Eigenfunction expansion of the refractory density

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1 Renewal process

Renewal processes keep memory of the last event, las firing time t^f. For those processes the spikes are generated according to a stochastic intensity called the hazard rate

$$\rho(t|\hat{t}) = \rho(\tau) \tag{1}$$

which depends on the age of the neuron τ, i.e the time since the last spike $\tau = t - \hat{\tau}$.

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, i.e the Probability

$$P(\tau) = P(t^f + \tau | t^f) \tag{2}$$

The ISI distribution satisfy

$$\int_0^\infty P(\tau) d\tau = 1 \tag{3}$$

and allows to compute the moment:

$$< \tau^n >= \int_0^\infty \tau^n P(\tau) d\tau \tag{4}$$

1.1 Survivor function

$$\tag{5}$$

Master equation

$$\frac{\partial q}{\partial t} = -\frac{\partial q}{\partial \tau} - \rho(\tau) q \tag{6}$$

boundary condition

$$q(0,t) = \int_0^\infty \rho(\tau) q(\tau, t) d\tau = A(t) \tag{7}$$

$$q(\infty, t) = 0 \tag{8}$$

q is normalised

$$q(0,t) = \int_0^\infty q(\tau, t) d\tau \tag{9}$$

We can expand the refractory density

$$q(\tau, t) = \sum_n a_n(t)\phi_n(\tau) \tag{10}$$

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

$$\mathcal{L}\phi_n = \lambda_n \phi_n \tag{11}$$

if the eigenvalues λ_n are complex, the complex conjugate of an eigenvalue is also an eigenvalue beacause $\mathcal{L}$ is a real operator

Because $\mathcal{L}$ cannot be generally brought to an Hermitian form we also need the eigenfunction ψ_n of the adjoint operator $\mathcal{L}^+$

$$\mathcal{L}^+\psi_n = \lambda_n^+ \psi_n \tag{12}$$

Defining the inner product one can show that the eigenvalues of eq.(11) and eq.(12) are the same:

$$(\psi, \phi) = \int_0^\infty \psi(\tau)\phi(\tau)d\tau \tag{13}$$

$$\begin{aligned}
\lambda_n(\psi_n, \phi_n) &= \int_0^\infty \psi(\tau)\mathcal{L}\phi(\tau)d\tau \\
&= (\psi_n, \mathcal{L}\phi_n) \\
&= (\mathcal{L}^+\psi_n, \phi_n) \\
&= \int_0^\infty \mathcal{L}^+\psi_n(\tau)\phi_n(\tau)d\tau \\
&= \lambda_n^+(\psi_n, \phi_n)
\end{aligned} \tag{14}$$

Eq.(14) implies that $\lambda_n = \lambda_n^+$ and

$$\mathcal{L}^+\psi_n = \lambda_n \psi_n \tag{15}$$

For different eigenvalues, the eigenfunctions ψ_i and phi_j are orthogonal:

$$\begin{aligned}
\lambda_j(\psi_i, \phi_j) &= (\psi_i, \mathcal{L}\phi_j) \\
&= (\mathcal{L}^+\psi_i, \phi_j) \\
&= \lambda_i(\psi_i, \phi_j)
\end{aligned} \tag{16}$$

We may thus normalize the functions according to

$$(\psi_i, \phi_j) = \delta_{ij} \tag{17}$$

If a stationary solution of Matser equation exists we have:

$$\lambda_0 = 0\,, \qquad \phi_0(\tau) = q_{st}(\tau)\,, \qquad \psi_0(\tau) = 1 \tag{18}$$

