

Chasse aux canards en environnement bruité

Nils Berglund

MAPMO, Université d'Orléans

CNRS, UMR 6628 et Fédération Denis Poisson

www.univ-orleans.fr/mapmo/membres/berglund

Collaborateurs:

Stéphane Cordier, Damien Landon, Simona Mancini, MAPMO, Orléans

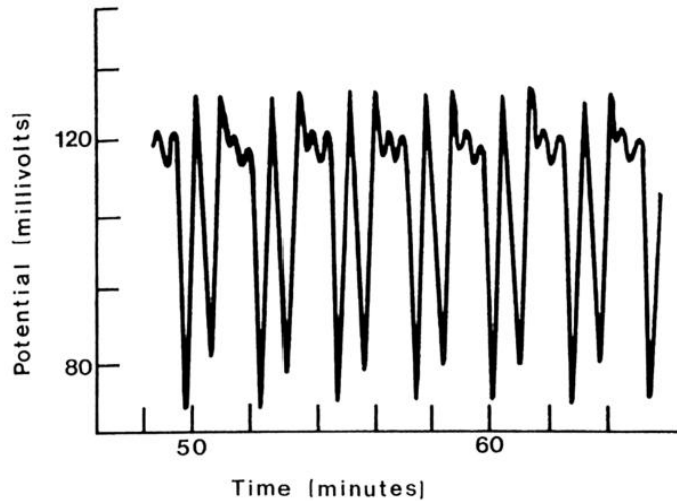
Barbara Gentz, University of Bielefeld

Christian Kuehn, Max Planck Institute, Dresden

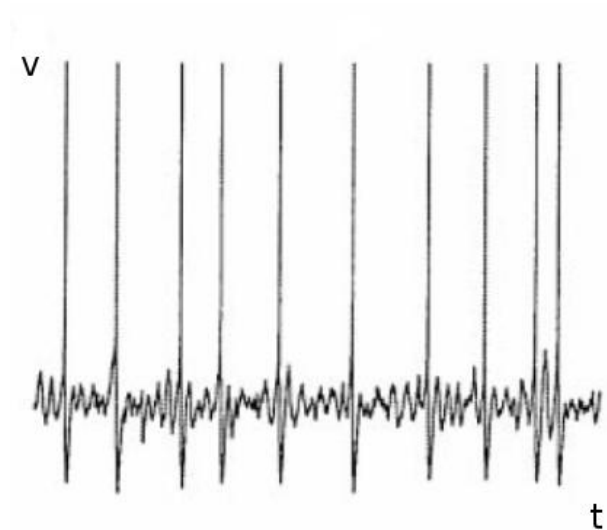
Projet ANR MANDy, Mathematical Analysis of Neuronal Dynamics

GdT Mathématiques et Neurosciences, IHP, Paris, 14 mars 2011

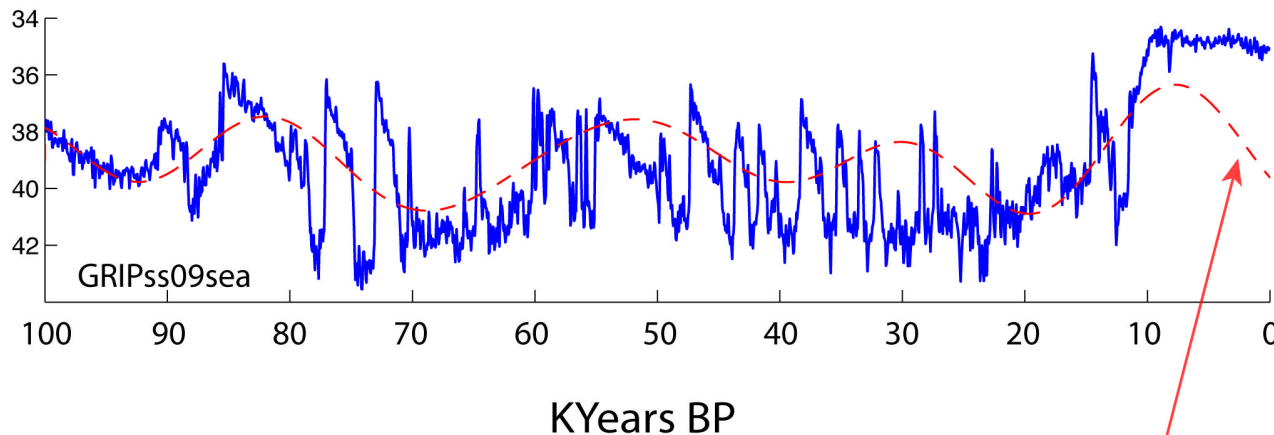
Oscillations in natural systems



Belousov-Zhabotinsky reaction [Hudson 79]

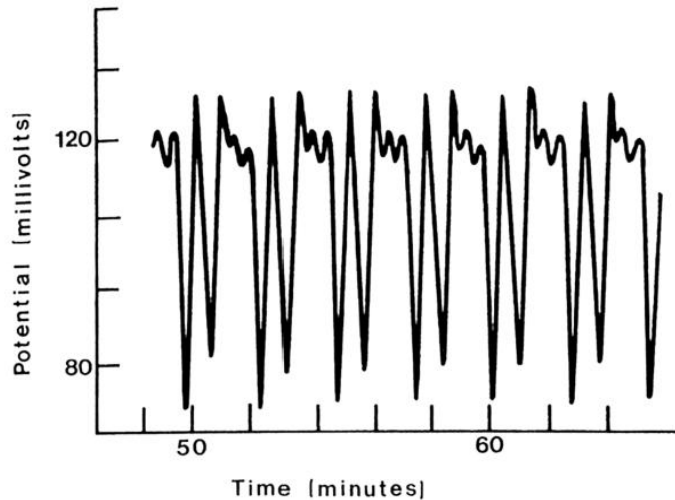


Stellate cells [Dickson 00]

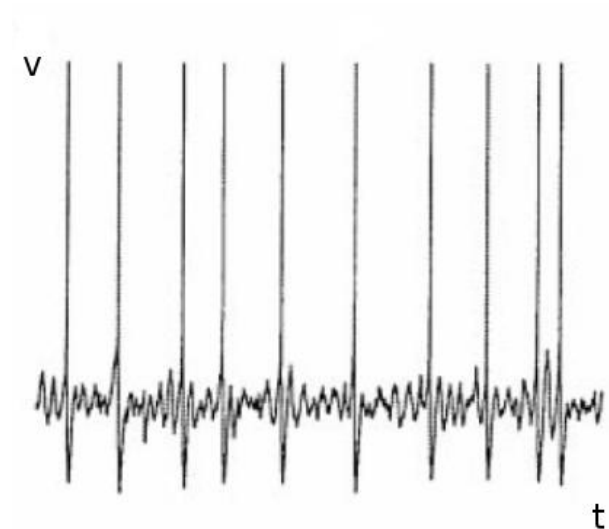


Mean temperature based on ice core measurements [Johnson et al 01]

