Neural Networks and Biological Modeling

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Answers to question set 1

Primer: linear, first order ODE

In this exercise, we are dealing with a first order, linear ODE. You have seen this type of equations in calculus. We quickly remind you how to solve it. The general form of this type of ODE is:

$y' = ay + q$

where y and q are functions of t. One method for solving this ODE is by multiplying it with an integrating factor:

$M = e^{\int -a dt} = e^{-at}$.

The equation then becomes $My' - May = Mq$.

Substituting M gives $e^{-at}y' - ae^{-at}y = e^{-at}q$. Convince yourself that the left hand side of this equation is equal to the derivative $(e^{-at}y)'$. Thus, integrating both sides becomes easy and we can solve for $y(t)$:

$\int_0^t (e^{-as}y)'\, ds = \int_0^t e^{-as} q\, ds$

$e^{-at}y(t) - e^{-a0}y(0) = \int_0^t e^{-as} q(s)\, ds$

$e^{-at}y(t) = y(0) + \int_0^t e^{-as} q(s)\, ds$

$y(t) = e^{at}y(0) + e^{at}\int_0^t e^{-as} q(s)\, ds$

In principle you can start from this equation, adapt the physical quantities, and plug in different input functions q(t). The following solutions however develop a more intuitive approach: In exercise 1.1 we find the solution by knowing the initial value (v_{rest}) and the steady-state value $y' = 0 = ay + q$. In between these values, we know (from calculus) that the solution to the linear differential equation grows (or decays) exponentially. The solution to 1.4 finally shows how to solve this linear ODE using the method known as "variation of parameters".

Exercise 1: Passive Membrane

1.1 On the one hand, $I(t) = 0$ for $t \le t_0$ and the neuron is at rest at $t = t_0$, so we know that $u(t) = u_{\text{rest}}$ for $t \le t_0$. On the other hand, after a long time, the membrane potential has reached a steady state which is defined by $\frac{du}{dt} = 0$, hence: $0 = -(u_\infty - u_{\text{rest}}) + RI_0$, from which follows that

$$u_\infty = RI_0 + u_{\text{rest}}. \tag{1}$$

The general solution of linear differential equations of first order involves the exponential function. The relevant time scale here is τ, so we can construct the total response to the step current by exponential interpolation between u_{rest} and u_∞:

$$u(t) = u_{\text{rest}} + RI_0\left(1 - e^{-(t-t_0)/\tau}\right) \quad (\text{for}\, t \ge t_0). \tag{2}$$

(Compare this result to the general solution (equation (5)) by plugging in $I(t) = I_0$.)

1.2 If $I(t)$ is a current pulse of duration Δ and amplitude q/Δ, the voltage starts by increasing exponentially towards the asymptotic value $u_{\text{rest}} + Rq/\Delta$ with a time constant τ for the duration of the pulse,

$$u(t) = u_{\text{rest}} + \frac{Rq}{\Delta}\left(1 - e^{-(t-t_0)/\tau}\right), \quad t_0 \le t \le t_0 + \Delta\,.$$

The voltage reaches a maximum at the end of the pulse, after which it decreases back to its resting value. If Δ is short relative to τ, the exponential term can be expanded as $e^{-(t-t_0)/\tau} \sim 1 - \frac{t-t_0}{\tau} + \ldots$, which gives

$$u(t) = u_{\text{rest}} + \frac{Rq}{\Delta\tau}(t - t_0)\,.$$

At $t = t_0 + \Delta$, we have $u = u_{\text{rest}} + q/C$, where C is defined by $\tau = RC$. Thus, in the limit where $\Delta \to 0$, the membrane potential instantaneously jumps an amount q/C and then decays exponentially to its resting value with a time constant τ. This is called the *impulse response.*

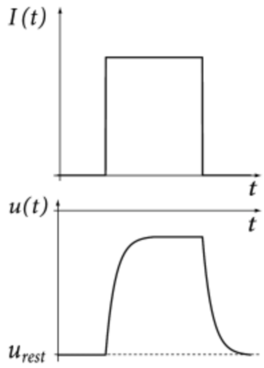

Figure 1: Step current I(t) and voltage response u(t).

1.3 For any value of Δ, the integral $\int_{t_0}^{t_1} f_\Delta(s)ds$ equals 1 if the integration range covers the interval $(t_0, t_0 + \Delta)$, and vanishes if the two intervals do not overlap. The conclusion follows by taking the limit $\Delta \to 0$.

