Neural Networks and Biological Modeling

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Answers to question set 12

Exercise 1: Flux across threshold

1.1 The fraction of neurons that jump across u_0 is made of all those whose voltage is more than $u_0 - \Delta u$ at time t, i.e.

$$a(t) = \int_{u_0 - \Delta u}^{u_0} p(u,t) du$$

1.2 We want to compute $J(t)$, the fraction of neurons that jump across a threshold u_0 per unit of time, at time t. Now not *all* neurons receive a spike, but we have stochastic spike arrival with a rate ν. Let us consider a very small time interval $[t, t + \Delta t]$. Δt is so small that there is either one or no pulse arriving during this time interval. The probability that there is one is $\nu \Delta t$.
From the neurons that receive a spike, those whose voltage is more than $u_0 - \Delta u$ at time t will cross the u_0 threshold. All the rest will not. Therefore, the expected fraction of neurons crossing threshold in this interval is

$$\langle a(t, t + \Delta t) \rangle = \nu \Delta t \times a(t) + (1 - \nu \Delta t) \times 0$$

where the 0 denotes the fact that no neuron jumps across the threshold if there is no pulse. Eventually, dividing by Δt and taking the limit $\Delta t \to 0$ yields the flux:

$$J(t) = \nu \int_{u_0 - \Delta u}^{u_0} p(u,t) du$$

1.3 The neurons that will cross the threshold u_0 from below are the ones that at time t are at $u_0 - \Delta u$ or more and receive an excitatory spike.
The neurons that will cross the threshold u_0 from above are the ones that at time t are at $u_0 + 2\Delta u$ or less and receive an inhibitory spike.

Following the logic of the previous question we have

$$J_{exc}(t) = \nu \int_{u_0 - \Delta u}^{u_0} p(u,t) du$$

and

$$J_{inh}(t) = \frac{\nu}{2} \int_{u_0 + 2\Delta u}^{u_0} p(u,t) du$$

The total flux would be

$$\begin{aligned} J_{tot}(t) &= \nu \int_{u_0 - \Delta u}^{u_0} p(u,t) du + \frac{\nu}{2} \int_{u_0 + 2\Delta u}^{u_0} p(u,t) du & (1) \\ &= \sum_k \nu_k \int_{u_0 - w_k}^{u_0} p(u,t) du & (2) \end{aligned}$$

where v_k the spike rate arriving at each synapse type k and w_k the corrsponding voltage jump that they cause.

Exercise 2: Ornstein-Uhlenbeck process

Consider the Ornstein-Uhlenbeck process

$$\tau \dot{u}(t) = -(u(t) - \mu(t)) + \sqrt{2\sigma^2\tau}\xi(t) \tag{3}$$

where $\xi(t)$ is a gaussian white noise, characterised by $\langle \xi(t) \rangle = 0$ and $\langle \xi(t)\xi(t') \rangle = \delta(t - t')$. To this differential equation (3), called a Langevin equation, corresponds the following Fokker-Planck equation that governs the distribution of the variable u :

$$\tau \frac{\partial}{\partial t} p(u,t) = \frac{\partial}{\partial u}\big((u - \mu(t))p(u,t)\big) + \sigma^2 \frac{\partial^2}{\partial u^2} p(u,t) \; . \tag{4}$$

These two descriptions are equivalent. Here we will solve the most general case.

First method Consider a Gaussian distribution of the form

$$p(u,t) = \frac{1}{\sqrt{2\pi\Sigma^2(t)}} \exp\left(-\frac{(u - \bar{u}(t))^2}{2\Sigma^2(t)} \right) . \tag{5}$$

Now calculate the partial derivatives (here we consider the general case $\Sigma(t) \neq \sigma$):

$$\frac{\partial p(u,t)}{\partial t} = \left[\frac{(u-\bar{u})\dot{\bar{u}}}{\Sigma^2} + \left(\frac{(u-\bar{u})^2}{\Sigma^2} - 1 \right) \frac{\dot{\Sigma}}{\Sigma} \right] p(u,t) \tag{6}$$

$$\frac{\partial p(u,t)}{\partial u} = -\frac{(u-\bar{u})}{\Sigma^2}\; p(u,t) \tag{7}$$

$$\frac{\partial^2 p(u,t)}{\partial u^2} = \frac{1}{\Sigma^2}\left(\frac{(u-\bar{u})^2}{\Sigma^2} - 1 \right) p(u,t) \tag{8}$$

