

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

MASTER PROJECT IN PHYSICS



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# Low-dimensional population dynamics of spiking neurons via eigenfunction expansion

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Carried out at **LCN**

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# Abstract



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# Chapter 1

## Introduction

This thesis is concerned with the mean activity of large homogeneous population of neuron. In the brain billion of neurons form complex network, they communicate with each other by short electrical pulse called action potential. Neurons encode stimuli by emitting spikes trains in response to sensory inputs. To uncover the corresponding neural code, the analysis of spike statistic is essential.

One of the most common ways to model large neuronal networks is to use a simplification called a firing rate model. It is equivalent to a mean field approach where rather than record the spiking trains of every single neuron, one tracks the averaged behavior of the spike rates of groups of neurons. This transition from a microscopic description to a mesoscopic description is illustrated in Fig.1.1. Firing rate model provides simple models which are computationally efficient and are mathematically tractable. The resulting models involves a compromise between accuracy and simplicity. Simple firing-rate models where the dynamics was governed by only one time constant fail to replicate certain dynamic features of populations of spiking neurons. To explain some phenomenological properties, heuristic model where developed but these model were not derived from the spiking neuron dynamics [Wilson and Cowan (1972),Ostojic and Brunel (2011)].

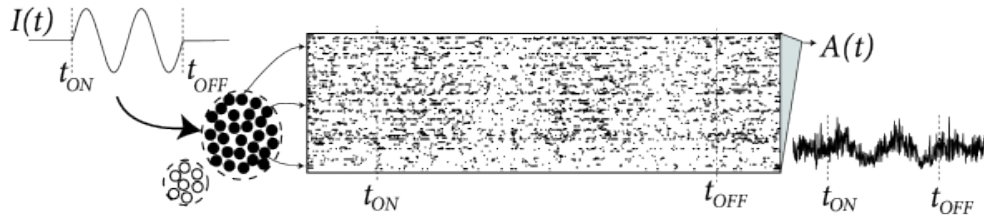


Figure 1.1: Response of population to a signal  $I(t)$ , represented by a sinusoidal modulation of the input starting at  $t_{ON}$  and ending at  $t_{OFF}$ , stimulates the population of 8000 excitatory neurons in a randomly coupled network of 8000 excitatory and 2000 inhibitory neurons (left). Each neuron produces a spike train (middle) illustrated here by lines of dots, each dot corresponding to a spike. Only 1% of the population is shown. At the mesoscopic level, the population activity  $A(t)$  (right) counts spikes in time bins of 1 ms averaged over the 8000 excitatory neurons. [Gerstner et al. (2014)]

In this project we consider a large homogeneous population of neurons modeled by time dependent renewal process. And the goal is to derive a low-dimensional population dynamics of spiking neurons, starting from a spectral expansion of the refractory density equation. Thus we will first introduce in Sections 1.1 and 1.3, renewal processes and the refractory density approach. Then we will recall some property of the spectral expansion in Section 1.4, which in previous studies was used to approximate the dynamics of spiking Networks, taking as state variable the membrane potential  $v$  [Mattia and Del Giudice (2002), Schaffer et al. (2013), Augustin et al. (2017)].

## 1.1 Renewal processes

A neuron model tells us how an input is transformed into output spikes. We define  $h(t)$  as the input potential, its time derivative is given by

$$\dot{h} = -h + \mu(t) + RI_{syn}(t) \quad (1.1)$$

where  $\mu(t)$  represents an external stimulus, and  $I_{syn}$  is the synaptic current, due to the spikes from other neurons.

Renewal processes keep memory of the last event, last firing time  $\hat{t}$ . The age, i.e the time elapsed since the last spike  $\tau = t - \hat{t}$ , is a state variable of the neuron. For those processes the spikes are generated according to a stochastic intensity called the hazard rate  $\rho(\tau, h)$ . The hazard rate  $\rho(\tau, h)$  define the probability to spike between  $t + \Delta t$  knowing that there were no spike between  $t$  and  $\hat{t}$ .

To generate a spike train according to the hazard rate  $\rho(\tau, h)$  in a simulation, one would proceed as follows

- At each time step  $\Delta t$  knowing the age  $\tau$  of the neuron and the current input potential  $h(t)$  the probability of the neuron to spike would be given by

$$p_{spike} = 1 - \exp(-\rho(\tau, h)\Delta t) \quad (1.2)$$

We see that the probability to spike is 0 for  $\rho(\tau, h) = 0$  and goes to 1 for  $\rho(\tau, h) \rightarrow +\infty$

- If the neuron spikes the age would be reset to 0, if not the age variable would be incremented by  $\Delta t$ .

### 1.1.1 Interval distribution and Survivor function

The renewal theory allows to define the probability of the next event given the age of the system, to calculate the interspike-interval (ISI) distribution  $P(\tau, h)$ , i.e the probability to spike at age  $\tau$ . The ISI distribution is normalized and therefore satisfy

$$\int_0^\infty P(\tau, h) d\tau = 1 \quad (1.3)$$

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The interval distribution  $P(\tau, h)$  is a probability density, which implies that integration of  $P(\tau, h)$  over age yields a probability. The probability that a neuron which has fired a spike at  $\hat{t}$  and fires the next spike at between  $\hat{t}$  and  $t$  is given by  $\int_0^\tau P(s, h)ds$ .

The interspike-interval (ISI) distribution can be linked to the survivor function

$$S(\tau, h) = 1 - \int_0^\tau P(s, h)ds \quad (1.4)$$

The survivor function  $S(\tau, h)$  define the probability that a neuron reach the age  $\tau$ , so that a neuron "survive" without firing between  $\hat{t}$  and  $t$ .  $P(\tau, h)$  describes the probability to spike at age  $\tau$ . This is given by the product of the probability to survive until age  $\tau$  times the momentary hazard  $\rho(\tau, h)$ .

$$P(\tau, h) = \rho(\tau, h)S(\tau, h) \quad (1.5)$$

The derivation of Eq.(1.4) yields to

$$P(\tau, h) = -\frac{d}{d\tau}S(\tau, h) \quad (1.6)$$

Inserting Eq.(1.5) in Eq.(1.6), we find that the hazard rate  $\rho(\tau, h)$  corresponds to the rate of decay of the survivor function:

$$\rho(\tau, h) = -\frac{\frac{d}{d\tau}S(\tau, h)}{S(\tau, h)} \quad (1.7)$$

Integrating eq.1.7 yields to the survivor function:

$$S(\tau, h) = \exp \left[ - \int_0^\tau \rho(s, h)ds \right] \quad (1.8)$$

Inserting Eq.(1.8) in Eq.(1.5) The interval distribution can be explicitly express in terms of the hazard, and is by itself normalized:

$$P(\tau, h) = -\frac{d}{d\tau}S(\tau, h) = \rho(\tau, h) \exp \left[ - \int_0^\tau \rho(s, h)ds \right] \quad (1.9)$$

Each of the three function  $\rho(\tau, h)$ ,  $P(\tau, h)$  and  $S(\tau, h)$  is sufficient to describe statistical properties of a renewal system.

### 1.1.2 Examples

Interval distribution and hazard functions have been measured in many experiments. Here are some examples widely used, for their simplicity and/or the agreement with experimental measurements.

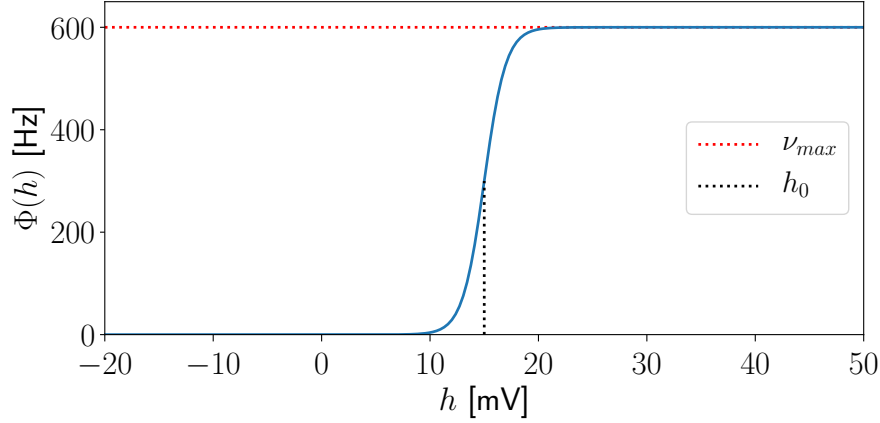
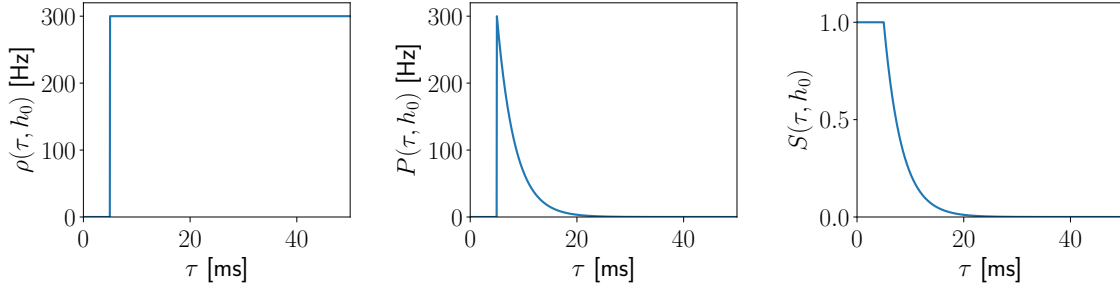


Figure 1.2: Rate  $\Phi(h)$  as a function of input potential  $h$ . With  $h_0 = 15$  mV ,  $\beta = 1$  mV<sup>-1</sup> and  $\nu_{max} = 0.6$  kHz.

(a)



(b)

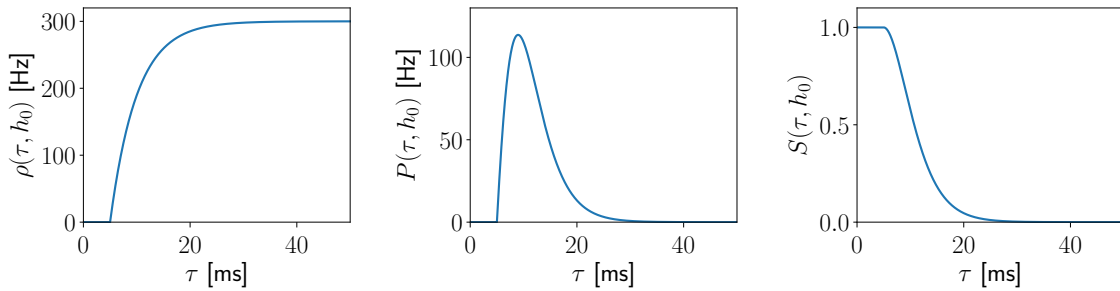


Figure 1.3: Hazard rate  $\rho(\tau, h)$  (left), interval distribution  $P(\tau, h)$  (middle) and survivor function  $S(\tau, h)$  (right) for different recovery function  $g(\tau)$ . (a) Recovery function corresponds to a Poisson neuron with absolute refractoriness  $\Delta$ , with  $\Delta = 5$  ms,  $h = h_0$ ,  $\nu_{max} = 600$  Hz. (b) Recovery function defined by  $g(\tau) = [1 - \exp(-\eta(\tau - \Delta))] \theta(\tau - \Delta)$  Poisson neuron with absolute refractoriness  $\Delta$ , with  $\Delta = 5$  ms,  $h = h_0$ ,  $\nu_{max} = 600$  Hz.

