Neural Coding

3. Inhomogeneous Poisson Process

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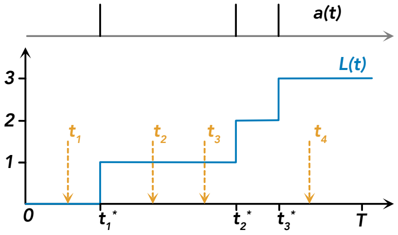
What did we learn already?

Last time:

- learned how to define a process with a constant rate and assign the probability to the spike trains generated by it.



What it gives us:

- We can assess the likelihood that a spike train was produced by the Poisson process with a given rate, compare it to alternatives

Today:

- A bit about inter-spike intervals
- What to do with changing rate?

Equally spaced sampling points

$$p_{t_1,\ldots,t_m}\left(L\left(t_1\right),\ldots,L\left(t_m\right)\right)=\prod_{j=1}^{m+1}\mathcal{P}_c\left(\underbrace{L\left(t_j\right)-L\left(t_{j-1}\right)}_{\Delta L_j}|\lambda\underbrace{\left(t_j-t_{j-1}\right)}_{\Delta t_j}\right)$$

$$\mathcal{P}_c=\mathcal{P}_{\mathbf{count}}(k|\mu)=\frac{\mu^k}{k!}e^{-\mu},\ \mu=\lambda\Delta t_j,\ k=\Delta L_j.$$

Let $L(T)=n$ Let us take $t_1:=\frac{T}{m+1}, t_2:=\frac{2T}{m+1},\ldots,t_m:=\frac{mT}{m+1}$ for $m\to\infty$

Then $\Delta t_j=t_j-t_{j-1}=\Delta t=\frac{1}{m+1}$

For sufficiently large m there are at most one spike per interval, and thus we have only factors $\mathcal{P}_c(1|\lambda\Delta t)$ and $\mathcal{P}_c(0|\lambda\Delta t)$

$$\begin{aligned}p_{t_1,\ldots,t_m}\left(L\left(t_1\right),\ldots,L\left(t_m\right)\right)&=\mathcal{P}_c^{m+1-n}(0|\lambda\Delta t)\mathcal{P}_c^n(1|\lambda\Delta t)\\&=(\lambda\Delta t)^n e^{-\lambda(m+1)\Delta t}=(\lambda\Delta t)^n e^{-\lambda T}\end{aligned}$$

If we divide this probability mass function by $(\Delta t)^n$, we obtain a *probability density* over the n spike times in the limit $\Delta t\to 0$, corresponding to $m\to\infty$.

Waiting times, ISI

$$p_{t_1,\ldots,t_m}\left(L\left(t_1\right),\ldots,L\left(t_m\right)\right)=\prod_{j=1}^{m+1}\mathcal{P}_c(\Delta L_j|\lambda\cdot\Delta t_j)$$

$$\mathcal{P}_c=\mathcal{P}_{\text{count}}(k|\mu)=\frac{\mu^k}{k!}e^{-\mu},\ \mu=\lambda\Delta t_j,\ k=\Delta L_j.$$

Waiting time distribution for the duration $t_k^\star-t_0$, where t_0 is an onset of the process, $L(t_0)=0$.

We have $\{(t_k^\star-t_0)<\tau\}\Leftrightarrow\{(L(t_0+\tau)-L\left(t_0\right))\geq k\}$ thus,

$$\begin{aligned}\mathcal{F}_{k-th}\,\text{spike}(\tau)&=P\left(t_k^\star<t_0+\tau\right)=P\left(L\left(t_0+\tau\right)-L\left(t_0\right)\geq k\right)\\&=1-\sum_{i=0}^{k-1}\mathcal{P}_{count}(i|\lambda\tau)=1-\sum_{i=0}^{k-1}\frac{(\lambda\tau)^i}{i!}e^{-\lambda\tau}\end{aligned}$$

It follows, that $\mathcal{F}_{1^{\text{st}}\text{spike}}(\tau)=1-e^{-\lambda\tau}$

$$\begin{aligned}\mathcal{F}_{ISI}(\tau)&=P\left(L\left(t_k^\star+\tau\right)\geq k+1|L\left(t_k^\star\right)=k\right)\\&=P\left(L\left(t_k^\star+\tau\right)-L\left(t_k^\star\right)\geq 1\right)=1-\mathcal{P}_{count}(0|\lambda\tau)=1-e^{-\lambda\tau}\end{aligned}$$

Memorylessness

Memorylessness property:

$$\Pr(X > t + s | X > t) = \Pr(X > s)$$

(Note: $S(t) = \Pr(X > t)$ is called survival function).

$$S\left(\tau_1 + \tau_2\right) = P\left(\tau > \tau_1 + \tau_2\right) = P\left(\tau > \tau_2\right) P\left(\tau > \tau_1\right) = S\left(\tau_1\right) S\left(\tau_2\right)$$

For exponential distribution $S(t) = e^{-\lambda t}$, it is memoryless (it is the only continuous memoryless distribution).

