

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

Noé Gallice

Professors: Wulfram Gerstner and Matthieu Wyart

Supervisor: Tilo Schwalger

Laboratory of Computational Neuroscience, EPFL

April 23, 2018



	<b>Complex system</b>	<b>Simplified model</b>	<b>Math. tractable / comput. efficiency</b>
<i>Neuron:</i>	Biophysical model	Hodgkin-Huxley model	IF model

	Complex system	Simplified model	Math. tractable / comput. efficiency
<i>Neuron:</i>	Biophysical model	Hodgkin-Huxley model	IF model
<i>Neuronal network:</i>	Spiking network	Population density equation	Firing rate model

	Complex system	Simplified model	Math. tractable / comput. efficiency
<i>Neuron:</i>	Biophysical model	Hodgkin-Huxley model	IF model
<i>Neuronal network:</i>	Spiking network	Population density equation	Firing rate model

M. Mattia, P. Del Giudice, *Phys. Review* (2002)

They derived a low dynamics of the collective firing rate from the spectral expansion of the Fokker-Plank equation.

	Complex system	Simplified model	Math. tractable / comput. efficiency
<i>Neuron:</i>	Biophysical model	Hodgkin-Huxley model	IF model
<i>Neuronal network:</i>	Spiking network	Population density equation	Firing rate model

M. Mattia, P. Del Giudice, *Phys. Review* (2002)

They derived a low dynamics of the collective firing rate from the spectral expansion of the Fokker-Plank equation.

**Aim:** Derive a low dimensional dynamics taking into account the slowest modes of the expansion of the refractory density.

# Overview

## 1. Theory

1.1 Refractory density equation

1.2 Eigenfunction expansion of the refractory density

1.3 Definition and property of the adjoint operator  $\mathcal{L}^+$

1.4 Recover the Activity

2.5 Resume of the theoretical derivation

## 2 Spectral expansion for different processes

2.1 Gamma process

2.2 Inverse Gaussian process

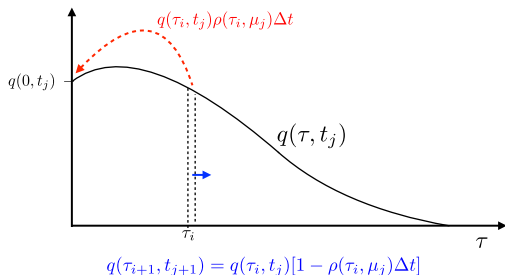
## 4. Summary and Future Work

# 1. Theory

## 1.1 Refractory density equation

In a large homogeneous population of neurons, spikes are generated at time  $t$  according to a hazard function  $\rho(\tau, \mu)$

The state variable  $\tau$  is the age of the neuron.

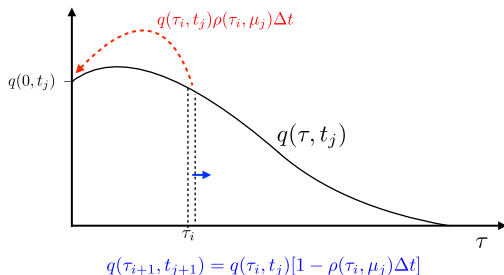


# 1. Theory

## 1.1 Refractory density equation

In a large homogeneous population of neurons, spikes are generated at time  $t$  according to a hazard function  $\rho(\tau, \mu)$

The state variable  $\tau$  is the age of the neuron.

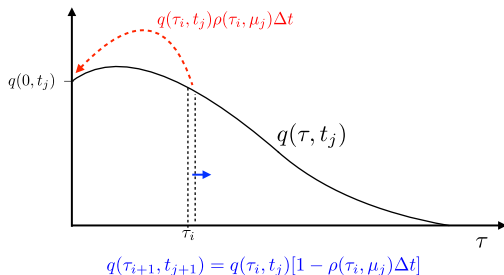


The refractory density  $q(\tau, t)$  obeys the master equation:

$$\partial_t q(\tau, t) + \partial_\tau q(\tau, t) = -\rho(\tau, \mu)q(\tau, t)$$



## 1.1 Refractory density equation



The refractory density  $q(\tau, t)$  obeys the master equation:

$$\partial_t q(\tau, t) + \partial_\tau q(\tau, t) = -\rho(\tau, \mu)q(\tau, t)$$

With boundary conditions:

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

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

## 1.2 Eigenfunction expansion of the refractory density

We consider first the time homogeneous case:  $\rho(\tau, \mu) = \rho(\tau)$

$$\begin{aligned}\partial_t q(\tau, t) &= -\partial_\tau q(\tau, t) - \rho(\tau)q(\tau, t) \\ &= \mathcal{L} q(\tau, t)\end{aligned}$$

with  $\mathcal{L} = -\partial_\tau - \rho(\tau)$

## 1.2 Eigenfunction expansion of the refractory density

$$\partial_t q(\tau, t) = \mathcal{L} q(\tau, t) \quad \text{with} \quad \mathcal{L} = -\partial_\tau - \rho(\tau)$$

We can expand the refractory density as:

$$q(\tau, t) = \sum_n a_n(t) \phi_n(\tau)$$

## 1.2 Eigenfunction expansion of the refractory density

$$\partial_t q(\tau, t) = \mathcal{L} q(\tau, t) \quad \text{with} \quad \mathcal{L} = -\partial_\tau - \rho(\tau)$$

We can expand the refractory density as:

$$q(\tau, t) = \sum_n a_n(t) \phi_n(\tau)$$

where  $\phi_n(\tau)$  are the eigenfunctions of the operator  $\mathcal{L}$

$$\mathcal{L} \phi_n = \lambda_n \phi_n$$

With eigenvalues  $\lambda_n$  and boundary conditions:

$$\begin{aligned} \phi_n(0) &= \int_0^\infty \rho(\tau) \phi_n(\tau) d\tau \\ \phi_n(\infty) &= 0 \end{aligned}$$

## 1.2 Eigenfunction expansion of the refractory density

Solving  $[-\partial_\tau - \rho(\tau)]\phi_n = \lambda_n\phi_n$  we have:

$$\phi_n(\tau) = \phi_n(0) \exp(-\lambda_n\tau - \int_0^\tau \rho(s)ds)$$

## 1.2 Eigenfunction expansion of the refractory density

Solving  $[-\partial_\tau - \rho(\tau)]\phi_n = \lambda_n\phi_n$  we have:

$$\phi_n(\tau) = \phi_n(0) \exp(-\lambda_n\tau - \int_0^\tau \rho(s)ds)$$

Using the boundary condition we find:

$$\phi_n(0) = \int_0^\infty \rho(\tau)\phi_n(0) \exp(-\lambda_n\tau - \int_0^\tau \rho(s)ds)$$

## 1.2 Eigenfunction expansion of the refractory density

Solving  $[-\partial_\tau - \rho(\tau)]\phi_n = \lambda_n\phi_n$  we have:

$$\phi_n(\tau) = \phi_n(0) \exp(-\lambda_n\tau - \int_0^\tau \rho(s)ds)$$

Using the boundary condition we find:

$$\phi_n(0) = \int_0^\infty \rho(\tau)\phi_n(0) \exp(-\lambda_n\tau - \int_0^\tau \rho(s)ds)$$

which can be written as:

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

with ISI density  $P(\tau) = \rho(\tau) \exp(-\int_0^\tau \rho(s)ds)$

## 1.2 Eigenfunction expansion of the refractory density

Solving  $[-\partial_\tau - \rho(\tau)]\phi_n = \lambda_n\phi_n$  we have:

$$\phi_n(\tau) = \phi_n(0) \exp(-\lambda_n\tau - \int_0^\tau \rho(s)ds)$$

Using the boundary condition we find:

$$\phi_n(0) = \int_0^\infty \rho(\tau)\phi_n(0) \exp(-\lambda_n\tau - \int_0^\tau \rho(s)ds)$$

which can be written as:

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

with ISI density  $P(\tau) = \rho(\tau) \exp(-\int_0^\tau \rho(s)ds)$

$\Rightarrow \lambda_0 = 0$  fulfilled the condition, it corresponds to the stationary density



### 1.3 Definition and property of the adjoint operator $\mathcal{L}^+$

To recover the activity we will need the eigenfunctions  $\psi_n$  of the adjoint operator  $\mathcal{L}^+$ :

$$\mathcal{L}^+ \psi_n = \lambda_n \psi_n$$

### 1.3 Definition and property of the adjoint operator $\mathcal{L}^+$

To recover the activity we will need the eigenfunctions  $\psi_n$  of the adjoint operator  $\mathcal{L}^+$ :

$$\mathcal{L}^+ \psi_n = \lambda_n \psi_n$$

Defining the inner product :  $(\psi, \phi) = \int_0^\infty \psi(\tau) \phi(\tau) d\tau$