**Simple model with recovery function** Because we are not only considering stationary renewal system, in this section we will use the notation  $\rho(\tau, h)$ , with  $h$  a time dependent

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parameter, to show explicitly that  $\rho(\tau)$  can change in time.  $h$  is a potential, its dynamics is given by

$$\tau_m \dot{h} = -h + \mu(t) \quad (1.10)$$

Where  $\mu(t)$  is a time dependent external input.

The hazard rate, can be expressed using a recovery function  $g(\tau)$

$$\rho(\tau, h) = \Phi(h)g(\tau) \quad (1.11)$$

With  $\Phi(h)$  the instantaneous Rate. A common choice a sigmoid function with threshold  $h_0$  illustrated on Fig.1.2. For  $h \gg h_0$  the firing rate goes to the value  $\nu_{max}$  for  $h \ll h_0$  it goes to 0.

$$\Phi(h) = \frac{\nu_{max}}{1 + \exp[-\beta(h - h_0)]} \quad (1.12)$$

The hazard rate, the survival probability, and the interval distribution are shown in Fig.1.3 for two examples of recovery function  $g$ , with potential  $h = h_0$  i.e  $\Phi(h) = \frac{\nu_{max}}{2}$ . Fig.1.3(a) corresponds to a Poisson process with absolute refractory period  $\Delta$ :

$$g(\tau) = \theta(\tau - \Delta) \quad (1.13)$$

$\theta(\tau - \Delta)$  denotes the Heaviside function. The recovery function for Fig.1.3(b) is given by

$$g(\tau) = [1 - \exp(-\eta(\tau - \Delta))] \theta(\tau - \Delta) \quad (1.14)$$

The main difference is that for the Poisson neuron with absolute refractoriness the recovery function Eq.(1.13) make a jump, whereas in Eq.(1.14) the transition is smooth. The time course of the recovery function given by Eq.(1.14), approximate well the recovery function measured for auditory neurons of the guinea-pig [Prijs et al. (1993)]

**Gamma process** The gamma process is often used to model spike trains as it is one of the easiest non-Poisson process to analyze. The interspike distribution is given by:

$$P(\tau) = \frac{\beta^\gamma}{\Gamma(\gamma)} \tau^{\gamma-1} e^{-\beta\tau} \quad (1.15)$$

Where  $\beta := \beta(h)$  is a rate which depend on the input potential  $h$

The rate of this process is  $R = \beta/\gamma$ , And the coefficient of variation is given by  $C_V = \gamma^{-\frac{1}{2}}$ . For  $\gamma = 1$  this corresponds to a Poisson process. For  $C_V > 1$  the Interspike distribution diverges as  $\tau$  goes to 0. One can see the gamma process as a succession of  $\gamma$  state, each state is Poisson neuron with firing rate  $\beta$ , one has to pass by each state before spiking, this implies that the global rate of the total chain is  $R = \beta/\gamma$ , and induces a relative refractoriness as shown on Fig.1.4

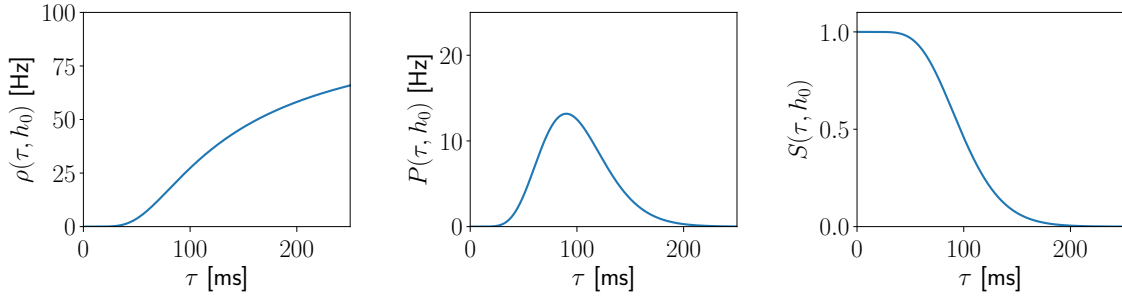


Figure 1.4: **Gamma process.** Hazard rate  $\rho(\tau)$  (left), interval distribution  $P(\tau)$  (middle) and survivor function  $S(\rho(\tau))$  (right) for a Gamma process with  $\beta = 100$  Hz  $\gamma = 10$

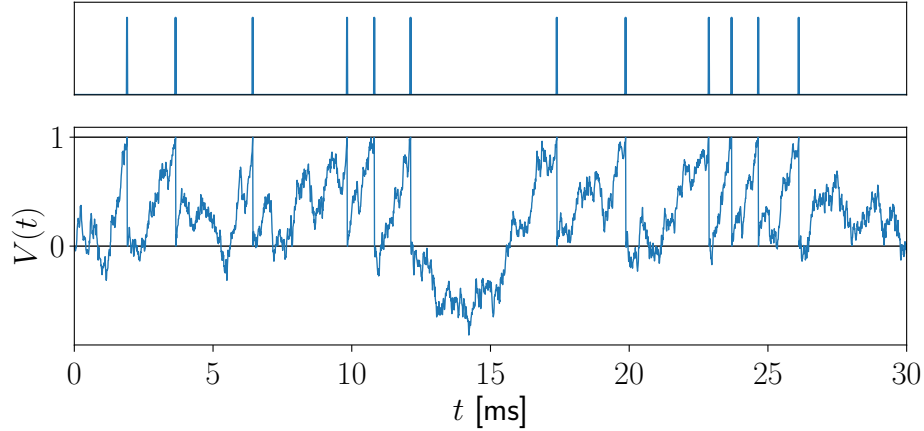


Figure 1.5: Typical realization  $V(t)$  for the PIF model driven with a white noise with  $f(h) = 0.3$   $V_{th}$ ,  $D = 0.1$   $V_{th}^2, \tau_v = 1$  ms  $V_{th} = 1$ . The generated spike train is indicated on the top.

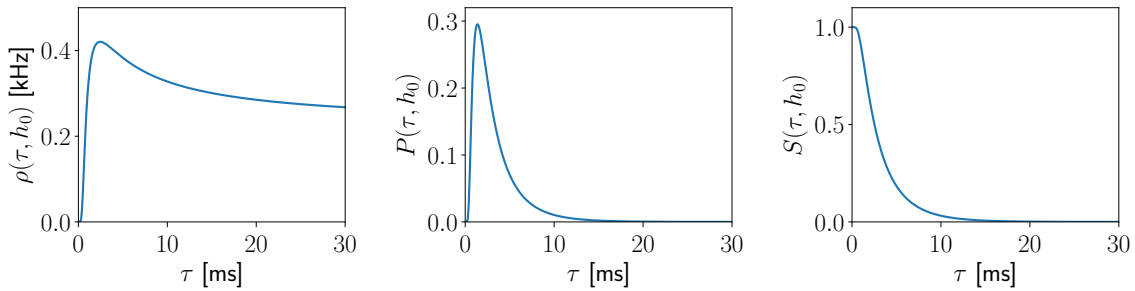


Figure 1.6: **PIF neurons.** Hazard rate  $\rho(\tau)$  (left), interval distribution  $P(\tau)$  (middle) and survivor function  $S(\rho(\tau))$  (right) for the PIF model.

**Perfect integrate-and-fire model driven by white noise** The perfect integrating-and fire model has been used to explain statistics of single neuron. The membrane potential  $V$  of a neuron can be seen as a Brownian-motion with drift  $f(h)$  driven by a white noise,

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which is reset to the value  $V_r$  when it hits the threshold  $V_{th}$ .  $f(h)$  is a mean current which depends on the input potential  $h$ .

$$\tau_v \dot{V} = f(h) + \sqrt{2D}\xi(t), \quad \text{if } V = V_{th} \rightarrow V_r \quad (1.16)$$

$$\langle \xi(t)\xi(s) \rangle = \delta(t-s) \quad (1.17)$$

A typical realization of the dynamics of  $V(t)$  for a single neuron and the corresponding spike train is illustrated on Fig.1.5. The statistic of such neurons are shown on Fig.1.6.

### 1.2 Moment of the interspike interval distribution $P(\tau)$

For a stationary spike train, the ISI distribution is also stationary.

Here  $h$  is the constant and  $P(\tau, h)$  is reduced to  $P(\tau)$ . The interval distribution allows to compute the  $k$ -th moment,

$$\langle \tau^k \rangle = \int_0^\infty \tau^k P(\tau) d\tau \quad (1.18)$$

It is useful to introduce the Laplace transform

$$P_L(\lambda) = \int_0^\infty d\tau e^{-\lambda\tau} P(\tau) \quad (1.19)$$

from which the  $k$ -th ISI moment can be generated

$$\langle \tau^k \rangle = (-1)^k \left. \frac{d^k P_L}{d\lambda^k} \right|_{\lambda=0} \quad (1.20)$$

Hence,  $P_L(\lambda)$  is called the ISI moment generating function. We can generate from this function the ISI cumulants defined by

$$\kappa_k = (-1)^k \left. \frac{d^k \ln P_L}{d\lambda^k} \right|_{\lambda=0} \quad (1.21)$$

The first two ISI cumulants are related to the ISI moments by

$$\kappa_1 = \langle \tau \rangle \quad (1.22)$$

$$\kappa_2 = \langle \tau^2 \rangle - \langle \tau \rangle^2 \quad (1.23)$$

The cumulants can be used to characterize the shape of the ISI density. The rate of a process  $R$  is given by

$$R = \langle \tau \rangle^{-1} = \kappa_1^{-1} \quad (1.24)$$

An important measure that quantifies the variability of ISI distribution is the coefficient of variation  $C_V$  defined as

$$C_V = \sqrt{\frac{\langle \tau^2 \rangle}{\langle \tau \rangle^2}} - 1 = \frac{\sqrt{\kappa_2}}{\kappa_1} \quad (1.25)$$

A Poisson process produces distributions with  $C_V = 1$  which indicate a highly irregular spike train. A value of  $C_V > 1$ , implies that a given spike train is less regular than a Poisson process with the same firing rate. If  $C_V < 1$ , then the spike train is more regular. Whereas  $C_V = 0$  indicates a perfectly regular spike train.

## 1.3 Populations of neurons and refractory density equations

### 1.3.1 Population model

There are more about hundred of billion neurons in the human brain, distributed in different brain area and which form elaborate neural networks. Within a brain area one can identify subregions and layers where neurons are organize in populations of cells with similar property. Eloquent example are barrel columns in the primary somatosensory cortex [Lefort et al. (2009)], and pool of motor neuron [Kandel et al. (2000)].

