On the Interspike Time Statistics in the Stochastic FitzHugh–Nagumo Equation

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

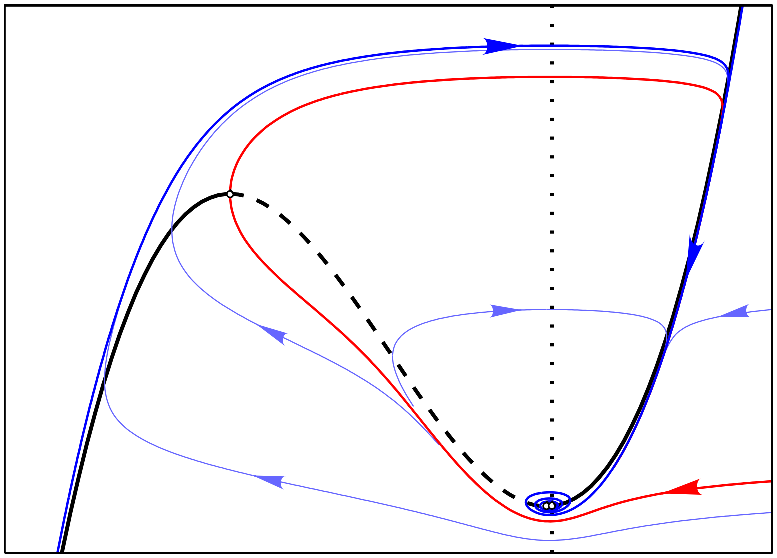
Linearisation has eigenvalues $\frac{-\delta \pm \sqrt{\delta^2 - \varepsilon}}{\varepsilon}$ where $\delta = \frac{3a^2 - 1}{2}$

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

Deterministic FitzHugh–Nagumo (FHN) equations

$\delta > 0$:

- $\triangleright$ P is asymptotically stable
- $\triangleright$ the system is excitable
- $\triangleright$ one can define a separatrix



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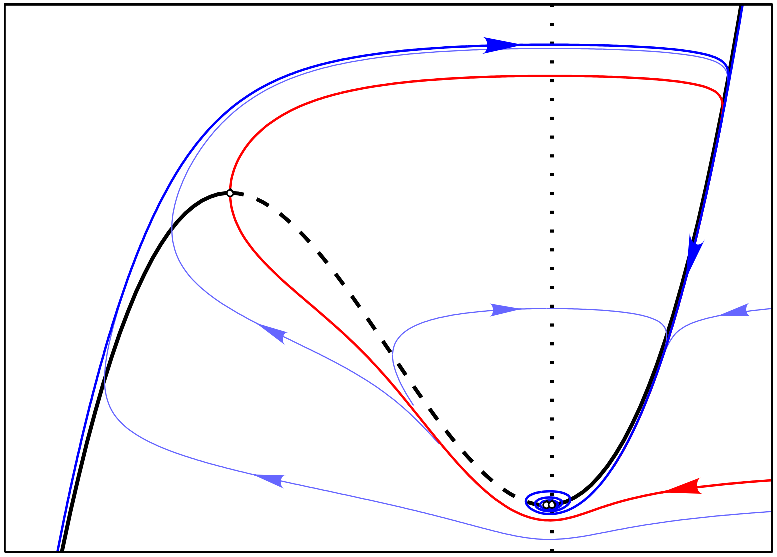

$\delta < 0$:

- ▷ P is unstable
- ▷ $\exists$ asympt. stable periodic orbit
- ▷ sensitive dependence on δ:
  canard (duck) phenomenon
  [Callot, Diener, Diener '78,
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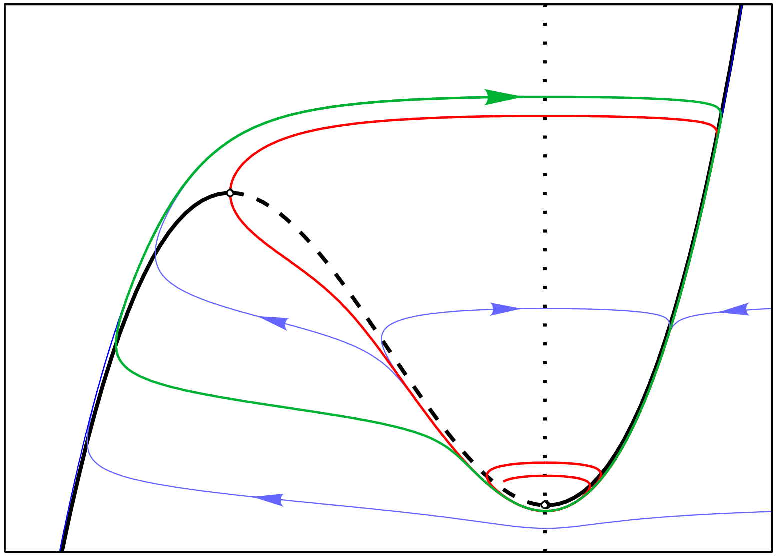

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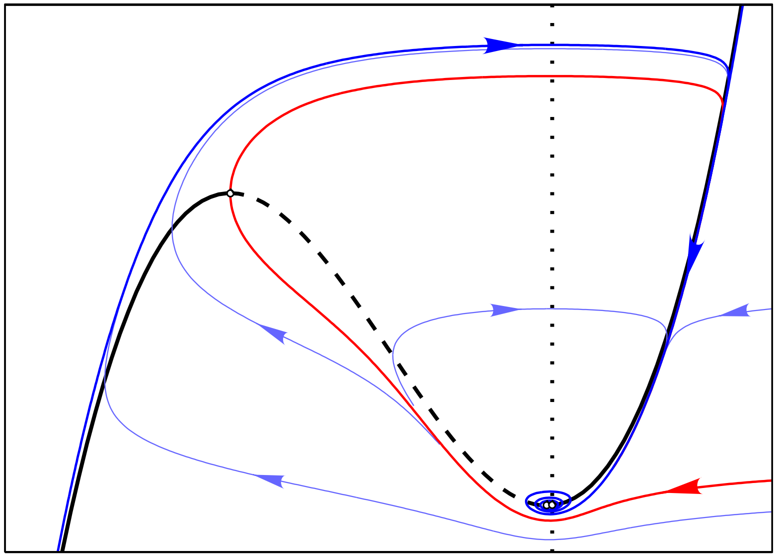

