Chasse aux canards en environnement bruité

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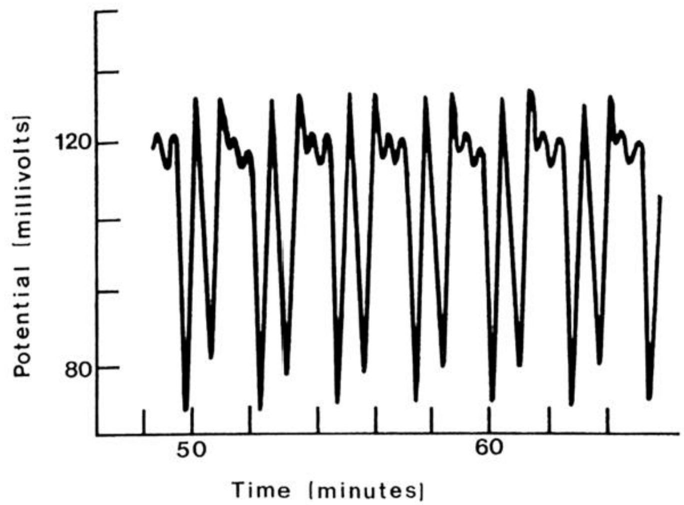
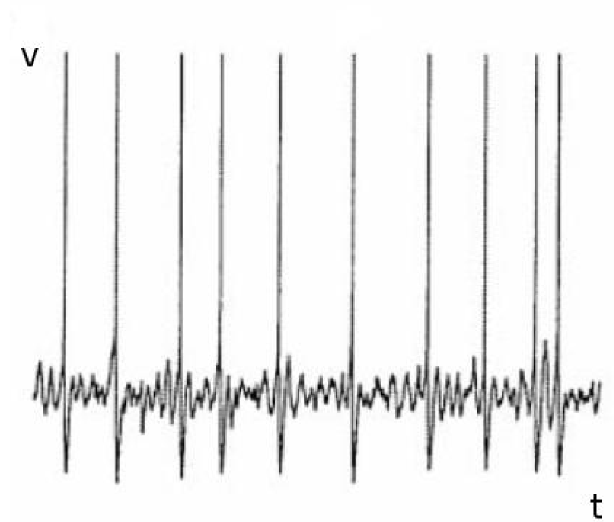
Projet ANR MANDy, Mathematical Analysis of Neuronal Dynamics

Nice, Laboratoire Dieudonné, 11 février 2011

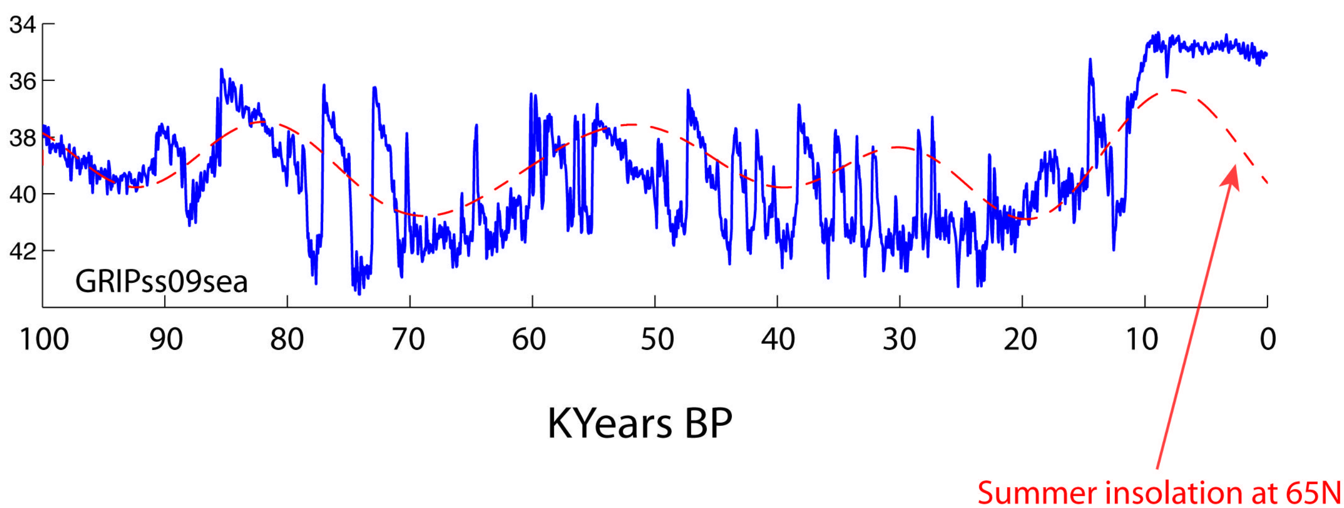
Oscillations in natural systems



Belousov-Zhabotinsky reaction [Hudson 79]

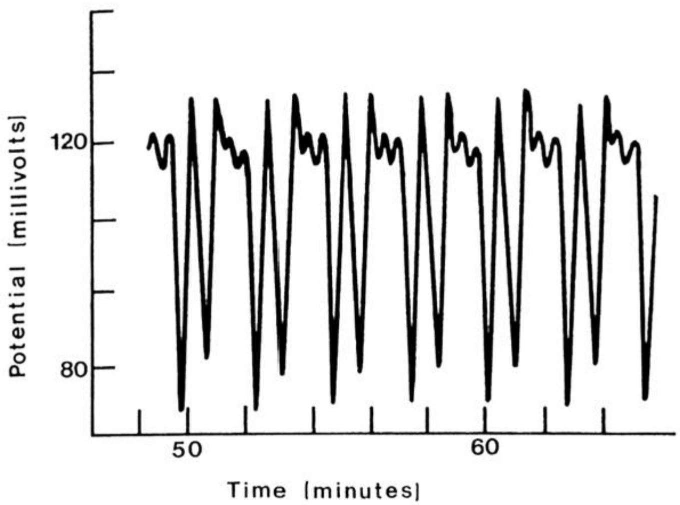


Stellate cells [Dickson 00]



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

Oscillations in natural systems



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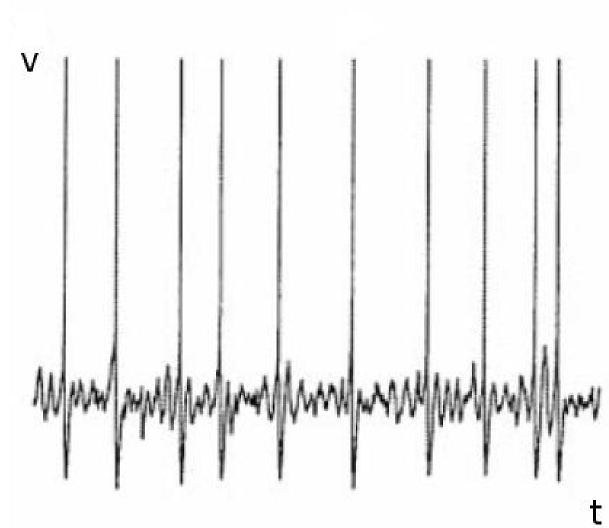

Stellate cells [Dickson 00]

- ▷ 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

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

$$\begin{aligned} \dot{x} &= y + x - \tfrac{1}{3}x^3 \\ \dot{y} &= -\varepsilon x \end{aligned} \quad \overset{t \mapsto \varepsilon t}{\Longleftrightarrow} \quad \begin{aligned} \varepsilon \dot{x} &= y + x - \tfrac{1}{3}x^3 \\ \dot{y} &= -x \end{aligned}$$