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

Example: Van der Pol oscillator

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

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

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

$$t \mapsto \varepsilon t$$

$$\iff$$

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

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

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

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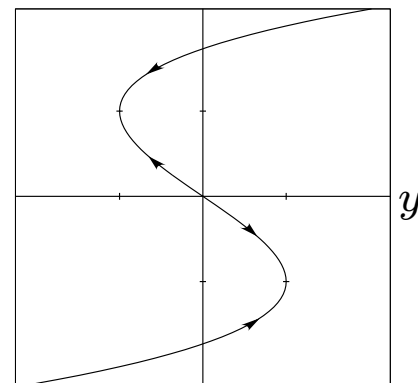
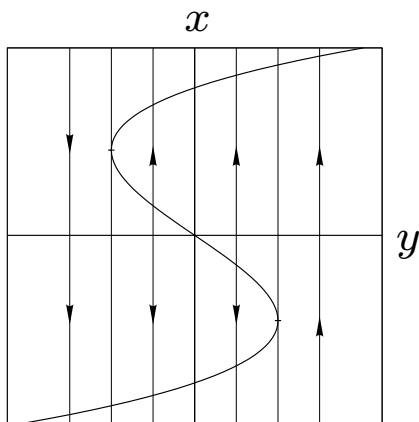
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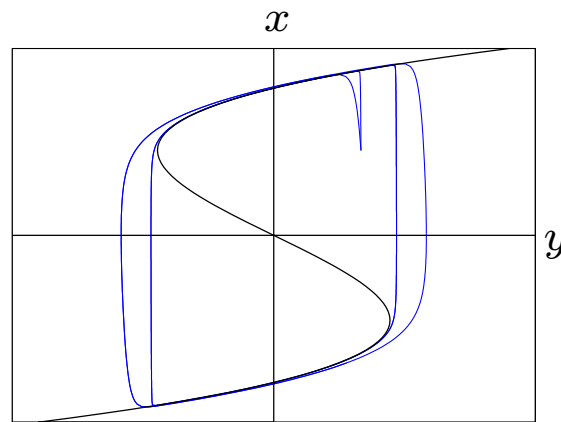


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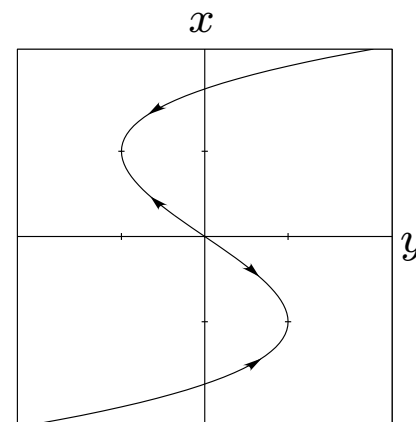
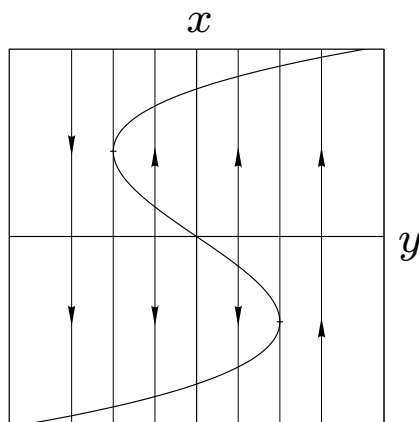
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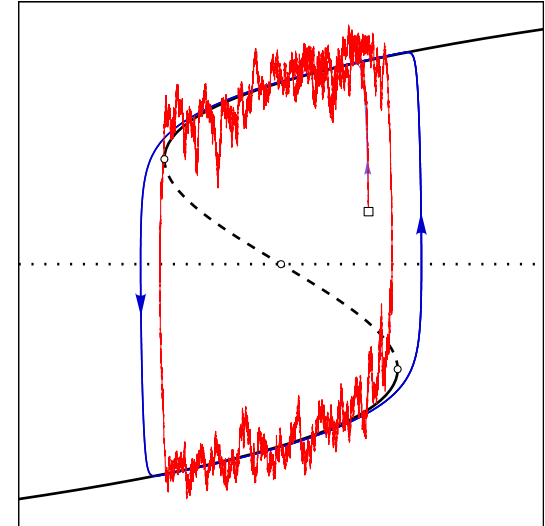


Relaxation oscillations



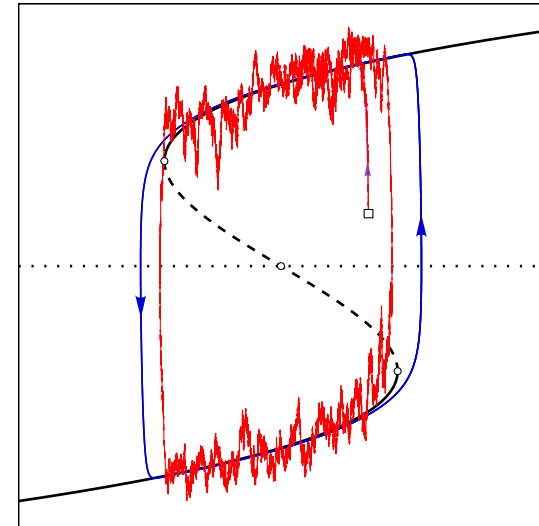
Effect of noise on the Van der Pol oscillator

$$dx_t = \left[y_t + x_t - \frac{x_t^3}{3} \right] dt + \sigma dW_t$$
$$dy_t = -\varepsilon x_t dt$$



Effect of noise on the Van der Pol oscillator

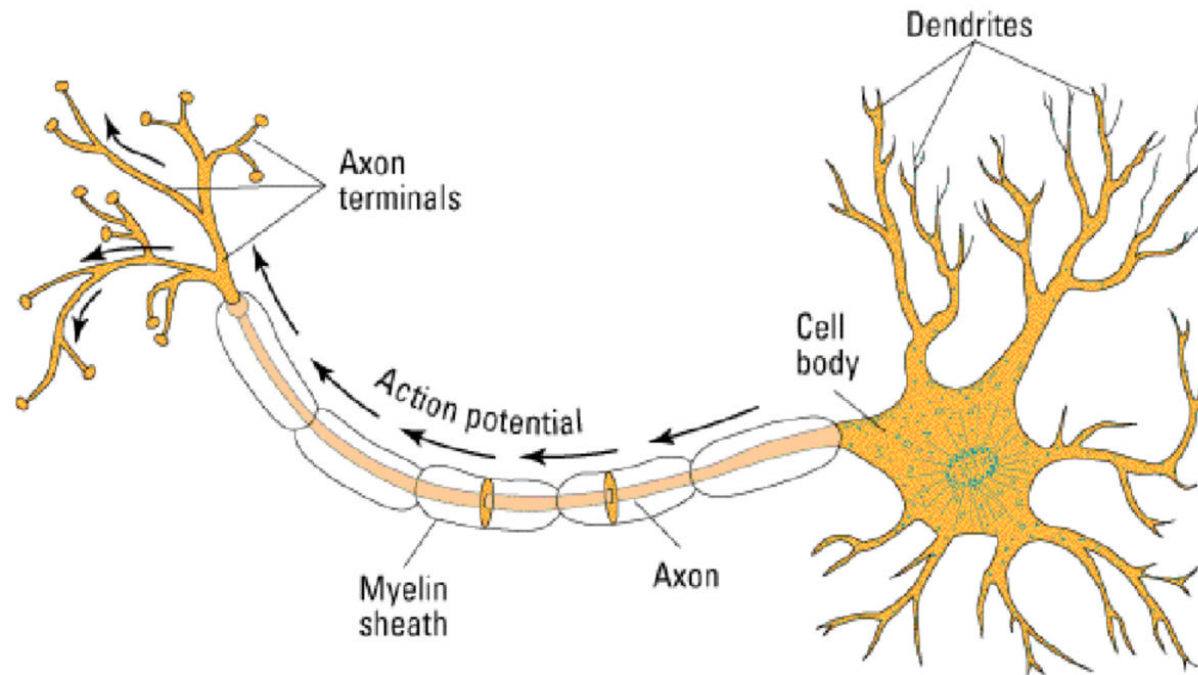
$$\begin{aligned} dx_t &= \left[y_t + x_t - \frac{x_t^3}{3} \right] dt + \sigma dW_t \\ dy_t &= -\varepsilon x_t dt \end{aligned}$$



