# Infinite systems of interacting chains with memory of variable length A stochastic model for biological neural nets

Antonio Galves Universidade de S.Paulo Fapesp Center for Neuromathematics

SPA Buenos Aires 2014

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- This article is dedicated to Errico Presutti

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# Spike trains

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- One emission of such an action potential is called a **spike**.
- Duration of spikes is very short (about 1 ms) : report if in a given time interval (of about 3 ms) there is **presence or absence of spike.**
- The point process with the times at which a neuron spikes is called a **spike train**.

Existence and Uniqueness Results Correlation of neighboring inter-spike intervals

## Spike trains

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

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### Important - and open - questions

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• How is information/external stimulus encoded in such patterns?

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- How to model brain plasticity?
- How to explain the appearance of synchronized spiking patterns (→ evoked potential)?

 $\operatorname{\mathsf{Goal}}$  : to find a model in which this type of questions can be addressed

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## The model

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## The model

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

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- 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* ∈ Z.

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 $X_t(i) \in \{0,1\}, X_t(i) = 1 \Leftrightarrow$  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.

Existence and Uniqueness Results Correlation of neighboring inter-spike intervals

## Background

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• Integrate and fire models : the membrane potential process of one neuron accumulates stimuli coming from other neurons.

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- Therefore the spiking train is a **chain with variable length memory :** the memory of each neuron goes back up to its last spike time.
- This is the framework considered by Cessac (2011) but only for a **finite** number of neurons.

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

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For any finite subset J of neurons,

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

where

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

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## The model II

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

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Here :

•  $W_{j \to i} \in \mathbb{R}$ : synaptic weight of neuron j on i.

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$$g : \mathbb{N} \to \mathbb{R}_+$$
 describes a **leaky** effect.

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$$g: \mathbb{N} \to \mathbb{R}_+$$
 describes a **leaky** effect.

• 
$$t - L_t^i$$
 describes an **aging** efect

### Excitatory versus inhibitory influence

Neurons who have a direct influence on i are those belonging to

$$\mathcal{V}_{\cdot \to i} := \{j : W_{j \to i} \neq 0\}$$
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Neurons who have a direct influence on i are those belonging to

$$\mathcal{V}_{\cdot \to i} := \{j : W_{j \to i} \neq 0\}$$
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Either excitatory :  $W_{j \rightarrow i} > 0$ . Or inhibitory :  $W_{j \rightarrow i} < 0$ .

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So it is an interesting mathematical object....

• The discrete time frame is not important – a continuous time description is analogous.

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- Our model is reminiscent 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 length memory.

## **Basic mathematical questions**

• Given  $(W_{i \rightarrow j})$ ,  $\Phi$  and g, does a chain with the above dynamics exist and if so, is it unique?

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- Yes under some conditions, see in two minutes.
- 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...

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

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

which depends on the space-time configuration of spike times

 $x_{L_{i}^{t}}^{t-1}(\mathcal{V}_{\rightarrow i})$ : 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 :

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

as  $k \to \infty$ .

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as  $k \to \infty$ . Since no summability is imposed on g.

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  $\delta$ :

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

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#### Theorem

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

there exists a unique stationary chain X<sub>t</sub>(i), t ∈ Z, i ∈ I, consistent with the dynamics.

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- there exists a unique stationary chain X<sub>t</sub>(i), t ∈ Z, i ∈ I, consistent with the dynamics.
- **2** the speed of convergence to equilibrium is bounded above :

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

where  $\varphi(s) \downarrow 0$  as  $s \to \infty$ .

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where  $\varphi(s) \downarrow 0$  as  $s \to \infty$ .

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  $\beta >> 1$ .

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## Proof : Conditional Kalikow-decomposition

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### Proof : Conditional Kalikow-decomposition

• 
$$\Phi(\cdot, \cdot) \ge \delta \Rightarrow$$
 **Coupling** with i.i.d. field  
 $\xi_t(i), t \in \mathbb{Z}, i \in \mathcal{I}, \xi_i(t) \sim \mathcal{B}(\delta)$   
 $X_i(i) \ge \xi_i(t)$  for all  $t, i$ .

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## Proof : Conditional Kalikow-decomposition

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

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

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

• We have to work in the configuration space conditioned on the realization of  $\boldsymbol{\xi}$  :

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

# Continuation of the proof

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

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

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

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### Proposition

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

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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 
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# Comments

- This is a conditional decomposition, conditional on the realization of spontaneous spikes.
- The "reproduction probabilities" λ(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

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

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

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.

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## Back to neuroscience

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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).

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

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#### **HOWEVER** :

Nawrot et al. (2007) in their article "Serial interval statistics of spontaneous activity in cortical neurons in vivo and in vitro"

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

We must describe in a more precise way the **directed graph defined by the synaptic weights :** 

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In such a graph there is a unique giant cluster, and we work in this giant cluster.

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#### Neuronal avalanches in neocortical circuits.

Beggs JM, Plenz D.

J Neurosci. 2003 Dec 3;23(35) :11167-77.

Networks of living neurons exhibit diverse patterns of activity, including oscillations, synchrony, and waves.(...) Here, we show that propagation of spontaneous activity in cortical networks is described by equations that govern avalanches. As predicted by theory for a **critical branching process**, the propagation obeys a power law with an exponent of -3/2 for event sizes, with a branching parameter close to the critical value of 1.( ...)

Critical directed Erdös-Rényi random graph

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

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- Here,  $p = \lambda/N$  and  $\lambda = 1 + \vartheta/N, \ \vartheta > 0.$
- Observe that W<sub>i→j</sub> and W<sub>j→i</sub> 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?

$$/ / / / / / / / 1 0 0 0 0 0 ?$$
  
Past  $L_t^i$  t 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*?

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

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

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# Proposition

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

N = number of neurons.

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

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#### This implies

#### Theorem

On a "good set" of random synaptic weights :

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

Moreover,

$$P(good set) \geq 1 - CN^{-1/2},$$

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Moreover,

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where  $\delta$  is the spontaneous spiking activity.

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

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#### Next steps

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 Hydrodynamic limit for interacting neurons
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- Statistical model selection for this class of stochastic processes.

#### NeuroMat Project | NeuroMat

#### 28/10/13 16:36

Contact



oject Team Postdoctoral Positions Related Projects

Research, Innovation and Dissemination Center for Neuromathematics



#### NeuroMat Project

This proposal concerns the creation of a mathematical Center aiming to integrate modeling with basic and applied research at the frontier of neuroscience. The goal of the Center is to develop a mathematical framework leading to the theoretical understanding of neural systems, fully integrated with experimental research in neuroscience. New models and theories will be developed in order to handle the huge quantity of data produced by concurrent experimental research and to provide a conceptual framework for the multiscale supect singlayed by neural phenomena.

Technology transfer and innovation will focus on products aimed at public health programs in re-habilition and will be offered through the Lucy



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