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

$$\begin{aligned}
(\psi, \mathcal{L}\phi) &= \int_0^\infty \psi(\tau)\mathcal{L}\phi(\tau)d\tau \\
&= \int_0^\infty \psi(\tau)[-\partial_\tau - \rho(\tau)]\phi(\tau)d\tau \\
&= -[\psi(\tau)\phi(\tau)]_0^\infty + \int_0^\infty \partial_\tau\psi(\tau)\phi(\tau)d\tau - \int_0^\infty \rho(\tau)\psi(\tau)\phi(\tau)d\tau \\
&= \psi(0)\phi(0) + \int_0^\infty [\partial_\tau - \rho(\tau)]\psi(\tau)\phi(\tau)d\tau \\
&= \int_0^\infty \psi(0)\rho(\tau)\phi(\tau)d\tau + \int_0^\infty [\partial_\tau - \rho(\tau)]\psi(\tau)\phi(\tau)d\tau \\
&= \int_0^\infty \{[\partial_\tau - \rho(\tau)]\psi(\tau) + \psi(0)\rho(\tau)\}\phi(\tau)d\tau \\
&= (\mathcal{L}^+\psi, \phi)
\end{aligned} \tag{19}$$

with

$$\mathcal{L}^+\psi(\tau) = [\partial_\tau - \rho(\tau)]\psi(\tau) + \psi(0)\rho(\tau) \tag{20}$$

From eq.(17) and eq.(10) we deduce that:

$$a_n = (\psi_n, q) \tag{21}$$

Taking the derivative of a_n with respect to time we have:

$$\begin{aligned}
\frac{da_n}{dt} &= (\psi_n, \partial_t q) \\
&= (\psi_n, \mathcal{L}q) \\
&= (\mathcal{L}^+\psi_n, q) \\
&= \lambda_n(\psi_n, q) \\
&= \lambda_n a_n
\end{aligned} \tag{22}$$

The solution of eq.(22) with initial refractory density $q(0, \tau)$ is:

$$
\begin{aligned}
a_n(t) =& a_n(0)\exp(\lambda_n t) && (23)\\
with \quad a_n(0) =& \int_0^\infty \psi_n(\tau) q(0,\tau) d\tau && (24)
\end{aligned}
$$

The solution eq.(11) and eq.(15) with initial refractory density $q(0,\tau)$ is:

$$
\begin{aligned}
\phi_n(\tau) &= \phi_n(0)\exp(-\lambda_n \tau - \int_0^\tau \rho(s)ds)\\
&= \phi_n(0)\exp(-\lambda_n \tau) S(\tau) \qquad (25)
\end{aligned}
$$

$$
\begin{aligned}
\psi_n(\tau) &= \psi_n(0)\exp\big(\lambda_n \tau + \int_0^\tau \rho(s)ds\big)\big[1 - \int_0^\tau \rho(x)\exp\big(-\lambda_n x - \int_0^x \rho(s)ds\big)dx\big]\\
&= \psi_n(0)\exp(\lambda_n \tau) S^{-1}(\tau)\big[1 - \int_0^\tau P(x)\exp\big(-\lambda_n x) dx\big] \qquad (26)
\end{aligned}
$$

Inserting eq.(25) et eq.(26) in eq.17 we have:

$$
\begin{aligned}
1 =& \int_0^\infty \phi_n(0)\psi_n(0)\big[1 - \int_0^\tau P(x)\exp\big(-\lambda_n x)dx\big]d\tau && (27)\\
\phi_n(0)\psi_n(0) =& \frac{1}{\int_0^\infty \big[1 - \int_0^\tau P(x)\exp\big(-\lambda_n x)dx\big]d\tau} && (28)
\end{aligned}
$$

In particular for $n = 0$, $\lambda_0 = 0$ and $\psi_0(0) = 1$, so we recover the relation:

$$
\phi_0(0) = \frac{1}{\int_0^\infty S(\tau)d\tau} \qquad (29)
$$

Inserting eq.(25) for $n = 0$ in eq.17 we have:

$$
\begin{aligned}
\int_0^\infty \phi_0(0)S(\tau) =& 1 && (30)\\
\phi_0(0) =& \frac{1}{\int_0^\infty S(\tau)} && (31)
\end{aligned}
$$

$$
A(t) = \sum_n a_n(t)\phi_n(0) \qquad (32)
$$

keeping only the first mode we have:

$$A(t) = \phi_0(0) + a_1(t)\phi_1(0) + a_{-1}(t)\phi_{-1}(0) \tag{33}$$

Where the term $a_{-1}(t)\phi_{-1}(0)$ is the complex conjugate of the term $a_1(t)\phi_1(0)$.