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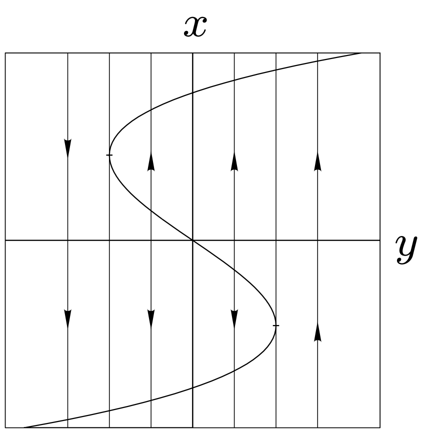

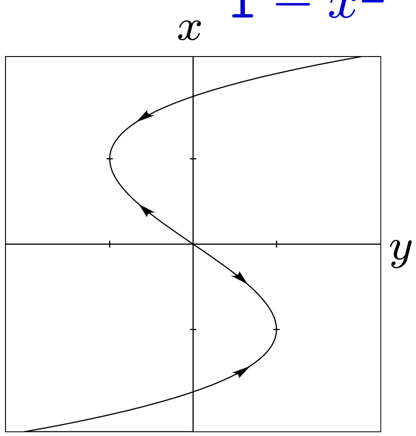

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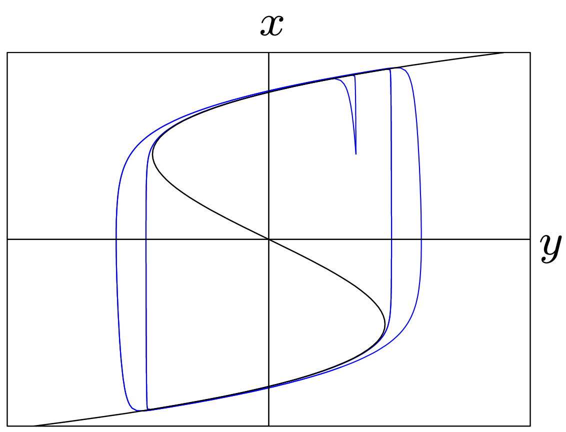
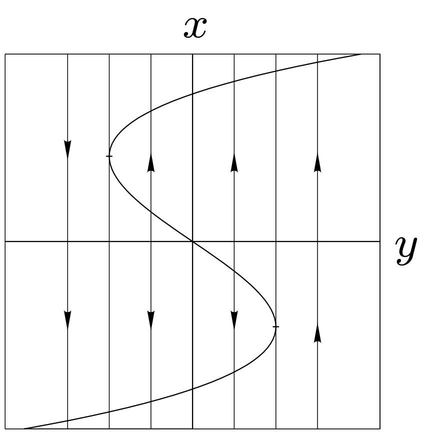
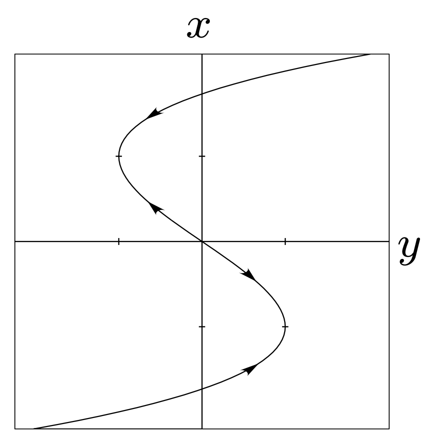


Relaxation oscillations

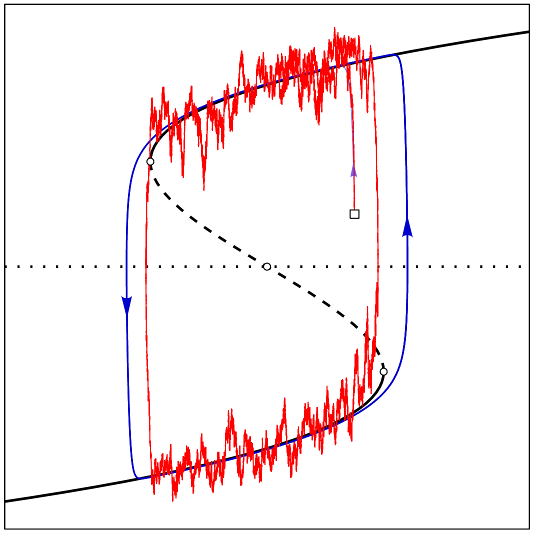




Effect of noise on the Van der Pol oscillator

$$\mathrm{d}x_t = \left[y_t + x_t - \frac{x_t^3}{3}\right]\mathrm{d}t + \sigma\,\mathrm{d}W_t$$

$$\mathrm{d}y_t = -\varepsilon x_t\,\mathrm{d}t$$



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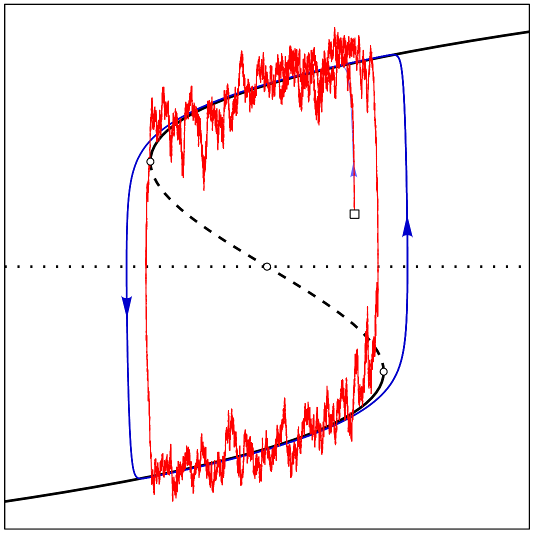
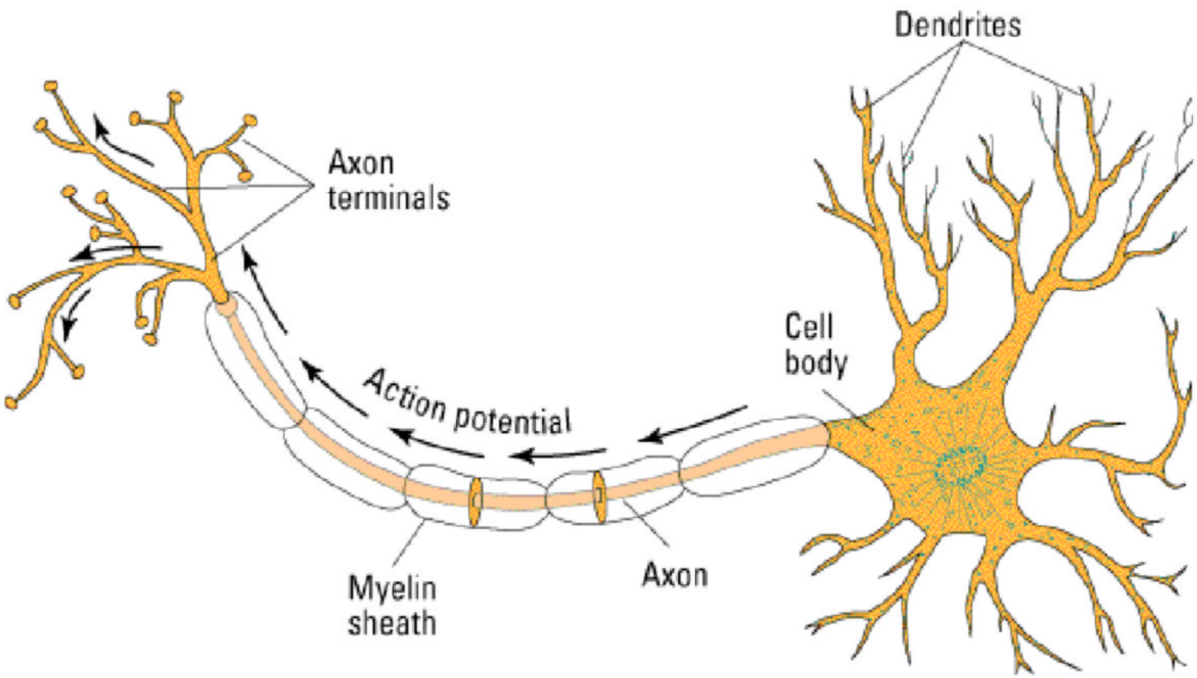


