DOING PHYSICS WITH PYTHON

THE PASSIVE CABLE EQUATION

Ian Cooper

Any comments, suggestions or corrections, please email me at

matlabvisualphysics@gmail.com

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mnsET01.py mnsET02.py

Solution $v_m(t,x)$ of the cable equation using a finite difference method.

Model parameters:

$$\lambda = 1.0\times10^{-3}\ \text{m} \quad \tau = 10\times10^{-3}\ \text{s} \quad C_1 = 0.10 \quad -5\,\lambda \le x \le 5\,\lambda$$

$$nX = 199 \quad dx = 5.05\times10^{-5}\ m$$

$$nT = 47045 \quad dt = 2.55\times10^{-6}\ \text{s} \quad t_{Max} = 12\,\tau$$

$$dt = \frac{C_1\,\tau\,dx^2}{\lambda^2}$$

INTRODUCTION

The passive cable equation in neuroscience models the spread of electrical signals along a neuronal cable (dendrite or axon) over time and space, and is modelled by a partial differential equation. The model is a passive one which means that membrane conductance is fixed. A subthreshold voltage signal that is initiated at one point along the axon or dendrite will decrease in amplitude with distance from the point of initiation. For example, the signal may correspond to synaptic input from another neuron. Understanding how geometry affects the spread of the signal helps determine whether the synaptic input will cause the cell to fire an action potential.

Assume the membrane is passive, so the analysis is more applicable to dendrites than to axons. Consider a cell that is shaped as a long cable of radius a and the current flow is along a single spatial dimension x, the distance along the cable. The membrane potential depends on the axial x variable and not on the radial. The cable equation is a partial differential equation that describes how the membrane potential $v_m(t,x)$ depends on currents entering, leaving, and flowing within the neuron. The equivalent circuit is shown in figure 1.

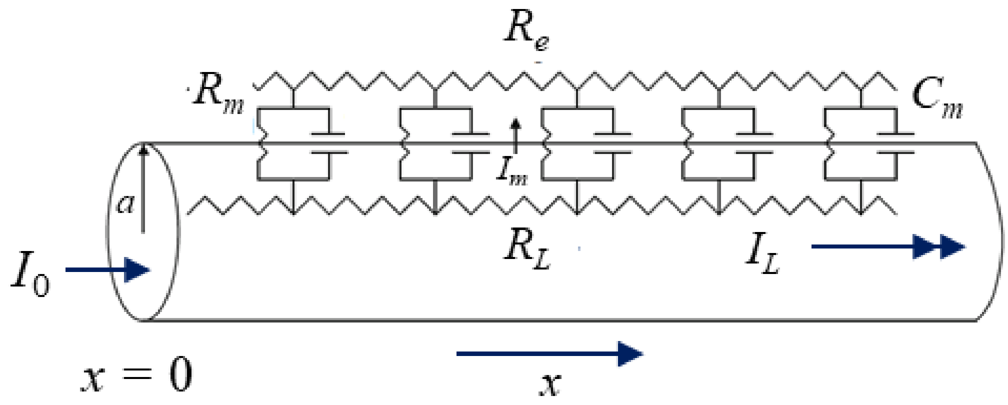


Fig. 1. Equivalent circuit for a uniform passive cable. I_L is the longitudinal (axial) current inside of the cable, I_m is the current across the membrane (membrane current), R_L is the longitudinal resistance (axial) inside the neuron (cytoplasm), R_e is the resistance of the extracellular space (assume extracellular space is isopotential, R_e = 0) , R_m is the membrane resistance (radial), and C_m is the membrane capacitance.

The typical problem of cable theory is to determine the distribution of voltage $v_m(x,t)$ along the length of the cable x and over time t, given a current input $I_0(t)$ at $x = 0$.

The axial current I_L flowing along the neuron is due to the voltage gradient along the cable. The longitudinal resistance R_L grows in proportion to the length of the cable and is inversely proportional to the cross-sectional area of the cable.

$$R_L = \frac{r_L \Delta x}{\pi a^2}$$

where r_L is the specific intracellular resistivity.

