Metastability of a system of interacting neurons

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Joint work with Eva Löcherbach

The model

- N neurons, potential $u \geqslant 0$.
- Jump rate (spikes) λ :

$$\mathbb{P}(\text{emits a spike during } [0,t]) \;=\; \lambda(u)\, t + \underset{t\to 0}{o}(t).$$

  At the jump time, reset to its resting value ($u = 0$).
- Mean-field and excitative network : when neuron j spikes,

$$u_i \leftarrow u_i + \frac{h}{N} \qquad i \neq j\,, h > 0\,.$$

- Between spikes :

$$\dot{u} = -\alpha u\,, \qquad \alpha > 0$$

- Parameters : h, α, λ.

A first interesting result

Introduced by Galves, Löcherbach (2013), studied by De Masi, Galves, Löcherbach, Presutti (2015) Fournier, Löcherbach (2016), Robert, Touboul (2016), Duarte, Ost (2016).

Assumption on λ (for the whole talk)

$\lambda : \mathbb{R}_+ \to \mathbb{R}_+$ is continuous bounded non-decreasing and $\lambda(0) = 0$.

Theorem (Duarte Ost 2016)

If λ is differentiable at 0 then, for all N, α, h, almost surely, there is only a finite number of spikes (i.e. there exists a random finite time after which there is no spike and the system relaxes towards 0).

Analogy with a population model

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- Death rate : $\mu > 0$.
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$$\mathbb{P}\,(\text{apocalypse}) \geqslant q_n = e^{-N\mu}(1 - e^{-\nu})^N > 0\,.$$

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- Law of large number : if n_0 is of order $N \to +\infty$, then

$$\partial_t n_t \simeq -\mu n_t + (1 - n_t/N)\nu n_t\,.$$

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- If $\nu > \mu$, x admits a unique fixed point $x_* > 0$, globally attractive.
- We expect $n_t/N \simeq x_*$ for all $1 \ll t \ll e^{\kappa N}$ for some $\kappa > 0$, and an abrupt (unpredictable) extinction : **metastability**.

The Markov process

The process $U^N(t) = U(t) = (U_i(t))_{i\in[\![1,N]\!]}$, with $U_i(t)$ the membrane potential of neuron i at time t, is a Markov process on $\mathbb{R}_+^N$ with generator A given by

$$A\varphi(u) \ = \ -\alpha u \cdot \nabla\varphi(u) + \sum_{i=1}^{N} \lambda(u_i)\left(\varphi(u+\Delta_i(u)) - \varphi(u)\right)$$

with

$$(\Delta_i(u))_j = \begin{cases} \frac{h}{N} & j \neq i \\ -u_i & j = i \end{cases},$$

Let L^N be the last spiking time (which is not a stopping time).

The non-linear limit process

Propagation of chaos phenomenon :

$$\frac{h}{N}\sharp\{\text{spike of a neuron } j \text{ during } [0,t],\ j\neq i\} \underset{N\to+\infty}{\simeq} h\int_0^t \mathbb{E}\left(\lambda(U_i(s))\right)\mathrm{d}s\,.$$

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Limit process $\bar{U}$ (non-linear/time inhomogeneous) with generator

$$\bar{A}_t\varphi(u) \ = \ \left(-\alpha u + h\int_0^{+\infty}\lambda(w)\eta_t(\mathrm{d}w)\right)\partial_u\varphi + \lambda(u)\left(\varphi(0)-\varphi(u)\right)$$

with $\eta_t = \mathcal{L}aw(\bar{U}(t))$, which solves

$$\begin{aligned} \partial_t\eta_t &= \partial_u\left[\left(\alpha u + h\int_0^{+\infty}\lambda(w)\eta_t(\mathrm{d}w)\right)\eta_t\right] - \lambda\eta_t \\ \eta_t(0) &= \int_0^{+\infty}\lambda(w)\eta_t(\mathrm{d}w)\,. \end{aligned}$$

The interaction, a jump mechanism, gives in the limit a non-linear deterministic drift.

