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## Spike train statistics and Gibbs distributions



B. Cessac, R. Cofré\*

NeuroMathComp team (INRIA, UNSA LJAD) 2004 Route des Lucioles, 06902 Sophia-Antipolis, France

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## ABSTRACT

This paper is based on a lecture given in the LACONEU summer school, Valparaiso, January 2012. We introduce Gibbs distribution in a general setting, including non stationary dynamics, and present then three examples of such Gibbs distributions, in the context of neural networks spike train statistics: (i) maximum entropy model with spatio-temporal constraints; (ii) generalized linear models; and (iii) conductance based integrate and fire model with chemical synapses and gap junctions.

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## 1. Introduction

Neurons communicate among them by generating action potentials or “spikes” which are pulses of electrical activity. When submitted to external stimuli, sensory neurons produce sequences of spikes or “spike trains” constituting a collective response and a dynamical way to encode information about those stimuli. However, neural responses are typically not exactly reproducible, even for repeated presentation of a fixed stimulus. Therefore, characterizing the relationship between sensory stimuli and neural spike responses can be framed as a problem of determining the most adequate probability distribution relating a stimulus to its neural response. There exist several attempts to infer this probability from data and/or general principles, based on Poisson or more general point processes (Ahmadian et al., 2011; Vere-Jones and Daley, 2003; Miller and Snyder, 1991), Bayesian approaches (Koyama et al., 2010; Gerwinn et al., 2009), maximum entropy (Schneidman et al., 2006; Vasquez et al., 2012) (for a review see Rieke et al., 1996). In this paper we present several situations where the notion of Gibbs distributions is appropriate to address this problem.

The concept of Gibbs distribution comes from statistical physics. We use it here in a more general sense than the one usually taught in standard physics courses, although it is part of mathematical statistical physics (Georgii, 1988). We argue here that Gibbs distributions might be canonical models for spike train statistics analysis. This statement is based on three prominent examples.

1. The so-called *Maximum Entropy Principle* allows one to propose spike train statistics models considering restrictions based on empirical observations. Although this approach

has been initially devoted to show the role of weak instantaneous pairwise correlations in the retina (Schneidman et al., 2006), it has been recently applied to investigate the role of more complex events such as instantaneous triplets (Ganmor et al., 2011) or spatio-temporal events (Vasquez et al., 2012). Probability distributions arising from the maximum entropy principle are Gibbs distributions.

2. Other approaches such as the Linear-Nonlinear (LN) or Generalized Linear Models (GLMs) propose an ad hoc form for the conditional probability that a neuron fires given the past network activity and given the stimulus. Those models have been proven quite efficient for retina spike trains analysis (Pillow et al., 2011). They are not limited by the constraint of stationarity, but they are based on a questionable assumption of *conditional independence between neurons*. As we show, the probability distributions coming out from those models are also Gibbs distributions.
3. Recent investigations on neural networks models (conductance based integrate-and-fire (IF) with chemical and electric synapses) show that statistics of spike trains generated by these models are Gibbs distributions reducing to 1 when dynamics is stationary, and reducing to 2 in specific cases (Cessac, 2011a,b; Cofré and Cessac, in press). In the general case, the spike trains produced by these models have Gibbs distributions which neither match 1 nor 2.

The paper is organized as follows. After some definitions regarding spike train statistics and a presentation of Gibbs distributions we develop these three examples, with a short discussion of their advantages and drawbacks in spike trains analysis. Then, we discuss some relations between these models, mainly based on the Hammersley-Clifford theorem (Hammersley and Clifford, unpublished; Besag, 1974; Moussouris, 1974; Clifford, 1990). This paper is a summary of several papers written by the authors and

\* Corresponding author. Tel.: +33 4 9238 2420; fax: +33 4 9238 7845.

E-mail addresses: [bruno.cessac@inria.fr](mailto:bruno.cessac@inria.fr) (B. Cessac), [rodrigo.cofre\\_torres@inria.fr](mailto:rodrigo.cofre_torres@inria.fr) (R. Cofré).

other collaborators (Cessac, 2011a,b; Nasser et al., 2013; Cessac and Palacios, 2012; Cofré and Cessac, in press). As such it does not contain original material (except the presentation).