Given the large number of neurons in a population, rather than track the spiking of individual neurons, instead it is appealing to describe the mean activity. Fig.1.1 illustrate the transition from a microscopic to a mesoscopic description. The theory of population dynamics date back to the 1970s [Knight (1972), Wilson and Cowan (1972)] and are still widely use to predict the temporal evolution of the activity  $A(t)$  [Schwalger et al. (2017)]. In a network of  $N$  neurons the population activity  $A(t)$  is defined as the proportion of active neuron, denoting by  $t_j^f$  the firing time  $f$  of the neuron  $j$ , the activity can be express as

$$A(t) = \frac{1}{N} \sum_{j=1}^N \sum_f \delta(t - t_j^f) \quad (1.26)$$

where  $\delta$  denotes the dirac function.

We consider large homogeneous population of neurons i.e all neuron are identical and receive the same input potential  $\mu(t)$

$$\mu(t) = RI_{ext}(t) + RI_{syn}(t) \quad (1.27)$$

Where  $I_{ext}$  denote an external input current, and  $I_{syn}$  the synaptic input

$$RI_{syn}(t) = JA(t) \quad (1.28)$$

$J$  denotes the coupling constant with the unite of voltage seconds, for a sake of simplicity we will consider all-to-all coupling, i.e. each neuron are coupled to each neuron and therefore receive the same input proportional to the mean activity.



### 1.3.2 Refractory density equation

An approach on the refractory density  $q(\tau, t)$  can be used to analyze the dynamic in an homogeneous population [Gerstner and Kistler (2002)].  $q(\tau, t)$  characterize the number of neuron at time  $t$  that are in a similar state of activity, i.e with age  $\tau = t - \hat{t}$ , where  $\hat{t}$  is the last spike time of the neuron. The population activity is thus given by

$$A(t) = q(0, t) \quad (1.29)$$

As long as a neuron does not fire, the age  $\tau$  increase at the speed of  $\frac{d\tau}{dt} = 1$ , therefore the flux along the refractory variable  $\tau$  is simply  $q(\tau, t)$  and the continuity equation is given by

$$\frac{\partial q}{\partial t} = -\frac{\partial q}{\partial \tau} \quad (1.30)$$

When a neuron fires, the trajectory along the refractory variable  $\tau$  stops at the current value and "reappears" at  $\tau = 0$ . The instantaneous probability to fire is given by the hazard function  $\rho(\tau, h)$ . Therefore the loss per unit time is given by  $-\rho(\tau, h)q(\tau, t)$  and the full dynamic is then given by the master equation:

$$\partial_t q(\tau, t) = -\partial_\tau q(\tau, t) - \rho(\tau, h)q(\tau, t) \quad (1.31)$$

The dynamics is schematize on Fig.1.7. At time  $t_j$  The proportion of neurons at age  $\tau_i$  whose are firing and will reappear at age 0, is given by  $q(\tau_i, \tau_j)\rho(\tau_i, h_j)\Delta t$  (red arrow). The neuron whose did not fire will reach the age  $\tau_{i+1}$  at time  $t_{j+1}$  (blue arrow). The sum of all trajectory that "disappear" at time  $t$  due to firing, are "reappearing" at  $\tau = 0$  and neuron will fire at some finite time, therefore the boundary condition are:

$$q(0, t) = \int_0^\infty \rho(\tau, h)q(\tau, t)d\tau = A(t) \quad (1.32)$$

$$q(\infty, t) = 0 \quad (1.33)$$

Additionally,  $q$  is normalized

$$\int_0^\infty q(\tau, t)d\tau = 1 \quad (1.34)$$

and has the initial density

$$q(\tau, 0) = q_0(\tau) \quad (1.35)$$

where  $q_0(\tau)$  is some function that satisfies the conditions Eq.(1.32),(1.34)

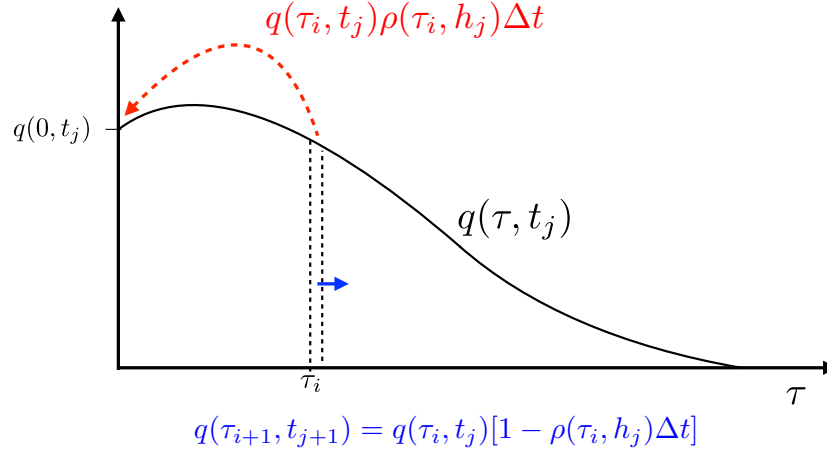


Figure 1.7: Scheme of refractory density dynamics. The red arrow represents the proportion of neurons with age  $\tau_i$  whose fire at time  $t_j$ , the blue one represents those that are not firing and will reach the age  $\tau_{i+1}$  at time  $t_{j+1}$ . Taking the limit  $\Delta t \rightarrow 0$  yields to Eq.(1.31)

## 1.4 Spectral decomposition method

We apply a probability density approach, which describes the evolution of the density of states  $q(x, t)$ , in the phase space of a specific choice of neuronal state variable  $x$ . Many approaches consider only one state, the membrane potential  $v$ , governed by the integrate and fire model. In the refractory density approach, the state variable is the age  $\tau$ , i.e the time elapsed since the last spike. Assuming that the state variable  $x$  can be described by a Markovian dynamics, we can write down an evolution equation for the state density  $q$  in the following form

$$\partial_t q(x, t) = \mathcal{L}q(x, t) \quad (1.36)$$

Where  $\mathcal{L}$  is the evolution operator. Taking the membrane potential  $v$  as a state variable the evolution operator corresponds to the Fokker-Planck operator [Mattia and Del Giudice (2002), Schaffer et al. (2013)]. We will first recall some property for a general evolution operator.

### 1.4.1 General properties of the evolution operator

The operator  $\mathcal{L}$  of Eq.1.36 has a set of eigenfunctions and associated eigenvalues

$$\mathcal{L}|\phi_n\rangle = \lambda_n|\phi_n\rangle \quad (1.37)$$

We use for notation  $\phi_n(x, t) = |\phi_n\rangle$  and  $\lambda_n(t) = \lambda_n$ . The time dependency provides a moving basis  $\{|\phi_n\rangle\}$ .

Because  $\mathcal{L}$  is a real operator, if an eigenvalue  $\lambda_n$  is complex, its complex conjugate  $\bar{\lambda}_n$  is also an eigenvalue of  $\mathcal{L}$ , with eigenfunction  $|\bar{\phi}_n\rangle$ . We will use the notation  $\bar{\lambda}_n = \lambda_{-n}$ , i.e

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the sums over the spectrum of  $\mathcal{L}$  range over all integer numbers. Note that  $\lambda_0 = 0$  is always an eigenvalue of the operator  $\mathcal{L}$  and corresponds to the stationary solution.

Because  $\mathcal{L}$  can not be generally brought to an Hermitian form we also need to define the eigenfunctions  $|\psi_n\rangle$  of the adjoint operator  $\mathcal{L}^+$

$$\mathcal{L}^+ |\psi_n\rangle = \tilde{\lambda}_n |\psi_n\rangle \quad (1.38)$$

The adjoint operator is defined as  $\langle\psi|\mathcal{L}\phi\rangle = \langle\mathcal{L}^+\psi|\phi\rangle$ , where we introduce the inner product

$$\langle\psi|\phi\rangle = \int \psi(x, t)\phi(x, t)dx \quad (1.39)$$

Using the properties of the operator, one can show that the eigenvalues of Eq.(1.37) and Eq.(1.38) are the same

$$\begin{aligned} \lambda_n \langle\psi_n|\phi_n\rangle &= \int \psi_n(x, t)\mathcal{L}\phi_n(x, t)dx \\ &= \langle\psi_n|\mathcal{L}\phi_n\rangle \\ &= \langle\mathcal{L}^+\psi_n|\phi_n\rangle \\ &= \int \mathcal{L}^+\psi_n(x, t)\phi_n(x, t)dx \\ &= \tilde{\lambda}_n \langle\psi_n, |\phi_n\rangle \end{aligned} \quad (1.40)$$

Eq.(1.40) implies that  $\lambda_n = \tilde{\lambda}_n$  and

$$\mathcal{L}^+ |\psi_n\rangle = \lambda_n |\psi_n\rangle \quad (1.41)$$

For different eigenvalues, the eigenfunctions  $\psi_i$  and  $\phi_j$  are orthogonal

$$\begin{aligned} \lambda_j \langle\psi_i|\phi_j\rangle &= \langle\psi_i|\mathcal{L}\phi_j\rangle \\ &= \langle\mathcal{L}^+\psi_i|\phi_j\rangle \\ &= \lambda_i \langle\psi_i|\phi_j\rangle \end{aligned} \quad (1.42)$$

And with an appropriate normalization the two set of eigenfunctions are biorthonormal

$$\langle\psi_i|\phi_j\rangle = \delta_{ij} \quad (1.43)$$

The density of state  $q(x, t)$  can be expressed in terms of this basis.

$$|q\rangle = \sum_n a_n |\phi_n\rangle \quad (1.44)$$

where  $a_n(t) = \langle\psi_n|q\rangle$  are the time dependent coefficients of the modal expansion. Since  $q$  is real,  $\bar{a}_n = a_{-n}$ .

