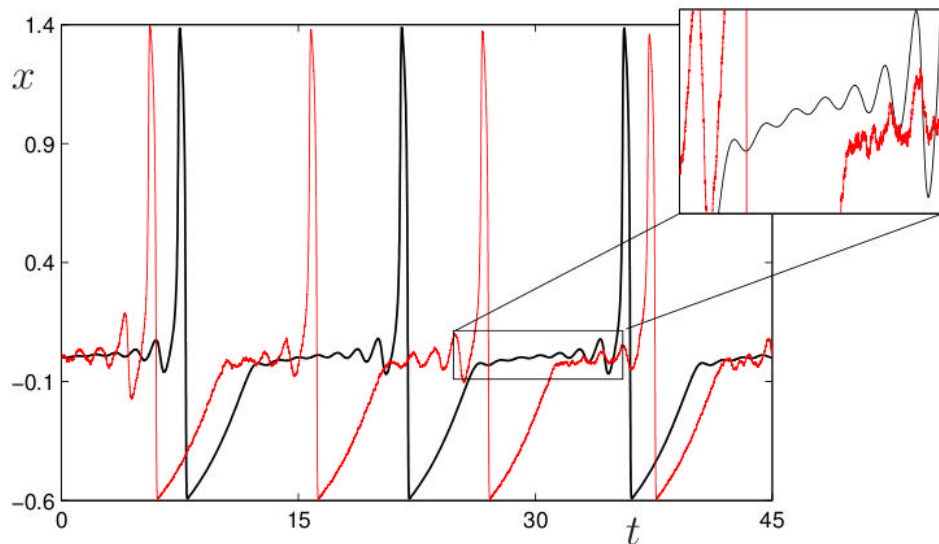
Picture: Mathieu Desroches

## Effect of noise

$$dx_t = \frac{1}{\varepsilon}(y_t - x_t^2) dt + \frac{\sigma}{\sqrt{\varepsilon}} dW_t^{(1)}$$

$$dy_t = [-(\mu + 1)x_t - z_t] dt + \sigma dW_t^{(2)}$$

$$dz_t = \frac{\mu}{2} dt$$



- Noise smears out small amplitude oscillations
- Early transitions modify the mixed-mode pattern

## Covariance tubes

Linearized stochastic equation around a canard  $(x_t^{\text{det}}, y_t^{\text{det}}, z_t^{\text{det}})$

$$d\zeta_t = A(t)\zeta_t dt + \sigma dW_t \quad A(t) = \begin{pmatrix} -2x_t^{\text{det}} & 1 \\ -(1+\mu) & 0 \end{pmatrix}$$

$$\zeta_t = U(t)\zeta_0 + \sigma \int_0^t U(t,s) dW_s \quad (U(t,s) : \text{principal solution of } \dot{U} = AU)$$

Gaussian process with covariance matrix

$$\text{Cov}(\zeta_t) = \sigma^2 V(t) \quad V(t) = U(t)V(0)U(t)^{-1} + \int_0^t U(t,s)U(t,s)^T ds$$

