

## A discrete time neural network model with spiking neurons: II: Dynamics with noise

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**Abstract** We provide rigorous and exact results characterizing the statistics of spike trains in a network of leaky Integrate-and-Fire neurons, where time is discrete and where neurons are submitted to noise, without restriction on the synaptic weights. We show the existence and uniqueness of an invariant measure of Gibbs type and discuss its properties. We also discuss Markovian approximations and relate them to the approaches currently used in computational neuroscience to analyse experimental spike trains statistics.

**Keywords** Neurons dynamics · Spike train statistics · Thermodynamic formalism · Gibbs distributions

**Mathematics Subject Classification (2000)** 37N25 · 92B20

### 1 Introduction

The neuronal activity is manifested by the emission of *action potentials* or *spikes*. While the shape of an action potential is essentially constant for a given neuron, the succession of spikes (*spike train*) that a neuron is able to emit, depending on its state and in response to excitations coming from other neurons or external stimuli, is simply overwhelming. About 20 different spike trains forms are classified in the literature

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(Izhikevich 2004). It is widely believed by the neuroscience community that spike trains emitted by a neuron assembly constitute somehow a “code” and deciphering this code is a big challenge (Rieke et al. 1996).

Spike train are usually not exactly reproducible when repeating the same experiment,<sup>1</sup> even with a very good control ensuring that the experimental conditions have not changed. Therefore, researchers are seeking statistical regularities in spike trains. For this, they define statistical indicators such as firing rate, probability of spike coincidence, spike response function, spike correlations (see Dayan and Abbott 2001; Gerstner and Kistler 2002b; Rieke et al. 1996, for a comprehensive introduction to spike train analysis). An early step for “reading the code” is therefore to provide an accurate model for spike train statistics, i.e. a probability distribution “fitting at best” the experimental data and/or matching what neuroscientists believe relevant in neurons communication via spikes.

For example, it has been long believed that firing rates (the probability that a neuron emits a spike in a certain time interval) were carrying most of the “information” exchanged by neurons. As a consequence the canonical statistical model, namely the probability distribution which reproduces the firing rates without additional assumptions, is a Bernoulli distribution (possibly with time dependent probabilities), and the probability that a given number of spikes is emitted within a definite time interval is Poisson. Actually, there are many mechanisms in the nervous system, such as the muscle commands (Adrian and Zotterman 1926), working essentially with rates. But more recent experiments evidenced the role of spikes timing, spike ordering, spike synchronization, in processes such as vision (Rullen and Thorpe 2001; Thorpe 1990; Thorpe et al. 1996) or interactions between perception and motion (Grammont and Riehle 1999, 2003; Riehle et al. 2000). Here, one has to consider more elaborated statistical models, such as the (weak) pairwise interactions model proposed by Schneidman and collaborators (Schneidman et al. 2006) in experiments on the salamander retina. Consequently, there is an intensive activity and wide debates, focusing on the determination of statistical models of spike train statistics, with a clear evidence: distinct statistical models lead to fundamentally distinct characterizations of the mechanisms at work in the piece of nervous system under study (Nirenberg and Latham 2003).

Clearly, obtaining statistical models from experimental data or selecting a model among many others are difficult task. Forgetting about all the experimental difficulties to obtain “clean” data with a good control on parameters experiments, one has still to solve delicate questions such as the control of finite sampling effects (finite duration, finite numbers of experiments), extrapolation of the probability distribution characterizing small neural assemblies to a large population of neurons (Roudy et al. 2009), non stationarity, effects of synaptic plasticity or adaptation mechanisms (Toyozumi et al. 2007). As a consequence, there is no general recipe to extract a statistical model from data and several approaches have been proposed (Marre et al. 2009; Pouzat and Chaffiol 2009; Schneidman et al. 2006).

It appears simpler to characterize spike trains statistics in neural networks *models* where one controls exactly the neural network parameters, the number of involved

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<sup>1</sup> Although, retinal responses to a natural image, seem to be almost reproducible spike by spike (Perrinet 2008).

neurons, the number of samples, and the duration of the experiment (with a possible mathematical extrapolation to infinite time). Especially, producing analytical (and when possible, rigorous) results on those statistics provides clues toward resolving the delicate experimental questions raised above, with possible outcomes toward new algorithms for data treatments (Vasquez et al. 2010). Obviously, for this, one needs models which are a good compromise between analytical tractability and biological realism.

Generalized Integrate-and-Fire (gIF) models (Rudolph and Destexhe 2006) constitute a good example of this. Besides the fact that they capture the conductance-based mechanisms for spike generation, without focusing to much on the biological machinery, it has been shown by authors like Jolivet et al. (2004, 2006) that they are “good enough” to reproduce spike trains from real neurons. Moreover, these models allow the analytical characterization of their dynamics (Cessac and Viéville 2008). Further simplifications of gIF models lead to the Leaky Integrate-and-Fire (LIF) model, which was in fact the first proposed to model neuron dynamics (in 1907!) (Lapicque 1907). In this setting, prominent mathematical results on spike statistics in the presence of noise, have been published. For example, Brunel and Hakim obtained a complete characterization of LIF models with noise and strong dilution of synaptic weights, using a mean-field approximation and assuming that the synaptic weights are inhibitory (Brunel and Hakim 1999). Also, Touboul and Faugeras (2007) obtained rigorous results on the probability distribution of inter-spike intervals for one LIF neuron submitted to noise. They recently extended their results in (Touboul and Faugeras 2009) to networks of IF neurons of several type considering different types of interactions and conclude that the spikes times can be modelled as a Markov chain.

In this paper, we proceed along similar lines, although using different methods and raising different conclusions, and make a complete characterization of spike train statistics for the discrete-time leaky Integrate-and-Fire model with noise and time-independent stimuli. This is somehow a continuation of the paper (Cessac 2008) proposing a complete classification of dynamics in this model, without noise, and of Cessac and Viéville (2008) extending these results to gIF models. It also rigorously supports the main assumption made in Cessac et al. (2009) where it was proposed to characterize spike train statistics in neural networks by Gibbs distributions, with an emphasis on synaptic plasticity effects. Here, we propose a framework allowing to handle dynamics with noise, with possible extensions to more realistic neural networks models such as gIF (see the conclusion section). We emphasize that we do not use any simplifying assumption in the model. Especially, our results hold for finite-sized networks, without restriction on the synaptic weights (except that they are finite) and all type of synaptic graph structures are allowed. Also, we are not constrained by an ad hoc choice of the initial conditions distribution of membrane potentials; instead we propose a procedure where this distribution is selected by dynamics and is uniquely determined, as we show.

Moreover, this work attempts to bridge a gap between the mathematical characterization of spike train statistics and empirical methods or algorithms currently used by the neuroscience community. As a consequence, this paper addresses to two distinct communities. On one hand, to specialists from mathematical statistical physics and ergodic theory, as far as the mathematics of this paper are concerned. From this point

of view the results exposed here are direct applications of classical results in ergodic theory. But, to the best of our knowledge, it is the first time that they are used in this context. On the other hand, this paper addresses to neuroscientists. Studying a fairly simple model, from the biological point of view, we nevertheless obtain conclusions which could be useful for the characterization of spike trains in real experiments, with concrete applications toward implementation of software for spike train analysis.

The paper is organized as follows. In Sect. 2 we define the model and infer some preliminary results. Especially we compute explicitly the probability that neurons fire at time  $t$  given the past. This defines a transition probability which is the main object of our study. A salient result obtained in Sect. 2 is the fact that this transition probability is *non Markovian*, it depends on an unbounded past. This defines a stochastic process, known under the name of “chain with complete connections” (Maillard 2007, and references therein), which is studied in Sect. 3. Especially, we show that there is a unique invariant probability measure (equilibrium state) whatever the model-parameters values, which satisfies a variational principle and is a Gibbs distribution. We also show that the entropy of the discrete-time leaky Integrate-and-Fire model with noise is always positive. In Sect. 4 we propose a Markovian approximation where memory depends on  $R$  time steps. This approximation allows the computation of the main quantities used in neuroscience for the characterization of raster plots statistics. The computation of these quantities is done in Sect. 5. We also show that, in this approximation, the equilibrium state can also be obtained via the Jaynes principle of statistical physics (maximizing the entropy under constraints), and we discuss in which sense the statistical models used in neuroscience community are approximations whose degree of accuracy can be controlled.

## 2 Definitions and preliminary results

### 2.1 Model definition

#### 2.1.1 The neural network

Fix  $N > 0$  a positive integer called “the dimension of the neural network” (the number of neurons). Let  $\mathcal{W}$  be a  $N \times N$  matrix, called “the matrix of synaptic weights”, with entries  $W_{ij}$ . It defines an oriented and signed graph, called “the neural network associated to  $\mathcal{W}$ ”, with vertices  $i = 1 \dots N$  called the “neurons”.<sup>2</sup> There is an oriented edge  $j \rightarrow i$  whenever  $W_{ij} \neq 0$ .  $W_{ij}$  is called “the synaptic weight”<sup>3</sup> from neuron  $j$  to neuron  $i$ . The synaptic weight is called “excitatory” if  $W_{ij} > 0$  and “inhibitory” if  $W_{ij} < 0$ . We assume that the synaptic weights are bounded i.e.  $W_{ij} \in [W_{\min}, W_{\max}]$ ,  $\forall i, j$  where  $-\infty < W_{\min} \leq W_{\max} < +\infty$ . Moreover, in this paper, the  $W_{ij}$ ’s do not evolve in time.

<sup>2</sup> Therefore, “neurons” are points here, i.e. they have no structure.

<sup>3</sup> On biological grounds, this corresponds to the maximal amplitude of the post-synaptic potential generated, at the dendrite connecting the pre-synaptic neuron  $j$  to the post-synaptic neuron  $i$ , when neuron  $j$  emits an action potential.

### 2.1.2 Membrane potential

Each vertex (neuron)  $i$  is characterized by a real variable  $V_i$  called the “membrane potential of neuron  $i$ ”. Fix a positive real number  $\theta > 0$  called the “firing threshold”. Let  $Z$  be the function  $Z(x) = \chi(x \geq \theta)$  where  $\chi$  is the indicatrix function. Namely,  $Z(x) = 1$  whenever  $x \geq \theta$  and  $Z(x) = 0$  otherwise.  $Z(V_i)$  is called the “firing state of neuron  $i$ ”. When  $Z(V_i) = 1$  one says that neuron  $i$  “fires” or “spikes” and when  $Z(V_i) = 0$  neuron  $i$  is “quiescent”. We extend the definition of  $Z$  to vectors:  $Z(V)$  is the vector with components  $Z(V_i)$ ,  $i = 1 \dots N$ .

### 2.1.3 Dynamics

Fix  $\gamma \in [0, 1[$ , called the “leak rate”. The discrete time and synchronous dynamics of our model is given by:

$$V(t + 1) = F(V(t)) + \sigma_B B(t), \tag{1}$$

where  $\sigma_B > 0$ ,  $V = (V_i)_{i=1}^N$  is the vector of membrane potentials and  $F = (F_i)_{i=1}^N$  with:

$$F_i(\mathbf{V}) = \gamma V_i (1 - Z[V_i]) + \sum_{j=1}^N W_{ij} Z[V_j] + I_i; \quad i = 1 \dots N.$$

We assume that initial conditions belong to some compact set in  $\mathbb{R}^N$  (i.e. the initial membrane potentials are bounded). The variable  $I_i$  is called “an external input applied to neuron  $i$ ”. We assume in this paper that it does not depend on time.

### 2.1.4 Noise

The vector  $B(t) = (B_i(t))_{i=1}^N$  is an additive noise.<sup>4</sup> It has Gaussian identically distributed and independent entries  $B_i(t)$  with zero mean and variance 1. We note  $\mathcal{N}(0, 1)$  the standard Gaussian law and :

$$\pi(x) = \frac{1}{\sqrt{2\pi}} \int_x^{+\infty} e^{-\frac{u^2}{2}} du.$$

The parameter  $\sigma_B$  in (1) tunes the noise amplitude.

### 2.1.5 Interpretation

To the best of our knowledge this model has been first introduced by [Soula et al. \(2006\)](#). It belongs to the family of the so-called leaky-Integrate-and-Fire models

<sup>4</sup> On phenomenological grounds, it mimics effects such as noise in synaptic transmission (neurotransmitters diffusion), randomness in ionic channels transitions, or effects of hidden degrees of freedom.

(Gerstner and Kistler 2002b). Its interpretation is the following. A neuron “fires” i.e. emits an action potential (or “spike”) whenever its membrane potential exceeds the threshold  $\theta$ . Here a spike is modelled by the function  $Z$ . For an isolated neuron, firing corresponds, in the model, to the reset of the membrane potential to a rest value  $V_{\text{rest}} = 0$ . In a network, each neuron  $i$  receives spikes from pre-synaptic neurons. When a pre-synaptic neuron  $j$  emits a spike this modifies the membrane potential of neuron  $i$  by an amount  $W_{ij}$ . Thus, according to Eq. (1), when a neuron fires, it immediately receives inputs from other neurons and from the environment (the constant input and the noise) (hence its value at the next time step is different from zero in general). If a neuron does not fire and does not receive influences from other neurons or input, then its membrane potential decays exponentially fast with a decay rate  $0 < \gamma < 1$ . The discussion of the biological relevance of this model and its extensions towards more elaborated models with adaptive conductances has been done in Cessac and Viéville (2008).