### 1.4.2 Rate equation

The activity  $A(t)$  can be defined as the flux operator  $\hat{J}$  on the the density of state  $q(x, t)$ .

$$A(t) = \hat{J}q(x, t) \quad (1.45)$$

Taking the membrane potential  $v$  as state variable, the flux operator  $\hat{J}$  is defined as

$$\hat{J}q(v, t) = -D(v, t)\partial_v q(v, t)|_{v=v_{th}} \quad (1.46)$$

$\hat{J}q(v, t)$  denotes the fractions of realisations per unit time crossing the threshold  $v_{th}$ . In the refractory approach with state variable  $\tau$ , i.e the times elapsed since the last spike, Eq.(1.32) implies that  $\hat{J}$  is given by

$$\hat{J}q(\tau, t) = \int_0^\infty \rho(\tau, t)q(\tau, t)d\tau \quad (1.47)$$

Expanding the refractory density on the eigenfunction basis Eq.(1.44), Eq.(1.45) can be rewritten as

$$\begin{aligned} A(t) &= \sum_n a_n \hat{J}|\phi_n\rangle \\ &= \vec{a} \cdot \vec{f} \end{aligned} \quad (1.48)$$

where  $\vec{a} = \{a_n\}$  and  $\vec{f} = \{\hat{J}|\phi_n\rangle\}$  corresponds to the operator  $\hat{J}$  acting on the eigenfunctions  $\{|\phi_n\rangle\}$ . The dynamics of the  $a_n$  can be determined directly from the evolution equation Eq.(1.36)

$$\begin{aligned} \dot{a}_n &= \langle \psi_n | \partial_t q \rangle + \langle \partial_t \psi_n | q \rangle \\ &= \langle \psi_n | \mathcal{L} q \rangle + \hbar \sum_m a_m \langle \partial_h \psi_n | \phi_m \rangle \\ &= \lambda_n a_n + \hbar \sum_m a_m \langle \partial_h \psi_n | \phi_m \rangle \end{aligned} \quad (1.49)$$

Here we have use the fact that the time dependence of  $\psi$  is due to the moment of  $\hbar$ , which is an external variable. An emission rate equation result

$$\dot{\vec{a}} = (\mathbf{\Lambda} + \mathbf{C}\hbar)\vec{a} \quad (1.50)$$

$$A = \vec{a} \cdot \vec{f} \quad (1.51)$$

The synaptic coupling are expressed in the he matrix  $\mathbf{C}$ :  $C_{nm} = \langle \partial_h \psi_n | \phi_m \rangle$ . And  $\mathbf{\Lambda}$  is the diagonal matrix of the eigenvalues of  $\mathcal{L}$ :  $\Lambda_{nm} = \lambda_n \delta_{nm}$

In previous studies a prominent choice of the state variable was the membrane potential  $v$  to analyze the dynamics of networks of integrate and fire neurons. In this case the evolution operator  $\mathcal{L}$  was the Fokker-Planck operator [Mattia and Del Giudice (2002), Gerstner and Kistler (2002), Schaffer et al. (2013)]. However neurons with different refractory state can have the same potential, and thus the membrane potential can be a weak predictor of the neuron complete state, but the age approximate quite well the refractory states, this encourage the use of a refractory approach. In this study, we re-evaluate the spectral decomposition for the refractory density Eq.(1.31).

### 1.5 Aim of the study

Starting with the spike statistic of a renewal process the goal of this thesis is to derive a low dimensional population dynamics keeping the first mode of the spectral expansion of the refractory density equation. In other word we would like to apply the eigenfunction expansion method presented in Section 1.4 to the operator of the refractory density. Therefore we will first introduce in Sections 2.1 and 2.2, the operator and adjoint operator of the refractory density and the corresponding eigenfunctions, to finally in Section 2.3 derive from this expansion a firing rate equation for a large population of homogeneous neuron.

In Chapter 3, we will present the spectrum for specific model and an approximation of the first eigenvalue for a general renewal process. We will then show the accuracy of the derived approximations using as model a large homogeneous population of Poisson neurons with absolute refractoriness. In Chapter 4 we will first consider the uncoupled case and analyze the effect of the refractory period  $\Delta$ . In Chapter 5 we will finally look at a network of synaptically coupled neurons.

# Chapter 2

## Theory

In this chapter we will follow the different step of the spectral expansion presented in Section 1.4, defining the operator and adjoint operator of the refractory density equation. Thanks to the derived spectrum and biorthonormal basis, we will obtained a low dimensional firing rate equation.

### 2.1 Operator of the refractory density, and eigenvalue spectrum $\{\lambda_n\}$

The master equation Eq.(1.31) can be rewritten introducing the operator :

$$\mathcal{L} = -\partial_\tau - \rho(\tau, h) \quad (2.1)$$

$$\partial_t q(\tau, t) = \mathcal{L} q(\tau, t) \quad (2.2)$$

The set of eigenfunctions and associated eigenvalues of  $\mathcal{L}$  obeys to

$$\mathcal{L} |\phi_n\rangle = \lambda_n |\phi_n\rangle \quad (2.3)$$

And respect the boundary conditions Eq.(1.32)

$$\phi_n(0, h) = \int_0^\infty \rho(\tau, h) \phi_n(\tau, h) d\tau \quad (2.4)$$

$$\phi_n(\infty, h) = 0 \quad (2.5)$$

To lighten the notation, we will omit the dependence on  $h$  (the time dependent potential) of the hazard rate  $\rho(\tau)$ , The ISI distribution  $P(\tau)$ , the survivor function  $S(\tau)$ , and of the set of eigenfunctions  $\{|\phi_n\rangle\}$  and eigenvalues  $\{\lambda_n\}$ .

## Chapter 2. Theory

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The solution of Eq.(2.3) is

$$\begin{aligned}\phi_n(\tau) &= \phi_n(0) \exp \left( -\lambda_n \tau - \int_0^\tau \rho(s) ds \right) \\ &= \phi_n(0) e^{-\lambda_n \tau} S(\tau)\end{aligned}\tag{2.6}$$

Inserting Eq.(2.6) in the boundary condition Eq.(2.4), we find the condition

$$\phi_n(0) = \int_0^\infty d\tau \rho(\tau) \phi_n(0) \exp \left( -\lambda_n \tau - \int_0^\tau \rho(s) ds \right)\tag{2.7}$$

which can be written as

$$1 = \int_0^\infty e^{-\lambda_n \tau} P(\tau) d\tau = P_L(\lambda_n)\tag{2.8}$$

The condition Eq.(2.8) was already derived by Tilo Schwalger in an unpublished paper. It states that the Laplace transform of the ISI density  $P_L(\lambda)$  at the (complex) arguments  $\lambda_n$  must be unity.

We can conclude some properties of the spectrum  $\lambda_n$  imposed by Eq.(2.8)

- As expected, the eigenvalue  $\lambda_0 = 0$  fulfilled the condition because the ISI density is normalized. This eigenvalue corresponds to the stationary density.
- The real part of  $\lambda_n$  cannot be positive, as expected for physical reason. Indeed the solution of the refractory density equation is directly related to the eigenvalues of  $\mathcal{L}$  and is expected to converge to  $\phi_0$ , instead of exploding which would be the case for positive eigenvalues. In fact for  $\Re(\lambda_n) > 0$ ,

$$\int_0^\infty e^{-\lambda_n \tau} P(\tau) d\tau < \int_0^\infty |e^{-\lambda_n \tau}| P(\tau) d\tau < \int_0^\infty P(\tau) d\tau = 1\tag{2.9}$$

which contradict Eq.(2.8).

## 2.2 Adjoint operator $\mathcal{L}^+$ , and normalization

Because  $\mathcal{L}$  cannot be generally brought to an Hermitian form we also need to define the set of eigenfunctions  $\{|\psi_n\rangle\}$  of the adjoint operator  $\mathcal{L}^+$

$$\mathcal{L}^+ |\psi_n\rangle = \lambda_n |\psi_n\rangle\tag{2.10}$$

We can find the adjoint operator  $\mathcal{L}$ , using integration by part

$$\begin{aligned}
 \langle \psi | \mathcal{L} \phi \rangle &= \int_0^\infty \psi(\tau) \mathcal{L} \phi(\tau) d\tau \\
 &= \int_0^\infty \psi(\tau) [-\partial_\tau - \rho(\tau)] \phi(\tau) d\tau \\
 &= -[\psi(\tau) \phi(\tau)]_0^\infty + \int_0^\infty \partial_\tau \psi(\tau) \phi(\tau) d\tau - \int_0^\infty \rho(\tau) \psi(\tau) \phi(\tau) d\tau \\
 &= \psi(0) \phi(0) + \int_0^\infty [\partial_\tau - \rho(\tau)] \psi(\tau) \phi(\tau) d\tau \\
 &= \int_0^\infty \psi(0) \rho(\tau) \phi(\tau) d\tau + \int_0^\infty [\partial_\tau - \rho(\tau)] \psi(\tau) \phi(\tau) d\tau \\
 &= \int_0^\infty \{ [\partial_\tau - \rho(\tau)] \psi(\tau) + \psi(0) \rho(\tau) \} \phi(\tau) d\tau \\
 &= \langle \mathcal{L}^+ \psi | \phi \rangle
 \end{aligned} \tag{2.11}$$

As we will normalize the eigenfunction to obtain a biorthonormal basis we can set  $\psi_n(0) = 1$ , and the adjoint operator can be express as

$$\mathcal{L}^+ \psi_n(\tau) = [\partial_\tau - \rho(\tau)] \psi_n(\tau) + \rho(\tau) \tag{2.12}$$

The solution of Eq.(2.10) is thus

$$\begin{aligned}
 \psi_n(\tau) &= \exp \left( \lambda_n \tau + \int_0^\tau \rho(s) ds \right) \left[ 1 - \int_0^\tau dx \rho(x) \exp \left( -\lambda_n x - \int_0^x \rho(s) ds \right) \right] \\
 &= e^{\lambda_n \tau} S^{-1}(\tau) \left[ 1 - \int_0^\tau dx P(x) e^{-\lambda_n x} \right]
 \end{aligned} \tag{2.13}$$

In particular we have

$$\psi_0(\tau) = 1 \tag{2.14}$$

Inserting Eq.(2.6) and Eq.(2.13) in Eq.(1.43) yields to the normalization of the biorthonormal basis

$$1 = \int_0^\infty d\tau \phi_n(0) \left[ 1 - \int_0^\tau dx P(x) e^{-\lambda_n x} \right] \tag{2.15}$$

$$\phi_n(0) = \frac{1}{\int_0^\infty [1 - \int_0^\tau P(x) e^{-\lambda_n x} dx] d\tau} \tag{2.16}$$

In particular for  $n = 0$ ,  $\lambda_0 = 0$  and we recover the relation

$$\phi_0(0) = \frac{1}{\int_0^\infty S(\tau) d\tau} \tag{2.17}$$



## 2.3 Firing rate equation

The spectrum  $\{\lambda_n\}$  of the operator  $\mathcal{L}$  provides a moving basis  $\{|\phi_n\rangle\}$ . The refractory density  $q(\tau, t)$  can be expressed with the eigenfunctions  $\{|\phi_n\rangle\}$ .

$$|q\rangle = \sum_n a_n |\phi_n\rangle \quad (2.18)$$

where  $a_n = \langle \psi_n | q \rangle$  are the time dependent coefficients of the modal expansion. In particular from Eq.(2.14), and Eq.(1.43) we have  $a_0(t) = 1$ . The dynamics of the  $a_n$  for  $n \neq 0$  can be determined directly using Eq.(2.1), and Eq.(2.2) as derived in Eq.(1.49)

