Neural Coding

2. Point processes as a model of spike trains. Homogeneous Poisson process

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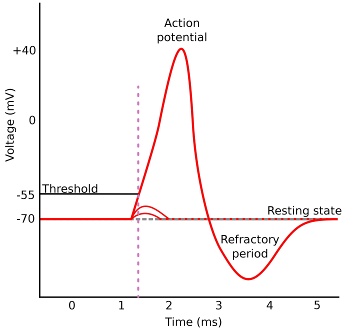
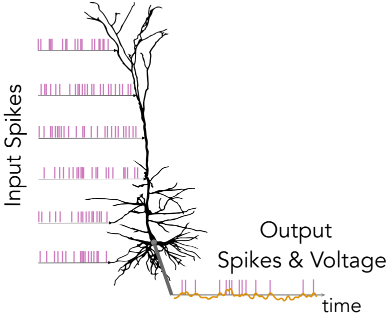
Spikes and how to represent them





- Our goal for today is to find a language to describe spike trains and define probability on them.

Dirac δ function

For spikes, we would like to have a function that notes the moment of a spike, allowing us to formulate in a mathematical way what happened as a response to it easily.

- Instead of definition:

$$\delta(x) = \begin{cases} +\infty, & x = 0 \\ 0, & x \neq 0 \end{cases} \qquad \int_{-a}^{a} \delta(x)dx = 1, \;\; \forall a > 0$$

- One possible limit:

$$F_{\Delta t}(t) = \begin{cases} 1/\Delta t & 0 < t < \Delta t \\ 0 & \text{otherwise} \end{cases} \qquad \delta(t) = \lim_{\Delta t \to 0} F_{\Delta t}(t)$$

- Another good option:

$$F_\sigma(t) = \frac{1}{\sqrt{2\pi\sigma}} e^{-\frac{t^2}{2\sigma^2}}. \qquad \delta(t) = \lim_{\sigma \to 0} F_\sigma(t)$$

Properties of Dirac δ function

- Property that is also used as a part of the definition

$$\int_{-\infty}^{\infty} f(t)\delta(t)dt = f(0) \qquad \int_{-\infty}^{\infty} f(t)\delta(t-T)dt = f(T)$$

- Symmetry: $\delta(-t) = \delta(t)$
  Reminder: $(f * g)(t) = \int_{-\infty}^{\infty} f(s)g(t-s)ds$
- Define $\delta_T(t) = \delta(t-T)$ - time-shifted version of δ function. Then

$$f * \delta_T(t) = \int_{-\infty}^{\infty} f(s)\delta(t-T-s)ds$$

$$= \int_{-\infty}^{\infty} f(s)\delta(s-(t-T))ds = f(t-T)$$

Back to spikes

Spike-times set:

$$\mathcal{S}_n(0, T) := \{t_1^\star, \ldots, t_n^\star : t_k^\star \in (0, T)\}$$

Number of spikes:

$$n = |\mathcal{S}_n(0, T)|$$

Neural response function:

$$a(t) = \sum_{t_k^\star \in \mathcal{S}_n(0,T)} \delta\left(t - t_k^\star\right) = \sum_{t_k^\star \in \mathcal{S}_n(0,T)} \delta_{t_k^\star}(t)$$

Counting function:

$$L(t) = [\Theta * a](t) = \sum_{t_k^\star \in \mathcal{S}_n(0,T)} \Theta\left(t - t_k^\star\right)$$

Impulse response function:

$$I(t) = [h * a](t) = \sum_{t_k^\star \in \mathcal{S}_n(0,T)} h\left(t - t_k^\star\right)$$

Discrete stochastic process

A sequence of Bernoulli trials $\{x_k\}_{k=1}^{\infty}$. $x_k \in \{0,1\}$, $p(x_k = 1) = \beta$. Same thing written differently: $p(x_k) = \beta^{x_k}(1-\beta)^{1-x_k}$. For n experiments:

$$p(x_1, \ldots, x_n) = \prod_{k=1}^{n} \beta^{x_k}(1-\beta)^{1-x_k} = \beta^L (1-\beta)^{n-L}$$

The probability of the infinite sequence is 0, but we can define marginal distributions. Some consistency is needed:

$$p(x_{k_2}, \ldots x_{k_m}) = \sum_{x_{k_1}} p(x_{k_1}, \ldots x_{k_m})$$

Probability of sequence of length n with L successes is given by the Binomial distribution $B(n, \beta)$

$$P(L|n) = \begin{pmatrix} n \\ L \end{pmatrix} \beta^L (1-\beta)^{n-L}$$

Interesting limit cases

- $f = L/n \in [0,1]$ (frequency of successes)

$$P(f|n) = \binom{n}{nf} \beta^{nf}(1-\beta)^{n(1-f)}$$

The mean of the $L \sim B(n,\beta)$ is $n\beta$, thus $\mathrm{E}f = L/n = \beta$. The variance of L is $\mathrm{Var}(L) = n\beta(1-\beta)$, thus $\mathrm{Var}(f) = \mathrm{Var}(L/n) = 1/n^2 \cdot \mathrm{Var}(L) = \beta(1-\beta)/n \to 0$ as $n \to \infty$. So we have for f:

$$P(f|n \to \infty) = \delta(f - \beta)$$

- another relevant case is a rare-event regime, where when time expands the number of successes remains the same: $n \cdot \beta_n = f$ then $B(n, \beta_n) \to \ldots$ (see exercises).

