Homework #1
Due 22 February 2022

1. Refractory periods

(a) **5 points** In class, we introduced the exponential distribution to model interspike intervals (ISI). Does the exponential distribution incorporate the concept of refractory periods? Please explain.

$\boxed{\textbf{No.}}$

The exponential distribution does not incorporate the concept of refractory periods since it assumes a high probability density for very short ISIs. But since neurons cannot fire during the absolute refractory period and are less likely to fire during the relative refractory period, due to the inactivation of sodium channels, the exponential distribution on its own isn't representative of realistic neuronal behavior. However, you can fix this by changing the probability of firing to equal 0 when the interspike interval is less than the refractory period.

(b) **(5 points)** If a model neuron spikes at 50 spikes per second according to a homogeneous Poisson process, what percentage of spikes would violate a 1 ms refractory period?

$$\lambda = 50\,\mathrm{Hz}$$
$$t_n \sim \exp(50)$$
$$f_t(t_n < 1) = 1 - e^{-\lambda t} = 1 - e^{-50*\left(\frac{1}{1000}\right)} = 0.04877$$

$\boxed{\textbf{4.88\% of spikes}}$

2. A neuron spikes according to a homogeneous Poisson process with rate λ.

(a) **(2 points)** What is the mean ISI of this neuron?

$t_1, ..., t_n \sim \exp(\lambda)$

$$\boxed{\mathbb{E}[t] = \tfrac{1}{\lambda}}$$

(b) **(5 points)** What is the probability that a given ISI is greater than the mean ISI?

$$\mathbb{P}(t_n > \mathbb{E}[t]) = \mathbb{P}(t_n > \frac{1}{\lambda}$$

$$F_T(t) = \mathbb{P}(T \leq t) = \begin{cases} 1 - e^{-\lambda t} & t \geq 0 \\ 0 & t < 0 \end{cases}$$

$$\mathbb{P}\left(T > \frac{1}{\lambda}\right) = 1 - \left(1 - e^{-\lambda\left(\frac{1}{\lambda}\right)}\right) = e^{-1} = 0.3679$$

$$\boxed{0.3679}$$

(c) **(8 points)** What is the expected ISI *given* that it is larger than the mean ISI?

$$\mathbb{E}\left[t_n | t_n > \frac{1}{\lambda}\right] = \frac{\int_{\frac{1}{\lambda}}^{\infty} t f_T\left(t > \frac{1}{\lambda}\right) dt}{\mathbb{P}\left(t_n > \frac{1}{\lambda}\right)} = \frac{\int_{\frac{1}{\lambda}}^{\infty} t\left(\lambda e^{-\lambda t}\right) dt}{e^{-1}}$$

$$\lambda \int_{\frac{1}{\lambda}}^{\infty} t e^{-\lambda t} dt \rightarrow$$

$$u = t \qquad dv = e^{-\lambda t}$$

$$du = 1dt \qquad v = \frac{-e^{-\lambda t}}{\lambda}$$

$$\int u dv = uv - \int v du = \frac{-te^{-\lambda t}}{\lambda} - \int \frac{-e^{-\lambda t}}{\lambda} dt$$

$$\int \frac{-e^{-\lambda t}}{\lambda} dt \qquad \rightarrow$$

$$u = -\lambda t \qquad dt = -\frac{1}{\lambda} du$$

$$\frac{du}{dt} = -\lambda$$

$$\int \frac{1}{\lambda} - e^u = \frac{e^u}{\lambda^2}$$

$$= \frac{-te^{-\lambda t}}{\lambda} - \frac{e^{-\lambda t}}{\lambda^2} = \cancel{\lambda}\left[\frac{1}{\lambda^{\cancel{2}}}\left(-t\lambda e^{-\lambda t} - e^{-\lambda t}\right)\right]$$

$$= -te^{-\lambda t} - \frac{e^{-\lambda t}}{\lambda}\Big|_{\frac{1}{\lambda}}^{\infty} = 0 - \left[-\frac{1}{\lambda}e^{-\lambda\left(\frac{1}{\lambda}\right)} - \frac{1}{\lambda}e^{-\lambda\left(\frac{1}{\lambda}\right)}\right]$$

$$= \frac{1}{\lambda}e^{-1} + \frac{1}{\lambda}e^{-1} = \frac{2}{\lambda}e^{-1}$$

$$\mathbb{E}\left[t_n | t_n > \frac{1}{\lambda}\right] = \frac{2}{\lambda}\cancel{e^{-1}}\frac{1}{\cancel{e^{-1}}} = \frac{2}{\lambda}$$

$$\boxed{\mathbb{E}\left[t_n | t_n > \tfrac{1}{\lambda}\right] = \tfrac{2}{\lambda}}$$