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

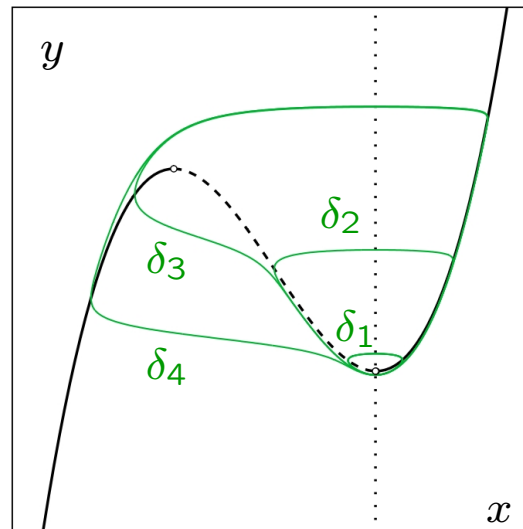
Fitzhugh–Nagumo model (1962)

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

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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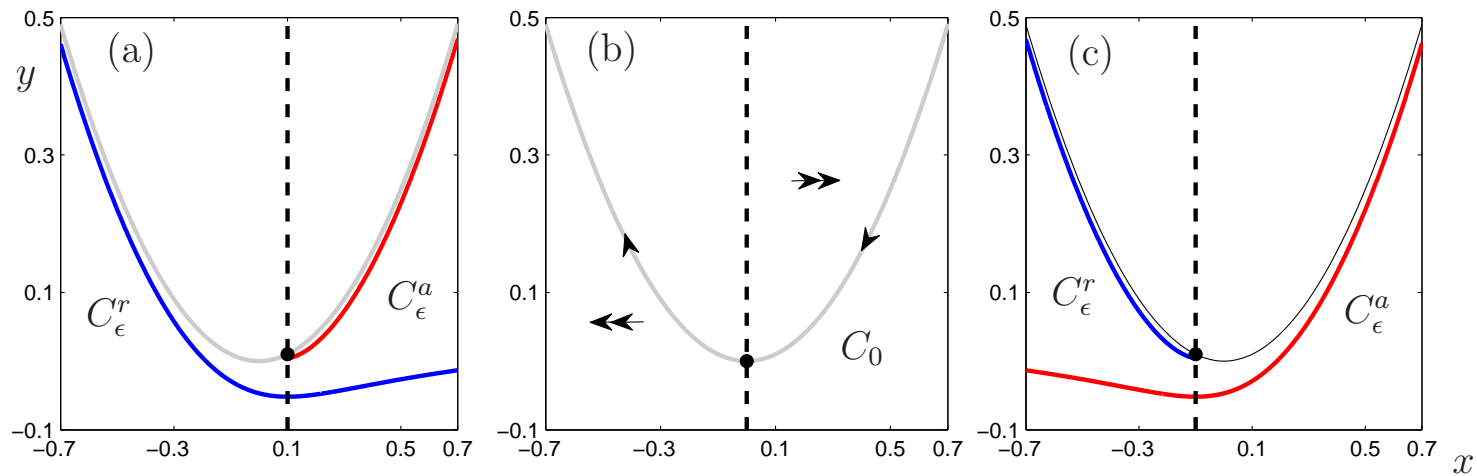
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The canard (french duck) phenomenon

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]:

