University of Colorado Boulder

APPM 4350

Propagation of Voltage in a Neuron

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Contents

1 Introduction

The purpose of this project is to determine the propagation of voltage in a neuron using the cable equation. The axon of a neuron has current flowing inside and outside of the cell membrane as well as current passing through the membrane. The resistances of the cell membrane creates the change of voltage throughout the axon. Using Kirchoff's loop law to sum the total flow of current, and Ohm's law to convert current to voltage, a partial differential equation called the cable equation emerges that models the change of voltage across the membrane (1).

$$\frac{\partial v(x,t)}{\partial t} = \frac{\partial^2 v(x,t)}{\partial x^2} + f(v(x,t)) + j_{ext}(x,t) \tag{1}$$

$v(x,t)$ represents the voltage at position x and time t across the membrane, $j_{ext}(x,t)$ represents the inward applied current per unit length, and $f(v(x,t))$ represents the ionic currents through the membrane.

Part two of this document concerns the passive membrane, meaning the ionic channels behave passive and obey Ohm's law such that $f(v(x,t)) = -v(x,t)$.

Part three is about adapting the model to ionic channels with nonlinear behavior, the local voltage is controlling and controlled by the current in the cell membrane. In this part a neural membrane acts like a wave, which is shown by modeling $f(v(x,t))$ as a bi-stable system where the two states are active and inactive. The nonlinear function $f(v) = -v + \Theta(\bar{v} - h)$ will describe the ionic channels.

2 Passive Membrane

2.1 Homogeneous Stationary Solution

With $\partial_t v(x,t)$ and $j_{ext}(x,t)$ set to 0, the resulting PDE equation is as following.

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

The solution of this PDE is simply a cosh and sinh or in exponential form:

$$v(x,t) = c_1 e^{x} + c_2 e^{-x} \tag{2}$$

With this, if the bounds of v(x,t) are bounded as x approaches $\pm\infty$. The resulting solutions means that c_1 and c_2 must equal 0, thus the final solution would be $v(x,t) = 0$.

2.2 Stationary Solution with a Spatial Impulse

For a spatial impulse, j_{ext} is replaced with a $\delta(x)$. The resulting equation is Fourier transformed.

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

Each term in the equation is Fourier transformed, with the transform of $\delta(x)$ being:

$$\delta(x) \xrightarrow{\mathcal{F}} \frac{1}{2\pi}$$

The derivation of V(w,t) is as following:

$$
\begin{aligned}
&0 = (-iw)^2 V(w,t) - V(w,t) + \frac{1}{2\pi} \\
&0 = -(w^2+1)V(w,t) + \frac{1}{2\pi} \\
&(w^2+1)V(w,t) + \frac{1}{2\pi} \\
&V(w,t) = \frac{1}{2\pi(w^2+1)}
\end{aligned}
$$

The inverse Fourier transform of V(w,t) will then get the solution to this problem.

$$
v(x,t) = \int_{-\infty}^{\infty} \frac{1}{2\pi(w^2+1)} e^{-iwx} dw
$$

$$
v(x,t) = \frac{1}{2\pi} e^{-|x|} \tag{3}
$$

2.3 General Stationary Solution

The ODE now takes the form

$$
\begin{aligned}
&0 = \partial_x^2 v_A(x) - v_A(x) + j_{ext}(x) \implies \\
&-\partial_x^2 v_A(x) + v_A(x) = j_{ext}(x) \implies \\
&L v_A(x) = j_{ext}(x)
\end{aligned}
$$

where L is the linear differential operator $-\partial_x^2 - 1$. From part 2.2, we know $Lv_F(x) = \delta(x)$. The rule of translated fundamental solutions is that the argument of a fundamental solution can be translated by any amount and still give a solution. For our case, this means $Lv_F(x-s) = \delta(x-s)$ is a valid equation for all real s. This translated equation will be modified below to yield $v_A(x)$.

Multiplying the translated equation by $j_{ext}(s)$, and then integrating over all possible s (by the rule of superposition) gives the equation

$$
\int_{-\infty}^{\infty} L v_F(x-s) j_{ext}(s) ds = \int_{-\infty}^{\infty} \delta(x-s) j_{ext}(s) ds
$$

By the properties of the δ function, the right side of the above equation becomes $j(x)$. But we also know $j(x) = Lv_A(x)$. Thus

$$
L v_A(x) = \int_{-\infty}^{\infty} L v_F(x-s) j_{ext}(s) ds
$$

Since L is a *linear* differential operator and since it does not operate on s, it can be pulled outside the integral, giving

$$
L v_A(x) = L \int_{-\infty}^{\infty} v_F(x-s) j_{ext}(s) ds
$$

The linearity of L finally suggests

$$
v_A(x) = \int_{-\infty}^{\infty} v_F(x-s) j_{ext}(s) ds = \int_{-\infty}^{\infty} \frac{1}{2} e^{-|x-s|} j_{ext}(s) ds \tag{4}
$$

2.4 Using Green's Function to Solve the PDE

$$
\begin{aligned}
&\partial_t v(x,t) = \partial_x^2 v(x,t) - v(x,t) + \delta(x)\delta(t) \implies \\
&Mv(x,t) = \delta(x)\delta(t)
\end{aligned}
$$

where M is the linear differential operator $\partial_t - \partial_x^2 + 1$. Take the Fourier transform with respect to x

$$
\begin{aligned}
&\partial_t V(w,t) = -w^2 V(w,t) - V(w,t) + \frac{1}{2\pi}\delta(t) \implies \\
&2\pi(\partial_t V(w,t) + (w^2+1)V(w,t)) = \delta(t)
\end{aligned}
$$

Let L be the linear differential operator

$$L = \partial_t + \gamma$$

With $\gamma = w^2 + 1$, the transformed PDE becomes

$$2\pi L V(w,t) = \delta(t)$$

A simple derivation (not shown) shows that for some single parameterized function $u(t)$, the equation

$$Lu(t) = \delta(t)$$

has the solution

$$u(t) = \Theta(t)e^{-\gamma t}$$

where $\Theta(t)$ is the Heaviside step function. Thus with $\gamma = w^2 + 1$, the equation

$$LV(w,t) = \delta(t)$$

has the solution

$$V(w,t) = \Theta(t)e^{-(w^2+1)t}$$

Furthermore, since L is a *linear* differential operator, the equation

$$2\pi L V(w,t) = \delta(t)$$

has the solution

$$V(w,t) = \frac{1}{2\pi}\Theta(t)e^{-(w^2+1)t}$$

which satisfies the transformed PDE.

Now $V(w,t)$ must be transformed from the wave domain back to the spatial domain. Taking the inverse Fourier transform with respect to x yields

$$
\begin{aligned}
v(x,t) &= \mathcal{F}_x^{-1}(V(w,t)) \\
&= \frac{1}{2\pi}\Theta(t)e^{-t}\mathcal{F}_x^{-1}(e^{-w^2 t}) \\
&= \frac{1}{2\pi}\Theta(t)e^{-t}\sqrt{\frac{\pi}{t}}e^{-\frac{x^2}{4t}} \\
&= \Theta(t)e^{-t}\frac{1}{\sqrt{4\pi t}}e^{-\frac{x^2}{4t}} \\
&= \Theta(t)e^{-t}\mathcal{N}(x|\mu = 0, \sigma^2 = 2t)
\end{aligned}
$$

where $\mathcal{N}$ is the normal distribution. This solution for $v(x,t)$ will be called Green's function on the infinite cable and be denoted by

$$G_\infty(x,t) = \Theta(t)e^{-t}\mathcal{N}(x|\mu = 0, \sigma^2 = 2t) \tag{5}$$

Plotting Eq (5) gives the following plots at t = 0, 1, 10, and 100. The physical representation of the PDE demonstrates that giving the membrane an impulse voltage causes the voltage across the membrane to decay. Over time, the magnitude of the voltage decreases significantly, and it can be expected to reach zero as t approaches ∞ because of that leakage voltage term in the PDE.