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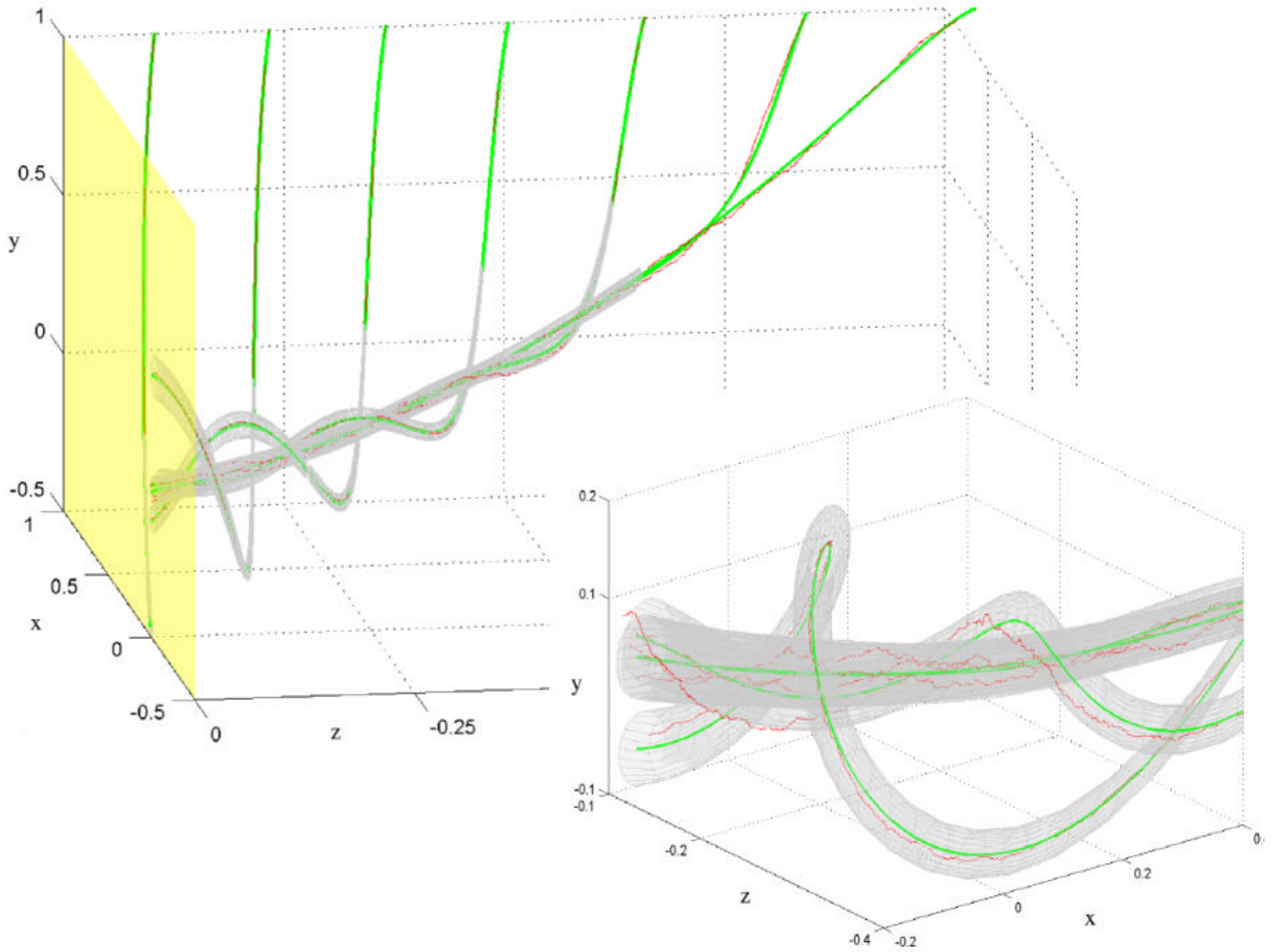
Covariance tube :

$$\mathcal{B}(h) = \left\{ \langle (x, y) - (x_t^{\text{det}}, y_t^{\text{det}}), V(t)^{-1} [(x, y) - (x_t^{\text{det}}, y_t^{\text{det}})] \rangle < h^2 \right\}$$

**Theorem** [B, Gentz, Kuehn 2010]

Probability of leaving covariance tube before time  $t$  (with  $z_t \leq 0$ ) :

$$\mathbb{P}\{\tau_{\mathcal{B}(h)} < t\} \leq C(t) e^{-\kappa h^2/2\sigma^2}$$



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Sketch of proof :

- ▷ (Sub)martingale :  $\{M_t\}_{t \geq 0}$ ,  $\mathbb{E}\{M_t | M_s\} = (\geq) M_s$  for  $t \geq s \geq 0$
- ▷ Doob's submartingale inequality :  $\mathbb{P}\left\{\sup_{0 \leq t \leq T} M_t \geq L\right\} \leq \frac{1}{L} \mathbb{E}[M_T]$



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- ▷ Linear equation :  $\zeta_t = \sigma \int_0^t U(t, s) dW_s$  is no martingale  
but can be approximated by martingale on small time intervals
- ▷  $\exp\{\gamma \langle \zeta_t, V(t)^{-1} \zeta_t \rangle\}$  approximated by submartingale
- ▷ Doob's inequality yields bound on probability of leaving  $\mathcal{B}(h)$  during small time intervals. Then sum over all time intervals

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▷ Nonlinear equation :  $d\zeta_t = A(t)\zeta_t dt + b(\zeta_t, t) dt + \sigma dW_t$

$$\zeta_t = \sigma \int_0^t U(t, s) dW_s + \int_0^t U(t, s) b(\zeta_s, s) ds$$

Second integral can be treated as small perturbation for  $t \leq \tau_{\mathcal{B}(h)}$

## Small-amplitude oscillations and noise

One shows that for  $z = 0$

- ▷ The distance between the  $k^{\text{th}}$  and  $k + 1^{\text{st}}$  canard has order  $e^{-(2k+1)^2\mu}$
- ▷ The section of  $\mathcal{B}(h)$  is close to circular with radius  $\mu^{-1/4}h$

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Sketch of proof :

- ▷ Dynamic diagonalization of equation linearized around central (“weak”) canard
- ▷  $V(t) = \sigma^{-2} \text{Cov}(\zeta_t)$  satisfies fast-slow equation

$$\mu \frac{dV}{dz} = A(z)V + VA(z)^T + \mathbb{1}$$

which can be studied by singular perturbation theory.

Note : Hopf bifurcation at  $z = 0$  !