(d) **(8 points)** What is the expected ISI *given* that it is smaller than the mean ISI?

$$\mathbb{E}\left[t_n|t_n < \frac{1}{\lambda}\right] = \frac{\int_0^{\frac{1}{\lambda}} t f_T\left(t < \frac{1}{\lambda}\right) dt}{\mathbb{P}\left(t_n < \frac{1}{\lambda}\right)} = \frac{\int_0^{\frac{1}{\lambda}} t\left(\lambda e^{-\lambda t}\right) dt}{(1-e^{-1})}$$
$$= \frac{-te^{-\lambda t} - \frac{e^{-\lambda t}}{\lambda}\Big|_0^{\frac{1}{\lambda}}}{(1-e^{-1})}$$
$$= \frac{\left[-\frac{1}{\lambda}e^{-\lambda\left(\frac{1}{\lambda}\right)} - \frac{1}{\lambda}e^{-\lambda\left(\frac{1}{\lambda}\right)}\right] - \left[0 - \frac{1}{\lambda}\right]}{(1-e^{-1})}$$
$$= \frac{\frac{-2e^{-1}}{\lambda} + \frac{1}{\lambda}}{(1-e^{-1})}$$
$$= \left(\frac{1-2e^{-1}}{\lambda}\right)\left(\frac{1}{(1-e^{-1})}\right) = \frac{e-2}{\lambda(e-1)}$$

$$\boxed{\mathbb{E}\left[t_n|t_n < \frac{1}{\lambda}\right] = \frac{e-2}{\lambda(e-1)}}$$

(e) **(8 points)** What is the expected number of spikes that will be fired before one sees an ISI greater than the mean ISI?

Success: $\mathbb{E}\left[t_n|t_n > \frac{1}{\lambda}\right] = \frac{2}{\lambda}$
Failure:$\mathbb{E}\left[t_n|t_n < \frac{1}{\lambda}\right] = \frac{e-2}{\lambda(e-1)}$

$$\hat{n} = \mathbb{E}\left[(1-p)^{n-1}p\right] - 1 = \frac{1}{p} - 1$$
$$= \frac{1}{e^{-1}} - 1 = e - 1 = 1.718$$

$$\boxed{\hat{n} = 1.718 \textbf{ spikes}}$$

(f) **(8 points)** What is the expected waiting time until (and including) an ISI greater than the mean ISI?

$$\hat{T} = \mathbb{E}\left[(1-p)^{n-1}p\right]\mathbb{E}\left[t_n|t_n < \frac{1}{\lambda}\right] + \mathbb{E}\left[t_n|t_n > \frac{1}{\lambda}\right]$$
$$= \cancel{(e-1)}\frac{e-2}{\lambda\cancel{(e-1)}} + \frac{2}{\lambda} = \frac{e}{\lambda}$$

$$\boxed{\hat{T} = \frac{e}{\lambda}}$$

3. A neuron spikes according to a homogeneous Poisson process with rate λ. On the nth experimental trial ($n = 1, ..., N$), we measure x_n spikes in a fixed window of duration one second. Assume that $x_1, ..., x_N$ are conditionally independent given λ.

(a) **(12 points)** Estimate the neuron's firing rate by finding the λ that maximizes $\mathbb{P}(x_1, ..., x_N|\lambda)$. (Hint: Work with log probabilities).