## 2.2 Technical definitions

### 2.2.1 Spiking sequences

Call  $\mathcal{M} = \mathbb{R}^N$  the phase space of our dynamical system. Given two integers  $s < t$  (possibly negative) we note  $V_s^t$  the piece of trajectory  $V(s), \dots, V(t)$ . To each membrane potential value,  $V_i(t)$ , we associate a variable  $\omega_i(t) = Z(V_i(t))$ . The “spiking pattern” of the neural network at time  $t$  is the vector  $\omega(t) = (\omega_i(t))_{i=1}^N$ : it tells us which neurons are firing at time  $t$ , ( $\omega_i(t) = 1$ ) and which neurons are not firing at time  $t$  ( $\omega_i(t) = 0$ ). We denote by  $\omega_s^t$  the sequence or *spike block*  $\omega(s) \dots \omega(t)$ . Associated with each piece of trajectory  $V_s^t$  there is a unique spike block  $\omega_s^t$  with  $\omega_i(n) = Z(V_i(n))$ ,  $i = 1 \dots N, s \leq n \leq t$ . We note  $Z(V_s^t) = \omega_s^t$ . Also we note  $\omega_s^{t_1} \omega_{t_1}^t = \omega_s^t$  the concatenation of the blocks  $\omega_s^{t_1}$  and  $\omega_{t_1}^t$ .

### 2.2.2 Raster plots

Call  $\mathcal{A}$  the set of spiking patterns (alphabet). An element of  $\mathcal{A}^{\mathbb{Z}}$ , i.e. a bi-infinite sequence  $\omega = \{\omega(t)\}_{t=-\infty}^{+\infty}$  of spiking patterns, is called a “raster plot”. It tells us which neurons are firing at each time  $t \in \mathbb{Z}$ . In experiments raster plots are obviously finite sequences of spiking pattern but the extension to  $\mathbb{Z}$ , especially the possibility of considering an arbitrary distant past (negative times) is quite useful in the present work. The set  $\mathcal{A}^{\mathbb{Z}}$  is a topological space for the product topology (Kitchens 1998). The open sets are the cylinder sets, namely the sets  $[\omega_s^t] = \{\omega' \in \mathcal{A}^{\mathbb{Z}}, \omega'(n) = \omega(n), n = s, \dots, t\}$ . Cylinder sets are also a countable basis for the  $\sigma$ -algebra in  $\mathcal{A}^{\mathbb{Z}}$ . There is a natural distance on  $\mathcal{A}^{\mathbb{Z}}$ ,

$$d_{\Theta}(\omega, \omega') = \begin{cases} (\Theta^N)^n, & \text{if } \omega \text{ and } \omega' \text{ differ for the first time in the } n\text{-th spiking pattern;} \\ 0, & \text{if } \omega = \omega', \end{cases} \quad (2)$$

for some  $0 < \Theta < 1$ . A classical choice is  $\Theta = \frac{1}{2}$ . Here, it can be convenient to take  $\Theta = \gamma$ .

### 2.2.3 Last firing time

For  $(s, t) \in \mathbb{Z}^2, s < t$ , and each  $i = 1 \dots N$ , we define the “last firing time of neuron  $i$  in the sequence  $\omega_s^t$ ” by:

$$\tau_i(\omega_s^t) \stackrel{\text{def}}{=} \begin{cases} s, & \text{if } \omega_i(k) = 0, \quad k = s, \dots, t; \\ \max \{s \leq k \leq t, \omega_i(k) = 1\}, & \text{if } \exists k \in \{s, \dots, t\} \text{ such that } \omega_i(k) = 1. \end{cases} \quad (3)$$

Therefore,  $\tau_i(\omega_s^t) = s$  either if neuron  $i$  fires at time  $s$  or if it does not fire during the whole time interval  $[s, t]$ . In this way, the name “last firing time” is a little bit confusing, but this has no incidence on the mathematical developments.

## 2.3 The asymptotic probability distribution of membrane potentials and raster plots

### 2.3.1 Conditional probability distribution of $V(t + 1)$

Call  $P = \mathcal{N}(0, 1)^{\otimes N\mathbb{Z}}$ , the joint distribution of the noise trajectories. Under  $P$  the membrane potential  $V$  is a stochastic process whose evolution is given in Eq. (1). Fix a pair of integers  $(s, t), s < t$ . The probability distribution of  $V(t + 1)$  can be explicitly obtained with the following remark. Since the cylinder sets  $[\omega_s^t]$  constitute a (countable) basis for the  $\sigma$ -algebra in  $\mathcal{A}^{\mathbb{Z}}$  and since to each piece of trajectory  $V_s^t$  is associated a unique sequence  $\omega_s^t$ , we consider first the probability distribution of  $V(t + 1)$  conditioned by  $Z(V_s^t) = \omega_s^t$  and by the initial condition  $V(s)$ , assumed here to be bounded. Then, the following holds as easily checked with a few algebra:

**Proposition 1** For each  $(s, t) \in \mathbb{Z}^2, s < t$ , conditionally to  $Z(V_s^t) = \omega_s^t$ , and given  $V(s)$ ,

$$V_i(t + 1) = \begin{cases} \gamma^{t+1-s} V_i(s) + C_i(\omega_s^t) + \sigma_B \xi_i(\omega_s^t), & \text{if neuron } i \text{ didn't fire in the time interval } [s, t]; \\ C_i(\omega_s^t) + \sigma_B \xi_i(\omega_s^t), & \text{otherwise.} \end{cases} \quad (4)$$

where

$$C_i(\omega_s^t) = \sum_{j=1}^N W_{ij} x_{ij}(\omega_s^t) + I_i \frac{1 - \gamma^{t+1-\tau_i(\omega_s^t)}}{1 - \gamma}, \quad (5)$$

$$x_{ij}(\omega_s^t) = \sum_{l=\tau_i(\omega_s^t)}^t \gamma^{t-l} \omega_j(l), \quad (6)$$

$$\xi_i(\omega_s^t) = \sum_{l=\tau_i(\omega_s^t)}^t \gamma^{t-l} B_i(l). \quad (7)$$

*Remark* – This equation expresses that the neuron loses its memory whenever it fires. This is due to the fact that we reset the membrane potential, after firing. This consequently simplifies the following analysis. For a discussion on dynamics of spiking neural phase models when the condition is relaxed see [Kirst et al. \(2009\)](#).

- Clearly, the membrane potential is the sum of a “deterministic” part,  $\gamma^{t+1-s} V_i(s) + C_i(\omega_s^t)$ , fixed by initial condition at time  $s$  and by the spike sequence  $\omega_s^t$ , and a stochastic part,  $\sigma_B \xi_i(\omega_s^t)$ , where the probability distribution of the noise  $\xi_i(\omega_s^t)$  is also fixed by the spike sequence  $\omega_s^t$ . More precisely, since the  $B_i$ ’s are independent, Gaussian with mean zero and variance 1, the  $\xi_i(\omega_s^t)$ ’s,  $i = 1 \dots N$  are, under  $P$ , Gaussian, independent, with zero mean and variance  $\frac{1 - \gamma^{2(t+1-\tau_i(\omega_s^t))}}{1 - \gamma^2}$ .

Denote by  $\mathbb{E}[\ ]$  the expectation under  $P$ . It follows that:

**Proposition 2** *For each  $(s, t) \in \mathbb{Z}^2, s < t$ , conditionally to  $Z(V_s^t) = \omega_s^t$ , and given  $V(s), V(t + 1)$  is Gaussian with mean:*

$$\begin{aligned} &\mathbb{E} [V_i(t + 1) | \omega_s^t, V(s)] \\ &= \begin{cases} \gamma^{t+1-s} V_i(s) + C_i(\omega_s^t), & \text{if neuron } i \text{ didn't fire in the time interval } [s, t]; \\ C_i(\omega_s^t), & \text{otherwise.} \end{cases} \end{aligned}$$

and covariance:

$$Cov [V_i(t + 1), V_j(t + 1) | \omega_s^t, V(s)] = \sigma_i^2(\omega_s^t) \delta_{ij}.$$

with:

$$\sigma_i^2(\omega_s^t) = \sigma_B^2 \frac{1 - \gamma^{2(t+1-\tau_i(\omega_s^t))}}{1 - \gamma^2}. \tag{8}$$

Thus, the  $V_i(t + 1)$ ’s,  $i = 1 \dots N$ , are conditionally independent.

*Remark* We used a slight abuse of notation since we condition by  $\omega_s^t$  instead of  $Z(V_s^t) = \omega_s^t$ .

### 2.3.2 The probability that some neuron $i$ does not fire within the time interval $[s, t]$

It is given by:

$$\begin{aligned} P \left( \bigcap_{n=s}^t \{V_i(n) < \theta\} \right) &= \sum_{\omega_s^t \in \mathcal{A}^{t-s}} P \left( \bigcap_{n=s}^t \{V_i(n) < \theta\} | \omega_s^t \right) P(\omega_s^t) \\ &= \sum_{\omega_s^t \in \mathcal{A}^{t-s}} \prod_{n=s+1}^t P \left( \{V_i(n) < \theta\} | \bigcap_{l=s}^{n-1} \{V_i(l) < \theta\} \cap \omega_s^t \right) P(\{V_i(s) < \theta\} | \omega_s^t) P(\omega_s^t) \\ &= \sum_{\omega_s^t \in \mathcal{A}^{t-s}} \prod_{n=s+1}^t P \left( \{V_i(n) < \theta\} | \bigcap_{l=s}^{n-1} \{V_i(l) < \theta\} \cap \omega_s^{n-1} \right) P(\{V_i(s) < \theta\} | \omega_s^s) P(\omega_s^s) \end{aligned}$$



From Proposition 2, we have:

$$P\left(\{V_i(n) < \theta\} \mid \bigcap_{l=s}^{n-1} \{V_i(l) < \theta\} \cap \omega_s^{n-1}\right) = P\left(\gamma^{n-s} V_i(s) + C_i(\omega_s^{n-1}) + \sigma_B \xi_i(\omega_s^{n-1}) < \theta\right),$$

where  $C_i(\omega_s^{n-1})$  and  $\xi_i(\omega_s^{n-1})$  are given by (5), (6), (7) with  $\tau_i(\omega_s^t) = s$ . Since, in this case,  $\xi_i(\omega_s^{n-1})$  is Gaussian, centered, with variance  $\frac{1-\gamma^{2(n-s)}}{1-\gamma^2}$  (Eq. 8) we have:

$$P\left(\{V_i(n) < \theta\} \mid \bigcap_{l=s}^{n-1} \{V_i(l) < \theta\} \cap \omega_s^{n-1}\right) = 1 - \pi\left(\frac{\theta - \gamma^{n-s} V_i(s) - C_i(\omega_s^{n-1})}{\sigma_B \sqrt{\frac{1-\gamma^{2(n-s)}}{1-\gamma^2}}}\right).$$

Since  $V_i(s)$  and the  $W_{ij}$ 's are assumed to be bounded we have, whatever  $n > s$ :

$$0 < \Pi_- < P\left(\{V_i(n) < \theta\} \mid \bigcap_{l=s}^{n-1} \{V_i(l) < \theta\} \cap \omega_s^{n-1}\right) < \Pi_+ < 1, \tag{9}$$

for some constants  $\Pi_-, \Pi_+$  depending on parameters  $\gamma, W_{ij}, i, j = 1 \dots N, I_i, i = 1 \dots N$ . Likewise,  $0 < a < P(\{V_i(s) < \theta\} \mid \omega_s^s) < b < 1$ . Without loss of generality, e.g. redefining  $\Pi_-$  as  $\min(\Pi_-, a)$  (redefining  $\Pi_+$  as  $\max(\Pi_+, b)$ ) we may write  $0 < \Pi_- < P(\{V_i(s) < \theta\} \mid \omega_s^s) < \Pi_+ < 1$ . As a consequence,

**Proposition 3** *The probability that some neuron  $i$  does not fire within the time interval  $[s, t]$  has the following bounds:*

$$0 < \Pi_-^{t-s} < P\left(\bigcap_{n=s}^t \{V_i(n) < \theta\}\right) < \Pi_+^{t-s} < 1.$$

As a consequence, whatever  $s < t, t - s$  finite, there is a positive probability that some neuron  $i$  does not fire within the time interval  $[s, t]$ . This probability vanishes exponentially fast as  $|t - s| \rightarrow +\infty$ .