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

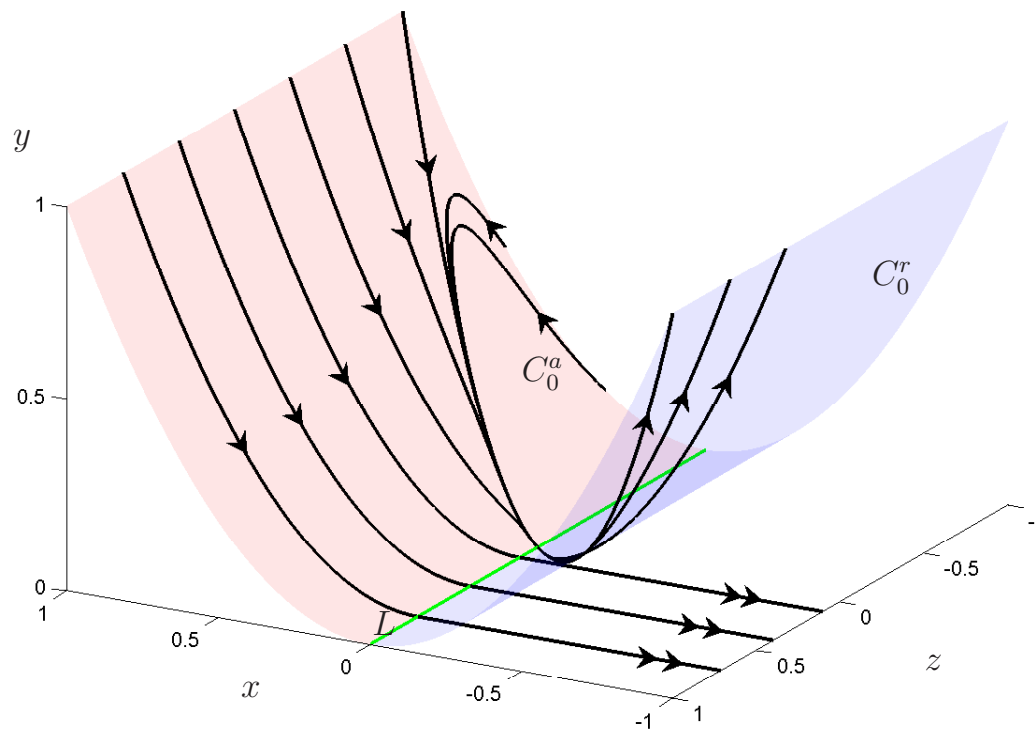
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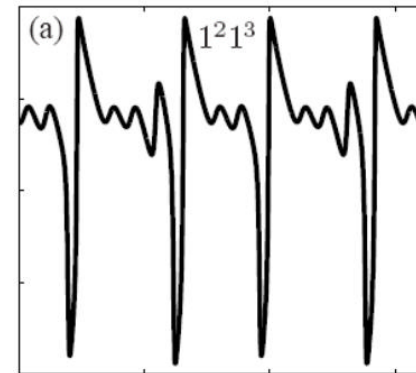
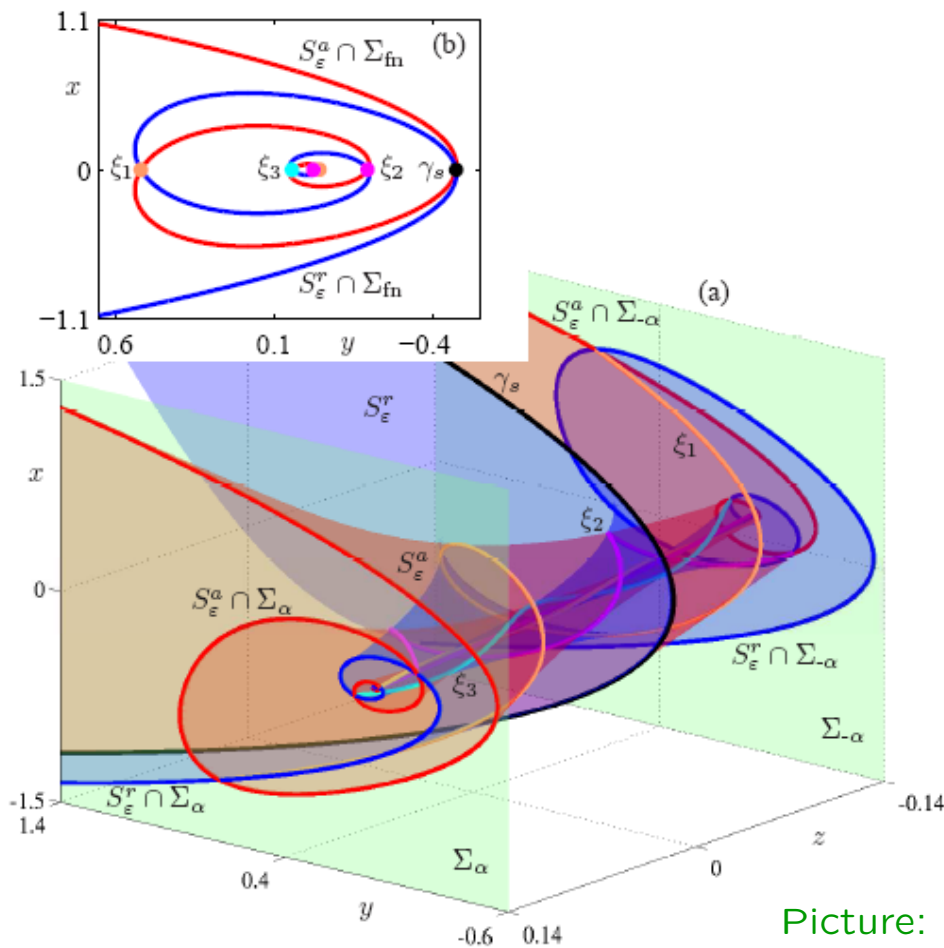


Folded node singularity

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

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

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



Mixed-mode oscillations (MMOs)

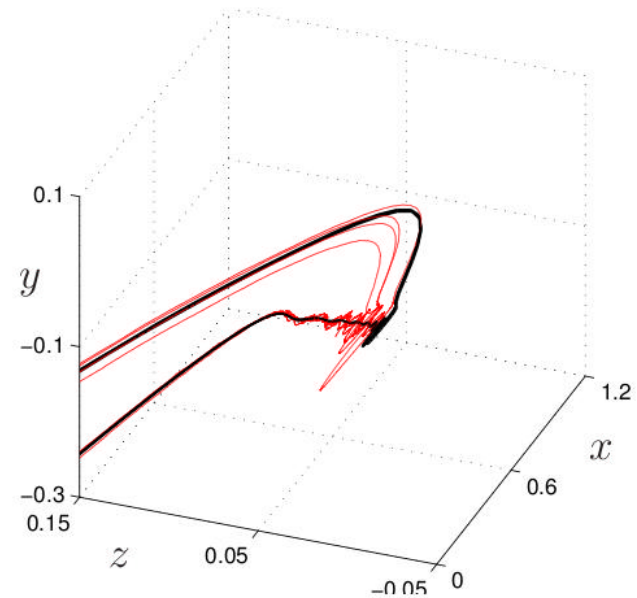
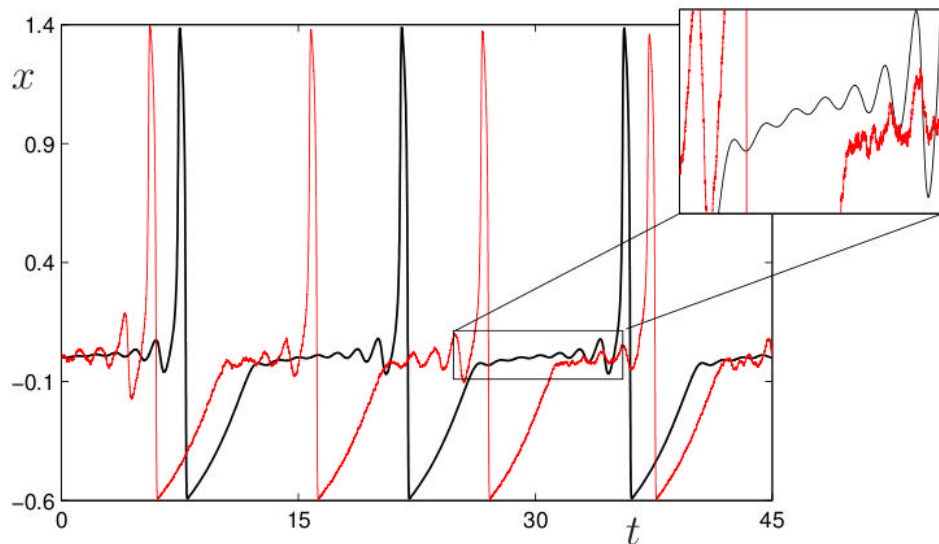
Picture: Mathieu Desroches

