Hopf bifurcation for a mean-field model of interacting neurons

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Introduction

- Model of noisy Integrate and Fire neurons in interaction.
- Mean-Field description through a McKean-Vlasov SDE.

From a **Dynamical System** point of view:

- What are the invariant measures (equilibrium points for ODEs), what can we say about their **stability** (local, global) ?
- What happens if the invariant measure is not locally stable (Oscillations via Hopf bifurcations) ?

The model: Interspikes dynamics

N neurons characterized by their membrane potential:

$$V_t^i \in \mathbb{R}_+$$

Between the spikes, $(V_t^i)_{t \geq 0}$ solves a simple deterministic ODE:

$$\frac{dV_t^i}{dt} = b(V_t^i).$$

(Example: $b \equiv$ constant: the potential of each neuron grows linearly between its spikes).

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The model: Spiking dynamics

- Each neuron i spikes randomly at a rate $f(V_t^i)$:

$$\mathbb{P}(V_t^i \text{ spikes between } [t, t+dt) \mid \mathcal{F}_t) = f(V_t^i)dt$$

- When such a spike occurs (say at time τ):
  1. The potential of the neuron i is reset to 0:

$$V^i_{\tau+} = 0.$$

  2. The potentials of the other neurons are increased by $J^N_{i \to j}$:

$$j \neq i, \quad V^j_{\tau+} = V^j_{\tau-} + J^N_{i \to j}.$$

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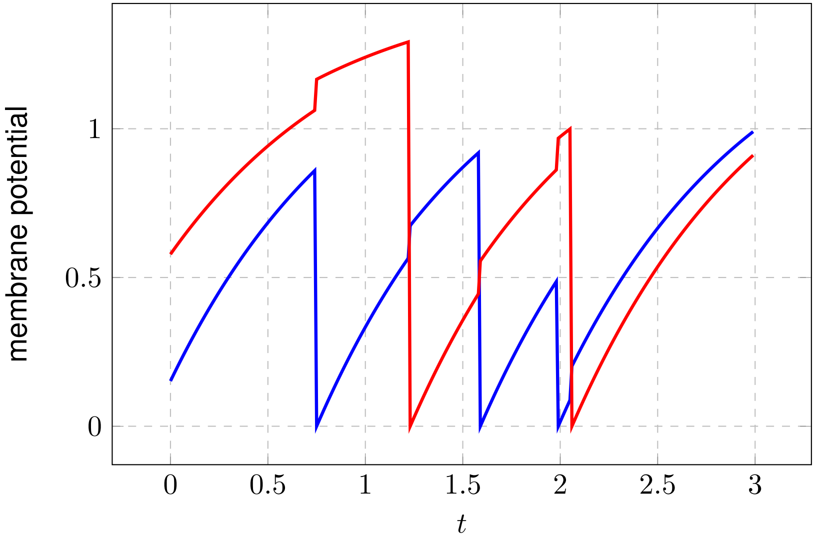
Illustration with $N = 2$ neurons



The parameters of the problem

The model is fully described by:

1. the drift $b : \mathbb{R}_+ \to \mathbb{R}$, with $b(0) > 0$. It gives the dynamic of the neurons between the spikes.

2. the rate function $f : \mathbb{R}_+ \to \mathbb{R}_+$ with $f(0) = 0$ and $f > 0$ on $\mathbb{R}_+^*$. It encodes the probability for a neuron of a given potential to spike at time t.

3. the connectivity parameters $(J^N_{i \to j})_{i,j}$.

4. the law of the initial potentials: we assume the neurons are initially i.i.d. with probability law ν.