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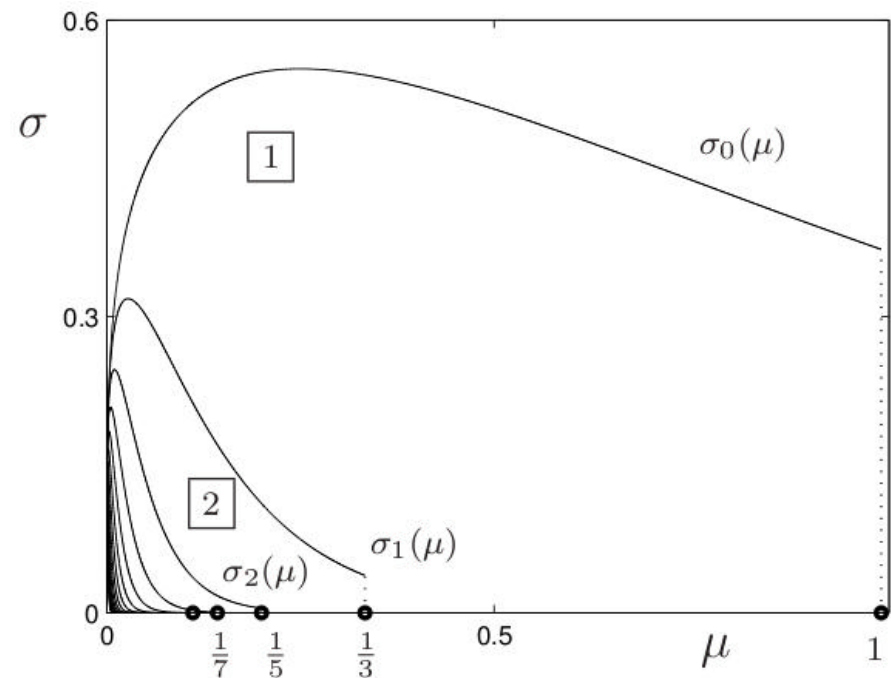
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### Corollary

Let

$$\sigma_k(\mu) = \mu^{1/4} e^{-(2k+1)^2\mu}$$

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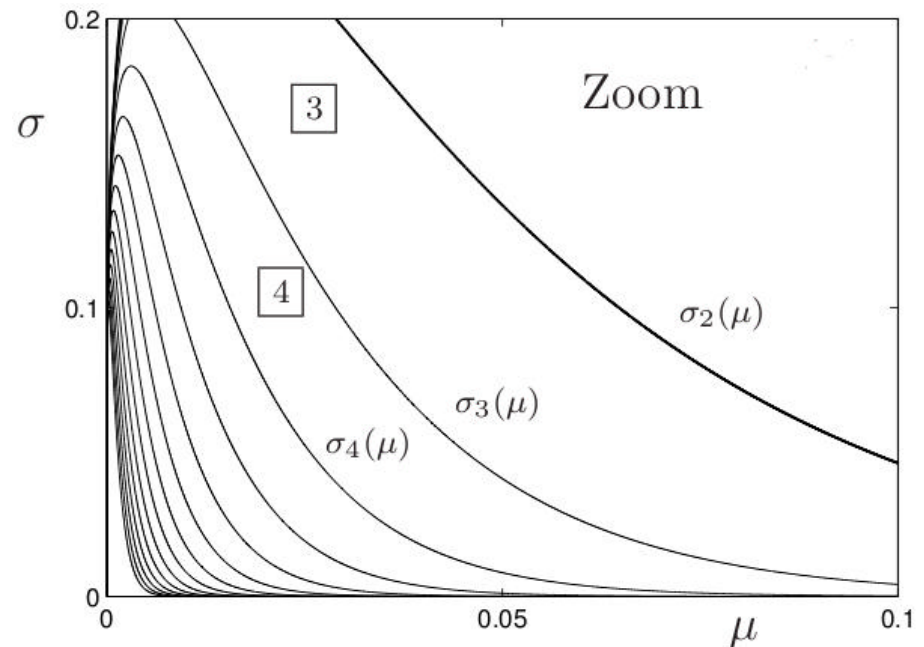
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## Early transitions

Let  $\mathcal{D}$  be neighbourhood of size  $\sqrt{z}$  of a canard for  $z > 0$  (unstable)

**Theorem** [B, Gentz, Kuehn 2010]

$\exists \kappa, C, \gamma_1, \gamma_2 > 0$  such that for  $\sigma |\log \sigma|^{\gamma_1} \leq \mu^{3/4}$  probability of leaving  $\mathcal{D}$  after  $z_t = z$  satisfies

$$\mathbb{P}\{z_{\tau_{\mathcal{D}}} > z\} \leq C |\log \sigma|^{\gamma_2} e^{-\kappa(z^2 - \mu)/(\mu |\log \sigma|)}$$

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Sketch of proof :

- ▷ Escape from neighbourhood of size  $\sigma |\log \sigma| / \sqrt{z}$  :  
compare with linearized equation on small time intervals + Markov property
- ▷ Escape from annulus  $\sigma |\log \sigma| / \sqrt{z} \leq \|\zeta\| \leq \sqrt{z}$  :  
use polar coordinates and averaging
- ▷ To combine the two regimes : use Laplace transforms