Units: R_L $[\Omega]$ r_L $[\Omega.m]$ Δx [m] a [m] I [A] v [V] t [s]

From Ohm's law, the decrease in $v_m(x,t)$ with increasing distance is equal the current times the resistance.

$$\Delta v_m = v_m(x+\Delta x, t) - v_m(x,t)$$

$$\Delta v_m = -R_L\, I_L = -\frac{r_L\, \Delta x\, I_L}{\pi\, a^2}$$

The minus sign is because, by convention, Δv_m is positive when voltage increases with x, and I_L is positive towards positive x.

The longitudinal current in the limit as $\Delta x \to 0$ is thus

$$I_L(x,t) = -\left(\frac{\pi\, a^2}{r_L}\right)\frac{\partial V_m(x,t)}{\partial x}$$

The membrane resistance R_m of a cylindrical segment of length Δx and circumference $2\pi\, a$ is

$$R_m = \frac{r_m}{2\pi\, a\, \Delta x}$$

where r_m is the specific resistance $[\Omega.m^2]$. The membrane current can be expressed as

$$I_m = 2\,\pi\, a\, \Delta x\, i_m$$

where i_m is the specific membrane current [A.m^{-2}]

For a passive cable, r_m is constant and Ohm's Law gives the relationship between the membrane voltage v_m and the membrane current (radial) I_m

$$v_m = I_m R_m = \left(2\pi a \Delta x \, i_m\right)\left(\frac{r_m}{2\pi a \Delta x}\right) = i_m r_m$$

After considering all flows into and out of a segment of length Δx, then the capacitor current I_{cap} will charge or discharge the capacitor. Hence, the rate of change of the membrane potential is determined by the membrane capacitance C_m [F].

$$I_{cap} = C_m \frac{d\,v_m}{d\,t} = \left(2\pi a \Delta x\right) c_m \frac{d\,v_m}{d\,t}$$

where c_m is the specific membrane capacitance [F.m^{-2}].

From Kirchhoff's current law, the change in intracellular axial current is equal to the amount of current that flows across the membrane. Hence,

$$I_L(x+\Delta x, t) - I_L(x,t) = -\left[I_{cap}(x,t) + I_m(x,t)\right]$$

$$\left(\frac{\pi a^2}{r_L}\right)\frac{\partial v_m(x+\Delta x, t)}{\partial x} - \left(\frac{\pi a^2}{r_L}\right)\frac{\partial v_m(x,t)}{\partial x}$$

$$= \left(2\pi a \Delta x\right) c_m \frac{\partial v_m}{\partial t} + 2\pi a \Delta x \, i_m$$

By dividing both sides of this equation by $\left(2\pi a \Delta x\right)$ and letting $\Delta x \to 0$, we obtain the **cable equation**

$$c_m \frac{\partial v_m}{\partial t} = \left(\frac{a}{2r_L}\right)\frac{\partial^2 v_m}{\partial x^2} - i_m = \left(\frac{a}{2r_L}\right)\frac{\partial^2 v_m}{\partial x^2} - \frac{v_m}{r_m}$$

Define the length (space) constant λ as

$$\lambda = \sqrt{\frac{a\, r_m}{2\, r_L}} \qquad \left[\frac{m.\Omega.m^2}{\Omega.m}\right]^{1/2} \rightarrow [m]$$

and the membrane time constant τ_m as

$$\tau_m = c_m\, r_m \qquad \left[F.m^{-2}.\Omega.m^2\right] \rightarrow \left[\frac{A.s}{V}.\frac{V}{A}\right] \rightarrow [s]$$

Thus, the cable equation can be expressed as

$$\tau_m \frac{\partial v_m}{\partial t} = \lambda^2 \frac{\partial^2 v_m}{\partial x^2} - v_m$$

- The time constant τ_m describes membrane potential attenuation over time.
- The length constant λ describes the attenuation over space.
- The time-derivative term $\partial v_m / \partial t$ relates to charging of the membrane capacitor.
- The second space-derivative term $\partial^2 v_m / \partial x^2$ relates to accumulation of longitudinal currents.

Typical values

cable radius $a \sim 5\text{x}10^{-6}$ m

specific intracellular resistivity $r_L \sim 1\ \Omega$.m

specific membrane resistivity $r_m \sim 1\ \Omega$.m.m^2

specific membrane capacitance $c_m \sim 10^{-2}$ F.m^{-2}

space constant $\lambda \sim 1\text{x}10^{-3}$ m

membrane time constant $\tau_m \sim 10^{-2}$ s

Steady-state solutions of the cable equation

We can calculate the steady-state solution $v_{SS}(x)$ of the cable equation where $\partial v_m / \partial t = 0$

$$\lambda^2 \frac{d^2 v_{SS}}{dx^2} - v_{SS} = 0$$

To solve this differential equation, we need to specify the cable geometry and the boundary conditions. Consider an infinite cable where $x \geq 0$ and a step current I_0 is injected at $x = 0$ resulting in the membrane potential at $x = 0$ to be v_0.

