Infinite systems of interacting chains with memory of variable length - a stochastic model for biological neural nets

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- This is a joint work with Eva Löcherbach

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- *This article is dedicated to Errico Presutti*

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- The point process with the times at which a neuron spikes is called a **spike train**.
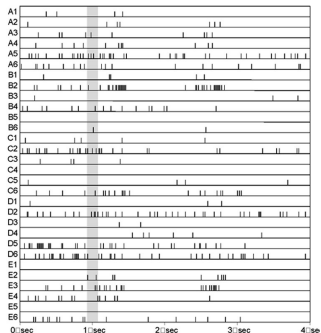
Spike trains

FIGURE: Spike trains of several neurons - Picture by W. Maass

Important - and open - questions

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Goal : to find a model in which this type of questions can be addressed

The model

- Huge system with $N \approx 10^{11}$ neurons that interact.

- Spike train : for each neuron i we indicate if there is a spike or not at time t, $t \in \mathbb{Z}$.

  $X_t(i) \in \{0, 1\}, X_t(i) = 1 \Leftrightarrow$ neuron i has a spike at time t .

- t is an index of the time window in which we observe the neuron. In the data we considered, the width of this window is typically 3 ms.

Background

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• Then : reset to a resting potential. Restart accumulating potentials coming from other neurons.

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• Hence : **Variable length memory :** the memory of the neuron goes back up to its last spike – at least at a first glance.

• This is the framework considered by Cessac (2011) - but only for a **finite** number of neurons.

The model

Chain $X_t \in \{0, 1\}^{\mathcal{I}}$,

$$X_t = (X_t(i), i \in \mathcal{I}), X_t(i) \in \{0, 1\}, t \in \mathbb{Z},$$

$\mathcal{I}$ countable is the set of neurons. **We will work in the case where $\mathcal{I}$ is infinite**.

Time evolution : At each time step, **given the past history of the system**, neurons update independently from each other :

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$$P(X_t(i) = a_i, i \in J | \mathcal{F}_{t-1}) = \prod_{i \in J} P(X_t(i) = a_i | \mathcal{F}_{t-1}),$$

where

$\mathcal{F}_{t-1}$ is the past history up to time $t-1$.

The model II

$$P(X_t(i) = 1|\mathcal{F}_{t-1}) = \Phi\left(\sum_j W_{j\to i} \sum_{s=L_t^i}^{t-1} g(t-s)X_s(j), t - L_t^i\right).$$

Here :

- $W_{j\to i} \in \mathbb{R}$: **synaptic weight** of neuron j on i.
- $L_t^i = \sup\{s < t : X_s(i) = 1\}$ **last spike time** of neuron i strictly before time t.
- $g : \mathbb{N} \to \mathbb{R}_+$ describes an **leaky** effect.
- $t - L_t^i$ describes an **aging** efect

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Either excitatory : $W_{j \to i} > 0$.
Or inhibitory : $W_{j \to i} < 0$.

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So it is an interesting mathematical object....

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- Our model is a version in discrete time of the so-called **Hawkes process** (see Brémaud& Massoulié 1991) – but : with an infinity of components and, locally, a structure of variable memory.

Basic mathematical questions

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• Are neighboring inter-spike intervals correlated ?

This is both a mathematical and a biological question,

and there are experimental facts that we have to explain. . .

The proof of existence and uniqueness is based on the study of the transition probability

$$(1) \quad p_{(i,t)}(1|x) = \Phi \left(\sum_{j \neq i} W_{j \to i} \sum_{s=L_t^i(x)}^{t-1} g(t-s)x_s(j), t - L_t^i(x) \right) :$$

which depends on the space-time configuration of spike times

$x_{L_t^i}^{t-1}(\mathcal{V}_{\cdot \to i})$: locally variable length in time, infinite range in space.

Globally of **infinite range memory** !

But attention : The function $x \mapsto p_{(i,t)}(1|x)$ in general is not continuous ! We do not have :

$$\sup_{x,x':x\overset{k}{=}x'} |p_{(i,t)}(1|x) - p_{(i,t)}(1|x')| \to 0$$

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Continuity is usually what is required in the study of **chains having infinite order** (see work by R. Fernández, G. Maillard, ...)

Hypotheses

1) Lipschitz : There exists some $\gamma > 0$: such that for all z, z', n,

$$|\Phi(z, n) - \Phi(z', n)| \leq \gamma |z - z'|.$$

2) Uniform summability of the synaptic weights

$$\sup_i \sum_j |W_{j \to i}| < \infty.$$

3) Spontaneous spiking activity with intensity δ :

$$\Phi(\cdot, \cdot) \geq \delta > 0.$$

Theorem

Under the above hypotheses : If $\delta \geq \delta_*$ and : fast decay of synaptic weigths, then

1. *there exists a unique stationary chain $X_t(i), t \in \mathbb{Z}, i \in \mathcal{I}$, consistent with the dynamics.*

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2. *the speed of convergence to equilibrium is bounded above :*

   $$(2) \quad |E[f(X_s^t(i))|\mathcal{F}_0] - E[f(X_s^t(i))]| \leq C(t-s+1)\|f\|_\infty \varphi(s),$$

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3. *If moreover*

   $$g(n) < Ce^{-\beta n},$$

   then we have in (2) that $\varphi(s) \leq C\varrho^s$ for some $\varrho \in]0, 1[$, if $\beta >> 1$.

