

Oscillations multimodales et chasse aux canards stochastiques

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[Christian Kuehn](#) (Vienne), [Damien Landon](#) (Orléans)

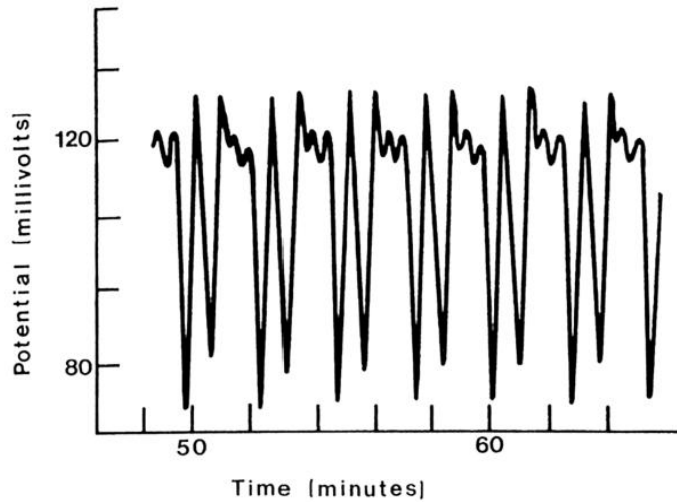
Projet ANR [MANDy](#), Mathematical Analysis of Neuronal Dynamics

Séminaire de Probabilités

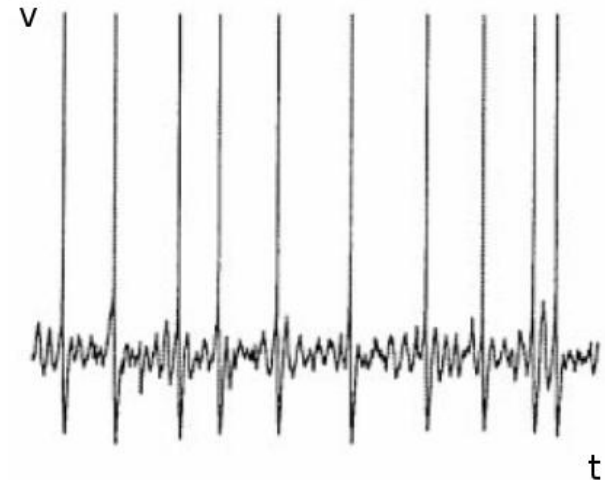
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7 février 2012

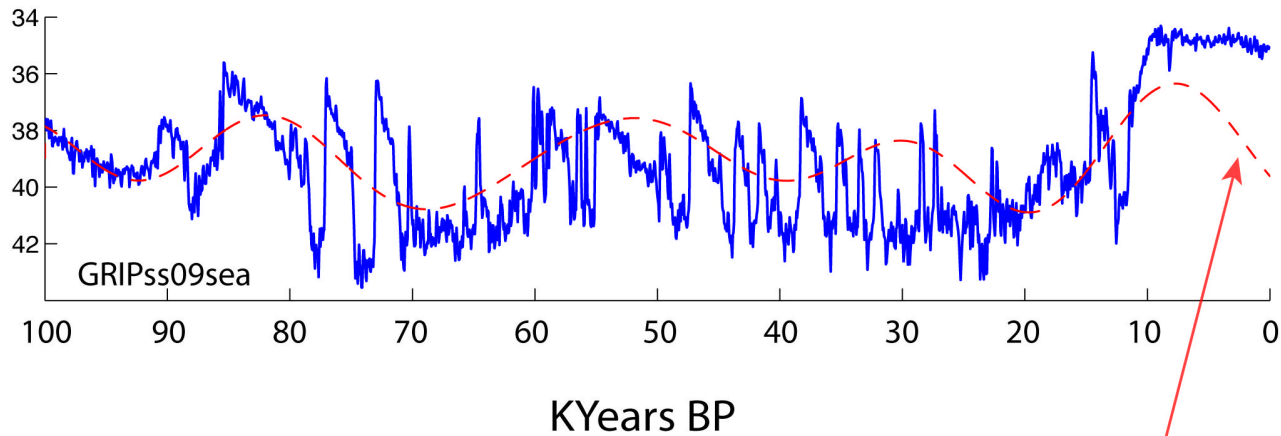
Mixed-mode oscillations (MMOs)



Belousov-Zhabotinsky reaction [Hudson 79]

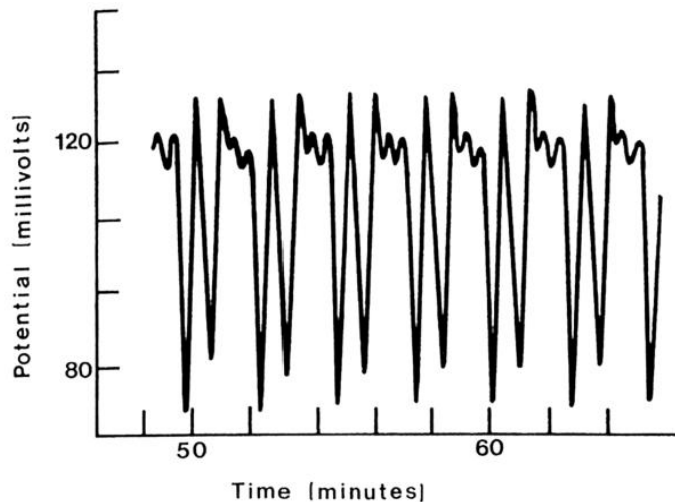


Stellate cells [Dickson 00]

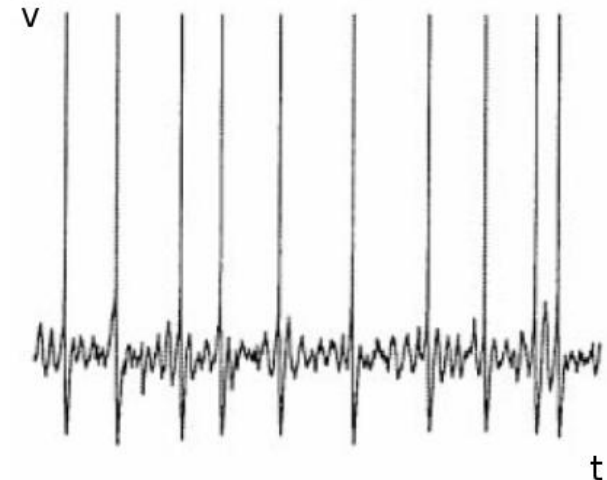


Mean temperature based on ice core measurements [Johnson et al 01]

Mixed-mode oscillations (MMOs)



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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

Noise may also induce oscillations not present in deterministic case

Part I

Where noise creates MMOs

Deterministic FitzHugh–Nagumo (FHN) equations

Consider the FHN equations in the form

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

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

- ▷ $x \propto$ membrane potential of neuron
- ▷ $y \propto$ proportion of open ion channels (recovery variable)
- ▷ $\varepsilon \ll 1 \Rightarrow$ fast–slow system

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Stationary point $P = (a, a^3 - a)$

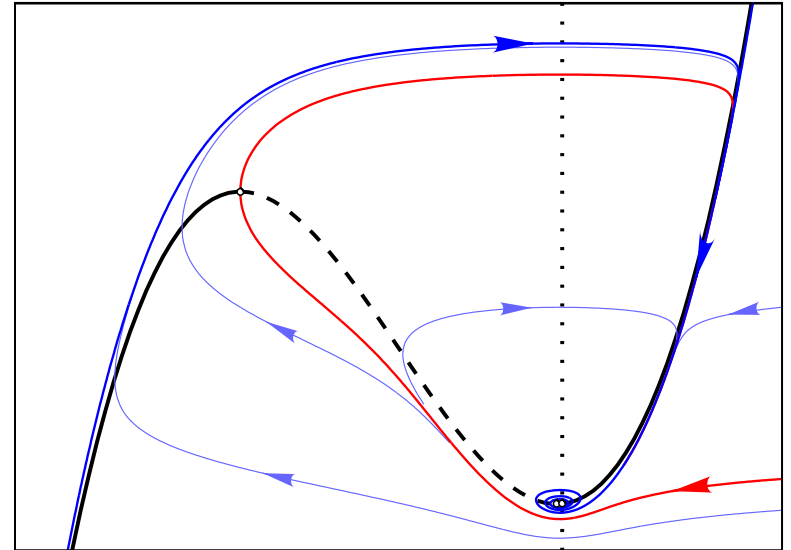
Linearisation has eigenvalues $\frac{-\delta \pm \sqrt{\delta^2 - \varepsilon}}{\varepsilon}$ where $\delta = \frac{3a^2 - 1}{2}$

- ▷ $\delta > 0$: **stable** node ($\delta > \sqrt{\varepsilon}$) or focus ($0 < \delta < \sqrt{\varepsilon}$)
- ▷ $\delta = 0$: **singular Hopf bifurcation** [Erneux & Mandel '86]
- ▷ $\delta < 0$: **unstable** focus ($-\sqrt{\varepsilon} < \delta < 0$) or node ($\delta < -\sqrt{\varepsilon}$)

Deterministic FitzHugh–Nagumo (FHN) equations

$\delta > 0$:

- ▷ P is asymptotically stable
- ▷ the system is excitable
- ▷ one can define a separatrix



Stochastic FHN equations

$$dx_t = \frac{1}{\varepsilon} [x_t - x_t^3 + y_t] dt + \frac{\sigma_1}{\sqrt{\varepsilon}} dW_t^{(1)}$$

$$dy_t = [a - x_t] dt + \sigma_2 dW_t^{(2)}$$

- ▷ $W_t^{(1)}, W_t^{(2)}$: independent Wiener processes
- ▷ $0 < \sigma_1, \sigma_2 \ll 1, \sigma = \sqrt{\sigma_1^2 + \sigma_2^2}$