$$
\begin{aligned}
\mathbb{P}_N(x_n) &= \frac{e^{-\lambda}\lambda^{x_n}}{x_n!} \\
\hat{\lambda}_{\text{MLE}} &= \text{argmax}\mathbb{P}(X|\lambda) = \text{argmax}\prod \mathbb{P}(x_n|\lambda) \\
\mathbb{L}(\lambda; x_1, ..., x_n) &= \prod^n f_N(x_n;\lambda) = \prod^n \frac{e^{-\lambda}\lambda^{x_n}}{x_n!} \\
\log\left(\mathbb{L}(\lambda; x_1, ..., x_n)\right) &= \ln\left(\prod^n \frac{e^{-\lambda}\lambda^{x_n}}{x_n!}\right) \\
l(\lambda; x_1, ..., x_n) &= \sum^n \ln\left(\frac{e^{-\lambda}\lambda^{x_n}}{x_n!}\right) = \sum^n \left[\ln\left(e^{-\lambda}\right) + \ln\left(\lambda^{x_n}\right) - \ln\left(x_n!\right)\right] \\
&= \sum^n \left[-\lambda + x_n\ln(\lambda) - \ln(x_n!)\right] = -n\lambda + \ln(\lambda)\sum^n x_n - \sum^n \ln(x_n!) \\
\frac{dl(\lambda; x_1, ..., x_n)}{d\lambda} &= \frac{d}{d\lambda}\left(-n\lambda + \ln(\lambda)\sum^n x_n - \sum^n \ln(x_n!)\right) \\
0 &= -n + \frac{1}{\lambda}\sum^n x_n \\
\frac{1}{\lambda}\sum^n x_n &= n \\
\lambda n &= \sum^n x_n \\
\hat{\lambda}_{\text{MLE}} &= \frac{1}{n}\sum^n x_n
\end{aligned}
$$

$$\boxed{\hat{\lambda}_{\textbf{MLE}} = \tfrac{1}{n}\sum^n x_n}$$

(b) **(12 points)** The approach taken in part (a) is referred to as *maximum likelihood estimation* because λ is estimated from the data alone, with no prior knowledge on λ. Here, we will incorporate the prior knowledge that λ is an exponentially-distributed random variable with parameter μ. Find the λ that maximizes $\mathbb{P}(\lambda|x_1, ..., x_N)$.

$$
\begin{aligned}
\mathbb{P}_N(x_n) &= \frac{e^{-\lambda}\lambda^{x_n}}{x_n!} \\
\hat{\lambda}_{\text{MAP}} &= \text{argmax}\mathbb{P}(x|\lambda)\mathbb{P}(\lambda) = \text{argmax}\log\left(\mathbb{P}(x|\lambda)\right) + \log\left(\mathbb{P}(\lambda)\right) \\
&= \text{argmax}\log\left(\prod \mathbb{P}(x_i|\lambda)\right) + \log\left(\mathbb{P}(\lambda)\right) = \text{argmax}\sum \log\left(\mathbb{P}(x_i|\lambda)\right) + \log\left(\mathbb{P}(\lambda)\right) \\
\log\left(\mathbb{P}(x_i|\lambda)\right) &= -n\lambda + \ln(\lambda)\sum^{n} x_n - \sum^{n}\ln(x_n!) \quad \rightarrow \quad \text{from 3a} \\
\mathbb{P}(\lambda;\mu) &= \mu e^{-\mu\lambda} \\
\log\left(\mathbb{P}(\lambda;\mu)\right) &= \ln(\mu) + \ln\left(e^{-\mu\lambda}\right) = \ln(\mu) - \mu\lambda \\
l(\lambda; x_1, ..., x_n) &= -n\lambda + \ln(\lambda)\sum^{n} x_n - \sum^{n}\ln(x_n!) + \ln(\mu) - \mu\lambda \\
\frac{dl}{d\lambda} &= \frac{d}{d\lambda}\left(-n\lambda + \ln(\lambda)\sum^{n} x_n - \sum^{n}\ln(x_n!) + \ln(\mu) - \mu\lambda\right) \\
0 &= -n + \frac{1}{\lambda}\sum^{n} x_n - \mu \\
\frac{1}{\lambda}\sum^{n} x_n &= n + \mu \\
\lambda(n+\mu) &= \sum^{n} x_n \\
\hat{\lambda}_{\text{MAP}} &= \frac{1}{n+\mu}\sum^{n} x_n
\end{aligned}
$$

$$\boxed{\hat{\lambda}_{\mathbf{MAP}} = \tfrac{1}{n+\mu}\textstyle\sum^{n} x_n}$$

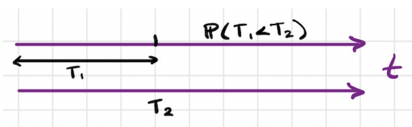
(c) **(2 points)** In part (b), λ is determined jointly by the data $x_1, ..., x_N$ and the prior knowledge on λ. This is referred to as *maximum a posteriori* (MAP) estimation. How does the relative influence of the data and prior change as the number of trials N increases? Please give a 1-2 sentence answer.

The prior is helpful for the MAP estimation when there are few trials, but as the number of trials N increases, the data has much more weight on the estimation than the prior does. As you collect more data, the information in that data overwhelms prior information if the data provides useful information (not just if the sample size iof N is large). So in a good dataset, the prior will get immediately swamped by data quickly (as N increases).