## Early transitions

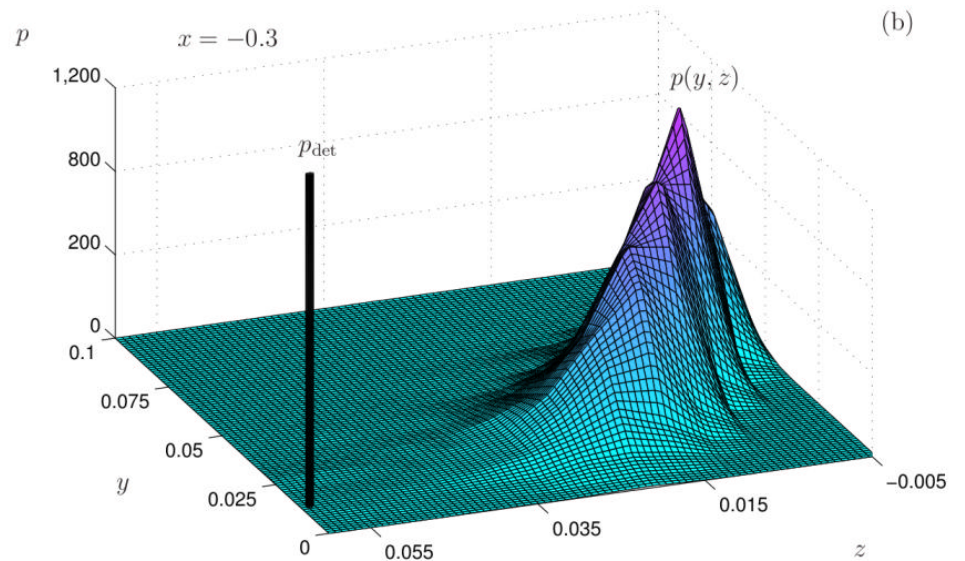
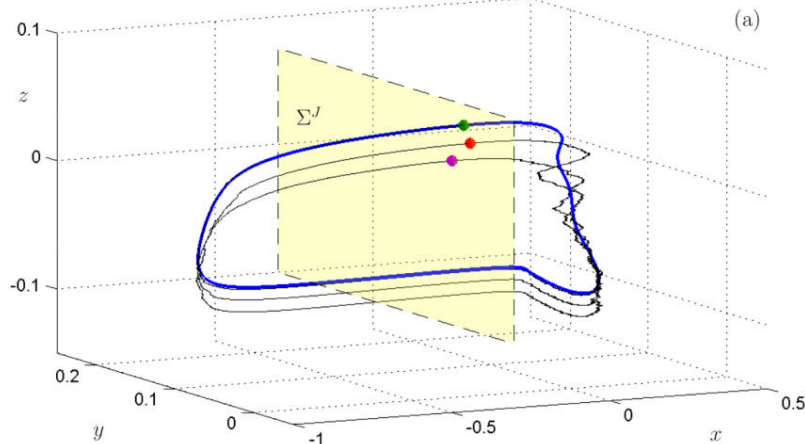
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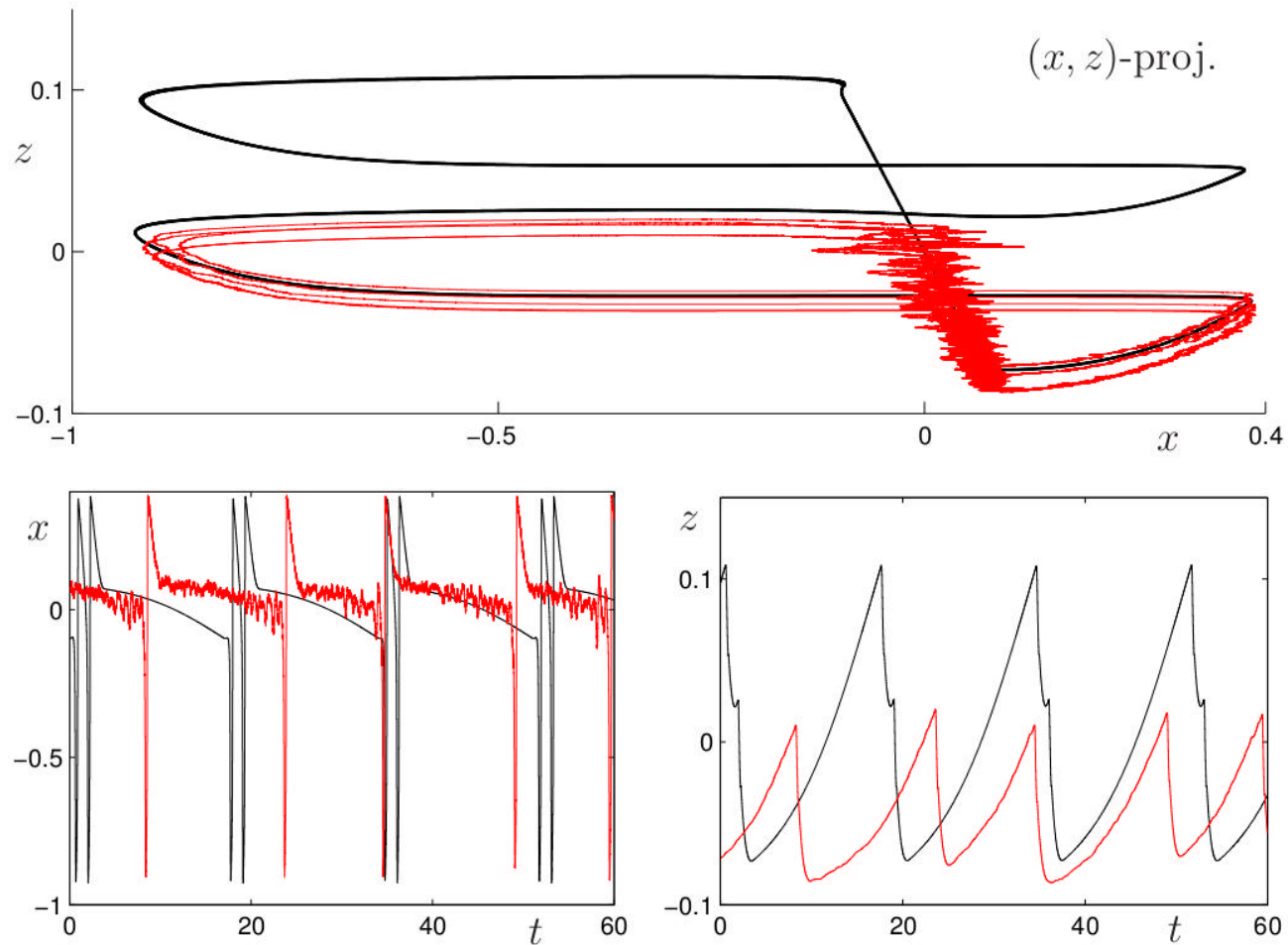