The particle system

- $(\mathbf{N}^i(du,dz))_{i=1,\dots,N}$: independent Poisson measures on $\mathbb{R}_+ \times \mathbb{R}_+$ with intensity measure $dudz$.
- $(V_0^i)_{i=1,\dots,N}$: random variables on $\mathbb{R}_+$, *i.i.d.* of law ν

Then (V_t^i) is a *càdlàg* process solution of the SDE:

$$\begin{cases} V_t^i = V_0^i + \int_0^t b(V_u^i)du + \sum_{j \neq i} J_{j \to i}^N \int_0^t \int_{\mathbb{R}_+} \mathbb{1}_{\{z \leq f(V_{u-}^j)\}} \mathbf{N}^j(du,dz) \\ \qquad - \int_0^t \int_{\mathbb{R}_+} V_{u-}^i \mathbb{1}_{\{z \leq f(V_{u-}^i)\}} \mathbf{N}^i(du,dz). \end{cases}$$

The limit equation

Simplification: $J^N_{i \to j} = \frac{J}{N}$ for some constant $J \geq 0$

$$V^i_t = V^i_0 + \int_0^t b(V^i_u)du + \frac{J}{N} \sum_{j \neq i} \int_0^t \int_{\mathbb{R}_+} \mathbb{1}_{\{z \leq f(V^j_{u-})\}} \mathbf{N}^j(du, dz) - \int_0^t \int_{\mathbb{R}_+} V^i_{u-} \mathbb{1}_{\{z \leq f(V^i_{u-})\}} \mathbf{N}^i(du, dz).$$

$N \to \infty$: the **Mean-Field** equation

$$V_t = V_0 + \int_0^t b(V_u)du + J \int_0^t \mathbb{E}\, f(V_u)du - \int_0^t \int_{\mathbb{R}_+} V_{u-} \mathbb{1}_{\{z \leq f(V_{u-})\}} \mathbf{N}(du, dz) \tag{M-F}$$

or equivalently:

$$\begin{cases} \dfrac{d}{dt} V_t = b(V_t) + J\, \mathbb{E}\, f(V_t) \\ + \, (V_t)_{t \geq 0} \text{ jumps to 0 with rate } f(V_t) \end{cases}$$

A brief tour of previous results

1. Many earlier considerations by physicists (**Keywords: hazard rate model, generalized I & F**)
2. A. De Masi, A. Galves, E. Löcherbach, E. Presutti, “Hydrodynamic limit for interacting neuron”
3. N. Fournier, E. Löcherbach, “On a toy model of interacting neurons” **results on the long time behavior for** $b \equiv 0$
4. A. Drogoul, R. Veltz “Hopf bifurcation in a nonlocal nonlinear transport equation stemming from stochastic neural dynamics” **numerical evidence of an Hopf bifurcation** in a closed setting.

Few words on existence and pathwise-uniqueness

$$V_t = V_0 + \int_0^t b(V_u)du + J\int_0^t \mathbb{E}\, f(V_u)du - \int_0^t \int_{\mathbb{R}_+} V_{u-}\mathbb{1}_{\{z \leq f(V_{u-})\}}\mathbf{N}(du, dz)$$

Introduce a **linearized version** of the N-L equation (M-F).
Given $\boldsymbol{a} \equiv (a_t)_{t\geq 0}$, consider

$$Y_t^{\boldsymbol{a},\nu} = Y_0^{\boldsymbol{a},\nu} + \int_0^t b(Y_u^{\boldsymbol{a},\nu})du + \int_0^t a_u du - \int_0^t \int_{\mathbb{R}_+} Y_{u-}^{\boldsymbol{a},\nu}\mathbb{1}_{\{z \leq f(Y_{u-}^{\boldsymbol{a},\nu})\}}\mathbf{N}(du, dz)$$

Then $(Y_t^{\boldsymbol{a},\nu})$ is a solution of (M-F) if and only if:

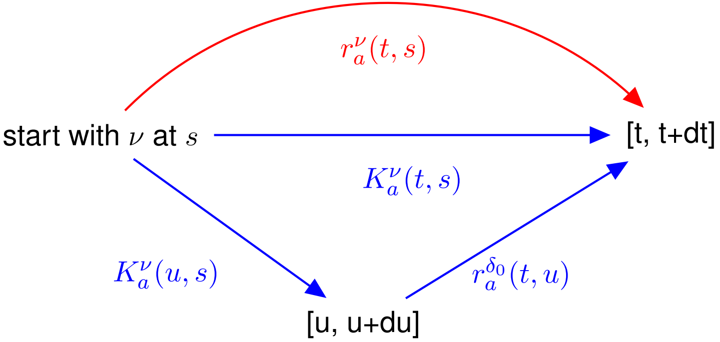
$$\forall t \geq 0, \quad a_t = J\,\mathbb{E}\, f(Y_t^{\boldsymbol{a},\nu}).$$