$$\begin{aligned}
\dot{a}_n &= (\psi_n, \partial_t q) + \dot{\mu}\,(\partial_\mu \psi_n, q) \\
&= (\psi_n, \mathcal{L}q) + \dot{\mu}\,\psi_n, \sum_m a_m \phi_m \\
&= (\mathcal{L}^+ \psi_n, q) + \dot{\mu} \sum_m a_m\,(\partial_\mu\,\psi_n, \phi_m) \\
&= \lambda_n(\psi_n, q) + \dot{\mu} \sum_m c_{nm} a_m \\
&= \lambda_n a_n + \dot{\mu} \sum_m c_{nm} a_m
\end{aligned} \tag{34}$$

Where we define $c_{nm} = \ (\partial_\mu\,\psi_n, \phi_m)$

So we can define

$$\mathcal{A}(t) = \phi_0(0) + 2a_1(t)\phi_1(0) \tag{35}$$

such that

$$A(t) = \Re(\mathcal{A}(t)) \tag{36}$$

$$\dot{\mathcal{A}}(t) = \dot{\mu}\partial_\mu \phi_0(0) + 2\dot{a}_1(t)\dot{\mu}\partial_\mu \phi_1(0) \tag{37}$$

with

$$\begin{aligned}
\dot{a}_1 =& \lambda_1 a_1 + \dot{\mu}(c_{10} + (c_{10} + c_{11}a_1 + c_{1-1}a_{-1}) \\
=& \lambda_1 a_1 + \dot{\mu}(c_{10} + (c_{10} + c_{11}a_1 + c_{-11}a_1)
\end{aligned} \tag{38}$$

$$\dot{\mathcal{A}}(t) = [\lambda_1 + \dot{\mu}(\partial_\mu \log(\phi_1(0)) + c_{11} + c_{-11})][\mathcal{A}(t) - \phi_0(0)] + \dot{\mu}[c_{10} + \partial_\mu \phi_0(0)] \tag{39}$$

Writing $\mathcal{A}(t) = A(t) + ßB(t)$ we obtained two non linear differential equation

$$\dot{A}(t) = f(t)(A(t) - \phi_0(0)) - g(t)B(t) + h(t) \tag{40}$$
$$\dot{B}(t) = f(t)B(t) + g(t)(A(t) - \phi_0(0)) + m(t) \tag{41}$$
$$\tag{42}$$

with

$$
\begin{aligned}
f(t) =& \Re[\lambda_1 + \dot{\mu}(\partial_\mu \log(\phi_1(0)) + c_{11} + c_{-11})] && (43)\\
g(t) =& \Im[\lambda_1 + \dot{\mu}(\partial_\mu \log(\phi_1(0)) + c_{11} + c_{-11})] && (44)\\
h(t) =& \Re[\dot{\mu}(c_{10} + \partial_\mu \phi_0(0))] && (45)\\
m(t) =& \Im[\dot{\mu}(c_{10} + \partial_\mu \phi_0(0))] && (46)
\end{aligned}
$$

2 poisson proccess with absolute refarctoriness

$$\rho(\tau) = \nu\, \Theta(\tau - \Delta) \tag{47}$$

$$P(\tau) = \nu \Theta(\tau - \Delta) \exp(-\nu(\tau - \Delta)) \tag{48}$$

$$S(\tau) = \Theta(\Delta - \tau) + \Theta(\tau - \Delta) \exp(-\nu(\tau - \Delta)) \tag{49}$$

$$
\begin{aligned}
P_L(\lambda) =& \int_0^\infty P(\tau) e^{-\lambda\tau} && (50)\\
=& \int_\Delta^\infty \nu \exp(-(\lambda + \nu)\tau)) \exp(\nu\Delta) && (51)\\
=& \frac{\nu}{\nu + \lambda} exp(-\lambda\Delta) && (52)
\end{aligned}
$$