## Further work

- ▷ Better understanding of distribution of noise-induced transitions
- ▷ Effect on mixed-mode pattern in conjunction with global return mechanism

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- ▷ Better understanding of distribution of noise-induced transitions
- ▷ Effect on mixed-mode pattern in conjunction with global return mechanism



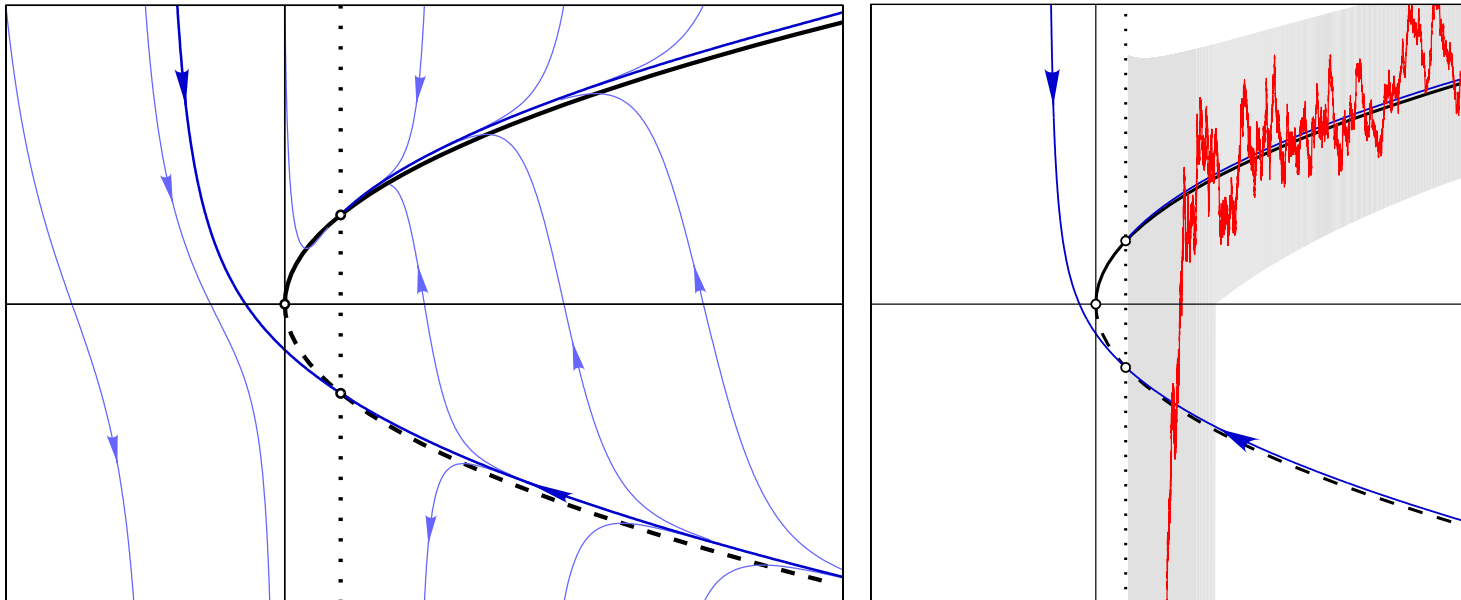
## Noise-induced MMOs

[D. Landon, PhD thesis, in progress]