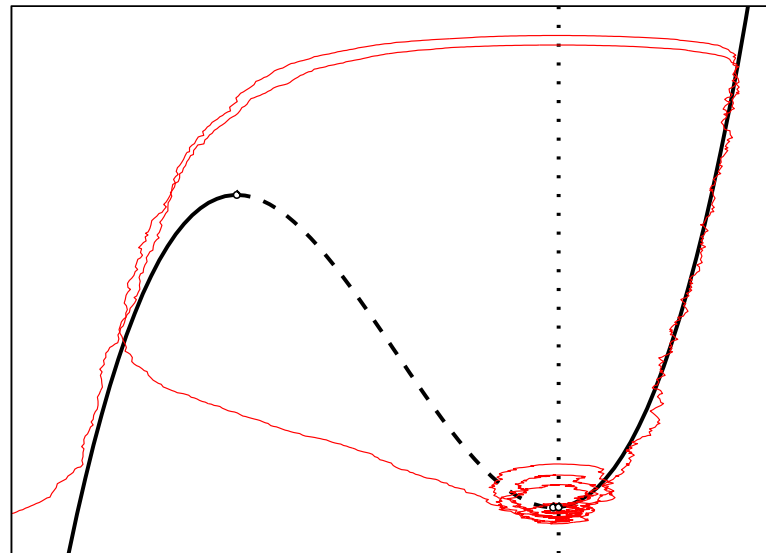
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$$\begin{aligned}\varepsilon &= 0.1 \\ \delta &= 0.02 \\ \sigma_1 &= \sigma_2 = 0.03\end{aligned}$$



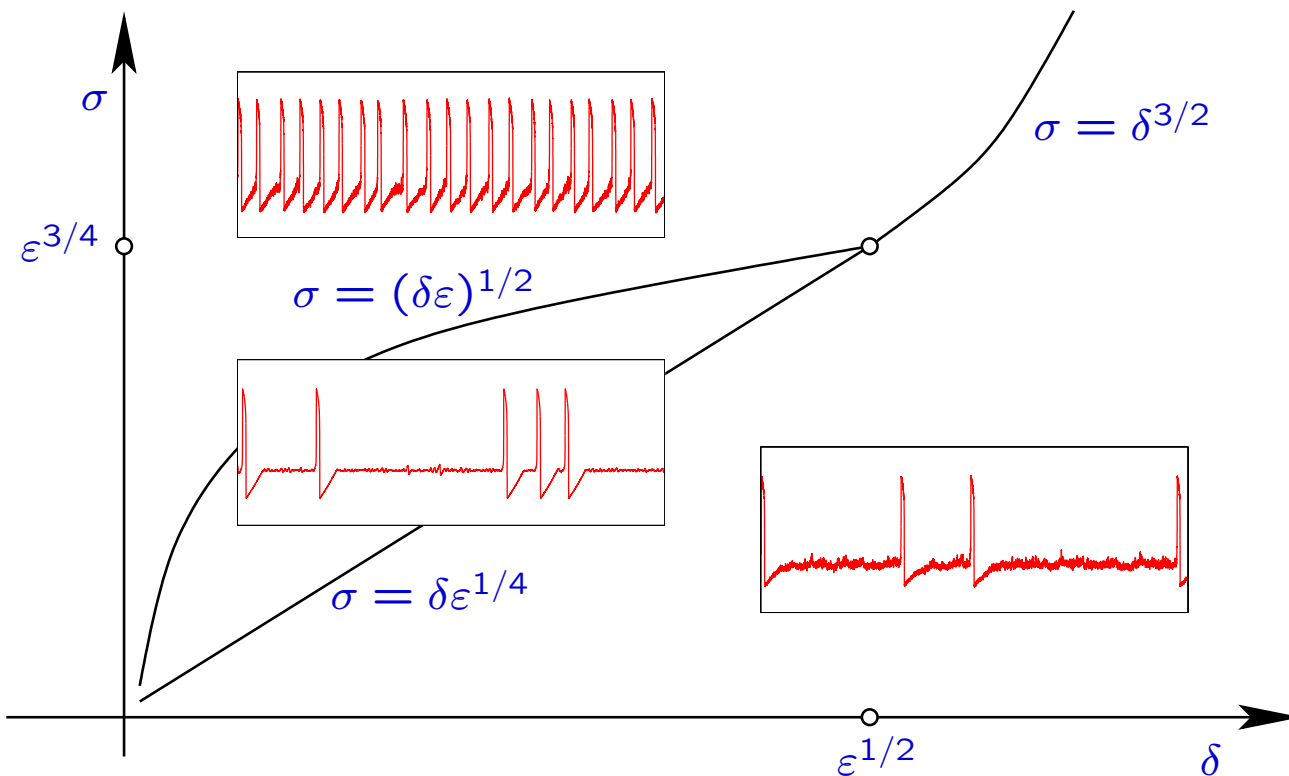
Some previous work

- ▷ Numerical: Kosmidis & Pakdaman '03, . . . , Borowski et al '11
- ▷ Moment methods: Tanabe & Pakdaman '01
- ▷ Approx. of Fokker–Planck equ: Lindner et al '99, Simpson & Kuske '11
- ▷ Large deviations: Muratov & Vanden Eijnden '05, Doss & Thieullen '09
- ▷ Sample paths near canards: Sowers '08

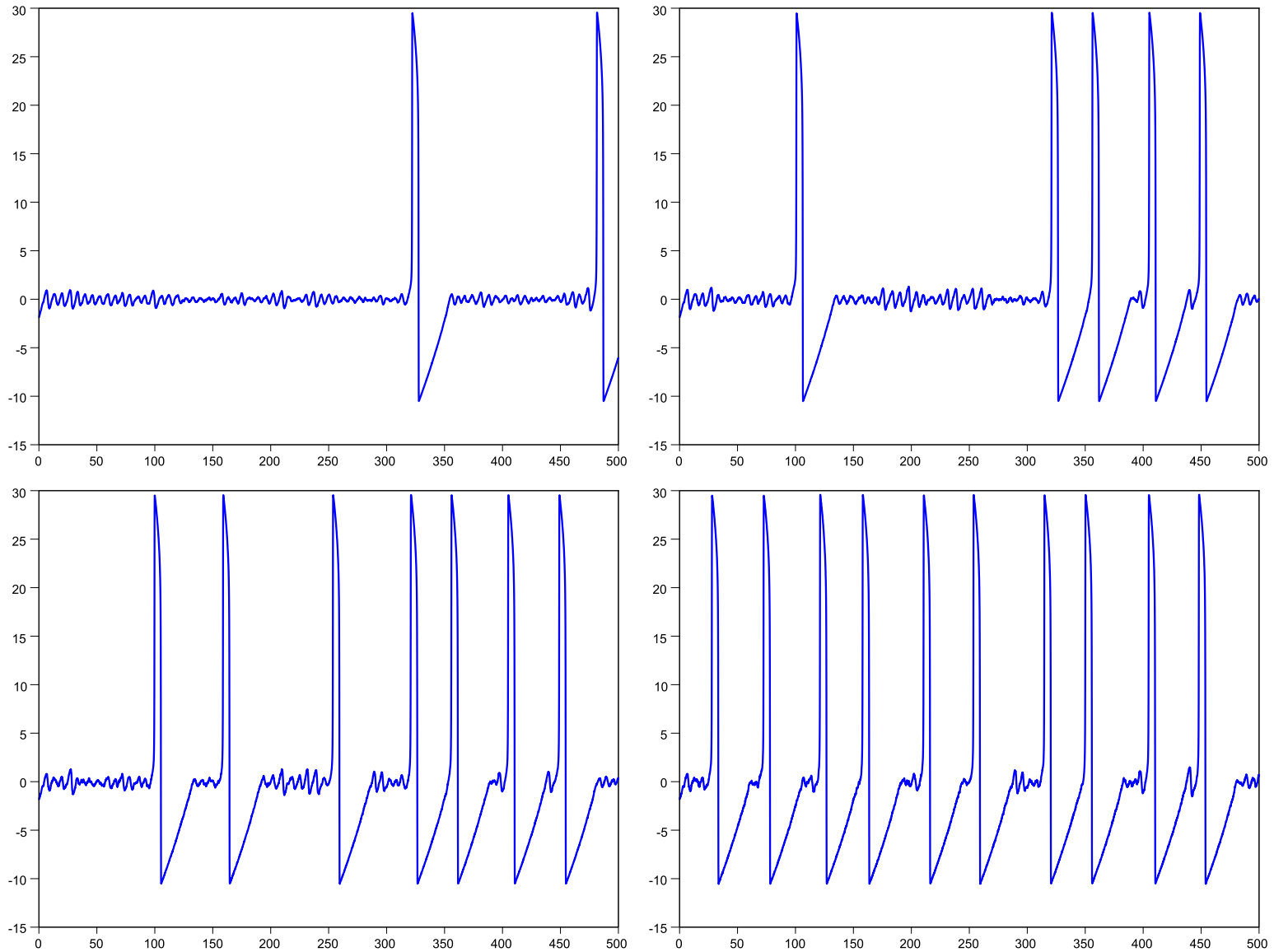
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Proposed “phase diagram” [Muratov & Vanden Eijnden '08]