A phase transition

Theorem

1. If $h\lambda'(0) > \alpha$, the non-linear system admits at least one non-zero stationary solution ($\eta_t = \mathcal{L}aw(\bar{U}(t)) = \eta_0$ for all $t \geqslant 0$ with $\eta_0 \neq \delta_0$) and there exists $c > 0$ such that for all initial condition $\nu_0 \neq \delta_0$, $\int_0^{+\infty} \lambda(w)\nu_t(\mathrm{d}w) \geqslant c$ for t large enough. The non-zero stationary solutions have a density of the form
$$g(x) = \frac{p}{hp - \alpha x} \exp\left(- \int_0^x \frac{\lambda(y)}{hp - \alpha y} dy \right) \mathbf{1}_{\{0 \leq x < hp/\alpha\}}$$
with $p = \int_0^{\infty} \lambda(w) g(x) \mathrm{d}x$.
2. If $h\lambda'(0) < \alpha$ and if λ is concave, the only stationary solution of the non-linear equation is δ_0, globally attractive in Wasserstein distance :
$$\mathbb{E}\left(\bar{U}(t)\right) \leqslant e^{-(\alpha - h\lambda'(0))t} \mathbb{E}\left(\bar{U}(0)\right).$$

Exponentially long survival

For simplicity, in the rest of the talk :

Hypothèse

$\lambda(u) = (ku) \wedge \lambda_*$ for some $k, \lambda * > 0$. We write $a = \alpha/(kh)$ and $b = \lambda_*/(kh)$.

We are interested in the case where a and b are small.

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Theorem

Assume that $a + b < 1$ and that for all $\varepsilon > 0$, there exists $x_0 > 0$ such that $\mathbb{P}(\sum_{i=1}^{N} \lambda(U_i^N(0)) \geqslant N x_0) \geqslant 1 - \varepsilon$ for all N large enough (ok if the $U_i(0)$ are i.i.d. non a.s. zero). Then, for all $\delta > 0$,

$$\lim_{N \to +\infty} \mathbb{P}\left(L^N \geqslant e^{(W_0 - \delta)N}\right) = 1, \qquad \text{with}$$

$$W_0 = \frac{\lambda_*}{kh}\left(\frac{kh - \lambda_*}{r} - 1 - \ln\left(\frac{kh - \lambda_*}{r}\right) - \frac{1}{2}\ln^2\left(\frac{kh - \lambda_*}{r}\right)\right) > 0\,.$$

Propagation of chaos

Theorem

Let $U^N = (U_1^N, \dots, U_N^N)$ be a system of interacting neurons with i.i.d. initial conditions and $\bar{U}^N = (\bar{U}_1^N, \dots, \bar{U}_N^N)$ be independent non-linear processes with $\bar{U}^N(0) = U^N(0)$, so that the jump times of both processes are defined with the same Poisson measures (synchronous coupling). Then for all $t \geqslant 0$ and $\varepsilon > 0$,

$$\mathbb{E}\left(\sum_{i=1}^N |\bar{U}_i^N(t) - U_i^N(t)|\right) \leqslant h\left(\sqrt{\lambda_* t} + 2t\lambda_*\right) e^{(\alpha+hk+\lambda_*)t}\sqrt{N}$$

$$\mathbb{P}\left(\sup_{s\in[0,t]} \sum_{i=1}^N |U_i^N(s) - \bar{U}_i^N(s)| \geqslant \varepsilon\right) \leqslant \frac{C_t\sqrt{N}}{\varepsilon},$$

with $C_t = 4h(1+\sqrt{\lambda_* t} + t\lambda_*)^2 e^{(2\alpha+hk+\lambda_*)t}$.