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Stochastic FHN equations

$$\mathrm{d}x_t = \frac{1}{\varepsilon}[x_t - x_t^3 + y_t]\,\mathrm{d}t + \frac{\sigma_1}{\sqrt{\varepsilon}}\,\mathrm{d}W_t^{(1)}$$

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▷ $0 < \sigma_1, \sigma_2 \ll 1$, $\sigma = \sqrt{\sigma_1^2 + \sigma_2^2}$

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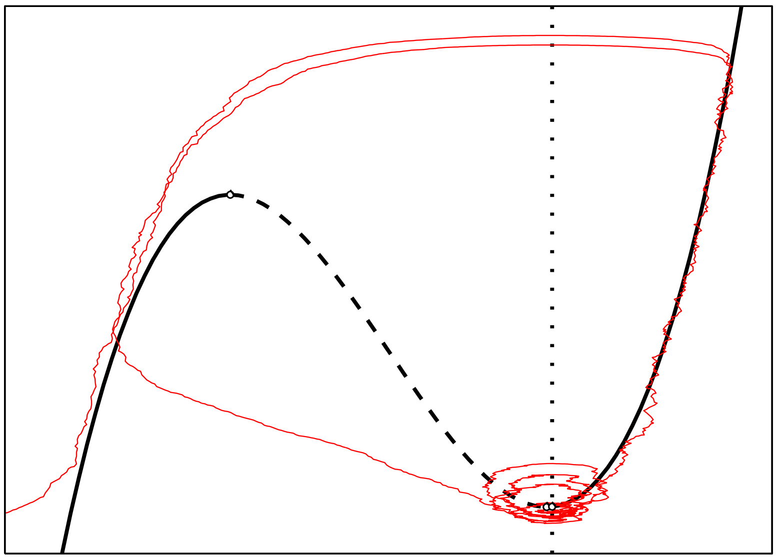
$\varepsilon = 0.1$
$\delta = 0.02$
$\sigma_1 = \sigma_2 = 0.03$



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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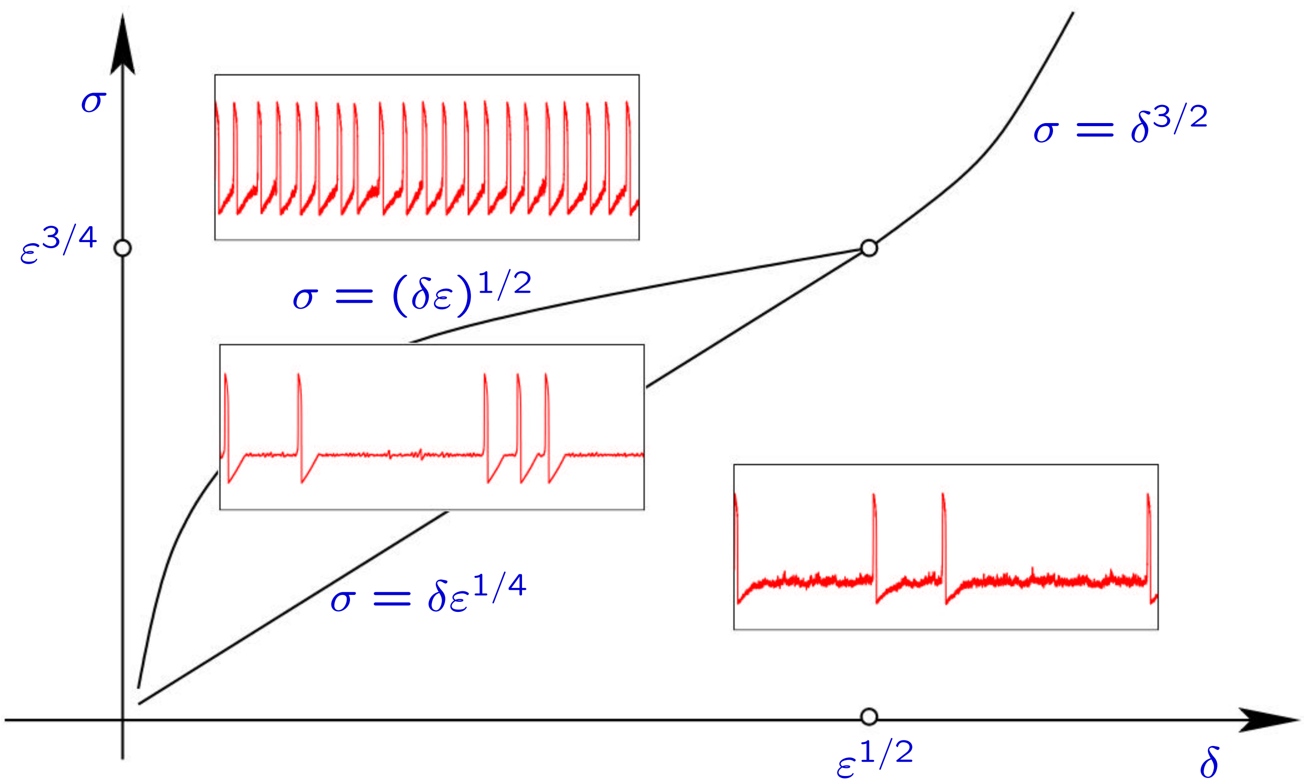
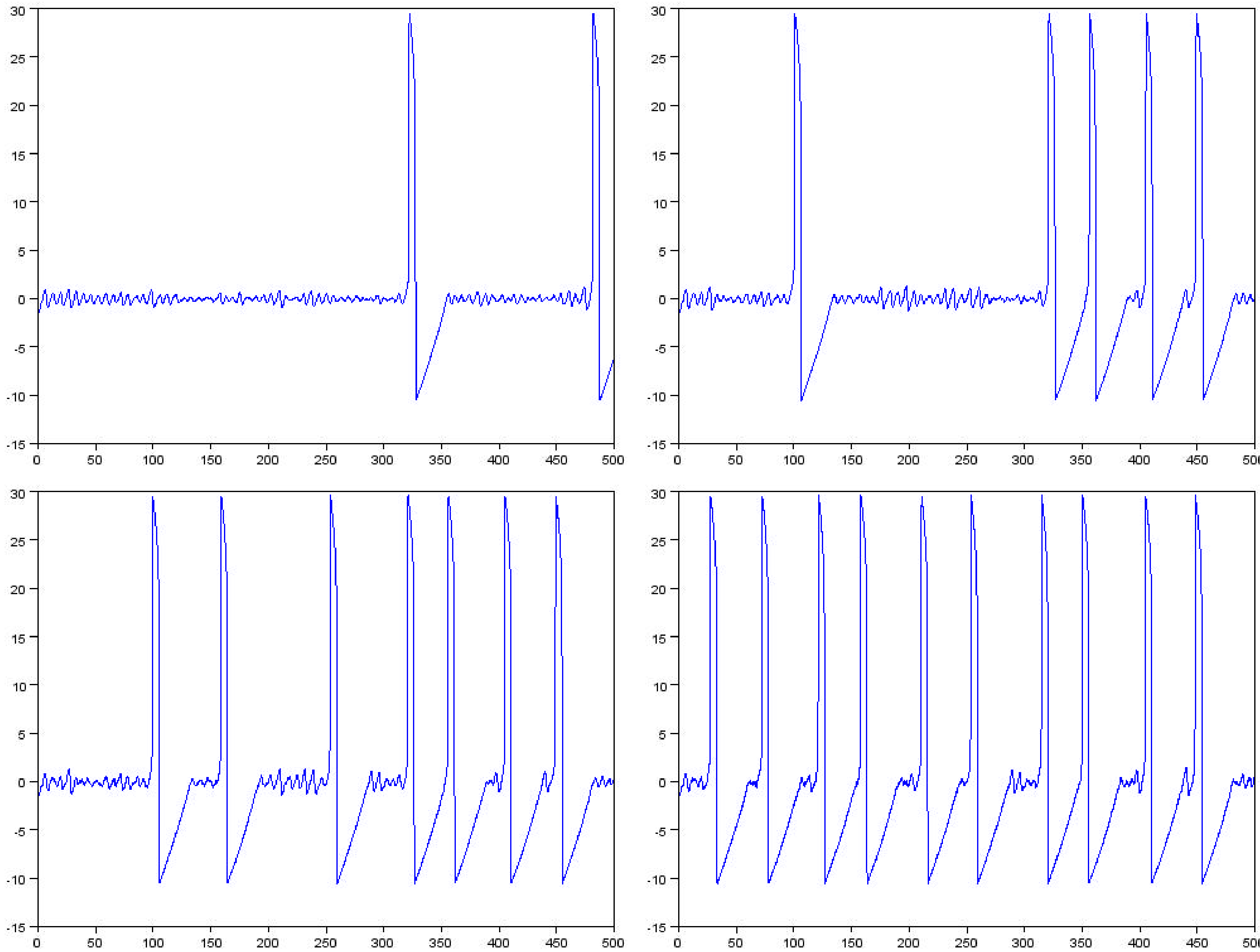
Proposed "phase diagram" [Muratov & Vanden Eijnden '08]