### 2.3.3 Permanent regime

The main drawback of the previous results is that we have to condition on the “initial” condition  $V(s)$  for spiking sequences such that some neuron does not fire between  $s$  and  $t$ . But the probability distribution of  $V(s)$  is not known. It has either to be “guessed” from ad hoc assumptions: is it Gaussian, uniform, “fractal” ...? Actually, the determination of initial conditions distribution is, to our opinion, one of the main obstacle toward realistic characterizations or simulations of neural network models, intended to somehow mimics the dynamics (of some part) of the brain, at some stage

of its evolution. Indeed, when considering the evolution of a set of neurons, one starts from some “initial” time  $s$  which corresponds to the beginning of the experiment. This is NOT the beginning of the system under study, which has undergone a previous evolution that actually determines the distribution of membrane potentials at time  $s$ . This distribution has little chances to be Gaussian or anything so mathematically “convenient”, unless one finds strong arguments to justify this. Actually, as we show, such assumption is wrong in model (1). Therefore, to compute the distribution of membrane potential at time  $s$  one has to consider the previous evolution of the system, which only postpones the problem, ...unless one assumes that this initial condition was drawn in an *infinite past*. On phenomenological grounds, “infinite past” means “a time quite longer than all characteristic time scales in the system”, though, mathematically, one may take it truly infinite. This is what we do here, focusing on what we call a “permanent regime” (by analogy with Physics) where the initial condition is fixed in the infinite past, namely  $s \rightarrow -\infty$ . In this case, indeed,  $\gamma^{t+1-s} V_i(s) \rightarrow 0$ . As we show, this procedure selects a *unique* probability distribution for membrane potentials, with a highly non trivial structure (see Eq. 33).

We therefore consider left-infinite sequences  $\omega_{-\infty}^t$  with corresponding last firing time:

$$\tau_i(\omega_{-\infty}^t) \stackrel{\text{def}}{=} \begin{cases} -\infty, & \text{if } \omega_i(k) = 0, \quad \forall k \leq t; \\ \max \{-\infty < k \leq t, \omega_i(k) = 1\} & \text{otherwise.} \end{cases} \tag{10}$$

We now show that Proposition 2 extends as well to the case  $s \rightarrow -\infty$ , namely:

**Proposition 4** *For each  $t \in \mathbb{Z}$ , conditionally to  $\omega_{-\infty}^t$ ,  $V(t + 1)$  is Gaussian with mean:*

$$\mathbb{E} [V_i(t + 1) | \omega_{-\infty}^t] = C_i(\omega_{-\infty}^t) = \sum_{j=1}^N W_{ij} x_{ij}(\omega_{-\infty}^t) + I_i \frac{1 - \gamma^{t+1-\tau_i(\omega_{-\infty}^t)}}{1 - \gamma}, \tag{11}$$

where,

$$x_{ij}(\omega_{-\infty}^t) = \sum_{l=\tau_i(\omega_{-\infty}^t)}^t \gamma^{t-l} \omega_j(l), \tag{12}$$

and covariance:

$$\text{Cov} [V_i(t + 1), V_j(t + 1) | \omega_{-\infty}^t] = \sigma_i^2(\omega_{-\infty}^t) \delta_{ij} = \sigma_B^2 \frac{1 - \gamma^{2(t+1-\tau_i(\omega_{-\infty}^t))}}{1 - \gamma^2} \delta_{ij}. \tag{13}$$

Thus, the  $V_i(t + 1)$ 's,  $i = 1 \dots N$ , are conditionally independent.

*Proof* Let us first show that the quantities defined by Eqs. (5), (6), (7) are well defined in the limit  $s \rightarrow -\infty$ . Consider first the limit of  $x_{ij}(\omega_s^t)$  given by Eq. (6). There are two possibilities. Either  $\omega_{-\infty}^t$  is such that  $\tau_i(\omega_{-\infty}^t) = n > -\infty$ . Then,  $x_{ij}(\omega_{-\infty}^t)$  is a finite sum  $\sum_{l=n}^t \gamma^{t-l} \omega_j(l)$  and is well defined. Or,  $\tau_i(\omega_{-\infty}^t) = -\infty$ . Then  $x_{ij}(\omega_{-\infty}^t) = \sum_{l=-\infty}^t \gamma^{t-l} \omega_j(l) = \sum_{l=0}^{+\infty} \gamma^l \omega_j(t-l)$ . This series converges since  $\gamma < 1$  and  $\omega_j(t-l) = 0, 1$ .

Moreover,  $\xi_i(\omega_s^t) = \sum_{l=\tau_i(\omega_s^t)}^t \gamma^{t-l} B_i(l)$  is a sum (possibly infinite) of independent Gaussian centered variables with finite variance. As a consequence,

$$\xi_i(\omega_{-\infty}^t) = \sum_{l=\tau_i(\omega_{-\infty}^t)}^t \gamma^{t-l} B_i(l), \tag{14}$$

is Gaussian centered with variance  $\frac{1-\gamma^{2(t+1-\tau_i(\omega_{-\infty}^t))}}{1-\gamma^2}$ . Finally, from (4)  $V_i(t+1) = C_i(\omega_{-\infty}^t) + \sigma_B \xi_i(\omega_{-\infty}^t)$ , and the proposition follows from the independence of the  $\xi_i(\omega_{-\infty}^t)$ 's and their Gaussian distribution.  $\square$

### 2.3.4 Elementary bounds

We have:

$$0 \leq x_{ij}(\omega_{-\infty}^t) \leq \frac{1}{1-\gamma}, \tag{15}$$

and,

$$C_i^- \stackrel{\text{def}}{=} I_i + \frac{1}{1-\gamma} \sum_{\substack{j=1 \\ W_{ij}<0}}^N W_{ij} \leq C_i(\omega_{-\infty}^t) \leq \frac{1}{1-\gamma} \left( \sum_{\substack{j=1 \\ W_{ij}>0}}^N W_{ij} + I_i \right) \stackrel{\text{def}}{=} C_i^+, \tag{16}$$

In the same way

$$\sigma_B^2 \leq \sigma_i^2(\omega_{-\infty}^t) \leq \frac{\sigma_B^2}{1-\gamma^2}. \tag{17}$$

### 2.3.5 The transition probability

We now compute the probability of a spiking pattern at time  $t+1$ ,  $\omega(t+1)$ , given the past  $\omega_{-\infty}^t$ . It is given by the following:

**Proposition 5** *The probability of  $\omega(t+1)$  conditionally to  $\omega_{-\infty}^t$  is given by:*

$$P(\omega(t+1)|\omega_{-\infty}^t) = \prod_{i=1}^N P(\omega_i(t+1)|\omega_{-\infty}^t), \tag{18}$$

with

$$P(\omega_i(t + 1) | \omega_{-\infty}^t) = \omega_i(t + 1) \pi \left( \frac{\theta - C_i(\omega_{-\infty}^t)}{\sigma_i(\omega_{-\infty}^t)} \right) + (1 - \omega_i(t + 1)) \left( 1 - \pi \left( \frac{\theta - C_i(\omega_{-\infty}^t)}{\sigma_i(\omega_{-\infty}^t)} \right) \right). \tag{19}$$

*Proof* We have, using the conditional independence of the  $V_i(t + 1)$ 's:

$$P(\omega(t + 1) | \omega_{-\infty}^t) = \prod_{i=1}^N \left[ \omega_i(t + 1) P(V_i(t + 1) \geq \theta | \omega_{-\infty}^t) + (1 - \omega_i(t + 1)) P(V_i(t + 1) < \theta | \omega_{-\infty}^t) \right].$$

Since the  $V_i(t + 1)$ 's are Gaussian, with mean  $C_i(\omega_{-\infty}^t)$  with a variance  $\sigma_i^2(\omega_{-\infty}^t)$  we directly obtain (18), (19). □

Consequently, it is possible, knowing the past sequence  $\omega_{-\infty}^t$ , to determine the probability of the spiking pattern  $\omega(t + 1)$ . In this way,  $P(\omega(t + 1) | \omega_{-\infty}^t)$  acts as a transition probability, as in Markov chains. But here, the length of the Markov chain depends on the last firing time of each neuron, since in fact,

$$P(\omega_i(t + 1) | \omega_{-\infty}^t) = P(\omega_i(t + 1) | \omega_{\tau_i(\omega_{-\infty}^t)}^t).$$

The problem here is that, according to Proposition 3, we cannot bound  $\tau_i(\omega_{-\infty}^t)$ . Although this time  $\tau_i(\omega_{-\infty}^t)$  is almost-surely finite, nevertheless, whatever  $T > 0$ , there is a positive probability set of sequences  $\omega$  such that  $\tau_i(\omega_{-\infty}^t) < t - T$ . So we have to consider a process where transition probability may have an *unbounded memory*. This type of process is called “variable length Markov chain” (Maillard 2007). Such processes can be studied in the general context of *chains with complete connections* and *g-measures*, developed in Sect. 3.

### 2.3.6 Stationarity

In the present setting where  $I_i$  does not depend on  $t$  we have the following property:

**Proposition 6** Fix a sequence  $a_{-\infty}^0, a(-n) \in \mathcal{A}, n \geq 0$ . Then,  $\forall t \in \mathbb{Z}$ ,

$$P(\omega(t) = a(0) | \omega_{-\infty}^{t-1} = a_{-\infty}^{-1}) = P(\omega(0) = a(0) | \omega_{-\infty}^{-1} = a_{-\infty}^{-1}). \tag{20}$$

*Proof* Assume that  $\omega(t - n) = a(-n)$ ,  $n \geq 0$ , as in the l.h.s of (20). Then, according to Eq. (10),  $\tau_i(\omega_{-\infty}^{t-1}) = t + \tau_i(a_{-\infty}^{-1})$ . Therefore, according to Eq. (12),

$$\begin{aligned} x_{ij}(\omega_{-\infty}^{t-1}) &= \sum_{l=\tau_i(\omega_{-\infty}^{t-1})}^{t-1} \gamma^{t-1-l} \omega_j(l) = \sum_{l=t+\tau_i(a_{-\infty}^{-1})}^{t-1} \gamma^{t-1-l} a_j(l-t) \\ &= \sum_{l'=\tau_i(a_{-\infty}^{-1})}^{-1} \gamma^{-1-l'} a_j(l') = x_{ij}(a_{-\infty}^{-1}), \end{aligned}$$

and, according to (11),

$$\begin{aligned} C_i(\omega_{-\infty}^{t-1}) &= \sum_{j=1}^N W_{ij} x_{ij}(\omega_{-\infty}^{t-1}) + I_i \frac{1 - \gamma^{t-\tau_i(\omega_{-\infty}^{t-1})}}{1 - \gamma}, \\ &= \sum_{j=1}^N W_{ij} x_{ij}(a_{-\infty}^{-1}) + I_i \frac{1 - \gamma^{-\tau_i(a_{-\infty}^{-1})}}{1 - \gamma} = C_i(a_{-\infty}^{-1}). \end{aligned}$$

Note that this last property holds because  $I_i$  does not depend on time. We have also, from the same arguments,

$$\sigma_i^2(\omega_{-\infty}^{t-1}) = \sigma_i^2(a_{-\infty}^{-1}).$$

Consequently,

$$\begin{aligned} &P\left(\omega(t) = a(0) \mid \omega_{-\infty}^{t-1} = a_{-\infty}^{-1}\right) \\ &= \prod_{i=1}^N \left[ \omega_i(t) \pi\left(\frac{\theta - C_i(\omega_{-\infty}^{t-1})}{\sigma_i(\omega_{-\infty}^{t-1})}\right) + (1 - \omega_i(t)) \left(1 - \pi\left(\frac{\theta - C_i(\omega_{-\infty}^{t-1})}{\sigma_i(\omega_{-\infty}^{t-1})}\right)\right) \right] \\ &= \prod_{i=1}^N \left[ a_i(0) \pi\left(\frac{\theta - C_i(a_{-\infty}^{-1})}{\sigma_i(a_{-\infty}^{-1})}\right) + (1 - a_i(0)) \left(1 - \pi\left(\frac{\theta - C_i(a_{-\infty}^{-1})}{\sigma_i(a_{-\infty}^{-1})}\right)\right) \right] \\ &= P\left(\omega(0) = a(0) \mid \omega_{-\infty}^{-1} = a_{-\infty}^{-1}\right). \end{aligned}$$

□

Therefore, instead of considering a family of transition probabilities depending on  $t$ , it suffices to define the transition probability at one time  $t \in \mathbb{Z}$ , for example  $t = 0$ .

### 3 The equilibrium state

In this section we show the existence of a unique invariant probability distribution for the dynamics (1) and characterize it explicitly. Especially, we show that it is an

*equilibrium state* and a *Gibbs state* in the sense of the thermodynamic formalism in ergodic theory (Chazottes and Keller 2009; Keller 1998). For this we use the concept of  $g$ -measures (Keane 1972), coming from ergodic theory, and very close (equivalent in the present setting) to the concept of chains with complete connections,<sup>5</sup> which comes from probability theory. However, all known theorems used here being formulated in the  $g$ -measure context, we use this formulation here. For the convenience of the reader we however provide examples and illustrations of the used notions. Our main reference are Bressaud et al. (1999), Chazottes (1999), Coelho and Quas (1998), Ledrappier (1974), and Maillard (2007).

We proceed in several steps leading us to the Theorems 1, 2 the main results of this paper.