4. You insert a pair of electrodes into the brain. Unbeknownst to you, electrode 1 sits next to a neuron with mean ISI of 20 ms, and electrode 2 sits next to a different neuron with mean ISI of 30 ms. Each neuron spikes independently according to a homogeneous Poisson process. A neuron is "detected" when it fires its first spike.

(a) **(10 points)** What is the probability that a neuron is detected on electrode 1 before electrode 2?

T_1 = time neuron 1 spikes
T_2 = time neuron 2 spikes



$$\mathbb{P}(T_1 = t_1) = \lambda_1 e^{-\lambda_1 t}$$

$$\mathbb{P}(T_1 < T_2 | T_2 = t_2) = 1 - e^{-\lambda_1 t_2}$$

$$\mathbb{P}(T_1 < T_2) = \int_0^\infty \mathbb{P}(T_1 < t | T_2 = t)\mathbb{P}(T_2 = t_2)dt = \int_0^\infty \mathbb{P}(T_1 < t)\mathbb{P}(T_2 = t)dt$$

$$\mathbb{P}(T_2 = t) = \frac{dF_{T_2}(t)}{dt} = \frac{d}{dt}\left(1 - e^{-\lambda_2 t}\right) = \lambda_2 e^{-\lambda_2 t}$$

$$= \int_0^\infty \left(1 - e^{-\lambda_1} t\right)\lambda_2 e^{-\lambda_2 t} dt$$

$$= \int_0^\infty \left(\lambda_2 e^{-\lambda_2 t} - \lambda_2 e^{-\lambda_2 t - \lambda_1 t}\right) dt$$

$$= \lambda_2 \int_0^\infty e^{-\lambda_2 t} dt - \lambda_2 \int_0^\infty e^{-\lambda_2 t - \lambda_1 t} dt$$

(1) $u = -\lambda_2 t \qquad dt = \frac{1}{-\lambda_2} du$

$$\frac{du}{dt} = -\lambda_2$$

$$-\frac{1}{\lambda^2}\int e^u du = -\frac{e^u}{\lambda_2}$$

(2) $u = -\lambda_2 t - \lambda_1 t \qquad dt = \frac{1}{-\lambda_2 - \lambda_1} du$

$$\frac{du}{dt} = -\lambda_2 - \lambda_1$$

$$-\frac{1}{\lambda_2 + \lambda_1}\int e^u du = -\frac{e^u}{\lambda_2 + \lambda_1}$$

$$= \frac{-e^{-\lambda_2 t}}{\lambda_2} + \lambda_2 \frac{e^{-\lambda_2 t - \lambda_1 t}}{\lambda_2 + \lambda_1} = -e^{-\lambda_2 t} + \frac{\lambda_2 e^{-\lambda_2 t - \lambda_1 t}}{\lambda_2 + \lambda_1}\Big|_0^\infty$$

$$= 0 - \left[-1 + \frac{\lambda_2}{\lambda_1 + \lambda_2}\right] = 1 - \frac{\lambda_2}{\lambda_1 + \lambda_2} = \frac{\lambda_1}{\lambda_1 + \lambda_2} = \frac{\frac{1}{20}}{\frac{1}{20} + \frac{1}{30}} = 0.6$$

$$\boxed{\mathbb{P}(T_1 < T_2) = 0.6}$$

(b) **(15 points)** What is the expected amount of time until a neuron is detected on both electrodes? (Hint: Intuitively, should the answer be less than or greater than 30 ms?)

Intuitively, the expected amount of time until a neuron is detected on both electrodes should be greater than 30ms. The faster neuron 1 fires, the closer the expected time for both to fire will get to 30ms.

$$\begin{aligned}
\mathbb{P}(T_1 < T_2) &= \frac{\lambda_1}{\lambda_1 + \lambda_2} \\
\mathbb{E}[N_1 \bigcap N_2] &= \mathbb{E}[N_1] + \mathbb{E}[N_2] - \mathbb{E}[N_1 \bigcup N_2] \\
&= \frac{1}{\lambda_1} + \frac{1}{\lambda_2} - \frac{\lambda_1}{\lambda_1 + \lambda_2} \\
&= 20 + 30 - 12 = 38
\end{aligned}$$

$$\boxed{\mathbb{E}[N_1 \bigcap N_2] = 38\,\mathrm{ms}}$$