Denote by $Y_{t,s}^{\boldsymbol{a},\nu}$ the solution starting at time s.
Consider τ the time of the first jump of $Y_{t,s}^{\boldsymbol{a},\nu}$ and define:

$$K_{\boldsymbol{a}}^{\nu}(t,s) = -\frac{d}{dt}\mathbb{P}(\tau > t) \quad \text{and} \quad r_{\boldsymbol{a}}^{\nu}(t,s) = \mathbb{E}\, f(Y_{t,s}^{\boldsymbol{a},\nu}).$$

Then

$$r_{\boldsymbol{a}}^{\nu}(t,s) = K_{\boldsymbol{a}}^{\nu}(t,s) + \int_s^t r_{\boldsymbol{a}}^{\delta_0}(t,u) K_{\boldsymbol{a}}^{\nu}(u,s)du$$



What are the invariant measures of the N-L process?

$$V_t = V_0 + \int_0^t b(V_u)du + J \int_0^t \mathbb{E}\, f(V_u)du - \int_0^t \int_{\mathbb{R}_+} V_{u-} \mathbb{1}_{\{z \leq f(V_{u-})\}} \mathbf{N}(du, dz)$$

In (M-F) replace the interactions $J\,\mathbb{E}\, f(V_u)$ by the constant $\alpha \geq 0$:

$$Y_t^\alpha = Y_0^\alpha + \int_0^t b(Y_u^\alpha)du + \alpha t - \int_0^t \int_{\mathbb{R}_+} Y_{u-}^\alpha \mathbb{1}_{\{z \leq f(Y_{u-}^\alpha)\}} \mathbf{N}(du, dz).$$

This process has a unique invariant measure given by:

$$\nu_\alpha^\infty(dx) = \frac{\gamma(\alpha)}{b(x) + \alpha} \exp\left(- \int_0^x \frac{f(y)}{b(y) + \alpha} dy \right) \mathbb{1}_{[0, \sigma_\alpha)}(x) dx,$$

- $\sigma_\alpha = \inf\{x \geq 0,\ b(x) + \alpha = 0\} \in \mathbb{R}_+^* \cup \{+\infty\}.$
- $\gamma(\alpha)$ is the normalizing factor (such that $\int \nu_\alpha^\infty(dx) = 1$.)
- It holds that $\gamma(\alpha) = \nu_\alpha^\infty(f)$.

The invariant measures of (M-F) are exactly: $\{\nu_\alpha^\infty : \alpha = J\gamma(\alpha),\ \alpha \geq 0\}$.

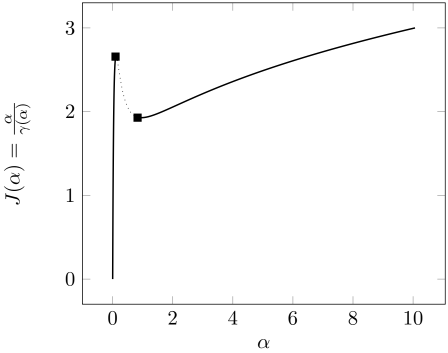
The case of small interactions

Theorem (C., Tanré, Veltz, SPA)

1. *the N-L SDE has a path-wise unique solution with* $\sup_{t\geq 0} \mathbb{E}\, f(V_t) < \infty$.
2. *if the interaction parameter J is small enough, then (V_t) has an* ***unique invariant measure*** *which is* ***globally stable****: starting from any initial condition, V_t converges in law to the unique invariant measure. The convergence is exponentially fast.*

Examples

The invariant measures are: $\{\nu_\alpha^\infty : J = \alpha/\gamma(\alpha),\ \alpha \geq 0\}$.
For $b(x) = 0.1 - x$, $f(x) = x^2$.