Inserting this in the Fokker-Planck equation (4), we get

$$\tau \left[\frac{(u-\bar{u})\dot{\bar{u}}}{\Sigma^2} + \left(\frac{(u-\bar{u})^2}{\Sigma^2} - 1 \right) \frac{\dot{\Sigma}}{\Sigma} \right] = 1 - (u-\mu)\frac{(u-\bar{u})}{\Sigma^2} + \frac{\sigma^2}{\Sigma^2}\left(\frac{(u-\bar{u})^2}{\Sigma^2} - 1 \right) . \tag{9}$$

We should also consider that the gaussian should be centered around $\bar{u}(t)$ which is the solution to the deterministic differential equation (i.e without the noise term).

$$\tau\dot{\bar{u}} = -(\bar{u} - \mu)$$

We can therefore replace μ by $\tau\dot{\bar{u}} + \bar{u}$ in the right hand side term of (9). We then obtain.

$$\left(\tau\frac{\dot{\Sigma}}{\Sigma} + 1 - \frac{\sigma^2}{\Sigma^2} \right)\left(\frac{(u-\bar{u})^2}{\Sigma^2} - 1 \right) = 0 \, . \tag{10}$$

We need to find a function $\Sigma(t)$ that verifies equation (10) for all u, t. In order to do so we set $\alpha(t) = \Sigma^2(t)$. The expression in the first parenthesis becomes

$$\frac{\tau}{2}\dot{\alpha} + \alpha = \sigma^2 \, ,$$

The solution with initial condition $\alpha(0) = \alpha_0$ is,

$$\alpha(t) = \alpha_0 e^{-2t/\tau} + \sigma^2\left(1 - e^{-2t/\tau}\right) . \tag{11}$$

We have thus shown that the function

$$p(u,t) = \frac{1}{\sqrt{2\pi\Sigma^2(t)}} \exp\left(-\frac{(u-\bar{u}(t))^2}{2\Sigma^2(t)}\right)$$

where

$$\bar{u}(t) = u_0 e^{-t/\tau} + \frac{1}{\tau}\int_0^t e^{-(t-s)/\tau}\mu(s)ds$$

and

$$\Sigma^2(t) = \Sigma_0^2 e^{-2t/\tau} + \sigma^2\left(1 - e^{-2t/\tau}\right)$$

is the solution of the Fokker-Planck equation (4) with the initial condition

$$p(u,0) = \frac{1}{\sqrt{2\pi\Sigma_0^2}} \exp\left(-\frac{(u-u_0)^2}{2\Sigma_0^2}\right) .$$

This condition becomes $p(u,0) = \delta(u-u_0)$ if $\Sigma_0 \to 0$.

Second method The problem can also be resolved by integrating directly the Langevin equation (3). We write

$$u(t) = u_0 e^{-t/\tau} + \frac{1}{\tau}\int_0^t e^{-(t-s)/\tau}\left(\mu(s) + \sqrt{2\sigma^2\tau}\xi(s)\right) ds\,,$$

where u_0 is initial distribution. If u_0 is a Gaussian, then u will also be a Gaussian since it is a linear combination of such Gaussians. Therefore we need only find its mean and variance to fully characterize it. We get

$$\begin{aligned}
\langle u(t)\rangle &= \left\langle u_0 e^{-t/\tau} + \frac{1}{\tau}\int_0^t e^{-(t-s)/\tau}\left(\mu(s) + \sqrt{2\sigma^2\tau}\xi(s)\right) ds \right\rangle \\
&= \langle u_0\rangle e^{-t/\tau} + \frac{1}{\tau}\int_0^t e^{-(t-s)/\tau}\left(\mu(s) + \sqrt{2\sigma^2/\tau}\langle\xi(s)\rangle\right) ds \\
&= \langle u_0\rangle e^{-t/\tau} + \frac{1}{\tau}\int_0^t e^{-(t-s)/\tau}\mu(s)ds
\end{aligned}$$

since $\langle\xi(s)\rangle = 0$. Moreover,

$$\begin{aligned}
u^2(t) = u_0^2\, e^{-2t/\tau} &+ 2u_0\, e^{-t/\tau}\frac{1}{\tau}\int_0^t e^{-(t-s)/\tau}\left(\mu(s) + \sqrt{2\sigma^2\tau}\xi(s)\right) ds \\
&+ \frac{1}{\tau^2}\int_0^t e^{-(t-s)/\tau}e^{-(t-s')/\tau}\left(\mu(s) + \sqrt{2\sigma^2\tau}\xi(s)\right)\left(\mu(s') + \sqrt{2\sigma^2\tau}\xi(s')\right) ds ds'\,,
\end{aligned}$$