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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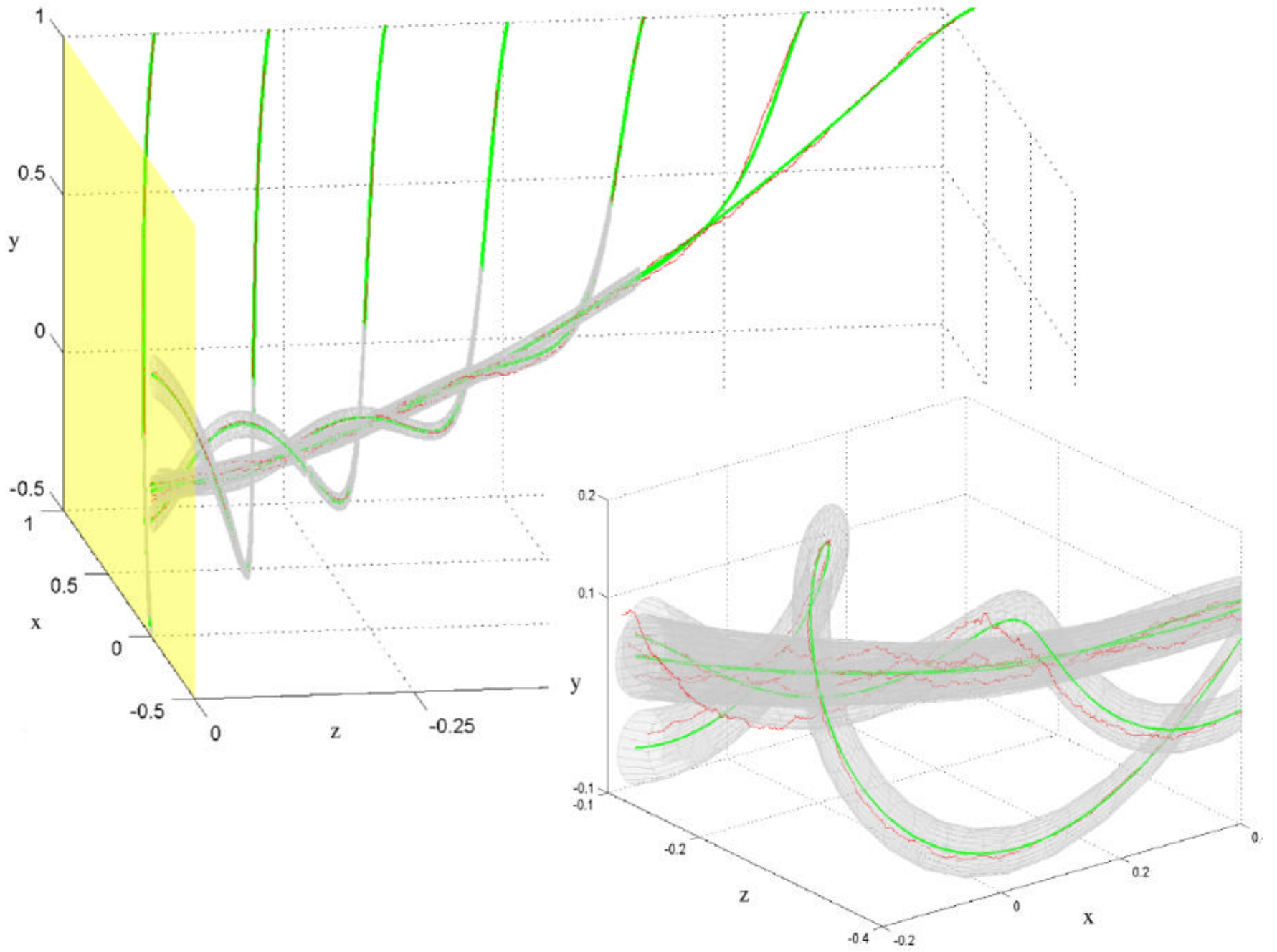
Covariance tube :

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

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^{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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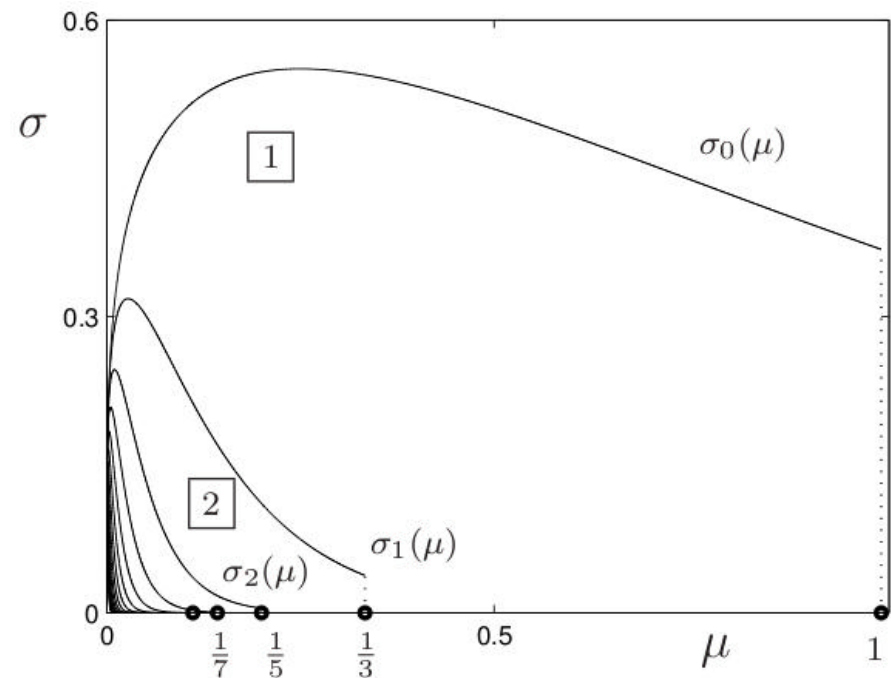
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Corollary

Let

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

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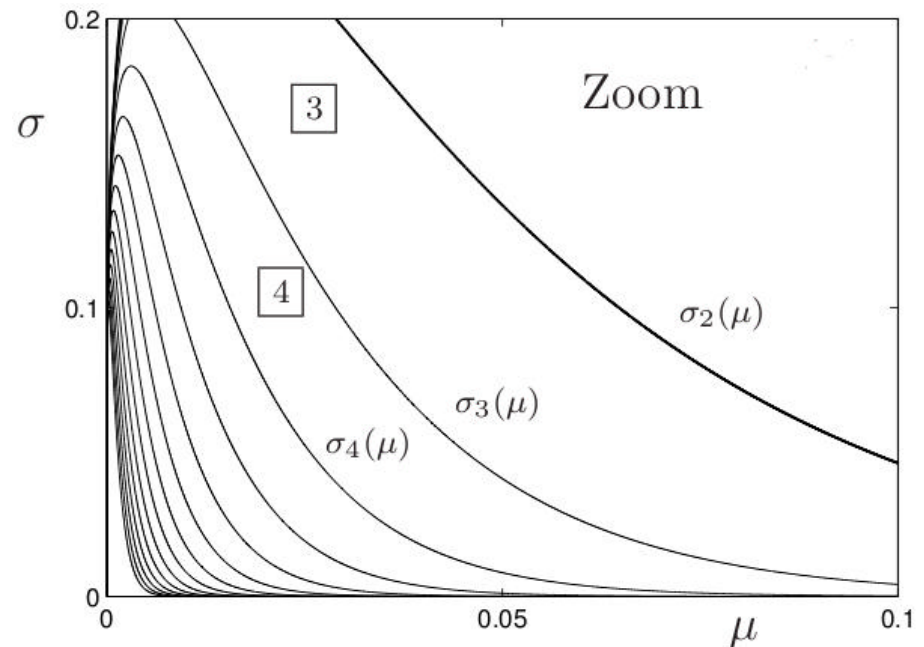
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Early transitions

