Spiking neural models: from point processes to partial differential equations.

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Outline

1. Introduction

2. A key tool: The thinning procedure

3. First approach: Mathematical expectation

4. Second approach: Mean-field interactions
1 Introduction
   - Neurobiologic context
   - Microscopic modelling
   - Macroscopic modelling

2 A key tool: The thinning procedure

3 First approach: Mathematical expectation

4 Second approach: Mean-field interactions
Biological context

- **Action potential**: brief and stereotyped phenomenon (*spike*).
- **Physiological constraint**: refractory period.
- **Model** interacting spiking neurons.
Microscopic modelling of spike trains

Time point processes = random countable sets of times (points of \( \mathbb{R} \) or \( \mathbb{R}_+ \)).

- Point process: \( N = \{ T_i, i \in \mathbb{Z} \} \) s.t. \( \cdots < T_0 \leq 0 < T_1 < \cdots \).
- Point measure: \( N(dt) = \sum_{i \in \mathbb{Z}} \delta_{T_i}(dt) \). Hence, \( \int f(t) N(dt) = \sum_{i \in \mathbb{Z}} f(T_i) \).
Microscopic modelling of spike trains

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- Age process: $(S_{t-})_{t \geq 0}$.

Age = delay since last spike.
Microscopic modelling

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- Age process: $(S_{t-})_{t \geq 0}$.

Stochastic intensity

- Heuristically,
  \[
  \lambda_t = \lim_{\Delta t \to 0} \frac{1}{\Delta t} \mathbb{P} \left( N([t, t+\Delta t]) = 1 \mid \mathcal{F}_{t-}^N \right),
  \]
  where $\mathcal{F}_{t-}^N$ denotes the history of $N$ before time $t$.
- Local behaviour: probability to find a new spike.
- May depend on the past (e.g. refractory period, aftershocks).
Some classical point processes in neuroscience

- Poisson process: $\lambda_t = \lambda(t)$ (deterministic, no refractory period).
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![Diagram of Poisson and Renewal processes](attachment:image.png)
Some classical point processes in neuroscience

- Poisson process: \( \lambda_t = \lambda(t) \) (deterministic, no refractory period).
- Renewal process: \( \lambda_t = f(S_t^-) \iff \text{i.i.d. ISIs. (refractory period)} \)
  
  ![Diagram of renewal process with ISIs](image)

- Linear Hawkes process: \( \lambda_t = \mu + \int_{-\infty}^{t^-} h(t-x)N(dx) \quad h \geq 0 \)
Some classical point processes in neuroscience

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- **Linear Hawkes process**: $\lambda_t = \mu + \int_{-\infty}^{t-} h(t-x)N(dx) \quad h \geq 0$
  
  $= \mu + \sum_{V \in N, V < t} h(t-V)$.
Age structured equations (K. Pakdaman, B. Perthame, D. Salort, 2010)

- Age = delay since last spike.
- \( n(t, s) = \begin{cases} 
  \text{probability density of finding a neuron with age } s \text{ at time } t. \\
  \text{ratio of the neural population with age } s \text{ at time } t.
\end{cases} \)

\[
\begin{align*}
\frac{\partial n(t, s)}{\partial t} + \frac{\partial n(t, s)}{\partial s} + p(s, X(t)) n(t, s) &= 0 \\
n(t, 0) &= \int_{0}^{+\infty} p(s, X(t)) n(t, s) \, ds.
\end{align*}
\] (PPS)
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\end{align*}
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Parameters

- rate function \( p \). For example, \( p(s,X) = 1\{s > \sigma(X)\}. \)

\[X(t) = \int_0^t d(t-x)n(x,0)dx \quad \text{(global neural activity)}\]

- Propagation time.
- \( d = \) delay function. For example, \( d(x) = e^{-\tau x}. \)
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- Propagation time.
- \( d = \text{delay function}. \) For example, \( d(x) = e^{-\tau x} \).