Using $\langle\xi(s)\xi(s')\rangle = \delta(s-s')$, we obtain

$$\begin{aligned}
\langle u^2(t)\rangle - \langle u(t)\rangle^2 &= \left(\langle u_0^2\rangle - \langle u_0\rangle^2\right) e^{-2t/\tau} + \frac{2\sigma^2}{\tau}\int_0^t e^{-(t-s)/\tau}ds \\
&= \Sigma_0^2\, e^{-2t/\tau} + \sigma^2\left(1 - e^{-2t/\tau}\right)\,,
\end{aligned}$$

where $\Sigma_0^2 = \langle u_0^2\rangle - \langle u_0\rangle^2$ is the variance of the initial distribution.

Exercise 3: Fokker-Plank equation with threshold

The aim is to solve

$$\frac{\partial p(u,t)}{\partial t} = -\frac{\partial J(u,t)}{\partial u} + \nu(t)\delta(u-u_r) \tag{12}$$

with the boundary condition

$$p(\vartheta, t) = 0\,, \forall t\,. \tag{13}$$

3.1 From the second line equation (2) of the question set we have

$$J(u) = -\frac{1}{\tau}(u + \sigma^2 \frac{\partial}{\partial u})p(u,t). \tag{14}$$

$p_1(u)$ indeed satisfies $J = 0$.

3.2 We check that p_2 satisfies equation (6) of the question set. Morevover it satisfies the boundary condition (13) and the form of J is that of a non-zero constant ($J(u) = \frac{\sigma c_2}{\tau}$). All the conditions are satisfied for p_2 to be the solution on the interval $[u_r, \theta]$.

3.3 Since we have found solutions of the differential equation (12) on both side of the singularity u_r we know that the solution is of the form

$$p(u) = \begin{cases} p_1(u) & , u < u_r \\ p_2(u) & , u_r < u < \vartheta\,. \end{cases} \tag{15}$$

The constraint of continuity for $p(u)$ at u_r is satisfied if

$$c_1 = c_2 \int_{u_r}^{\theta} e^{\frac{x^2}{2\sigma^2}} dx.$$

3.4 We can write the solution on the whole interval $[-\infty, \theta]$,

$$p(u) = \frac{c_2}{\sigma} e^{-\frac{u^2}{2\sigma^2}} \int_{\max(u,u_r)}^{\theta} e^{\frac{x^2}{2\sigma^2}} dx$$

and c_2 is

$$c_2 = \left(\int_{-\infty}^{\theta} e^{-\frac{u^2}{2\sigma^2}} \int_{\max(u,u_r)}^{\theta} e^{\frac{x^2}{2\sigma^2}} dx\, du \right)^{-1}.$$

3.5 $\nu = J(\theta) = \frac{\sigma c_2}{\tau} \Rightarrow$

$$\nu = \frac{\sigma^2}{\tau} \left(\int_{-\infty}^{\theta} e^{-\frac{u^2}{2\sigma^2}} \int_{\max(u,u_r)}^{\theta} e^{\frac{x^2}{2\sigma^2}} dx\, du \right)^{-1}$$