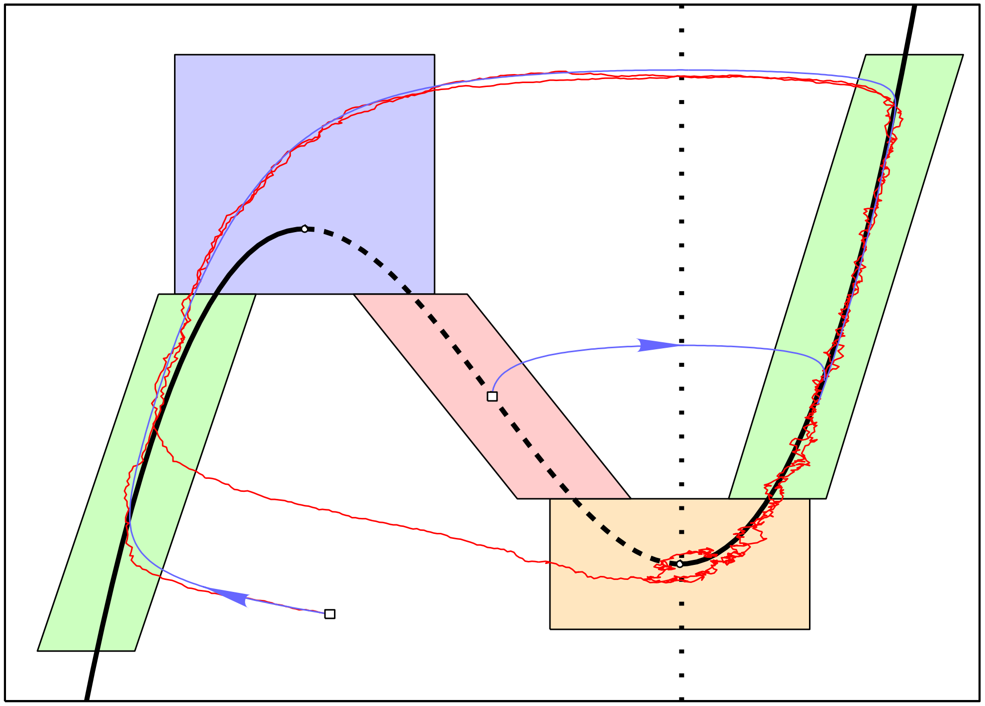


Intermediate regime: mixed-mode oscillations (MMOs)