Cornerstone: \( X(t) \leftrightarrow \int_{0}^{t-} h(t-x)N(dx) \).
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2. A key tool: The thinning procedure

3. First approach: Mathematical expectation

4. Second approach: Mean-field interactions
Lewis and Shedler’s Thinning, 1979

- \( \Pi \) is a Poisson process with intensity 1.
- \( \Pi(dt, dx) = \sum \delta_x \).
- \( \mathbb{E}[\Pi(dt, dx)] = dtdx \).
- Spatial independence.

\( \mathbb{R}_+ \)

0

\( t \)
Lewis and Shedler’s Thinning, 1979

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Spatial independence.

\( \lambda \) is deterministic.
\( N \) admits \( \lambda \) as an intensity.
Ogata’s Thinning, 1981

- Π is a Poisson process with intensity 1.
- Π(dt, dx) = \sum \delta_x.
- E [Π(dt, dx)] = dt dx.
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Ogata’s Thinning, 1981

- $\Pi$ is a Poisson process with intensity 1.
- $\Pi(dt, dx) = \sum \delta_x$.
- $\mathbb{E}[\Pi(dt, dx)] = dt dx$.
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- $\lambda$ is random.
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Spatial independence.

\[ \lambda \text{ is random.} \]

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Introduction

1/ Expectation

Ogata's Thinning, 1981

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Spatial independence.

\[ \lambda \text{ is random.} \]
\[ N \text{ admits } \lambda \text{ as an intensity.} \]
1. Introduction

2. A key tool: The thinning procedure

3. First approach: Mathematical expectation
   - The system satisfied in expectation
   - Coming back to the examples

4. Second approach: Mean-field interactions
Technical construction

- (PPS) system: $n(t,.)$ is the probability density of the age at time $t$.
- One neuron scale: at fixed time $t$, the distribution is a Dirac mass at $S_t$.
Technical construction

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Microscopic measure

- We construct an ad hoc random measure \( U \) which satisfies a system of SDEs driven by Poisson noise similar to (PPS) (thinning).

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U(t, ds) = \delta_{S_t^-}(ds)
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**Microscopic measure**
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  \]

**Macroscopic measure**
- We consider the expectation measure \( u(dt,ds) = \mathbb{E}[U(dt,ds)] \).
  \( u(t,.) \) is the distribution of \( S_t^- \).
System in expectation

Theorem

Let \( \lambda_t \) be some non negative predictable process which is \( L_{loc}^1 \) in expectation. The measure \( u \) satisfies the following system,

\[
\begin{align*}
\frac{\partial}{\partial t} u(dt, ds) + \frac{\partial}{\partial s} u(dt, ds) + \rho_{\lambda, P_0}(t, s) u(dt, ds) &= 0, \\
u(dt, 0) &= \int_{s \in \mathbb{R}_+} \rho_{\lambda, P_0}(t, s) u(t, ds) dt,
\end{align*}
\]

(PPS-\( \rho \))

in the weak sense where \( \rho_{\lambda, P_0}(t, s) = \mathbb{E}[\lambda_t | S_{t-} = s] \) for almost every \( t \).
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Corollary (LLN)

The empirical measure $\frac{1}{n} \sum_{i=1}^{n} \delta_{S_{i^-}}(ds)$ of the age processes associated to some i.i.d. point processes converges (in some weak sense) as $n \to \infty$ towards the mean measure $u$. 
The system in expectation

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where \( \rho_{\lambda, P_0}(t, s) = \mathbb{E}[\lambda_t | S_{t^-} = s] \).