Convergence to equilibrium for the non-linear process

For $\nu, \mu \in \mathcal{P}(\mathbb{R}_+)$, we consider the Wasserstein distance

$$\mathcal{W}_1(\nu, \mu) = \inf\{\mathbb{E}(|X - Y|), \ X \sim \nu, \ Y \sim \mu\}.$$

Theorem

For a and b small enough (explicit condition), there exists $\kappa \in (0,1)$ such that : for all $\gamma > 0$, there exists $C_\gamma > 0$ so that for all initial conditions μ_0^1, μ_0^2 with $\int_0^\infty \lambda(w)\mu_0^i(w)\mathrm{d}w \geqslant \gamma$, the corresponding solutions of the non-linear equation satisfy, for all $t \geqslant 0$,

$$W_1(\mu_t^1, \mu_t^2) \leqslant C_\gamma \kappa^t W_1(\mu_0^1, \mu_0^2).$$

In particular there is a unique globally attractive equilibrium (if $\mu_0 \neq \delta_0$).

Asymptotic exponentiality

Theorem

Suppose that a and b are small enough (explicit condition), write $\bar\lambda(u) = N^{-1}\sum_{i=1}^N \lambda(u_i)$ and $\tau = \inf\{t \geqslant 0,\ U^N \notin \mathcal{D}\}$ with either :

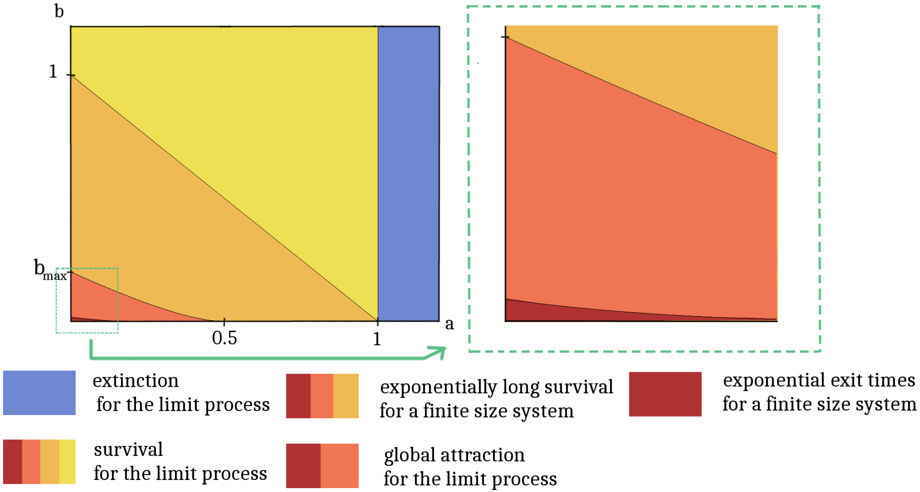
1. $\mathcal{D} = \{\bar\lambda \geqslant \gamma\}$ for $\gamma > 0$ small enough (explicit condition).
2. $\mathcal{D}$ measurable $\mathbb{R}_+^N$ such that, for some $\delta > 0$, $\{p_* - \delta \leqslant \bar\lambda \leqslant p_* + \delta\} \subset \mathcal{D} \subset \{\bar\lambda \geqslant \delta\}$, with $p_* = \int_0^{+\infty} \lambda(w) g(\mathrm{d}w)$ where g is the unique non-linear equilibrium.

In the case (1) set $\mathcal{K} = \{\bar\lambda \geqslant \delta\}$ for some $\delta > \gamma$ and in the case (2), $\mathcal{K} = \{p_* - \gamma \leqslant \bar\lambda \leqslant p_* + \gamma\}$ for some $\gamma \in (0, \delta)$. Then, in both cases, there exist C, θ, N_0 such that $N \geqslant N_0$,

$$\sup_{u,v\in\mathcal{K}} \left| \frac{\mathbb{E}_u(\tau)}{\mathbb{E}_v(\tau)} - 1 \right| + \sup_{t\geqslant 0}\sup_{u\in\mathcal{K}} \left| \mathbb{P}_u(\tau \geqslant t\mathbb{E}_u(\tau)) - e^{-t} \right| \leqslant \varepsilon(N)$$

with $\varepsilon(N) = Ce^{-\theta N}$ in the case (1) and $C \ln N / N^{1/4}$ in the case (2).