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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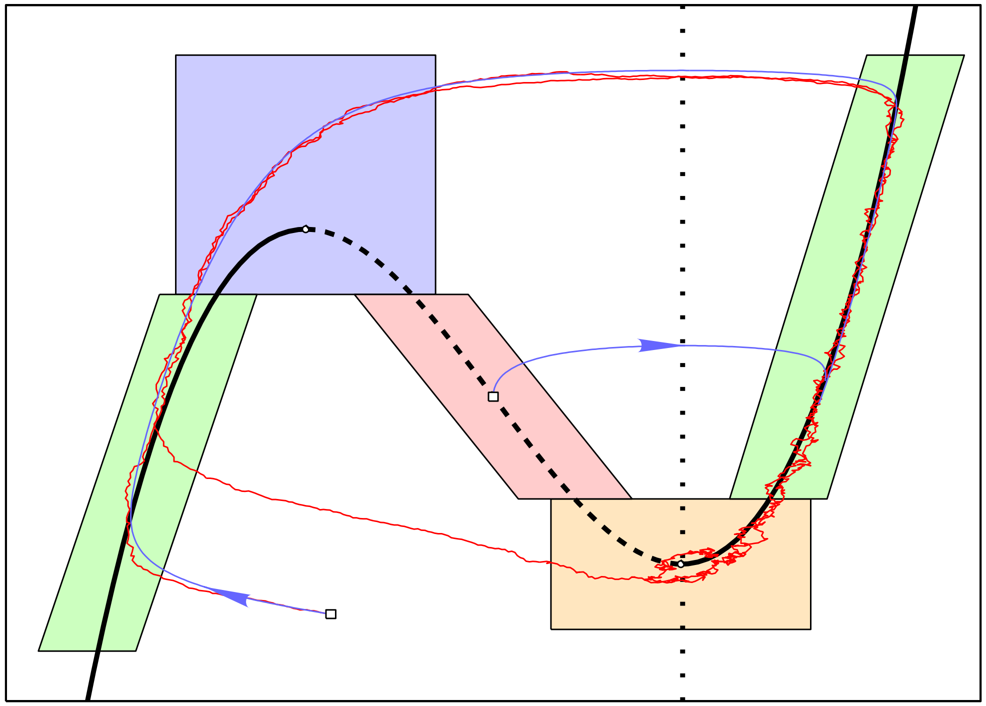
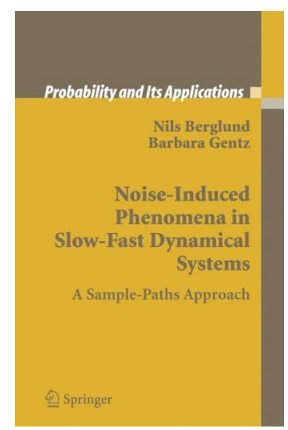


▷ Dynamics near stable branch, unstable branch and saddle–node bifurcation: already done in [B & Gentz '05]