Theorem [B & Gentz 2006]

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

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)

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

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

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

▷ $i \in \{\mathsf{Na}^+, \mathsf{K}^+, \dots\}$ describes different types of ion channels

▷ $\varphi_i^*(v), \chi_i^*(v)$ sigmoïdal 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)

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

Conductance-based models for membrane potential

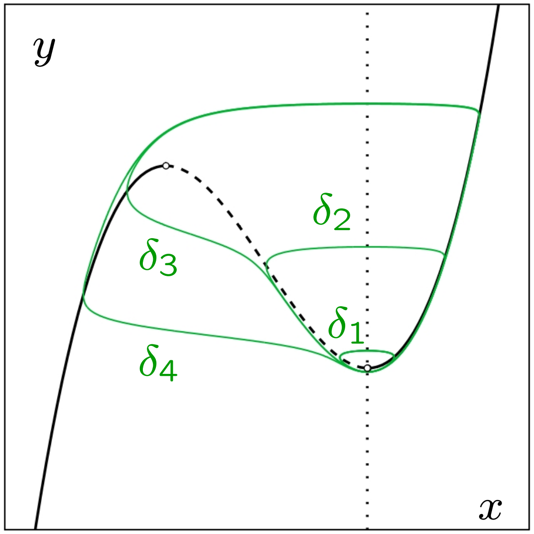
Fitzhugh–Nagumo model (1962)

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

The canard (french duck) phenomenon

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

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



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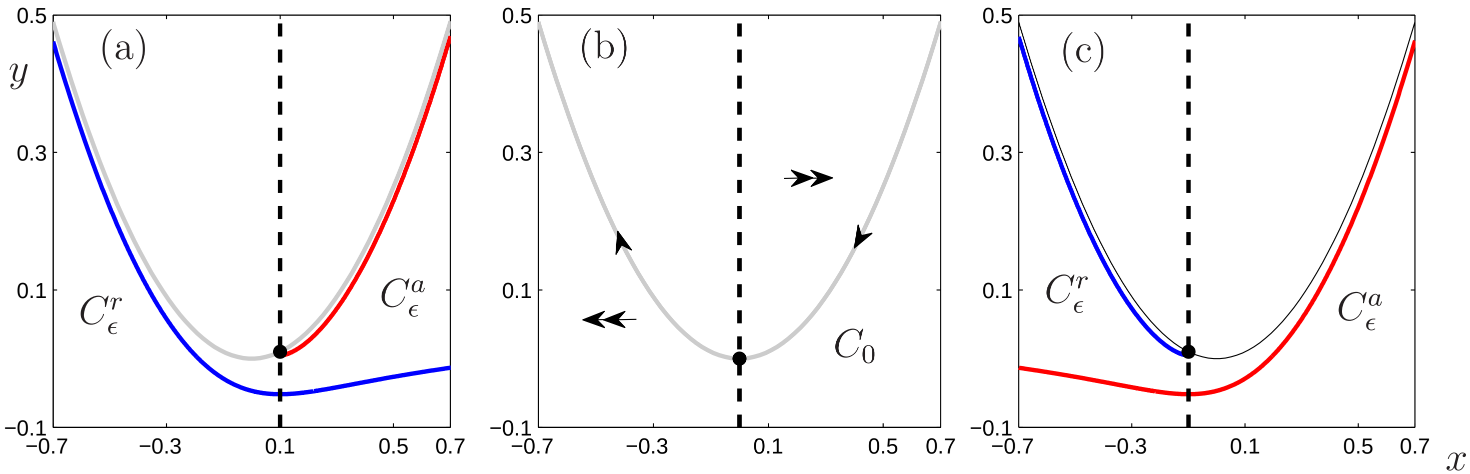
The canard (french duck) phenomenon

Normal form near fold point

$$\varepsilon\dot{x} = y - x^2$$
$$\dot{y} = \delta - x$$

(+ higher-order terms)



Folded node singularity

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

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

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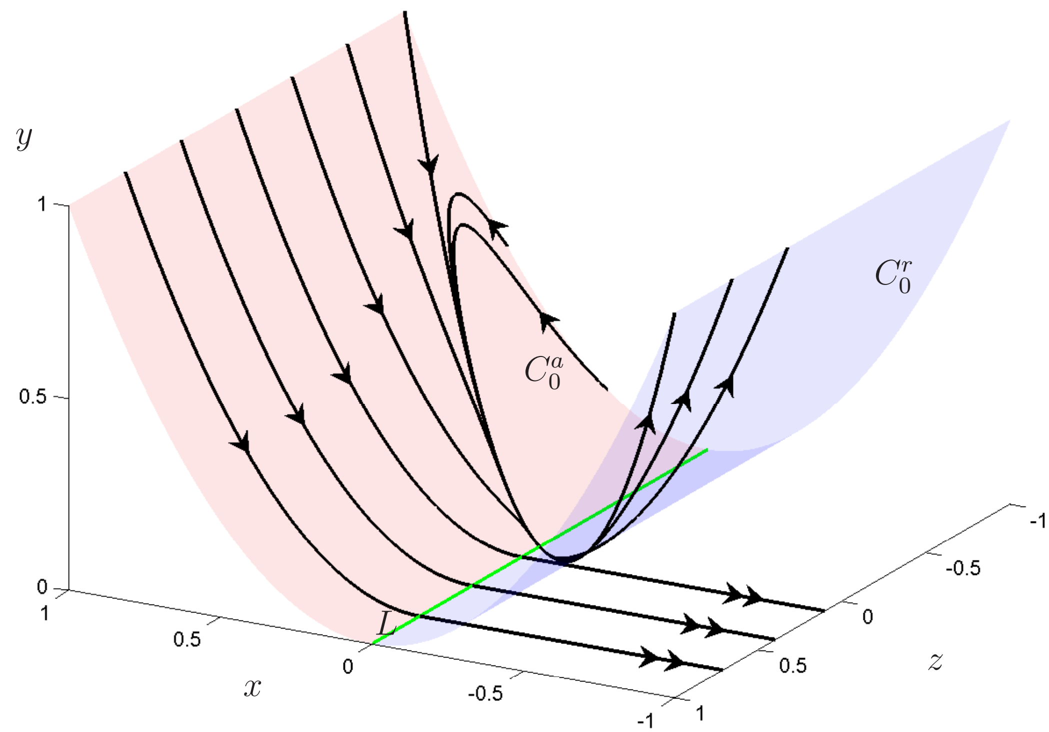
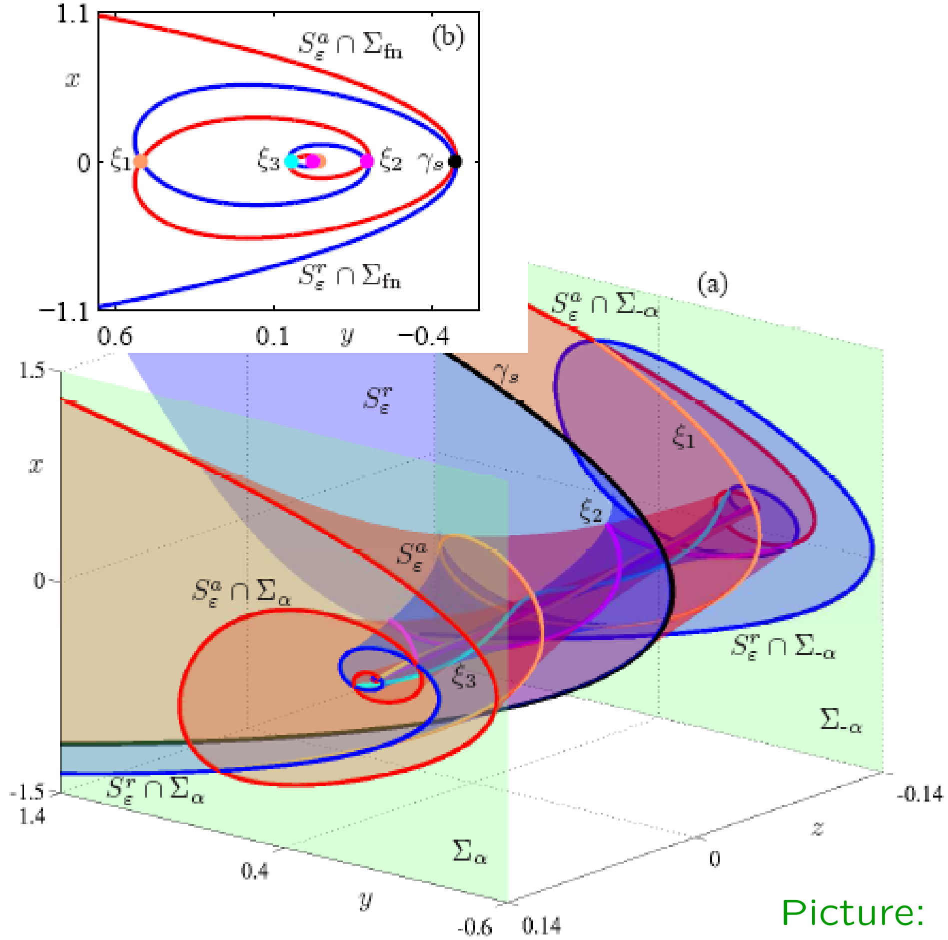
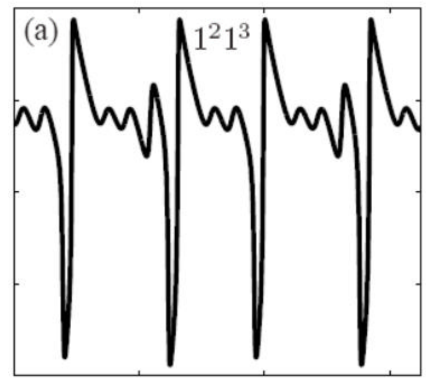