The longitudinal current and membrane potential

$$I_L(x,t) = -\left(\frac{\pi a^2}{r_L}\right)\frac{\partial V_m(x,t)}{\partial x}$$

$$\frac{dV_m(x)}{dx} = -\left(\frac{r_L}{\pi a^2}\right) I_L(x)$$

The boundary condition is

$$\left.\frac{dV_m}{dx}\right|_{x=0} = -\left(\frac{r_L}{\pi a^2}\right) I_L(0) = -\left(\frac{r_L}{\pi a^2}\right) I_0$$

The solution of the differential equation is

$$v_{SS}(x) = \left(\frac{\lambda\, r_L\, I_0}{\pi\, a^2} \right) \exp(-x / \lambda) = v_0 \exp(-x / \lambda) \quad v_0 = \frac{\lambda\, r_L\, I_0}{\pi\, a^2}$$

This solution when differentiated and evaluated at $x = 0$ satisfies the boundary conditions.

Thus, the membrane potential decays exponentially. The distance at which the potential has decayed to $1/e$ is the space constant λ

$$\lambda = \sqrt{\frac{a\, r_m}{2\, r_L}}$$

Since the space constant λ is proportional to the square root of the cable's radius *a*, we conclude that thicker axons or dendrites have larger space constants than narrower processes. This means that thicker axons or dendrites are able to transmit signals for greater distances. Thicker cells with a larger space constant λ are more easily excited and are able to generate faster action potentials.

The input resistance R_{inp} is defined to be the ratio of the steady-state membrane potential to the injected current at $x = 0$

$$R_{inp} = \frac{v_{SS}(0)}{I_0} = \frac{r_L\, \lambda}{\pi\, a^2} = \frac{1}{\pi\, a^{3/2}} \sqrt{\frac{r_m\, r_L}{2}} \qquad \lambda = \sqrt{\frac{a\, r_m}{2\, r_L}}$$

The input resistance R_{inp} of the cable varies with the -3/2 power of the cable radius. Therefore, the input conductance G_{inp} is directly proportional to the 3/2 power of the cable radius.

$$G_{inp} = \pi a^{3/2} \sqrt{\frac{2}{r_m r_L}}$$

The input resistance is important because it is something that can be measured experimentally. Since it is also possible to measure the space constant λ, one can compute r_m and r_L from experimental data.

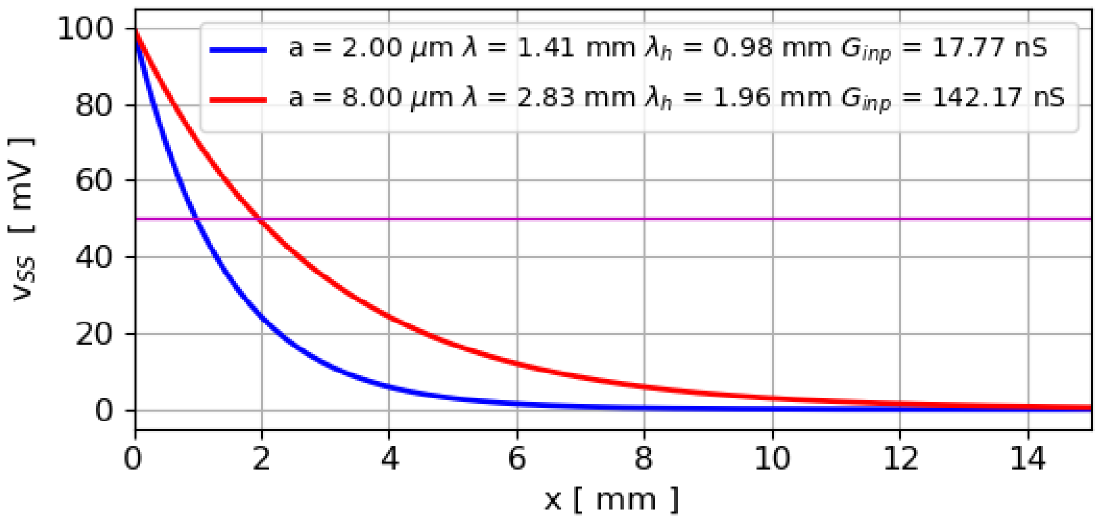


Fig. 2. Steady-state solutions of the cable equation for two values of the cable radius a. The membrane potential decreases exponentially from the stimulus. λ_h distance for the membrane potential to decrease by half.

