# Neural Networks and Biological Modeling

Professor Wulfram Gerstner
Laboratory of Computational Neuroscience

## Answers to question set 11

### Exercise 1: Poisson neuron

**1.1** We present two methods to solve this problem.

**Method 1:** The probability that the neuron does not fire during a *small* time interval $\Delta t$ 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.,

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

Although this expression is correct for a discrete process, it has the drawback of being dependent on the discretization time step $\Delta t$. 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

$$S(t) = \lim_{n\to\infty} \left(1 - \frac{\rho t}{n}\right)^n = e^{-\rho t} \,. \tag{2}$$

Alternatively, one can use the identity

$$(1 - \rho\Delta t)^n = \exp\left[\sum_{i=1}^{n} \log\left(1 - \rho \Delta t\right)\right] \,, \tag{3}$$

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

$$S(t) = \lim_{n\to\infty} \exp\left[-\sum_{i=1}^{n} \rho \Delta t\right] \to \exp\left[-\int_0^t \rho dt\right] = exp\left[-\rho t\right] \,. \tag{4}$$

The latter calculation has the advantage that it also works for time dependent rates $\rho = \rho(t)$, which is less obvious from Eq.(2).

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

$$S(t + \Delta t) = S(t)S(\Delta t) \,, \tag{5}$$

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

$$\frac{S(t + \Delta t) - S(t)}{\Delta t} = -\rho S(t) \,, \tag{6}$$

which becomes as $\Delta t \to 0$

$$\frac{d}{dt} S(t) = -\rho S(t) \,, \tag{7}$$

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

**1.2** Again, due to independence, we have

$$\begin{aligned} P(t, t + \Delta t) \equiv P\left(\text{fire for the first time in } (t, t + \Delta t)\right) &= P\left(\text{not fire until } t\right) \times P\left(\text{fire in } (t, t + \Delta t)\right) \\ &= e^{-\rho t} \times \rho \Delta t \,. \end{aligned} \tag{8}$$

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

$$p(\text{fire at } t) = \lim_{\Delta t \to 0} \frac{P(t, t+\Delta t)}{\Delta t} = \rho e^{-\rho t} . \tag{9}$$

**1.3** 这里的频率就是速度ρ

**(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

$$P(\text{ISI} < 20\text{ms}) = \int_0^{20\text{ms}} \rho e^{-\rho s} ds = \left[-e^{-\rho s}\right]_{s=0}^{20\text{ms}} = 1 - e^{-20\rho} . \tag{10}$$

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 $\rho$, the observer can determine the strength of the input with fair confidence after observing a few spikes.

**1.4** 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:

$$P = \frac{\langle N_{coinc} \rangle}{N} . \tag{11}$$

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 $S_1$:

$$P \approx \frac{2\Delta \rho_0 N}{N} = 2\rho_0 \Delta = 8\% . \tag{12}$$

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

## Exercise 2: 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 2.1 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] $\left\langle \sum_f \delta(s - (t' - t^f)) \right\rangle = \nu$,

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

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

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

**2.2** The general solution is given by Eq. (18).

## Exercise 3: Renewal process

Given an output spike at $t = \hat{t}$, the survivor function $S(t - \hat{t})$ is given by

$$S(t - \hat{t}) = \exp\left[ - \int_{\hat{t}}^{t} \rho(t'|\hat{t}) dt' \right] = \exp\left[ - \int_{\hat{t}}^{t} \rho(t' - \hat{t}) dt' \right] = \exp\left[ - \int_{0}^{t-\hat{t}} \rho(s) ds \right].$$

where we made the variable change $s = t' - \hat{t}$.
The interspike interval distribution is $P(t - \hat{t}) = \rho(t - \hat{t}) S(t - \hat{t})$. Thus we only need to calculate the integral of the hazard function $\rho(t - \hat{t})$. This gives

$$\int_0^{t-\hat{t}} \rho(s) ds = \begin{cases} \int_0^{t_{\text{abs}}} \rho(s) ds = 0 & \text{for } s < t_{\text{abs}} \\ \int_0^{t_{\text{abs}}} \rho(s) ds + \int_{t_{\text{abs}}}^{t-\hat{t}} \rho(s) ds = \frac{\rho_0}{4} \left( t - \hat{t} - t_{\text{abs}} \right)^2 & \text{for } t_{\text{abs}} < s < t_{\text{abs}} + 2 \\ \int_0^{t_{\text{abs}}} \rho(s) ds + \int_{t_{\text{abs}}}^{t_{\text{abs}}+2} \rho(s) ds + \int_{t_{\text{abs}}+2}^{t-\hat{t}} \rho(s) ds = \rho_0 \left( -1 + t - \hat{t} - t_{\text{abs}} \right) & \text{for } t_{\text{abs}} + 2 < s \,. \end{cases}$$

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

## 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 $e^x = \sum_{n=0}^{\infty} \frac{x^n}{n!}$.