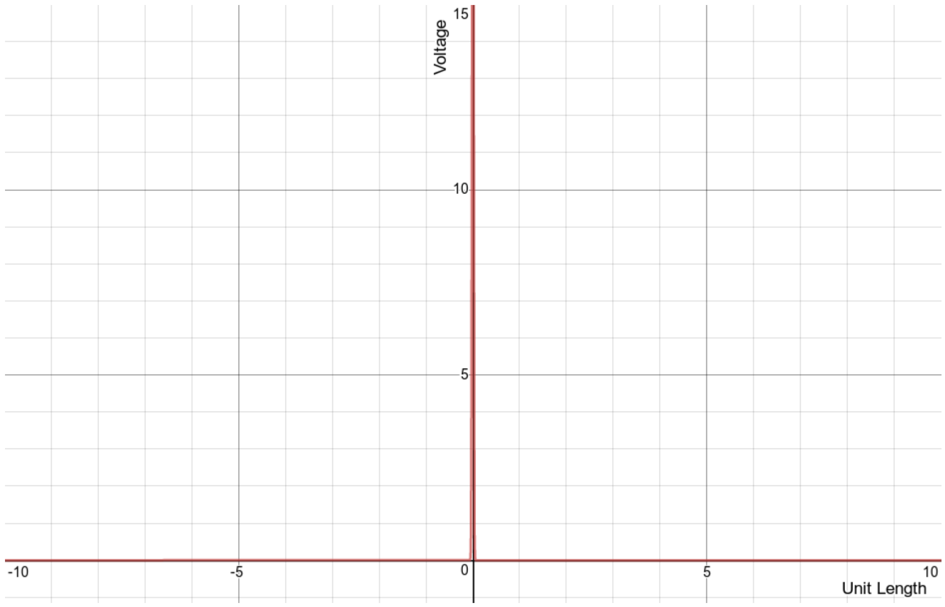

Figure 1: G_∞ at t = 0.0001

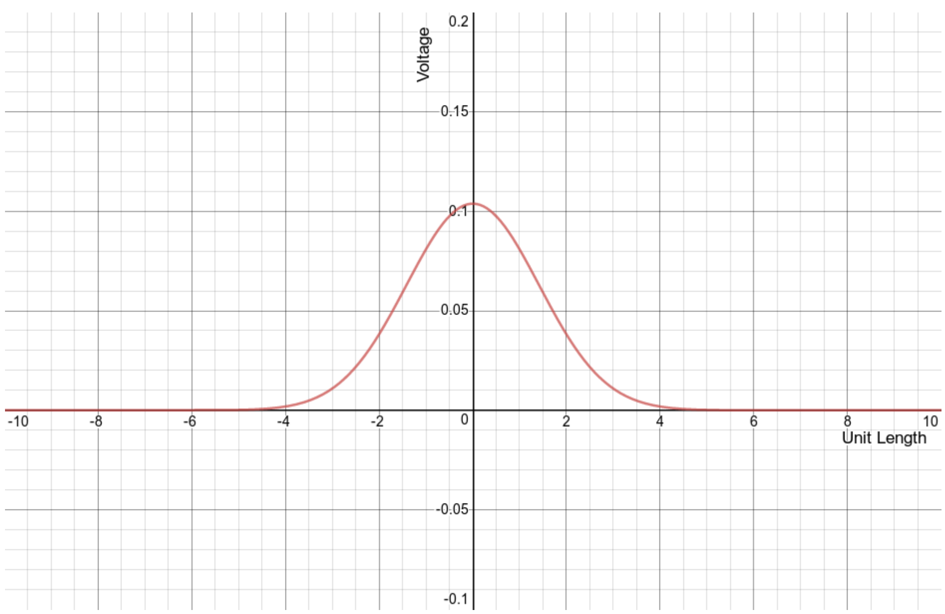

Figure 2: G_∞ at t = 1

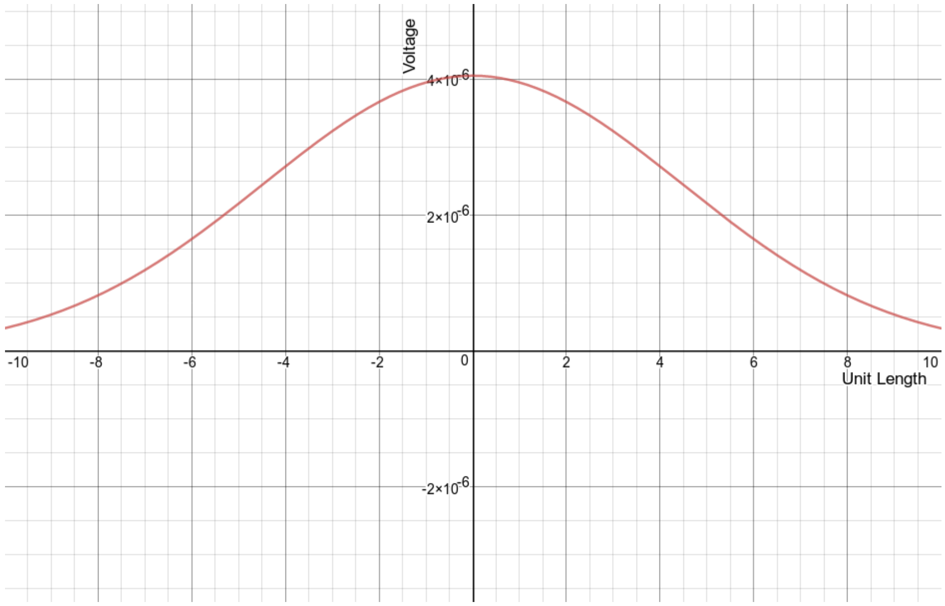

Figure 3: G_∞ at t = 10

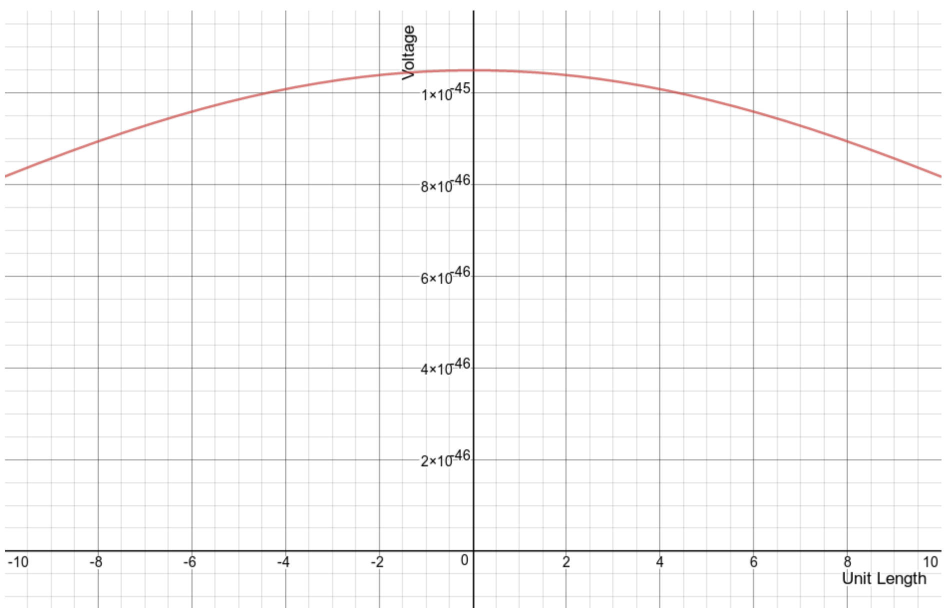

Figure 4: G_∞ at t = 100

Referring to the beginning of part (d), it is evident that

$$MG_\infty(x,t) = \delta(t)\delta(x)$$

Again for clarity, $M = \partial_t - \partial_x^2 + 1$.
At $x = 0$ and $t > 0$

$$G_\infty(x,t) = \frac{1}{\sqrt{4\pi t}} e^{-t} \tag{6}$$

The numerator decreases with time, and the denominator increases with time, so the quantity is monotone decreasing. At $x = 2$ and $t > 0$

$$G_\infty(x,t) = \frac{1}{\sqrt{4\pi t}} e^{-t-\frac{1}{t}}$$

The plot of this function (not shown) initially goes up and then comes back down, meaning that the derivative is non-monotonic.

The total voltage $\bar{G}(t)_\infty = \int_{-\infty}^{\infty} G(x,t)_\infty dx$ can be computed noting that the integral of $\mathcal{N}(x|0,2t)$ with respect to x over infinite bounds is 1 as a property of the normal distribution. Thus

$$\bar{G}(t)_\infty = \Theta(t)e^{-t} \tag{7}$$

which for $t > 0$ reduces to the monotonic decreasing function e^{-t}.

2.5 Modeling the PDE

The PDE now takes the form

$$\begin{aligned}&\partial_t v(x,t) = \partial_x^2 v(x,t) - v(x,t) + j_{ext}(x,t) \implies \\ &Mv(x,t) = j_{ext}(x,t)\end{aligned}$$

where M is the linear differential operator $\partial_t - \partial_x^2 + 1$. From part (d) we know $MG_\infty(x,t) = \delta(x)\delta(t)$. The rule of translated fundamental solutions is that the arguments of a fundamental solution can be translated by any amount and still give a solution. For our case, this means $MG_\infty(x-x', t-t') = \delta(x-x')\delta(t-t')$ is a valid equation for all real x' and t'. This translated equation will be modified below to yield $v(x,t)$.

Multiplying the translated equation by $j_{ext}(x', t')$, and then integrating over all possible x' and t' (by the rule of superposition) gives the equation

$$\iint_{-\infty}^{\infty} MG_\infty(x-x', t-t')j_{ext}(x', t')dx'dt' = \iint_{-\infty}^{\infty} \delta(x-x')\delta(t-t')j_{ext}(x', t')dx'dt'$$

By the properties of the δ function, the right side of the above equation becomes $j(x,t)$. But from the beginning of part (e) we know $j(x,t) = Mv(x,t)$. Thus

$$Mv(x,t) = \iint_{-\infty}^{\infty} MG_\infty(x-x', t-t')j_{ext}(x', t')dx'dt'$$

Since M is a *linear* differential operator and since it does not operate on x' or t', it can be pulled outside the integral, giving

$$Mv(x,t) = M\iint_{-\infty}^{\infty} G_\infty(x-x', t-t')j_{ext}(x', t')dx'dt'$$

The linearity of M finally suggests

$$v(x,t) = \iint_{-\infty}^{\infty} G_\infty(x-x', t-t')j_{ext}(x', t')dx'dt'$$

$$v(x,t) = \iint_{-\infty}^{\infty} \Theta(t-t')e^{-t+t'} \frac{1}{\sqrt{4\pi(t-t')}} e^{-\frac{(x-x')^2}{4(t-t')}} j_{ext}(x', t')dx'dt' \tag{8}$$

2.5.1 $j_{ext} = (\delta(x-1) + \delta(x+1))\delta(t)$

When setting $j_{ext} = (\delta(x-1)+\delta(x+1))\delta(t)$, the resulting integral is easy to do because the property of the delta where

$$\int g(x)\delta(x)dx = g(0)$$

As a result, the integral simply becomes

$$\begin{aligned} v(x,t) &= \iint_{-\infty}^{\infty} G_\infty(x-x', t-t')(\delta(x'-1)+\delta(x'+1))\delta(t')dx'dt' \\ &= \int_{-\infty}^{\infty} G_\infty(x-x', t)(\delta(x'-1)+\delta(x'+1))dx' \\ &= G_\infty(x-1,t) + G_\infty(x+1,t) \end{aligned}$$

$$v(x,t) = \Theta(t)e^{-t}\frac{1}{\sqrt{4\pi(t)}}e^{-\frac{(x-1)^2}{4(t)}} + \Theta(t)e^{-t}\frac{1}{\sqrt{4\pi(t)}}e^{-\frac{(x+)^2}{4(t)}} \tag{9}$$

The plot of Eq (9) is similar to just one delta, where the voltage decays, but the one interesting factor is what occurs at x = 0. The membrane at the center sees an increase of voltage, but then decays again. Physically, it may represent the membrane voltage that was leaking from nearby, being added up.