Summary of the results (except propagation of chaos)



Synchronous coupling

Given a process $(Y_t)_{t\geqslant 0}$ with jump rate $y \mapsto \lambda(y)$, the jumps of Y can be realized as the jumps of

$$\int_{[0,t]\times\mathbb{R}_+} \mathbf{1}_{z\leqslant\lambda(Y_{s-})}\pi(\mathrm{d}s,\mathrm{d}z)$$

with π a standard Poisson measure over $\mathbb{R}_+ \times \mathbb{R}_+$.

Most our results are based on synchronous couplings : we define two different processes Y and Z with the same Poisson measure. In other words, the processes are forced to jump together as much as possible. Asynchronous jumps occur at rate $|\lambda(Y_t) - \lambda(Z_t)|$.

An auxiliary process

To prove that the last spiking time is exponentially large with N, we would like to study

$$\Lambda_N(t) \;=\; \frac{1}{N}\sum_{i=1}^{N}\lambda\left(U_i(t)\right)$$

(this is just a real number, containing the useful information concerning the jump times). However it is not Markov (there is no closed equation for its evolution).

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The idea : design a proces Z_N on $\mathbb{R}_+$ with the following properties :

- Z_N Markov (simple explicit evolution)
- $Z_N(t) \leqslant \Lambda_N(t)$ for all $t \geqslant 0$.
- All jumps of Z_N are jumps of U^N.

Then we bound the last jump time of U^N by the one of Z_N, that we compare to $\inf\{t \geqslant 0, Z_N \leqslant z\}$ for some small $z > 0$, which is then studied with classical Large Deviations results.

Evolution of Λ_N

- Between jump times, $\dot{U}_i = -\alpha U_i(t)$, where

$$\dot{\Lambda}_N \geqslant -\alpha \Lambda_N$$

- At a spiking time t of the neuron i, $\lambda(U_i)$ decreases at most by λ_*, and for all $j \neq i$ with $U_j \leqslant \lambda_*/k - h/N$, $\lambda(U_j)$ increases by kh/N. Besides, since λ is non-decreasing,

$$\sharp \left\{ j \in [\![1, N]\!],\ U_j(t-) \leqslant \frac{\lambda_*}{k} - \frac{h}{N} \right\} \geqslant N \left(1 - \frac{\Lambda_N(t-)}{\lambda_*(1 - kh/N)} \right),$$

and thus

$$\Lambda_N(t) - \Lambda_N(t-) \ \geqslant \ -\frac{\lambda_*}{N} + \frac{kh}{N} \left(1 - \frac{\Lambda_N(t-)}{\lambda_*(1 - kh/N)} \right).$$

In particular, if $\lambda_* < kh$ (i.e. $b < 1$), below some positive threshold, a jump can only increase Λ_N.

- Jumps occur at a rate $N\Lambda_N$.

Construction of Z_N

Z_N designed by taking the worst cases in the evolution of Λ_N :

- Between jumps, $\dot{Z}_N = -\alpha Z_N$.
- At a jump time,

$$Z_N(t) \;=\; -\frac{\lambda_*}{N} + \frac{kh}{N}\left(1 - \frac{Z_N(t-)}{\lambda_*(1-kh/N)}\right)_+$$

  (with a slight modification close to $z_* := \lambda_*(1-\lambda_*/kh)$, above which the jump of Λ_N can be negative : we have to avoid the situation where $\Lambda_N > z_* > Z_N$ and Λ_N jumps alone and pass below Z_N).
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The synchronous coupling of U^N and Z_N (with $Z_N(0) = max(z_*, \Lambda_N(0))$) ensures that $\Lambda_N(t) \geqslant Z_N(t)$ for all $t \geqslant 0$ (and in particular any jump Z_N is a jump of U^N).

Asymptotic of Z_N

For $N \to +\infty$, on any time interval $[0, t]$, Z_N converges to the solution of

$$\dot{z} \;=\; -\alpha z + \left(kh\left(1 - \frac{z}{\lambda_*}\right) - \lambda_* \right) \max(z, z_*)\,,$$

which, under the condition $\lambda_* + \alpha < kh$ (i.e. $a + b < 1$) has a unique positive equilibrium.