- $J < J_1$: one unique invariant measure.
- $J_1 < J < J_2$: **three** invariant measures, 2 are stable: **bi-stability**.
- $J > J_2$: one unique invariant measure.

Examples

Setting

$b(x) = 2 - 2x$, $f(x) = x^{10}$.

Always exactly one invariant measure. But if $J \in [0.71, 1.04]$ spontaneous oscillation of $t \to \mathbb{E} f(V_t)$ appears! The law of V_t asymptotically oscillates (Video !).

The invariant measure looses its stability. There is a Hopf bifurcation for $J \approx 0.71$.

Stability of an invariant measure

Consider ν_α^∞ such that $\alpha = J\gamma(\alpha)$.
Let $\mathcal{M}(f^2) := \{\nu \in \mathcal{P}(\mathbb{R}_+), \ \ \nu(f^2) < \infty\}$, equipped with

$$d(\nu, \mu) = \int_{\mathbb{R}_+} \left(1 + f^2(x)\right) |\nu - \mu|(dx).$$

Definition

We say that ν_α^∞ is locally exponentially stable with rate $\lambda > 0$ if $\forall \epsilon > 0$, $\exists \rho > 0$ such that

$$\forall \nu \in \mathcal{M}(f^2), \quad d(\nu, \nu_\alpha^\infty) < \rho \implies \sup_{t \geq 0} |J\,\mathbb{E}\, f(X_t^\nu) - \alpha| e^{\lambda t} < \epsilon.$$

Stability of an invariant measure

Theorem (2020, Arxiv)

Consider ν_α^∞ *such that* $\alpha = J\gamma(\alpha)$*. Define*

$$\forall t \geq 0, \quad \Theta_\alpha(t) = \int_0^\infty \frac{d}{dx} r_\alpha^x(t) \nu_\alpha^\infty(dx),$$

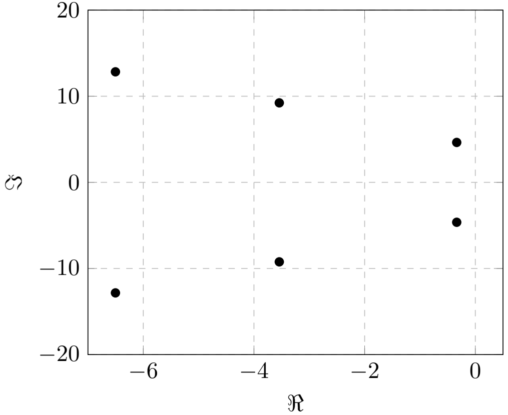
where $r_\alpha^x(t) = \mathbb{E}\, f(Y_{t,0}^{\alpha,\delta_x})$*. Assume that*

$$\sup\{\Re(z),\ z \in \mathbb{C},\ J\widehat{\Theta_\alpha}(z) = 1\} < 0.$$

Then ν_α^∞ *is locally stable.*

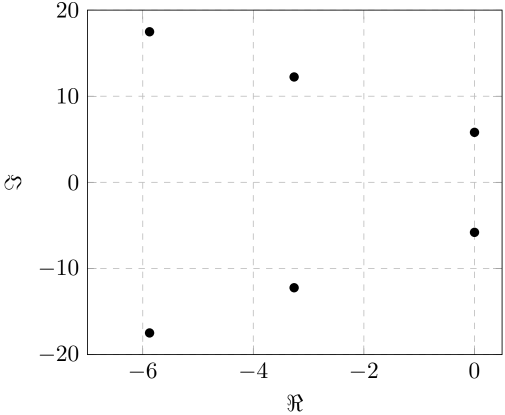
$\widehat{\Theta_\alpha}(z) := \int_0^\infty e^{-zt}\Theta_\alpha(t)dt$.
If $f + b' \geq 0$, this criteria is automatically satisfied.