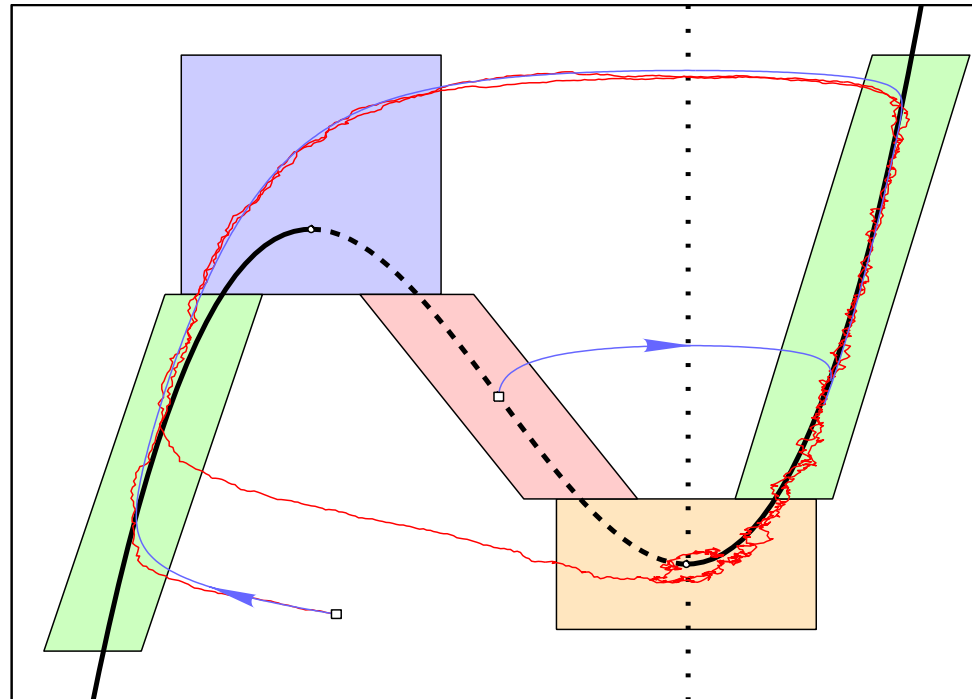


Intermediate regime: mixed-mode oscillations (MMOs)

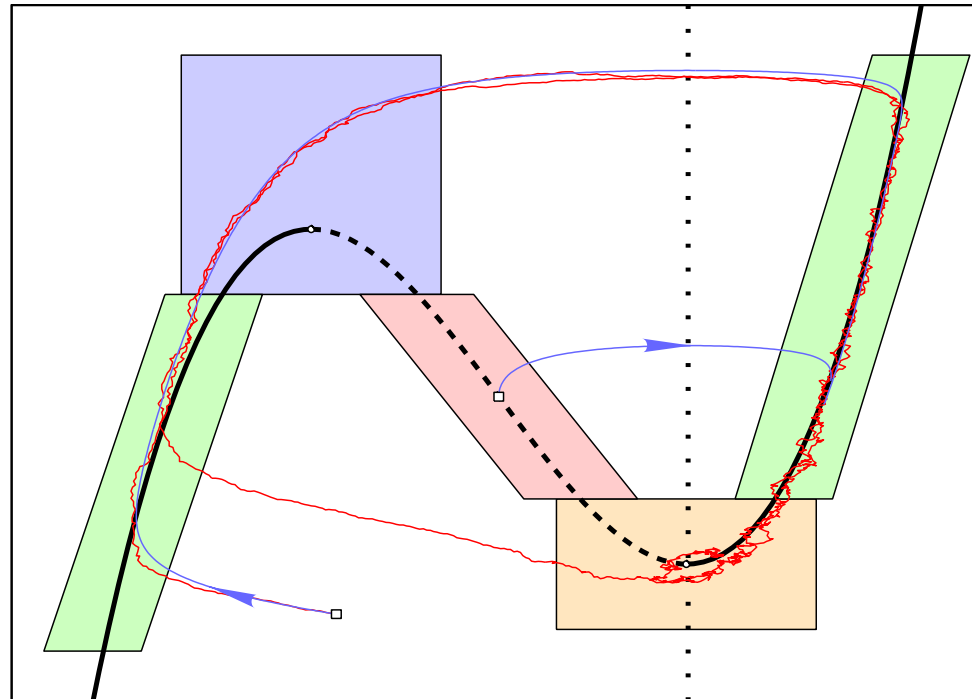


Time series $t \mapsto -x_t$ for $\varepsilon = 0.01$, $\delta = 3 \cdot 10^{-3}$, $\sigma = 1.46 \cdot 10^{-4}, \dots, 3.65 \cdot 10^{-4}$

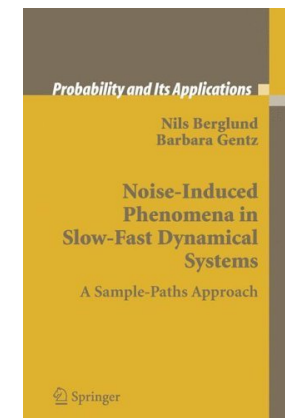
Precise analysis of sample paths



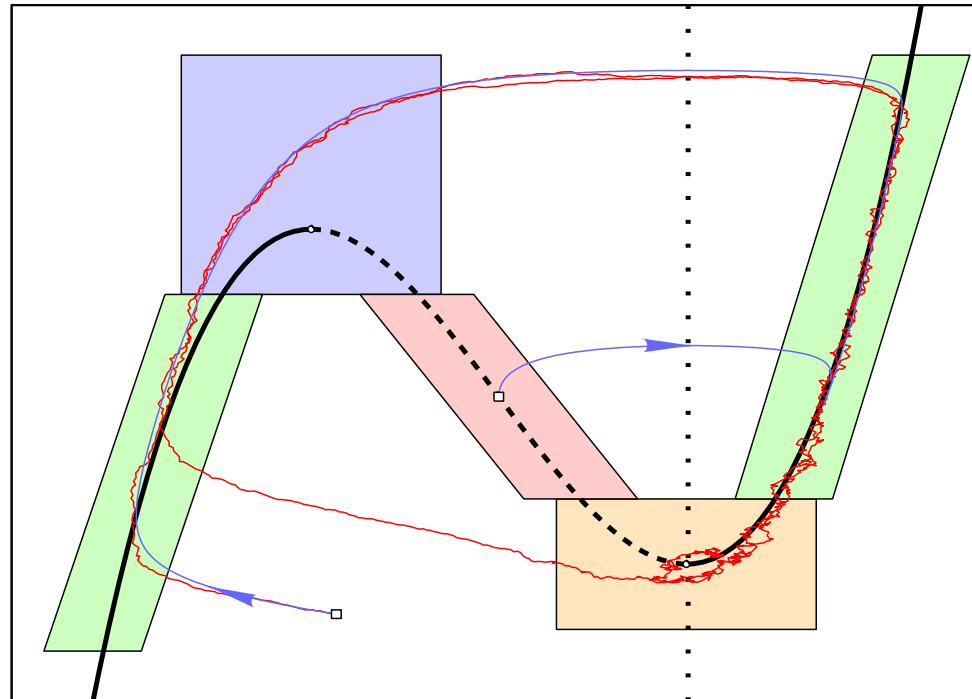
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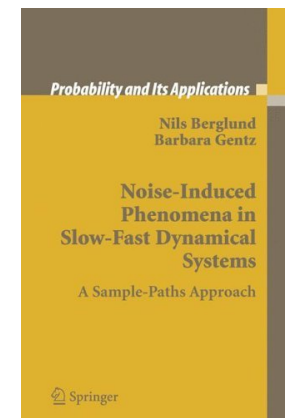
- ▷ Dynamics near **stable branch**, **unstable branch** and **saddle–node bifurcation**: already done in [B & Gentz '05]



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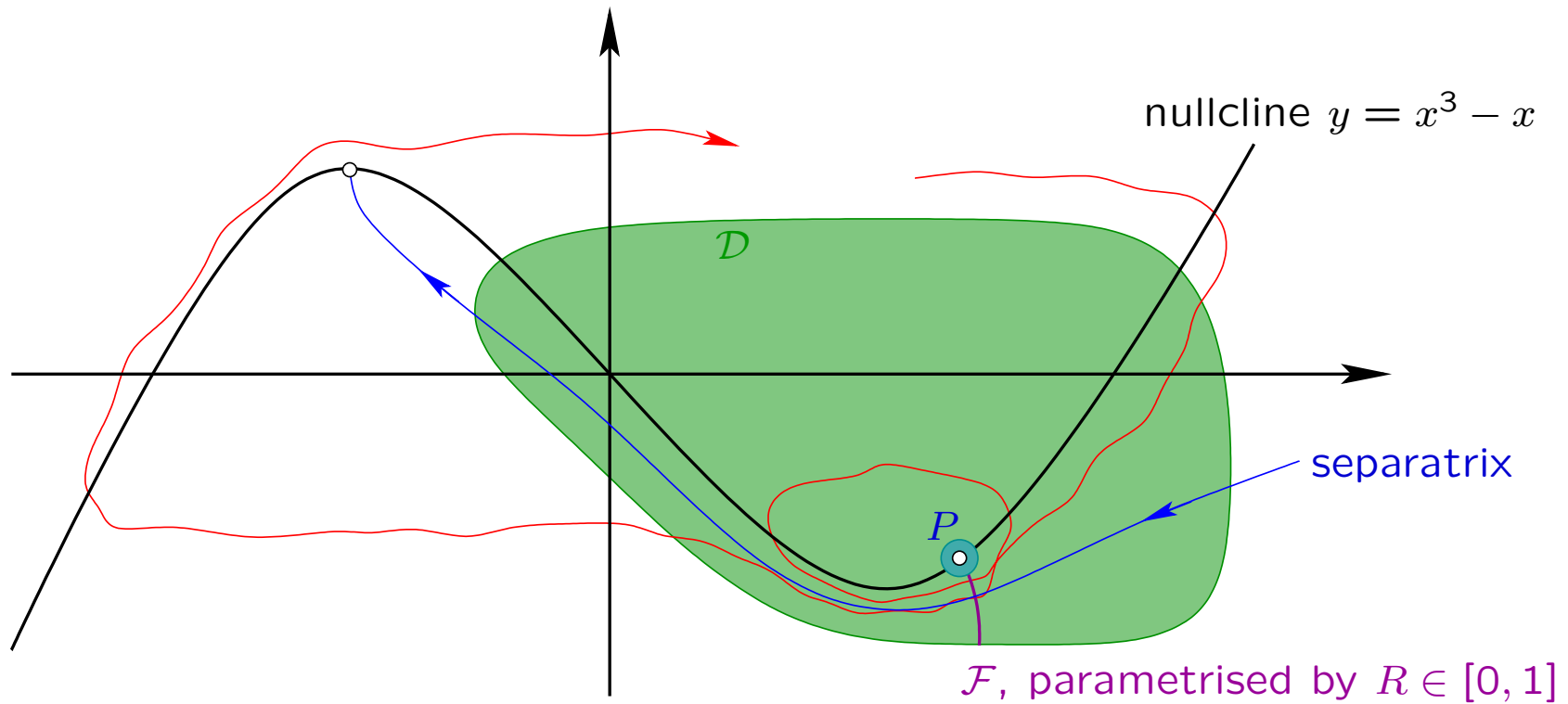