1. From a Large Deviation result on Z_N we deduce that the extinction of U^N is exponentially large.
2. Combining this with propagation of chaos (in finite time), we get that a solution of the non-linear equation satisfies $\mathbb{E}\left(\lambda(\bar{U}(t))\right) \geqslant z(t)$ with z a solution of the ODE (hence the instability of δ_0 ; this is also an ingredient involved in the global convergence toward equilibrium).

A general framework

Let $(X_t)_{t\geqslant 0}$ be a Markov process on a polish space E, $\mathcal{D},\mathcal{K}\subset E$ measurables with $\emptyset\neq\mathcal{K}\subset\mathcal{D}$, and we write $\tau_A=\inf\{t\geqslant 0,\ X_t\in A\}$ for $A\subset E$. Let $\varepsilon_1,\varepsilon_2,\varepsilon_3\in[0,1]$ and $s_1\geqslant s_2>0$ such that :

1. Exit from $\mathcal{D}$ from the stable zone $\mathcal{K}$ unlikely in a time s_1 :

$$\varepsilon_1 \ \geqslant\ \sup_{x\in\mathcal{K}} \mathbb{P}_x\left(\tau_{\mathcal{D}^c}\leqslant s_1\right).$$

2. From a point of $\mathcal{D}$, if we haven't exited before time s_2, we are probably in the stable zone $\mathcal{K}$:

$$\varepsilon_2 \ \geqslant\ \sup_{x\in\mathcal{D}} \mathbb{P}_x\left(\tau_{\mathcal{D}^c}\wedge\tau_{\mathcal{K}}>s_2\right).$$

3. Loss of memory in $\mathcal{K}$ in time s_1 : for all $x,y\in\mathcal{K}$ there exists a coupling $(X_t,Y_t)_{t\geqslant 0}$ of two processes initially at x and y with

$$\mathbb{P}\left(X_t=Y_t\ \forall t\geqslant s_1\right)\ \geqslant\ 1-\varepsilon_3\,.$$

A general result

Adapting a result of Brassesco, Olivieri, Vares (1998) for low-temperature diffusions :

Theorem

Suppose that $\varepsilon_1 + \varepsilon_2 + \varepsilon_3 \leqslant 1/2$ and $\tau := \tau_{\mathcal{D}^c}$ is $\mathbb{P}_{x_0}$-a.s. for some $x_0 \in \mathcal{K}$. Then there exist $\beta > 0$ such that $\mathbb{P}_{x_0}(\tau > \beta) \in [1/4, 3/4]$. Suppose that there exist $C, \delta, M \geqslant 0$ such that

$$\frac{s_2}{\beta} \vee (\varepsilon_2 + \varepsilon_3) \leqslant Ce^{-\delta M}.$$

then there exist $K, M_0 > 0$ (depending only on C, δ, not on M) such that, if $M \geqslant M_0$, then $\sup_{x \in \mathcal{D}} \mathbb{E}_x(\tau) < +\infty$ and for all $x, y \in \mathcal{K}$,

$$\left| \frac{\mathbb{E}_x(\tau)}{\mathbb{E}_y(\tau)} - 1 \right| + \sup_{t \geqslant 0} \left| \mathbb{P}_x(\tau \geqslant t\mathbb{E}_x(\tau)) - e^{-t} \right| \leqslant K' M^3 e^{-\min(\delta/3, 1/2)M}$$

For the neuron model

- The return time to $\mathcal{K}$ and the exit time from $\mathcal{D}$ from $\mathcal{K}$ are easily obtaining by comparison with the auxiliary process Z_N or with the limit process $\bar{U}$.
- For the coupling from $\mathcal{K}$, we start by proving that

$$\mathbb{E}\left(\sum_{i=1}^{N}|\lambda(U_i^N(t))-\lambda(\tilde{U}_i^N(t))|\right) \quad \leqslant \quad C\left(\kappa^t N + e^{-\theta N}\right)$$

following the strategy used for the convergence of the non-linear system.
- Then we couple $U^N(t)=\tilde{U}^N(t)$ in a time $t=N^\alpha$, $\alpha\in(0,1]$:
  - At half the time, $N^\alpha/2$, the rates are close. There is probably no asynchronous jump in the interval $[N^\alpha/2, N^\alpha]$.
  - Moreover, on this interval, each pair $(U_i^N, \tilde{U}_i^N)$ probably has a (synchronous) spike, from which $U_i^N(s)=\tilde{U}_i^N(s)$ (up to the first asynchronous jump in the system).