FitzHugh–Nagumo, normal form near bifurcation point:

$$\begin{aligned} dx_t &= (y_t - x_t^2) dt + \sigma dW_t \\ dy_t &= \varepsilon(\delta - x_t) dt \end{aligned}$$

- ▷  $\delta > \sqrt{\varepsilon}$ : equilibrium  $(\delta, \delta^2)$  is a node, effectively 1D problem
  - $\sigma \ll \delta^{3/2}$ : rare spikes, approx. exponential interspike times
  - $\sigma \gg \delta^{3/2}$ : repeated spikes



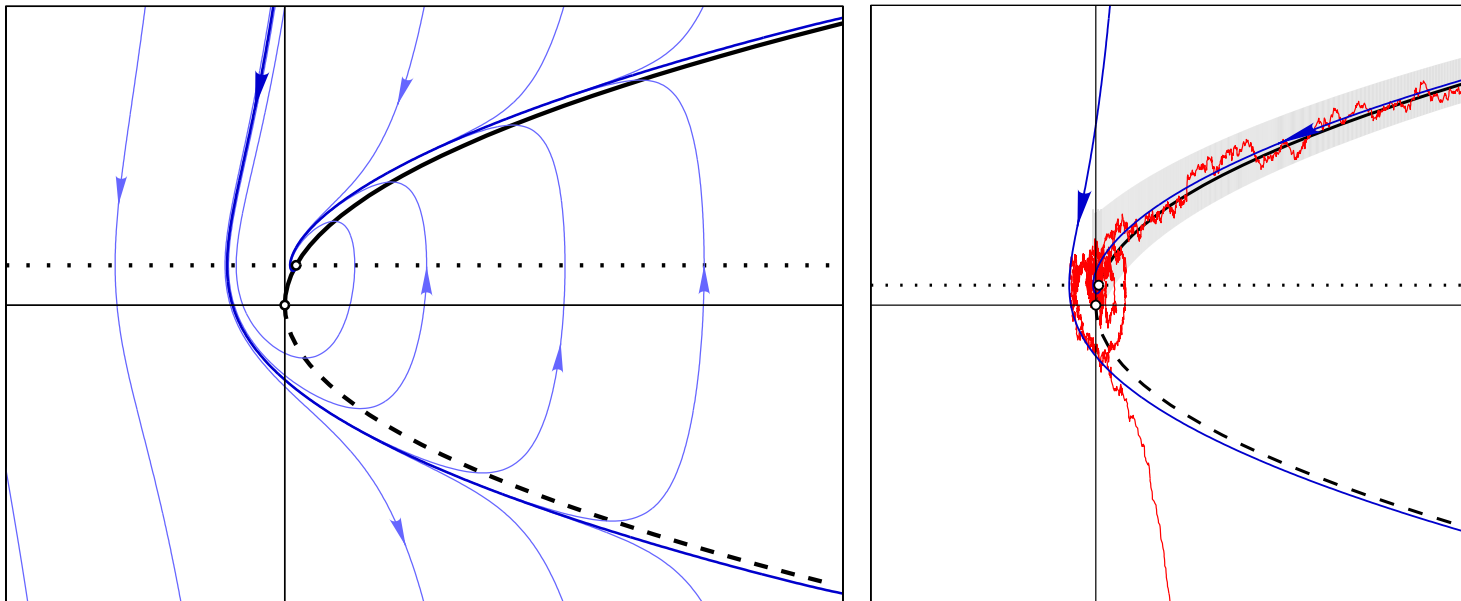
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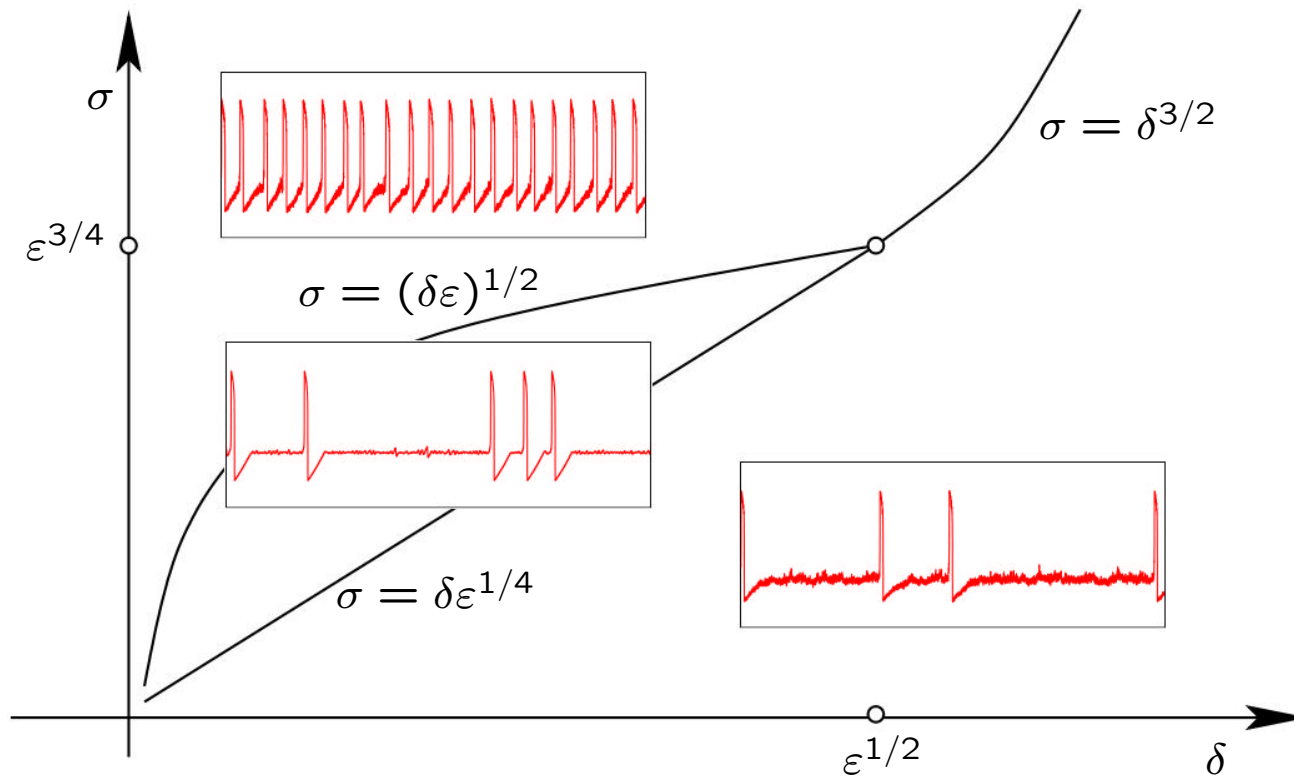
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  - $\sigma \ll \delta^{3/2}$ : rare spikes, approx. exponential interspike times
  - $\sigma \gg \delta^{3/2}$ : repeated spikes
- ▷  $\delta < \sqrt{\varepsilon}$ : equilibrium  $(\delta, \delta^2)$  is a focus. Two-dimensional problem