and using the property:  $(\psi, \mathcal{L}\phi) = (\mathcal{L}^+\psi, \phi)$

### 1.3 Definition and property of the adjoint operator $\mathcal{L}^+$

To recover the activity we will need the eigenfunctions  $\psi_n$  of the adjoint operator  $\mathcal{L}^+$ :

$$\mathcal{L}^+ \psi_n = \lambda_n \psi_n$$

Defining the inner product :  $(\psi, \phi) = \int_0^\infty \psi(\tau) \phi(\tau) d\tau$

and using the property:  $(\psi, \mathcal{L}\phi) = (\mathcal{L}^+\psi, \phi)$

One can obtained the adjoint operator  $\mathcal{L}^+$ :

$$\mathcal{L}^+ \psi(\tau) = [\partial_\tau - \rho(\tau)]\psi(\tau) + \psi(0)\rho(\tau)$$

### 1.3 Definition and property of the adjoint operator $\mathcal{L}^+$

To recover the activity we will need the eigenfunctions  $\psi_n$  of the adjoint operator  $\mathcal{L}^+$ :

$$\mathcal{L}^+ \psi_n = \lambda_n \psi_n$$

Defining the inner product :  $(\psi, \phi) = \int_0^\infty \psi(\tau) \phi(\tau) d\tau$

and using the property:  $(\psi, \mathcal{L}\phi) = (\mathcal{L}^+\psi, \phi)$

One can obtained the adjoint operator  $\mathcal{L}^+$ :

$$\mathcal{L}^+ \psi(\tau) = [\partial_\tau - \rho(\tau)]\psi(\tau) + \psi(0)\rho(\tau)$$

$\psi_n, \phi_n$  form a biorthonormal basis:

$$(\psi_i, \phi_j) = \delta_{ij}$$

## 1.4 Recover the Activity

The activity is given by:

$$A(t) = q(t, 0) = \sum_n a_n(t) \phi_n(0)$$

## 1.4 Recover the Activity

The activity is given by:

$$A(t) = q(t, 0) = \sum_n a_n(t) \phi_n(0)$$

We derived  $a_n(t)$  by projecting  $q(\tau, t)$  on the eigenbasis:

$$a_n(t) = (\psi_n, q)$$

## 1.4 Recover the Activity

The activity is given by:

$$A(t) = q(t, 0) = \sum_n a_n(t) \phi_n(0)$$

We derived  $a_n(t)$  by projecting  $q(\tau, t)$  on the eigenbasis:

$$a_n(t) = (\psi_n, q)$$

From which we obtained:

$$\begin{aligned} \frac{da_n}{dt} &= (\psi_n, \partial_t q) \\ &= (\psi_n, \mathcal{L}q) \\ &= (\mathcal{L}^+ \psi_n, q) \\ &= \lambda_n a_n \end{aligned}$$

$$a_n(t) = a_n(0) \exp(\lambda_n t)$$

## 1.4 Recover the Activity

The activity is given by:

$$A(t) = q(t, 0) = \sum_n a_n(t) \phi_n(0)$$

Keeping the two first modes, one can obtain a second order differential equation for the firing rate :

$$\ddot{A}(t) = [2\text{Re}(\frac{1}{\lambda_1})\dot{A}(t) - A(t) + A_\infty]|\lambda_1|^2$$

M. Mattia, *Low-dimensional firing rate dynamic of spiking neuron networks* (2016)



## 2.5 Resume of the theoretical derivation

We can expand the refractory density as:

$$q(\tau, t) = \sum_n a_n(t) \phi_n(\tau)$$

## 2.5 Resume of the theoretical derivation

We can expand the refractory density as:

$$q(\tau, t) = \sum_n a_n(t) \phi_n(\tau)$$

from this expansion we found a condition for the eigenvalues  $\lambda_n$ :

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

## 2.5 Resume of the theoretical derivation

We can expand the refractory density as:

$$q(\tau, t) = \sum_n a_n(t) \phi_n(\tau)$$

from this expansion we found a condition for the eigenvalues  $\lambda_n$ :

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

Knowing the eigenvalues and the hazard function we can analytically define the eigenfunctions  $\phi_n$  and  $\psi_n$ .

## 2.5 Resume of the theoretical derivation

We can expand the refractory density as:

$$q(\tau, t) = \sum_n a_n(t) \phi_n(\tau)$$

from this expansion we found a condition for the eigenvalues  $\lambda_n$ :

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

Knowing the eigenvalues and the hazard function we can analytically define the eigenfunctions  $\phi_n$  and  $\psi_n$ .

