Low-dimensional population dynamics of spiking neurons via eigenfunction expansion

Noé Gallice

Professor: Wulfram Gerstner   Supervisor: Tilo Schwalger

Laboratory of Computational Neuroscience, EPFL

April 12, 2018

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

	Complex system	**Simplified model**	**Math. tractable / comput. efficiency**
Neuron:	Biophysical model	Hodgkin-Huxley model	IF model

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

	Complex system	**Simplified model**	**Math. tractable / comput. efficiency**
Neuron:	Biophysical model	Hodgkin-Huxley model	IF model
Neuronal network:	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**
Neuron:	Biophysical model	Hodgkin-Huxley model	IF model
Neuronal network:	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. Refractory density $q(\tau, t)$
   1.1 Refractory density equation
   1.2 The refractory density for a LIF neuron
2. Theoretical derivation
   2.1 Eigenfunction expansion of the refractory density
   2.2 Definition and property of the adjoint operator $\mathcal{L}^+$
   2.3 Recover the Activity
   2.4 Resume of the theoretical derivation
3. Spectral expansion for different processes
   3.1 LIF neuron with exponential link function
   3.2 Inverse Gaussian process
   3.3 Gamma process
4. Summary and Future Work

1. Refractory density $q(\tau, t)$

1.1 Refractory density equation

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

1. Refractory density $q(\tau, t)$

1.1 Refractory density equation

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

The state variable τ is the age of the neuron.

1. Refractory density $q(\tau, t)$

1.1 Refractory density equation

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

The state variable τ is the age of the neuron.

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

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

1. Refractory density $q(\tau, t)$

1.1 Refractory density equation

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

The state variable τ is the age of the neuron.

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

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

With boundary conditions:

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

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

The hazard function for a LIF neuron with exponential link function is:

$$\rho(\tau, t) = C \exp(\tfrac{u(\tau,t)-V_{th}}{\Delta})$$

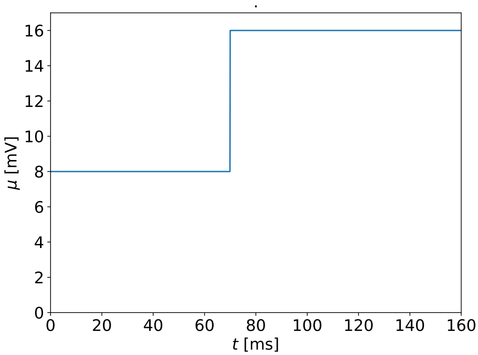
with membrane potential:

$$u(\tau, t) = V_r e^{-\tau/\tau_m} + \tfrac{1}{\tau_m} \int_0^\tau e^{-s/\tau_m} \mu(t-s))ds$$

where $\mu(t)$ is a time dependent input current, V_r is a reset potential and Δ sets the sharpness of the threshold at V_{th}.

1.2 The refractory density for a LIF neuron

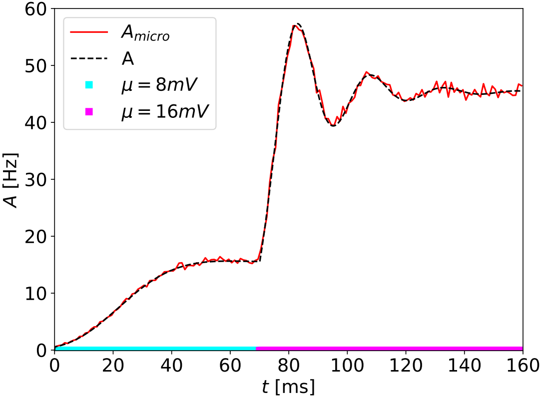
The refractory density for a step current input μ:



$V_{th} = 15$ mV, $V_r = 0$ mV, $\Delta = 2$ mV, $C = 1000$ Hz, $\tau_m = 20$ ms
$dt = 0.1$ ms, $N_{micro} = 10^5$

1.2 The refractory density for a LIF neuron

The activity is defined as: $A(t) = q(0,t) = \int_0^\infty \rho(\tau,t) q(\tau,t) d\tau$



$V_{th} = 15$mV, $V_r = 0$ mV, $\Delta = 2$ mV, $C = 1000$ Hz, $\tau_m = 20$ ms
$dt = 0.1$ ms, $N_{micro} = 10^5$

Overview

2. Theoretical derivation

2.1 Eigenfunction expansion of the refractory density

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

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

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

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

We can expand the refractory density as:

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

2. Theoretical derivation

2.1 Eigenfunction expansion of the refractory density

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

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

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

$$\mathcal{L} = -\partial_\tau - \rho(\tau) \qquad \mathcal{L}\phi_n = \lambda_n \phi_n$$

With eigenvalues λ_n and boundary conditions:

$$\phi_n(0) = \int_0^\infty \rho(\tau) \phi_n(\tau) d\tau$$

$$\phi_n(\infty) = 0$$

2. Eigenfunction expansion of the refractory density

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

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

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:

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

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

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

$\Rightarrow \lambda_0 = 0$ fulfilled the condition, The eigenvalues must be complex, and the real part of λ_n cannot be positive.

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

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

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

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

To recover the activity we will need the eigenfunctions ψ_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: $(\psi, \mathcal{L}\phi) = (\mathcal{L}^+\psi, \phi)$

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

To recover the activity we will need the eigenfunctions ψ_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 $\mathcal{L}^+$:

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

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

To recover the activity we will need the eigenfunctions ψ_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 $\mathcal{L}^+$:

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

ψ_n, ϕ_n form a biorthonormal basis:

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

2.3 Recover the Activity

The activity is given by:

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

2.3 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:

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

2.3 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 $\frac{da_n}{dt} = \lambda_n a_n$ and:

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

2.3 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 $\frac{da_n}{dt} = \lambda_n a_n$ and:

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

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

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

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

2.4 Resume of the theoretical derivation

We can expand the refractory density as:

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

2.4 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 λ_n:

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

2.4 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 λ_n:

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

Knowing the eigenvalues and the hazard function we can analytically define the eigenfunctions ϕ_n and ψ_n.

2.4 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 λ_n:

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

Knowing the eigenvalues and the hazard function we can analytically define the eigenfunctions ϕ_n and ψ_n.

Thanks to those eigenfunctions we can recover the activity:

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

Overview

3. Spectral expansion for different processes

3.1 LIF neuron with exponential link function

In the case of the LIF neuron with exponential link function we can not find λ_n from the condition:

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

3. Spectral expansion for different processes

3.1 LIF neuron with exponential link function

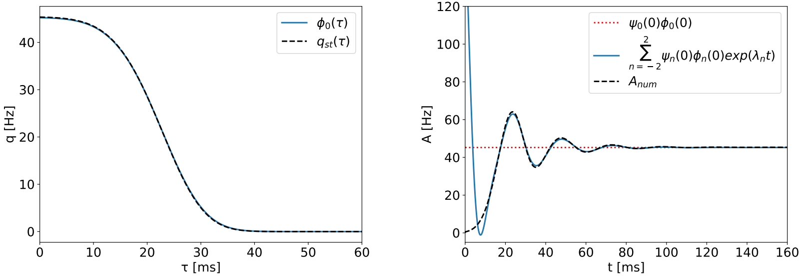
In the case of the LIF neuron with exponential link function we can not find λ_n from the condition:

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

We can express the operator $\mathcal{L}$ in matrix form.
And recover the activity computing the eigenvalues and eigenvectors of this matrix.

3.1 LIF neuron with exponential link function

$$\lambda_0 = 0 \Rightarrow \partial_t q(\tau, t) = 0 \qquad A(t) = \sum_n \psi_n(0)\phi_n(0)\exp(\lambda_n t)$$



$$\mu = 16 \text{ mV}, V_{th} = 15 \text{ mV}, V_r = 0 \text{ mV}, \Delta = 2 \text{ mV}, C = 1000 \text{ Hz},$$
$$\tau_m = 20 \text{ ms } dt = 0.1 \text{ ms}$$

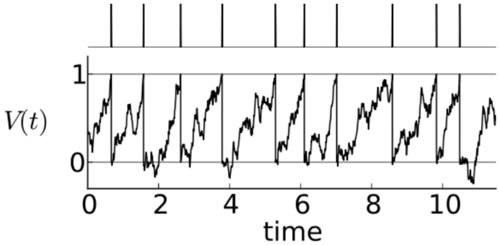
3.2 Spectral expansion for different processes

3.1 Inverse Gaussian process

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

$$\dot{V} = \mu + \sqrt{2D}\xi(t) \qquad\qquad < \xi(t)\xi(s) >= \delta(t-s)$$

if $V = V_{th}: \; V \to V_r$



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

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

3.2 Inverse Gaussian process

The ISI distribution is given by:

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

3.2 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:

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

3.2 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:

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

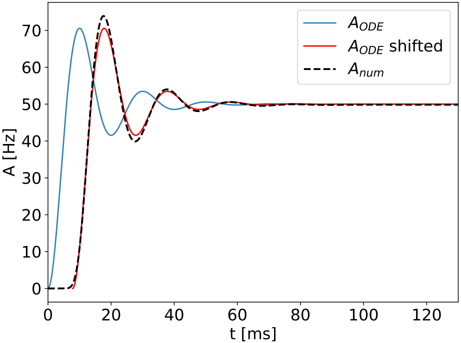
Solving $\bar{P}(\lambda_n) = 1$ we find:

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

3.2 Inverse Gaussian process

Recover the activity solving the second order differential equation:

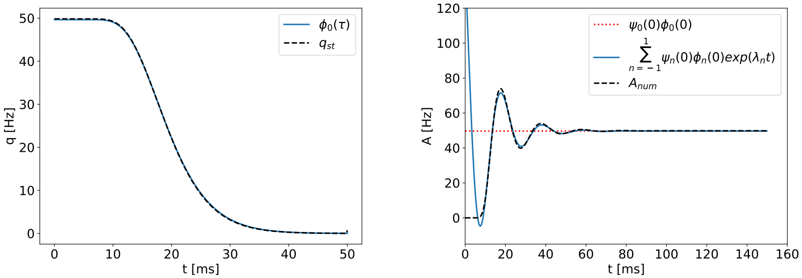
$$\ddot{A}(t) = [2Re(\frac{1}{\lambda_1})\dot{A}(t) - A(t) + A_\infty]|\lambda_1|$$



$\mu = 50$ mV, $D = 7.5$, $V_{th} = 1$

3.2 Inverse Gaussian process

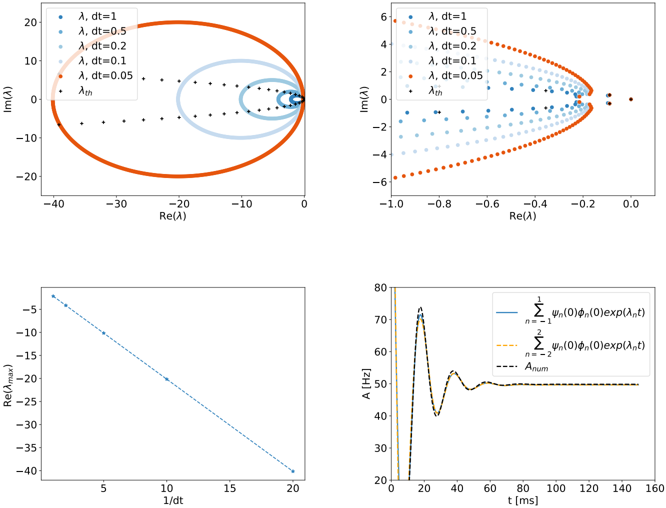
$$\lambda_0 = 0 \Rightarrow \partial_t q(\tau, t) = 0 \qquad A(t) = \sum_n \psi_n(0)\phi_n(0)\exp(\lambda_n t)$$



$$\mu = 50 \text{ mV}, D = 7.5,\ V_{th} = 1$$

3.2 Inverse Gaussian process

Comparison of the theoretical spectrum and the eigenvalues obtained from the matrix form of $\mathcal{L}$



3.3 Gamma process

The ISI distribution is given by:

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

3.3 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:

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

3.3 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:

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

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

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

4. Summary and Future Work

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

4. Summary and Future Work

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

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

4. Summary and Future Work

- We made an expansion of the refractory density for time homogeneous hazard rates $\rho(t, \tau) = \rho(\tau)$
- 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.
$$\frac{da_n}{dt} = \lambda_n a_n + \frac{d\nu}{dt}\left(\frac{\partial \psi_n}{\partial \nu}, q\right)$$
- Understand if there is an other constraint on the eigenvalues or if it's a numerical error.

Thanks for your attention

one can show that for different eigenvalues, the eigenfunctions ψ_i and ϕ_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:

$$\begin{aligned}\psi_n(\tau) =& \psi_n(0)\exp(\lambda_n\tau + \int_0^\tau \rho(s)ds)\\ &- \psi_n(0)\int_0^\tau \rho(x)\exp\left[\lambda_n(\tau - x) + \int_0^{\tau - x} \rho(s)ds\right]dx\end{aligned}$$

Second order differential equation for the firing rate for uncoupled neurons

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

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