# Noise-induced MMOs

[D. Landon, PhD thesis, in progress]

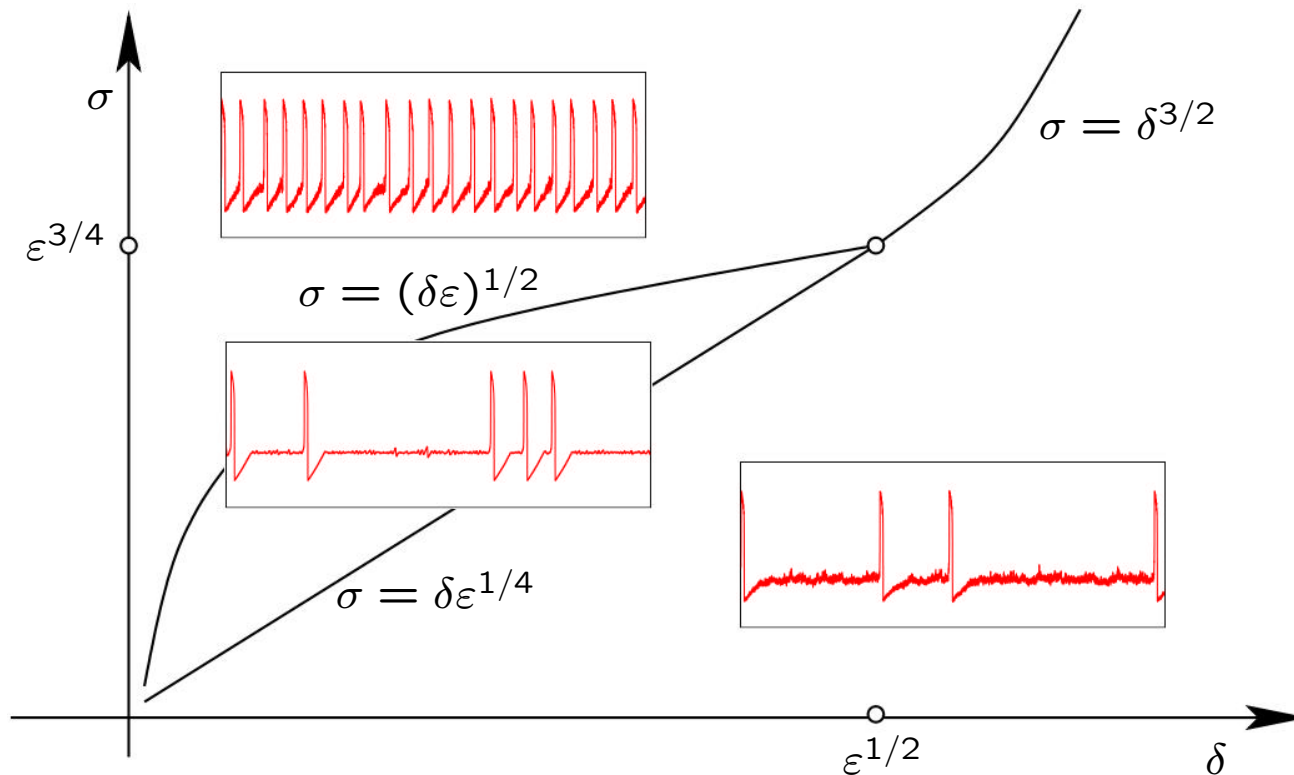
Conjectured bifurcation diagram [Muratov and Vanden Eijnden (2007)] :