$$a \to 4a \quad \lambda \to 2\lambda \quad \lambda_h \to 2\lambda_h \quad G_{inp} \to 8\,G_{inp}$$ **mnsET01.py**

Linear potential profile

Let $v_m(x,t) = f(x)\,g(t)$ where the linear potential profile is given by

$$f(x) = m\,x + b$$

$$d^2 f(x)/dx^2 = 0 \Rightarrow \frac{\partial^2 V(x,y)}{\partial x^2} = 0$$

and the cable equation reduces to $\tau_m \frac{\partial V(x,t)}{\partial t} = -V(x,t)$ and the solution for $g(t)$ is of the form $\exp(-t/\tau_m)$. Therefore, the solution can be expressed as

$$v_m(x,t) = (m\,x + b)\exp(-t/\tau_m)$$

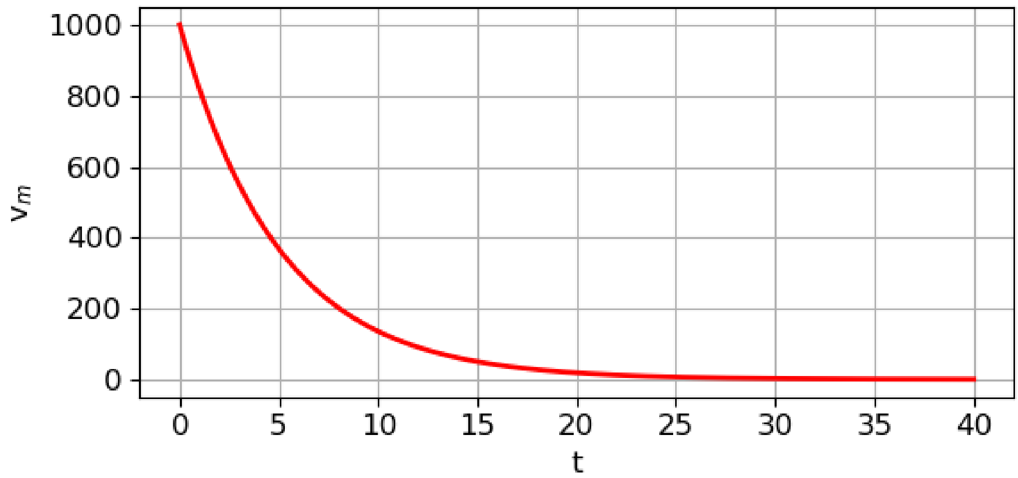


Fig. 3. For all values of x, the membrane potential relaxes to zero with time. **mnsET01.py**

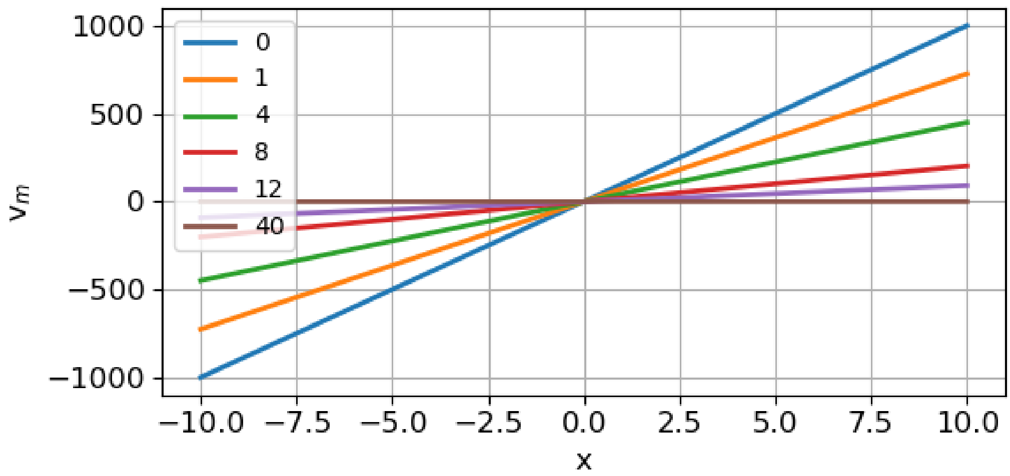
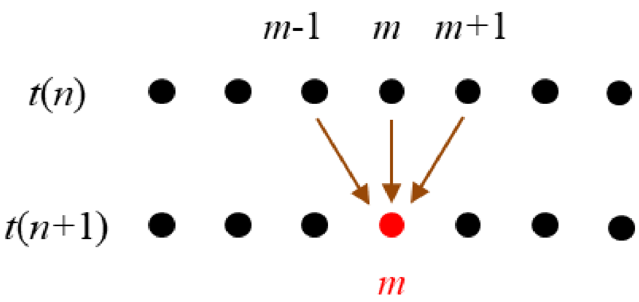