Folded node singularity

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



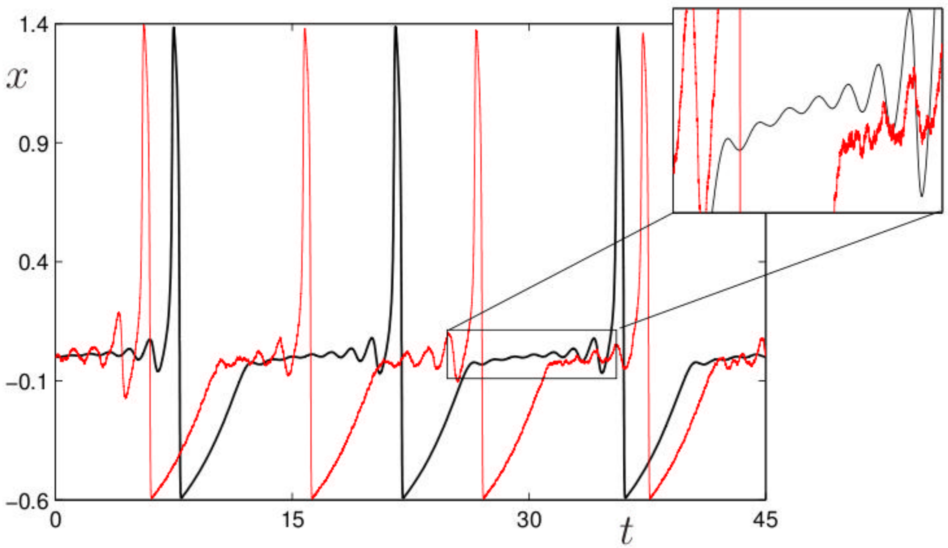


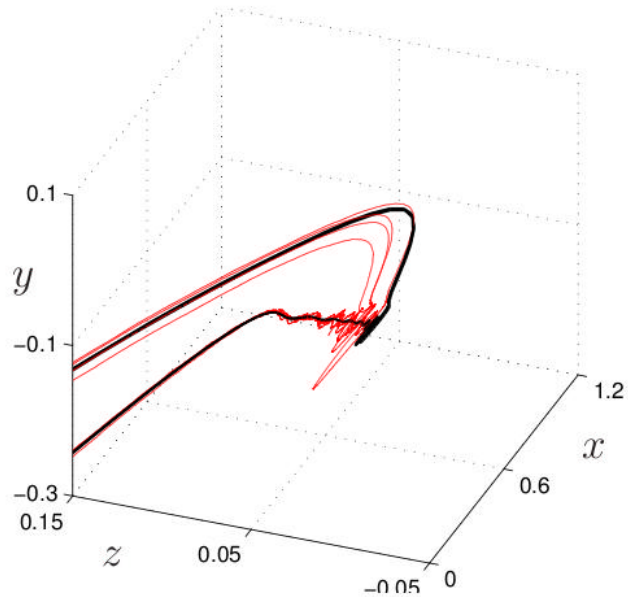
Mixed-mode oscillations (MMOs)

Picture: Mathieu Desroches

Effect of noise

$$\mathrm{d}x_t = \frac{1}{\varepsilon}(y_t - x_t^2)\,\mathrm{d}t + \frac{\sigma}{\sqrt{\varepsilon}}\,\mathrm{d}W_t^{(1)}$$
$$\mathrm{d}y_t = [-(\mu+1)x_t - z_t]\,\mathrm{d}t + \sigma\,\mathrm{d}W_t^{(2)}$$
$$\mathrm{d}z_t = \frac{\mu}{2}\,\mathrm{d}t$$





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

Covariance tubes

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

$$\mathrm{d}\zeta_t = A(t)\zeta_t \,\mathrm{d}t + \sigma \,\mathrm{d}W_t \qquad A(t) = \begin{pmatrix} -2x_t^{\text{det}} & 1 \\ -(1+\mu) & 0 \end{pmatrix}$$

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

Gaussian process with covariance matrix

$$\mathrm{Cov}(\zeta_t) = \sigma^2 V(t) \qquad V(t) = U(t)V(0)U(t)^{-1} + \int_0^t U(t,s)U(t,s)^T \,\mathrm{d}s$$