## Noise-induced MMOs

[D. Landon, PhD thesis, in progress]

Conjectured bifurcation diagram [Muratov and Vanden Eijnden (2007)] :



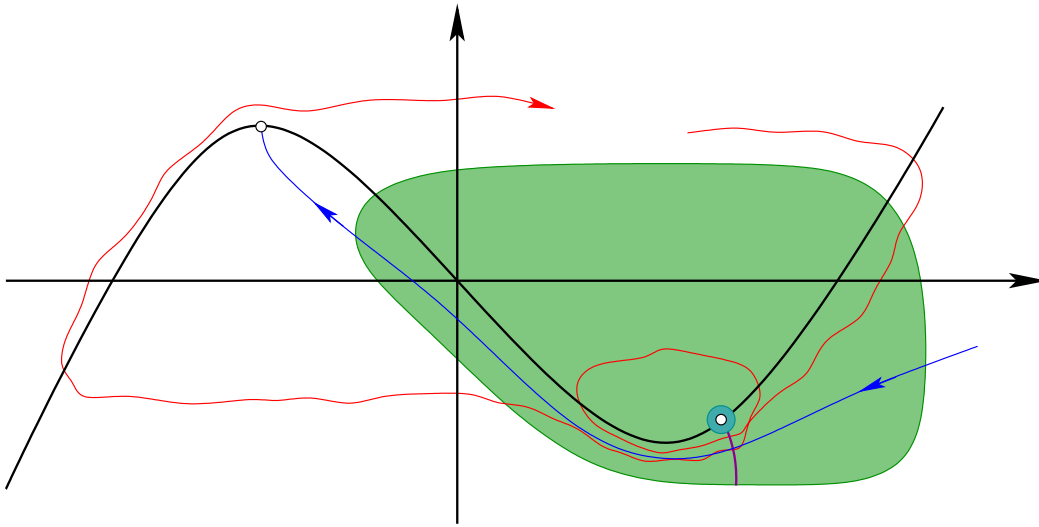
Work in progress :

- ▷ Prove bifurcation diagram is correct
- ▷ Characterize interspike time statistics and spike train statistics
- ▷ Characterize distribution of mixed-mode patterns

## Noise-induced MMOs

[D. Landon, PhD thesis, in progress]

Definition of random number of SAOs  $N$ :



$N$  = survival time of substochastic Markov chain

**Theorem** (2011):

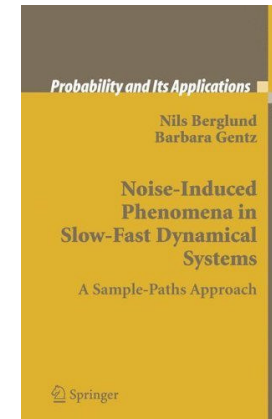
- $\lim_{n \rightarrow \infty} \mathbb{P}\{N = n + 1 | N > n\} = 1 - \lambda_0$ ,  $\lambda_0$  = principal ev
- Weak noise:  $\sigma_1^2 + \sigma_2^2 \leq (\varepsilon^{1/4} \delta)^2 \Rightarrow 1 - \lambda_0 \leq e^{-\kappa(\varepsilon^{1/4} \delta)^2 / (\sigma_1^2 + \sigma_2^2)}$
- Increasing noise:

$$1 - \lambda_0 \simeq \Phi\left(-\frac{(\pi\varepsilon)^{1/4}(\delta - \sigma_1^2/\varepsilon)}{\sqrt{\sigma_1^2 + \sigma_2^2}}\right)$$

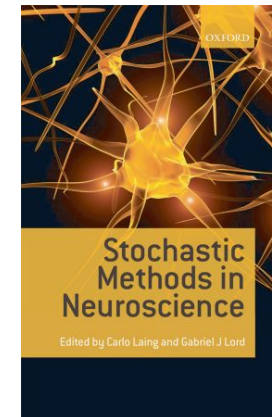


## References

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