### 3.1 Definitions and elementary results

#### 3.1.1 Setting and notations

The main object under study here is the family of transitions probabilities (18). Using the stationarity Proposition 6 we can restrict to transition probabilities of the form  $P(\omega(0)|\omega_{-\infty}^{-1})$ . Namely, we may focus on sequences in  $\mathcal{A}_{-\infty}^0$ . From now on we set  $\omega = \omega_{-\infty}^0$ ,  $\underline{\omega} = \omega_{-\infty}^{-1}$  (a sequence  $\omega$  is called an “history”),  $X = \mathcal{A}_{-\infty}^0$ ,  $\underline{X} = \mathcal{A}_{-\infty}^{-1}$ . The  $\sigma$ -algebra (the set of cylinders) on  $X$  (resp.  $\underline{X}$ ) is denoted  $\mathcal{F}$  (resp.  $\underline{\mathcal{F}}$ ).

Call  $T$  the *right* shift over  $X$  i.e.  $(T\omega)(t) = \omega(t - 1)$ ,  $t \leq 0$ . The use of the right shift, instead of the left shift currently used in dynamical systems theory, is related to the formulation of the problem in terms of transitions probabilities (see for example Bressaud et al. (1999)). We note  $\omega a$ , the right concatenation of  $\omega$  and  $a \in \mathcal{A}$ , namely, this is the sequence  $\omega'$  such that  $\omega'(t - 1) = \omega(t)$ ,  $t \leq 0$  and  $\omega'(0) = a$ . Note that  $T(\omega a) = \omega$ .

#### 3.1.2 $g$ -Functions

**Definition 1** A  $g$ -function over  $(X, T)$  is a measurable function  $g : X \rightarrow [0, 1]$  which satisfies, for all  $\omega \in X$ :

$$\sum_{\omega', T(\omega')=\omega} g(\omega') = 1. \quad (21)$$

<sup>5</sup> The concept of chains with complete connections, dates back to 1935 (Onicescu and Mihoc 1935). They are a generalization of Markov chains with an infinite memory. More precisely, they are induced by conditional probabilities of the form:  $P(\omega(t + 1) | \omega_{-\infty}^t)$ . These transition probabilities appear to be an extension of the notion of  $k$ -step Markov chain with an infinite  $k$ . These objects must be taken with some precautions because, in the non-Markovian case, the conditioning is always on an event of probability zero (see Maillard (2007) for proper definition). The transition probabilities given by Eqs. (18), (19) define a system of such transition probabilities.

Examples of  $g$  functions are precisely transition probabilities of type (18). Indeed, for  $\omega \in X$ , set:

$$g_0(\omega) = P(\omega(0)|\underline{\omega}) = \prod_{i=1}^N \left[ \omega_i(0)\pi\left(\frac{\theta - C_i(\underline{\omega})}{\sigma_i(\underline{\omega})}\right) + (1 - \omega_i(0))\left(1 - \pi\left(\frac{\theta - C_i(\underline{\omega})}{\sigma_i(\underline{\omega})}\right)\right) \right]. \tag{22}$$

Then, by definition, all  $\omega'$ 's in the sum (21) have the form  $\omega' = \omega a$ , and:

$$\sum_{\omega', T(\omega')=\omega} g_0(\omega') = \sum_{a \in \mathcal{A}} P(a|\underline{\omega}) = 1.$$

We now give two properties of  $g_0$  used below.

### 3.1.3 $g_0$ is non-null

A  $g$  function is *non null* on  $X$  if for all  $\omega \in X$ ,  $g(\omega) > 0$ . We have:

**Proposition 7** *The  $g$ -function  $g_0$ , given by (22), is non-null.*

*Proof* It suffices to check that  $P(\omega(0)|\underline{\omega}) > 0$ . If there exists  $\omega \in X$  such that  $P(\omega(0)|\underline{\omega}) = 0$ , then, for some  $i \in \{1 \dots N\}$ ,  $\pi\left(\frac{\theta - C_i(\underline{\omega})}{\sigma_i(\underline{\omega})}\right) = 0$  or 1. This imposes that either  $C_i(\underline{\omega}) = \pm\infty$  or  $\sigma_i(\underline{\omega}) = 0$  which is not possible since these quantities are bounded by bounds (16), (17).  $\square$

### 3.1.4 $g_0$ is continuous

**Definition 2** The *variation* of a  $g$ -function  $g$  is:

$$var_k(g) = \sup \{ |g(\omega) - g(\omega')| : \omega, \omega' \in X, \omega(t) = \omega'(t), \forall t \in \{-k, \dots, 0\} \}.$$

**Definition 3** A  $g$ -function is *continuous* if  $var_k(g) \rightarrow 0$  as  $k \rightarrow +\infty$ .

**Proposition 8**  $g_0$  is continuous.

*Proof* We shall use the following inequalities.

1. For a collection  $0 \leq a_i, b_i \leq 1, \forall i = 1 \dots N$ , we have<sup>6</sup>

$$\left| \prod_{i=1}^N a_i - \prod_{i=1}^N b_i \right| \leq \sum_{i=1}^N |a_i - b_i|, \tag{23}$$

as easily proved by recursion.

<sup>6</sup> We thank one reviewer for this useful remark.

2. For  $0 \leq x < 1$ , write  $\sqrt{1-x} = 1 - \sum_{n=1}^{+\infty} f_n x^n$ , where  $f_n = \frac{4^{-n}(2n)!}{(n!)^2(-1+2n)} \geq 0$  are the series coefficients of  $\sqrt{1-x}$ . Then, for  $A, B$  real,  $0 \leq u, v < 1$ ,

$$\begin{aligned} |A\sqrt{1-u} - B\sqrt{1-v}| &\leq |A - B| + \sum_{n=1}^{+\infty} f_n |Au^n - Bv^n| \\ &\leq |A - B| + \sum_{n=1}^{+\infty} f_n (|A|u^n + |B|v^n). \end{aligned} \tag{24}$$

Fix  $i \in \{1, \dots, N\}$ . Set  $y_i = \frac{\theta - C_i(\omega)}{\sigma_i(\omega)}$ ,  $y'_i = \frac{\theta - C_i(\omega')}{\sigma_i(\omega')}$ ,  $C_i = C_i(\omega)$ ,  $C'_i = C_i(\omega')$ ,  $\sigma_i = \sigma_i(\omega)$ ,  $\sigma'_i = \sigma_i(\omega')$ ,  $\tau_i = \tau_i(\omega)$ ,  $\tau'_i = \tau_i(\omega')$  to alleviate notations in the proof. We have, for  $k > 0$ ,

$$var_k(g_0) = \sup \left\{ \left| \prod_{i=1}^N a_i - \prod_{i=1}^N b_i \right| : \omega, \omega' \in X, \omega(t) = \omega'(t), \forall t \in \{-k, \dots, 0\} \right\}.$$

where  $a_i = \omega_i(0)\pi(y_i) + (1 - \omega_i(0))(1 - \pi(y_i))$ ,  $b_i = \omega_i(0)\pi(y'_i) + (1 - \omega_i(0))(1 - \pi(y'_i))$ . Moreover, since either  $\omega_i(0) = 0$  or  $\omega_i(0) = 1$ ,  $|a_i - b_i| = |\pi(y_i) - \pi(y'_i)|$ . Therefore, using inequality (23),

$$var_k g_0 \leq \sum_{i=1}^N \sup \{ |\pi(y_i) - \pi(y'_i)| : \omega, \omega' \in X, \omega(t) = \omega'(t), \forall t \in \{-k, \dots, 0\} \}.$$

Fix  $k > 0$ . Then, for all  $\omega$  such that  $\tau_i(\omega) \in \{-k \dots 0\}$ ,  $\pi(y_i) = \pi(y'_i)$ . Therefore, the sup is realized for those  $\omega, \omega'$  such that  $\tau_i, \tau'_i < -k$ . Since  $\gamma < 1$  we have therefore  $\gamma^{-\tau} < \gamma^k$  and  $\frac{1}{1-\gamma^{-\tau}} < \frac{1}{1-\gamma^k}$ , for  $\tau = \tau_i, \tau'_i$ . We have  $|\pi(y_i) - \pi(y'_i)| \leq |y_i - y'_i| \|\pi'\|_\infty$  with  $\|\pi'\|_\infty = \frac{1}{\sqrt{2\pi}}$ . Moreover,  $|y_i - y'_i| \leq \theta \left| \frac{1}{\sigma_i} - \frac{1}{\sigma'_i} \right| + \left| \frac{C'_i \sigma_i - C_i \sigma'_i}{\sigma_i \sigma'_i} \right|$ .

We have,

$$\begin{aligned} \left| \frac{1}{\sigma_i} - \frac{1}{\sigma'_i} \right| &= \frac{\sqrt{1-\gamma^2}}{\sigma_B} \left| \frac{1}{\sqrt{1-\gamma^{-2\tau_i}}} - \frac{1}{\sqrt{1-\gamma^{-2\tau'_i}}} \right| \\ &= \frac{\sqrt{1-\gamma^2}}{\sigma_B \sqrt{1-\gamma^{-2\tau_i}} \sqrt{1-\gamma^{-2\tau'_i}}} \left| \sqrt{1-\gamma^{-2\tau'_i}} - \sqrt{1-\gamma^{-2\tau_i}} \right| \\ &\leq \frac{2\sqrt{1-\gamma^2}}{\sigma_B(1-\gamma^{2k})} \gamma^{2k} S(\gamma), \end{aligned}$$



with

$$S(\gamma) = \sum_{n=1}^{+\infty} f_n \gamma^{2k(n-1)}, \tag{25}$$

the last inequality coming from (24).

Likewise,

$$\begin{aligned} \left| \frac{C'_i \sigma_i - C_i \sigma'_i}{\sigma_i \sigma'_i} \right| &= \frac{\sqrt{1-\gamma^2}}{\sigma_B \sqrt{1-\gamma^{-2\tau_i}} \sqrt{1-\gamma^{-2\tau'_i}}} \left| C'_i \sqrt{1-\gamma^{-2\tau_i}} - C_i \sqrt{1-\gamma^{-2\tau'_i}} \right| \\ &\leq \frac{\sqrt{1-\gamma^2}}{\sigma_B (1-\gamma^{2k})} \left( |C'_i - C_i| + \sum_{n=1}^{+\infty} f_n \gamma^{2kn} (|C'_i| + |C_i|) \right) \\ &\leq \frac{\sqrt{1-\gamma^2}}{\sigma_B (1-\gamma^{2k})} \left( |C'_i - C_i| + 2\gamma^{2k} |C_i^+| S(\gamma) \right) \end{aligned}$$

where  $C_i^+$  is given by (16).

We have,

$$\begin{aligned} |C'_i - C_i| &= \left| \sum_{j=1}^N W_{ij} \left( \sum_{l=\tau_i}^{-1} \gamma^{-l-1} \omega_j(l) - \sum_{l=\tau'_i}^{-1} \gamma^{-l-1} \omega'_j(l) \right) + \frac{I_i}{1-\gamma} (\gamma^{-\tau_i} - \gamma^{-\tau'_i}) \right| \\ &\leq \sum_{j=1}^N |W_{ij}| \left| \sum_{l=\tau_i}^{-1} \gamma^{-l-1} \omega_j(l) - \sum_{l=\tau'_i}^{-1} \gamma^{-l-1} \omega'_j(l) \right| + \frac{|I_i|}{1-\gamma} |\gamma^{-\tau_i} - \gamma^{-\tau'_i}|. \end{aligned}$$

Remark that

$$\sum_{l=-k}^{-1} \gamma^{-l-1} \omega_j(l) = \sum_{l=-k}^{-1} \gamma^{-l-1} \omega'_j(l),$$

since  $\omega_j(l) = \omega'_j(l), l = -k \dots - 1$ . Therefore,

$$\left| \sum_{l=\tau_i}^{-1} \gamma^{-l-1} \omega_j(l) - \sum_{l=\tau'_i}^{-1} \gamma^{-l-1} \omega'_j(l) \right| = \left| \sum_{l=\tau_i}^{-k-1} \gamma^{-l-1} \omega_j(l) - \sum_{l=\tau'_i}^{-k-1} \gamma^{-l-1} \omega'_j(l) \right| \leq \frac{2\gamma^k}{1-\gamma}.$$

Moreover,

$$\frac{|I_i|}{1-\gamma} |\gamma^{-\tau_i} - \gamma^{-\tau'_i}| \leq 2 \frac{|I_i|}{1-\gamma} \gamma^k$$

Finally,

$$|C'_i - C_i| \leq \frac{2\gamma^k}{1-\gamma} \left( \sum_{j=1}^N |W_{ij}| + |I_i| \right).$$

Summarizing,

$$\begin{aligned} \left| \frac{C'_i \sigma_i - C_i \sigma'_i}{\sigma_i \sigma'_i} \right| &\leq \gamma^k \frac{2\sqrt{1-\gamma^2}}{\sigma_B(1-\gamma^{2k})} \left( \frac{1}{1-\gamma} \left( \sum_{j=1}^N |W_{ij}| + |I_i| \right) + \gamma^k |C_i^+| S(\gamma) \right) \\ \|\pi(y_i) - \pi(y'_i)\| &\leq \sqrt{\frac{2}{\pi}} \frac{\sqrt{1-\gamma^2}}{\sigma_B(1-\gamma^{2k})} \left( \frac{1}{1-\gamma} \left( \sum_{j=1}^N |W_{ij}| + |I_i| \right) + \gamma^k (\theta + |C_i^+|) S(\gamma) \right) \gamma^k, \end{aligned}$$

and,

$$var_k g_0 \leq \sqrt{\frac{2}{\pi}} \frac{\sqrt{1-\gamma^2}}{\sigma_B(1-\gamma^{2k})} \left( \frac{1}{1-\gamma} \left( \sum_{i,j=1}^N |W_{ij}| + \sum_{i=1}^N |I_i| \right) + \gamma^k \left( N\theta + \sum_{i=1}^N |C_i^+| \right) S(\gamma) \right) \gamma^k,$$

Remarking that  $S(\gamma) \rightarrow f_1$  as  $k \rightarrow +\infty$  we conclude that  $var_k g_0 \rightarrow 0$  as  $k \rightarrow +\infty$  and behaves like  $K\gamma^k$ , where the constant

$$K = \sqrt{\frac{2}{\pi}} \frac{1}{\sigma_B} \sqrt{\frac{1+\gamma}{1-\gamma}} \left[ \sum_{i,j=1}^N |W_{ij}| + \sum_{i=1}^N |I_i| \right], \tag{26}$$

depends on model parameters (synaptic weights and current) and  $N$ . □

*Remark* Note that  $g_0$  is therefore Hölderian for the metric (2) (with an exponent  $\frac{\log \gamma}{\log \Theta}$  so it is Lipschitz for  $\Theta = \gamma$ ).