Thanks to those eigenfunctions we can recover the activity:

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

# Overview

## 1. Theory

1.1 Refractory density equation

1.2 Eigenfunction expansion of the refractory density

1.3 Definition and property of the adjoint operator  $\mathcal{L}^+$

1.4 Recover the Activity

2.5 Resume of the theoretical derivation

## 2 Spectral expansion for different processes

2.1 Gamma process

2.2 Inverse Gaussian process

## 4. Summary and Future Work

## 2 Spectral expansion for different processes

### 2.1 Gamma process

The ISI distribution is given by:

$$P(\tau) = \frac{\beta^\gamma}{(\gamma-1)!} \tau^{\gamma-1} e^{-\beta\tau} \text{ for integer } \gamma \text{ and } \beta > 0.$$

## 2 Spectral expansion for different processes

### 2.1 Gamma process

The ISI distribution is given by:

$$P(\tau) = \frac{\beta^\gamma}{(\gamma-1)!} \tau^{\gamma-1} e^{-\beta\tau} \text{ for integer } \gamma \text{ and } \beta > 0.$$

The Laplace transform can be derived analytically:

$$\bar{P}(\lambda) = \left(\frac{\beta}{\beta+\lambda}\right)^\gamma$$

## 2 Spectral expansion for different processes

### 2.1 Gamma process

The ISI distribution is given by:

$$P(\tau) = \frac{\beta^\gamma}{(\gamma-1)!} \tau^{\gamma-1} e^{-\beta\tau} \text{ for integer } \gamma \text{ and } \beta > 0.$$

The Laplace transform can be derived analytically:

$$\bar{P}(\lambda) = \left(\frac{\beta}{\beta+\lambda}\right)^\gamma$$

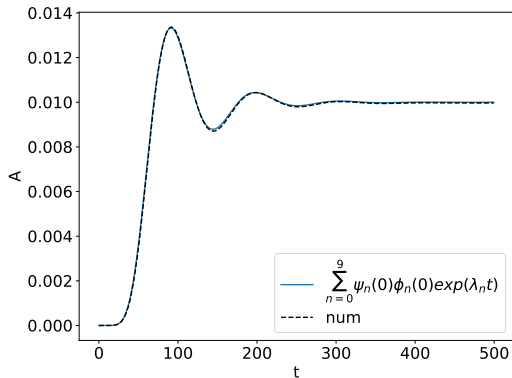
Solving  $\bar{P}(\lambda_n) = 1$  we find:

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



## 2.1 Gamma process

Initial condition  $q(\tau, 0) = \delta(\tau) \rightarrow A(t) = \sum_{n=0}^{\gamma-1} \psi_n(0)\phi_n(0)\exp(\lambda_n t)$



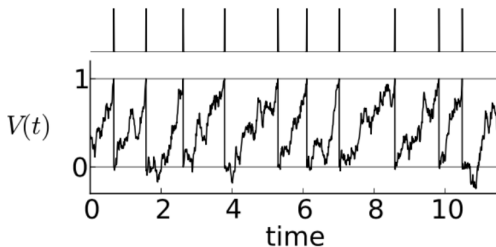
$$\beta = 0.1, \gamma = 10$$

## 2.2 Inverse Gaussian process

The perfect integrate fire model driven by a Gaussian white noise:

$$\dot{V} = \mu + \sqrt{2D}\xi(t) \quad \langle \xi(t)\xi(s) \rangle = \delta(t-s)$$

if  $V = V_{th}$  :  $V \rightarrow V_r$



$$\mu = 1, D = 0.125 \text{ and } V_{th} = 1$$

figure: T. Schwalger, *The interspike-interval statistics of non-renewal neuron models* (2013)

## 2.2 Inverse Gaussian process

The ISI distribution is given by:

$$P(\tau) = \frac{V_{th}}{\sqrt{4\pi D\tau^3}} \exp\left(-\frac{(\mu\tau - V_{th})^2}{4D\tau}\right)$$

## 2.2 Inverse Gaussian process

The ISI distribution is given by:

$$P(\tau) = \frac{V_{th}}{\sqrt{4\pi D\tau^3}} \exp\left(-\frac{(\mu\tau - V_{th})^2}{4D\tau}\right)$$

The Laplace transform can be derived analytically:

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

## 2.2 Inverse Gaussian process

The ISI distribution is given by:

$$P(\tau) = \frac{V_{th}}{\sqrt{4\pi D\tau^3}} \exp(-\frac{(\mu\tau - V_{th})^2}{4D\tau})$$

The Laplace transform can be derived analytically:

$$\bar{P}(\lambda) = \exp(\frac{\mu V_{th}}{2D} [1 - \sqrt{1 + \frac{4D\lambda}{\mu^2}}])$$