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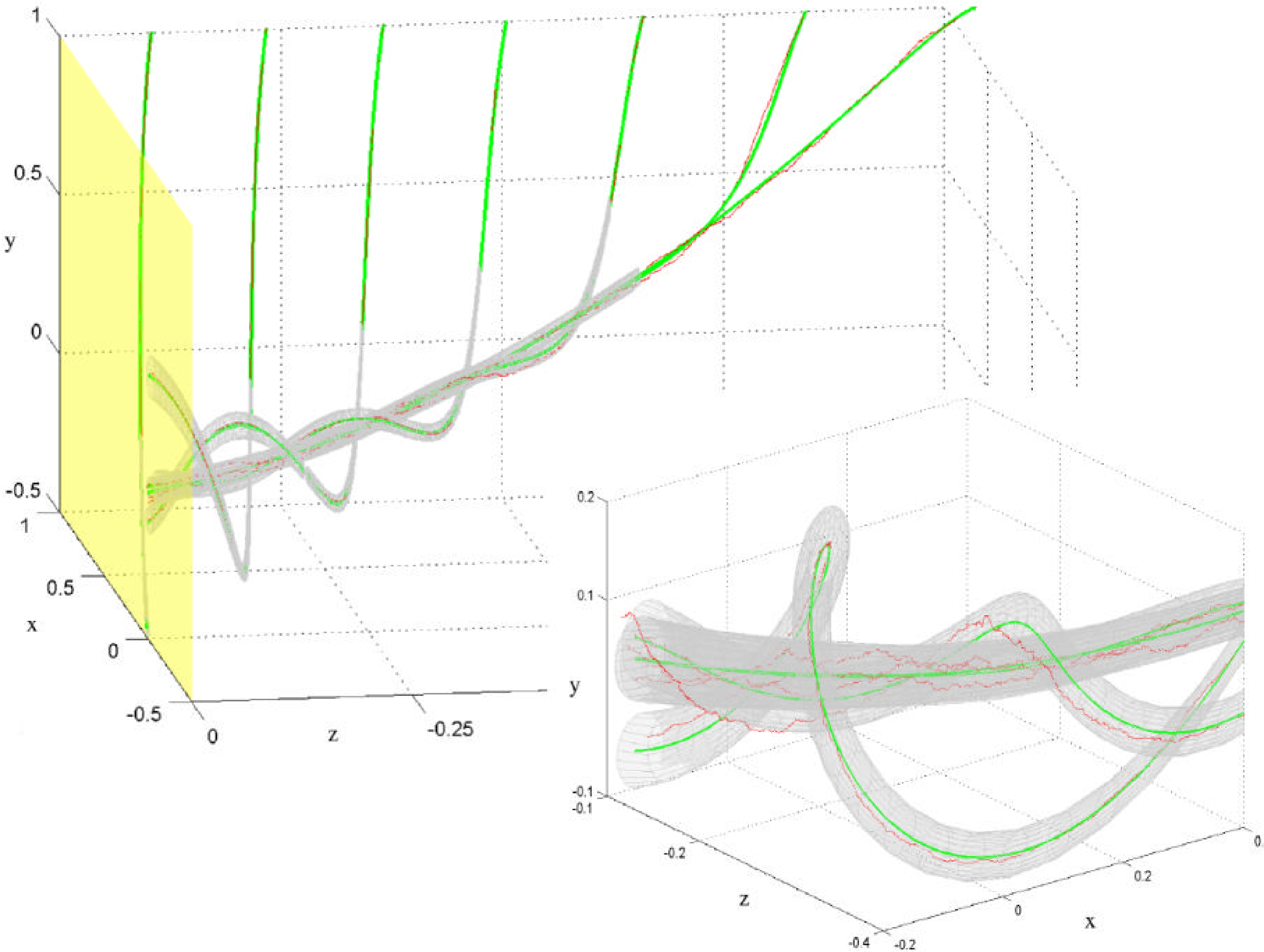
Covariance tube :

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

Theorem [B, Gentz, Kuehn 2010]

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

$$\mathbb{P}\Bigl\{ \tau_{\mathcal{B}(h)} < t \Bigr\} \leqslant C(t)\,\mathrm{e}^{-\kappa h^2/2\sigma^2}$$



9-b

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Sketch of proof :

- ▷ (Sub)martingale : $\{M_t\}_{t\geqslant 0}$, $\mathbb{E}\{M_t|M_s\} = (\geqslant) M_s$ for $t \geqslant s \geqslant 0$
- ▷ Doob's submartingale inequality : $\mathbb{P}\Big\{\sup\limits_{0\leqslant t\leqslant T} M_t \geqslant L\Big\} \leqslant \dfrac{1}{L}\mathbb{E}[M_T]$

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- ▷ Linear equation : $\zeta_t = \sigma \displaystyle\int_0^t U(t,s)\,\mathrm{d}W_s$ 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 : $\mathrm{d}\zeta_t = A(t)\zeta_t\,\mathrm{d}t + b(\zeta_t,t)\,\mathrm{d}t + \sigma\,\mathrm{d}W_t$

$$\zeta_t = \sigma\int_0^t U(t,s)\,\mathrm{d}W_s + \int_0^t U(t,s)b(\zeta_s,s)\,\mathrm{d}s$$

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

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 $\mathrm{e}^{-(2k+1)^2\mu}$
- ▷ 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
- ▷ $V(t) = \sigma^{-2}\,\mathrm{Cov}(\zeta_t)$ satisfies fast-slow equation

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

which can be studied by singular perturbation theory.
Note : Hopf bifurcation at $z = 0$!

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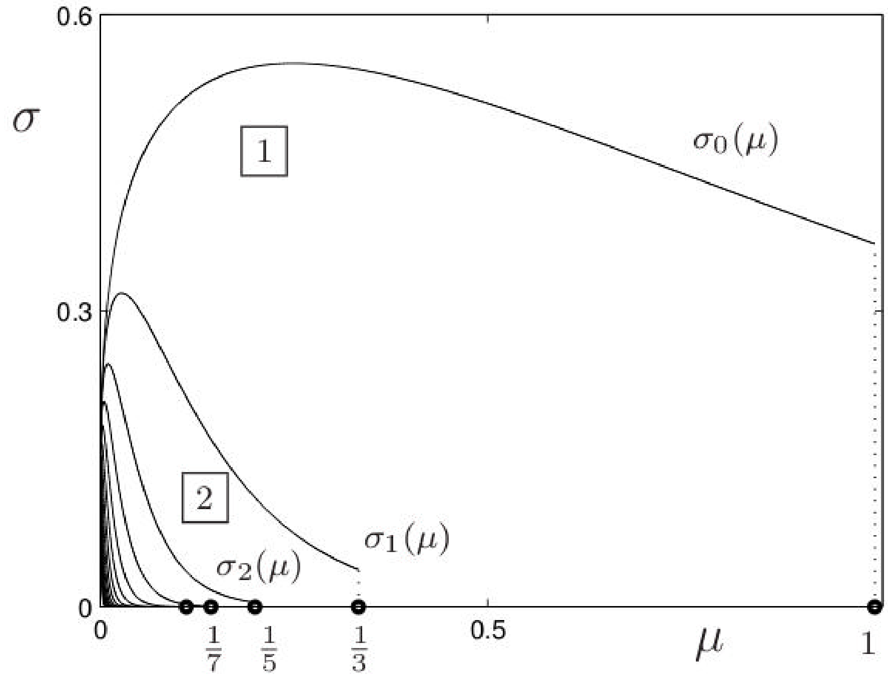
Corollary

Let

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

Canards with $\frac{2k+1}{4}$ oscillations become indistinguishable from noisy fluctuations for $\sigma > \sigma_k(\mu)$