- ▷ Dynamics near **stable branch**, **unstable branch** and **saddle–node bifurcation**: already done in [B & Gentz '05]
- ▷ Dynamics near **singular Hopf bifurcation**: To do



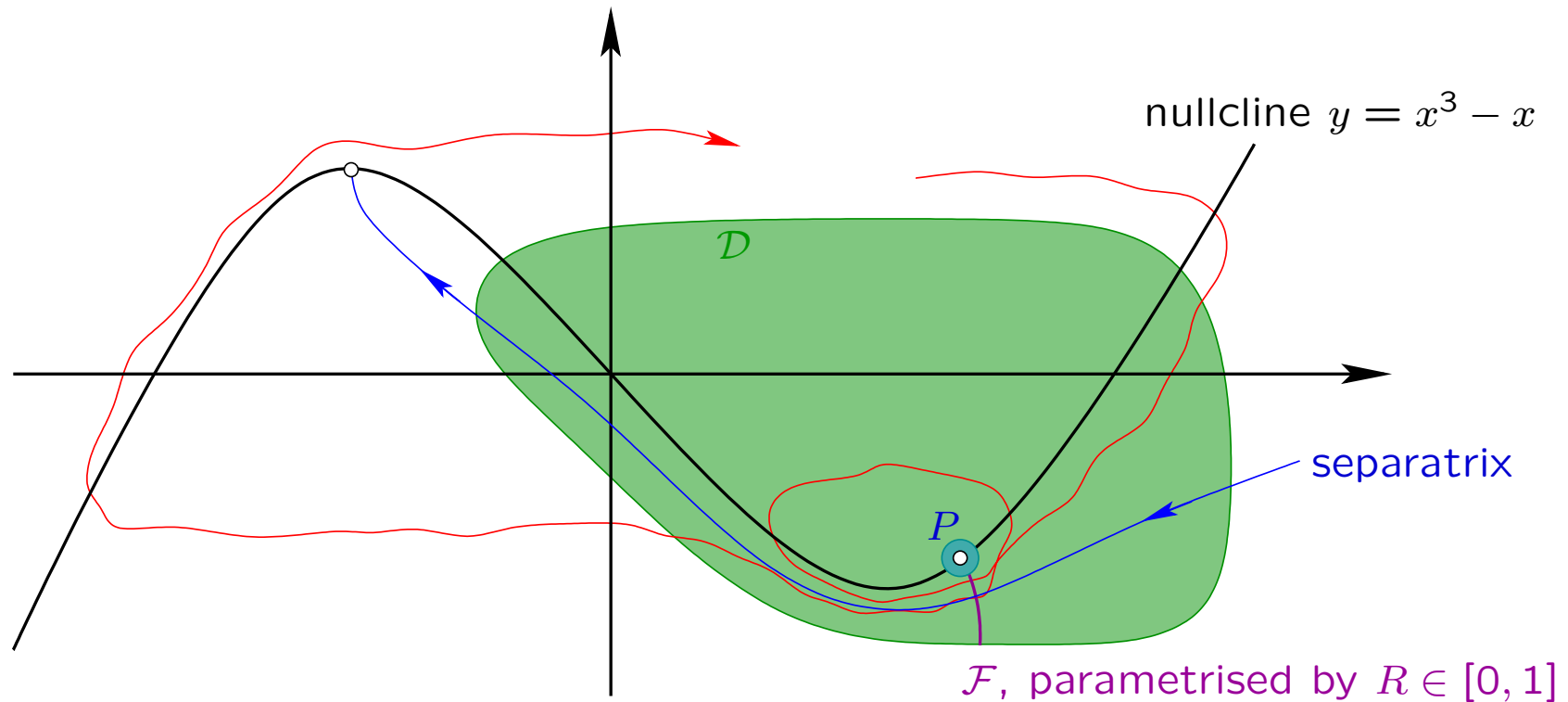
Small-amplitude oscillations (SAOs)

Definition of random number of SAOs N :



Small-amplitude oscillations (SAOs)

Definition of random number of SAOs N :



$(R_0, R_1, \dots, R_{N-1})$ substochastic Markov chain with kernel

$$K(R_0, A) = \mathbb{P}^{R_0}\{R_\tau \in A\}$$

$R \in \mathcal{F}$, $A \subset \mathcal{F}$, $\tau =$ first-hitting time of \mathcal{F} (after turning around P)

$N =$ number of turns around P until leaving \mathcal{D}

General results on distribution of SAOs

General theory of continuous-space Markov chains: [Orey '71, Nummelin '84]

Principal eigenvalue: eigenvalue λ_0 of K of largest module. $\lambda_0 \in \mathbb{R}$

Quasistationary distribution: prob. measure π_0 s.t. $\pi_0 K = \lambda_0 \pi_0$

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Theorem 1: [B & Landon, 2011] Assume $\sigma_1, \sigma_2 > 0$

- ▷ $\lambda_0 < 1$
- ▷ K admits quasistationary distribution π_0
- ▷ N is almost surely finite
- ▷ N is asymptotically geometric:

$$\lim_{n \rightarrow \infty} \mathbb{P}\{N = n + 1 | N > n\} = 1 - \lambda_0$$

- ▷ $\mathbb{E}[r^N] < \infty$ for $r < 1/\lambda_0$, so all moments of N are finite

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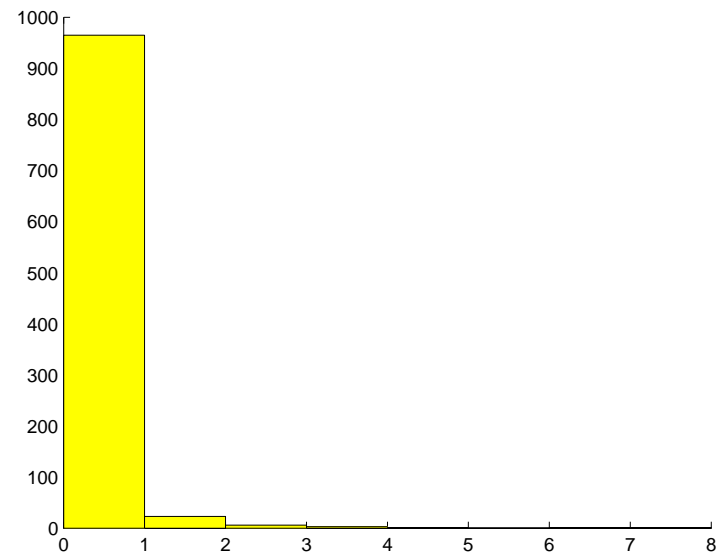
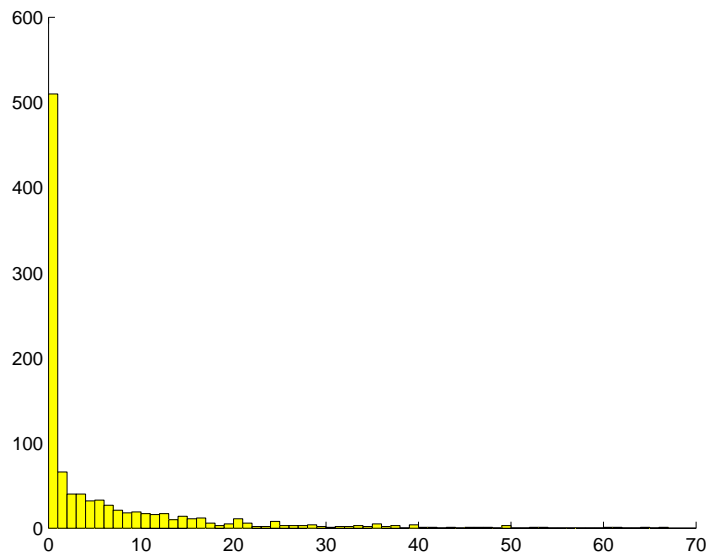
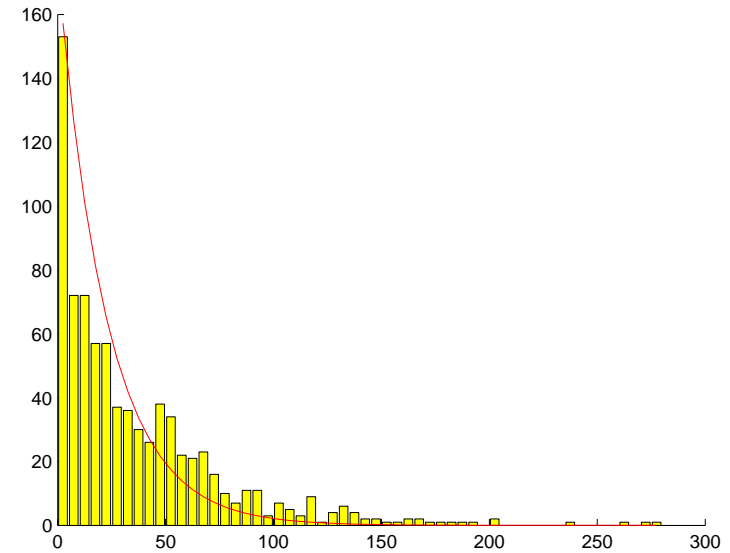
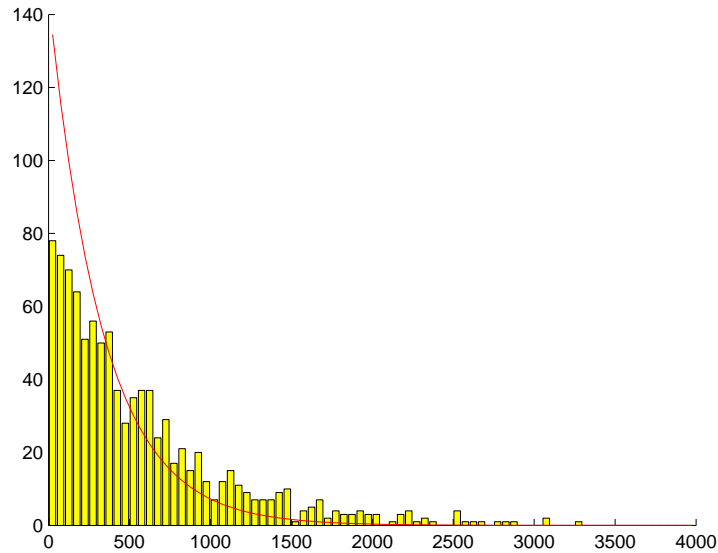
- ▷ $\mathbb{E}[r^N] < \infty$ for $r < 1/\lambda_0$, so all moments of N are finite