Defining the coupling coefficient as  $C_{nm} = \langle \partial_h \psi_n | \phi_m \rangle$  we can rewrite Eq.1.49

$$\dot{a}_n = \lambda_n a_n + \dot{h} \sum_m C_{nm} a_m \quad (2.19)$$

We can finally express the activity  $A(t) = q(0, t)$  as

$$A(t) = \sum_n a_n(t) \phi_n(0) \quad (2.20)$$

Keeping only the first mode, and using the fact that  $|\phi_{-n}\rangle = |\bar{\phi}_n\rangle$  and  $a_{-n} = \bar{a}_n$ , Eq.(2.20) becomes

$$\begin{aligned} A(t) &= \phi_0(0) + a_1 \phi_1(0) + a_{-1} \phi_{-1}(0) \\ &= \phi_0(0) + 2 (\Re[a_1] \Re[\phi_1(0)] - \Im[a_1] \Im[\phi_1(0)]) \end{aligned} \quad (2.21)$$

And the dynamics of the  $a_1$  is given by

$$\dot{a}_1 = \lambda_1 a_1 + \dot{h} [C_{10} + C_{11} a_1 + C_{1-1} a_{-1}]$$

Separating explicitly the real part  $X(t)$  and the imaginary part  $Y(t)$  of  $a_1(t)$

$$a_1(t) = X(t) + iY(t) \quad (2.22)$$

we derived from Eq.(2.22) two non linear first order differential equations

$$\dot{X} = \Re[f]X - \Im[g]Y + \Re[C_{10}]\dot{h} \quad (2.23)$$

$$\dot{Y} = \Re[g]Y + \Im[f]X + \Im[C_{10}]\dot{h} \quad (2.24)$$

$$(2.25)$$

with

$$f = \lambda_1 + \dot{h}(c_{11} + c_{1-1}) \quad (2.26)$$

$$g = \lambda_1 + \dot{h}(c_{11} - c_{1-1}) \quad (2.27)$$

We have finally a set of three non linear differential equation  $\dot{h}$ ,  $\dot{X}$ ,  $\dot{Y}$ . Eq.(2.21) can be rewritten as

$$A(t) = \phi_0(0) + 2 \left( X \Re[\phi_1(0)] - Y \Im[\phi_1(0)] \right) \quad (2.28)$$

# Chapter 3

## Spectrum

### 3.1 Spectral derivation for specific model

#### 3.1.1 Poisson neuron with absolute refractoriness

In this section we consider a Poisson neuron with absolute refractory period  $\Delta$ , the hazard rate is defines by the recovery function Eq.(1.13). For the sake of simplicity in the notation we will use the variable  $\nu$  such that  $\nu = \Phi(h)$ . The hazard rate is then given by

$$\rho(\tau) = \nu \Theta(\tau - \Delta) \quad (3.1)$$

And the interspike interval distribution is

$$P(\tau) = \nu \exp(-\nu(\tau - \Delta))\Theta(\tau - \Delta) \quad (3.2)$$

For this process we can compute the Laplace transform of the ISI density

$$\begin{aligned} P_L(\lambda) &= \int_0^\infty P(\tau)e^{-\lambda\tau} \\ &= \frac{\nu}{\nu + \lambda} \exp(-\lambda\Delta) \end{aligned} \quad (3.3)$$

By the change of variable  $w = (\nu + \lambda_n)\Delta$ , the condition Eq.(2.8), can be rewritten as

$$\Delta\nu e^{\nu\Delta} = we^w \quad (3.4)$$

The solution of equation Eq.(3.4) is given introducing the Lambert W-function  $W(z, n)$

$$w = W(\Delta\nu e^{\nu\Delta}, n) \quad (3.5)$$

from which we read the eigenvalue spectrum  $\{\lambda_n\}$

$$\lambda_n = \frac{1}{\Delta} W(\Delta\nu e^{\nu\Delta}, n) - \nu \quad (3.6)$$

We can explicitly express the eigenfunctions,  $|\phi_n\rangle$  of the operator  $\mathcal{L}$  and  $|\psi_n\rangle$  of the adjoint operator  $\mathcal{L}^+$

$$\phi_n(\tau) = \frac{\nu + \lambda_n}{1 + \Delta(\nu + \lambda_n)} e^{-\lambda_n \tau} [\Theta(\Delta - \tau) + \Theta(\tau - \Delta) e^{-\nu(\tau - \Delta)}] \quad (3.7)$$

$$\psi_n(\tau) = \Theta(\Delta - \tau) e^{\lambda_n \tau} + \Theta(\tau - \Delta) \frac{\nu}{\nu + \lambda_n} \quad (3.8)$$

$$= \Theta(\Delta - \tau) e^{\lambda_n \tau} + \Theta(\tau - \Delta) e^{\lambda_n \Delta} \quad (3.9)$$

On can verify that the set eigenfunctions satisfy indeed Eq.(1.43).

In order to define the coupling coefficient we need first to compute  $\frac{d\psi_n(\tau)}{d\nu}$

$$\frac{\partial \psi_n(\tau)}{\partial \nu} = \frac{\lambda_n}{\nu[1 + \Delta(\nu + \lambda_n)]} [\Theta(\Delta - \tau) \tau e^{\lambda_n \tau} + \Theta(\tau - \Delta) \Delta e^{\lambda_n \Delta}] \quad (3.10)$$

The coupling coefficient are then

$$\begin{aligned} C_{nn} &= \frac{\partial \nu}{\partial h} \int_0^\infty \frac{d\psi_n(\tau)}{d\nu} \phi_n(\tau) d\tau \\ &= \frac{\lambda_n \Delta (1 + \frac{1}{2} \lambda_n (\nu + \lambda_n))}{\nu (1 + \Delta(\nu + \lambda_n))} \frac{\partial \nu}{\partial h} \end{aligned} \quad (3.11)$$

$$\begin{aligned} C_{nm} &= \frac{\partial \nu}{\partial h} \int_0^\infty \frac{d\psi_n(\tau)}{d\nu} \phi_m(\tau) d\tau \\ &= \frac{\lambda_n (\nu + \lambda_m)}{\nu (\lambda_n - \lambda_m) (\nu + \lambda_n) (1 + \Delta(\nu + \lambda_m))} \frac{\partial \nu}{\partial h} \end{aligned} \quad (3.12)$$

### Gamma process

In this section we consider a gamma process. Taking the Laplace transform of the ISI density Eq. (1.15) yields:

$$P_L(\lambda) = \left( \frac{\beta}{\beta + \lambda} \right)^\gamma \quad (3.13)$$

The condition given by Eq.(2.8) leads then to the solutions

$$\lambda_n = \beta \left( \exp \left( \frac{2\pi i}{\gamma} n \right) - 1 \right), \quad n = 0, \dots, \gamma - 1 \quad (3.14)$$

### Chapter 3. Spectrum

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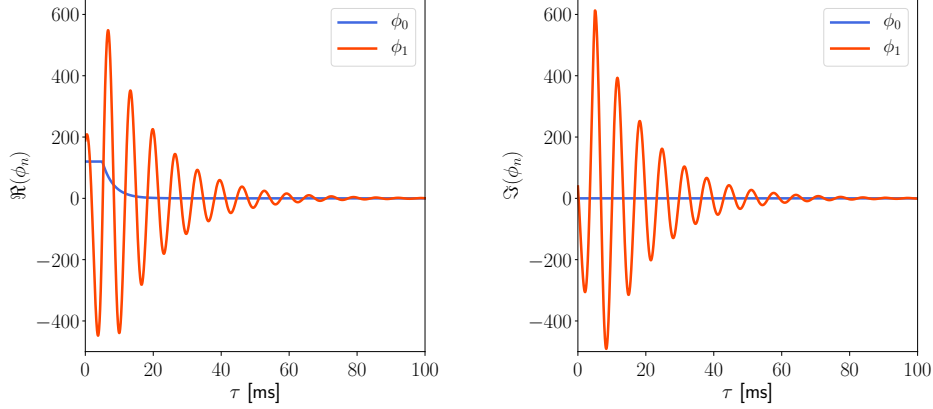


Figure 3.1: Real part (left) and imaginary part (right) of the eigenfunctions  $\phi_n$  and  $\psi_n$  of the first modes for **Poisson neuron with absolute refractory period**  $\Delta$ , with  $\Delta = 5$  ms,  $h = h_0$ ,  $\nu_{max} = 0.6$  kHz.  $\phi_{-1}$  is the complex conjugate of  $\phi_1$

Interestingly the gamma process has a finite basis. This can be rewritten in function of the rate  $R$  and the coefficient of variation  $C_v$  as

$$\lambda_n = RC_V^{-2} (\exp(2\pi i C_V^2 n) - 1) \quad (3.15)$$

And the normalization Eq.2.14 yields to

$$\phi_n(0) = \frac{1}{\gamma \beta^\gamma (\beta + \lambda_n)^{-(\gamma+1)}} \quad (3.16)$$

#### PIF neuron

In this section we will consider a perfect integrating and fire neuron. The Laplace transform of the ISI density Eq. (??) is

$$P_L(\lambda) = \exp\left(\frac{\mu V_{th}}{2D} \left[1 - \sqrt{1 + \frac{4D\lambda}{\mu^2}}\right]\right) \quad (3.17)$$

The condition given by Eq.(2.8) leads then to the solutions

$$\lambda_n = -\frac{2\pi\mu}{V_{th}} n \left( \frac{2\pi D}{\mu V_{th}} n + i \right) \quad (3.18)$$

The spectrum can be rewritten as a function of the rate  $R$  and the coefficient of variation  $C_v$

$$\lambda_n = -2\pi^2 R^2 C_V^2 n^2 + 2\pi R i n \quad (3.19)$$

We could not find an analytical solution for the normalization equation Eq.2.14.