Zeros of $J(\alpha)\widehat{\Theta}_\alpha(z) - 1$, $\alpha = 0.5$, $J(\alpha) \approx 0.558$



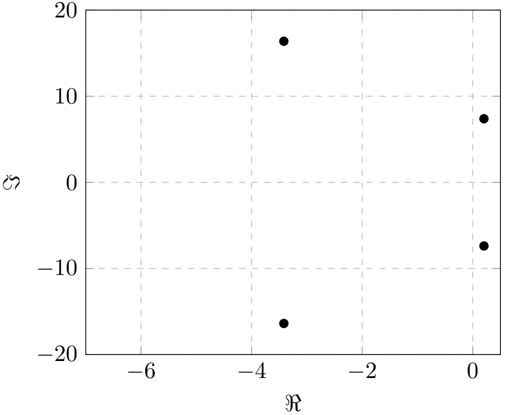
Example with $b(x) = 2 - 2x$ and $f(x) = x^{10}$.

Zeros of $J(\alpha)\widehat{\Theta}_\alpha(z) - 1$, $\alpha = 0.825$, $J(\alpha) \approx 0.71$



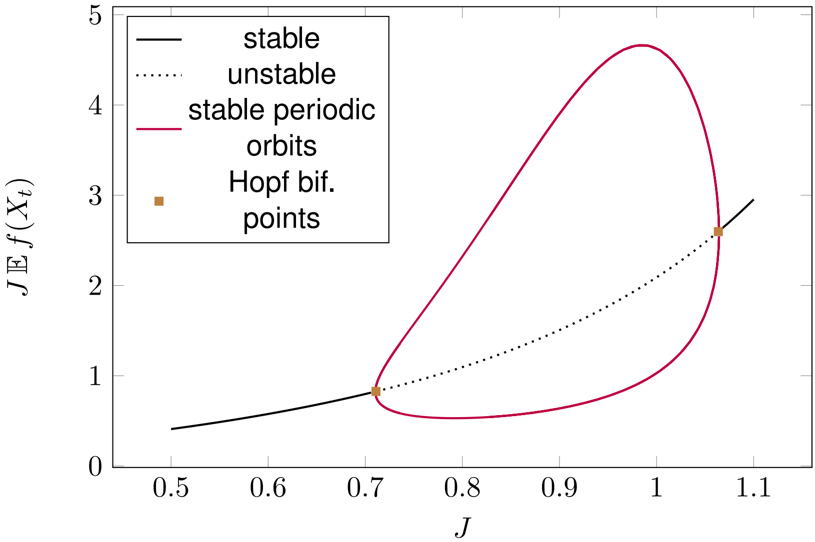
Example with $b(x) = 2 - 2x$ and $f(x) = x^{10}$.

Zeros of $J(\alpha)\widehat{\Theta}_\alpha(z) - 1$, $\alpha = 1.3$, $J(\alpha) \approx 0.85$



Example with $b(x) = 2 - 2x$ and $f(x) = x^{10}$.

Bifurcation diagram



Hopf bifurcation: spectral assumptions

Consider $\nu^{\infty}_{\alpha_0}$ an invariant measure of (N-L), for $J(\alpha_0) = \frac{\alpha_0}{\gamma(\alpha_0)}$. Assume

$$J(\alpha_0)\widehat{\Theta}_{\alpha_0}(\tfrac{i}{\tau_0}) = 1 \quad \text{and} \quad \frac{d}{dz}\widehat{\Theta}_{\alpha_0}(\tfrac{i}{\tau_0}) \neq 0.$$

Moreover assume that for all $n \in \mathbb{Z}\backslash\{-1, 1\}$,

$$J(\alpha_0)\widehat{\Theta}_{\alpha_0}(\tfrac{in}{\tau_0}) \neq 1.$$

The Implicit function theorem yields the existence of $\mathfrak{Z}_0(\alpha)$ such that around $(\alpha_0, \frac{i}{\tau_0})$,

$$J(\alpha)\widehat{\Theta}_{\alpha}(z) = 1 \iff z = \mathfrak{Z}_0(\alpha).$$

We assume that the zero crosses the imaginary axis with non-vanishing speed:

$$\Re \mathfrak{Z}_0'(\alpha_0) \neq 0, \quad \mathfrak{Z}_0'(\alpha) = \frac{d}{d\alpha}\mathfrak{Z}_0(\alpha)$$