## 2. Definitions

### 2.1. Spike trains

We consider a network of  $N$  neurons. We assume that there is a minimal time scale  $\delta > 0$  corresponding to the minimal resolution of the spike time, constrained by biophysics and by measurements methods (typically  $\delta \sim 1$  ms) (Cessac and Viéville, 2008; Cessac et al., 2010). Without loss of generality (change of time units) we set  $\delta = 1$ , so that spikes are recorded at integer times. One then associates to each neuron  $k$  and each integer time  $n$  a variable  $\omega_k(n) = 1$  if neuron  $k$  fires at time  $n$  and  $\omega_k(n) = 0$  otherwise. A *spiking pattern* is a vector  $\omega(n) \stackrel{\text{def}}{=} [\omega_k(n)]_{k=1}^N$  which tells us which neurons are firing at time  $n$ . We note  $\mathcal{A} = \{0, 1\}^N$  the set of spiking patterns. A *spike block* is a finite ordered list of spiking patterns, written:

$$\omega_{n_1}^{n_2} = \{\omega(n)\}_{\{n_1 \leq n \leq n_2\}},$$

where spike times have been prescribed between the times  $n_1$  to  $n_2$  (i.e.,  $n_2 - n_1 + 1$  time steps). The *range* of a block is  $n_2 - n_1 + 1$ , the number of time steps from  $n_1$  to  $n_2$ . The set of such blocks is  $\mathcal{A}^{n_2 - n_1 + 1}$ . Thus, there are  $2^{Nn}$  possible blocks with  $N$  neurons and range  $n$ . We call a *raster plot* a bi-infinite sequence  $\omega \stackrel{\text{def}}{=} \{\omega(n)\}_{n=-\infty}^{+\infty}$ , of spiking patterns. Obviously experimental rasters are finite, but the consideration of infinite sequences is more convenient mathematically. The set of raster plots is denoted  $\Omega = \mathcal{A}^{\mathbb{Z}}$ .

### 2.2. Transition probabilities

The probability that a neuron emits a spike at some time  $n$  depends on the history of the neural network. However, it is impossible to know explicitly its form in the general case since it depends on the past evolution of all variables determining the neural network state. A possible simplification is to consider that this probability depends *only* on the spikes emitted in the past by the network. In this way, we are seeking a family of transition probabilities of the form  $\mathbb{P}_n[\omega(n)|\omega_{n-D}^{n-1}]$ , the probability that the firing pattern  $\omega(n)$  occurs at time  $n$ , given a past spiking sequence  $\omega_{n-D}^{n-1}$ . Here,  $D$  is the *memory depth* of the probability, i.e., how far in the past does the transition probability depend on the past spike sequence. We use the convention that  $\mathbb{P}_n[\omega(n)|\omega_{n-D}^{n-1}] = \mathbb{P}_n[\omega(n)]$  if  $D = 0$  (memory-less case).

The index  $n$  of  $\mathbb{P}_n[\cdot|\cdot]$  indicates that transition probabilities depend explicitly on the time  $n$ . We say that those transition probabilities are *time-translation invariant* or *stationary* if for all  $n$ ,  $\mathbb{P}_n[\omega(n)|\omega_{n-D}^{n-1}] = \mathbb{P}_D[\omega(D)|\omega_0^{D-1}]$  whenever  $\omega_{n-D}^{n-1} = \omega_0^{D-1}$  (i.e. the probability does not depend explicitly on time). In this case we drop the index  $n$ .

Transition probabilities depend on the neural network characteristics such as neurons conductances, synaptic responses or external currents. They give information about the dynamics that takes place in the observed neural network. Especially, they have a *causal* structure where the probability of an event depends on the past. This reflects underlying biophysical mechanisms in the neural network, which are also causal.

### 2.3. Gibbs distribution

We define here Gibbs distributions (or Gibbs measures) in a more general setting that the one usually taught in statistical

physics courses, where Gibbs distributions are considered in the realm of stationary process and maximum entropy principle. Here, we do not assume stationarity and the definition encompasses the maximum entropy distributions. The Gibbs distributions considered here are called *chains with complete connections* in the realm of stochastic processes (Fernandez and Maillard, 2005; Maillard, 2007) and *g-measures* in ergodic theory (Keane, 1972). They are also studied in mathematical statistical physics (Georgii, 1988).