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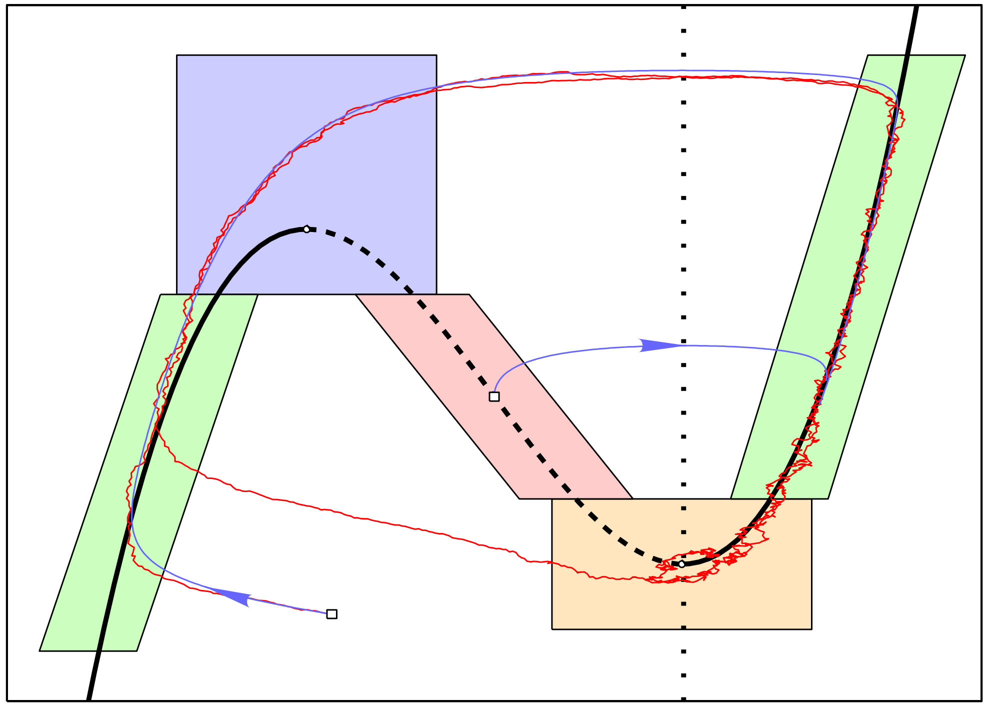
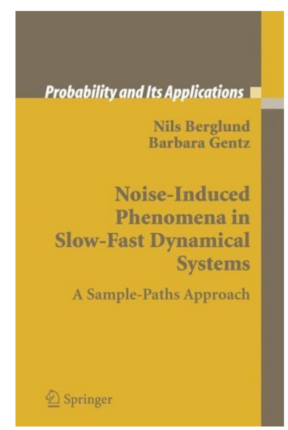
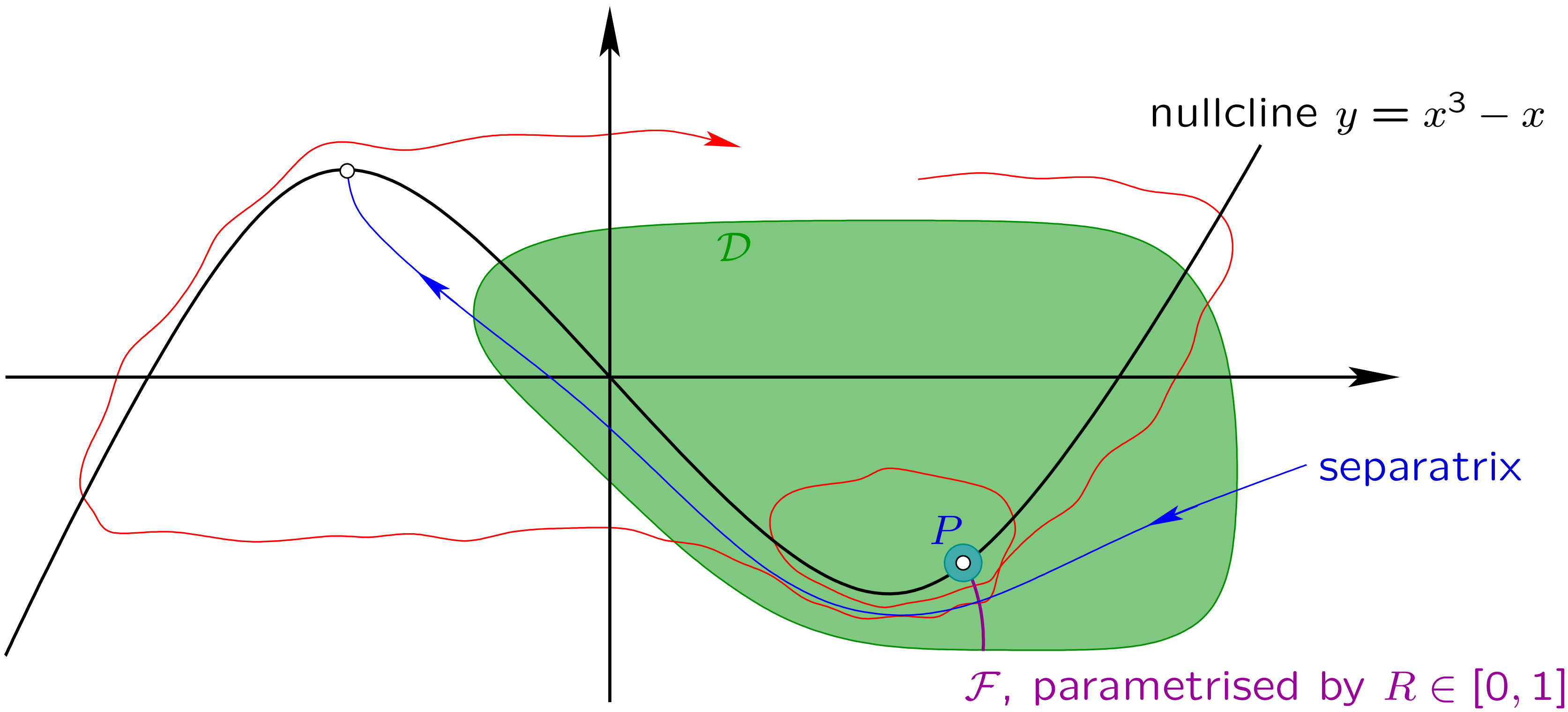


- ▷ Dynamics near stable branch, unstable branch and saddle–node bifurcation: already done in [B & Gentz '05]
- ▷ Dynamics near singular Hopf bifurcation: To do



Small-amplitude oscillations (SAOs)

Definition of random number of SAOs N:



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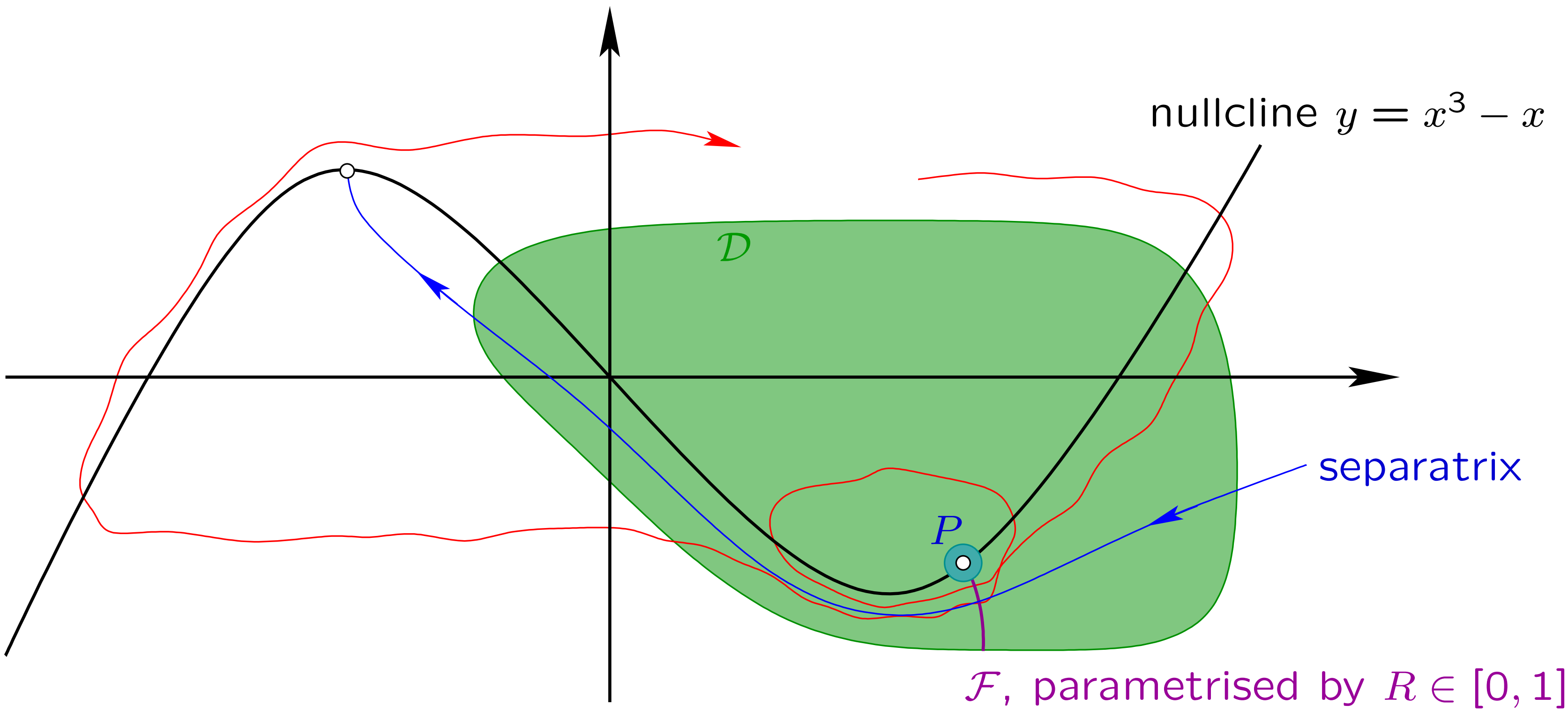