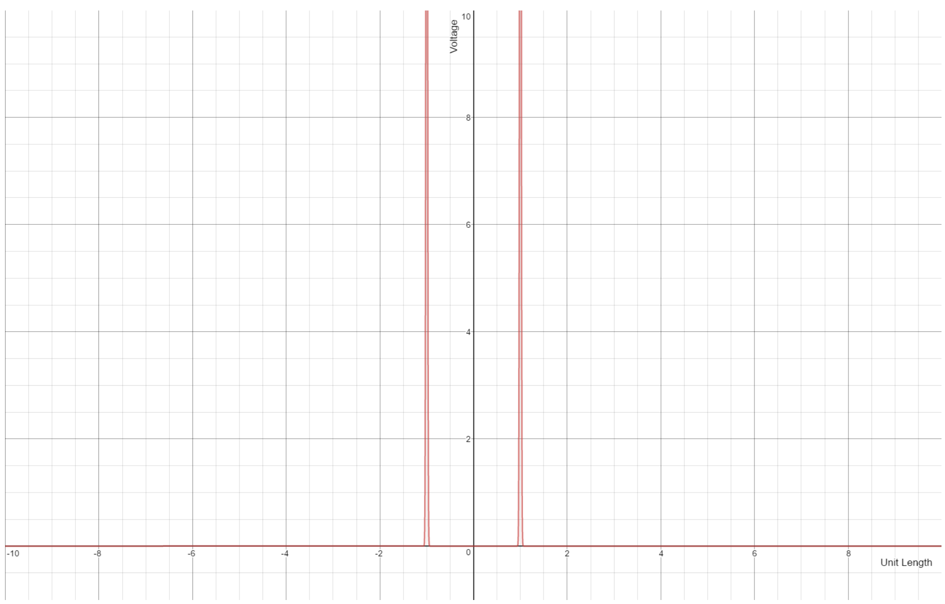

Figure 5: G_∞ at t = 0.0001

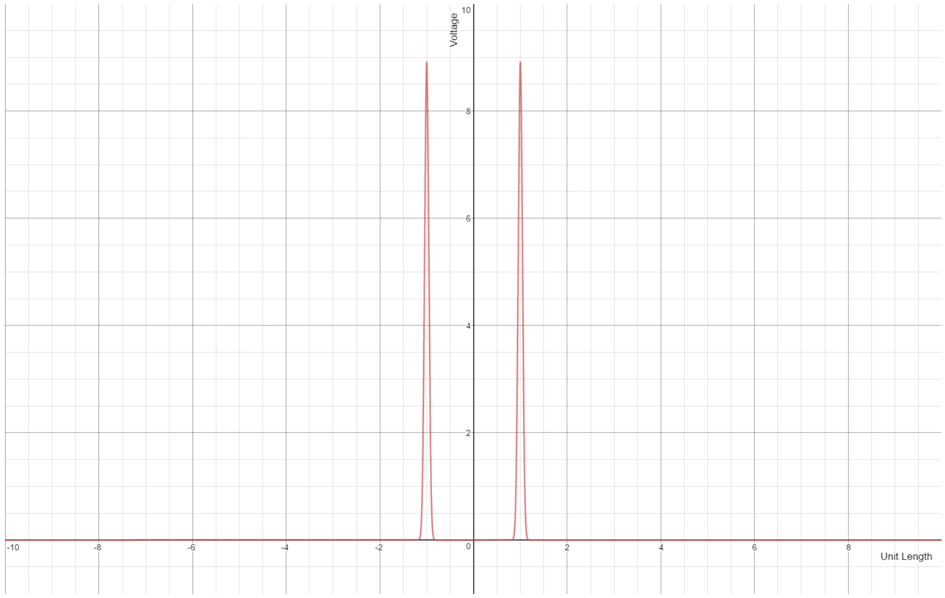

Figure 6: G_∞ at t = .001

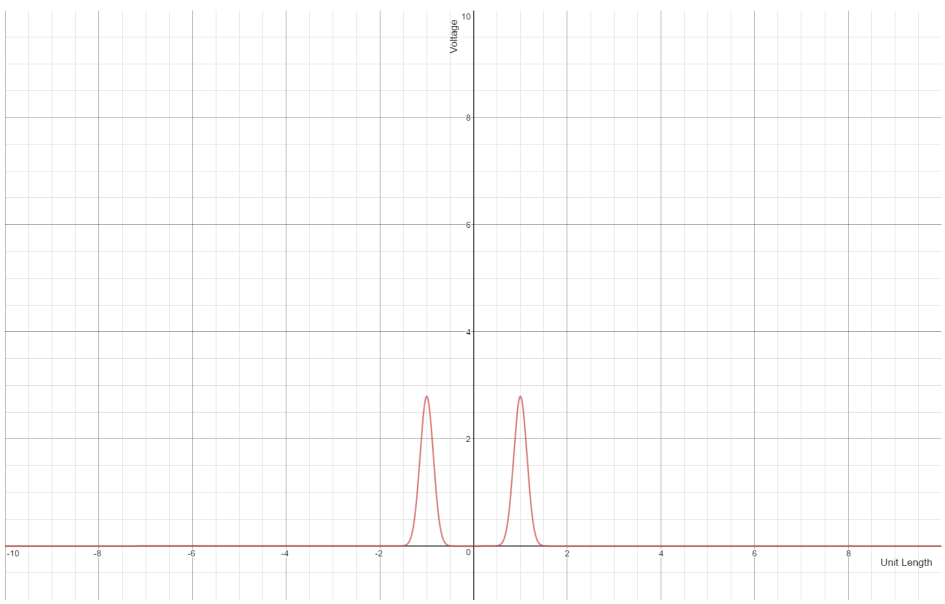

Figure 7: G_∞ at t = .01

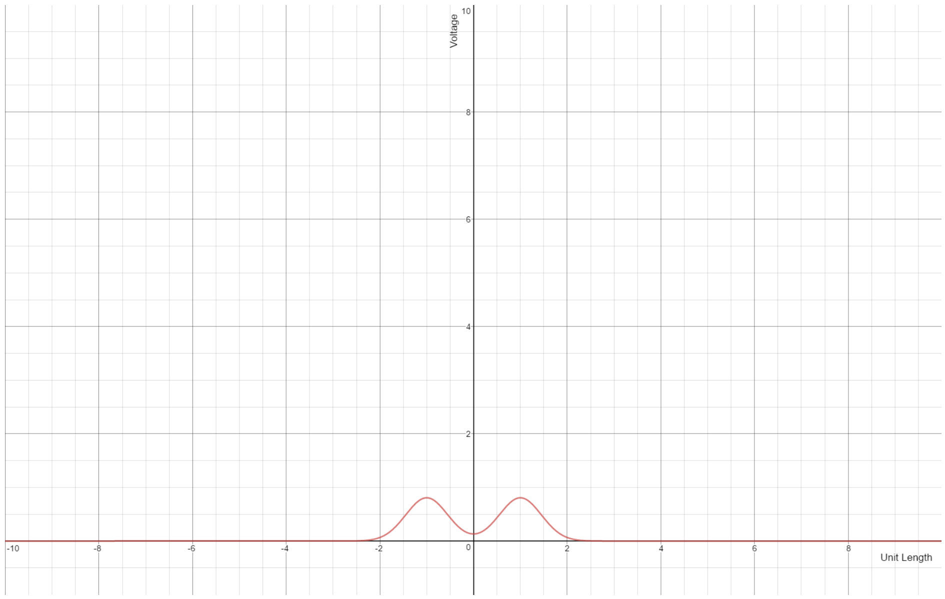

Figure 8: G_∞ at t = .1

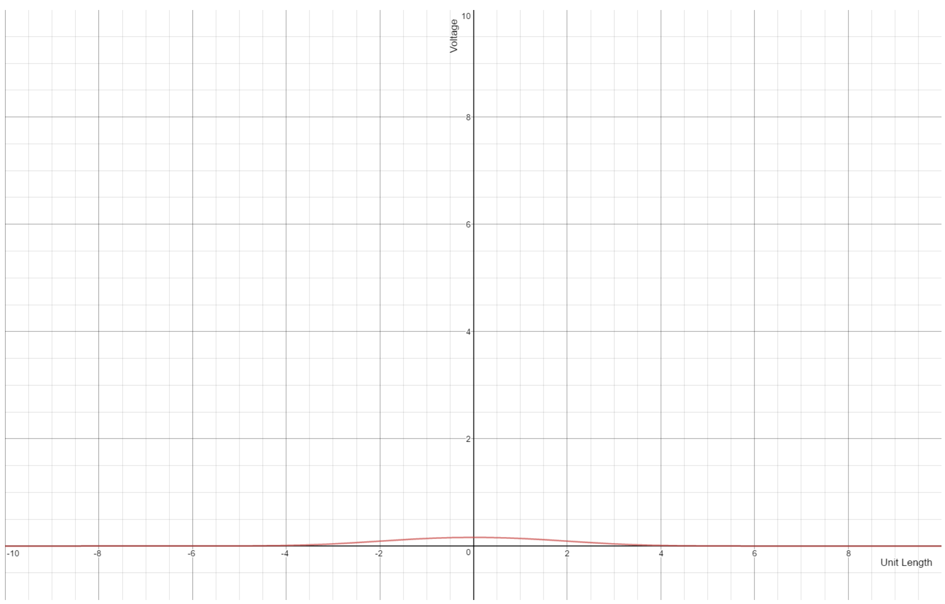

Figure 9: G_∞ at t = 1

2.5.2 $j_{ext} = Sin(x)$

Thus, the resulting equation for the first plot ($j_{ext}(x,t)$ =sin(x)) is:

$$\begin{aligned} v(x,t) &= \iint_{-\infty}^{\infty} \Theta(t-t')e^{-t+t'} \frac{1}{\sqrt{4\pi(t-t')}} e^{-\frac{(x-x')^2}{4(t-t')}} \sin(x) dx' dt' \\ &= \int_{-\infty}^{\infty} \Theta(t-t')e^{-t+t'} \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi(t-t')}} e^{-\frac{(x-x')^2}{4(t-t')}} \sin(x) dx' dt' \end{aligned}$$