### 3.2 The Gibbs equilibrium state

We now prove that the system (1) admits a unique invariant probability measure (also called a  $g$ -measure). This measure satisfies a variational principle (equilibrium state) and has the form of a Gibbs distribution in statistical physics.

#### 3.2.1 $g$ -Measure

**Definition 4** Let  $g$  be a  $g$ -function. A probability measure  $\mu$  in  $\mathcal{P}(X, \mathcal{F})$  is a  $g$ -measure if:

$$\int f(\omega)g(\omega a)\mu(d\omega) = \int_{\{\omega(0)=a\}} f(\omega)\mu(d\omega),$$

$\forall a \in \mathcal{A}$  and  $\forall f$  measurable with respect to  $\underline{\mathcal{F}}$ .

3.2.2 *There exists a g-measure for (1) and it is unique*

Since  $g_0$  is continuous there is always a  $g$ -measure. Now, a theorem of [Johansson and Oberg \(2003\)](#) states that if  $g_0$  is a continuous, non-null  $g$  function on  $X$  satisfying:

$$\sum_{k \geq 0} var_k^2(\log g_0) < +\infty, \tag{27}$$

then the  $g$ -measure is unique.

**Theorem 1** *The dynamical system (1) has a unique  $g_0$ -measure whatever the values of parameters  $W_{ij}, i, j = 1 \dots N, I_i, i = 1 \dots N, \gamma, \theta$ .*

*Proof* This follows from the theorem of Johansson and Oberg. Indeed, using a proof similar to Proposition 8 and the same notations, we have, for  $k > 0$ , and using that

$$\begin{aligned} \log [\omega_i(0)\pi(y_i) + (1 - \omega_i(0))(1 - \pi(y_i))] &= \omega_i(0) \log (\pi(y_i)) \\ &+ (1 - \omega_i(0)) \log (1 - \pi(y_i)), \\ var_k(\log g_0) &= \sup \left\{ \left| \sum_{i=1}^N \left[ \omega_i(0) \left[ \log \left( \frac{\pi(y_i)}{\pi(y'_i)} \right) \right] + (1 - \omega_i(0)) \left[ \log \left( \frac{1 - \pi(y_i)}{1 - \pi(y'_i)} \right) \right] \right] \right| \right. \\ &\quad \left. \times : \omega, \omega' \in X, \omega(t) = \omega'(t), \forall t \in \{-k, \dots, 0\} \right\} \\ &\leq \sum_{i=1}^N \sup \left\{ \left| \log \left( \frac{\pi(y_i)}{\pi(y'_i)} \right) \right| + \left| \log \left( \frac{1 - \pi(y_i)}{1 - \pi(y'_i)} \right) \right| : \right. \\ &\quad \left. \times \omega, \omega' \in X, \omega(t) = \omega'(t), \forall t \in \{-k, \dots, 0\} \right\}. \end{aligned}$$

From the bounds (16), (17),

$$\sqrt{1 - \gamma^2} \frac{\theta - C_i^+}{\sigma_B} \leq y_i, y'_i \leq \frac{\theta - C_i^-}{\sigma_B}.$$

Set  $a \stackrel{\text{def}}{=} \sqrt{1 - \gamma^2} \min_{i=1 \dots N} \frac{\theta - C_i^+}{\sigma_B}$  and  $b \stackrel{\text{def}}{=} \max_{i=1 \dots N} \frac{\theta - C_i^-}{\sigma_B} < \infty$ . Denote  $\|f\|_{[a,b]} \stackrel{\text{def}}{=} \sup_{x \in [a,b]} |f(x)|$ , we have:

$$var_k(\log g_0) \leq 2 \left\| \frac{\pi'}{\pi} \right\|_{[a,b]} \sum_{i=1}^N \sup \{ |y_i - y'_i| : \omega, \omega' \in X, \omega(t) = \omega'(t), \forall t \in \{-k, \dots, 0\} \},$$

where the norm

$$\left\| \frac{\pi'}{\pi} \right\|_{[a,b]} = \frac{e^{-\frac{b^2}{2}}}{\int_b^{+\infty} e^{-\frac{u^2}{2}} du},$$

is finite since  $b$  is finite. For the term  $\max_i \sup \{|y_i - y'_i| \mid \omega, \omega' \in X, \omega(t) = \omega'(t), \forall t \in \{-k, \dots, 0\}\}$ , we have the same majoration as in the proof of Proposition 8. Thus,

$$\text{var}_k(\log g_0) \leq K' \gamma^k,$$

with

$$K' = \sqrt{2\pi} \left\| \frac{\pi'}{\pi} \right\|_{[a,b]} K, \tag{28}$$

$K$  given by (26). It follows that  $\sum_{k \geq 0} \text{var}_k^2(\log g_0) \leq K'^2 \sum_{k \geq 0} (\gamma^2)^k < \infty$ . Then the  $g_0$  measure is unique. □

Let us now characterize the structure of this  $g$ -measure.

### 3.2.3 The Ruelle–Perron–Frobenius operator

For the  $g$ -function  $g_0$  define the *transfer operator* or *Ruelle–Perron–Frobenius operator*  $\mathcal{L}_{g_0}$  from  $C(X, \mathbb{R})$  to  $C(X, \mathbb{R})$ , where  $C(X, \mathbb{R})$  is the set of continuous real functions on  $X$ , by:

$$\mathcal{L}_{g_0} f(\omega) = \sum_{\omega': T(\omega')=\omega} g_0(\omega') f(\omega'). \tag{29}$$

Denoting  $\mathcal{L}_{g_0}^n, n > 0$ , the  $n$ -iterates of the RPF operator,  $\mathcal{L}_{g_0}^n f$  is the conditional expectation of  $f$  on the time interval  $[0, n - 1]$  given the history  $\underline{\omega}$ . The Ruelle–Perron–Frobenius is the extension of matrices of probability transitions for Markov chains.

The adjoint of  $\mathcal{L}_{g_0}$  maps the set of probability measures on  $X$  to itself and is defined by:

$$\mathcal{L}_{g_0}^* \mu(f) = \mu(\mathcal{L}_g f).$$

A probability measure  $\mu$  on  $X$  is a  $g$ -measure if and only if  $\mathcal{L}_{g_0}^* \mu = \mu$  (Ledrappier 1974).

### 3.2.4 Equilibrium state

Let  $\psi$  be a continuous function  $X \rightarrow \mathbb{R}$  such that  $\sum_{k=0}^{\infty} \text{var}_k(\psi) < \infty$  (also called a *regular potential*, Keller 1998). Call  $P_T(X)$  the set of  $T$ -invariant finite measures on

$X$ . For  $\mu \in P_T(X)$  let

$$h(\mu) = \limsup_{n \rightarrow +\infty} \frac{1}{n+1} \sum_{[\omega]_0^n} \mu([\omega]_0^n) \log \mu([\omega]_0^n), \tag{30}$$

be the entropy of  $\mu$ , where the sum holds over all cylinders  $[\omega]_0^n$  of length  $n + 1$ . Note that the entropy can be defined in a more general setting (see Keller 1998). Here we take a definition which corresponds more to the one used in neural networks dynamics analysis.

**Definition 5** An equilibrium state,  $\mu_\psi$ , is a  $T$ -invariant measure on  $X$ , such that:

$$P(\psi) \stackrel{\text{def}}{=} h(\mu_\psi) + \mu_\psi(\psi) = \sup_{\mu \in P_T(X)} h(\mu) + \mu(\psi). \tag{31}$$

The quantity  $P(\psi)$  is called the “topological pressure” (Bowen 2008; Ruelle 1978; Sinai 1972). This is a fundamental quantity and we come back to it in Sect. 4. It is zero whenever the potential  $\psi$  is normalized, which is the case here since  $\psi$  is the log of a conditional probability.

Ledrappier has shown (Ledrappier 1974) that if  $\psi$  is a regular potential then the equilibrium states for  $\psi$  are the  $g$ -measures for a continuous  $g$  function. In our case where the  $g$ -measure is unique,  $g_0$  is related to the potential  $\psi$  given by:

$$\psi(\omega) = \log g_0(\omega).$$

Therefore, the following holds.

**Theorem 2** Whatever the parameters values the system (1) has a unique  $g_0$  probability measure,  $\mu_\psi$ , which is an equilibrium state for the potential

$$\begin{aligned} \psi(\omega) &\equiv \psi(\omega_{-\infty}^0) = \log g_0(\omega) \\ &= \sum_{i=1}^N \left[ \omega_i(0) \log \left( \pi \left( \frac{\theta - C_i(\omega)}{\sigma_i(\omega)} \right) \right) + (1 - \omega_i(0)) \log \left( 1 - \pi \left( \frac{\theta - C_i(\omega)}{\sigma_i(\omega)} \right) \right) \right]. \end{aligned} \tag{32}$$

### 3.3 Consequences

#### 3.3.1 Asymptotic distribution of membrane potentials

A first consequence of Proposition 4 and Theorem 1 is:

**Proposition 9** *The membrane potential vector  $V$  is stationary with a product density  $\rho_V(v) = \prod_{i=1}^N \rho_{V_i}(v_i)$  where:*

$$\rho_{V_i}(v) = \int_{\underline{X}} \frac{1}{\sqrt{2\pi}\sigma_i(\underline{\omega})} \exp\left(-\frac{1}{2}\left(\frac{v - C_i(\underline{\omega})}{\sigma_i(\underline{\omega})}\right)^2\right) d\mu_\psi(\underline{\omega}). \quad (33)$$

*Its expectation is  $\mu_\psi [C_i(\underline{\omega})]$  and its variance  $\mu_\psi [\sigma_i^2(\underline{\omega})]$ .*

**Comments.** This density is a ‘‘mixture’’ of Gaussian densities, but it is not Gaussian. Each Gaussian density in the decomposition depends on a specific history  $\underline{\omega}$ , and the integral holds on the set of all possible histories with a weight  $\mu_\psi(\underline{\omega})$ . Therefore, to obtain a closed form for the stationary density of membrane potential we need to know the invariant probability  $\mu_\psi$  which weights the possible histories *over an unbounded past*. It has therefore a highly non trivial structure as announced in Sect. 2.3.3.

### 3.3.2 Firing rates

Define:

$$r_i(\underline{\omega}) \stackrel{\text{def}}{=} P(\omega_i(0) = 1 | \underline{\omega}) = \pi \left[ \frac{\theta - C_i(\underline{\omega})}{\sigma_i(\underline{\omega})} \right], \quad (34)$$

the probability that neuron  $i$  fires at time 0 given the past  $\underline{\omega}$  and,

$$r_i \stackrel{\text{def}}{=} \mu_\psi(\omega_i(0) = 1), \quad (35)$$

called ‘‘the firing rate’’ of neuron  $i$ . We have:

$$r_i = \mu_\psi(r_i(\underline{\omega})) = \mu_\psi \left( \pi \left[ \frac{\theta - C_i(\underline{\omega})}{\sigma_i(\underline{\omega})} \right] \right). \quad (36)$$

### 3.3.3 Entropy

It results from (31) and the normalization of the potential  $\psi$  that  $0 = h(\mu_\psi) + \mu_\psi(\psi)$ . Therefore:

$$\begin{aligned} h(\mu_\psi) = & - \sum_{i=1}^N \mu_\psi \left( \omega_i(0) \log \left( \pi \left[ \frac{\theta - C_i(\underline{\omega})}{\sigma_i(\underline{\omega})} \right] \right) \right. \\ & \left. + (1 - \omega_i(0)) \log \left( 1 - \pi \left[ \frac{\theta - C_i(\underline{\omega})}{\sigma_i(\underline{\omega})} \right] \right) \right). \end{aligned}$$

Since either  $\omega_i(0) = 0$  or 1, we have:

$$h(\mu_\psi) = - \sum_{i=1}^N \left[ r_i \mu_\psi \left( \log \left( \pi \left[ \frac{\theta - C_i(\underline{\omega})}{\sigma_i(\underline{\omega})} \right] \right) \right) + (1 - r_i) \mu_\psi \left( \log \left( 1 - \pi \left[ \frac{\theta - C_i(\underline{\omega})}{\sigma_i(\underline{\omega})} \right] \right) \right) \right],$$

and finally,

$$h(\mu_\psi) = - \sum_{i=1}^N \left[ r_i \mu_\psi (\log r_i(\omega)) + (1 - r_i) \mu_\psi (\log(1 - r_i(\omega))) \right]. \tag{37}$$

This looks like the classical entropy for a Bernoulli scheme but with a crucial difference: one has to take the expectation of the log of the probability instead of the log of the expectation.