Inhomogeneous process, general definition

Instead of the constant rate, we have a rate function $\lambda(t)$, also called instantaneous firing rate.

$$\lambda : [0, T] \to [0, \infty), \quad t \mapsto \lambda(t)$$

We define the inhomogeneous Poisson process using the counting function $L(t)$:

$$p_{t_1,\ldots,t_m}\left(L\left(t_1\right), \ldots, L\left(t_m\right)\right) = \prod_{j=1}^{m+1} \mathcal{P}_c\left(L\left(t_j\right) - L\left(t_{j-1}\right) \middle| \int_{t_{j-1}}^{t_j} \lambda(t)dt\right)$$

Reminder:

$$\mathcal{P}_c = \mathcal{P}_{\text{count}}(k|\mu) = \frac{\mu^k}{k!}e^{-\mu},\ \mu = \int_{t_{j-1}}^{t_j} \lambda(t)dt,\ \ k = \Delta L_j.$$

We can rewrite the definition of the Poisson process in terms of *spike count expectation* function

$$\mu(t) = \int_0^t \lambda\left(t'\right) dt'$$

For the homogeneous Poisson process, $\mu(t) = \lambda t$. The marginal distribution can then be rewritten as

$$\begin{aligned} p_{t_1,\ldots,t_m}\left(L\left(t_1\right),\ldots,L\left(t_m\right)\right) &= \prod_{j=1}^{m+1} \mathcal{P}_c\left(L\left(t_j\right) - L\left(t_{j-1}\right) \middle| \mu\left(t_j\right) - \mu\left(t_{j-1}\right)\right) \\ &= \prod_{j=1}^{m+1} \mathcal{P}_c\left(\Delta L_j | \Delta\mu_j\right) = \prod_{j=1}^{m+1} \frac{\left(\Delta\mu_j\right)^{\Delta L_j}}{\left(\Delta L_j\right)!} e^{-\Delta\mu_j} \end{aligned}$$

Waiting times, ISIs

Using the joint marginal distribution, same as for homogeneous PP:

$$\mathcal{F}_{k-th\ spike}(\tau) = 1 - \sum_{i=0}^{k-1} \frac{(\mu(\tau))^i}{i!} e^{-\mu(\tau)}$$

For the inter-spike-intervals, if there is a spike at time $t^\star_{k-1}$ we can compute the density:

$$\rho_{ISI}\left(\tau_k | t^\star_{k-1}\right) = \frac{1}{Z_k\left(t^\star_{k-1}\right)} e^{-\Delta\mu_k(\tau_k)} = \frac{1}{Z_k\left(t^\star_{k-1}\right)} e^{-\left(\mu\left(t^\star_{k-1}+\tau_k\right)-\mu\left(t^\star_{k-1}\right)\right)}$$

with $Z_k\left(t^\star_{k-1}\right) = \int_0^\infty e^{-\Delta\mu_k(\tau_k)} d\tau_k$

Density of inhomogeneous Poisson Process 1

We want to compute a full joint probability measure for the whole $[0, T]$ $\{L(t) : t \in [0, T]\}$. To do so, consider the two-step process:

- Find the total number of spikes in $[0, T]$ by drawing a value from distribution: $\mathcal{P}_c\left(k \,\middle|\, \int_0^T \lambda(t)dt\right)$
- Then we draw k iid spike-times from the univariate density $\rho_1(t) := \lambda(t)/\mu(T)$, where $\mu(t) = \int_0^T \lambda\left(t'\right) dt'$

The joint density is then given by:

$$\rho\left(t_1, \ldots, t_k\right) = \prod_{j=1}^{k} \rho_1\left(t_j\right) = \prod_{j=1}^{k} \frac{\lambda\left(t_j\right)}{\mu(T)}$$

Thus, for the spike train (because so far we draw t_i iid, and the spike-trains satisfy $t_0 < t_1 < \ldots < t_k$

$$\rho\left(\mathcal{S}_k(0, T)|k\right) = k! \prod_{j=1}^{k} \frac{\lambda\left(t_j\right)}{\mu(T)}$$

