Neural Networks and Biological Modeling

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Question set 12

Exercise 1: The flux due to stochastic spike arrival

Assume that we have a population of N neurons which currently (at time t) have a distribution of membrane potential $p(u,t)$.

1.1 Each neuron in the population receives an excitatory input which causes a δ-shaped current pulse leading to a jump in the membrane potential by an amount Δu. What is the fraction of the neurons that will be kicked by the spike arrival across a threshold u_0?

1.2 Assume that arrival of excitatory spikes occurs at a rate ν. What is the flux $J(u,t)$ across a reference potential u_0?

1.3 Assume that excitatory spikes arrive at a rate ν and cause a jump Δu and inhibitory spikes arrive at a rate $\nu/2$ and cause a jump by an amount $-2\Delta u$. What is the excitatory and inhibitory flux across u_0, separately? What is the total flux? What if $u_0 = \vartheta$ is the firing threshold of an integrate-and-fire neuron?

Exercise 2: Ornstein-Uhlenbeck process

Consider the Ornstein-Uhlenbeck process with time-dependent mean and variance,

$$\tau \dot{u}(t) = -u(t) + \mu(t) + \sqrt{2\sigma^2\tau}\,\xi(t) \tag{1}$$

where $\mu(t) = RI(t)$ is the input and $\xi(t)$ is a Gaussian white noise, i.e. $\langle\, \xi(t) \,\rangle = 0$ and $\langle\, \xi(t)\xi(t') \,\rangle = \delta(t-t')$.

The probability distribution of the variable u obeys the Fokker-Planck equation

$$\begin{aligned}\tau \frac{\partial}{\partial t} p(u,t) &= \frac{\partial}{\partial u}\big((u-\mu(t))p(u,t)\big) + \sigma^2 \frac{\partial^2}{\partial u^2} p(u,t) \\ &= \frac{\partial}{\partial u}\left\{u - \mu(t) + \sigma^2 \frac{\partial}{\partial u}\right\} p(u,t)\,. \end{aligned} \tag{2}$$

Voltage distribution

Consider the Gaussian distribution

$$p(u,t) = \frac{1}{\sqrt{2\pi\Sigma^2(t)}} \exp\left(-\frac{(u-\bar{u}(t))^2}{2\Sigma^2(t)}\right) \tag{3}$$

where $\bar{u}(t)$ is the (deterministic) solution of equation

$$\tau \frac{d\overline{u}}{dt} = \mu(t) - \overline{u}\,, \qquad \overline{u}(0) = u_0$$

and

$$\Sigma^2(t) = \sigma^2[1 - e^{-\frac{2t}{\tau}}].$$

2.1 Show that for constant $\Sigma(t) = \sigma$, Eq.(3) solves the Fokker-Planck equation (2). Note that the initial condition is $p(u,0) = (2\pi\sigma^2)^{-\frac{1}{2}} \exp\left(-\frac{(u-u_0)^2}{2\sigma^2}\right)$. What is the physical interpretation of this initial condition?

2.2 Assume that all trajectories start at $u = u_0$. This corresponds to the initial condition $p(u,0) = \delta(u-u_0)$. Show that for constant $\mu(t) = \mu$, Eq.(3) solves the Fokker-Planck equation (2). What is the physical interpretation of the initial condition?

Exercise 3: Fokker-Planck equation with threshold

Take $\mu = 0$ and rewrite the Fokker-Planck equation in the form of a conservation law

$$\frac{\partial p(u,t)}{\partial t} = -\frac{\partial J(u,t)}{\partial u} \tag{4}$$

where $J(u,t)$ is the probability current. To incorporate the spike threshold, we impose an absorbing boundary condition at $u = \vartheta$, i.e.,

$$p(\vartheta, t) = 0\,, \forall t\,. \tag{5}$$

Furthermore, the reset is described by adding a source term in the equation,

$$\frac{\partial p(u,t)}{\partial t} = -\frac{\partial J(u,t)}{\partial u} + \nu(t)\delta(u-u_r) \tag{6}$$

where $\nu(t) = J(u,t)\mid_{u=\theta}$ is the average firing frequency. This means that the probability current flowing through the threshold is reinjected at the reset potential, which is necessary to ensure the conservation of probability.