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

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

Small for $z \gg \sqrt{\mu |\log \sigma| / \kappa}$

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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

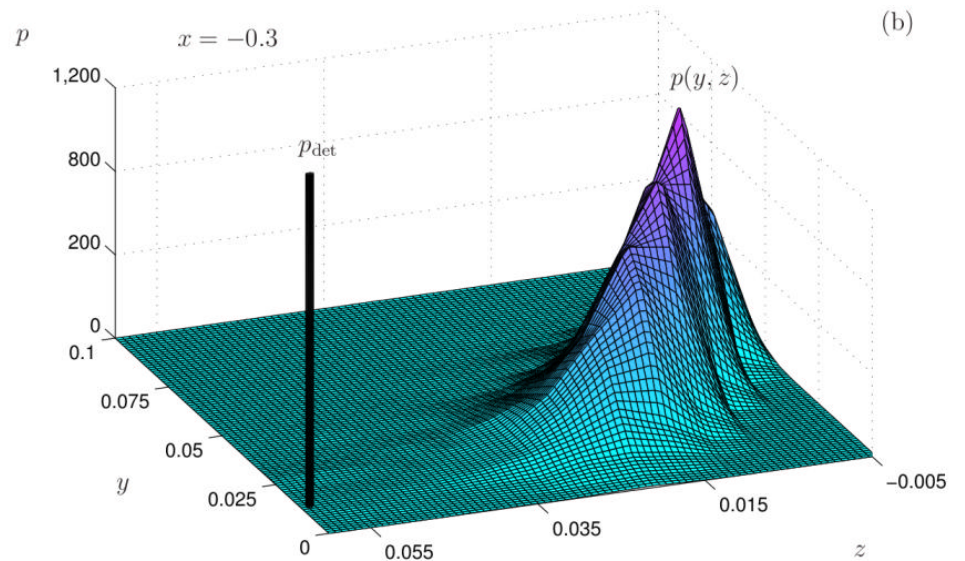
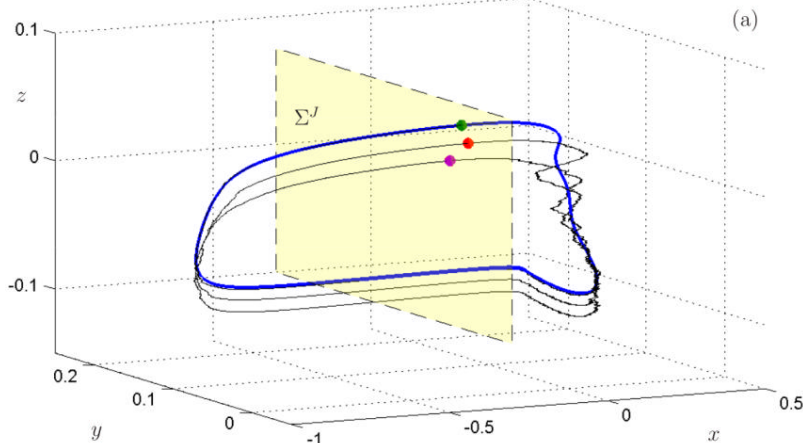
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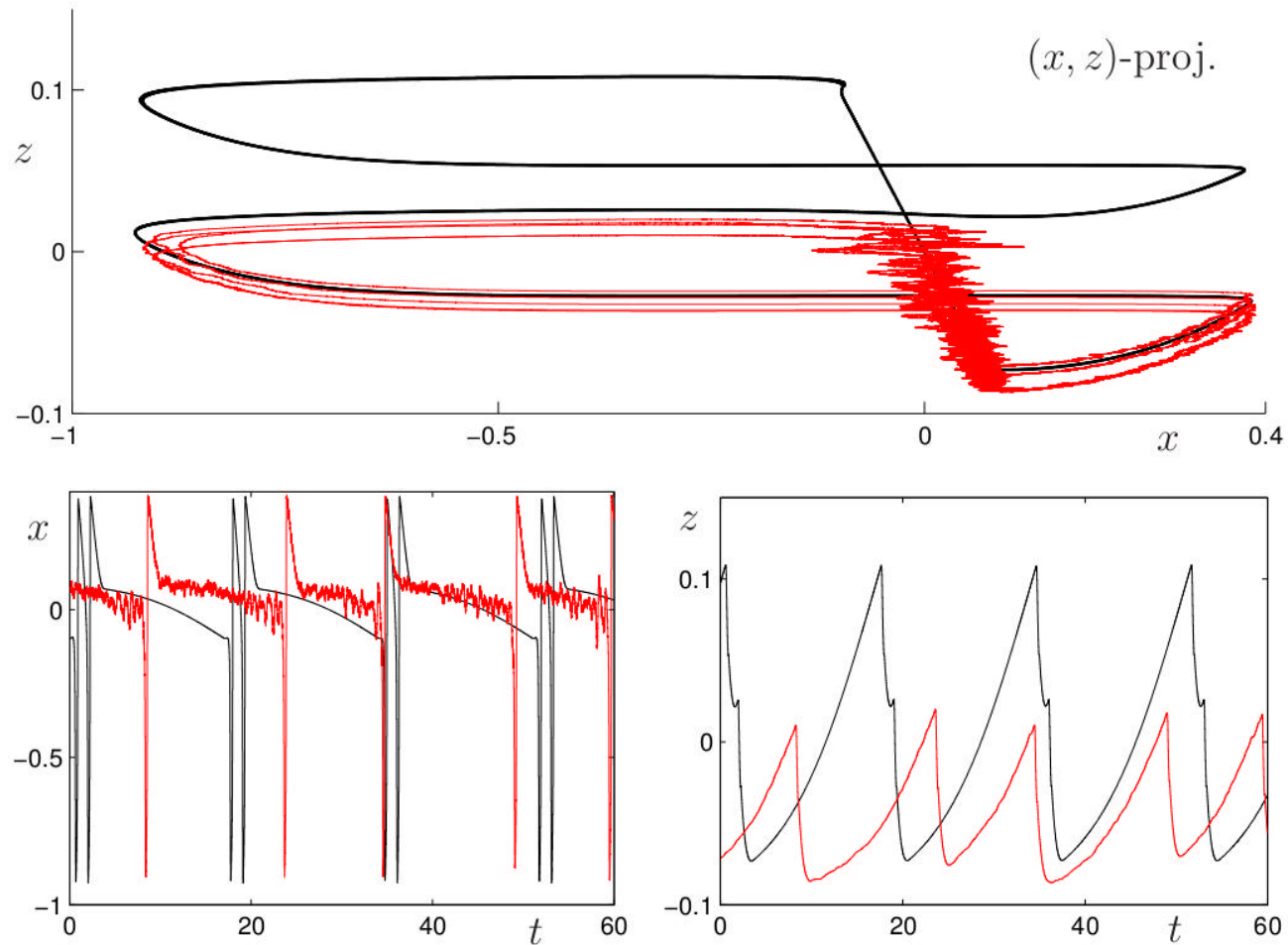