Density of inhomogeneous Poisson Process 2

To get the joint distribution of spike counts and time we have to multiply by $\mathcal{P}_c(k|\mu(T))$

$$\rho\left(\mathcal{S}_k(0,T)|k,\rho_1\right)\mathcal{P}_{count}(k|\mu(T)) = \left(k!\prod_{j=1}^{k}\frac{\lambda\left(t_j\right)}{\mu(T)}\right)\frac{\mu^k(T)}{k!}e^{-\mu(T)}$$

$$= e^{-\mu(T)}\prod_{j=1}^{k}\lambda\left(t_j\right)$$

Lemma

Obtained in this two-step procedure, the joint distribution of spike times and spike counts coincides with the distribution from the definition of the Poisson point process

Steps for the proof of the Lemma* 1

We take the joint distribution at equidistant points in a limit $\{L(T/m), L(2T/m), \ldots, L((m-1)T/m), L(T)\}$, $m \to \infty$.

- Simplest case: no spikes in this spike train, so $L(iT/m) = 0$

$$p_{t_1,\ldots,t_m}\left(L\left(t_1\right), \ldots, L\left(t_m\right)\right) = \prod_{j=1}^{m+1} \mathcal{P}_c(0|\Delta\mu_j) = \prod_{j=1}^{m+1} e^{-\Delta\mu_j} = e^{-\mu(T)}$$

- One spike at time $t_1^\star$, if $m = 1$
  $p(L(0), L(T)) = \mathcal{P}_c(1|\mu(T)) = \mu(T)e^{-\mu(T)}$. For $m = 2$:

$$\begin{aligned}
&p(L(0), L(T/2), L(T)) \\
&= \mathcal{P}_c\left(\Theta\left(T/2 - t_1^\star\right)|\mu(T/2)\right)\mathcal{P}_c\left(\Theta\left(t_1^\star - T/2\right)|\,\mu(T) - \mu(T/2)\right) \\
&= \left[\Theta\left(T/2 - t_1^\star\right)\mu(T/2) + \Theta\left(t_1^\star - T/2\right)\left(\mu(T) - \mu(T/2)\right]e^{-\mu(T)}
\end{aligned}$$

$$p(L(t_1), L(t_2), \ldots, L(t_m)) = \left(\mu\left(t_+\right) - \mu\left(t_-\right)\right)e^{-\mu(T)}$$

With $t_- := \max\left(t < t_1^\star : t \in \{0, T/m, 2T/m, \ldots, T\}\right)$ and $t_+ = t_- + T/m$

Steps for the proof of the Lemma* 2

However, in the limit, there is a problem:

$$\lim_{m\to\infty} \mu\left(t_{+}\right) - \mu\left(t_{-}\right) = \lim_{m\to\infty} \int_{t_{-}}^{t_{-}+\frac{T}{m}} \lambda(t)dt = \lim_{m\to\infty} \lambda\left(t_{1}\right) \frac{T}{m} = 0$$

So instead of the probability, we consider a probability density ρ

$$\rho\left(\mathcal{S}_{1}(0, T) | k=1\right) \mathcal{P}(k=1 | \mu(t)) = \lambda\left(t_{1}^{\star}\right) e^{-\mu(T)}$$

Methods to Generate Inhomogeneous Poisson Processes

- **1. Sampling from the known density** $\lambda(t)$
  - \+ Exact and simple conceptually
  - – Requires analytical or numerically normalized $\lambda(t)/\mu(T)$.
  - – Might be hard to sample from $\rho_1(t) := \lambda(t)/\mu(T)$.

Thinning Method (Ogata, Lewis & Shedler)

Algorithm:

1. Choose $\lambda_{\text{max}} \geq \lambda(t)$ for all $t \in [0, T]$
2. Initialize $t \leftarrow 0$
3. While $t < T$:
   - Draw $\tau \sim \text{Exp}(\lambda_{\text{max}})$, set $t \leftarrow t + \tau$
   - Draw $U \sim \mathcal{U}[0, 1]$
   - Accept t as spike if $U < \lambda(t)/\lambda_{\text{max}}$

Why it works:

Consider a small interval $[t, t + \Delta t]$:

- Probability that a point from the homogeneous process occurs:

$$P_{\text{raw}} = \lambda_{\text{max}} \cdot \Delta t + o(\Delta t)$$

- Probability that it is accepted:

$$P_{\text{accept}} = \lambda_{\text{max}} \cdot \Delta t \cdot \frac{\lambda(t)}{\lambda_{\text{max}}} = \lambda(t) \cdot \Delta t$$

- So the resulting process has intensity $\lambda(t)$, as desired.