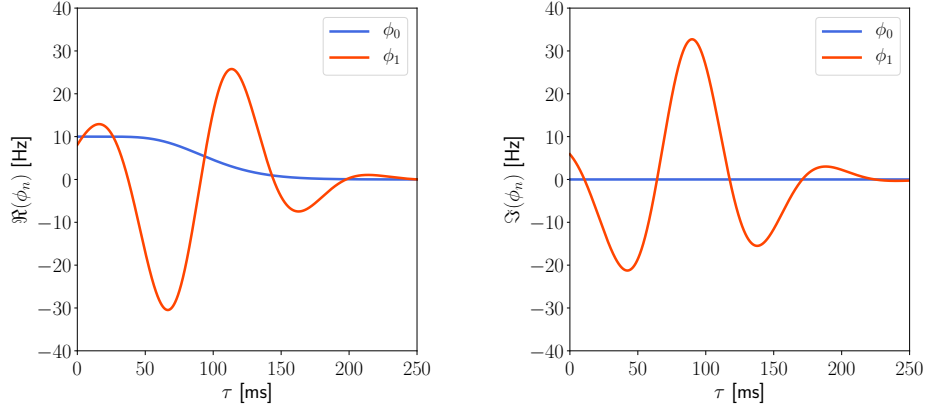


Figure 3.2: Real part (left) and imaginary part (right) of the eigenfunction  $\phi_n$  of the first modes for a **Gamma Process** with  $\beta = 100$   $\gamma = 10$ .  $\phi_{-1}$  is the complex conjugate of  $\phi_1$

## 3.2 A general approximation of the spectrum

In the previous sections we derived the spectrum  $\{\lambda_n\}$  for different specific model. But for a general ISI distribution  $P(\tau)$ , it is not always possible to obtained a analytical form of the Laplace transform  $P_L(\lambda)$ . Thats why we would like to find a method to approximate the first eigenvalue  $\lambda_1$ . From Eq.(1.20) one can see that the the Laplace transform of ISI distribution can be rewritten with the cumulant  $\kappa_n$  as:

$$P_L(\lambda) = \exp \left[ \sum_{k=1}^{+\infty} (-1)^k \kappa_k \frac{\lambda^k}{k!} \right] \quad (3.20)$$

The condition Eq.(2.8) can be then rewritten as:

$$\sum_{k=1}^{+\infty} (-1)^k \kappa_n \frac{\lambda_n^k}{k!} = 2\pi i n \quad (3.21)$$

We can approximate the first eigenvalue  $\lambda_1$ , neglecting the cumulant  $\kappa_k$  for  $k > 2$ . Consequently Eq.(3.21) becomes

$$\frac{\kappa_2}{2} \lambda_1^2 - \kappa_1 \lambda_1 - 2\pi i = 0 \quad (3.22)$$

$\lambda_1$  correspond to the roots of Eq.(3.22) with the negative real parts, as we shown before a positive real part would be unphysical and does not satisfy Eq.(2.8). The approximation of  $\lambda_1$  can be rewritten in terms of the rate  $R$  and the coefficient of variation  $C_V$ :

$$\lambda_1 \simeq RC_V^{-2} \left( 1 - \sqrt{1 + 4\pi i C_V^2} \right) \quad (3.23)$$

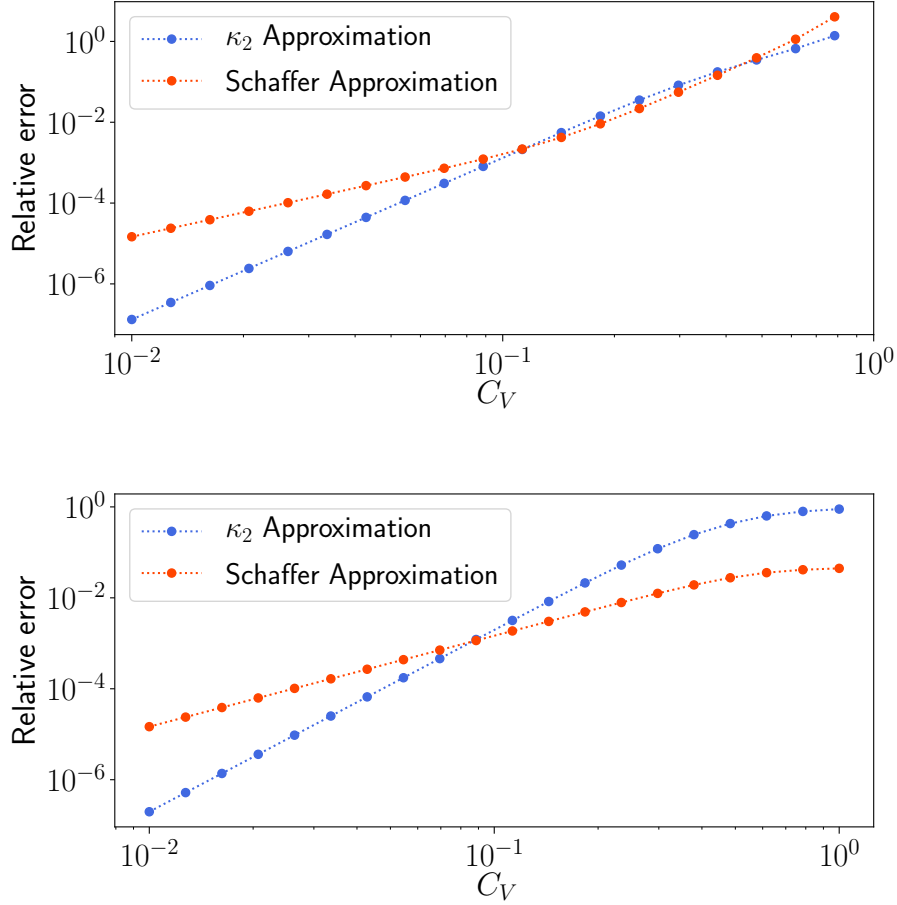


Figure 3.3: **Top:** Gamma process. **Bottom:** PIF neuron. Relative error on the eigenvalue for the spectrum approximations derived by Schaffer et al. (2013) Eq.(3.24), and by Eq.(3.23) using the cumulant expansion as a function of  $C_V$ .

Schaffer et al. (2013) determine the first eigenvalue  $\lambda_1$  for different renewal processes by fitting the dependency of the real part and the imaginary part on the rate  $R$  and the coefficient of variation squared  $C_V^2$ . They found as a relationship for small  $C_V$ :

$$\lambda_1 \simeq -R \left( \left( \frac{C_V}{0.22} \right)^2 + 2\pi i \right) \quad (3.24)$$

Note that for small  $C_V$  we can expand Taylor expand the square root in Eq.(3.23) and recover an expression close to Eq.(3.24)

$$\lambda_1 \simeq -R (2\pi^2 C_V^2 + 2\pi i) + \mathcal{O}(C_V^4) \quad (3.25)$$

Indeed  $\frac{1}{(0.22)^2} \simeq 20.7$  and  $2\pi^2 \simeq 19.7$ .

Fig.3.3 shows the relative error  $\frac{|\lambda_1 - \hat{\lambda}_1|}{|\lambda_1|}$  for the different approximation  $\hat{\lambda}_1$  of the first eigenvalue  $\lambda_1$ . For the Gamma process the relative error is below 0.1 for  $C_V < 0.3$  for the approximation obtained by Schaffer et al Eq.(3.24) and the one given by Eq.(3.23). For  $C_V < 0.1$  Eq.(3.23) is a better approximation. For the PIF neuron model, the  $\kappa_2$  approximation has a relative error below 0.1 for  $C_V < 0.1$ . It becomes better than the Schaffer approximation for  $C_V > 0.1$ . Actually Eq.(3.25) is exact and we saw that the Schaffer approximation is close to this expression. It seems that the truncation of the cumulant sum to second order gives a good approximation of the first eigenvalue  $\lambda_1$  for small  $C_V$ .



# Chapter 4

## General renewal neuron

### 4.1 Transient response of the population activity starting with a delta distribution $q(\tau, 0) = \delta(\tau)$

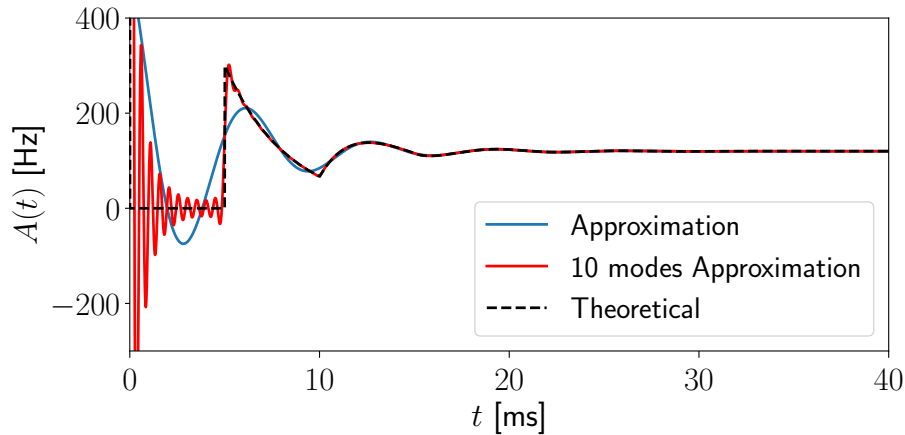


Figure 4.1: Activity  $A(t)$  of a population of neuron of poisson neuron with absolute refractoriness  $\Delta$ . The approximation given by Eq.(2.21), and the 10 modes approximation is given by by Eq.2.20 with  $n = 10$ . The parameters used are  $h = h_0$ ,  $\Delta = 5$  ms, and  $\nu_{max} = 0.6$  kHz and the initial condition is  $q(\tau, 0) = \delta(\tau)$

In this section we will look at the result of the approximation for the gamma process and for a population of Poisson neurons with absolute refractoriness. For a sake of simplicity we consider first large homogeneous population of uncoupled neurons with a constant input potential. The initial distribution of the refractory density  $q$  is given by a delta pic  $q(\tau, 0) = \delta(\tau)$ , i.e all neurons spike at time  $t = 0$ . As expected we need infinitely many modes to recover the exact initial distribution. We will see later that keeping only the first mode is good approximation for not too fast changes, which is not the case of a delta pic

#### 4.1. Transient response of the population activity starting with a delta distribution $q(\tau, 0) = \delta(\tau)$

nevertheless fig.4.1 one can see that we quantitatively reproduce with the approximation given by Eq.(2.21) the oscillations of the activity, and we even recover the shape of the first pic taking the 10 first mode of Eq.(2.20). For the Gamma process we saw that we had a finite basis and we see on fig.4.1 that we recover exactly the activity  $A(t)$  taking the complete expansion.

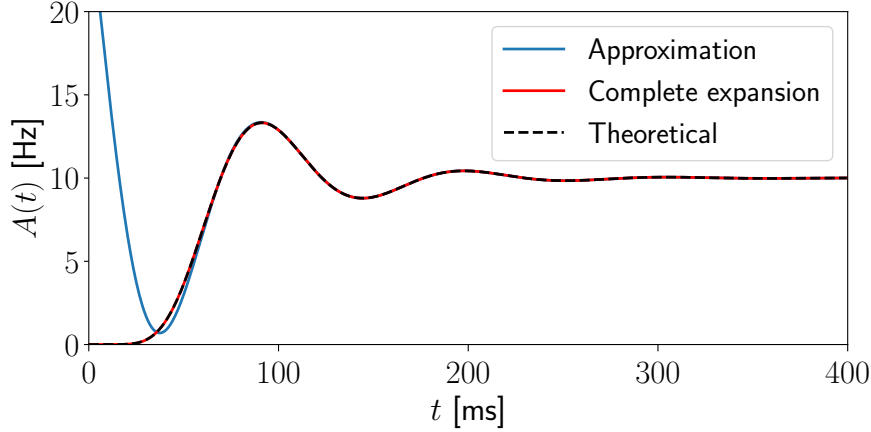


Figure 4.2: Activity  $A(t)$  of a population of neuron having an ISI density given by the gamma distribution with  $\beta = 100$  Hz and  $\gamma = 10$  starting with a delta distribution  $q(\tau, 0) = \delta(\tau)$ . With the approximation given by Eq.(2.21), and the complete expansion given by Eq.2.20