Proof : Conditional Kalikow-decomposition

- $\Phi(\cdot, \cdot) \geq \delta \Rightarrow$ **Coupling** with i.i.d. field

$$\xi_t(i), t \in \mathbb{Z}, i \in \mathcal{I}, \xi_i(t) \sim \mathcal{B}(\delta) :$$

$X_i(i) \geq \xi_i(t)$ for all t, i.

- We have to work in the configuration space conditioned on the realization of ξ :

$$\mathcal{S}^\xi = \{x \in \{0,1\}^{\mathbb{Z} \times \mathcal{I}} : x_t(i) \geq \xi_t(i) \forall t, \forall i\}.$$

Continuation of the proof

Each site (i, t) has its memory bounded by

$$R_t^i = \sup\{s < t : \xi_s(i) = 1\}.$$

Introduce : $V_i(0) := \{i\}$, $V_i(k) \uparrow \mathcal{V}_i = \{j : W_{j \to i} \neq 0\} \cup \{i\}$.

Proposition

$$p_{(i,t)}(a|x) = \lambda(-1)p^{[-1]}(a) + \sum_{k \geq 0} \lambda(k)p^{[k]}(a|x_{R_t^i}^{t-1}(V_i(k))),$$

where $\lambda(k) \in [0,1], \sum \lambda(k) = 1$,

$$\lambda(k) \leq 2\gamma \sum_{s=R_t^i}^{t-1} g(t-s) \sum_{j \notin V_i(k-1)} |W_{j \to i}|, \ k \geq 1.$$

Comments

- This is a conditional decomposition, conditional on the realization of spontaneous spikes.

- The "reproduction probabilities" $\lambda(k)$ are random variables depending on ξ.

- We get uniqueness via a "dual process", the **Clan of Ancestors :** in order to decide about the value of (i, t), we have to know the values of all sites in

  $$C^1_{(i,t)} = V_i(k) \times [R^i_t, t-1], \text{ chosen with probability } \lambda(k)....$$

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Iterate ! If this process stops in finite time a.s., then we are done. This is granted by a comparison with a multi-type branching process in random environment.

Back to neuroscience

Goldberg et al. (1964) in their article "Response of neurons of the superior olivary complex of the cat to acoustic stimuli of long duration" observe :

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In many experimental setups the empirical correlation between successive inter-spike intervals is very small –

"indicating that a description of spiking as a **stationary renewal process** is a good approximation" (Gerstner and Kistler 2002).

In the same direction :

The statistical analysis of the activity of several (but not all !)
neurons in the hippocampus selects as best model a

renewal process.

– *Data registered by Sidarta Ribeiro (Brain Institute UFRN), in
2005.*

– *Data analyzed by Andrés Rodríguez and Karina Y. Yaginuma,
using the SMC (smallest maximiser criterion).*

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Can we account for these apparently contradictory facts with our model ?

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In what follows this graph will be a realization of a critical directed Erdös-Rényi graph. In such a graph there is a unique giant cluster, and we work in this giant cluster.

Critical directed Erdös-Rényi random graph

- Large but finite system of neurons with
  $\mathcal{I} = \{1, \ldots, N\}, N \approx 10^{11}$.

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- Here, $p = \lambda/N$ and $\lambda = 1 + \vartheta/N$, $\vartheta > 0$.

- Observe that $W_{i \to j}$ and $W_{j \to i}$ are distinct and independent :
  being influenced by neuron i is different from influencing
  neuron i....

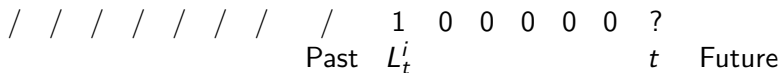# Does the past before the last spike of a neuron influence the future ?

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Does it affect the future whether the last spike before L_t^i took place immediately before L_t^i or whether it took place many steps before ?

The point is : the last spike of neuron i before time L_t^i affects many neurons – different from i, which in turn affect other neurons and so on. How long does it take until this influence returns to the starting neuron i ?

This time is a sort of *recurrence time* in the random graph :

$$C_1^i = \{j : W_{j \to i} \neq 0\}, \ldots, C_n^i = \{j : \exists k \in C_{n-1}^i : W_{j \to k} \neq 0\}.$$

Then the recurrence time is

$$T_i = \inf\{n : i \in C_n^i\}.$$

Proposition

$$P(\text{recurrence time} \leq k) \leq \frac{k}{N} e^{\vartheta k / N}.$$

$N = $ number of neurons.

$\vartheta = $ parameter appearing in the definition of the synaptic weight probabilities, $Np = 1 + \vartheta/N$.

This implies

Theorem

On a "good set" of random synaptic weights :

$|Covariance\ of\ neighboring\ inter\text{-}spike\ intervals| \leq C\dfrac{1}{\delta^2}N(1-\delta)^{\sqrt{N}}.$

Moreover,

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This conciliates the empirical results both of Goldberg et al. (1964) and of Nawrot et al. (2007) !