Fig. 4. The linear membrane potential at times 0, 1,4, 8, 12, and 40. For all values of x the membrane potential relaxes towards zero with time. **mnsET01.py**

Solution $v_m(t,x)$ of the cable equation using a finite difference method. **mnsET02.py**



Cable equation

$$\tau_m \frac{\partial v_m}{\partial t} = \lambda^2 \frac{\partial^2 v_m}{\partial x^2} - v_m$$

Finite difference equation:

time step (Δt) m, total steps nT

space step (Δx) n, total steps nX

$$v_m(m+1,n) = v_m(m,n) + C_1\left[v_m(m,n+1) - 2v_m(m,n) + v_m(m,n-1)\right] - C_2 v_m(m,n)$$

$$C_1 = \frac{\lambda^2}{\tau_m \Delta x^2} \quad C_2 = \frac{\Delta t}{\tau_m}$$

$C_1 < 0.1$ for stability of the solution

Boundary Conditions: The membrane potentials at the ends of the cable are set to zero at all time steps.

The stimulus is applied at the centre of the cable.

Stimulus: Membrane potential fixed at the Origin $x = 0$

$v_m(t,0) = 100$ mV

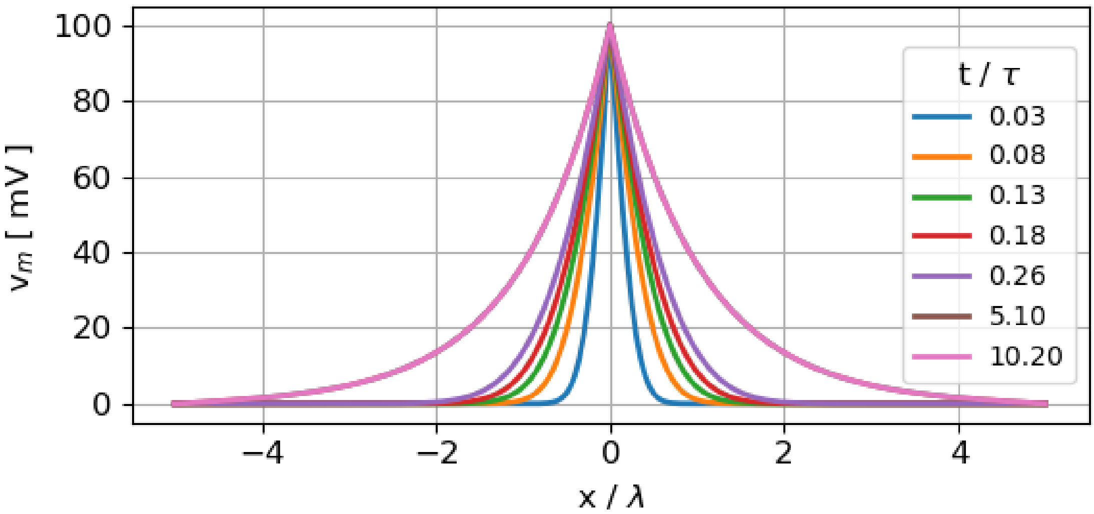


Fig. 5A. Membrane potential fixed at the Origin. Membrane potential along the length of the cable at different times. **mnsET02.py**