##### 4.1.1 Population response to time-dependent input

In this section we will study the response of a large population of uncoupled Poisson neuron with absolute refractoriness to an external time dependent input potential  $\mu(t)$ . The differential equation for the input potential  $h$  is given by Eq.(1.10), and the firing rate of the Poisson neurons is given by  $\Phi(h)$  Eq.(1.12). We will compare the population activity approximation given by Eq.(2.21), to the theoretical one computed as

$$A(t) = \Phi(h) \left( 1 - \int_{t-\Delta}^t A(s) ds \right) \quad (4.1)$$

We will use as an error measure the normalized root-mean-square deviation NRMS. The NRMS of predicted values  $\hat{y}_t$  for times  $t$  of a regression's dependent variable  $y_t$  with variables observed over  $T$  times, is computed for  $T$  different predictions as the square root of the mean of the squares of the deviations normalized by the range of value of  $y$

$$NRMS = \frac{1}{y_{max} - y_{min}} \sqrt{\frac{\sum_{t=1}^T (\hat{y}_t - y_t)^2}{T}} \quad (4.2)$$

## Chapter 4. General renewal neuron

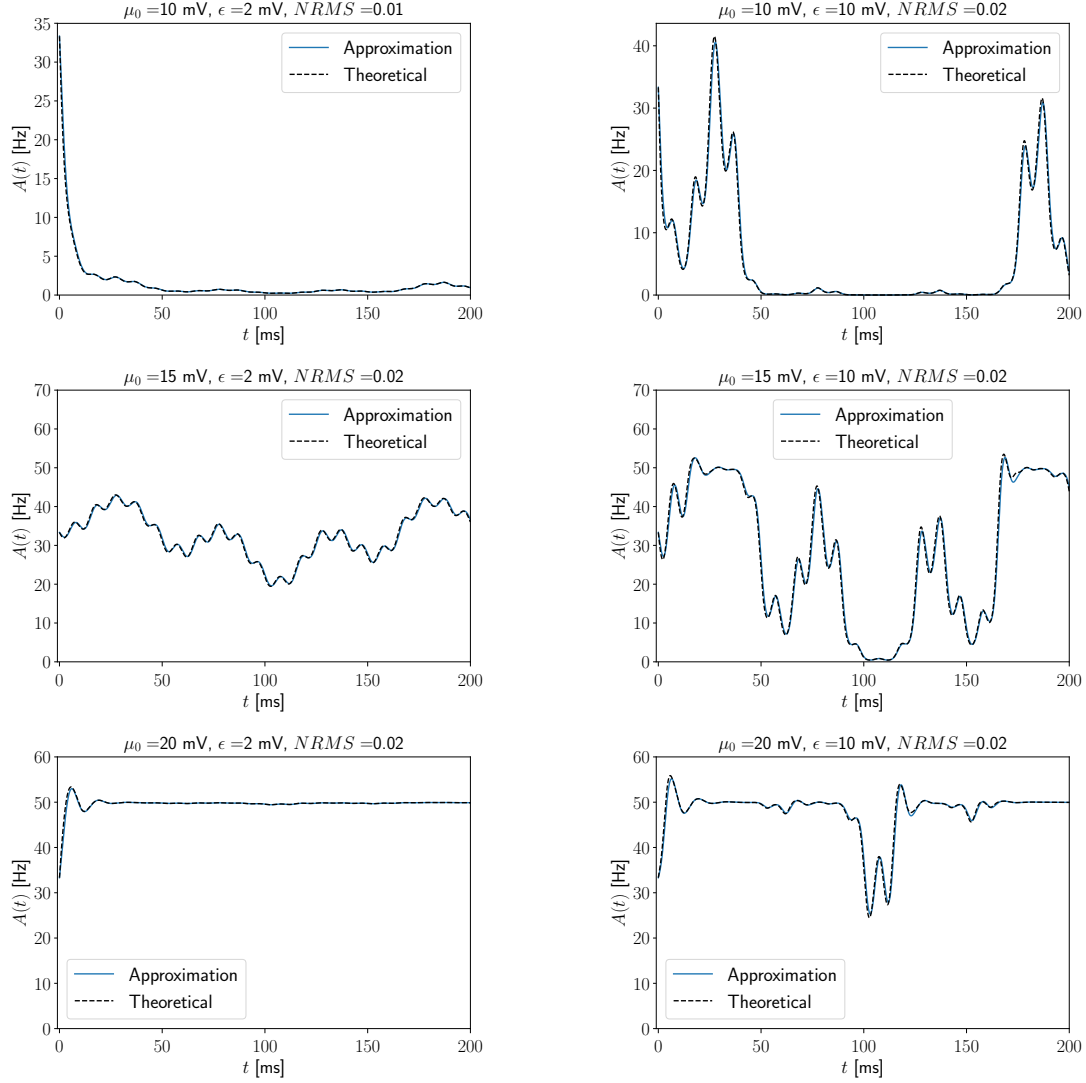


Figure 4.3: Response of a population of uncoupled Poisson neurons with absolute refractoriness to a fluctuating external input given by Eq.(4.4). For different amplitude  $\epsilon$  of the oscillating function  $f_{cos}(t)$  (left:  $\epsilon = 2$  mV, right:  $\epsilon = 10$  mV), for different baseline of the external potential input, top:  $\mu_0 < h_0$ , middle  $\mu_0 = h_0$  and bottom:  $\mu_0 > h_0$ . The parameters of the neurons are  $\nu_{max} = 100$  Hz,  $\Delta = 10$  ms,  $\beta = 1$  mV $^{-1}$ ,  $h_0 = 15$  mV. The time constant of the input potential  $h$  is  $\tau_m = 10$  ms.

Our approximation Eq.(2.21) only keeps the slowest mode, so we expect that the theory breaks down for too fast inputs. To study the accuracy of our approximation, we looked at the response of the model to a sinusoidal modulation of the external input potential  $\mu(t)$  with an angular frequency  $\omega_s$

#### 4.1. Transient response of the population activity starting with a delta distribution

$q(\tau, 0) = \delta(\tau)$

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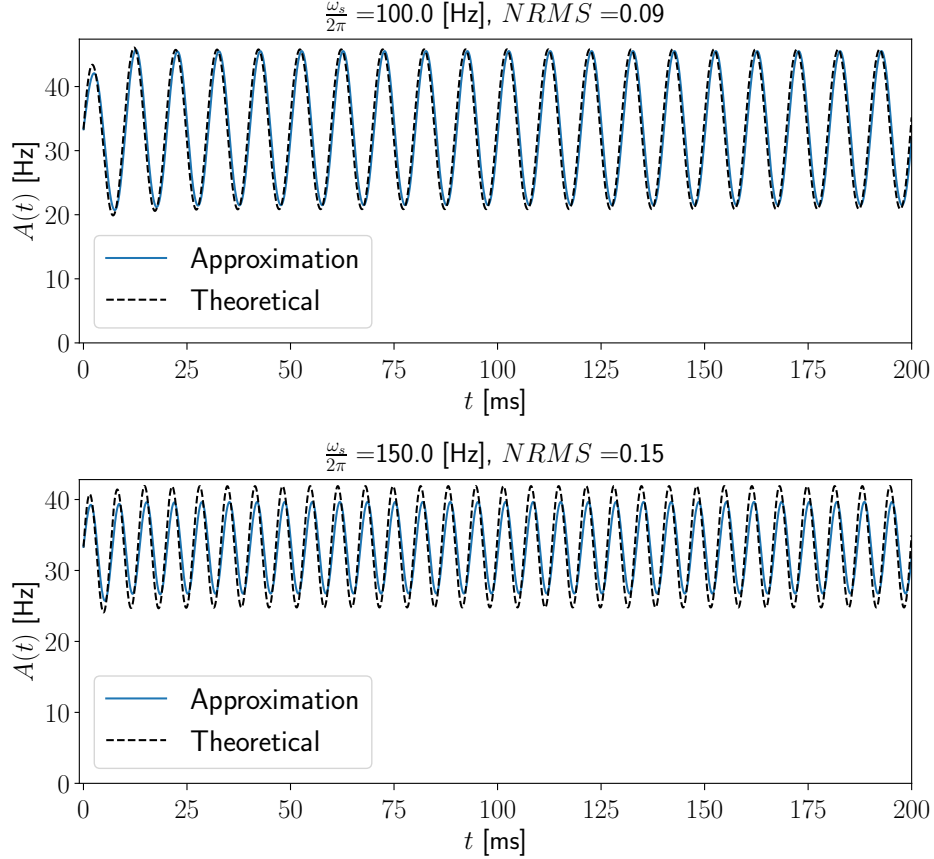


Figure 4.4: Population response to an oscillating input  $\mu(t)$  with angular frequency  $\omega_s$  (top: 100 Hz, bottom 150 Hz), for a large populations of uncoupled Poisson neurons with absolute refractoriness. The parameters of the neurons are  $\nu_{max} = 100$  Hz,  $\Delta = 10$  ms,  $\beta = 1$  mV<sup>-1</sup>,  $h_0 = 15$  mV. The time constant of the input potential  $h$  is  $\tau_m = 10$  ms.

$$\mu(t) = \mu_0 + \epsilon \cos(\omega_s t) \quad (4.3)$$

The input potential was initialized as the population activity was at a stationary state with  $h(0) = \mu_0 = h_0$ .

The results are summarize in Fig.4.5. For frequencies higher than 100 Hz, the NRMS becomes high thus the approximation does not hold anymore. On Fig.4.4, one can see that for a frequency of 150 Hz the activity amplitude of the approximation becomes lower than the theoretical one.

To study the population response to more complex signals we used as external

## Chapter 4. General renewal neuron

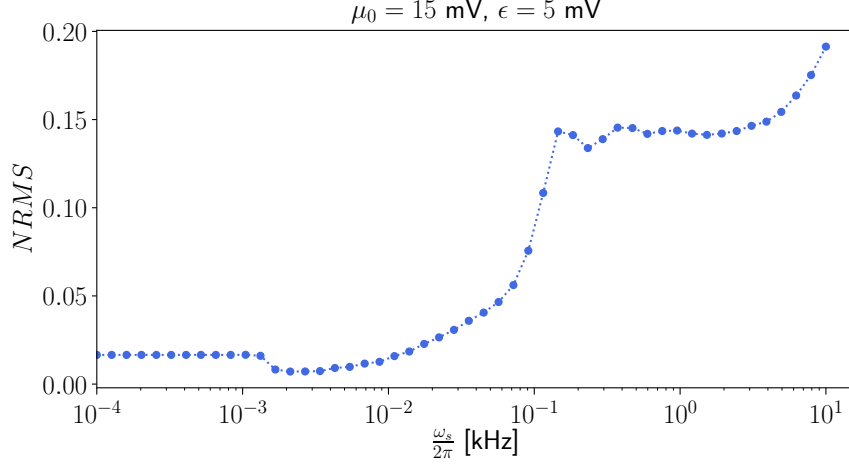


Figure 4.5: NRMS on the response of population of uncoupled Poisson neurons with absolute refractoriness as a function of the angular frequency  $\omega_s$  of the sinusoidal modulation of the external input potential  $\mu(t)$  Eq.(4.3). The parameters of the neurons are  $\nu_{max} = 100$  Hz,  $\Delta = 10$  ms,  $\beta = 1$  mV $^{-1}$ ,  $h_0 = 15$  mV. The time constant of the input potential  $h$  is  $\tau_m = 10$  ms.