Proof:

- ▷ uses Frobenius–Perron–Jentzsch–Krein–Rutman–Birkhoff theorem
- ▷ [Ben Arous, Kusuoka, Stroock '84] implies uniform positivity of K
- ▷ which implies spectral gap

Histograms of distribution of SAO number N (1000 spikes)

$$\sigma = \varepsilon = 10^{-4}, \delta = 1.2 \cdot 10^{-3}, \dots, 10^{-4}$$



The weak-noise regime

Theorem 2: [B & Landon 2011]

Assume ε and $\delta/\sqrt{\varepsilon}$ sufficiently small

There exists $\kappa > 0$ s.t. for $\sigma^2 \leq (\varepsilon^{1/4}\delta)^2 / \log(\sqrt{\varepsilon}/\delta)$

The weak-noise regime

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▷ Expected number of SAOs:

$$\mathbb{E}^{\mu_0}[N] \geq C(\mu_0) \exp\left\{\kappa \frac{(\varepsilon^{1/4}\delta)^2}{\sigma^2}\right\}$$

where $C(\mu_0)$ = probability of starting on \mathcal{F} above separatrix

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Proof:

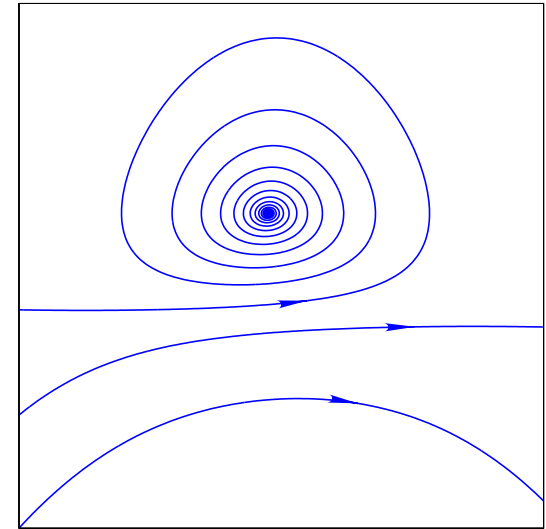
- ▷ Construct $A \subset \mathcal{F}$ such that $K(x, A)$ exponentially close to 1 for all $x \in A$
- ▷ Use two different sets of coordinates to approximate K :
Near separatrix, and during SAO

Dynamics near the separatrix

Change of variables:

- ▷ Translate to Hopf bif. point
- ▷ Scale space and time
- ▷ Straighten nullcline $\dot{x} = 0$

⇒ variables (ξ, z) where nullcline: $\{z = \frac{1}{2}\}$



$$d\xi_t = \left(\frac{1}{2} - z_t - \frac{\sqrt{\varepsilon}}{3} \xi_t^3 \right) dt$$

$$dz_t = \left(\tilde{\mu} + 2\xi_t z_t + \frac{2\sqrt{\varepsilon}}{3} \xi_t^4 \right) dt$$

where

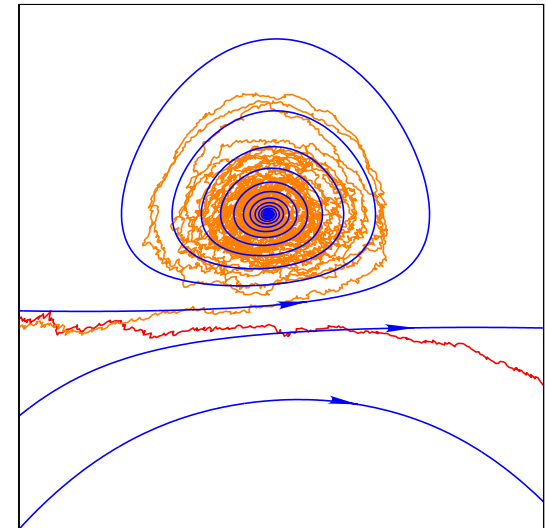
$$\tilde{\mu} = \frac{\delta}{\sqrt{\varepsilon}}$$

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$$d\xi_t = \left(\frac{1}{2} - z_t - \frac{\sqrt{\varepsilon}}{3} \xi_t^3 \right) dt + \tilde{\sigma}_1 dW_t^{(1)}$$

$$dz_t = \left(\tilde{\mu} + 2\xi_t z_t + \frac{2\sqrt{\varepsilon}}{3} \xi_t^4 \right) dt - 2\tilde{\sigma}_1 \xi_t dW_t^{(1)} + \tilde{\sigma}_2 dW_t^{(2)}$$

where

$$\tilde{\mu} = \frac{\delta}{\sqrt{\varepsilon}} - \tilde{\sigma}_1^2 \quad \tilde{\sigma}_1 = -\sqrt{3} \frac{\sigma_1}{\varepsilon^{3/4}} \quad \tilde{\sigma}_2 = \sqrt{3} \frac{\sigma_2}{\varepsilon^{3/4}}$$

Upward drift dominates if $\tilde{\mu}^2 \gg \tilde{\sigma}_1^2 + \tilde{\sigma}_2^2 \Rightarrow (\varepsilon^{1/4} \delta)^2 \gg \sigma_1^2 + \sigma_2^2$

Rotation around P : use that $2z e^{-2z-2\xi^2+1}$ is constant for $\tilde{\mu} = \varepsilon = 0$

Transition from weak to strong noise

Linear approximation:

$$dz_t^0 = (\tilde{\mu} + tz_t^0) dt - \tilde{\sigma}_1 t dW_t^{(1)} + \tilde{\sigma}_2 dW_t^{(2)}$$

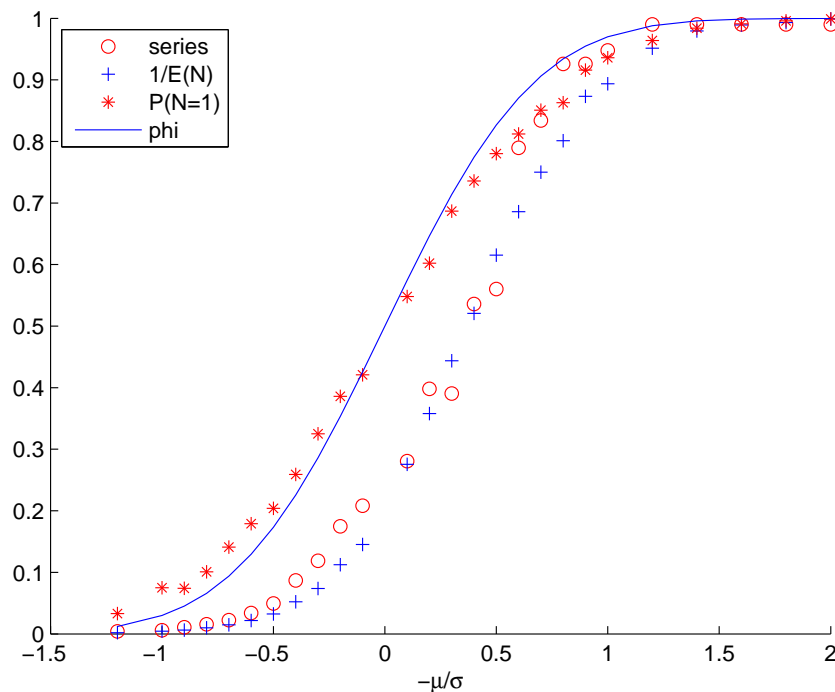
$$\Rightarrow \mathbb{P}\{\text{no SAO}\} \simeq \Phi\left(-\pi^{1/4} \frac{\tilde{\mu}}{\sqrt{\tilde{\sigma}_1^2 + \tilde{\sigma}_2^2}}\right) \quad \Phi(x) = \int_{-\infty}^x \frac{e^{-y^2/2}}{\sqrt{2\pi}} dy$$

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*: $\mathbb{P}\{\text{no SAO}\}$