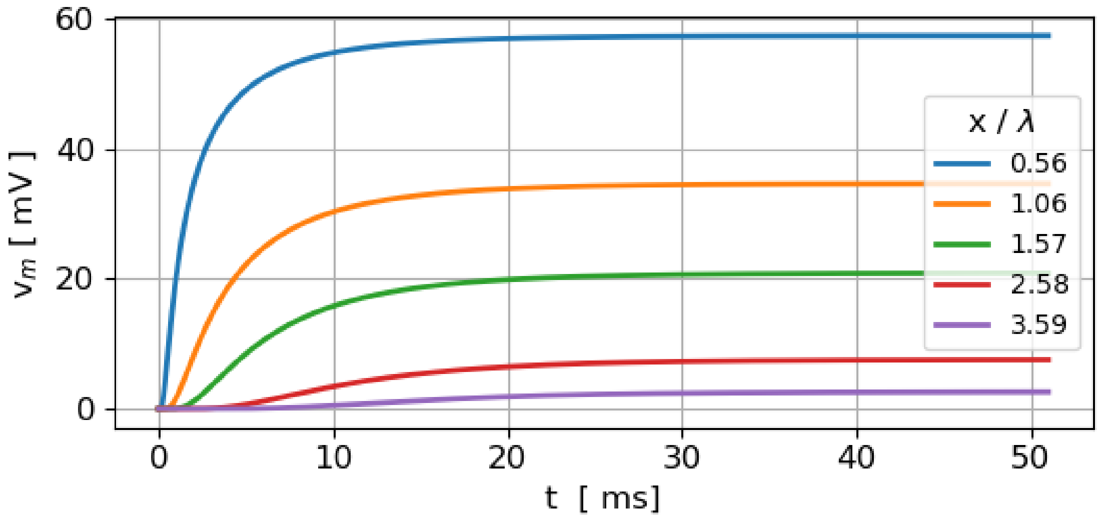


Fig. 5B. Membrane potential fixed at the Origin. Time evolution of the membrane potential at different times positions long the cable. **mnsET02.py**

Stimulus: Membrane potential at the Origin $x = 0$ decreases with time with a Gaussian profile.

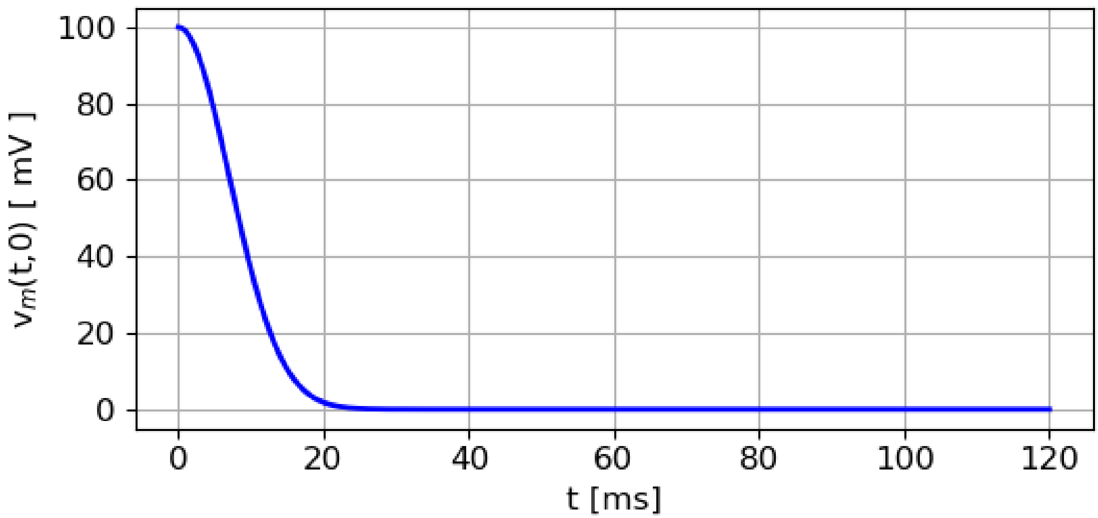


Fig. 6A. Stimulus applied at Origin: Gaussian decrease in membrane potential with time at the Origin $x = 0$. **mnsET02.py**