Moreover  $\psi(\omega) < 0$  (the strict inequality comes from proposition 7). Therefore,  $\mu_\psi(\psi) < 0$  and:

**Proposition 10** *The entropy  $h(\mu_\psi)$ , given by (37), is positive whatever the value of parameters  $W_{ij}, i, j = 1 \dots N, I_i, i = 1 \dots N, \theta, \gamma$ .*

Though this result appears “evident” a priori, it is proved here, as an easy consequence of the variational principle (31). Moreover, it provides an explicit value for the entropy, which depends on parameters.

### 3.3.4 Gibbs state

In the present setting equilibrium states are Gibbs states (Keller 1998). A Gibbs state for the potential  $\psi$  is a probability measure  $\mu_\psi$  such that one can find some constants  $P(\psi), c_1, c_2$  with  $0 < c_1 \leq 1 \leq c_2$  such that for all  $n \geq 0$  and for all  $\omega \in X$ :

$$c_1 \leq \frac{\mu_\psi([\omega]_0^n)}{\exp[-(n + 1)P(\psi) + \sum_{k=0}^n \psi(T^k\omega)]} \leq c_2. \tag{38}$$

Basically, the condition (38) expresses that the measure of the cylinder  $[\omega]_0^n$  behaves like:

$$\mu_\psi([\omega]_0^n) \sim \frac{\exp \sum_{k=0}^n \psi(\omega_{-\infty}^k)}{Z_\psi^{(n+1)}(\omega)}, \tag{39}$$

which has therefore the classical form of Gibbs distribution where spins chains are replaced by sequences of spiking patterns and where the normalization factor  $Z_\psi^{(n+1)}(\omega)$  is analog to a “partition function” (but depends on  $\omega$ ). Note that  $P(\psi) = \lim_{n \rightarrow +\infty} \frac{1}{n+1} \log Z_\psi^{(n+1)}(\omega)$ , where the limit exists and is constant for  $\mu_\psi$ -almost-every  $\omega$ . Thus the topological pressure  $P(\psi)$  is analog to a free energy density.

### 3.3.5 Kullback–Leibler divergence

Let  $\mu, \nu$  be two  $T$ -invariant measures. The Kullback–Leibler divergence between  $\mu$  and  $\nu$  is given by:

$$d(\mu, \nu) = \limsup_{n \rightarrow +\infty} \frac{1}{n+1} \sum_{[\omega]_0^n} \mu([\omega]_0^n) \log \left[ \frac{\mu([\omega]_0^n)}{\nu([\omega]_0^n)} \right], \tag{40}$$

where the sum holds on all possible cylinders  $[\omega]_0^n$ . It provides some notion of asymmetric “distance” between  $\mu$  and  $\nu$ . Minimizing this divergence, corresponds to minimizing “what is not explained in the empirical measure  $\mu$  by the theoretical measure  $\nu$ ”.

The following holds. For  $\mu$  an ergodic measure and  $\mu_\psi$  a Gibbs state with a potential  $\psi$ , both defined on the same set of sequences, one has (Bowen 2008; Chazottes and Keller 2009; Keller 1998; Ruelle 1969):

$$d(\mu, \mu_\psi) = P(\psi) - \mu(\psi) - h(\mu). \tag{41}$$

This result is used in the next section.

## 4 Finite range approximations

### 4.1 Constructing a Markov chain with finite memory

The main difficulty in handling the transition probabilities (18) and the related equilibrium state is that they depend on an history dating back to  $\tau_i(\omega_{-\infty}^t)$ , where  $\tau_i(\omega_{-\infty}^t)$  is unbounded. On the other hand, the influence of the activity of the network, say at time  $-l$ , on the membrane potential  $V_i$  at time 0, appearing in the term  $x_{ij}(\omega_{-\infty}^0) = \sum_{l=\tau_i(\omega_{-\infty}^0)}^0 \gamma^{-l} \omega_j(l)$ , (Eq. 12) decays exponentially fast as  $l \rightarrow -\infty$ . Thus, one may argue that after a characteristic time depending on  $\frac{1}{|\log(\gamma)|}$  the past network activity has little influence on  $V_i(0)$ . We now make this statement precise, especially evaluating the error attached to this approximation, before exploring its consequences in Sect. 5.

#### 4.1.1 Range- $R$ approximation

Assume that we want to approximate the statistics of spikes, given by the dynamics (1), by fixing a finite time horizon  $R$  such that the membrane potential at time 0 depends on the past only up to some finite time  $-R$ . In this way, we truncate the histories and we approximate the transition probabilities  $P(\omega(0)|\omega_{-\infty}^{-1})$ , with unbounded memory, by transition probabilities  $P(\omega(0)|\omega_{-R}^{-1})$  where  $\tau_i(\omega_{-\infty}^{-1})$  is replaced by  $\tau_i(\omega_{-R}^{-1})$  (see Eq. (3)), thus limiting memory to at most  $R$  time steps in the past.



These approximated transition probabilities constitute therefore a Markov chain with a memory depth  $R$ . How good is this approximation? To answer this question let us first construct the Markov chain within more details.

### 4.1.2 Blocks coding

Since we are now only considering finite histories given by spike blocks of length  $R$ , of the form  $\omega_{-R}^{-1}$ , we may encode each of these blocks by an integer

$$w = \sum_{i=1}^N \sum_{n=-R}^{-1} 2^{(i-1)+(n+R)N} \omega_i(n). \tag{42}$$

We write  $w \sim \omega_{-R}^{-1}$ . These integers or *words* constitute the states of the Markov chain. We note

$$\Omega^R \stackrel{\text{def}}{=} \{0, \dots, 2^{NR} - 1\},$$

the set of words.

### 4.1.3 Transition matrix

From Proposition 6, this chain is homogeneous, i.e. transition probabilities does not depend on time. They are encoded in a  $2^{NR} \times 2^{NR}$  matrix  $\mathcal{L}^{(R)}$  with entries:

$$\mathcal{L}_{w',w}^{(R)} \stackrel{\text{def}}{=} \begin{cases} P\left(\omega(0) | \omega_{-R}^{-1}\right), & \text{if } w' \sim \omega_{-R}^{-1}, w \sim \omega_{-R+1}^0, \\ 0, & \text{otherwise.} \end{cases} \tag{43}$$

If  $w' \sim \omega_{-R}^{-1}, w \sim \omega_{-R+1}^0$  we say that  $w$  “follows”  $w'$  or that the transition  $w' \rightarrow w$  is “legal”. Note that when using a matrix representation where  $w' \in \Omega^R, w \in \Omega^R$  not all transition are legal ( $w', w$  must correspond to overlapping blocks). We therefore use the convention that non-legal transitions have a zero probability.

It results from Proposition 7 that any legal transition has a positive probability. Note that the transition matrix  $\mathcal{L}^{(R)}$  corresponds to the matrix representation of the Ruelle–Perron–Frobenius (29) operator in the case of a finite memory.

### 4.1.4 Incidence matrix

The set of transitions is encoded in a  $2^{NR} \times 2^{NR}$  matrix  $\mathcal{I}$ , called *incidence matrix* with entries:

$$\mathcal{I}_{w'w} = \begin{cases} 1, & \text{if } w' \rightarrow w \text{ is legal} \\ 0; & \text{otherwise.} \end{cases} \tag{44}$$

It is easy to show that  $\mathcal{I}$  is primitive namely  $\exists m > 0$  such that  $\forall w, w' \in \Omega^R \times \Omega^R$ ,  $\mathcal{I}^m_{w'w} > 0$ , where  $\mathcal{I}^m$  is the  $m$ -th power of  $\mathcal{I}$ . Indeed, having  $\mathcal{I}^m_{w'w} > 0$  means that there exists a raster plot  $\omega$  which contains the block  $w'$  and the block  $w$  where the first spiking pattern of each block is separated by  $m$  time steps. Therefore, taking  $m = R + 1$  any raster containing the concatenation of blocks  $w'w$  satisfies the requirement.

#### 4.1.5 Range $R + 1$ potential

Using the same representation as (42), but with blocks of size  $R + 1$ , to each block  $\omega_{-R}^0$  of length  $R + 1$  we associate a word  $W = \sum_{i=1}^N \sum_{n=-R}^0 2^{(i-1)+(n+R)N} \omega_i(n) \sim \omega_{-R}^0$  and define:

$$\begin{aligned} \psi^{(R)}(W) = \sum_{i=1}^N \left[ \omega_i(0) \log \left( \pi \left( \frac{\theta - C_i(\omega_{-R}^{-1})}{\sigma_i(\omega_{-R}^{-1})} \right) \right) \right. \\ \left. + (1 - \omega_i(0)) \log \left( 1 - \pi \left( \frac{\theta - C_i(\omega_{-R}^{-1})}{\sigma_i(\omega_{-R}^{-1})} \right) \right) \right], \end{aligned} \tag{45}$$

called a *range- $R + 1$  potential*. It corresponds to an approximation of the potential (32) when the memory depth of the chain is  $R$ . Then:

$$\mathcal{L}_{w',w}^{(R)} = e^{\psi^{(R)}(W)} \mathcal{I}_{w'w}.$$

#### 4.1.6 The Perron–Frobenius theorem

Since  $\mathcal{I}$  is primitive and since all legal transitions have a positive probability,  $\mathcal{L}^{(R)}$  is primitive and the Perron–Frobenius theorem holds (Gantmacher 1998; Seneta 2006).  $\mathcal{L}^{(R)}$  has a real positive eigenvalue  $s$  with maximal modulus, isolated from the rest of the spectrum. Moreover, since  $\mathcal{L}^{(R)}$  is a transition probability,  $s = 1$ . The quantity

$$P(\psi^{(R)}) = \log s = 0$$

is the topological pressure of the potential  $\psi^{(R)}$  (Keller 1998).

The corresponding left and right eigenvectors are respectively denoted  $l$  and  $r$  i.e.  $l\mathcal{L}^{(R)} = sl$  and  $\mathcal{L}^{(R)}r = sr$  where  $r$  as positive entries  $r_w > 0$ . Without of generality we may assume that  $\langle l, r \rangle = 1$ , where  $\langle \cdot, \cdot \rangle$  denotes the standard scalar product.

The Markov chain has a unique invariant probability measure  $\mu_{\psi^{(R)}} = lr$  (i.e.  $\forall w \in \Omega^R$ ,  $\mu_{\psi^{(R)}}(w) = l_w r_w$ ). From this, one can compute the probability of spike blocks of arbitrary length by the Chapman–Kolmogorov formula:

$$\mu_{\psi^{(R)}}([\omega]_s^{t+R}) = \mu_{\psi^{(R)}}(w(s)) \prod_{n=s}^{t-1} \mathcal{L}_{w(n)w(n+1)}^{(R)},$$

with  $w(n) \sim \omega_n^{n+R}$ .

Then, one can check that  $\mu_{\psi^{(R)}}$  is a Gibbs distribution (Keller 1998) (see Eq. 38). Moreover, it is also an equilibrium state in the sense of (31). As a result  $0 = h(\mu_{\psi^{(R)}}) + \mu_{\psi^{(R)}}(\psi^{(R)})$ , therefore

$$h(\mu_{\psi^{(R)}}) = -\mu_{\psi^{(R)}}(\psi^{(R)}).$$

### 4.2 Convergence of the approximation

Let us now discuss how well the range- $R$  potential (45) approximates the infinite range potential (32). By definition of a range- $R + 1$  potential  $\psi^{(R)}(\omega) = \psi^{(R)}(\omega_{-R}^0)$  so that we can compare  $\psi$  and  $\psi^{(R)}$ . One has:

$$\begin{aligned} \|\psi - \psi^{(R)}\|_\infty &\leq \sup \{ |\psi(\omega) - \psi(\omega')| : \omega, \omega' \in X, \omega(t) = \omega'(t), \\ &\forall t \in \{-R, \dots, 0\} \} \stackrel{\text{def}}{=} \text{var}_R(\psi), \end{aligned}$$

so that, from Theorem 1,

$$\|\psi - \psi^{(R)}\|_\infty \leq K' \gamma^R, \tag{46}$$

where  $K'$  is given by (28). Therefore,  $\psi^{(R)}$  approaches  $\psi$  exponentially fast, as  $R$  grows, with a rate  $\gamma$ . This is in fact a classical result in ergodic theory: regular potential are approximated by finite-range potential in the sup norm where  $\|\psi - \psi^{(R)}\|_\infty \leq C \Theta^R$ , for some  $0 < \Theta < 1$  (see Eq. 2). Here it is natural to take  $\Theta = \gamma$ .