- This result may seem OK, but \( \rho \) is not explicit.
- In particular, this system may seem linear, but it is non-linear in general.
Review of the examples

The system in expectation

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- \( \lambda_t = f(t, S_{t-}) \) (Poisson, renewal).

\[ \rightarrow \rho_{\lambda, P_0}(t, s) = f(t, s) \] and the system admits a unique solution.
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\[\rightarrow \rho_{\lambda, P_0}(t, s) = f(t, s) \text{ and the system admits a unique solution.}\]

\[\rightarrow \rho_{\lambda, P_0} \text{ is much more complex.}\]
Review of the examples

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\rightarrow \quad \rho_{\lambda, P_0} \text{ is much more complex.}
\]

The integral \( v(t, s) := \int_s^{+\infty} u(t, d\sigma) \) satisfies a closed system.
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1 Introduction

2 A key tool: The thinning procedure

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4 Second approach: Mean-field interactions
   - Generalities
   - Actual and limit dynamics
   - Coupling of these two dynamics
   - Mean-field approximation
Propagagation of chaos: a tool to link the two scales

Mean-field $n$-particle system

- The particles are dependent, but they are exchangeable.
- Homogeneous weak interactions.
- The dynamics is described by a system of $n$ equations.
Propagtion of chaos: a tool to link the two scales

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Asymptotic when $n \to +\infty$

- The particles become independent.
- Their distribution is described by one non-linear PDE.
Thinning procedure

1/ Expectation

2/ Mean-field

Summary

Propagation of chaos: a tool to link the two scales

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- Homogeneous weak interactions.
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Mean-field in biology

- Neuroscience: Intrinsic spiking (Stannat et al. 2014), I&F (Delarue et al. 2015), point processes models (Galves and Löcherbach 2015).
Multivariate Hawkes processes

- Multivariate HP: \( (i = 1, \ldots, n) \)

\[
\lambda^i_t = \Phi \left( \int_0^{t-} h_{i \rightarrow i}(t-x)N^i(dx) + \sum_{j \neq i} \int_0^{t-} h_{j \rightarrow i}(t-x)N^j(dx) \right).
\]
### Multivariate Hawkes processes

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\]

Interaction function \(h_{j \rightarrow i} \leftrightarrow\) synaptic weight of neuron \(j\) over neuron \(i\).
Generalized Hawkes processes

Renewal process

\[ \lambda_t = f(S_t) \]

Multivariate HP

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$$\lambda^i_t = \Phi\left( \sum_{j=1}^{n} \int_{0}^{t-} h_{j \rightarrow i}(t-x) N^j(dx) \right)$$

Example:
$$\Psi(s, x) = \Phi(x) 1_{s \geq \delta} \Rightarrow \text{strict refractory period of length } \delta$$
Generalized Hawkes processes

Renewal process
\[ \lambda_t = f(S_{t^-}) \]

Multivariate HP
\[ \lambda^i_t = \Phi \left( \sum_{j=1}^{n} \int_{0}^{t^-} h_{j \rightarrow i}(t-x) N^{j}(dx) \right) \]

Age dependent Hawkes process \((n\text{-neurons system})\)

It is a multivariate point process \((N^{n,i})_{i=1,\ldots,n}\) with intensity given for all \(i = 1,\ldots,n\) by
\[ \lambda^{n,i}_t = \psi \left( S^{n,i}_{t^-}, \frac{1}{n} \sum_{j=1}^{n} \int_{0}^{t^-} h(t-z) N^{n,j}(dz) \right), \quad "h_{j \rightarrow i} = \frac{1}{n} h". \]

- Example: \(\psi(s,x) = \Phi(x)1_{s \geq \delta} \rightsquigarrow \) strict refractory period of length \(\delta\).
The idea is to find a suitable coupling between the particles of the $n$-particle system and $n$ i.i.d. copies of a \textit{limit process}. 
The idea is to find a suitable coupling between the particles of the $n$-particle system and $n$ i.i.d. copies of a limit process.

1. Find a good candidate for the limit process.

2. Show that it is well-defined (McKean-Vlasov fixed point problem).

3. Couple the dynamics in the right way.

4. Show the convergence.
Scheme of the coupling method

Idea of coupling

The idea is to find a suitable coupling between the particles of the $n$-particle system and $n$ i.i.d. copies of a limit process.