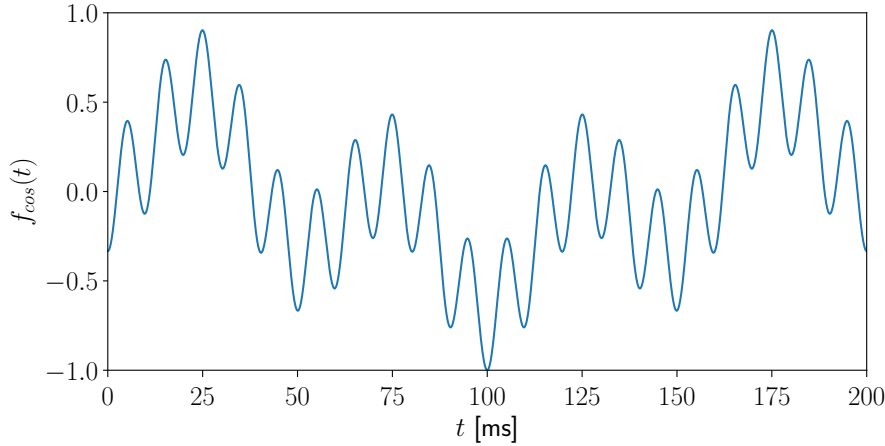


Figure 4.6: Mix of equal amplitude sinusoidal oscillation with different frequencies: 5, 20 and 100 Hz.  $f_{cos}(t) = \frac{1}{3} (\cos(\omega_1 t) - \cos(\omega_2 t) - \cos(\omega_3 t))$

$$\mu(t) = m\mu_0 + \epsilon f_{cos}(t) \quad (4.4)$$

Where  $\mu_0$  and  $\epsilon$  are constant and  $f_{cos}(t)$  is composed of equal-amplitude sinusoidal oscillation with different frequencies.  $f_{cos}(t)$  is represented in Fig.4.6. Fig.4.5 illustrates the response for different  $\mu_0$  and  $\epsilon$ . In the sub threshold  $m\mu_0 \ll h_0$  the activity is shut down due to the sigmoid rate function  $\Phi(h)$ . In the suprathreshold limit  $\mu_0 \gg h_0$  the activity goes toward the value  $\frac{\nu_{max}}{1+\Delta\nu_{max}}$ . Fig.?? illustrates the accuracy of the approximation for the different input. For the different input the NRMS stay below 2.5% which highlights the

#### 4.1. Transient response of the population activity starting with a delta distribution $q(\tau, 0) = \delta(\tau)$

validity of the approximation.

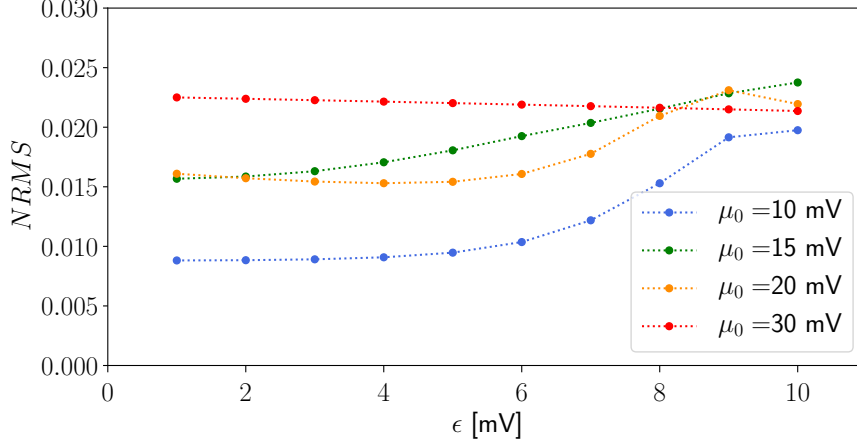


Figure 4.7: NRMS on the response of population of uncoupled Poisson neurons with absolute refractoriness to a fluctuating external input given by Eq.(4.4). For different amplitude  $\epsilon$  of the oscillating function  $f_{cos}(t)$ , for different baseline potential, top:  $\mu_0$ . The parameters of the neurons are  $\nu_{max} = 100$  Hz,  $\Delta = 10$  ms,  $\beta = 1$  mV $^{-1}$ ,  $h_0 = 15$  mV. The time constant of the input potential  $h$  is  $\tau_m = 10$  ms.

Finally we analyzed the response of the population activity to an abrupt change in the external input with a step function, from 15mV to  $\mu(t) = \mu_0$  for  $t > 0$ . The results are shown on Fig.4.8. The response shows an oscillatory behavior, the amplitude of the oscillation increases with  $\mu_0$ , as well as the NRMS (Fig.??).

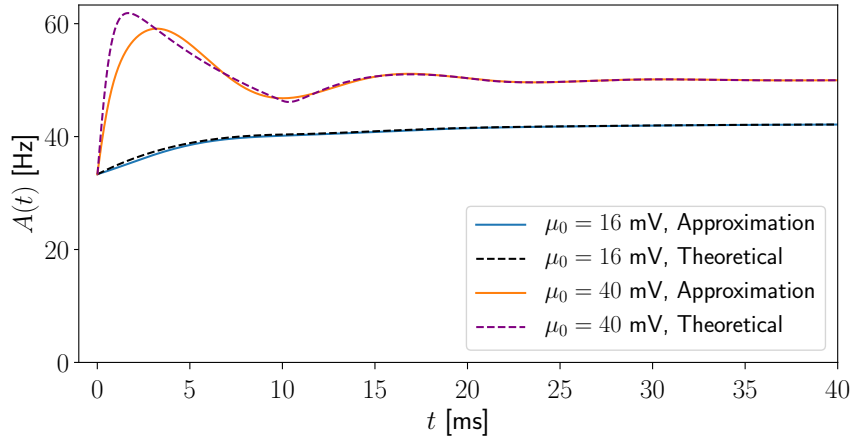


Figure 4.8: Transient response of the population activity receiving as external input a step function  $\mu(t)$ . The parameters of the neurons are  $\nu_{max} = 100$  Hz,  $\Delta = 10$  ms,  $\beta = 1$  mV $^{-1}$ ,  $h_0 = 15$  mV.

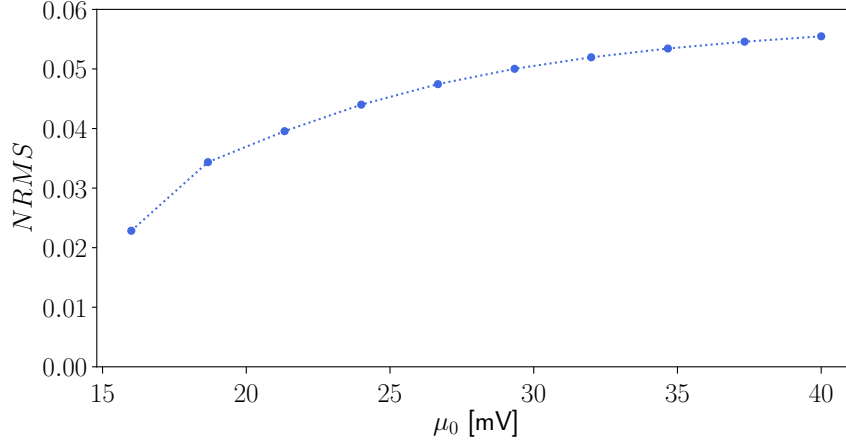


Figure 4.9: NRMS on the response of population of uncoupled Poisson neurons with absolute refractoriness to a abrupt change in the input potential  $\mu(t)$ . for different step from 15 mV to  $\mu_0$ . The parameters of the neurons are  $\nu_{max} = 100$  Hz,  $\Delta = 10$  ms,  $\beta = 1$  mV<sup>-1</sup>,  $h_0 = 15$  mV. The time constant of the input potential  $h$  is  $\tau_m = 10$  ms.

## 4.2 Effect of the refractoriness

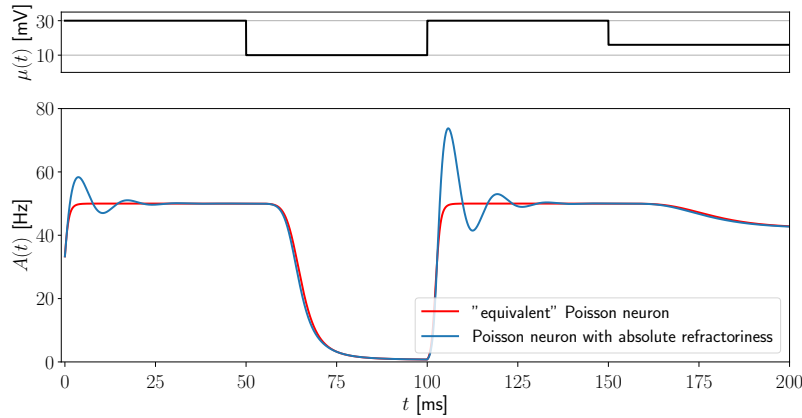


Figure 4.10: Transient response of the population activity (bottom) receiving as external input an step function  $\mu(t)$  (top). The blue line correspond to the response of poisson neuron with absolute refractory period .The parameters of the neurons are  $\nu_{max} = 100$  Hz,  $\Delta = 10$  ms,  $\beta = 1$  mV<sup>-1</sup>,  $h_0 = 15$  mV. The red line correspond to the "equivalent" poputaltion of poisson neuron with firing rate given by Eq.(4.5)

To analyze the effect of the refractory period on the transient response to an external input  $\mu(t)$ , we will compare the activity of a population of Poisson neuron with refractoriness to

an "equivalent" population of Poisson neuron. We know that the mean firing rate  $R$  of a population of Poisson neuron with absolute refractoriness  $\Delta$  is given by

$$R = \frac{\Phi(h)}{1 + \Phi(h)} \quad (4.5)$$

Therefore the "equivalent" population of Poisson neuron is defined as a population of Poisson neuron with firing rate given by Eq.(4.5).

Fig.4.10 illustrates the difference in the response between a population of Poisson neurons with absolute refractoriness (blue line) and an "equivalent" population of Poisson neurons to abrupt change in the input potential  $\mu(t)$ . the external input  $\mu(t)$  was a step function changing every 50 ms (30 mV/10 mV/30 mV/16 mV). Note that the blue line was obtained using the approximation Eq.2.21, with an  $NMRS = 0.02$ . Contrary to the "equivalent" population of Poisson neuron, for the Poisson neurons with absolute refractoriness the response of the population activity to an abrupt change shows an oscillatory behavior in the approach to the new stationary state. The oscillations are absent in a quasi-stationary state and as expected the population becomes the same. When the input is lowered, the response of the population is delayed and doesn't show oscillation. The response of the population of Poisson neurons with absolute refractoriness is a bit faster.



## Chapter 5

# Population dynamics of coupled neurons

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