The dx' integral is convolution in the time domain.

$$\sin(x') \xrightarrow{\mathcal{F}} \frac{\delta(w-1)-\delta(w+1)}{4i\pi}$$

$$\frac{1}{\sqrt{4\pi(t-t')}}e^{-\frac{(x-x')^2}{4(t-t')}} \xrightarrow{\mathcal{F}} \frac{1}{2}e^{-(w'^2)(t-t')}$$

Using the Fourier property

$$g(x) * f(x) \xrightarrow{\mathcal{F}} 2\pi G(w)F(w)$$

v(x,t) in the Fourier domain becomes:

$$\begin{aligned} V(w,t) &= \frac{1}{4i}\int_{-\infty}^{\infty}\Theta(t-t')e^{-t+t'}e^{-(w'^2)(t-t')}[\delta(w-1)-\delta(w+1)]dt' \\ &= \frac{1}{4i}[\delta(w-1)-\delta(w+1)]\int_{-\infty}^{t}e^{-(t-t')(w^2+1)}dt' \end{aligned}$$

because

$$\int_{-\infty}^{t}e^{-(t-t')(w^2+1)}dt' = 1$$

$$V(w,t) = \frac{1}{4i}[\delta(w-1)-\delta(w+1)]$$

The inverse Fourier transform of V(w,t) is

$$v(x,t) = \frac{\sin x}{2} \tag{10}$$

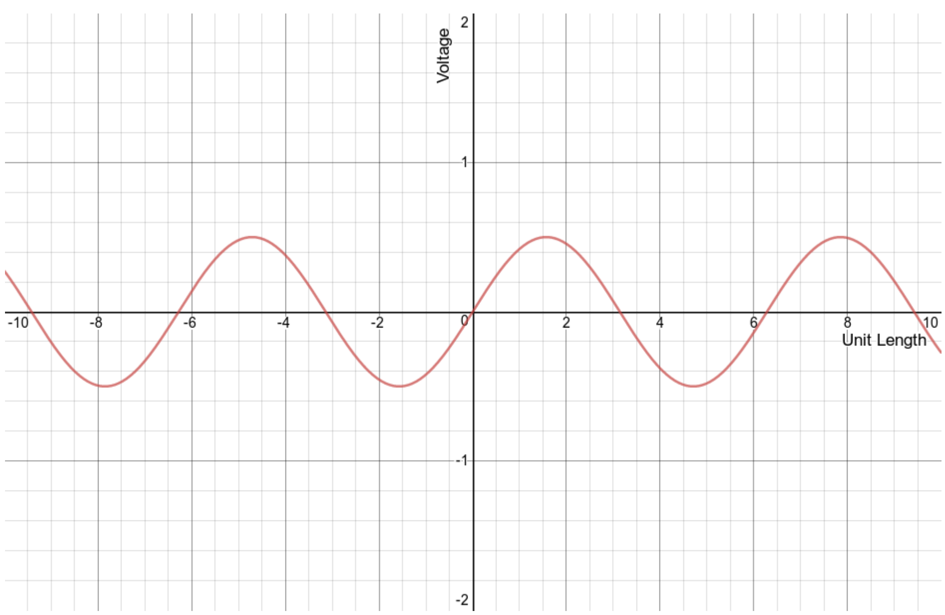

Figure 10: Solution to the PDE when $J_{ext} = sin(x)$

2.5.3 $j_{ext} = 1$

$$
\begin{aligned}
v(x,t) &= \iint_{-\infty}^{\infty} \Theta(t-t')e^{-t+t'} \frac{1}{\sqrt{4\pi(t-t')}} e^{-\frac{(x-x')^2}{4(t-t')}} dx'dt' \\
&= \int_{-\infty}^{\infty} \Theta(t-t')e^{-t+t'} \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi(t-t')}} e^{-\frac{(x-x')^2}{4(t-t')}} dx'dt'
\end{aligned}
$$

The dx' integral of the normal distribution from negative to positive infinity is equal to 1.

$$
\begin{aligned}
v(x,t) &= \int_{-\infty}^{\infty} \Theta(t-t')e^{-t+t'} dt' \\
&= \int_{-\infty}^{t} e^{-t+t'} dt'
\end{aligned}
$$

$$v(x,t) = 1 \tag{11}$$

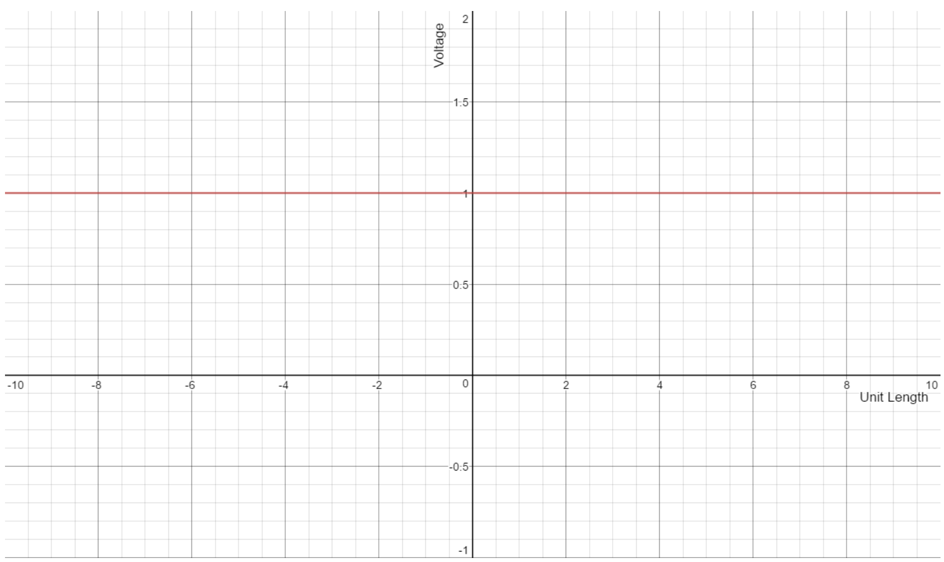

Figure 11: Solution to the PDE when $J_{ext} = 1$

2.6 Finite Difference Approximation of the Passive Membrane

Using the resources provided, the PDE was transformed using the explicit method. Using the heat equation example, the code was rewritten to follow the PDE.

```
clear;

%Input Parameters
Jext = ''; %Options: init, 2△, sin, 1
timePlots = [1 ;10; 50; 100; 250; 1000; 10000];
axisValues = [-10 10 0 1]; % Xmin Xmax Ymin Ymax

% Parameters to define the equation and the range in space and time
L = 20; % Length of the wire
T = 50; % Final time

% Parameters needed to solve the equation within the explicit method
```

```
dt = .001;
dx = .1;
timeSteps = T/dt; % Number of time steps
spaceSteps = L/dx; % Number of space steps

%defining the real x and t values
xValues = -10:dx:10;
tValues = 0:dt:50;

% Initial Condition
for x = 1:spaceSteps+1
    if strcmp(Jext, 'init')
        V(x,1) = 10*exp(-25*xValues(x)^2);  %init impulse at the center
    elseif strcmp(Jext, 'sin') || strcmp(Jext, '1')
        V(x,1) = 0;  %No initial conditions when sin(x) or 1
    elseif strcmp(Jext, '2∆')
        if(xValues(x) == 1 || xValues(x) == -1)
            V(x,1) = 1; %Impulses at t = 0 and x = 1 and x = -1
        else
            V(x,1) = 0;
        end;
    end
end

% Implementation of the explicit method
for t=1:timeSteps % Time Loop
    for x=2:spaceSteps; % Space Loop
        V(x,t+1) = (dt/(dx*dx))*(V(x+1,t) - 2*V(x,t) + V(x-1,t)) - ...
            (dt*V(x,t)) + V(x,t);

        if strcmp(Jext, 'sin') %Adding Jext if needed
            V(x,t+1) = V(x,t+1) + dt*sin(xValues(x));
        elseif strcmp(Jext, '1')
            V(x,t+1) = V(x,t+1) + dt*1;
        end

    end
end

% Graphical representation of the voltage at different selected times
figure(1)
timeLegends = timePlots*dt;
suptitle('Passive Membrane when Jext = );

subplot(1,2,1);
plot(xValues,V(:,timePlots(1)),'-',...
    xValues,V(:,timePlots(2)),'-',...
    xValues,V(:,timePlots(3)),'-',...
    xValues,V(:,timePlots(4)),'-',...
    xValues,V(:,timePlots(5)),'-',...
    xValues,V(:,timePlots(6)),'-','LineWidth',3)

%Plot Cleanup
legend(strcat(num2str(timeLegends), ' seconds'));
xlabel('X');ylabel('V')
subplot(1,2,2);
mesh(xValues,tValues,V')
xlabel('X');ylabel('Time');zlabel('V')
```