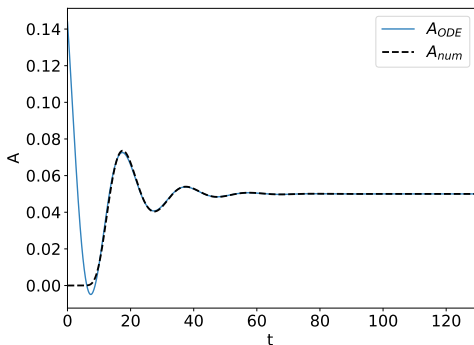
Solving  $\bar{P}(\lambda_n) = 1$  we find:

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

## 2.2 Inverse Gaussian process

Recover the activity solving the second order differential equation:

$$\ddot{A}(t) = [2\text{Re}(\frac{1}{\lambda_1})\dot{A}(t) - A(t) + A_\infty]|\lambda_1|^2$$



$$\mu = 0.05, D = 0.002, V_{th} = 1$$

## 4. Summary and Future Work

- ▶ We made an expansion of the refractory density for time homogeneous hazard rates  $\rho(\tau, \mu) = \rho(\tau)$

## 4. Summary and Future Work

- ▶ We made an expansion of the refractory density for time homogeneous hazard rates  $\rho(\tau, \mu) = \rho(\tau)$
- ▶ We obtained a low dimensional dynamics for the firing rate in the case of uncoupled neuron



## 4. Summary and Future Work

- ▶ We made an expansion of the refractory density for time homogeneous hazard rates  $\rho(\tau, \mu) = \rho(\tau)$
- ▶ We obtained a low dimensional dynamics for the firing rate in the case of uncoupled neuron

Future work:

- ▶ Derive a low-dimensional ordinary differential equation for the firing rate in the case of a coupled network.

$$\frac{da_n}{dt} = \lambda_n a_n + \frac{d\mu}{dt} \left( \frac{\partial \psi_n}{\partial \mu}, q \right)$$

## 4. Summary and Future Work

- ▶ We made an expansion of the refractory density for time homogeneous hazard rates  $\rho(\tau, \mu) = \rho(\tau)$
- ▶ We obtained a low dimensional dynamics for the firing rate in the case of uncoupled neuron

Future work:

- ▶ Derive a low-dimensional ordinary differential equation for the firing rate in the case of a coupled network.

$$\frac{da_n}{dt} = \lambda_n a_n + \frac{d\mu}{dt} \left( \frac{\partial \psi_n}{\partial \mu}, q \right)$$

- ▶ Find a efficient method to approximate the first eigenvalue for any hazard rate  $\rho(\tau, \mu)$

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

Thanks for your attention

one can show that for different eigenvalues, the eigenfunctions  $\psi_i$  and  $\phi_j$  are orthogonal:

$$\begin{aligned}\lambda_j(\psi_i, \phi_j) &= (\psi_i, \mathcal{L}\phi_j) \\ &= (\mathcal{L}^+\psi_i, \phi_j) \\ &= \lambda_i(\psi_i, \phi_j)\end{aligned}$$

## 2.2 Definition and property of the adjoint operator $\mathcal{L}^+$

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

with  $\mathcal{L}^+ \psi(\tau) = [\partial_\tau - \rho(\tau)] \psi(\tau) + \psi(0) \rho(\tau)$

## 2.2 Definition and property of the adjoint operator $\mathcal{L}^+$

$$\begin{aligned}\mathcal{L}^+ \psi_n(\tau) &= [\partial_\tau - \rho(\tau)]\psi_n(\tau) + \psi_n(0)\rho(\tau) \\ &= \lambda_n \psi_n(\tau)\end{aligned}$$

The solution of this equation is:

$$\psi_n(\tau) = \psi_n(0) \exp(\lambda_n \tau) S^{-1}(\tau) \left[ 1 - \int_0^\tau P(x) \exp(-\lambda_n x) dx \right]$$

$$1 = \int_0^\infty \phi_n(0)\psi_n(0) \left[ 1 - \int_0^\tau P(x) \exp(-\lambda_n x) dx \right] d\tau$$

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

## Second order differential equation for the firing rate for uncoupled neurons

M. Mattia, *Low-dimensional firing rate dynamic of spiking neuron networks* (2016)

$$\ddot{A}(t) = [2\text{Re}(\frac{1}{\lambda_1})\dot{A}(t) - A(t) + A_\infty]|\lambda_1|^2$$