3.6 See Figure 1.

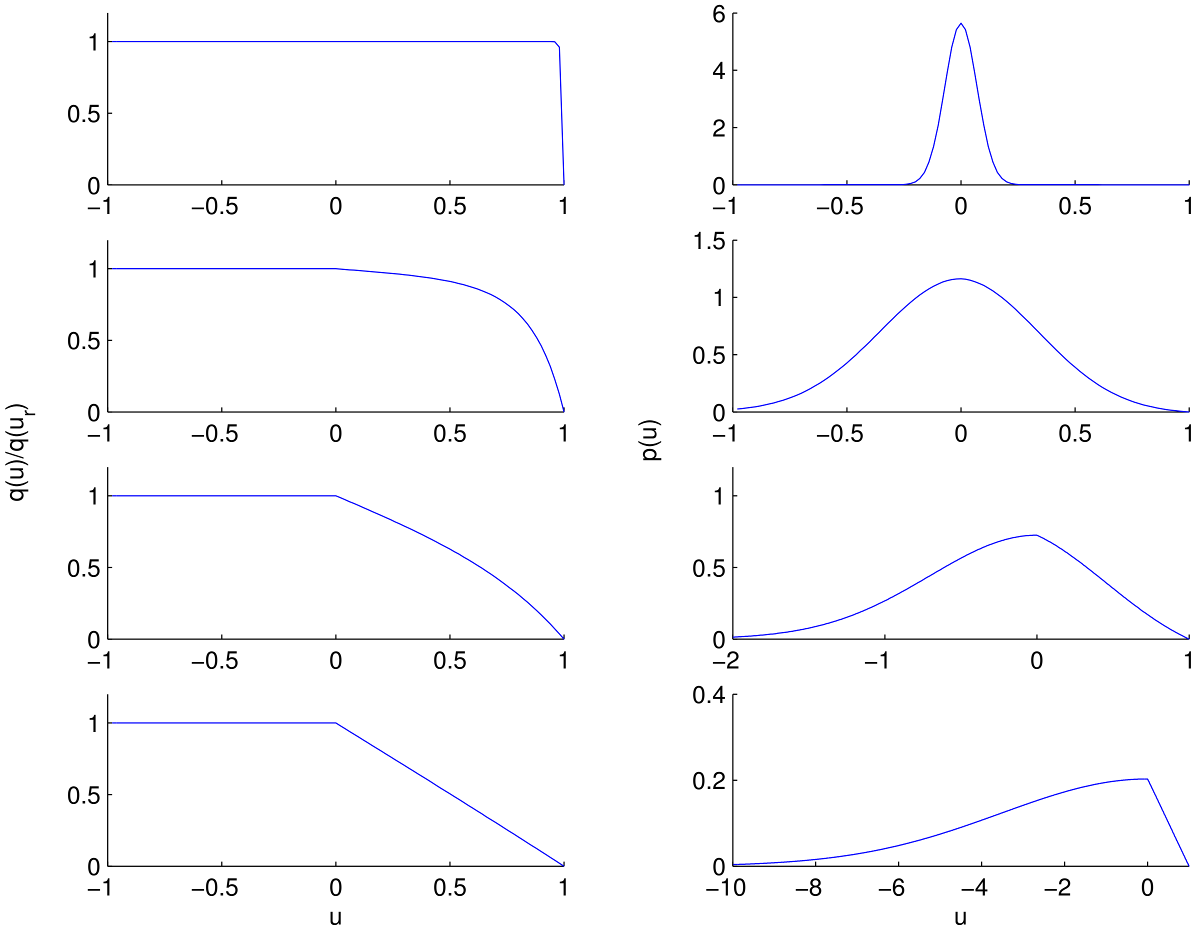

Figure 1: The normalized function $q(u)/q(u_r)$, and stationnary distribtion $p(u)$ for different values of σ. $\sigma = 0.1$ (top), 0.5, 1, et 5mV (bottom). The other parameters are $\tau = 10$ms, $\mu = 0$, $v_r = 0$ et $\theta = 1$mV.

Exercise 4: Brunel Network

4.1 The total 'drive' μ is given by [1]

$$\mu(t) = \tau_m \sum_k \nu_k(t) w_k.$$

This sum can be split in an excitatory and an inhibitory term so that

$$\begin{aligned} \mu(t) &= \tau_m w_0 K A(t) + \tau_m (-g) w_0 \frac{K}{4} A(t) \\ &= \tau_m w_0 K A(t)(1 - \frac{g}{4}) \end{aligned} \tag{16}$$

[1] [For personal interest] A complete derivation of the drive and diffusion is shown in 4.8

4.2 The amount of diffusive noise $\sigma^2(t)$ is

$$\begin{aligned}\sigma^2(t) &= \tau_m \sum_k \nu_k(t) w_k^2 \\ &= \tau_m w_0^2 K A(t) + \tau_m g^2 w_0^2 \frac{K}{4} A(t) \\ &= \tau_m w_0^2 K A(t)(1 + \frac{g^2}{4}) \end{aligned} \tag{17}$$

4.3 The balance state is obtained when inhibition counterbalance excitation, which is obtained with $g = 4$ in Eq. 16.

4.4 A change in the number of neurons without changing the connectivity does not affect the network dynamic as long as the network is large enough ($N >> K$) so that the inputs can be considered uncorrelated. Both the driving potential and the diffusion constant grow linearly with K.

4.5 As long as the network is in a balanced state ($g = 4$), the driving potential will be clamped to zero. Hence N and K can be increased while keeping the driving potential at 0. However, in this case the variance will increase linearly with K.

4.6 If $w_0^2 = 1/K$, the driving potential and the diffusion become

$$\mu(t) = \tau_m \sqrt{K} A(t)(1 - \frac{g}{4}) \tag{18}$$

$$\sigma^2(t) = \tau_m A(t)(1 + \frac{g^2}{4}) \tag{19}$$

To keep the driving potential at zero the balanced state is sufficient. The scaling of the jump amplitudes $w_0^2 = 1/K$ allows to keep the diffusion term fixed even if K is changing.

