Neural Networks and Biological Modeling

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Answers to question set 10

Exercise 1: Firing Statistics

Defining $p(t, t')$ as the probability density of observing a spike a t and a spike at t', and $p(t|t')$ the conditional probability intensity (it is not really a prob. density because it does not integrate to one) of observing a spike at t given a spike at t', we have:

$$\langle\, S(t)S(t')\,\rangle = p(t,t') = p(t|t')p(t') \tag{1}$$

The first equality comes from the definition of the expected value as the sum of all possible results weighted by their probability to happen. The second equality is simply the expansion of the joint probability.

If $t \neq t'$, we know that $p(t|t') = p(t)$ and therefore:

$$\langle\, S(t)S(t')\,\rangle = \lim_{\Delta t \to 0} \frac{P_{\Delta t}(t)P_{\Delta t}(t')}{\Delta t^2} = \nu^2.$$

Otherwise, when $t = t'$, we have:

$$\langle\, S(t)S(t)\,\rangle = \lim_{\Delta t \to 0} \frac{P_{\Delta t}(t|t)P_{\Delta t}(t)}{\Delta t^2}$$

$P_{\Delta t}(t|t)$ is the probability of spiking between $t - \frac{\Delta t}{2}$ and $t + \frac{\Delta t}{2}$ given a spike at t. $P_{\Delta t}(t|t) = 1$:

$$\langle\, S(t)S(t)\,\rangle = \lim_{\Delta t \to 0} \frac{\nu}{\Delta t} \to \infty.$$

We can summarize the two cases by writing

$$\langle\, S(t)S(t')\,\rangle = \nu^2 + \nu\delta(t - t'). \tag{2}$$

Exercise 2: Poisson neuron

2.1 We present two methods to solve this problem.

Method 1: The probability that the neuron does not fire during a *small* time interval Δt is given by $S(\Delta t) = 1 - \rho\Delta t$. Since a Poisson process is independent of its past history, the probability that the neuron does not fire during n such time intervals is the product of the probabilities for each time intervals, i.e.,

$$S(n\Delta t) = (1 - \rho\Delta t)^n\,. \tag{3}$$

Although this expression is correct for a discrete process, it has the drawback of being dependent on the discretization time step Δt. Thus it is desirable to take the limit as $\Delta t \to 0$. This can be done by setting $t = n\Delta t$ and taking the limit as $n \to \infty$ with t fixed. Remembering the formula $\lim_{n\to\infty}(1 + \frac{a}{n})^n = e^a$, one concludes that

$$S(t) = \lim_{n\to\infty} \left(1 - \frac{\rho t}{n}\right)^n = e^{-\rho t}\,. \tag{4}$$

Alternatively, one can use the identity

$$(1-\rho\Delta t)^n = \exp\left[\sum_{i=1}^{n} \log(1-\rho\Delta t)\right] , \tag{5}$$

and expand the logarithm as $\log(1+x) = x + \ldots$, which yields

$$S(t) = \lim_{n\to\infty} \exp\left[-\sum_{i=1}^{n} \rho\Delta t\right] \to \exp\left[-\int_0^t \rho dt\right] = exp\,[-\rho t] \, . \tag{6}$$

The latter calculation has the advantage that it also works for time dependent rates $\rho = \rho(t)$, which is less obvious from Eq.(4).

Method 2 A different way to obtain this result is to consider the variation of $S(t)$ during a small time interval Δt. Because of independence, we have

$$S(t+\Delta t) = S(t)S(\Delta t) \, , \tag{7}$$

where $S(\Delta t) = 1 - \rho\Delta t$ by assumption. Rearranging. we obtain

$$\frac{S(t+\Delta t) - S(t)}{\Delta t} = -\rho S(t) \, , \tag{8}$$

which becomes as $\Delta t \to 0$

$$\frac{d}{dt} S(t) = -\rho S(t) \, , \tag{9}$$

the solution of which is indeed $S(t) = e^{-\rho t}$.

2.2 Again, due to independence, we have

$$\begin{aligned} P(t, t+\Delta t) \equiv P\,(\text{fire for the first time in } (t, t+\Delta t)) &= P\,(\text{not fire until } t) \times P\,(\text{fire in } (t, t+\Delta t)) \\ &= e^{-\rho t} \times \rho\Delta t \, . \end{aligned} \tag{10}$$

As $\Delta t \to 0$, this probability vanishes; however, the probability density, defined by $p(t)dt = P(t, t+dt)$, has finite value,

$$p(\text{fire at } t) = \lim_{\Delta t \to 0} \frac{P(t, t+\Delta t)}{\Delta t} = \rho e^{-\rho t} \, . \tag{11}$$

2.3

(i) The interval distribution was calculated earlier, $P(t) = \rho e^{-\rho t}$.

(ii) The probability to observe an interspike interval smaller than 20 ms is

$$P(\text{ISI} < 20\text{ms}) = \int_0^{20\text{ms}} \rho e^{-\rho s} ds = \left[-e^{-\rho s}\right]_{s=0}^{20\text{ms}} = 1 - e^{-20\rho} \, . \tag{12}$$

Due to independence, the probability of getting a burst of two such intervals is just the square of this probability. Thus, for $\rho = 2\text{Hz} = 2 \cdot 10^{-3}\text{ms}^{-1}$, we get $p_{\text{burst}} \simeq 0.0015$, whereas for $\rho = 20\text{Hz}$, $p_{\text{burst}} \simeq 0.109$.

(iii) Given knowledge of the interspike interval distribution and survivor function as a function of the firing rate ρ, the observer can determine the strength of the input with fair confidence after observing a few spikes.