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 $e^{-(2k+1)^2\mu}$
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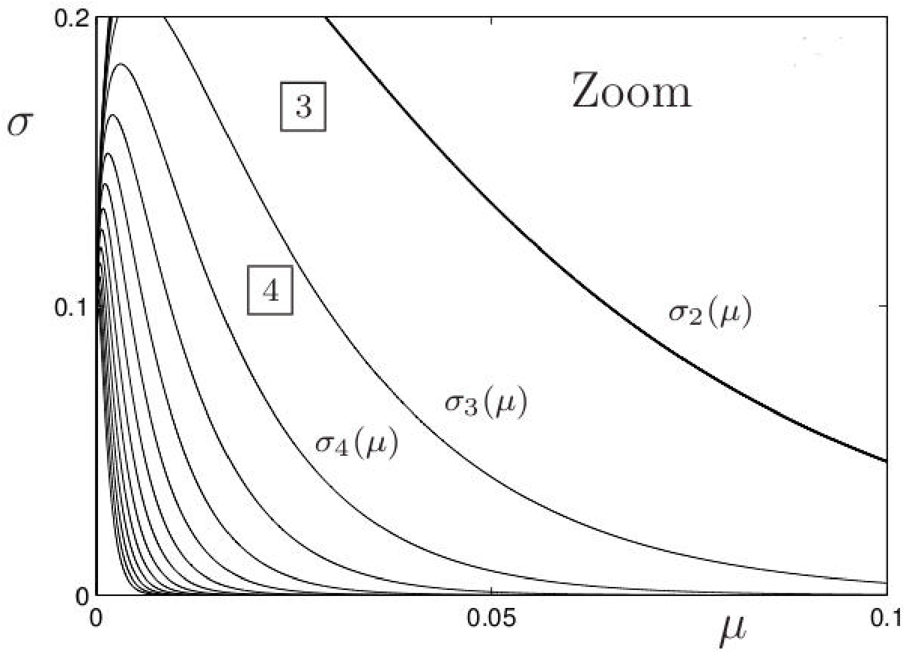

Early transitions

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 $\sigma|\log\sigma|^{\gamma_1} \leqslant \mu^{3/4}$ probability of leaving $\mathcal{D}$ after $z_t = z$ satisfies

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

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

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

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 $\sigma|\log\sigma|/\sqrt{z} \leqslant \|\zeta\| \leqslant \sqrt{z}$:
  use polar coordinates and averaging
- ▷ To combine the two regimes : use Laplace transforms

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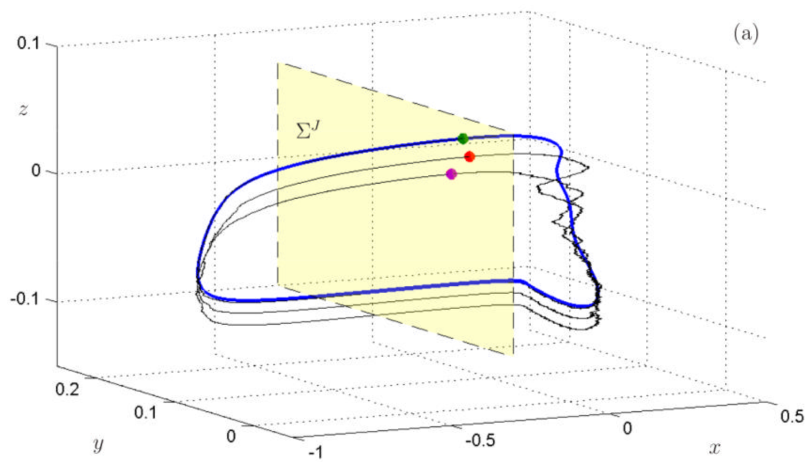
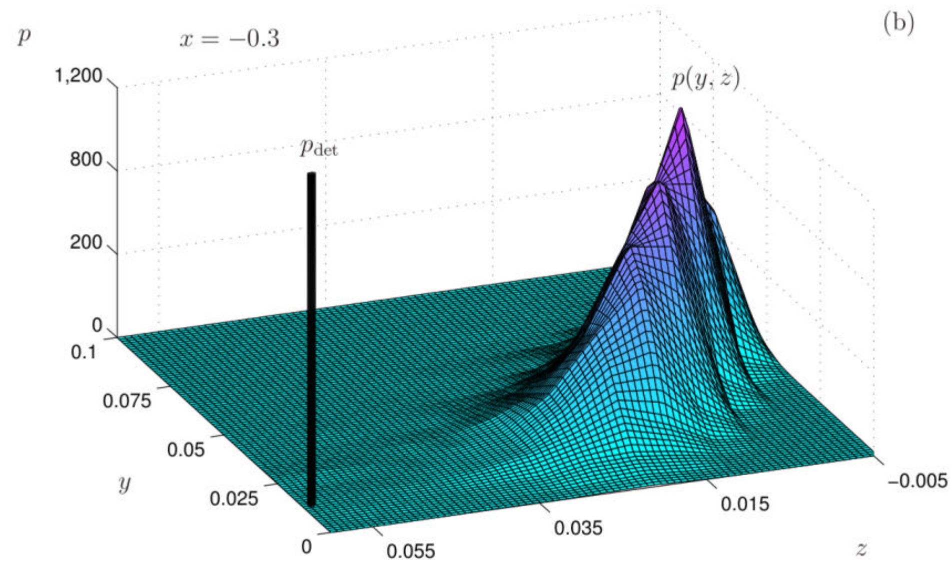
$$\mathbb{P}\Big\{z_{\tau_{\mathcal{D}}} > z\Big\} \leqslant C|\log\sigma|^{\gamma_2}\,\mathrm{e}^{-\kappa(z^2-\mu)/(\mu|\log\sigma|)}$$

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





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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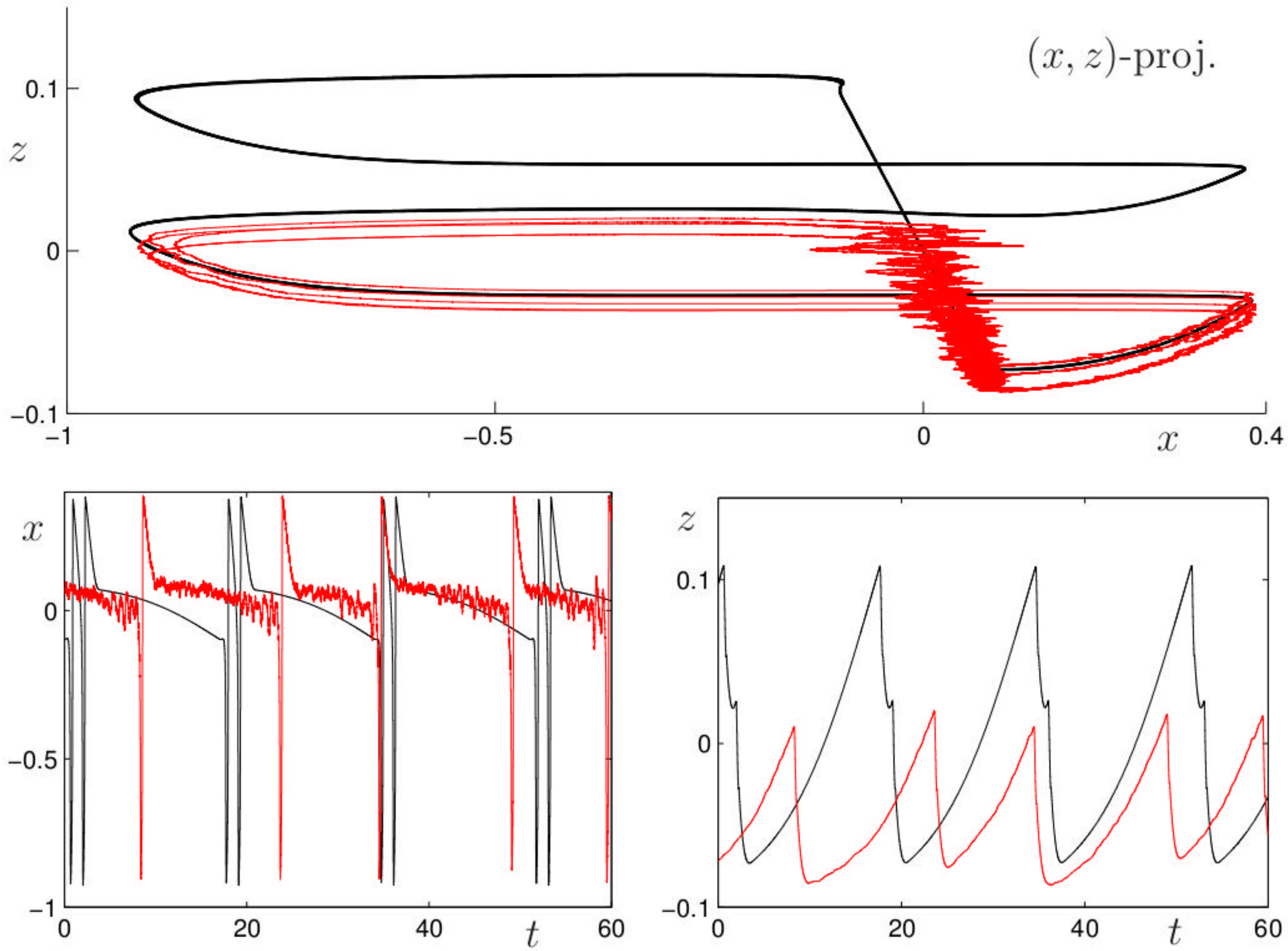