+: $1/\mathbb{E}[N]$

o: $1 - \lambda_0$

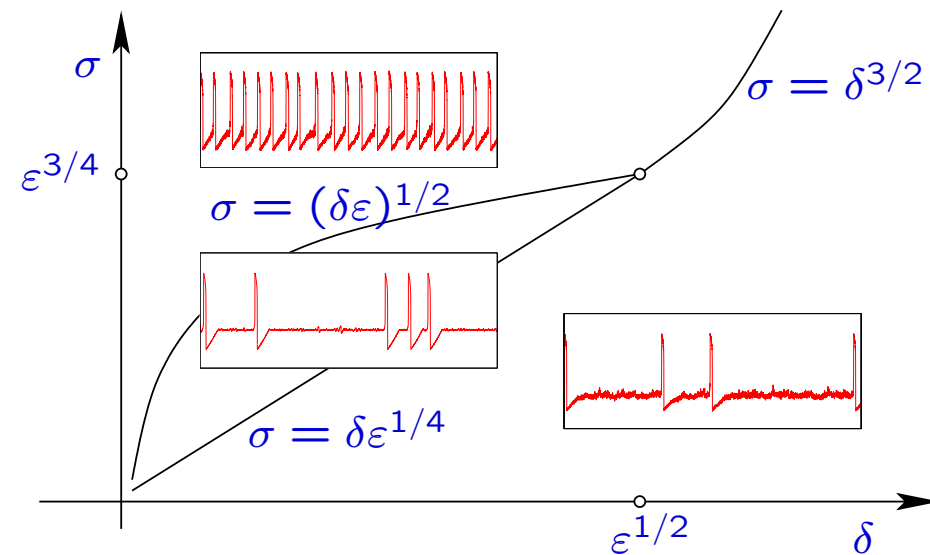
curve: $x \mapsto \Phi(\pi^{1/4}x)$

$$x = \frac{\tilde{\mu}}{\sqrt{\tilde{\sigma}_1^2 + \tilde{\sigma}_2^2}} = \frac{\varepsilon^{1/4}(\delta - \sigma_1^2/\varepsilon)}{\sqrt{\sigma_1^2 + \sigma_2^2}}$$

Conclusions

Three regimes for $\delta < \sqrt{\varepsilon}$:

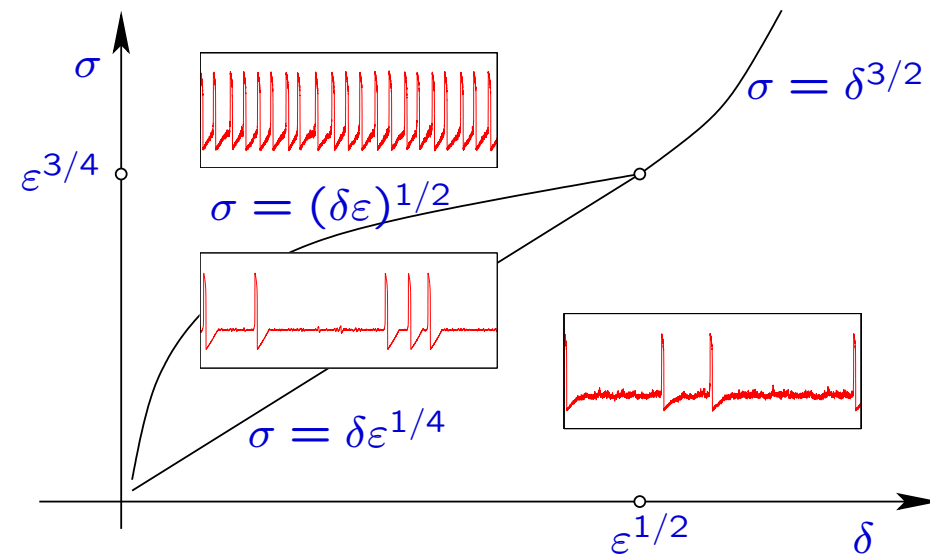
- ▷ $\sigma \ll \varepsilon^{1/4}\delta$: rare isolated spikes
interval $\simeq \mathcal{E}xp(\sqrt{\varepsilon} e^{-(\varepsilon^{1/4}\delta)^2/\sigma^2})$
- ▷ $\varepsilon^{1/4}\delta \ll \sigma \ll \varepsilon^{3/4}$: transition
geometric number of SAOs
 $\sigma = (\delta\varepsilon)^{1/2}$: geometric(1/2)
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Outlook

- ▷ sharper bounds on λ_0 (and π_0)
- ▷ relation between $\mathbb{P}\{\text{no SAO}\}$, $1/\mathbb{E}[N]$ and $1 - \lambda_0$
- ▷ consequences of postspike distribution $\mu_0 \neq \pi_0$
- ▷ interspike interval distribution \simeq periodically modulated exponential – how is it modulated?

Part II

Where noise modifies or suppresses
MMOs

Folded node singularity

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

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

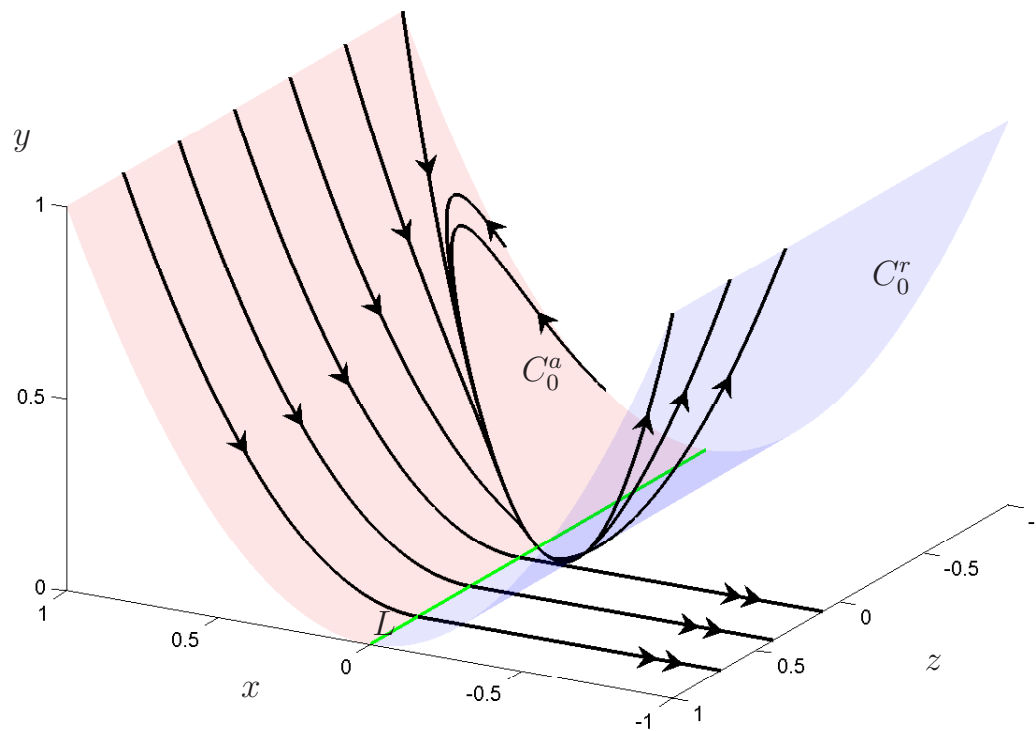
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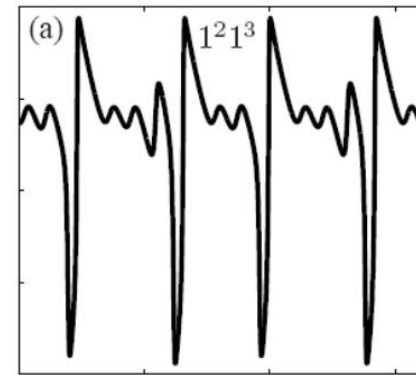
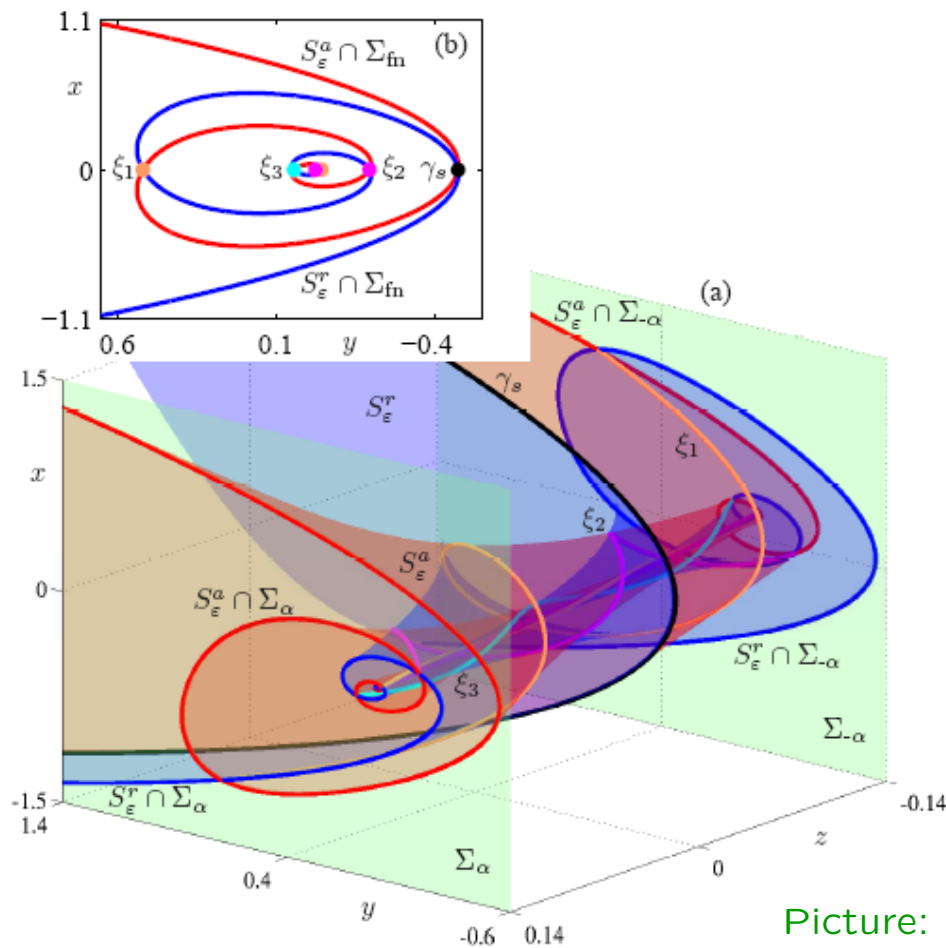