$$\frac{\nu}{\nu + \lambda} exp(-\lambda_n \Delta) = 1 \tag{53}$$

$$\Delta \nu e^{\nu\Delta} = w e^w \qquad w = (\nu + \lambda_n)\Delta \tag{54}$$

$$w = W(\Delta \nu e^{\nu\Delta}, n) \tag{55}$$

$$\lambda_n = \frac{1}{\Delta} W(\Delta \nu e^{\nu\Delta}, n) - \nu \tag{56}$$

$$
\begin{aligned}
\phi_n(0) =& \frac{1}{\int_0^\infty \big[1 - \int_0^\tau \nu \Theta(x - \Delta) \exp(-\nu(x - \Delta)) \exp\big(- \lambda_n x) dx \big] d\tau} && (57)\\
=& \frac{\nu + \lambda_n}{1 + \Delta(\nu + \lambda_n)} && (58)
\end{aligned}
$$

$$\phi_n(\tau) = \frac{\nu+\lambda_n}{1+\Delta(\nu+\lambda_n)} \exp(-\lambda_n\tau)\big[\Theta(\Delta-\tau) + \Theta(\tau-\Delta)\exp(-\nu(\tau-\Delta))\big] \quad (59)$$

$$\begin{aligned}
\psi_n(\tau) =& \Theta(\Delta-\tau)\exp(\lambda_n\tau) + \Theta(\tau-\Delta)\frac{\nu}{\nu+\lambda_n} && (60)\\
=& \Theta(\Delta-\tau)\exp(\lambda_n\tau) + \Theta(\tau-\Delta)\exp(\lambda_n\Delta) && (61)\\
& && (62)
\end{aligned}$$

$$\frac{d\psi_n(\tau)}{d\nu} = \frac{\lambda_n}{\nu[1+\Delta(\nu+\lambda_n)]}\big[\Theta(\Delta-\tau)\tau\exp(\lambda_n\tau) + \Theta(\tau-\Delta)\Delta\exp(\lambda_n\Delta)\big] \quad (63)$$

$$\begin{aligned}
c_{nn} =& \int_0^\infty \frac{d\psi_n(\tau)}{d\nu}\phi_n(\tau)d\tau && (64)\\
=& \frac{\lambda_n\Delta(1+\frac{1}{2}\lambda_n(\nu+\lambda_n))}{\nu(1+\Delta(\nu+\lambda_n))} && (65)
\end{aligned}$$

$$\begin{aligned}
c_{nm} =& \int_0^\infty \frac{d\psi_n(\tau)}{d\nu}\phi_m(\tau)d\tau && (66)\\
=& \frac{\lambda_n(\nu+\lambda_m)}{\nu(\lambda_n-\lambda_m)(\nu+\lambda_n)(1+\Delta(\nu+\lambda_m))} && (67)
\end{aligned}$$

For a LIF neuron with exponential link function the hazard rate is given by:
$\rho(\tau,t) = C\exp(\frac{u(\tau,t)-V_{th}}{\Delta})$
with membrane potential: $u(\tau,t) = V_r e^{-\tau/\tau_m} + \frac{1}{\tau_m}\int_0^\tau e^{-s/\tau_m}\mu(t-s))ds$
$\tau_m\frac{du(\tau,t)}{d\tau} = -u(\tau,t) + \mu(t)$
$V_{th} = 15mV\ \Delta = 2mV\ C = 1000Hz\ dt = 0.1ms\ tau = 20ms\ V_r = 0$

In theoretical neuroscience one common way of understanding neuronal dynamics in the brain is to pass from complex system to simplified model and the last step is to derived mathematical tractable equation, that we can well undertsand and where we can apply tools from dynamical system theory for example.

For population density equation the last step is not trivial. and we dont have a simple ODE for the firing rate.

My work is focus on this step and based on the work where they derived...

References

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