Neural Networks and Biological Modeling

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Answers to question set "Cable Equation"

Exercise 1: Cable equation

1.1 We need to verify that $u(t,x) = G_\infty(t,x)$ fulfils Eq. 1 for a short current pulse injected at $t = 0$ and $x = 0$, i.e $r_T i_{\text{ext}}(t,x) = \delta(x)\delta(t)$.

$$\frac{\partial}{\partial t} u(t,x) - \frac{\partial^2}{\partial x^2} u(t,x) = -u(t,x) + r_T i_{\text{ext}}(t,x)\,, \tag{1}$$

We re-write it and substitute $G_\infty(t,x)$ and the current δ-pulse

$$\begin{aligned} \frac{\partial}{\partial t} u(t,x) - \frac{\partial^2}{\partial x^2} u(t,x) + u(t,x) = r_T i_{\text{ext}}(t,x) \\ \frac{\partial}{\partial t} G_\infty(t,x) - \frac{\partial^2}{\partial x^2} G_\infty(t,x) + G_\infty(t,x) = \delta(x)\delta(t) \end{aligned} \tag{2}$$

We need to show that Eq. 2 is valid. Let's define $K(t,x) = \frac{1}{\sqrt{4\pi t}} \exp\left(-t - \frac{x^2}{4t}\right)$. Then we have $G_\infty(t,x) = \Theta(t)K(t,x)$. We then work on the left-hand side of the equation and find

$$\begin{aligned} \frac{\partial}{\partial t} \Theta(t)K(t,x) - \frac{\partial^2}{\partial x^2} \Theta(t)K(t,x) + \Theta(t)K(t,x) = \\ K(t,x)\frac{\partial}{\partial t} \Theta(t) + \Theta(t)\frac{\partial}{\partial t} K(t,x) - \frac{\partial^2}{\partial x^2} \Theta(t)K(t,x) + \Theta(t)K(t,x) = \\ K(t,x)\delta(t) + \Theta(t)(\frac{\partial}{\partial t} K(t,x) - \frac{\partial^2}{\partial x^2} K(t,x) + K(t,x)) = \\ \delta(t)K(t,x) + \Theta(t)LK(t,x) \end{aligned}$$

where we defined an operator $L = \frac{\partial}{\partial t} - \frac{\partial^2}{\partial x^2} + 1$.

For $t \neq 0$ the term $\delta(t)K(t,x)$ vanishes. We need to consider the limit $t \to 0$ and we have

$$\lim_{t\to 0} K(t,x) = \lim_{t\to 0} \frac{1}{\sqrt{4\pi t}} \exp\left(-t - \frac{x^2}{4t}\right) = \delta(x).$$

The above comes by the definition of the $\delta(x)$ as a Gaussian whose width goes to 0.

After a few calculations we can find that

$$LK(t,x) = \frac{\partial}{\partial t} K(t,x) - \frac{\partial^2}{\partial x^2} K(t,x) + K(t,x) = 0$$

Taking the left-hand side of Eq. 2 we therefore have

$$\begin{aligned} \frac{\partial}{\partial t} G_\infty(t,x) - \frac{\partial^2}{\partial x^2} G_\infty(t,x) + G_\infty(t,x) = \\ \delta(t)K(t,x) + \Theta(t)(LK(t,x)) = \delta(t)K(t,x) = \delta(t)\delta(x) \quad \text{q.e.d.} \end{aligned}$$

Remarks :

- You can also have a look at section 3.2.2 of the book [1] (in HTML format on `http//neuronaldynamics.epfl.ch/online/Ch3.S2.html`).
- G_∞ is called the Green's function of the given partial differential equation. It is the solution of a linear differential equation for a Dirac δ-pulse as input. With such functions we can write the general solution of the inhomogeneous equation for any input

$$Lu(t,x) = I(t,x)$$

in terms of an integral (superposition) of Green's functions, due to linearity. Indeed the solution can be written

$$u(t,x) = \int_{-\infty}^{t} dt' \int_{-\infty}^{+\infty} dx' G_\infty(t-t', x-x') I(t', x') \tag{3}$$

(i) & **(ii)** The solution of the diffusion equation $\frac{\partial u}{\partial t} - \frac{\partial^2 u}{\partial x^2} = 0$ is given by $u(t,x) = \frac{1}{\sqrt{4\pi t}} \exp\left(\frac{-x^2}{4t}\right)$. In this case, there is transport (the width of the Gaussian increases with time) but there is no dissipation of energy ($\int u(t,x)dx$ = constant). In the cable equation it is the term "1" in the differential operator $L = \frac{\partial}{\partial t} - \frac{\partial^2}{\partial x^2} + 1$ which is responsible of the dissipation of energy. This term represents the voltage loss due to the leaks through the membrane, and gives the exponentially decaying term in the solution.