Folded node singularity

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)

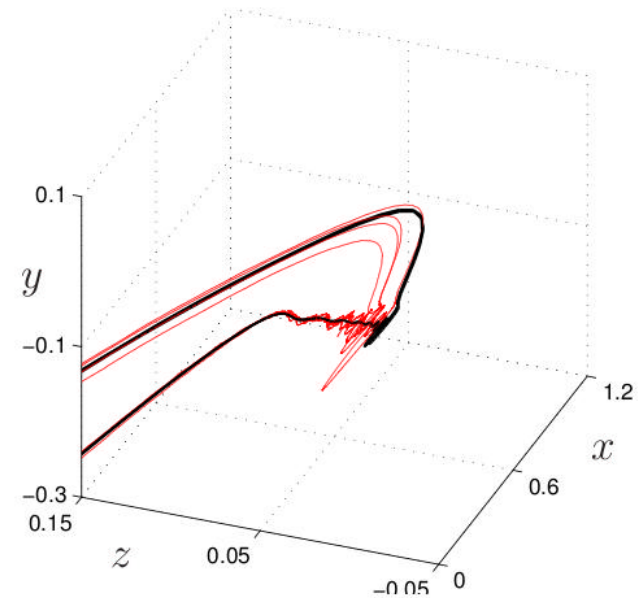
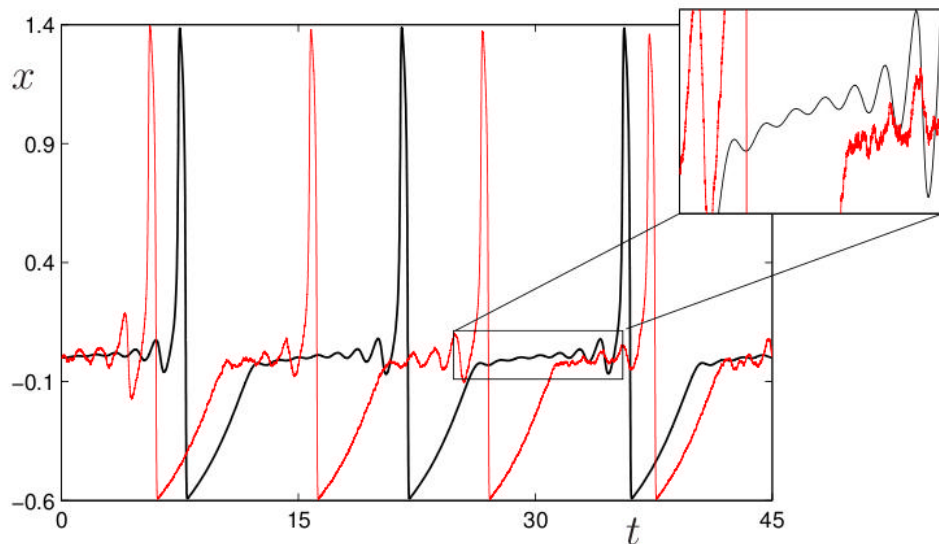
Picture: Mathieu Desroches

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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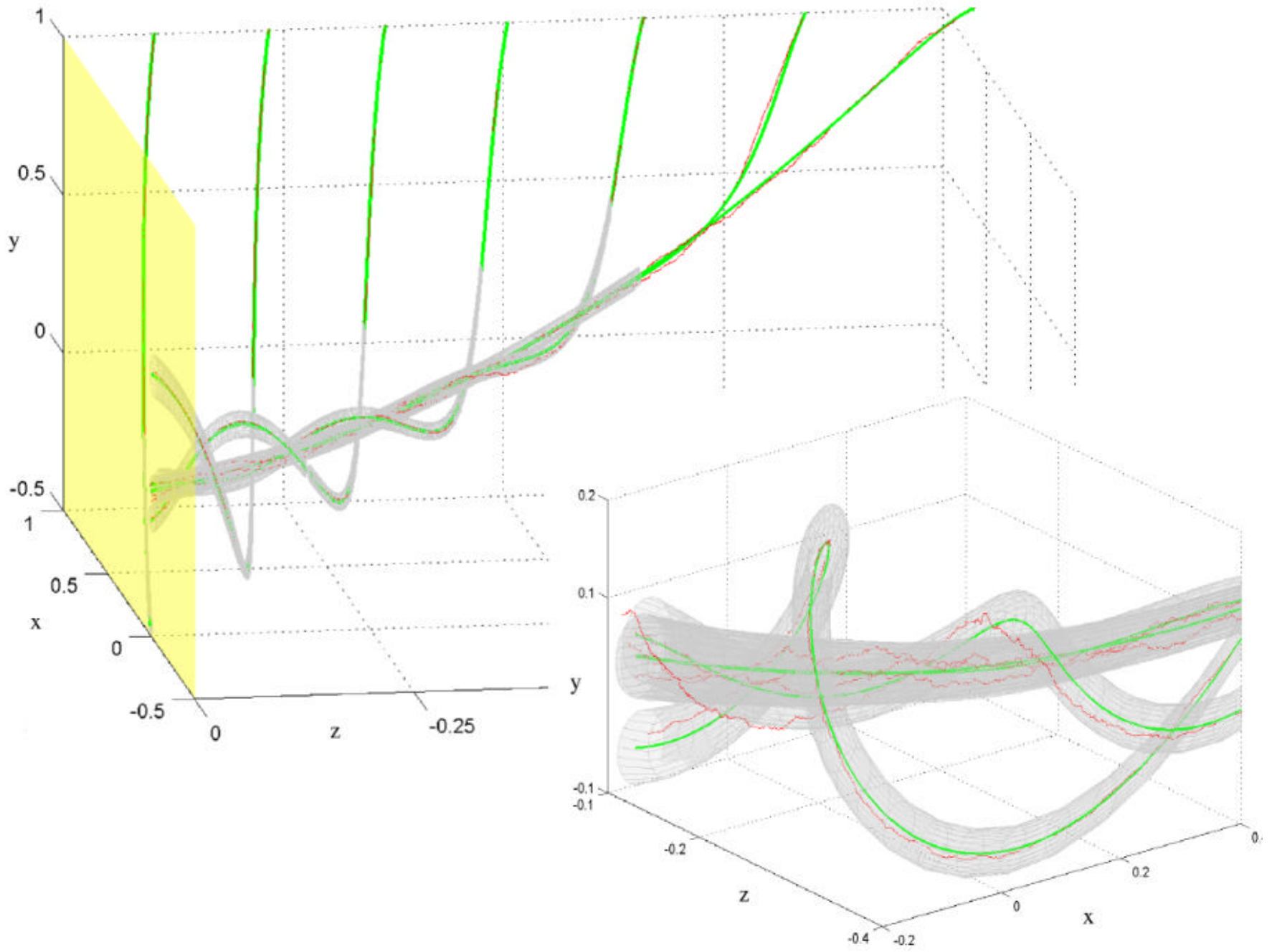
Covariance tube :

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

Theorem 3: [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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- ▷ (Sub)martingale : $\{M_t\}_{t \geq 0}$, $\mathbb{E}\{M_t | M_s\} = (\geq) M_s$ for $t \geq s \geq 0$
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but can be approximated by martingale on small time intervals
- ▷ $\exp\{\gamma \langle \zeta_t, V(t)^{-1} \zeta_t \rangle\}$ approximated by submartingale
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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 $z = 0$