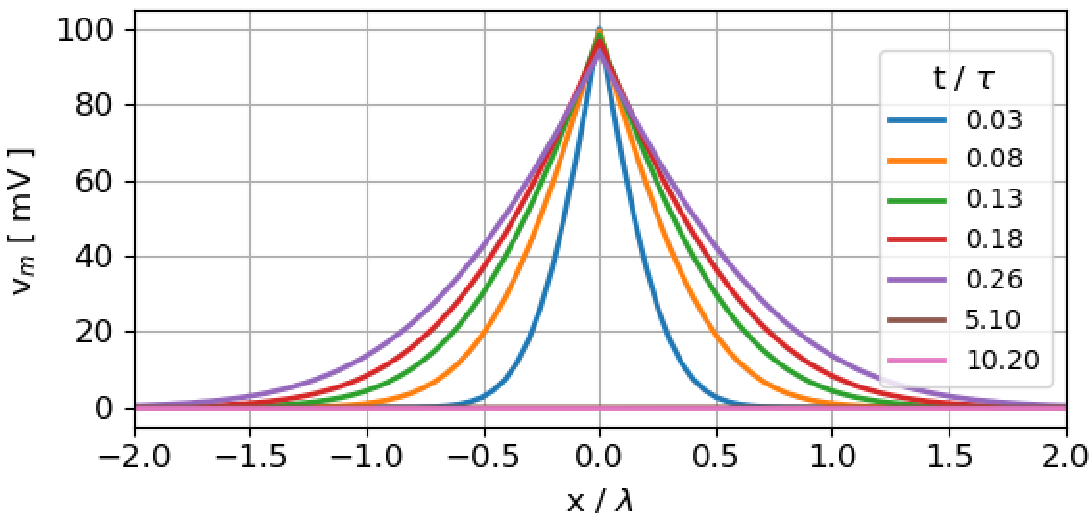


Fig. 6B. Membrane potential along the length of the cable at different times. **mnsET02.py**

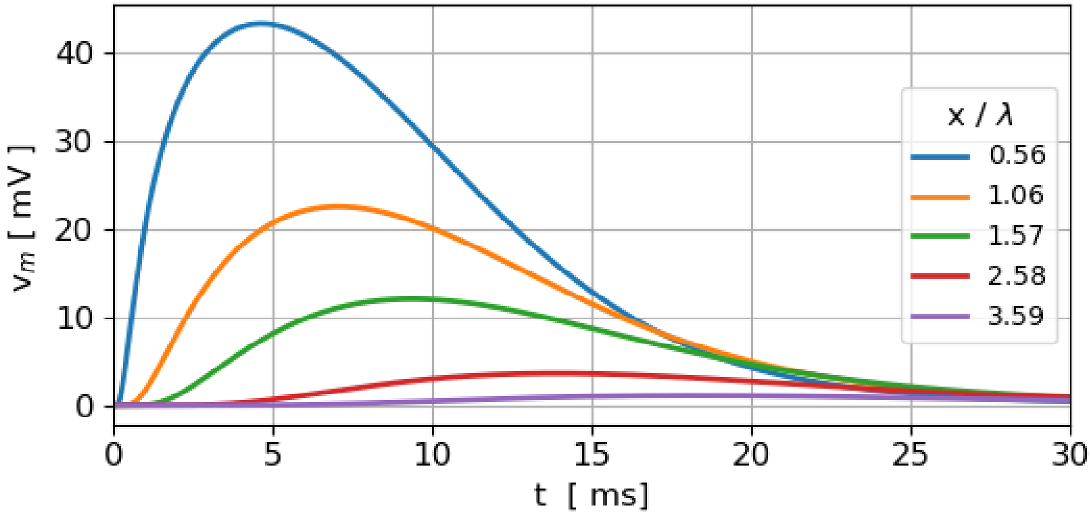


Fig. 6C. The peak in the membrane potential at each time step propagates away from the Origin at a conduction speed v_{cond}.

Theory: Local peak voltage propagates with speed

$$v_{cond} = \frac{2\lambda}{\tau} = 0.20 \text{ m.s}^{-1} \quad \lambda = 1.0 \times 10^{-3} \quad \tau = 10 \times 10^{-3} \text{ s}$$

Simulation: Peak 1 $x/\lambda = 0.56 \quad t/\tau = 4.66$

Peak 2 $x/\lambda = 1.06 \quad t/\tau = 7.18$

$$v_{cond} = (1.06 - 0.56)/(7.18 - 4.66) = 0.20 \text{ m.s}^{-1}$$

Agrees with theoretical prediction

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