Theorem (C., Tanré, Veltz, 2020, Arxiv)

Under these spectral assumptions, there exists a family of $2\pi\tau_v$-periodic solutions of (N-L), parametrized by $v \in (-v_0, v_0)$, for some $v_0 > 0$. That is, there exists a continuous curve $\{(\nu_v(\cdot), \alpha_v, \tau_v),\ v \in (-v_0, v_0)\}$ such that for all $v \in (-v_0, v_0)$:

- $(\nu_v(t))_{t\in\mathbb{R}}$ *is a $2\pi\tau_v$-periodic solution of (N-L) with $J = J(\alpha_v)$.*
- *The curve passes through $(\nu^\infty_{\alpha_0}, \alpha_0, \tau_0)$ for $v = 0$.*
- *Define the "periodic current" $\boldsymbol{a}_v$*

$$a_v(t) := J(\alpha_v) \int_{\mathbb{R}_+} f(x)\nu_v(t, dx).$$

It's mean over a period is equals to α_v

$$\frac{1}{2\pi\tau_v} \int_0^{2\pi\tau_v} a_v(u)du = \alpha_v.$$

Sketch of the Proof

Step 1. Given the "external current" $\boldsymbol{a} \in C_T$ (T-periodic),

$$Y^{\boldsymbol{a},\nu}_{t,s} = Y^{\boldsymbol{a},\nu}_{s,s} + \int_s^t b(Y^{\boldsymbol{a},\nu}_{u,s})du + \int_s^t a_u du - \int_s^t \int_{\mathbb{R}_+} Y^{\boldsymbol{a},\nu}_{u-,s} \mathbb{1}_{\{z \leq f(Y^{\boldsymbol{a},\nu}_{u-,s})\}} \mathbf{N}(du, dz).$$

Let $r^{\nu}_{\boldsymbol{a}}(t,s) := \mathbb{E}\, f(Y^{\boldsymbol{a},\nu}_{t,s})$ its jump rate.
We want to define the "asymptotic" periodic jump rate by:

$$\forall t \in \mathbb{R}, \quad \rho_{\boldsymbol{a}}(t) = \lim_{k \in \mathbb{N},\ k \to \infty} r^{\delta_0}_{\boldsymbol{a}}(t, -Tk).$$

Does this limit exists? What are the properties of $\rho_{\boldsymbol{a}}$?

Let τ be the time of the first jump of Y and $K^{\nu}_{\boldsymbol{a}}(t,s) = -\frac{d}{dt}\mathbb{P}(\tau > t)$.
Recall the Volterra Integral equation

$$r^{\delta_0}_{\boldsymbol{a}}(t,-kT) = K^{\delta_0}_{\boldsymbol{a}}(t,-kT) + \int_{-kT}^{t} K^{\delta_0}_{\boldsymbol{a}}(t,u) r^{\delta_0}_{\boldsymbol{a}}(u,-kT)du$$

The limit $k \to \infty$ gives:

$$\begin{aligned}\rho_{\boldsymbol{a}}(t) &= \int_{-\infty}^{t} K^{\delta_0}_{\boldsymbol{a}}(t,u)\rho_{\boldsymbol{a}}(u)du.\\ &= \int_{0}^{T} K^{T}_{\boldsymbol{a}}(t,u)\rho_{\boldsymbol{a}}(u)du, \quad \text{with} \quad K^{T}_{\boldsymbol{a}}(t,u) := \sum_{k\geq 0} K^{\delta_0}_{\boldsymbol{a}}(t,u-kT).\end{aligned}$$

Problem: this equation does not characterize $\rho_{\boldsymbol{a}}$ (if $\rho_{\boldsymbol{a}}$ is solution then $2\rho_{\boldsymbol{a}}$ is also solution).