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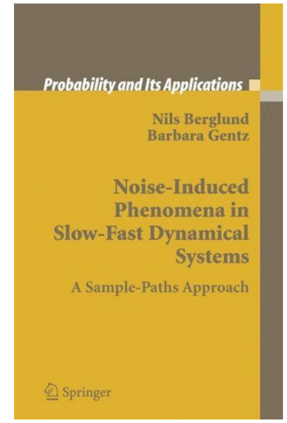

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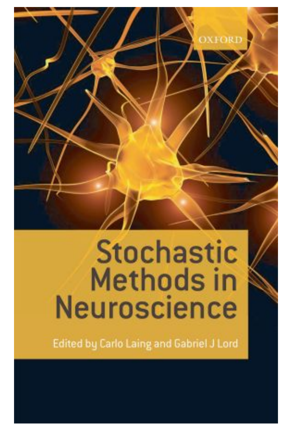

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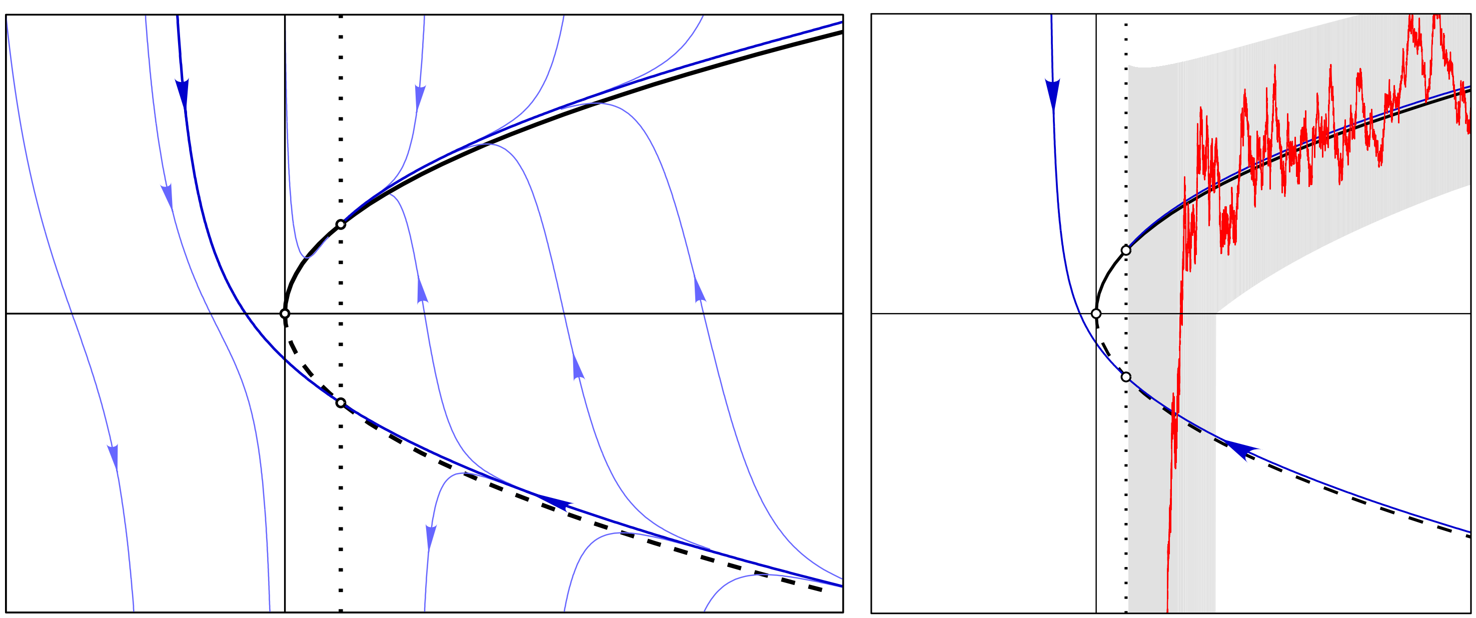
Noise-induced MMOs [D. Landon, PhD thesis, in progress]

FitzHugh–Nagumo, normal form near bifurcation point:

$$\begin{aligned} \mathrm{d}x_t &= (y_t - x_t^2)\,\mathrm{d}t + \sigma\,\mathrm{d}W_t \\ \mathrm{d}y_t &= \varepsilon(\delta - x_t)\,\mathrm{d}t \end{aligned}$$

▷ $\delta > \sqrt{\varepsilon}$: 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



Noise-induced MMOs [D. Landon, PhD thesis, in progress]