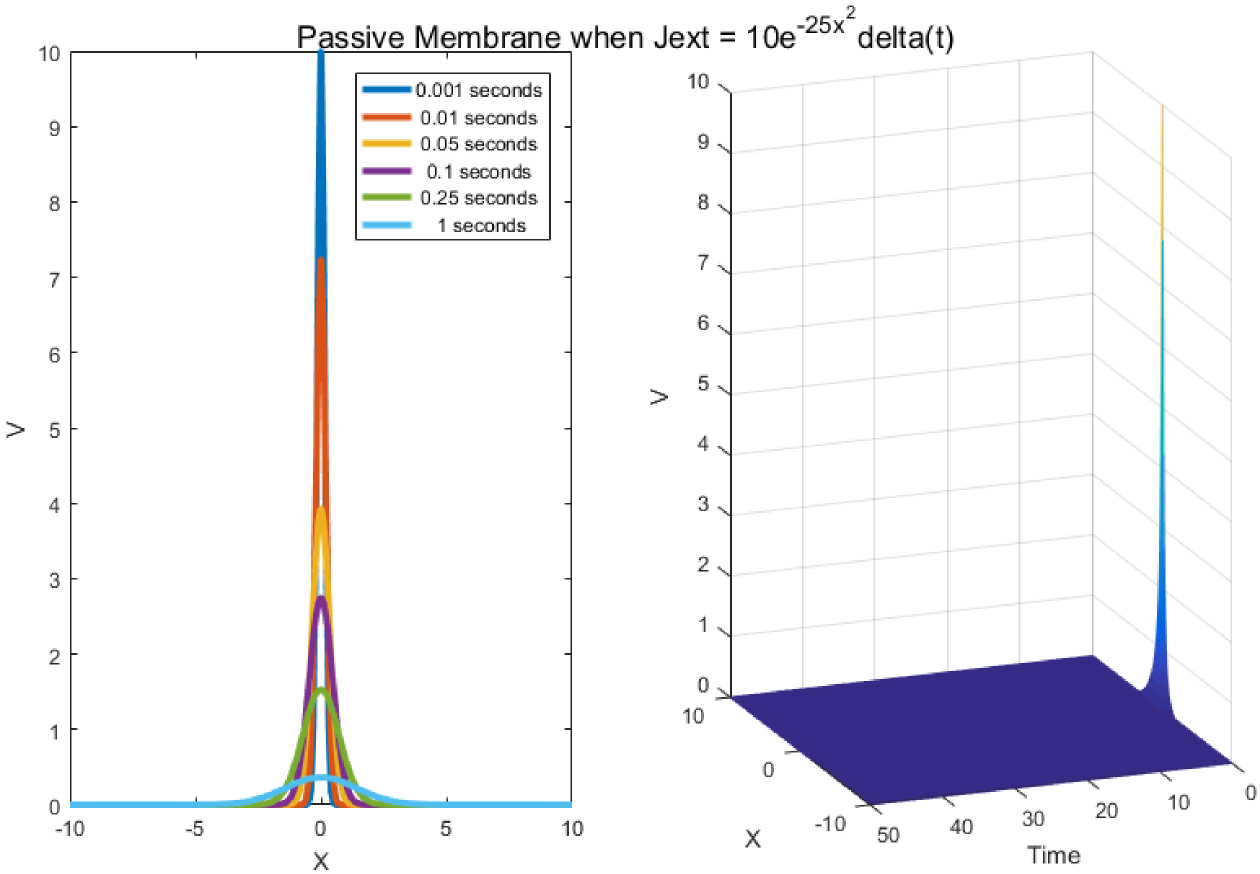

Figure 12: $J_{ext} = 10e^{-25x^2}\delta(t)$

With an initial delta at time $= 0$, the overall membrane will see the voltage have an exponential decay. It is a very short amount of time until the entire membrane is back at equilibrium, seeing that the entire voltage across the membrane is 0 at around 2 seconds. This is similar to the plot when simulating an impulse at $\delta(x)\delta(t)$ since the voltage where the impulse was is decreasing very quickly.

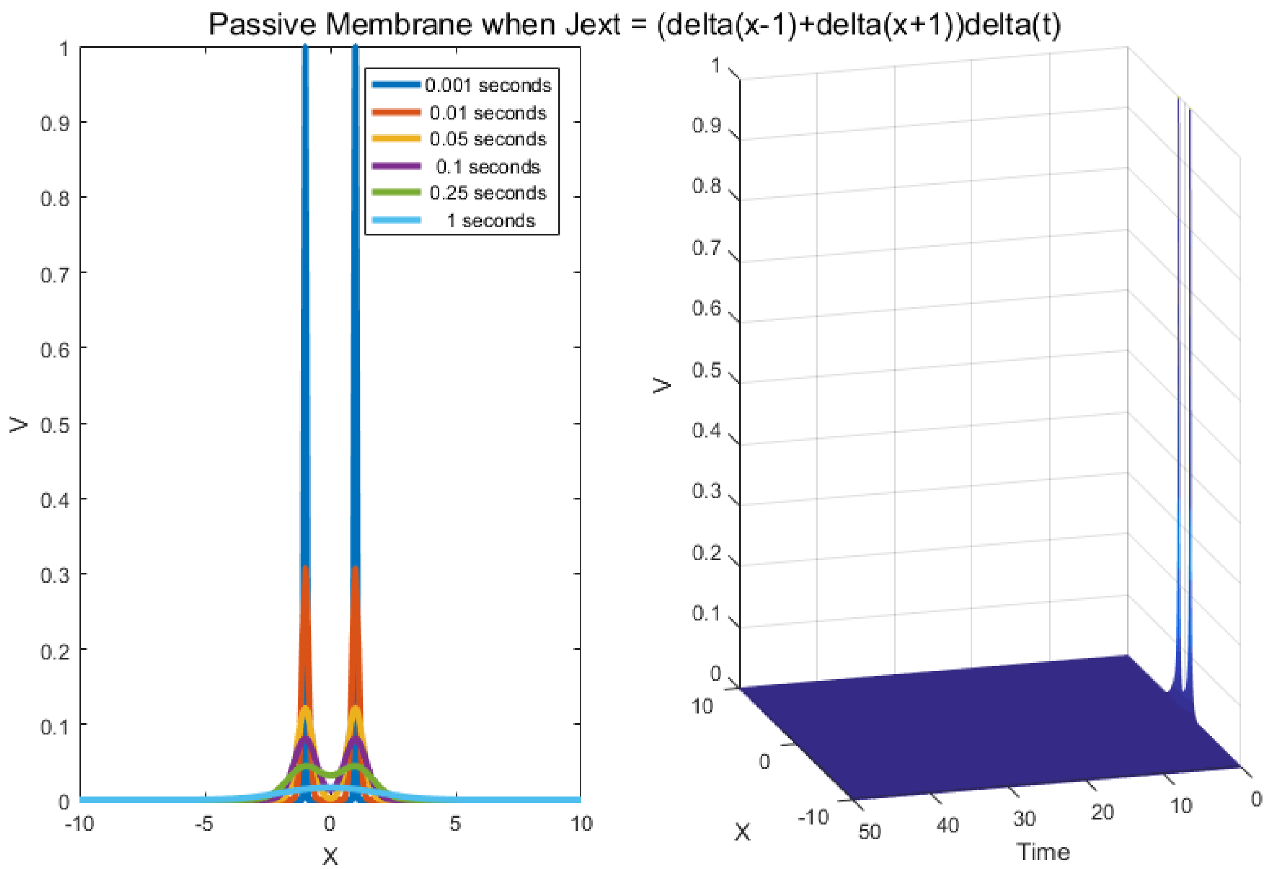

Figure 13: $J_{ext} = (\delta(x-1) + \delta(x+1))\delta(t)$

With two impulses, the membrane follows a similar pattern to a single impulse. The only difference is that as the two voltages decrease, the membrane at the center sees an increase in its voltage due to its neighbor. Similar to the first simulation, the membrane quickly equalizes back to 0 volts. This can be seen in Eq (9), where the center membrane sees an increase in voltage and then decreases again at around t = .1.

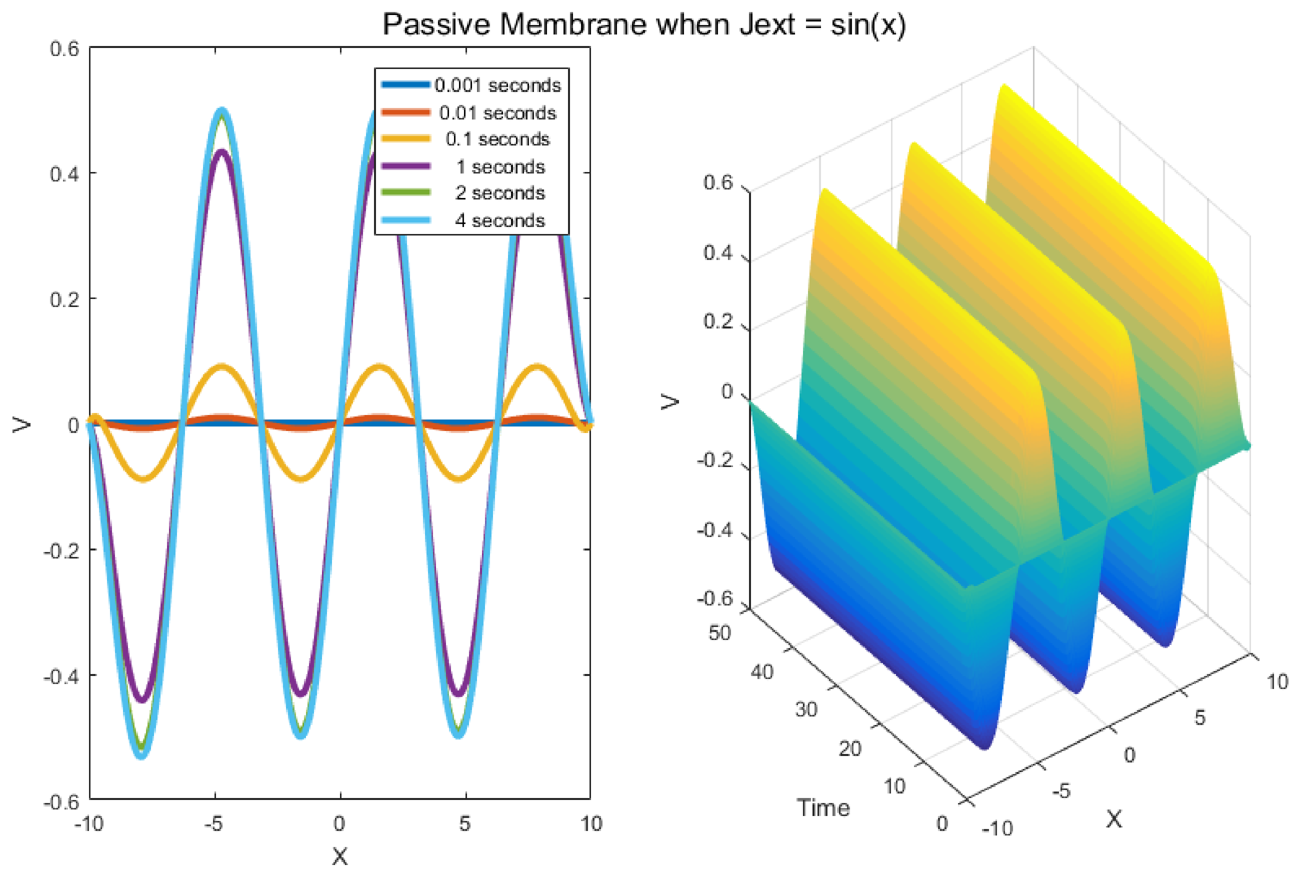

Figure 14: $J_{ext} = sin(x)$

Unlike the impulses, the membrane is seeing a continuous increase in the voltage from the sin input. Thus, over time, the voltage across the membrane is simply a sine function, with its magnitude cut in half. Seeing the previous image, it matches the overall shape from the calculations done. The one interesting thing to note is the gradual increase of the membrane. Instead of immediately starting with a magnitude of 1/2, the membrane sees a slow increase in voltage. This may be an issue with the finite dimensional representation of the PDE.