A probabilistic interpretation

Define $(\tau_i)_{i\geq 1}$ the times of the successive jumps of $(Y_t^{\boldsymbol{a},\nu})_{t\geq 0}$. Let $\phi_i \in [0,T)$ be the **phase** of the i-ith jump

$$\phi_i := \tau_i - \left\lfloor \frac{\tau_i}{T} \right\rfloor T.$$

Then $(\phi_i)_{i\geq 0}$ **is a Markov Chain on** $[0,T]$**, with a transition probability given by** $K_{\boldsymbol{a}}^T$**.**
The asymptotic jump rate $\rho_{\boldsymbol{a}}$ is proportional to the invariant measure of this Markov Chain.

Step 2. To find a periodic solution, it suffices to find $\boldsymbol{a} \in C_T$ such that

$$\forall t \in [0, T], \quad a(t) = J\rho_{\boldsymbol{a}}(t).$$

A difficulty: the period T itself is unknown. For $\boldsymbol{a} \in C_{2\pi}$ and $\tau > 0$, we define

$$\forall t \in \mathbb{R}, \quad \rho_{\boldsymbol{a},\tau}(t) := \rho_{\boldsymbol{d}}(\tau t),$$

with $d(t) := a(t/\tau)$. We then show that

$$\rho_{\boldsymbol{a},\tau} : C_{2\pi} \times \mathbb{R}_+^* \to C_{2\pi}$$

is $\mathcal{C}^2$ Fréchet differentiable.

A key property

Let $C^0_{2\pi} := \{h \in C_{2\pi}, \int_0^{2\pi} h(u)du = 0\}$.
Write $\boldsymbol{a} = \alpha + \boldsymbol{h}$ with $\boldsymbol{h} \in C^0_{2\pi}$ and $\alpha > 0$.

The mean number of spikes per period is

$$\frac{1}{2\pi}\int_0^{2\pi} \rho_{\boldsymbol{\alpha}+\boldsymbol{h},\boldsymbol{\tau}}(u)du = \gamma(\alpha).$$

It is independent of $\boldsymbol{h}$!

Let $C^0_{2\pi} := \{h \in C_{2\pi}, \int_0^{2\pi} h(u)du = 0\}$.
Step 3. We now look at the zeros of:

$$G(h, \alpha, \tau) := (\alpha + h) - J(\alpha)\rho_{\alpha+h,\tau}.$$

We have for all $\alpha, \tau > 0$:

$$G(0, \alpha, \tau) = \alpha - J(\alpha)\gamma(\alpha) = 0.$$

Those are the trivial zeros. We need to find the **non-trivial** zeros of G.
We apply the Lyapounov-Schmidt reduction method to reduce to **dimension 2**.

The differential of G: $D_h G(0, \alpha_0, \tau_0)$ can be written using a convolution involving Θ_{α_0}. For $h \in C^0_{2\pi}$, we have

$$D_h G(0, \alpha_0, \tau_0) \cdot h = h - J(\alpha_0) \int_{\mathbb{R}} \tau_0 \Theta_{\alpha_0}(\tau_0 u) h(t-u) du.$$

By Lyapounov-Schmidt, we reduce the problem to dimension 2:

$$\text{dim}\,(\text{Ker} D_h G(0, \alpha_0, \tau_0)) = 2.$$

We then characterize all the solutions locally in a neighborhood of $(0, \alpha_0, \tau_0)$.

Conclusion and perspectives

- The mean-field equation is a McKean-Vlasov SDE and we study its long time behavior.
- A key tool: the **Volterra integral equation**.
- Small connectivity (J small enough) $\implies$ relaxation to equilibrium.
- J arbitrary: spectral condition ensuring the **local stability**.
- When the invariant measure losses its stability, this typically leads to a **Hopf bifurcation**.

The two papers on arXiv
"Mean-field model of Integrate-and-Fire neurons: non-linear stability of the stationary solutions"
"Hopf bifurcation in a Mean-Field model of spiking neurons"