Further work

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

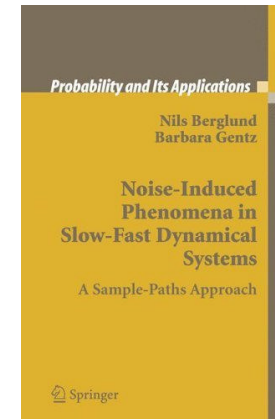
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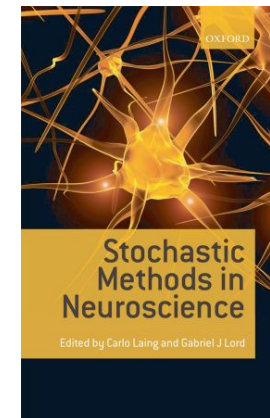


References

N.B. and Barbara Gentz, *Noise-induced phenomena in slow-fast dynamical systems, A sample-paths approach*, Springer, Probability and its Applications (2006)



N.B. and Barbara Gentz, *Stochastic dynamic bifurcations and excitability*, in C. Laing and G. Lord, (Eds.), *Stochastic methods in Neuroscience*, p. 65-93, Oxford University Press (2009)



N.B., Barbara Gentz and Christian Kuehn, *Hunting French Ducks in a Noisy Environment*, hal-00535928, submitted (2010)



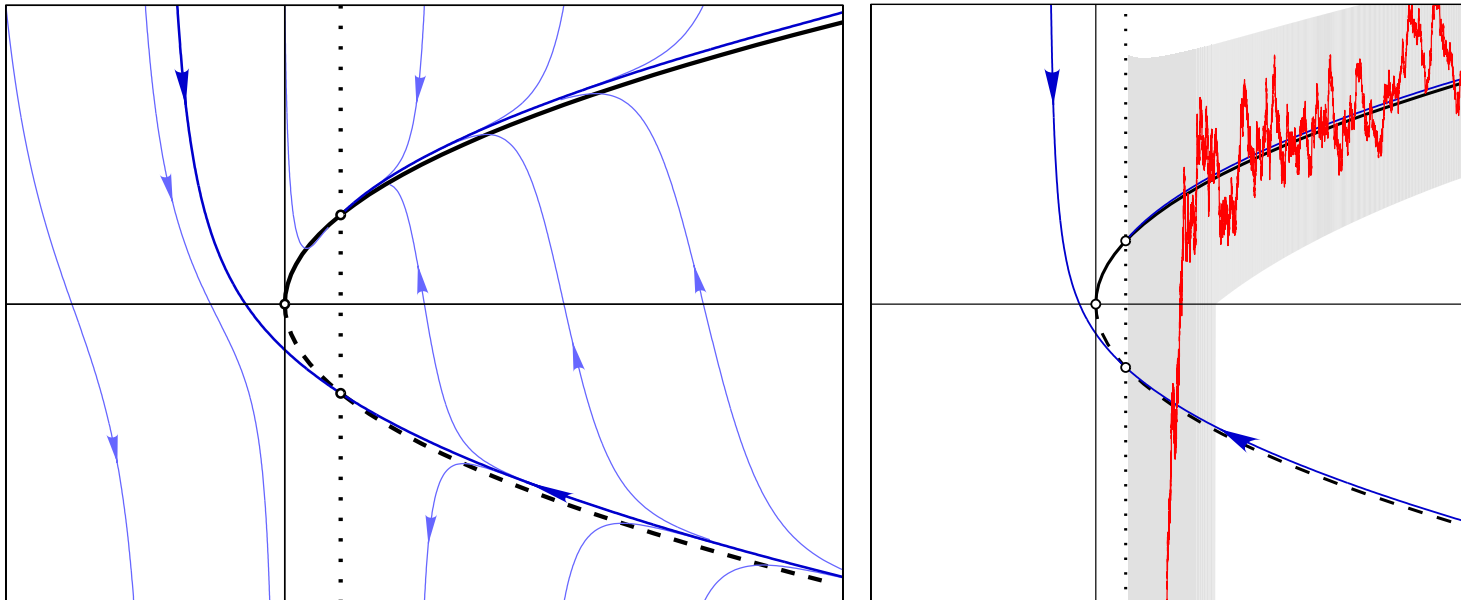
Noise-induced MMOs

[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 (δ, δ^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