Stationary solution

We look for a stationary solution of (5-6), characterized by $\partial p/\partial t = 0$ and $\nu(t) = \nu = \text{cst}$. Integrating (6) once, we obtain

$$J(u,t) = \nu H(u-u_r)\,, \tag{7}$$

where H is the Heaviside function, and we have used the "natural" condition: $\lim_{u\to-\infty} J(u,t) = 0$.

3.1 Comparing Eq. 4 with Eq. 2, we see that the probability current is related to the stationary probability density according to: $J(u) = \left(-u - \sigma\frac{\partial}{\partial u}\right) p(u)$. With the results of exercise 2 show that the Gaussian distribution

$$p_1(u) = \frac{c_1}{\sigma} e^{-\frac{u^2}{2\sigma^2}} \tag{8}$$

is a solution of the Fokker-Planck equation (6-7) on the interval $[-\infty, u_r]$. Conclude that it is the desired solution for the interval $[-\infty, u_r]$.

3.2 Consider the "modified" Gaussian

$$p_2(u) = \frac{c_2}{\sigma} e^{-\frac{u^2}{2\sigma^2}} \int_u^{\vartheta} e^{\frac{x^2}{2\sigma^2}}\, dx \tag{9}$$

Show that it satisfies the solution for the current (7), the Fokker-Planck equation (6), and the boundary condition (5).

3.3 Set

$$p(u) = \begin{cases} p_1(u) & , u < u_r \\ p_2(u) & , u_r < u < \vartheta\,. \end{cases} \tag{10}$$

Find the relation between c_1 and c_2 which ensures the continuity of $p(u)$.

3.4 Normalize the probability density to find an expression for the constants.

3.5 What is the firing rate of this neuron $\nu = J(\vartheta)$.

3.6 Note that $p(u)$ can be written $p(u) = \bar{p}(u)q(u)$ where $\bar{p}(u)$ is the stationary solution of the problem *without* boundary condition (c.f. Ex.2). Sketch the form of $\bar{p}$, q, and p and give an interpretation.

Exercise 4: Brunel Network

The Brunel network (Brunel, 2000) of excitatory and inhibitory neurons is famous because it can be analyzed mathematically while it shows rich dynamics that are interesting from a biological point of view. We analyze the Brunel network here and use it as a starting point for combining network arguments and noise arguments from earlier weeks.

In the Brunel network we simulate a large network of leaky integrate-and-fire neurons (10 000 or more). 20% of the neurons are inhibitory, the others excitatory (say 8000 excitatory and 2000 inhibitory). Each neuron receives exactly K excitatory (say 500) and $K/4$ inhibitory input synapses (say 125). Arrival of an input spike at an excitatory synapses causes a jump in the membrane potential by $w_0 = 0.1$ mV. Arrival of an input spike at an inhibitory synapse causes a jump by $(-g)w_0$,with $g > 1$. All neurons in the network have the same parameters, and you may assume that all neurons fire at the same firing rate $\nu = A_0 =$ constant.

4.1 Calculate the driving potential $\mu(t)$ that determines the voltage drift $\gamma(u) = \mu - u$ in the Fokker-Planck equation (Hint: calculate the mean membrane potential in the absence of a threshold, using the tricks from last week; or use directly the results of this week).

4.2 Calculate the diffusion constant in the Fokker-Planck equation (Hint: calculate the variance of the membrane potential in the absence of a threshold, using the tricks from last week; or use directly the results of this week).

4.3 What are the conditions that the mean driving potential is zero ('balanced state')?

4.4 What happens if we increase the number of neurons (from 10 000 to 20 000) while keeping K fixed? What happens if we increase K (from 500 to 1000) while keeping N fixed?

4.5 Can we increase N and K (with $p = K/N$ fixed) AND at the same time keep the driving potential at zero? What happens to the variance (diffusion term)?

4.6 Scale the weights with $w^2 = 1/K$ and repeat the steps in 4.5.
Can we increase N and K (with $p = K/N$ fixed) AND at the same time keep the driving potential at zero AND keep the variance (diffusion term) fixed?

4.7 Going back to the original Brunel network, what happens if the firing rate is NOT constant in time? Can you make statements for the time dependent case where the firing rate is the same for all neurons, but potentially different from one time step to the next?
Write down the Fokker-Planck equation for the time-dependent case.