4.7 The Fokker-Planck equation is given by

$$\tau_m \frac{\partial}{\partial t} p(u,t) = -\frac{\partial}{\partial u}\big((-u + \mu(t))p(u,t)\big) + \frac{1}{2}\sigma^2(t)\frac{\partial^2}{\partial u^2} p(u,t) + A(t)\big(\delta(u - u_r) - \delta(u - \vartheta)\big),$$

with $\mu(t)$ and $\sigma^2(t)$ given in Eq. 16 and 17 (or their scaled version Eq. 18 and 19). The balanced state condition and scaling effects discussed earlier hold for time-dependent firing rate.

4.8 Derivation of the mean drive and diffusion

[**These two formulas were given in class, we give here their derivation if you are curious.**]

The dynamics of the menbrane potential in the absence of a threshold is given by

$$\tau_m \dot{V} = -V + E_L + R I_s, \tag{20}$$

where $I_s(t)$ is the synaptic input current:

$$R I_s(t) = \tau_m \sum_k w_k S_k(t). \tag{21}$$

Here, $S_k(t)$ is is a Poissonian spike train with rate ν_k. That is, the mean is given by

$$\langle S_k(t) \rangle = \nu_k(t) \tag{22}$$

and the auto-correlation function is

$$\langle S_k(t) S_l(t') \rangle = \nu_k \delta_{k,l} \delta(t - t') + \nu_k \nu_l. \tag{23}$$

Here, the Kronecker delta $\delta_{k,l}$ expresses the fact that inputs are uncorrelated across neurons and the Dirac delta function $\delta(t-t')$ means that spikes are uncorrelated in time (Poisson assumption). The aim is to approximate the synaptic input by its mean and a white Gaussian noise (so-called diffusion approximation), i.e.

$$RI_s(t) \approx \mu(t) + \sigma(t)\sqrt{\tau_m}\xi(t), \tag{24}$$

where $\langle \xi(t) \rangle = 0$ and $\langle \xi(t)\xi(t') \rangle = \delta(t-t')$. Thus, the goal is to derive the $\mu(t)$ and $\sigma(t)$ for the Poissonian shot noise, Eq. (21).

Solution A. We simply match the mean and auto-correlation of the noise in Eq. (21) and (24). For the diffusion approximation, we have the mean

$$\langle RI_s(t) \rangle = \mu(t) \tag{25}$$

and the auto-correlation function for $\delta I_s = I_s - \langle I_s \rangle = \sigma\sqrt{\tau_m}\xi/R$

$$R^2\langle \delta I_s(t)\delta I_s(t') \rangle = \tau_m\sigma(t)\sigma(t')\langle \xi(t)\xi(t') \rangle = \tau_m\sigma^2(t)\delta(t-t'). \tag{26}$$

On the other hand, for the shot noise Eq. (21), we have the mean

$$\langle RI_s(t) \rangle = \tau_m \sum_k w_k \langle S_k(t) \rangle = \tau_m \sum_k w_k \nu_k(t) \tag{27}$$

and correlation function ($R\delta I_s = \tau_m \sum_k [w_k(S_k - \nu_k)]$)

$$R^2\langle \delta I_s(t)\delta I_s(t') \rangle = \tau_m^2 \sum_{k,l} w_k w_l \langle [S_k(t) - \nu_k(t)][S_l(t') - \nu_l(t')] \rangle \tag{28}$$

$$= \tau_m^2 \sum_{k,l} w_k w_l \, [\langle S_k(t)S_l(t') \rangle \tag{29}$$

$$-\nu_k(t)\langle S_l(t') \rangle - \langle S_k(t) \rangle \nu_l(t') + \nu_k(t)\nu_l(t')] \tag{30}$$

$$= \tau_m^2 \sum_{k,l} w_k w_l \, [\langle S_k(t)S_l(t') \rangle - \nu_k(t)\nu_l(t')] \tag{31}$$

$$= \tau_m^2 \sum_{k,l} w_k w_l \nu_k(t)\delta_{k,l}\delta(t-t') \tag{32}$$

$$= \tau_m^2 \sum_k w_k^2 \nu_k(t)\delta(t-t') \tag{33}$$

Comparing Eq. (25) with Eq. (27) and Eq. (26) with Eq. (33) we conclude that

$$\mu(t) = \tau_m \sum_k w_k \nu_k(t), \qquad \sigma^2(t) = \tau_m \sum_k w_k^2 \nu_k(t). \tag{34}$$

This solution works for the time-dependent case (see 4.7).