Methods to Generate Inhomogeneous Poisson Processes

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- **2. Thinning method (Ogata, Lewis & Shedler)**
  - \+ Works with unnormalized or numerically defined $\lambda(t)$.
  - \+ Easy to implement, even for time-varying or stochastic $\lambda(t)$.
  - − Can be inefficient if $\lambda(t)$ is much lower than $\lambda_{\max}$.
  - − Random number usage can be high for sparse processes.

- **3. Time-rescaling method**
  - \+ Elegant and efficient when $\mu(t) = \int_0^t \lambda(s)\,ds$ is tractable.
  - \+ Generates interspike intervals directly.
  - − Requires computing and inverting $\mu(t)$.
  - − Not suitable when $\lambda(t)$ is noisy or non-smooth.

See homework 2 for more information and implementation of them

Law of total variance. General definitions

For two random variables X and Y, $E(X \mid Y)(y) = E(x \mid Y = y)$

- X and Y are independent, then $E(X \mid Y) = EX$
- Law of total expectation:

$$E(E(X \mid Y)) = EX$$

- Law of total variation

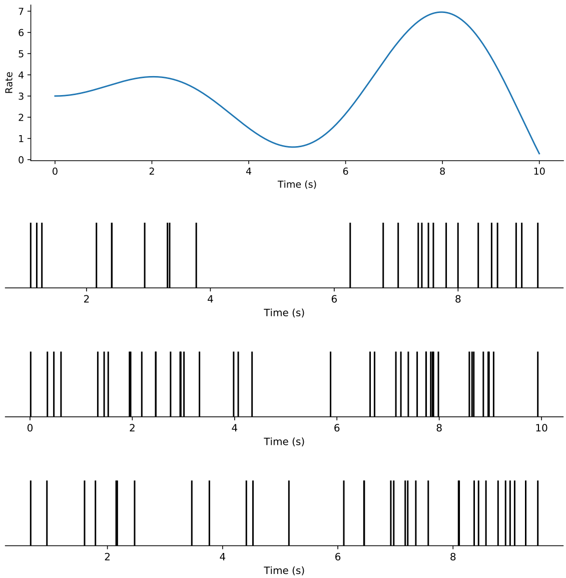
$$Var(X) = E(Var(X \mid Y)) + Var(E(X \mid Y))$$

Proof:

$$E(Var(X \mid Y)) = E\left(E(X^2 \mid Y) - [E(X \mid Y)]^2\right) = EX^2 - E\left[E(X \mid Y)\right]^2$$

$$Var(E(X \mid Y) = E[E(X \mid Y)]^2 - (E(E(X \mid Y))^2 = E[E(X \mid Y)]^2 - (EX)^2$$

Law of total variance for spike-trains



Law of total variance for spike-trains

Problem: We are measuring spikes from a neuron during time $t \in (0, T]$ and assume that they are from an inhomogeneous Poisson Process with the rate $\lambda(t)$. Where the variability of spike counts within a bin of size Δt may come?

- from stochasticity in spike generation for given $\lambda(t)$
- from changes in the rate between the bins

Law of total variance for spike-trains, formal

$$Var(X) = E(Var(X \mid Y) + Var(E(X \mid Y)$$

Imagine, the rate in the ith bin $\Delta t_i = (\Delta t \cdot (i-1), \Delta t \cdot i]$ is λ_i. N_i is a number of spikes in a bin Δt_i. Using the law of the total variance:

$$\begin{aligned} Var(N_i) &= Var[E(N_i \mid \lambda_i)] + E(Var[N_i \mid \lambda_i]) = Var[\lambda_i \Delta t] + E(\lambda_i \Delta t) \\ &= (\Delta t)^2 Var[\lambda_i] + \Delta t E(\lambda_i) = (\Delta t)^2 Var[\lambda_i] + \frac{\Delta t \int_0^T \lambda(t) dt}{T} \end{aligned}$$

We can use this relation to find the (unknown) variance of the rate, using N total number of spikes as a proxy for $\int_0^T \lambda(t) dt$:

$$Var[\lambda_i] = \frac{Var(N_i)}{\Delta t^2} - \frac{N}{T \cdot \Delta t}$$

Summary

We covered today:

- Distribution of inter-spike intervals for homogeneous Poisson process
- Definition of inhomogeneous Poisson process

What it gives us:

- Way to describe the neuronal spike trains if the rate is a function of time
- Method to find the variance of the firing rate from the spikes observation in trial data

Next time:

- Simple encoding-decoding scheme
- Tuning curves
- Fisher Information