1. Model and results

2. Some ideas of the proofs
   - Coupling with an auxiliary process
   - Exponentiality of exit times
   - Convergence for the non-linear system

Synchronous coupling

Consider a non-linear process solving (witing $\bar{\lambda}_t = \mathbb{E}(\lambda(\bar{U}(t)))$

$$d\bar{U}(t) = -\alpha\bar{U}(t)dt + h\bar{\lambda}_t dt - \bar{U}(t-)\int_{\mathbb{R}_+} \mathbf{1}_{\{z\leq\lambda(\bar{U}(t-))\}}\pi(dt,dz),$$

and a similar $\hat{U}$ (same π) but with a different initial law. We want

$$\mathbb{E}\left(|\bar{U}(t) - \hat{U}(t)|\right) \leqslant C\kappa^t, \qquad \kappa\in(0,1).$$

We first prove

$$\mathbb{E}\left(\left|\lambda\left(\bar{U}(t)\right) - \lambda\left(\hat{U}(t)\right)\right|\right) \leqslant C\kappa^t, \qquad \kappa\in(0,1),$$

The first point is then proven similarly and by using this first information.

Synchronous coupling

- Saturation : for $u \geqslant u_* = \lambda_*/k$, $\lambda(u) = \lambda_*$. for a and b small enough and $\bar{\lambda}_0$ large enough (which we can assume), the solution of

$$d\bar{U}(t) = -\alpha\bar{U}(t)dt + h\bar{\lambda}_t dt \tag{1}$$

starting from 0 upcrosses the threshold u_* (and stays above).

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- Without any spike, the two processes $\bar{U}$ and $\hat{U}$ upcrosses the threshold and then $\lambda(\tilde{U}(s)) = \lambda(\hat{U}(s))$ up to the next jump (which will thus be synchronous).

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- Problem : at this synchronous jump, the derivatives being different, the (rates of the) processes immediatly split. Then there can be asynchronous jumps.
- Solution : if a and b are small enough, not only (1) upcrosses the threshold u_*, but it upcrosses it *fast*, which means the time window for asynchronous jumps is short.

Truncated Gronwall

Considering the different cases (no jump, only synchronous jumps, at least one asynchronous jump), we get that $f(t) := \mathbb{E}\left(|\lambda(\bar{U}(t)) - \lambda(\hat{U}(t))|\right)$ satisfies

$$f(t) \leqslant \theta \int_{(t-t_*)_+}^{t} f(s)\mathrm{d}s + \left(kf \int_0^t f(s)\mathrm{d}s + f(0)\right) \mathbf{1}_{t\in[0,t_*]}$$

with $\theta = kh\lambda_* t_* + \lambda_*$ and t_* (roughly) the hitting time of u_* by (1). Iterating Gronwall's lemma, for $n \in \mathbb{N}$ and $t \in [nt_*, (n+1)t_*]$,

$$f(t) \leqslant (\theta t_* e^{\theta t_*})^n e^{(\theta+kh)t_*} f(0) .$$

Finally, for a, b small enough, θt_* is smaller than the solution x of $xe^x = 1$, which concludes.

Conclusion

- Can we get the asymptotic exponentiality of L^N ?
- Could the (quantitative) bounds proven to establish the asymptotic exponentiality be used to get the convergence of the process conditioned to have stayed in $\mathcal{D}$ toward its quasi-stationary distribution (with a rate independent from N, or at least polynomial in N) ?

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Thanks for your attention !