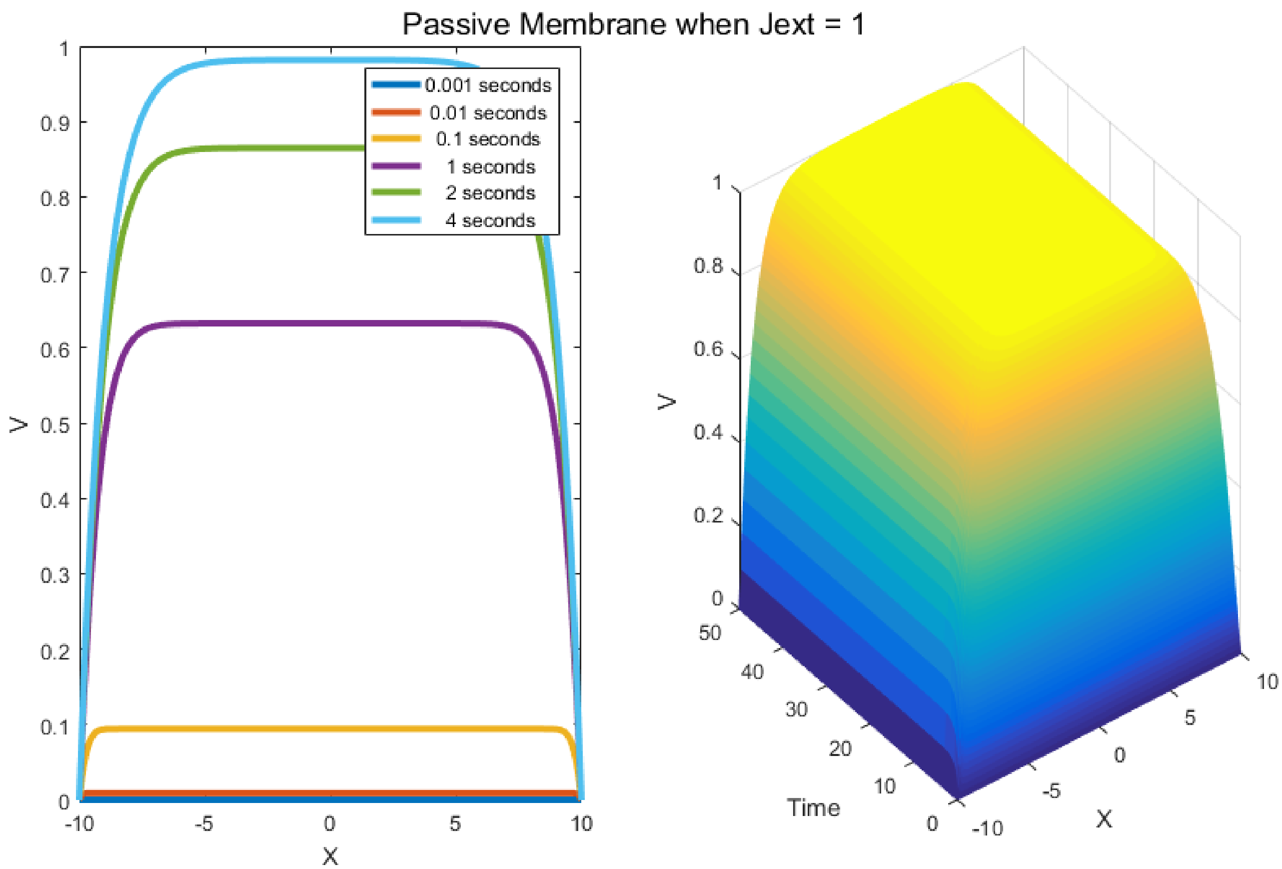

Figure 15: $J_{ext} = 1$

Like the sine function, a constant values cause the membrane to hit an overall 1 volts across the membrane, except for the extremes. At the boundaries, there is a sharp curve.

When adjusting the Δt value, too large of a value causes oscillations and instability where decreasing the Δt value causes the entire Matlab program to freeze up so it is hard to say what would happen when increasing the Δt value. It is possible to predict that it would be a more accurate representation.

3 Traveling Wave Solutions

3.1 Homogeneous Solutions

We identify the two possible constant solutions for v, $\bar{v}^+$ and $\bar{v}^-$, satisfying the homogeneous version of equation (reference). In the analytical part of this project I will denote the threshold by h, while in the simulations and plot the threshold is denoted by θ.

$$\begin{aligned} &0 = 0 - \bar{v} + \Theta(\bar{v} - h) + 0 \implies \\ &\bar{v} = \Theta(\bar{v} - h) \end{aligned}$$

For $\Theta = 1$, $\bar{v} - h > 0 \implies \bar{v} > h$. In this case, $\bar{v} = \bar{v}^+ = 1$, and so $1 > h$.
For $\Theta = 0$, $\bar{v} - h < 0 \implies \bar{v} < h$. In this case, $\bar{v} = \bar{v}^- = 0$, and so $0 < h$.
Thus the two solutions are $\bar{v}^+ = 1$ and $\bar{v}^- = 0$ and the condition on h is $0 < h < 1$.

3.2 Change of Variables

We make a change of variables $v(x, t) \to z(\xi)$, $\xi = x - ct$. This implies $\partial_t v = -cz'$ and $\partial_x^2 v = z''$. The boundary conditions also change from $\lim_{x\to\pm\infty} \partial_x v = 0$ to $\lim_{\xi\to\pm\infty} z' = 0$. The PDE becomes

$$-cz' = z'' - z + \Theta(z - h) \tag{12}$$

3.3 Solving for the Shape of the Wave

To begin solving the new PDE, we consider the two cases for $\Theta(z - h)$:

- $\Theta(z - h) = 1 \implies z - h > 0 \implies z > h$. By assumption, this occurs when $\xi < 0$.
- $\Theta(z - h) = 0 \implies z - h < 0 \implies z < h$. By assumption, this occurs when $\xi > 0$.

As a result of these two cases, we correspondingly break the PDE into two different PDEs. We will be solving for the two corresponding traveling wave solutions. For these two solutions to resemble a single wave, they must share the same value at $\xi = 0$. For the resembled wave to have a single velocity at $\xi = 0$. These boundary conditions are not listed in the piecewise representation below. The ODE can be written piecewise as

- For $\xi < 0$:

$$\begin{aligned} &-cz_1' = z_1'' - z_1 + 1 \\ &\lim_{\xi\to-\infty} z_1' = 0, \ \lim_{\xi\to-\infty} z_1 = \bar{v}^+|\bar{v}^- \end{aligned}$$

- For $\xi > 0$:

$$\begin{aligned} &-cz_2' = z_2'' - z_2 \\ &\lim_{\xi\to\infty} z_2' = 0, \ \lim_{\xi\to\infty} z_2 = \bar{v}^-|\bar{v}^+ \end{aligned}$$

3.4 Solving the ODE

- For $\xi > 0$: Let $z_2(\xi) = \exp(r\xi)$. Then

$$\begin{aligned} &r^2 + cr - 1 = 0 \implies 2r = -c \pm \sqrt{c^2 + 4c^2} \\ &r_1 = -\frac{1}{2}(c + \sqrt{c^2 + 4}) < 0, \ r_2 = -\frac{1}{2}(c - \sqrt{c^2 + 4}) > 0 \implies \\ &z_2(\xi) = a(c)\exp(r_1\xi) + b(c)\exp(r_2\xi) \end{aligned}$$

  Considering the boundary condition $\lim_{\xi\to\infty} z_2' = 0$ leaves

$$z_2(\xi) = a(c)\exp(r_1\xi)$$

  and the second boundary condition holds as $\lim_{\xi\to\infty} z_2 = 0 = \bar{v}^-$

- For $\xi < 0$: The homogeneous solution take the the same general form as the solution z_2

$$h_1(\xi) = a(c)\exp(r_1\xi) + b(c)\exp(r_2\xi)$$

Considering the boundary condition $\lim_{\xi\to-\infty} z_1' = 0$ leaves $h_1(\xi) = b(c)\exp(r_2\xi)$. A particular solution is evidently 1. So the full solution is

$$z_1(\xi) = b(c)\exp(r_2\xi) + 1$$

and the second boundary condition holds as $\lim_{\xi\to-\infty} z_1 = 1 = \bar{v}^+$

Now we apply the conditions that the $z_1(0) = z_2(0)$ and $z_1'(0) = z_2'(0)$.

$$\begin{aligned} z_1(0) = z_2(0) &\implies b(c) + 1 = a(c) \\ z_1'(0) = z_2'(0) &\implies r_2 b(c) = r_1 a(c) \end{aligned}$$