1. Find a good candidate for the limit process.
1’. Use the PDE to find the distribution of the limit process.
2. Show that it is well-defined (McKean-Vlasov fixed point problem).
3. Couple the dynamics in the right way.
4. Show the convergence.
1/ Limit process (heuristic)

Recall the intensities of the \( n \)-neurons system

\[
\lambda_t^{n,i} = \psi\left( S_{t^-}^{n,i}, \frac{1}{n} \sum_{j=1}^{n} \int_{0}^{t^-} h(t - z) N_j^n(dz) \right).
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1/ Limit process (heuristic)

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\]

- Independence at the limit \( \Rightarrow \) Law of Large Numbers.
1/ Limit process (heuristic)

Recall the intensities of the $n$-neurons system

$$\lambda_{t,i}^n = \psi \left( S_{t^-}^n, \frac{1}{n} \sum_{j=1}^{n} \int_{0}^{t^-} h(t-z) \mathbb{N}^n_j(dz) \right).$$

- Independence at the limit $\Rightarrow$ Law of Large Numbers.

Limit process

It is a point process $\overline{N}$ with intensity given by

$$\overline{\lambda}_t = \psi \left( \overline{S}_{t^-}, \int_{0}^{t^-} h(t-z) \mathbb{E} [\mathbb{N}(dz)] \right).$$
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$$\overline{\lambda}_t = \psi\left(\overline{S}_{t-}, \int_{0}^{t-} h(t-z) \mathbb{E}[\overline{N}(dz)] \right).$$

- The intensity of $\overline{N}$ depends on the time and the age.
1’/ Study the associated PDE system

Limit system

\[
\begin{align*}
&\frac{\partial u(t,s)}{\partial t} + \frac{\partial u(t,s)}{\partial s} + \Psi(s,X(t)) u(t,s) = 0, \\
&u(t,0) = \int_{s \in \mathbb{R}_+} \Psi(s,X(t)) u(t,s) \, ds,
\end{align*}
\]

(PPS-NL)

where for all \( t \geq 0, \ X(t) = \int_0^t h(t - z) u(z,0) \, dz.\)

Main assumption

The rate function \( \Psi \) is bounded and uniformly Lipschitz w.r.t. \( X(t) \).
1’/ Study the associated PDE system

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\frac{\partial u(t,s)}{\partial t} + \frac{\partial u(t,s)}{\partial s} + \psi(s,X(t))u(t,s) &= 0, \\
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(PPS-NL)

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Main assumption

The rate function \( \psi \) is bounded and uniformly Lipschitz w.r.t. \( X(t) \).

Linear version:

\[
\begin{aligned}
\frac{\partial u(t,s)}{\partial t} + \frac{\partial u(t,s)}{\partial s} + f(t,s)u(t,s) &= 0, \\
u(t,0) &= \int_{s \in \mathbb{R}_+} f(t,s)u(t,s) \, ds.
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\]  

(PPS-L)
1’/ Study the associated PDE system 2

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(PPS-L)

**Proposition**

Assume that \( f : \mathbb{R}^+ \times \mathbb{R}^+ \to \mathbb{R} \) is bounded and continuous (uniformly in the second variable) with respect to the first variable. Assume that \( u^{\text{in}} \) belongs to \( \mathcal{M}(\mathbb{R}^+) \).

Then, there exists a unique solution in the weak sense \( u \) such that \( t \mapsto u(t, \cdot) \) belongs to \( BC(\mathbb{R}^+, \mathcal{M}(\mathbb{R}^+)) \) with initial condition \( u(0, \cdot) = u^{\text{in}} \).

1' Study the associated PDE system 2

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\end{align*}
\] (PPS-L)

**Proposition**

Assume that \( f : \mathbb{R}_+ \times \mathbb{R}_+ \to \mathbb{R} \) is bounded and continuous (uniformly in the second variable) with respect to the first variable. Assume that \( u^{\text{in}} \) belongs to \( \mathcal{M}(\mathbb{R}_+) \).

Then, there exists a unique solution in the weak sense \( u \) such that \( t \mapsto u(t,\cdot) \) belongs to \( BC(\mathbb{R}_+, \mathcal{M}(\mathbb{R}_+)) \) with initial condition \( u(0,\cdot) = u^{\text{in}} \).