The implications on statistics is related to the Kullback–Leibler divergence (40). Indeed, since  $\mu_\psi$  and  $\mu_{\psi^{(R)}}$  are Gibbs distributions for the right shift  $T$  we may use (41), giving:

$$d(\mu_{\psi^{(R)}}, \mu_\psi) = P(\psi) - \mu_{\psi^{(R)}}(\psi) - h(\mu_{\psi^{(R)}}) = \mu_{\psi^{(R)}}(\psi^{(R)} - \psi),$$

where we used  $P(\psi) = 0$  (normalization of  $\psi$ ) and  $h(\mu_{\psi^{(R)}}) = -\mu_{\psi^{(R)}}(\psi^{(R)})$  (see e.g. Chazottes 1999 for a more general proof). Therefore,

$$d(\mu_{\psi^{(R)}}, \mu_\psi) < K' \gamma^R. \tag{47}$$

Therefore, the Kullback–Leibler divergence between the two measures  $\mu_\psi, \mu_{\psi^{(R)}}$ , decays exponentially fast with a decay rate  $\gamma$ .

A practical consequence of this result is that it might be sufficient, for practical purposes, to approximate  $\psi$  with a potential of range:

$$R \sim -\frac{\log K'}{\log \gamma}. \tag{48}$$

Note however that the constant  $K'$  depend on several parameters. Especially, it diverges when  $\sigma_B \rightarrow 0$  (or  $\gamma \rightarrow 1$ ). As a consequence, depending on these parameters, the effective range can be quite large.

## 5 Raster plots statistics

As discussed in the introduction, the neuroscience community is confronted to the delicate problem of characterizing statistical properties of raster plots from finite time spike trains and/or from finite number of experiments. This requires an a priori guess for the probability of raster plots, what we call a *statistical model*. These models can be extrapolated from heuristic arguments or from principles such as the Jaynes argument from statistical physics (Jaynes 1957) (see Sect. 5.3.2). In this section, we show that Markovian approximations introduced in the previous section constitute such statistical models, from which classical statistical indicators used by the neuroscience community can be explicitly computed in the case of model (1).

### 5.1 Two representations of the potential $\psi^{(R)}$

#### 5.1.1 Spike-block representation

The potential  $\psi^{(R)}$  is a function of  $W \sim \omega_{-R}^0$ . Therefore, it takes only  $L = 2^{N(R+1)}$  values, *explicitly given by* (45). To each possible block  $\omega_{-R}^0$  we associate a word  $W_n, n = 1 \dots L$ . Call  $\chi_n(W)$  the characteristic function, equal to 1, if  $W = W_n$ , and 0 otherwise. Then:

$$\psi^{(R)}(W) = \sum_{n=1}^{L=2^{N(R+1)}} \alpha_n \chi_n(W) \equiv \psi_{\alpha}^{(R)}(W), \tag{49}$$

where  $\alpha_n = \psi^{(R)}(W_n)$ . This decomposition of the potential is called the *spike-block representation* of  $\psi^{(R)}$  and the index  $\alpha$  in (49) (which is the vector  $(\alpha_n)_{n=1}^L$ ) makes this representation explicit. Note that  $\alpha$  depend (analytically) on the model-parameters  $W_{ij}, i, j = 1 \dots N, I_i, i = 1 \dots N, \gamma, \theta$ .

#### 5.1.2 Interpretation

This representation is quite natural since  $e^{\alpha_n}$  is nothing but the probability  $P(\omega(0) | \omega_{-R}^{-1})$  with  $W_n \sim \omega_{-R}^0$ , namely a matrix element of the transition matrix (43). This function corresponds to the so-called “conditional intensity” introduced in neuroscience data analysis by researchers like Pouzat and Chaffiol (2009) and the exponential distribution introduced by these authors is actually our Gibbs distribution. Here, we are able to compute explicitly this distribution, because we are dealing with a model, while Pouzat and Chaffiol are coping with real world data.

Fixing an history  $\omega_{-R}^{-1}$  the sum of  $e^{\alpha_n}$ 's, over all blocks  $W_n$  having an history  $\omega_{-R}^{-1}$  and such that  $\omega_i(0) = 1$ , is the probability that neuron  $i$  fires given the history  $\omega_{-R}^{-1}$ . More generally, the product of the transition matrix  $\mathcal{L}$  elements (43) provides the probability of a certain sequence of spikes (“response”) given a certain history. If one focuses on the response  $\mathcal{R}$  of a subset of neurons in the network, to spikes emitted by an another subset of neurons in the network-corresponding to a given history and

considered as a stimulus  $\mathcal{S}$ - the matrix  $\mathcal{L}$  in the  $\alpha$ -representation allows the computation of the probability  $P(\mathcal{R}|\mathcal{S})$ . Then, by Bayesian inference, and *since the probability  $P(\mathcal{S})$  of the stimulus is known* (it is given by the invariant measure of the Markov chain), one infers  $P(\mathcal{S}|\mathcal{R})$ . This provides one way of characterizing the “neural code”, in the sense of Rieke et al. (1996), at the level of networks of neurons, where stimuli are spike trains.

### 5.2 The spikes-uplets representation

Though natural the  $\alpha$ -representation is not the most commonly used. Let us introduce another representation.

#### 5.2.1 Monomials

An *order- $n$  monomial* is a product  $\omega_{i_1}(t_1) \dots \omega_{i_n}(t_n)$ , where  $1 \leq i_1 \leq i_2 \leq \dots \leq i_n \leq N$  and  $-\infty < t_1 \leq t_2 \leq \dots \leq t_n < +\infty$ , and where there is no repeated pair of indexes  $(i, t)$ . Since  $\omega_i(t)^k = \omega_i(t), \forall i = 1 \dots N, t \in \mathbb{Z}, k > 1$  the last requirement avoids redundancies. A polynomial is a linear combination of monomials.

The monomial  $\omega_{i_1}(t_1) \dots \omega_{i_n}(t_n)$  takes values in  $\{0, 1\}$  and is 1 if and only if each neuron  $i_l$  fires at times  $t_l, l = 1 \dots n$ . On phenomenological grounds this corresponds to a spike  $n$ -uplet  $(i_1, t_1), \dots, (i_n, t_n)$  (neuron  $i_1$  fires at time  $t_1$ , and neuron  $i_2$  fires at time  $t_2, \dots$ ).

#### 5.2.2 Spikes-uplets expansion of $\psi$

Returning to the spike-block representation (49), the characteristic function of the word  $W_n, \chi_n(W)$ , reads:

$$\chi_n(W) = Q_n(W)R_n(W),$$

with

$$Q_n(W) = \prod_{(i,t), \omega_i(t)=1} \omega'_i(t),$$

where  $W$  represents a spike block  $\omega^0_{-R}$ , while the product holds over all pairs  $(i, t), 1 \leq i \leq N, -R \leq t \leq 0$  such that  $\omega_i(t) = 1$ , in the word  $W_n \sim \omega^0_{-R}$ . Likewise,

$$R_n(W) = \prod_{(j,s), \omega_j(s)=0} (1 - \omega'_j(s)) = \sum_{m=1}^{k_n} (-1)^m R_{n,m}(W),$$

where  $R_{n,m}$  are monomials of order  $\leq R$ . Since  $\omega_i(t)^k = \omega_i(t), k \geq 1, Q_n, R_n$  are monomials of order  $\leq R$  and all  $\chi_n(W)$ 's are polynomials of order  $\leq R$ .

For  $N, R \in \mathbb{Z}$ , we note  $\mathcal{P}(N, R)$  the set of non repeated pairs of integers  $(i, n)$  with  $i \in \{1, \dots, N\}$  and  $t \in \{-R, \dots, 0\}$ . We have just proved that  $\psi$  is approximated by a range- $R$  polynomial expansion of the form:

$$\psi_{\lambda}^{(R)}(W) = \sum_{l=0}^R \sum_{(i_1, t_1), \dots, (i_l, t_l) \in \mathcal{P}(N, R)} \lambda_{i_1, t_1, \dots, i_l, t_l}^{(l)} \omega_{i_1}(t_1) \dots \omega_{i_l}(t_l), \tag{50}$$

where  $W \sim \omega_0^R$ . This is called the ‘‘spike-uplets representation’’. It is obviously equivalent to the spike-block representation  $\psi_{\alpha}^{(R)}$  (the  $\lambda_i$ ’s are linear combinations of the  $\alpha_l$ ’s) but this expansion is more convenient to discuss the link between our results and the standard approaches used in the neuroscience community. Note that a spike-block contains 0’s and 1’s (it tells us which neurons are firing and which neurons are not firing) while a spike-uplet takes only into account firing neurons. As a consequence there is some redundancy in the spike-block representation that can be removed in the spike-uplets representation (see details below).

### 5.2.3 Interpretation

Since the analytic function  $\log(\pi(x))$  has a series expansion for  $x \in \mathbb{R}$ , setting  $x = \frac{\theta - C_i(\omega_{-R}^{-1})}{\sigma_i(\omega_{-R}^{-1})}$  in (45)  $x^n$  is a sum of terms  $\omega_{i_1}(t_1) \dots \omega_{i_n}(t_n)$  and using the series expansion<sup>7</sup> one can compute explicitly the coefficients of the spike-uplets expansion. Due to stationarity (see details below) one can only consider spike-uplets of the form  $\omega_i(0)\omega_{j_1}(t_1) \dots \omega_{j_l}(t_l)$ , with  $t_1, \dots, t_l < 0$ . They are combinations of terms proportional to  $W_{i j_1} W_{i j_2} \dots W_{i j_l} \gamma^{-(t_1+t_2+\dots+t_l)}$  which have a nice interpretation. The sum of these terms corresponds to the cumulative effect of spikes emitted by neurons  $j_1, \dots, j_l$  at times  $t_1, \dots, t_l$  in the past, on neuron  $i$  at time 0. Actually, these terms are related to a linear response theory as developed in a different context in Cessac and Sepulchre (2004, 2006).

## 5.3 Statistical models

### 5.3.1 The topological pressure as a cumulant generator

Let us return to the transition matrix  $\mathcal{L}^{(R)}$  and related topological pressure  $P(\psi^{(R)})$  introduced in Sects. 4.1.3, 4.1.6. These quantities depend on  $\alpha$  or  $\lambda$  according to the representation (which is nothing but a change of variables).

<sup>7</sup> Since  $\omega_i(t)^k = \omega_i(t), \forall i = 1 \dots N, t \in \mathbb{Z}, k > 1$ , the terms of the series can be grouped together giving rise to a finite sum of monomials.

The pressure is differentiable with respect to  $\lambda$  and one has<sup>8</sup>:

$$\frac{\partial P(\psi^{(R)})}{\partial \lambda_{(i_1, t_1), \dots, (i_l, t_l)}^{(l)}} = \mu_{\psi^{(R)}} [\omega_{i_1}(t_1) \dots \omega_{i_l}(t_l)],$$

Therefore, the derivation of the pressure with respect to the quantity  $\lambda_{(i_1, t_1), \dots, (i_l, t_l)}^{(l)}$  provides the  $\mu_{\psi^{(R)}}$ -probability of the spike  $n$ -uplet  $\omega_{i_1}(t_1) \dots \omega_{i_l}(t_l)$ .

In particular:

$$\frac{\partial P(\psi^{(R)})}{\partial \lambda_{i_1, t_1}^{(1)}} = \mu_{\psi^{(R)}} [\omega_{i_1}(t_1)], \tag{51}$$

the firing rate of neuron  $i_1$  at time  $t_1$ . Since dynamics is stationary this quantity does not depend on  $t$  (see Eq. (35)). As a consequence all terms  $\lambda_{i,t}$ ,  $i$  fixed and  $t \in \{-R, \dots, 0\}$  play the same role and we can simplify the potential (50) in keeping, as first order terms, the monomials of form  $\lambda_i^{(1)} \omega_i(0)$ ,  $i = 1 \dots N$ .

In the same way:

$$\frac{\partial P(\psi^{(R)})}{\partial \lambda_{(i_1, t_1), (i_2, t_2)}^{(2)}} = \mu_{\psi^{(R)}} [\omega_{i_1}(t_1) \omega_{i_2}(t_2)],$$

From stationarity it follows that this quantity depends only on  $t_2 - t_1$ . So, there are redundant terms in the expansion (50) and we may write the part of the expansion corresponding to pairs of spikes as  $\sum_{\tau=-R/2}^{R/2} \sum_{i_1, i_2=1}^N \lambda_{i_1, i_2, \tau}^{(2)} \omega_{i_1}(0) \omega_{i_2}(\tau)$ .

Higher order redundant terms can be removed as well, taking into account the stationarity of the process. As a consequence we may write the spike-uplets expansion of  $\psi$  in the form:

$$\psi_{\lambda}^{(R)}(W) = \sum_{l=0}^K \lambda_l \phi_l(W), \tag{52}$$

where  $l$  enumerates all non redundant monomials  $\phi_l$  of order  $\leq R$ , including the constant monomial  $\phi_0(W) = 1$ .