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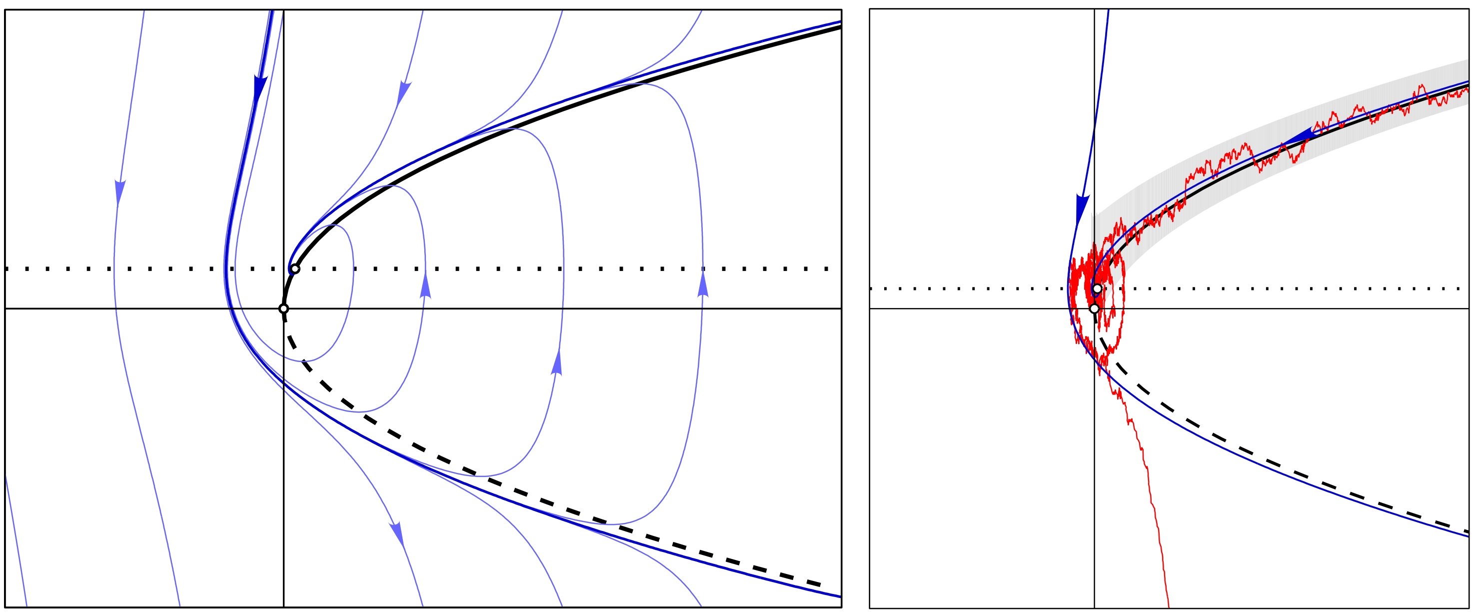
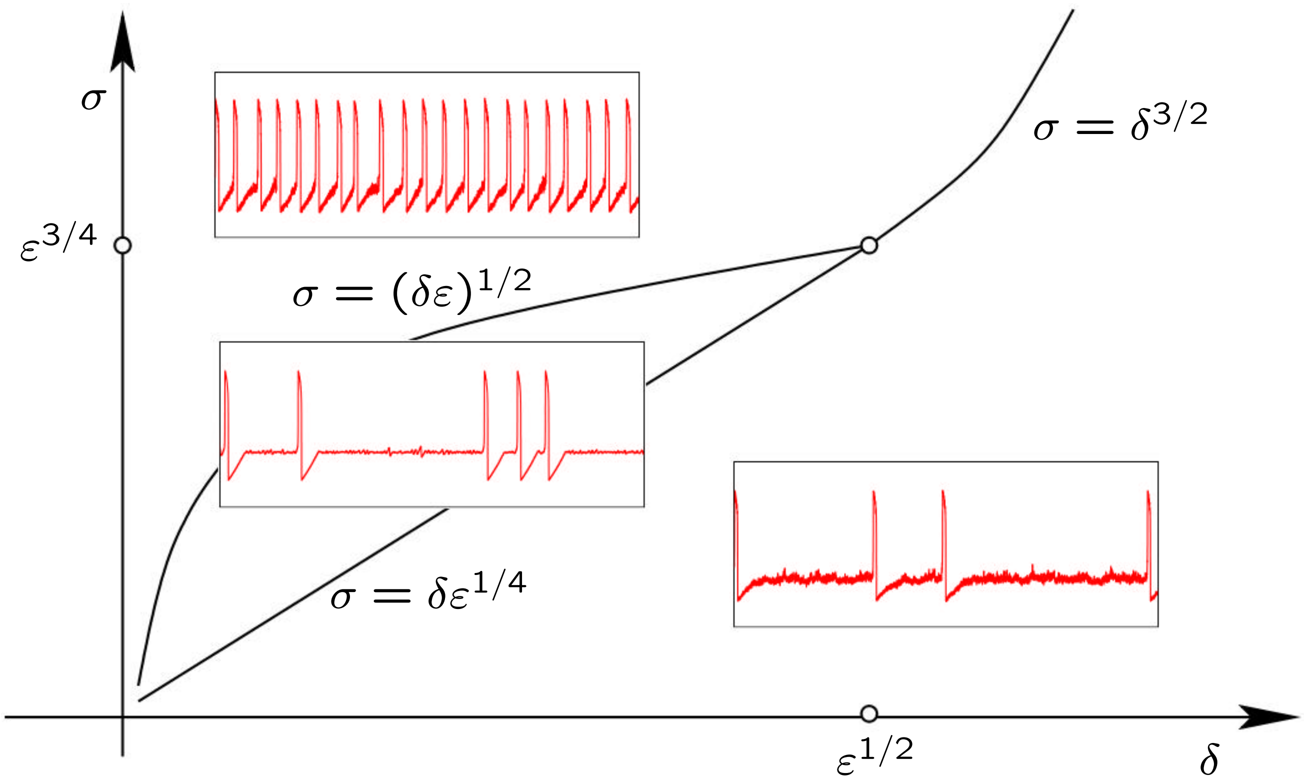
- $\sigma \ll \delta^{3/2}$: rare spikes, approx. exponential interspike times
- $\sigma \gg \delta^{3/2}$: repeated spikes

▷ $\delta < \sqrt{\varepsilon}$: equilibrium (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)] :



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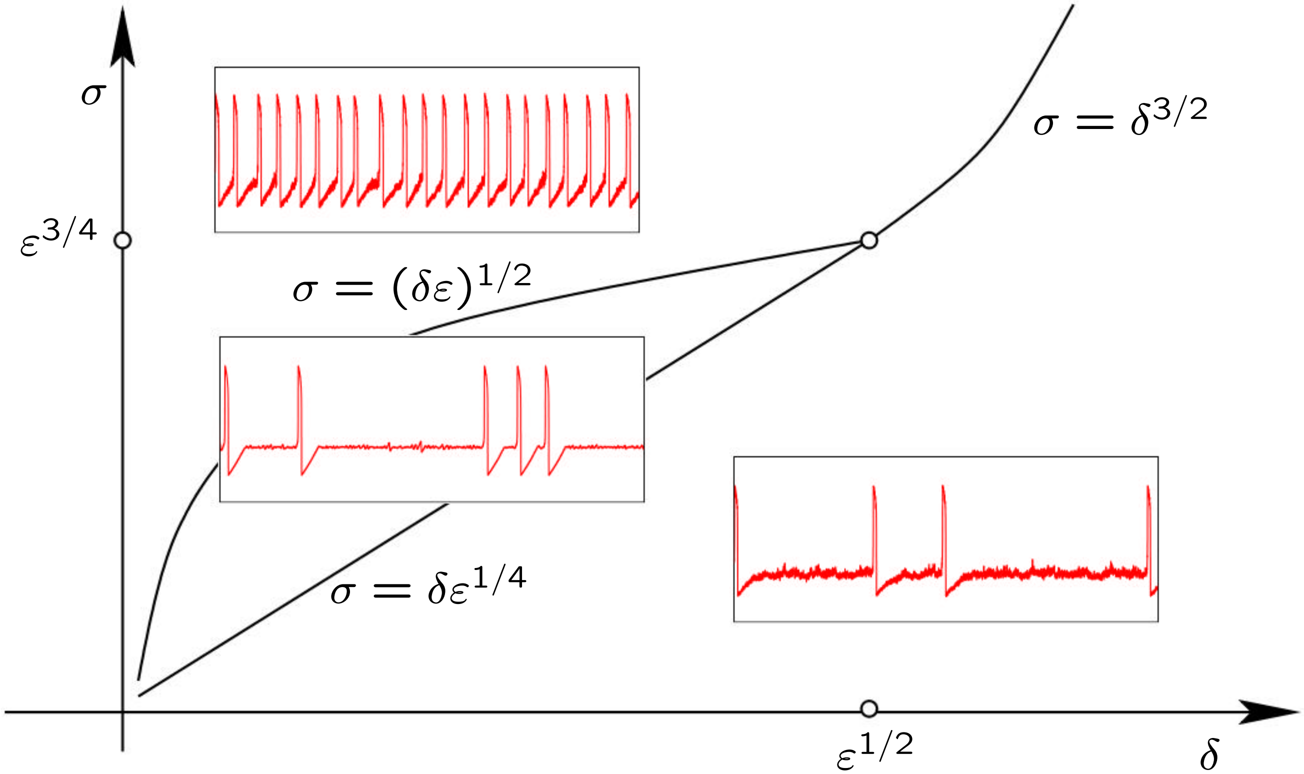

Work in progress :

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