$(R_0, R_1, \dots, R_{N-1})$ substochastic Markov chain with kernel

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

$R \in \mathcal{F}$, $A \subset \mathcal{F}$, τ = 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:

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

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

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Proof uses Frobenius–Perron–Jentzsch–Krein–Rutman–Birkhoff theorem and uniform positivity of K, which implies spectral gap

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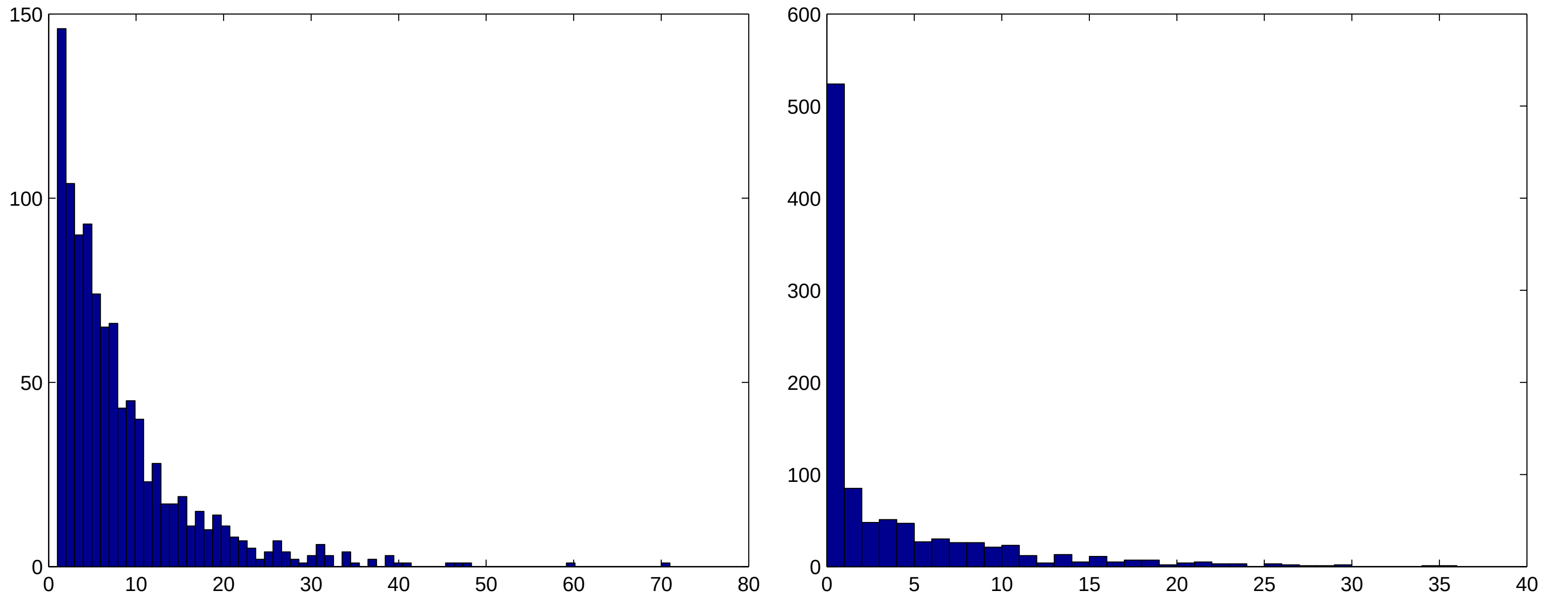

Histogramms of distribution of SAO number N (1000 spikes)