1.2 We are looking for a solution of the equation

$$Lu = r_T q \delta(x - x_0)\delta(t) + r_T q \delta(x + x_0)\delta(t)$$

which corresponds to an instantaneous injection of a charge q at time $t = 0$ at position $x = x_0$ and to an instantaneous injection of an imaginary "virtual" charge q at time $t = 0$ at position $x = -x_0$. The "virtual" charged is placed in order to account for the boundary condition $\frac{du}{dx}\mid_{x=0}= 0$, i.e. $i(t, x = 0) = 0$.

Since the cable equation is linear we can find the solution of the above equation by superposition of the Green's functions for each of the two input current pulses. The solution is then

$$u(t,x) = r_T q \left[G_\infty(t, x - x_0) + G_\infty(t, x + x_0)\right]$$

We can indeed verify that the derivative satisfies $\frac{du}{dx}\mid_{x=0}= 0$. Therefore, if we restrict ourselves to the interval $x \geq 0$, $u(t,x)$ satisfies both $Lu = r_T q\delta(x - x_0)\delta(t)$ and $\frac{du}{dx}\mid_{x=0}= 0$. It is the solution we were looking for.

(i) & **(ii)** If $x = 0$ represents the soma (i.e the cell body), the flat derivative boundary condition expresses the fact that no charge can diffuse any further. The electrical charges accumulate there. If we substitute $G_\infty(t, x - x_0)$ and $G_\infty(t, x + x_0)$ and calculate the solution at $x = 0$ we have

$$u(t, x = 0) = \frac{2 r_T q \Theta(t)}{\sqrt{4\pi t}} \exp\left(-t - \frac{x_0^2}{4t}\right) \tag{4}$$

One can therefore see that the further the injection point in the dendrite, the weaker the resulting potential at the soma. This phenomenon is indeed present in neurons; without any mechanisms for active amplification, input in distal dendrites leads to weak and broad responses at the cell body.

References

[1] Gerstner W. et al. *Neuronal dynamics: From single neurons to networks and models of cognition.* Cambridge University Press, 2014.

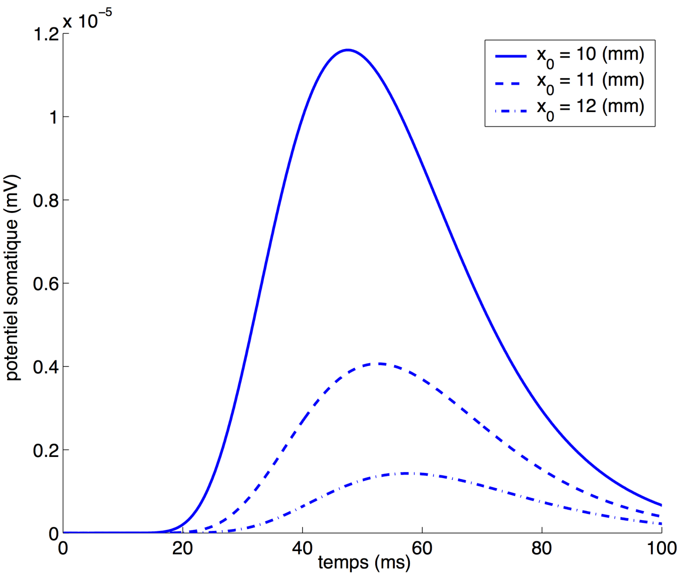

Figure 1: Time-dependence of the somatic potential following a 1 μC charge at a distance x_0 from the soma. In this example $\lambda = 1$ mm et $\tau = 10$ ms.