From the definition of the δ-function (with $t_0 = 0$), an instantaneous current pulse can be defined as $I(t) = q\delta(t - t^f)$. Note that this is consistent in terms of physical units because the δ-function has units of 1/time, and an electrical current has units of electrical charge/time.

1.4 We start by computing the solution of

$$\tau\frac{du}{dt} = -(u(t) - u_{\text{rest}}) + R\,I(t)\,. \tag{3}$$

This is a linear equation for $u(t)$. Its general solution consists of a sum of (i) the solution to the homogeneous equation and (ii) a particular solution of (3). We first solve the homogeneous equation where we neglect terms that are independent of $u(t)$:

$$\tau\frac{du}{dt} + u(t) = 0 \quad \Leftrightarrow \quad \frac{du/dt}{u} = -\frac{1}{\tau}\,.$$

Integrating, we find $\log(u) = -t/\tau + \text{const}$, which leads to $u(t) = ke^{-t/\tau}$, where k is an integration constant. A particular solution can be obtained by the "variation of parameters" method (variation de la constante): we write $u(t) = k(t)e^{-t/\tau}$ and replace it in (3):

$$\begin{aligned} \tau\left(\frac{dk(t)}{dt} - \frac{1}{\tau}k(t)\right)e^{-t/\tau} + k(t)e^{-t/\tau} &= u_{\text{rest}} + RI(t) \\ \frac{dk(t)}{dt} &= \frac{1}{\tau}(u_{\text{rest}} + RI(t))e^{t/\tau}\,. \end{aligned}$$

Integrating, we find $k(t) = k_2 + \frac{1}{\tau}\int_{t_0}^{t}(u_{\text{rest}} + RI(s))e^{s/\tau}ds$ where k_2 is a new integration constant. Denoting the initial condition by $u_0 = u(t_0)$, we obtain

$$u(t) = u_{\text{rest}} + (u_0 - u_{\text{rest}})e^{-(t-t_0)/\tau} + \frac{1}{\tau}\int_{t_0}^{t} RI(s)e^{-(t-s)/\tau}ds\,. \tag{4}$$

Using the particular initial condition $u(t_0) = u_{\text{rest}}$, the equation simplifies to:

$$u(t) = u_{\text{rest}} + \frac{1}{\tau}\int_{t_0}^{t} RI(s)e^{-(t-s)/\tau}ds\,. \tag{5}$$

Exercise 2: Integrate-and-Fire Model

2.1 From Eq. (2), we see that the membrane potential approaches its limiting value $RI_0 + u_{\text{rest}}$ from below. Thus the threshold ϑ is attained only if $RI_0 + u_{\text{rest}} > \vartheta$, i.e., $I_{min} = (\vartheta - u_{\text{rest}})/R$.

2.2 In the case where $I_0 > I_{min}$, the neuron fires repetitively at regular intervals. The interval between two spikes equals the time it takes for the neuron to go from the reset potential (here, $u_{\text{reset}} = u_{\text{rest}}$) to the firing threshold ϑ. Thus, the period T is the solution of $u(T) = \vartheta$, where $u(t)$ satisfies Eq. (2) with $t_0 = 0$. Solving for T, we obtain

$$T = \tau \ln\left(\frac{RI_0}{RI_0 - (\vartheta - u_{\text{rest}})}\right)\,. \tag{6}$$

2.3 The firing frequency is $f = 1/T$, i.e., $g(I_0) = T^{-1}$ for $RI_0 > \vartheta - u_{\text{rest}}$, and $g(I_0) = 0$ otherwise.

Exercise 3: Integrate-and-Fire Models

3.1 The resting potential u_{rest} must correspond to the stable fixed point of the dynamics. It is the leftmost intersection between F and the voltage axis. By contrast, the threshold u_{th} corresponds to an unstable fixed point. It is the second point where $F(u) = 0$.

3.2 For $u(t = 0) = u_1$, $F(u)$ is positive and the voltage increases slowly to u_{rest}. For $u(t = 0) = u_2$, $F(u)$ is negative and the voltage decreases slowly to u_{rest}. In the case of QIF and EIF, for $u(t = 0) = u_3$, $F(u)$ is positive and large, and $u(t)$ increases rapidly to infinity. In the case of LIF the figure does not define $F(u)$ above the spike threshold.

3.3 u_{rest} is the voltage at which the neuron model will remain if no external force is acting on it, i. e. when the model neuron is resting. The threshold serves to replace the action potential with a reset of the voltage. u_{th} sets the voltage at which the action potential is triggered.

3.4 The Quadratic IF fires last. This can be seen because the onset of the spike is much slower than that of the exponential IF (compare $F(u)$ for the two models).