#### 2.3.1. Continuity with respect to a raster

For  $n \in \mathbb{Z}$ , we note  $\mathcal{A}_{-\infty}^{n-1}$  the set of sequences  $\omega_{-\infty}^{n-1}$ . Assume that we are given a set of transitions probabilities, like in the previous section, possibly depending on an infinite past<sup>1</sup>, i.e. of the form  $\mathbb{P}_n[\omega(n)|\omega_{-\infty}^{n-1}]$ . We give in Section 3.3 an example of neural network model where such transition probabilities with an infinite memory do occur.

Even if transition probabilities involve an infinite memory  $\omega_{-\infty}^{n-1}$ , it is reasonable to consider situations where the effects of past spikes decreases exponentially with their distance in the past. This corresponds to the mathematical notion of *continuity with respect to a raster*. We note, for  $n \in \mathbb{Z}$ ,  $m \geq 0$ , and  $r$  integer:

$$\omega \stackrel{m,n}{=} \omega' \quad \text{if} \quad \omega(r) = \omega'(r), \quad \forall r \in \{n-m, \dots, n\}.$$

Consider a function  $f$  depending both on discrete time  $n$  and on the raster part of  $\omega$  anterior to  $n$ . We write  $f(n, \omega)$  instead of  $f(n, \omega_{-\infty}^{n-1})$ . The function  $f$  is *continuous with respect to the raster*  $\omega$  if its *m-variation*:

$$\text{var}_m[f(n, \cdot)] := \sup\{|f(n, \omega) - f(n, \omega')| : \omega \stackrel{m,n}{=} \omega'\}, \quad (1)$$

tends to 0 as  $m \rightarrow +\infty$ . This precisely means that the effect, on the value of  $f$  at time  $n$ , as this change is more distant in the past.

#### 2.3.2. Gibbs distribution

**Definition 2.1.** A Gibbs distribution is a probability measure  $\mu: \Omega \rightarrow [0, 1]$  such that:

(i) For all  $n \in \mathbb{Z}$  and all  $\mathcal{F}_{\leq n}$ -measurable functions  $f$ :

$$\int f(\omega_{-\infty}^n) \mu(d\omega) = \int \sum_{\omega(n) \in \mathcal{A}} f(\omega_{-\infty}^{n-1} \omega(n)) \mathbb{P}_n[\omega(n)|\omega_{-\infty}^{n-1}] \mu(d\omega).$$

(ii)  $\forall n \in \mathbb{Z}, \forall \omega_{-\infty}^{n-1} \in \mathcal{A}_{-\infty}^{n-1}, \mathbb{P}_n[\omega(n)|\omega_{-\infty}^{n-1}] > 0$ .

(iii) For each  $n \in \mathbb{Z}$ ,  $\mathbb{P}_n[\omega(n)|\omega_{-\infty}^{n-1}]$  is continuous with respect to  $\omega$ .

The condition (i) is a natural extension of the condition defining the invariant probability of an homogeneous Markov chain (see Eq. (2) next section). In its most general sense (i) does not require stationarity and affords the consideration of an infinite memory. It defines so-called *compatibility conditions*. They state that the average of a function  $f(n, \omega)$  with respect to  $\mu$ , at time  $n$  (left hand side), is equal to the average computed from transition probabilities (right hand side). This equality must hold for any time  $n$ .

There exist several theorems guaranteeing the existence and uniqueness of a Gibbs distribution (Georgii, 1988; Fernandez and Maillard, 2005): this holds if the variation of transition probability decays sufficiently fast with time (typically exponentially) as  $n - m \rightarrow -\infty$ .

<sup>1</sup> In this case, one has to assume that (i) for every  $\omega(n) \in \mathcal{A}$ ,  $\mathbb{P}_n[\omega(n)|\cdot]$  is measurable with respect to  $\mathcal{F}_{\leq n-1}$ , the sigma-algebra on  $\mathcal{A}_{-\infty}^{n-1}$ ; (ii) for every  $\omega_{-\infty}^{n-1} \in \mathcal{A}_{-\infty}^{n-1}, \sum_{\omega(n) \in \mathcal{A}} \mathbb{P}_n[\omega(n)|\omega_{-\infty}^{n-1}] = 1$ .

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