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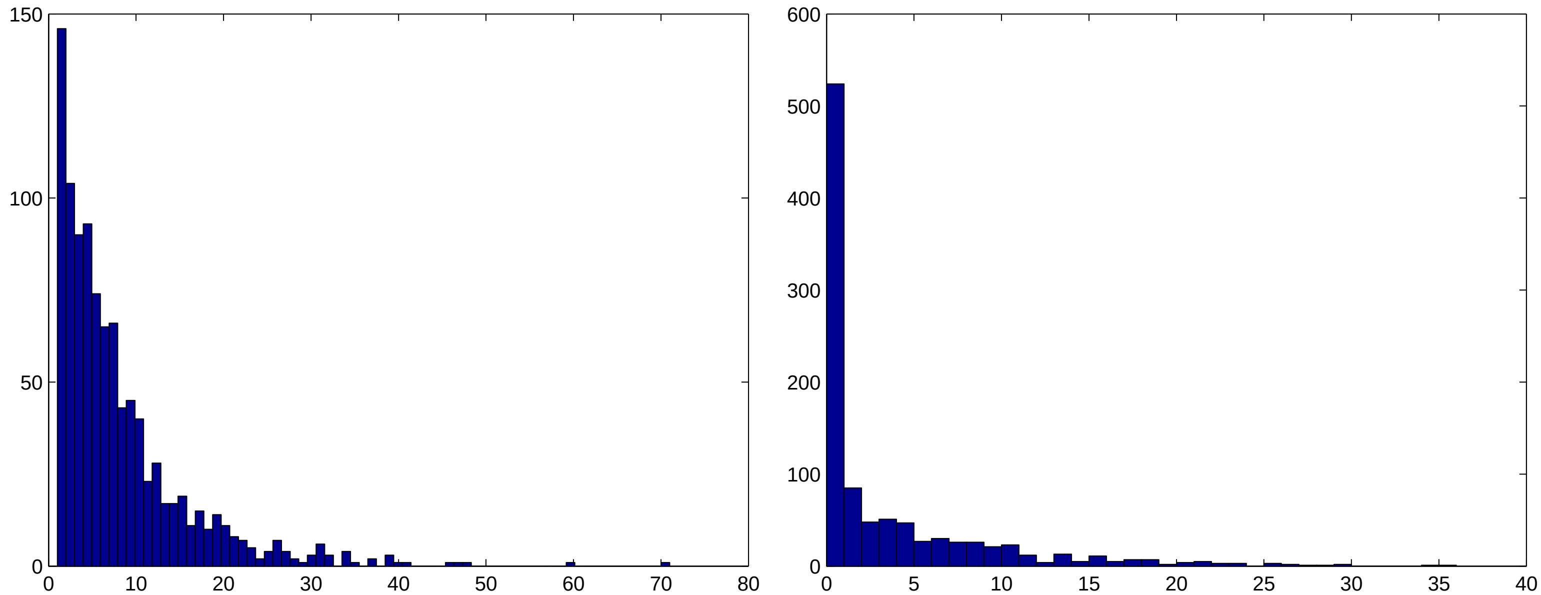

Histogramms of distribution of SAO number N (1000 spikes)

Remark: $\mathbb{P}\{$cluster of spikes of length $k\} \simeq p^k(1-p)$ where

- ▷ $p = \mathbb{P}^{\mu_0}\{N \leqslant n_0\}$
- ▷ μ_0 = incoming distribution after a spike
- ▷ n_0 = maximal number of SAOs between spikes in a cluster

The weak-noise regime

Theorem 2: [B & Landon 2011]
Assume ε and $\delta/\sqrt{\varepsilon}$ sufficiently small
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$$\mathbb{E}^{\mu_0}[N] \geqslant C(\mu_0)\exp\left\{\kappa\frac{(\varepsilon^{1/4}\delta)^2}{\sigma^2}\right\}$$

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

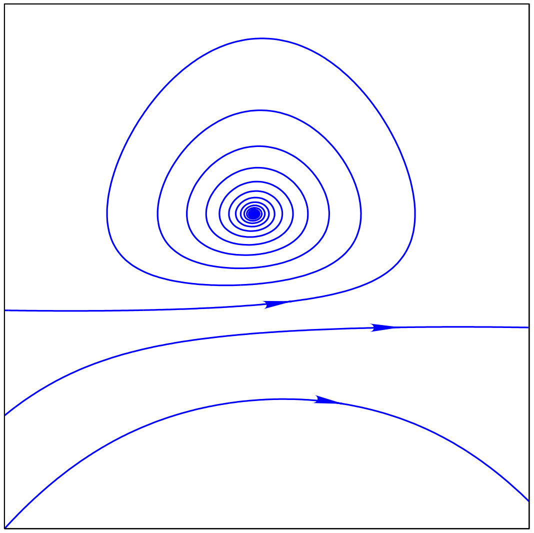
Change of variables:

▷ Translate to Hopf bif. point

▷ Scale space and time

▷ Straighten nullcline $\dot{x} = 0$

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



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

$$\mathrm{d}z_t = \left(\tilde{\mu} + 2\xi_t z_t + \frac{2\sqrt{\varepsilon}}{3}\xi_t^4\right)\mathrm{d}t - 2\tilde{\sigma}_1\xi_t\,\mathrm{d}W_t^{(1)} + \tilde{\sigma}_2\,\mathrm{d}W_t^{(2)}$$

where

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

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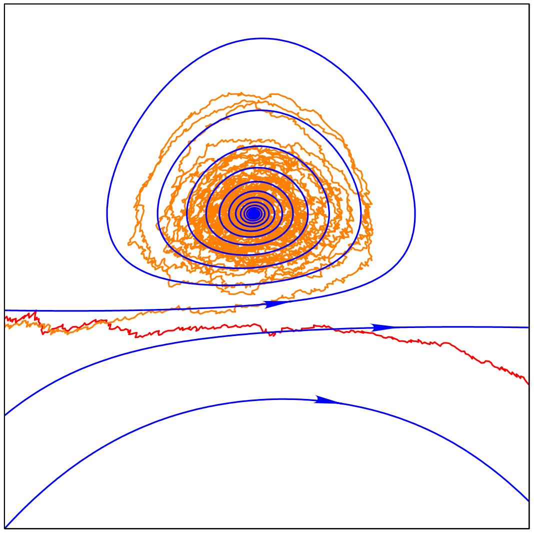

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Upward drift dominates if $\tilde{\mu}^2 \gg \tilde{\sigma}_1^2 + \tilde{\sigma}_2^2 \Rightarrow (\varepsilon^{1/4}\delta)^2 \gg \sigma_1^2 + \sigma_2^2$

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

Transition from weak to strong noise

Linear approximation:

$$\mathrm{d}z_t^0 = \left(\tilde{\mu} + t z_t^0\right)\mathrm{d}t - \tilde{\sigma}_1 t\,\mathrm{d}W_t^{(1)} + \tilde{\sigma}_2\,\mathrm{d}W_t^{(2)}$$