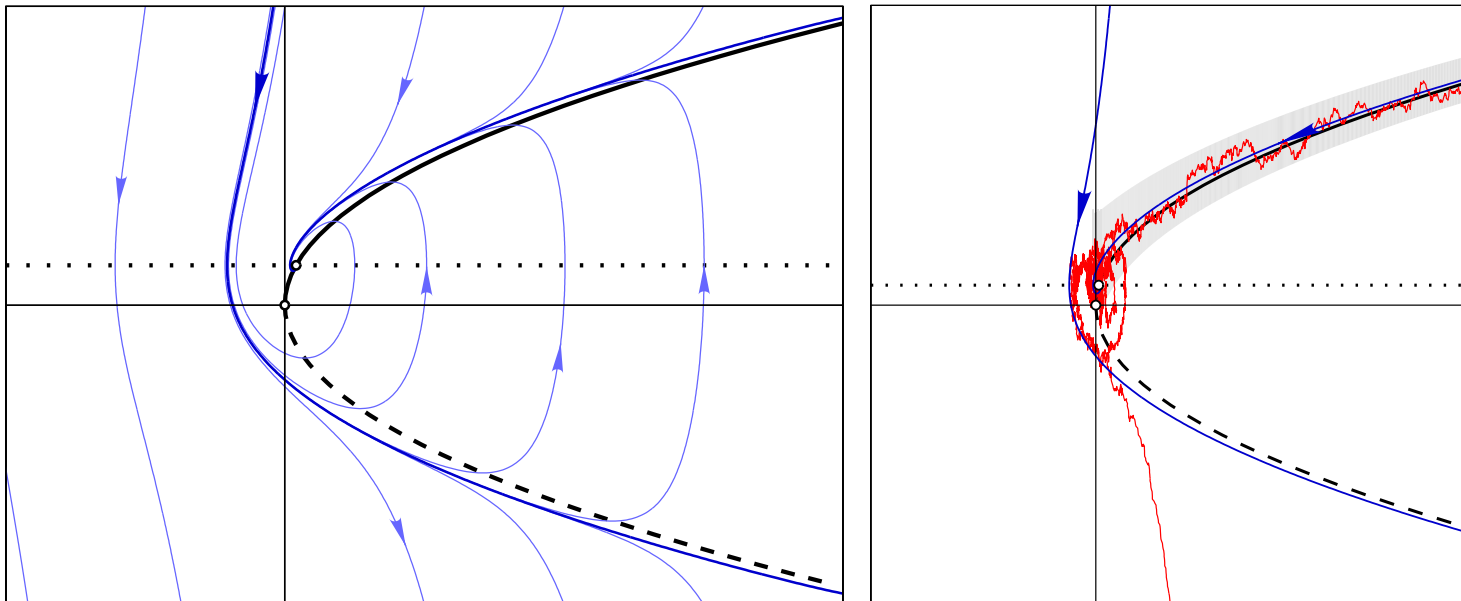
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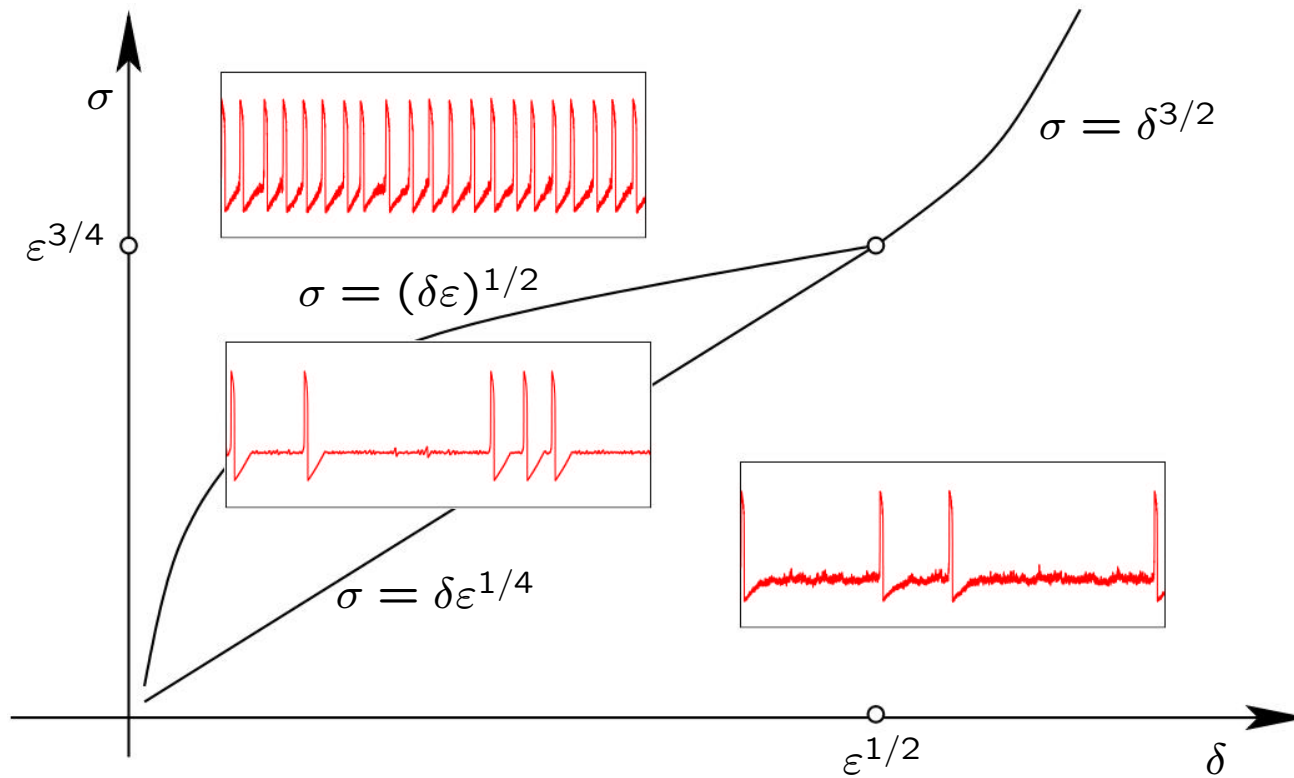
- ▷ $\delta > \sqrt{\varepsilon}$: equilibrium (δ, δ^2) is a node, effectively 1D problem
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 - $\sigma \gg \delta^{3/2}$: repeated spikes
- ▷ $\delta < \sqrt{\varepsilon}$: equilibrium (δ, δ^2) is a focus. Two-dimensional problem



Noise-induced MMOs

[D. Landon, PhD thesis, in progress]

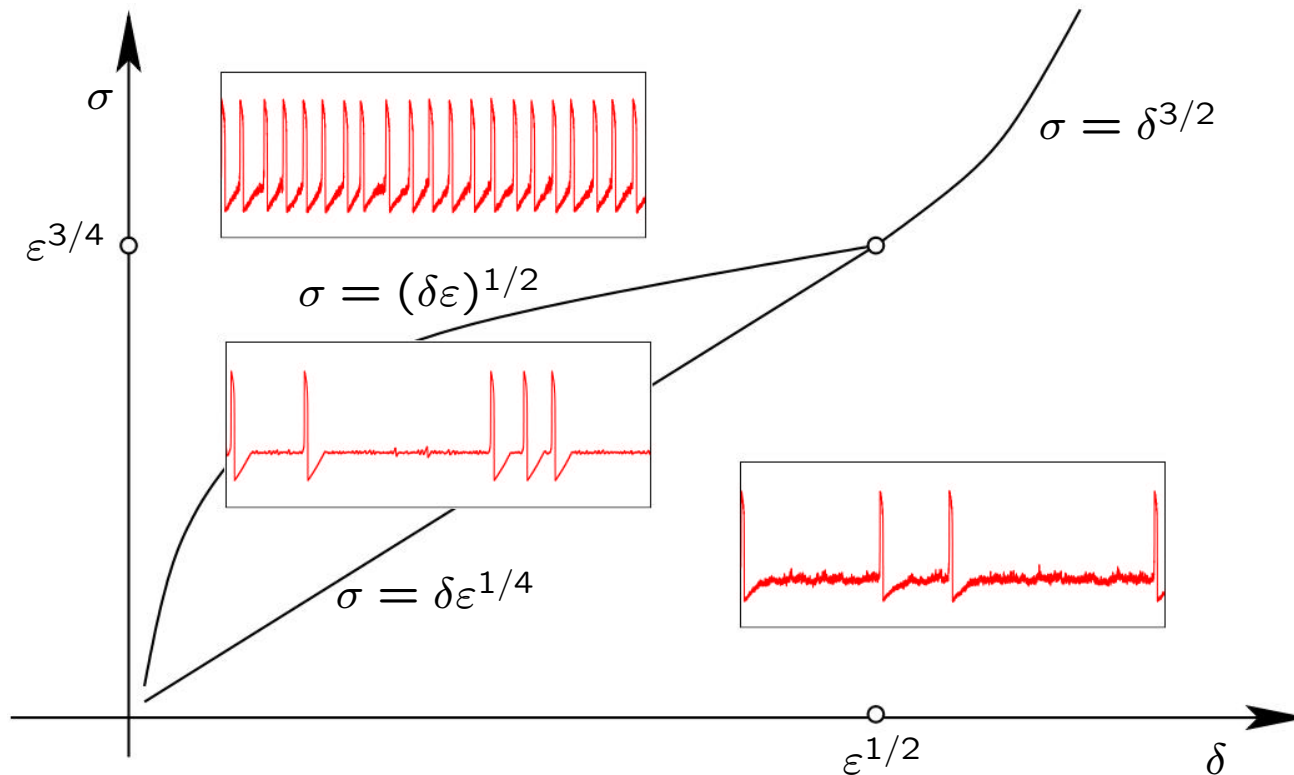
Conjectured bifurcation diagram [Muratov and Vanden Eijnden (2007)] :



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