Exercise 3: Stochastic spike arrival

We first need to solve the linear equation

$$\tau \frac{du}{dt} = -(u - u_{\text{rest}}) + RI(t) \tag{13}$$

We know (c.f. exercise set 1) that the solution is given by

$$u(t) = u_{\text{rest}} + \frac{R}{\tau} \int_{-\infty}^{t} e^{-(t-t')/\tau} I(t') dt' \,. \tag{14}$$

Let us first solve the general problem with arbitrary presynaptic current shape $\alpha(t - t^f)$. The case of problem 3.1 then corresponds to the choice $\alpha(t - t^f) = q\delta(t - t^f)$.
So for $I(t) = \sum_f \alpha(t - t^f)$ we have:

$$u(t) = u_{\text{rest}} + R \int_{-\infty}^{t} \frac{e^{-(t-t')/\tau}}{\tau} \sum_f \alpha(t' - t^f) dt' \,. \tag{15}$$

Writing $\alpha(t' - t^f) = \int_{-\infty}^{\infty} \alpha(s)\delta(s - (t' - t^f))ds$, we obtain

$$u(t) = u_{\text{rest}} + R \int_{-\infty}^{t} dt' \int_{-\infty}^{\infty} ds \frac{e^{-(t-t')/\tau}}{\tau} \alpha(s) \sum_f \delta(s - (t' - t^f)) \,. \tag{16}$$

Taking the average over all possible spike trains,

$$\langle\, u(t) \,\rangle = u_{\text{rest}} + R \int_{-\infty}^{t} dt' \int_{-\infty}^{\infty} ds \frac{e^{-(t-t')/\tau}}{\tau} \alpha(s) \left\langle \sum_f \delta(s - (t' - t^f)) \right\rangle \tag{17}$$

because all the deterministic quantities can be pulled out of the average.
Now since[1] $\left\langle \sum_f \delta(s - (t' - t^f)) \right\rangle = \nu$,

$$\begin{aligned} \langle\, u(t) \,\rangle &= u_{\text{rest}} + R\nu \underbrace{\int_{-\infty}^{t} dt' \frac{e^{-(t-t')/\tau}}{\tau}}_{=1} \int_{-\infty}^{\infty} ds \alpha(s) \\ &= u_{\text{rest}} + R\nu \int_{-\infty}^{\infty} \alpha(s) ds \,. \end{aligned} \tag{18}$$

3.1 With $\alpha(t - t^f) = q\delta(t - t^f)$, we obtain:

$$\langle\, u(t) \,\rangle = u_{\text{rest}} + R\nu q. \tag{19}$$

[1] this can be seen by remarking that $\int \delta(s)ds = 1$ so that $\frac{1}{T} \sum_f \int_0^T \delta(s - t^f)ds = \frac{\#\text{ of spikes in }(0,T)}{T} = \nu$.

3.2 The general solution is given by Eq. (18).

Exercise 4: Homework

4.1 We take the limit and use Stirling's approximation and $\lim_{n\to\infty}(1-x/n)^n = e^{-x}$:

$$
\begin{aligned}
P_k(T) &= \lim_{N\to\infty} \frac{N!}{k!(N-k)!}\left(1-\frac{\nu T}{N}\right)^{N-k}\left(\frac{\nu T}{N}\right)^k && (20)\\
&= \frac{(\nu T)^k}{k!}\lim_{N\to\infty}\frac{N^N e^{-N}}{(N-k)^{N-k}e^{-N+k}}\left(1-\frac{\nu T}{N}\right)^{N-k}\left(\frac{1}{N}\right)^k && (21)\\
&= \frac{(\nu T)^k e^{-k}}{k!}\lim_{N\to\infty}\frac{\left(1-\frac{\nu T}{N}\right)^{N-k}}{(1-k/N)^{N-k}} && (22)\\
&= \frac{(\nu T)^k e^{-k}}{k!}\frac{e^{-\nu T}}{e^{-k}} && (23)\\
&= \frac{(\nu T)^k}{k!}e^{-\nu T} && (24)
\end{aligned}
$$

The expected number of spikes in an interval of duration T can be calculated from the definition of expectation,

$$
\begin{aligned}
\langle k \rangle &= \sum_{k=0}^{\infty} k P_k(T) && (25)\\
&= \sum_{k=0}^{\infty} k\frac{(\nu T)^k}{(k)!}e^{-\nu T} && (26)\\
&= e^{-\nu T}\sum_{k=1}^{\infty} k\frac{(\nu T)^k}{(k)!} && (27)\\
&= e^{-\nu T}\sum_{k=1}^{\infty} \frac{(\nu T)^k}{(k-1)!} && (28)\\
&= e^{-\nu T}(\nu T)\sum_{k=0}^{\infty} \frac{(\nu T)^k}{k!} && (29)\\
&= \nu T\,. && (30)
\end{aligned}
$$

For the third equality we considered that for $k = 0$ the sum is 0, so we can start with $k = 1$. For the fourth equality we performed a change of variables and for the last one we used the definition of the exponential function $e^x = \sum_{n=0}^{\infty}\frac{x^n}{n!}$.

4.2 Let us label the spike trains corresponding to each neuron S_1 and S_2. The percentage is the number of spikes in S_1 coincident with a spike in S_2, N_{coinc}, divided by the total number of spikes (N) in spike train one:

$$P = \frac{\langle N_{coinc} \rangle}{N}\,. \qquad (31)$$

And $\langle N_{coinc} \rangle$ is just the probability to observe a spike in S_2 within a small observation window size $2\Delta = 4$ ms, times the number of spikes in S_1:

$$P \approx \frac{2\Delta\rho_0 N}{N} = 2\rho_0\Delta = 8\%\,. \qquad (32)$$

Here, we had to assume that the observation windows do not overlap, i. e. $\Delta \ll \rho_0$.