Continuous stochastic process

Main object is a set of random variables $\{x(t) : t \in [0, T]\}$. Again, we speak about joint marginals

$$p_{t_1,\dots,t_m}\left(x\left(t_1\right),\dots,x\left(t_m\right)\right)$$

Homogeneous Poisson process

Counting function:

$$L(t) := \int_0^t \sum_{t_k^* \in \mathcal{S}_n(0,T)} \delta\left(s - t_k^\star\right) ds = \sum_{t_k^\star \in \mathcal{S}_n(0,T)} \Theta\left(t - t_k^\star\right)$$

By definition $L(0) = 0$, $L(T) = n$.
We set $0 = t_0 < t_1 < \ldots < t_m < t_{m+1} = T$. We define the homogeneous Poisson process by setting the marginals of the counting function to obey:

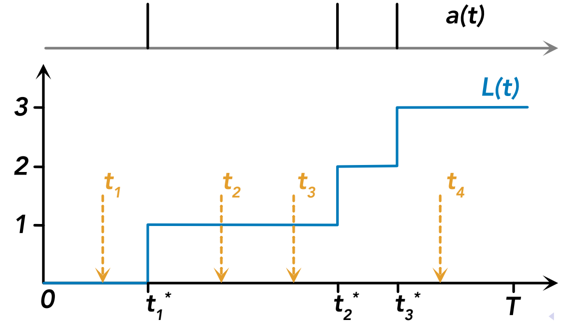
$$p_{t_1,\ldots,t_m}\left(L\left(t_1\right),\ldots,L\left(t_m\right)\right) = \prod_{j=1}^{m+1} \mathcal{P}_c\left(\underbrace{L\left(t_j\right) - L\left(t_{j-1}\right)}_{\Delta L_j} | \lambda \underbrace{\left(t_j - t_{j-1}\right)}_{\Delta t_j}\right)$$

Where counting probability is given by the Poison distribution:

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

Example

$$p_{t_1,\ldots,t_4}\left(L\left(t_1\right),\ldots,L\left(t_4\right)\right)=\mathcal{P}_c\left(0|\lambda\Delta t_1\right)\cdot\mathcal{P}_c\left(1|\lambda\Delta t_2\right)\cdot\mathcal{P}_c\left(0|\lambda\Delta t_3\right)$$
$$\cdot\mathcal{P}_c\left(2|\lambda\Delta t_4\right)\cdot\mathcal{P}_c\left(0|\lambda\Delta t_5\right)$$
$$=e^{-\lambda\Delta t_1}\cdot\frac{(\lambda\Delta t_2)^2}{1!}e^{-\lambda\Delta t_2}\cdot e^{-\lambda\Delta t_3}\cdot\frac{(\lambda\Delta t_4)^2}{2!}e^{-\lambda\Delta t_4}\cdot e^{-\lambda\Delta t_5}$$
$$=\frac{(\lambda\Delta t_2)^1}{1!}\frac{(\lambda\Delta t_4)^2}{2!}e^{-\lambda(\Delta t_1+\Delta t_2+\Delta t_3+\Delta t_4+\Delta t_5)}=\frac{1}{2}\lambda\Delta t_2\left(\lambda\Delta t_4\right)^2e^{-\lambda T}$$



Simple properties

- Events **can not** occur at the same time
  To check it, we need to show that
  $\lim_{\Delta t \to 0} \mathbb{P}(\Delta L > 1 \mid \Delta L > 0) = 0$:

$$\lim_{\Delta t \to 0} \frac{p_{t,t+\Delta t}(L(t), L(t+\Delta t) > L(t)+1)}{p_{t,t+\Delta t}(L(t), L(t+\Delta t) > L(t))} =$$

$$\lim_{\Delta t \to 0} \frac{\mathcal{P}_c(\Delta L > 1 | \lambda \Delta t)}{\mathcal{P}_c(\Delta L > 0 | \lambda \Delta t)} < \lim_{\Delta t \to 0} C \frac{(\lambda \Delta t)^2}{\lambda \Delta t} = 0$$

- Independence
  Let $L(t)$ be a homogeneous Poisson process, and let

$$0 < t_1 < \cdots < t_{m_1} < \tilde{t}_1 < \cdots < \tilde{t}_{m_2}.$$

Then the random variables

$$\{L(t_1), \ldots, L(t_{m_1})\} \quad \text{and} \quad \{L(\tilde{t}_1), \ldots, L(\tilde{t}_{m_2})\}$$

are independent.

Equally spaced sampling points

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 maximal 1 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, Inter-spike intervals (ISI)

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 $\{(t_k^\star - t_0) < \tau\} \Leftrightarrow \{(L(t_0 + \tau) - L(t_0)) \geq k\}$ 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 $\mathcal{F}_{1^{\text{st}}\text{spike}}(\tau) = 1 - e^{-\lambda\tau}$

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

Thus probability density of inter-spike intervals is $\rho_{ISI}(\tau) = \lambda e^{-\lambda\tau}$

Memorylessness

Memorylessness property:

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

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

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

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

Summary

- We learned how to define the Poisson process with the constant rate λ
- This way, we can now define probabilities of spike trains if the input and other parameters influencing the response of the neuron do not change
- Next time: what if the input changes? -> Define inhomogeneous poison processes

Literature:

- I have a bit more verbal (than on slides) script, uploaded to the "Additional sources and scripts" ILIAS folder
- Some of the material can be found in Dayan and Abbott, "Theoretical Neuroscience" (but not very detailed there)
- For the mathematical part, you can also consult books on point processes. I added one to the "Additional sources and scripts" ILIAS folder

Homework

- All homework tasks are in the Homework folder in ILIAS
- Unless specified differently, the homework solutions need to be uploaded before the next tutorial
- For now, you can solve homework in pairs; each person uploads a homework solution but clearly indicates with whom it was made. Only one of the two will normally be checked
- If you do not yet have a HW partner but would like to have one - there is a topic in the ILIAS forum to search for a partner
- There will be around 8 Homework.