Solving this system of equations yields

$$a(c) = \frac{r_2}{r_2 - r_1},\ b(c) = \frac{r_1}{r_2 - r_1}$$

Simplifying $a(c)$ and $b(c)$, $z(\xi)$ can be written piecewise as

$$z(\xi) = \begin{cases} -\frac{1}{2}(\frac{c}{\sqrt{c^2+4}} + 1)\exp(-\frac{1}{2}(c - \sqrt{c^2+4})\xi) + 1 & \xi < 0 \\ -\frac{1}{2}(\frac{c}{\sqrt{c^2+4}} - 1)\exp(-\frac{1}{2}(c + \sqrt{c^2+4})\xi) & \xi > 0 \end{cases}$$

3.5 Speed of the Traveling Front

We now solve for c in terms of h by applying the assumption that $z(0) = h$.

$$\begin{aligned} z(0) = h &\implies \frac{r_2}{r_2 - r_1} = h \\ &\implies \ldots\text{algebra}\ldots \implies \\ c &= \pm\frac{2h-1}{\sqrt{h(1-h)}} \end{aligned}$$

With $0 < h < 1$, the numerator has the range $(-1, 1)$. The denominator has the range $(0, 1/2]$. Thus c has the range $(-\infty, \infty)$. There are two options for the sign of c. In the inactive state of $h \to 1$, $v(\xi) \to 0$ and by previous analysis this means $\xi \to \infty$. But $\xi \to \infty$ implies $c \to -\infty$. Thus we can choose the sign for c such that $c \to -\infty$ as $h \to 1$. The negative sign is the appropriate choice. That is,

$$c = \frac{1-2h}{\sqrt{h(1-h)}}$$

To make sense of this further, consider a low threshold so that the axon is active. In this case, the voltage approaches the homogeneous solution of equilibrium 1. This homogeneous solution appears as $\xi \to -\infty$, and hence as $c \to \infty$. In other words, an active membrane occurs with a jump in voltage to the higher equilibrium.

3.6 Linear Stability Solution

Given the PDE with $v = v(x, t)$

$$\partial_t v = \partial_x^2 v + f(v),\ f(v) = -v + \Theta(v - h)$$

we make the change $v(x,t) \to z(\xi) + \epsilon\psi(\xi,t)$.

$$\begin{aligned}
&\partial_t v = \partial_\xi z \partial_t \xi + \epsilon(\partial_\xi \psi \partial_t \xi + \partial_t \psi) = -cz' - c\epsilon\partial_\xi\psi + \epsilon\partial_t\psi \\
&\partial_x v = \partial_\xi z \partial_x \xi + \epsilon(\partial_\xi \psi \partial_x \xi + 0) = z' + \epsilon\partial_\xi\psi \\
&\partial_x^2 v = z'' + \epsilon\partial_\xi^2\psi \\
&f(v(x,t)) = f(z(\xi) + \epsilon\psi(\xi,t))
\end{aligned}$$

We will Taylor expand f around z and since ϵ is small, we will only expand to a linear function.

$$\begin{aligned}
&f(z+\epsilon\psi) \approx f(z) + \epsilon\psi f'(z) \\
&f(z) = -z + \Theta(z-h) \\
&f'(z) = -1 + \Theta(z-h) = -1 + \frac{\Theta(\xi)}{|z'(0)|}
\end{aligned}$$

where the last equality follows from a property of the dirac function that exploits 0 as a root of $z(\xi) - h$. Writing out the PDE with the change of variables gives

$$\begin{aligned}
&-cz' - c\epsilon\partial_\xi\psi + \epsilon\partial_t\psi = z'' + \epsilon\partial_\xi^2\psi - z + \Theta(z-h) + \epsilon\psi(-1 + \frac{\Theta(\xi)}{|z'(0)|}) \implies \\
&-c\epsilon\partial_\xi\psi + \epsilon\partial_t\psi = \epsilon\partial_\xi^2\psi - \epsilon\psi + \epsilon\psi\frac{\Theta(\xi)}{|z'(0)|}) = 0 \implies \\
&\partial_\xi^2\psi + c\partial_\xi\psi - \partial_t\psi - \psi + \psi\frac{\Theta(\xi)}{|z'(0)|}) = 0
\end{aligned}$$

Using separation of variables, $\psi(\xi,t) = g(\xi)h(t)$. Plugging back into the PDE and using separation constant λ, this yields

$$\begin{aligned}
&h'(t) = \lambda h(t) \\
&g''(\xi) + cg(\xi) - v'(\xi)(\lambda+1) + v'(\xi)\frac{\delta(\xi)}{|z'(0)|}) = 0
\end{aligned}$$

This means $h(t) = e^{\lambda t}$. For the solution to be stable in the case of a perturbation, $h(t)$ must not grow over time. That is, $\lambda \leq 0$. So clearly, solutions exist of the form $\psi(\xi,t) = g(\xi)e^{\lambda t}$ for $t < 0$. For a solution that does not grow over time, but does not decay either, occurs with $\lambda = 0$. In this case, $\psi(\xi,t) = g(\xi)$. Below it is verified that $g(\xi) = z'(\xi)$ is such a solution. Plugging in z' for g and integrating over infinite bounds gives

$$\begin{aligned}
&v''(\infty) - v''(-\infty) + cv'(\infty) - cv'(-\infty) - (v(\infty) - v(-\infty))(\lambda+1) \\
&\quad + \int_{-\infty}^{\infty} \frac{v'(\xi)\delta(\xi)}{|v'(0)|} d\xi \implies = 0 \\
&0 - 0 + c(0) - c(0) - (0-1)(\lambda+1) - 1 \implies \lambda = 0
\end{aligned}$$

confirming the assumption that $\lambda = 0$. The last implication occurs noting that $v'(0) < 0$.

3.7 Finite Difference Approximation of the Traveling Wave

The Matlab code solves the partial differential equation of the traveling wave. Theta is threshold that determines whether the axon is active or inactive overtime. The areas of the axon that have voltage less than the threshold at time 0 becomes in active voltage. The areas of the axon that have greater voltage than the threshold at time zero stay active at 1 volt. For the second plot we compute the value of c.

```
%Might try this for initial condition:
clear;
```

```
%Input Parameters
timePlots = [1 ;50; 100; 501; 25000];
axisValues = [-10 10 -10 10]; % Xmin Xmax Ymin Ymax
theta = .2;

% Parameters to define the equation and the range in space and time
L = 20; % Length of the wire
T = 50; % Final time

% Parameters needed to solve the equation within the explicit method
dt = .001;
dx = .1;
timeSteps = T/dt; % Number of time steps
spaceSteps = L/dx; % Number of space steps

%defining the real x and t values
xValues = -10:dx:10;
tValues = 0:dt:50;

%Initial Condition
for x = 1:101
    V(x,1) = .8;
end

for x = 102:201
    V(x,1) = .2;
end



%Implementation of the explicit method
for t = 1:timeSteps
    for x = 2:spaceSteps
        V(x,t+1) = (dt/(dx*dx))*(V(x+1,t) - 2*V(x,t) + V(x-1,t)) - ...
         (dt*V(x,t)) + dt*heaviside(V(x,t) - theta) + V(x,t);
    end
end

%create matrices
XX(1,1) = 0;
YY(1,1) = 0;

% computing c
% v(0) = theta
% 0 = x-ct
%c=x/t
count = 0;
for t = 1: timeSteps
    for x = 1:spaceSteps
        if(V(x,t)< (theta + .00001) && V(x,t)>(theta - .00001))
            count = count +1;
            XX(count)=x;
            YY(count)=t;
        end
    end
end

 c = xValues(XX)./tValues(YY);

% Graphical representation of the voltage at different selected times
figure(1)
suptitle('Traveling Wave Solution');
subplot(1,2,1);

timeLegends = timePlots*dt;
plot(xValues,V(:,timePlots(1)),'-',...
    xValues,V(:,timePlots(2)),'-',...
```

```
    xValues,V(:,timePlots(3)),'-',...
    xValues,V(:,timePlots(4)),'-',...
    xValues,V(:,timePlots(5)),'-')

%Plot Cleanup
legend(strcat(num2str(timeLegends), ' seconds'));
xlabel('X');ylabel('V')

subplot(1,2,2);
mesh(xValues,tValues,V')
xlabel('Distance');ylabel('Time');zlabel('V')
```