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

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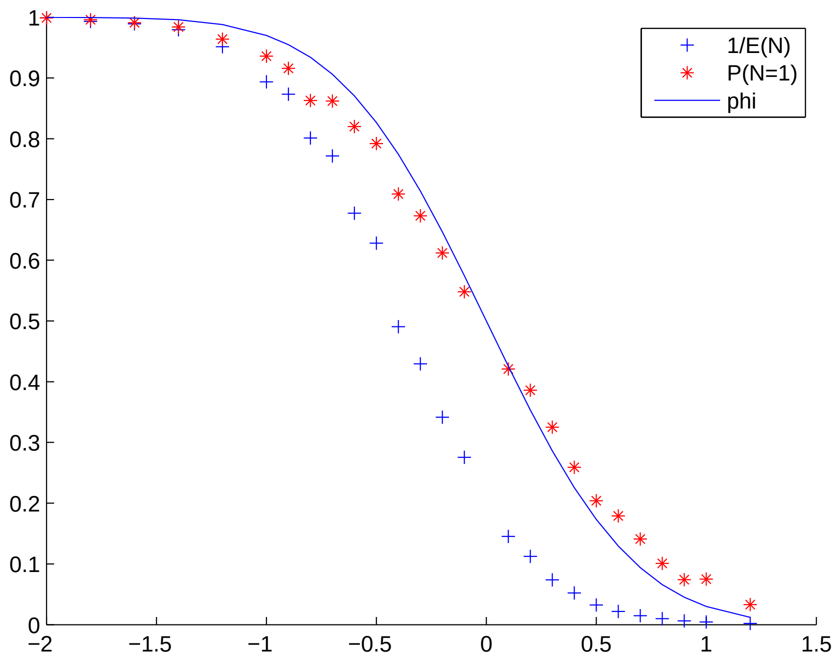

$*$: $\mathbb{P}\{\text{no SAO}\}$

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

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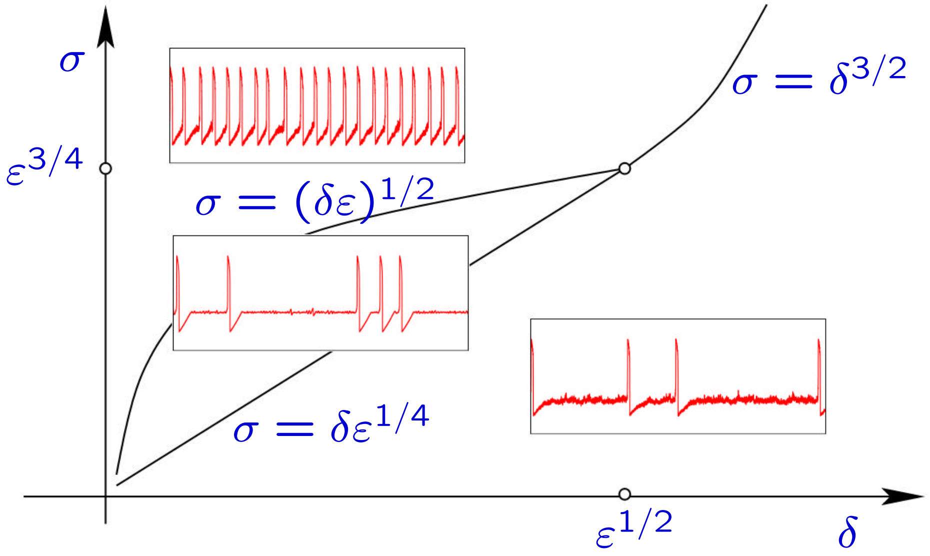

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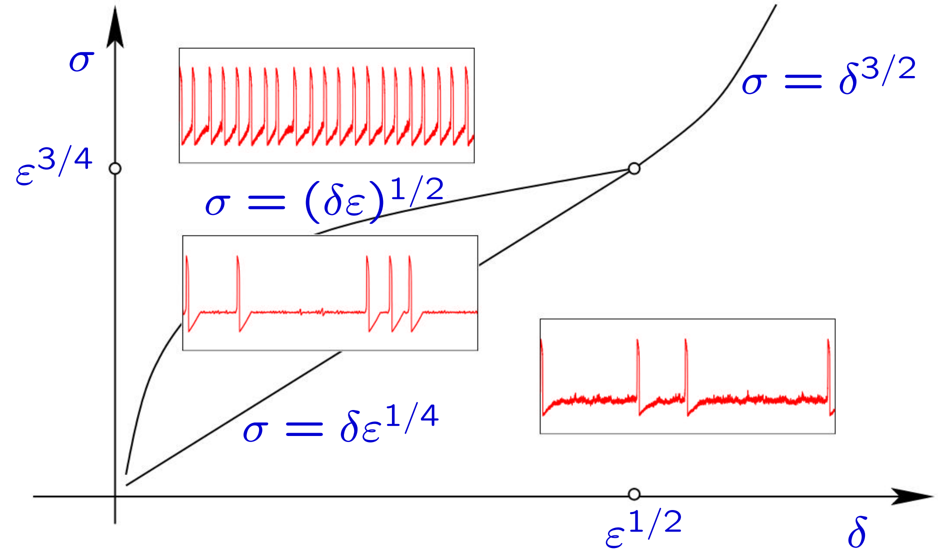
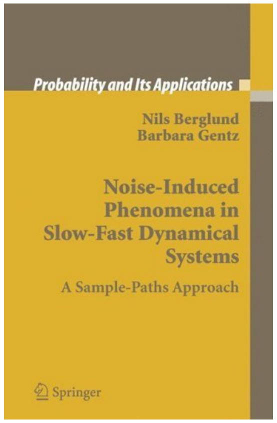


Outlook

- ▷ sharper bounds on λ_0 (and π_0)
- ▷ relation between $\mathbb{P}\{$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?

Some references

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



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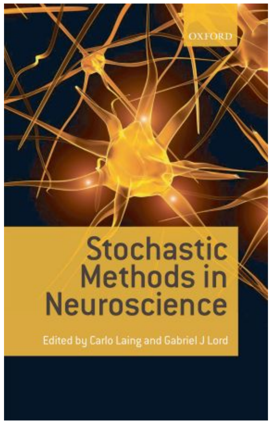

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