- Mass-conservative and conservation of positivity.
- Conservation of a probability density.
1’/ Study the associated PDE system

\[
\begin{cases}
\frac{\partial u(t,s)}{\partial t} + \frac{\partial u(t,s)}{\partial s} + \Psi(s,X(t))u(t,s) = 0, \\
u(t,0) = \int_{s\in\mathbb{R}_+} \Psi(s,X(t))u(t,s) \, ds,
\end{cases}
\]

(PPS-NL)

where for all \( t \geq 0 \), \( X(t) = \int_0^t h(t - z)u(z,0) \, dz \).

**Theorem**

Assume that \( h : \mathbb{R}_+ \rightarrow \mathbb{R} \) is locally integrable and that \( u^\text{in} \) is a non-negative function such that both \( \int_0^{+\infty} u^\text{in}(s) \, ds = 1 \) and there exists \( M > 0 \) such that for all \( s \geq 0 \), \( 0 \leq u^\text{in}(s) \leq M \).

Then, there exists a unique solution in the weak sense \( u \) such that \( t \mapsto u(t,\cdot) \) belongs to \( BC(\mathbb{R}_+, \mathcal{P}(\mathbb{R}_+)) \) (Moreover, the solution is in \( C(\mathbb{R}_+, L^1(\mathbb{R}_+)) \)).
1'/ Study the associated PDE system

\[
\begin{cases}
\frac{\partial u(t,s)}{\partial t} + \frac{\partial u(t,s)}{\partial s} + \Psi(s,X(t)) u(t,s) = 0, \\
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**Sketch of Proof**

1. For any continuous function \( Y \), consider the system with \( Y \) replacing \( X \).
1’ Study the associated PDE system

\[
\begin{align*}
\frac{\partial u(t,s)}{\partial t} + \frac{\partial u(t,s)}{\partial s} + \Psi(s,X(t))u(t,s) &= 0, \\
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**Sketch of Proof**

1. For any continuous function \( Y \), consider the system with \( Y \) replacing \( X \).
2. This new system is linear. Apply the previous results.
1’/ Study the associated PDE system

\[
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**Theorem**

Assume that \( h : \mathbb{R}_+ \to \mathbb{R} \) is locally integrable and that \( u^{\text{in}} \) is a non-negative function such that both \( \int_0^{+\infty} u^{\text{in}}(s)\,ds = 1 \) and there exists \( M > 0 \) such that for all \( s \geq 0 \), \( 0 \leq u^{\text{in}}(s) \leq M \).

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**Sketch of Proof**

1. For any continuous function \( Y \), consider the system with \( Y \) replacing \( X \).
2. This new system is linear. Apply the previous results.
3. Study the fixed point of \( Y \mapsto \int_0^t h(t-z)u_Y(z,0)\,dz \) (\( u_Y \): solution associated to \( Y \)).
2/ Show that the limit process is well-posed

Recall the intensity of the limit process

\[ \bar{\lambda}_t = \Psi \left( S_t, \int_0^t h(t-z) \mathbb{E} \left[ N(dz) \right] \right). \]

Recall the associated system (PPS-NL),

\[
\begin{cases}
\frac{\partial u(t,s)}{\partial t} + \frac{\partial u(t,s)}{\partial s} + \Psi(s,X(t)) u(t,s) = 0, \\
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2/ Show that the limit process is well-posed

Recall the intensity of the limit process

$$\bar{\lambda}_t = \Psi \left( \bar{S}_{t-}, \int_0^{t-} h(t-z) \mathbb{E} \left[ N(dz) \right] \right).$$

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**Proposition**

- The distribution of the age $\bar{S}_{t-}$ is the unique solution of (PPS-NL).
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where for all \( t \geq 0 \), \( X(t) = \int_0^t h(t-z)u(z,0) \, dz \).