### 5.3.2 Statistics of raster plots from Jaynes formalism

We would like now to relate the present analysis to a standard problem in spike train analysis. Assume that we have generated a (finite) raster plot  $\omega_{exp}$  from the dynamical

<sup>8</sup> Here the pressure  $P(\psi^{(R)})$  is considered as a function of the  $\lambda$ 's, where these parameters are arbitrary. As a consequence the corresponding potential  $\psi_{\lambda}^{(R)}$  is no longer normalized. In this case the topological pressure is defined as the logarithm of the maximal eigenvalue of the matrix  $\mathcal{L}^{(R)}$ . The fact that a potential of the form (50) are in general *not normalized* has deep practical consequences widely discussed in the paper (Vasquez et al. 2010).

system (1) and that we want to recover the probability distribution  $\mu_{\psi}$  from this raster plot, without any other information. A usual approach consist of computing the average value of some prescribed spike-uplets, and infer the corresponding probability distribution from a variational principle introduced by Jaynes (1957). The Jaynes approach has been used by several authors in the field of experimental spike train analysis (Marre et al. 2009; Schneidman et al. 2006; Tkacik et al. 2006).

So, let us assume that, from the raster plot  $\omega_{exp}$ , we have computed, by time average,<sup>9</sup> the average value  $C_l$  of an a priori fixed set of monomials  $\phi_l, l = 1 \dots M$ . To find a probability distribution  $\mu_{\psi_{test}}$  which matches these average values, without making additional assumptions, one maximizes the statistical entropy under the constraints  $\mu_{\psi_{test}}(\phi_l) = C_l, l = 1 \dots M$ . In the context of thermodynamic formalism *this amounts to finding a set of parameters  $\lambda_l$  satisfying the variational equation (31) for a finite range potential  $\psi_{test} = \sum_{l=1}^M \lambda_l \phi_l$* . The  $\lambda_l$ 's are adjustable Lagrange multipliers, which have to be tuned using (51), so that the average of  $\phi_l$  with respect to  $\mu_{\psi_{test}}$  is equal to  $C_l$

Let us give two classical examples.

### 5.3.3 Homogeneous Bernoulli statistics

The simplest example consists of only measuring, thus, constraining the value of firing rates. This amount to considering a range-1 potential (Dayan and Abbott 2001; Gerstner and Kistler 2002a; Rieke et al. 1996):

$$\psi_{test}(W) = \sum_{i=1}^N \lambda_i^{(1)} \omega_i(0),$$

corresponding to a probability:

$$\mu_{\psi_{test}}(\omega(0)) = \prod_{i=1}^N \frac{e^{\lambda_i^{(1)} \omega_i(0)}}{1 + e^{\lambda_i^{(1)}}}.$$

Therefore, taking only the first order monomials allows one to select a probability distribution under which neurons fire independently with a time-independent rate:

$$r_i = \frac{e^{\lambda_i^{(1)}}}{1 + e^{\lambda_i^{(1)}}}.$$

### 5.3.4 Pairwise interactions

This statistical model has been introduced, in the context of spike trains statistics, by Schneidman et al. (2006). Here, still  $R = 1$  and  $\psi_{test}$  does not depend on  $t$  but pairs

<sup>9</sup> This argument extends to the case where several empirical raster plots have been generated. Then, average values are obtained by combinations of time average and sample average.



of spikes occurring at the same time are considered. Then,

$$\psi_{test}(W) = \sum_{i=1}^N \lambda_i^{(1)} \omega_i(0) + \sum_{1 \leq i_1 < i_2 \leq N} \lambda_{i_1, i_2}^{(2)} \omega_{i_1}(0) \omega_{i_2}(0).$$

Here, the related probability measure does not factorize any more but all information about spike train statistics is contained in the first and second order spike-uplets.

### 5.3.5 Choosing an a priori set of monomials

More general potentials can be considered as well (Marre et al. 2009). In view of the present analysis, fixing an a priori set of observables, often fixed from a priori hypotheses on the relative role of spike-uplets (e.g. rate versus synchronization), amounts to fixing a test potential  $\psi_{test}$ . Therefore, there are as many models as possible choices of observables. How to discriminate them ?

The probability distribution  $\mu_{\psi_{test}}$  is the Gibbs distribution for the potential  $\psi_{test}$ . It provides an approximation of the invariant measure  $\mu_{\psi}$  in two senses. First,  $\psi_{test}$  contains only some terms in the polynomial expansion of a finite range potential  $\psi^{(R)}$ , which are fixed from the a priori choice of observables. Second,  $\psi^{(R)}$  is a finite-range approximation of the exact, infinite-range, potential  $\psi$ . The “error” is measured by the Kullback–Leibler divergence (40):

$$d(\mu_{\psi_{test}}, \mu_{\psi}) = \mu_{\psi_{test}}(\psi_{test} - \psi).$$

It is upper-bounded by  $C\gamma^{NR}$ . This fixes, for model (1), an estimate for the value of  $R$  given by (48).

Nevertheless, the number of terms increases exponentially with  $R$  and  $N$  and therefore, especially if  $\gamma$  is close to 1 there is an overwhelming number of monomials. Now, it might be, that some terms  $\phi_l$  are less important than others: the corresponding coefficient  $\lambda_l$  vanishes or is small compared to others terms. As discussed in Cessac et al. (2009) and shortly commented in Sect. 6.3, neural mechanisms such as plasticity certainly reinforce some of these terms (especially rates and spike pairs). On a more abstract setting, our analysis shows that the Kullback–Leibler divergence (40) gives an indication of the distance between the probability reconstructed from Jaynes principle, with a “guess” potential, and the true probability  $\mu_{\psi}$ . This opens up a way to compare and select statistical models by minimizing the Kullback–Leibler divergence, using Eq. (40). This aspect and its numerical implementation are discussed in Vasquez et al. (2010).

## 6 Discussion and conclusion

In this paper we have addressed the question of characterizing the spike train statistics of a network of LIF neurons with noise, in the stationary case, with two aims. Firstly, to obtain analytic and rigorous results allowing the characterization of the process

of spike generations. For this, we have used the realm of ergodic theory and thermodynamic formalism, which looks well adapted for this purpose. We have obtained unexpected results, especially the fact that, even so simple models of neural networks have, strictly speaking, an unbounded memory rendering spike train statistics non-Markovian. The common wisdom in the field of neural networks dynamics suggests, however, that there is a characteristic time scale after which the system essentially loses its memory. Here, this time scale is controlled by  $\gamma$ , the leak rate, closely related to synaptic response time.

The second goal was to make a connection from this mathematical analysis toward the empirical methods used in neuroscience community for the analysis of spike trains. Here, we have shown that the Jaynes method, based on an a priori choice of a “guess” potential, with finite range, amounts to approximate the exact probability distribution by the Gibbs distribution of a Markov chain (Csiszar 1984). The degree of approximation can be controlled by the Kullback–Leibler divergence which can be computed using a classical result in the thermodynamic formalism. This analysis opens up the possibility of developing efficient algorithms to estimate at best the statistic of spike trains from experimental data, using several guess potentials and selecting the one which minimizes the KL divergence (Vasquez et al. 2010).

Clearly, this work is just a beginning, since, especially, it deals with a rather simple model. Let us now briefly comment several possible extensions.

## 6.1 Conductance based Integrate-and-Fire neurons

A natural extension of the present work concerns the so-called Generalized Integrate-and-Fire models (Rudolph and Destexhe 2006), which are closer to biology (Jolivet et al. 2004, 2006). The occurrence of a post-synaptic potential on synapse  $j$ , at time  $t_j^{(n)}$ , results in a change of membrane potential. In conductance based models this change is integrated in the adaptation of conductances. It has been shown in Cessac and Viéville (2008) that, under natural assumptions on spike-time precision that the continuous-time evolution of these equations reduces to the discrete time dynamics:

$$V_i(t+1) = \gamma_i(t, \omega_{-\infty}^t) [1 - Z(V_i(t))] V_i(t) + J_i(t, \omega_{-\infty}^t), \quad i = 1 \dots N,$$

where:

$$\gamma_i(t, \omega_{-\infty}^t) \stackrel{\text{def}}{=} e^{-\int_t^{t+1} g_i(s, \omega_{-\infty}^t) ds} < 1,$$

is the integral of the conductance  $g_i(s, \omega_{-\infty}^t)$  over the time interval  $[t, t+1[$ . Conductances depend on the past spikes via the relation:

$$g_{ij}(t, \omega_{-\infty}^t) = G_{ij} \sum_{n=1}^{M_j(\omega_{-\infty}^t)} \alpha_j(t - t_j^{(n)}).$$

In this equation,  $M_j(\omega^t_{-\infty})$  is the number of times neuron  $j$  has fired at time  $t$  (it can be infinite).  $\alpha$  is the synaptic profile (it decays exponentially fast) and  $t_j^{(n)}$  is the time of occurrence of the  $n$ -th spike in the raster  $\omega$ .  $G_{ij}$  is a positive constant proportional to the synaptic efficacy

$$\begin{cases} W_{ij} = E^+ G_{ij} & \text{if } j \in \mathcal{E}, \\ W_{ij} = E^- G_{ij} & \text{if } j \in \mathcal{I}, \end{cases}$$

where  $E_L, E^+, E^-$  are respectively the Nernst potentials for the leak, the excitatory (set  $\mathcal{E}$ ) and the inhibitory synapses (set  $\mathcal{I}$ ).

The term,

$$J_i(t, \omega^t_{-\infty}) = \int_t^{t+1} i_i(s, \omega^t_{-\infty}) v_i(s, t + 1, \omega^t_{-\infty}) ds,$$

is the corresponding integrated synaptic current with:

$$i_i(t, \omega^t_{-\infty}) = \frac{E_L}{\tau_L} + E^+ \sum_{j \in \mathcal{E}} g_{ij}(t, \omega^t_{-\infty}) + E^- \sum_{j \in \mathcal{I}} g_{ij}(t, \omega^t_{-\infty}) + i_i^{(ext)}(t),$$

$$v_i(s, t + 1, \omega^t_{-\infty}) = e^{-\int_s^{t+1} g_i(s', \omega^t_{-\infty}) ds'}.$$

The difficulty here is that the coefficient  $\gamma_i(t, \omega^t_{-\infty})$ , which is the analog of  $\gamma$  in Eq. (1) depends on the whole past. This introduces another non-Markovian effect in the dynamics. In this case the computation of the potential corresponding to (32) is clearly more complex. This case is under current investigations.

### 6.2 Non stationarity

One weakness of the present work is that it only considers stationary dynamics, where e.g. the external current  $I_i$  is independent of time. Besides, we have taken the limit  $s \rightarrow -\infty$  in Sect. 2 to remove the dependence in the initial condition  $V(s)$ . However, real neural systems are submitted to non static stimuli, and transients play a crucial role. To extend the present analysis to these case one needs the proper mathematical framework. The non stationarity requires to handle time dependent Gibbs measures. In the realm of ergodic theory applied to non equilibrium statistical physics, Ruelle has introduced the notion of time-dependent SRB measure (Ruelle 1999). A similar approach could be used here, at least formally.

Handling the transients is an even more tricky question. The main difficulty is to propose a probability distribution for the initial condition  $V(s)$ . From the dynamical systems point of view it is natural to take e.g. Lebesgue, and extensions toward this case are under current investigations. But if one wants to make serious extrapolations of mathematical results towards neuroscience one has to ask why the ‘‘initial state’’ of a neural network, namely the state in which the neural network is as the experiment

starts, should be uniform in the phase space (or Gaussian or whatsoever), as soon as this initial state is the result of a previous (phylogenetic and ontogenetic) evolution ?

### 6.3 Synaptic plasticity

In neural networks, synaptic weights are not fixed, as in (1), but they evolve with the activity of the pre- and post-synaptic neuron (synaptic plasticity). This means that synaptic weights evolve according to spike train statistics, while spike train statistics is constrained by synaptic weights. This interwoven evolution has been considered in Cessac et al. (2009) under the assumption that spike-train statistics is characterized by a Gibbs distribution. Actually, the present work confirms this hypothesis in the case of LIF models. The main conclusion of Cessac et al. (2009) is that synaptic mechanism occurring on a time scale which is slow compared to neural dynamics are associated with a variational principle. There is a function, closely related to the topological pressure, which decreases when the synaptic adaptation process takes place. Moreover, the synaptic adaptation has the effect of reinforcing specific terms in the potential, directly related to the form of the synaptic plasticity mechanism. The interest of this result is that it provides an a priori guess of the relevant terms in the potential expansion. A contrario, it allows one to constrain the spike train statistics of a LIF model, using synaptic plasticity with an appropriate rule which can be determined from the form of the expected potential.

Finally, an interesting issue fitting together with the discussion of non stationarity and synaptic plasticity, is to analyse spike frequency adaptation in this context (Benda and Herz 2003; Benda et al. 2005; Crook et al. 1998; Ermentrout et al. 1926).

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