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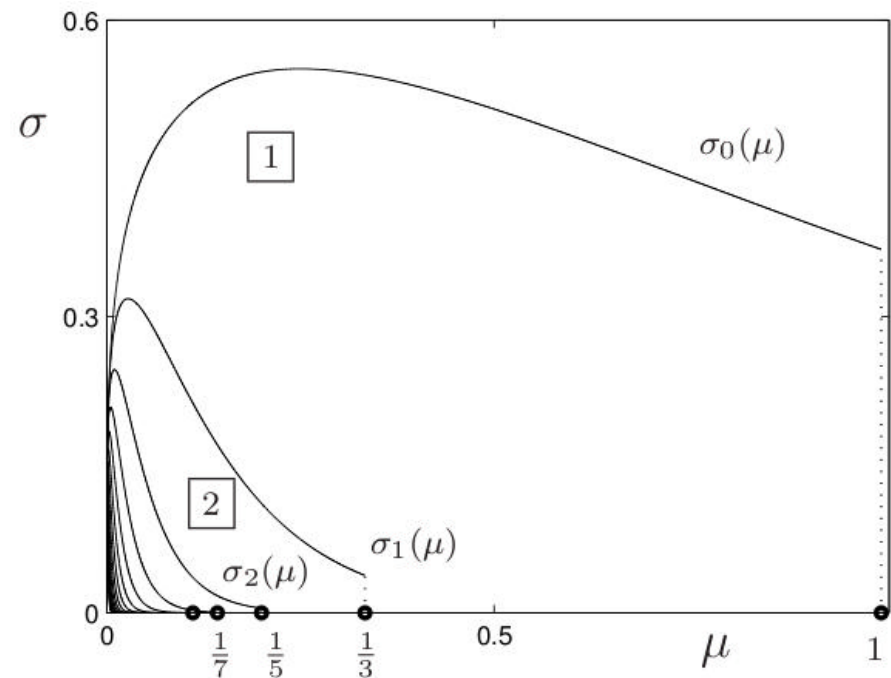
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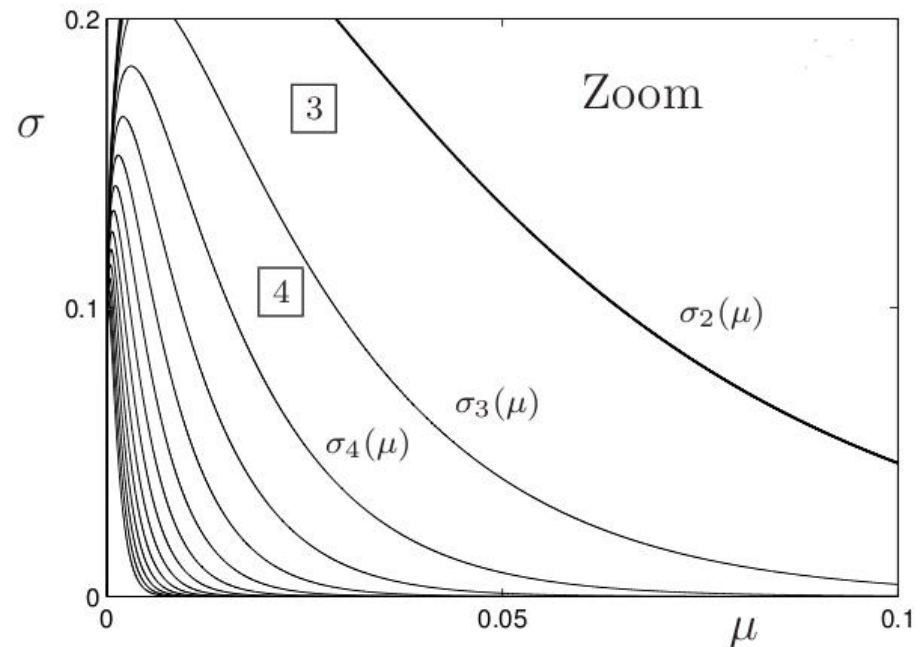
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Early transitions

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

Theorem 4: [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 $z \gg \sqrt{\mu |\log \sigma| / \kappa}$

Early transitions

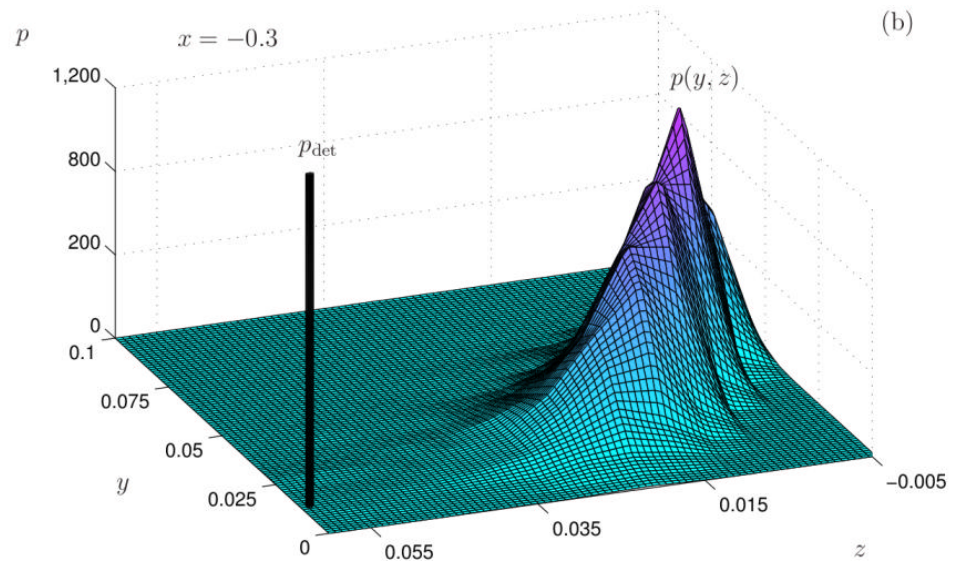
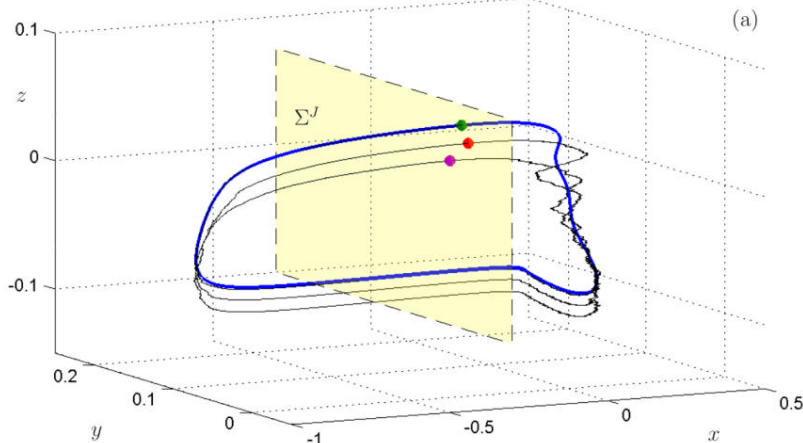
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Sketch of proof :

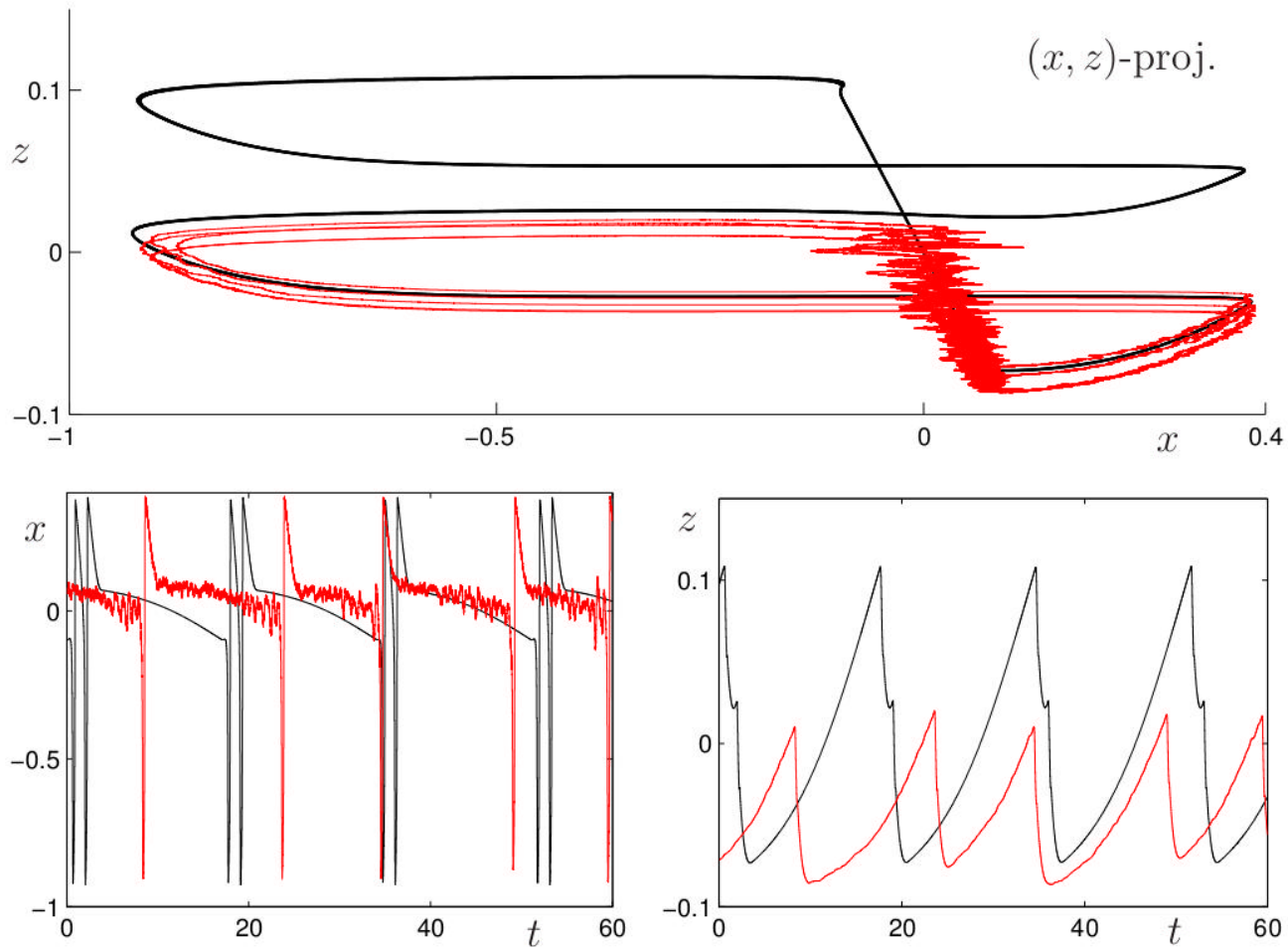
- ▷ Escape from neighbourhood of size $\sigma |\log \sigma| / \sqrt{z}$:
compare with linearized equation on small time intervals + Markov property
- ▷ Escape from annulus $\sigma |\log \sigma| / \sqrt{z} \leq \|\zeta\| \leq \sqrt{z}$:
use polar coordinates and averaging
- ▷ To combine the two regimes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

Further work

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Further reading

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*, arXiv:1011.3193, to appear in J. Differential Equations (2012)

N.B. and Damien Landon, *Mixed-mode oscillations and interspike interval statistics in the stochastic FitzHugh–Nagumo model*, arXiv:1105.1278, submitted (2011)

N.B., *Kramers' law: Validity, derivations and generalisations*, arXiv:1106.5799, submitted (2011)