Proposition

- The distribution of the age \( \bar{S}_{t-} \) is the unique solution of (PPS-NL).
- The intensity of the limit process is given by

\[ \bar{\lambda}_t = \Psi \left( \bar{S}_{t-}, \int_0^{t} h(t-z)u(z,0) \, dz \right) . \]

- Hence the limit process is well-defined.
3/ The coupling

Six realizations of a Poisson process with intensity 2 on [0, 1].
3/ The coupling

- $\mathbb{R}^+$
- $t_0$

- $\times$: Poisson process $\Pi^i$
- $\circ$: Point process $N_{n,i}^n$
- $\bullet$: Limit process $\overline{N}^i$

- 1/ Expectation
- 2/ Mean-field
- 3/ The coupling
- Summary

Introduction

Thinning procedure
3/ The coupling

\( \mathbb{R}_+ \)

\( \lambda_{n,i} \)

\( \Pi^i \)

\( N_{n,i} \)

\( \overline{N}^i \)

- Poisson process
- Point process
- Limit process
3/ The coupling

\[ \mathbb{R}_+ \]

- \( \lambda_{n,i}^t \)
- \( \bar{\lambda}_t^i \)
- \( \Pi^i \)
- \( \lambda_{t}^n \)
- \( N^{n,i} \)
- \( \overline{N}^i \)

\( \times \): Poisson process \( \Pi^i \)
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\( \bigcirc \): Limit process \( \overline{N}^i \)
4/ Control/Convergence 1

**Theorem**

The coupling described in the previous slide is such that

\[
E \left[ \text{Card} \left( (\mathcal{N}^{n,i} \triangle \overline{\mathcal{N}}^i) \cap [0, \theta] \right) \right] = \int_0^\theta E \left[ |\lambda_{t}^{n,i} - \lambda_{t}^{i}| \right] dt \lesssim n^{-1/2}.
\]

The constant depends on \( \theta, \Psi \) and \( h \).
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The constant depends on $\theta$, $\Psi$ and $h$.

Corollary

If the distribution of the initial value of the age is bounded then the coupling described in the previous slide is such that

$$\mathbb{E} \left[ \sup_{t \in [0,\theta]} |S_t^{n,i} - \overline{S}_t^i| \right] \lesssim n^{-1/2}.$$
### Propagation of chaos

Fix $k$ in $\mathbb{N}$. Then, the processes $N^{n,1}, \ldots, N^{n,k}$ of the $n$-neurons system behave (when $n \to +\infty$) as i.i.d. copies of the limit process $\bar{N}$. 

```latex
If the ages at time 0 are i.i.d. with common density $\nu$ in $\mathbb{R}$, then for all $t \geq 0$,
\[
\frac{1}{n} \sum_{i=1}^{n} \delta_{S^{n,i}(t)} \to_{n \to \infty} \nu(t, \cdot),
\]
where $\nu$ is the unique solution of the (PPS-NL) system with initial condition $\nu$.

Link between (PPS) and a well-designed microscopic model.

Goodness-of fit tests: Renewal and Hawkes processes.
4/ Control/Convergence 2

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Theorem

If the ages at time 0 are i.i.d. with common density $u^{\text{in}}$, then for all $t \geq 0$, $\frac{1}{n} \sum_{i=1}^{n} \delta_{S_{t-i}^{n,i}} \xrightarrow{n \to \infty} u(t, \cdot)$,

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- Goodness-of fit tests: Renewal and Hawkes processes.
Summary

- First approach:
  - Link with an i.i.d. network.
  - Ends up with (PPS) for Renewal or Poisson processes.
  - Ends up with a more intricate system with linear Hawkes processes.
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- **First approach:**
  - Link with an i.i.d. network.
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- **Second approach:**
  - Network of weakly dependent neurons (asymptotically independent).
  - Refractory period possible for the limit process. Its distribution is given by (PPS).

Remark: The $h_j \rightarrow i$'s can be i.i.d. Dependence with respect to the past before time 0 can be added.

Outlook:
- Study of the system in expectation for linear Hawkes processes.
- Fluctuations around the mean limit behaviour (Central Limit Theorem).
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