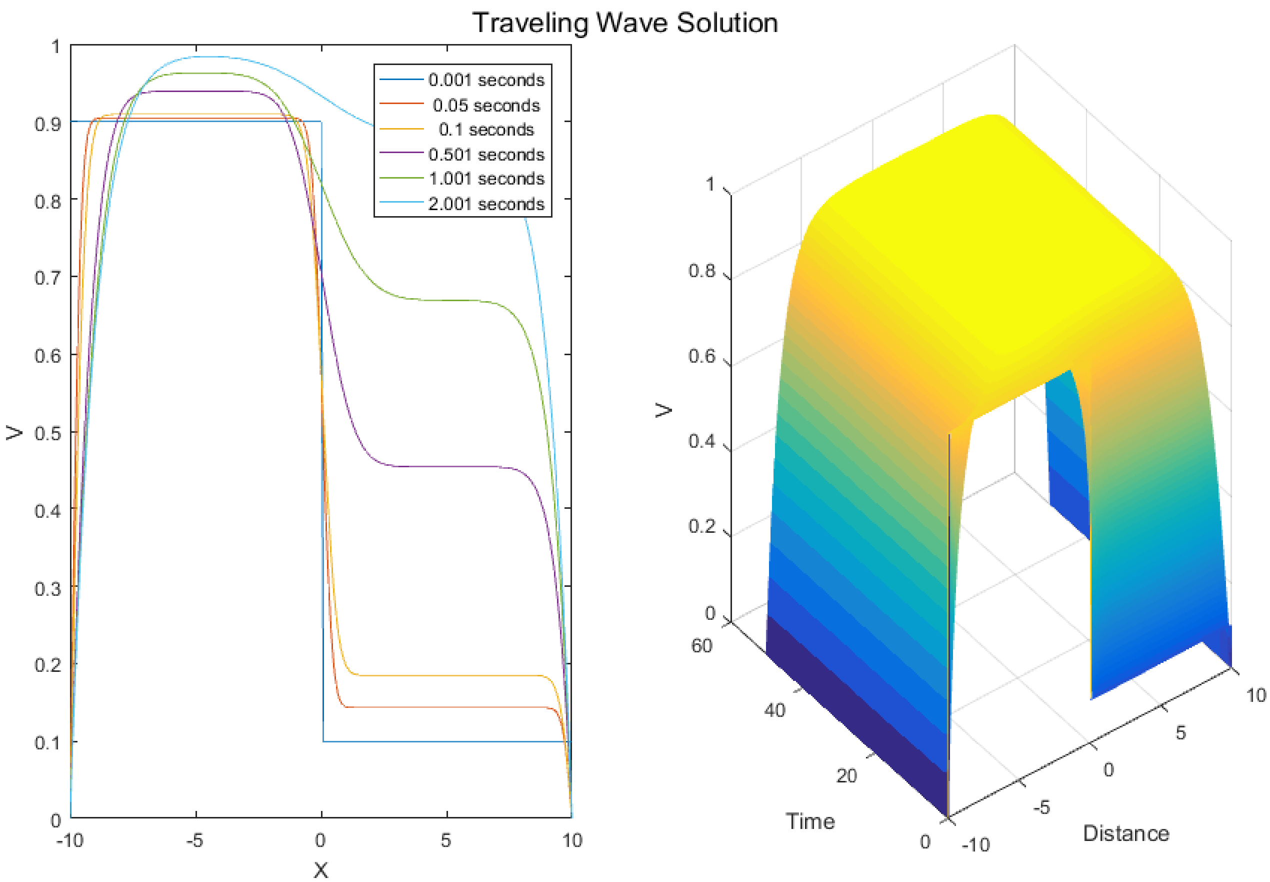

Figure 16: $\theta = 0.05$, $v(x, 0) = 0.9$ when $x < 0$ and $v(x, 0) = 0.1$ when $x > 0$

In this plot, the theta value is lower than the voltage across the membrane, and thus, it is seen that the voltage overall increases throughout the membrane. In addition, when looking at the points at x = 0, the overall front of the wave propagates to the right.

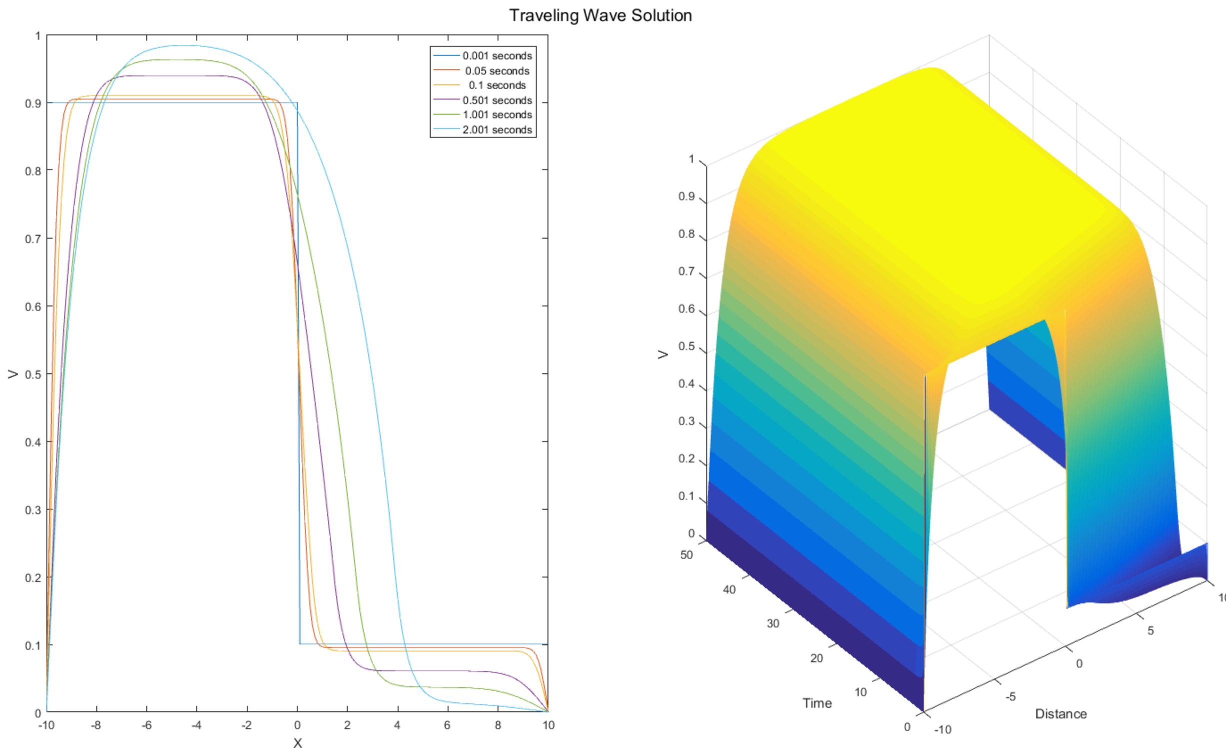

Figure 17: $\theta = 0.2$, $v(x, 0) = 0.9$ when $x < 0$ and $v(x, 0) = 0.1$ when $x > 0$

Now with the threshold above 0.2, the membrane that is below the threshold voltage decays. Looking at x = 0, the front of the wave is traveling to the right. In order to calculate the speed, the intersection of the wave at 0.001 seconds and 0.05 seconds and then calculate the speed. We choose this graph to compute the speed of the traveling front, c. As the front moves to the right, for every adjacent pair of lines, we compute the change in x divided by the change in t along a horizontal line (we choose the line $v = 0.1$). Given a computation of c for ever adjacent pair of lines, we take the average of these c computations and our result is ≈ 1.5. This makes sense because this graph has a threshold of 0.2 and computing c analytically from $\theta = 0.2$ yields $c = 1.5$.

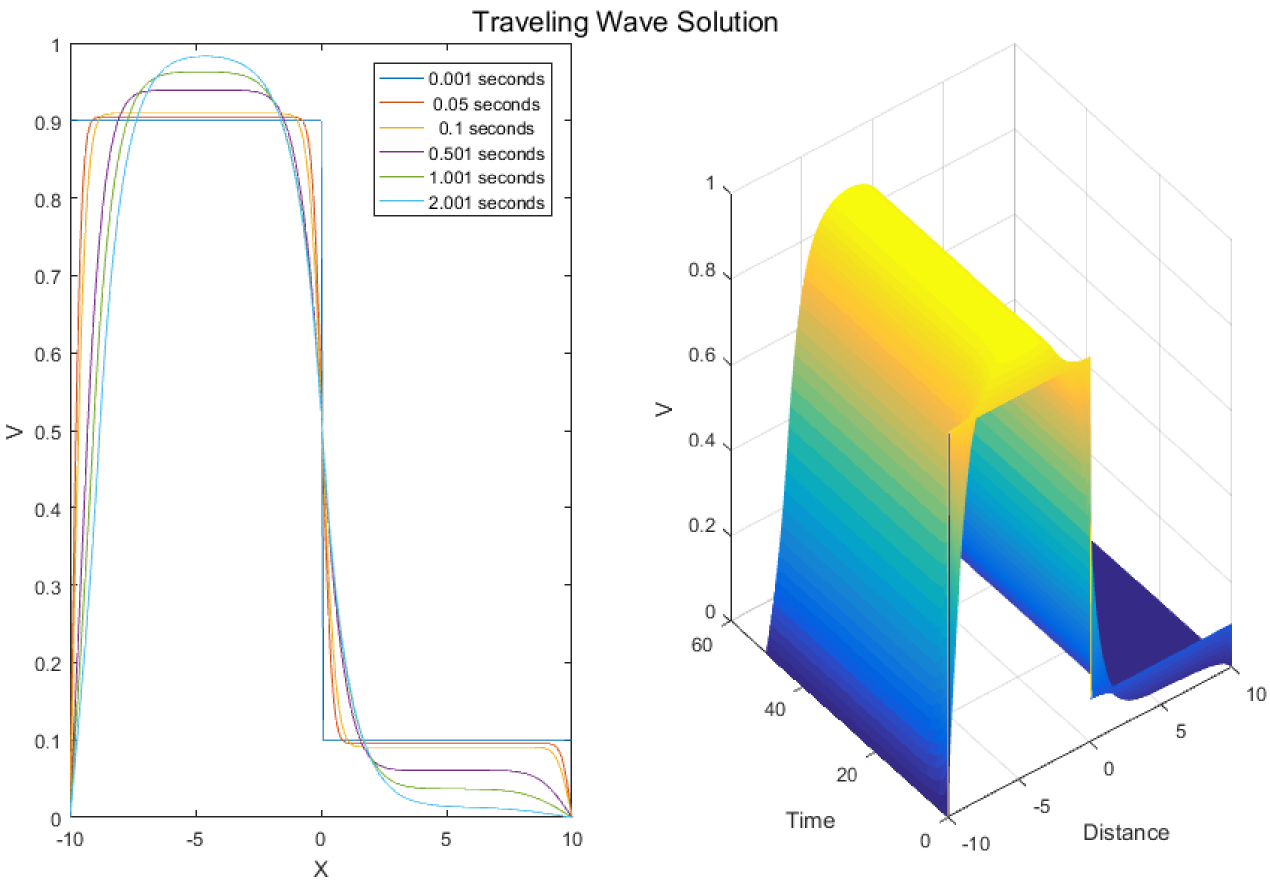

Figure 18: $\theta = 0.5$, $v(x,0) = 0.9$ when $x < 0$ and $v(x,0) = 0.1$ when $x > 0$

The graphs show the voltage becoming inactive where $x > 0$ and active where $x < 0$ over time. Looking at x $= 0$, the wave is stationary because with $\theta = 0.5$ because in this case, $c = 0$.

4 Conclusion

This document discussed how the ionic currents affect the voltage in a neuron. In the first part, the passive cell membrane has linear current representing Ohm's Law. We learned that over time all of the voltage in the neuron axon decays exponentially to zero volts. In the stationary solution (2), the voltage equals zero because voltage is bounded, causing the coefficients of the stationary solution to be zero. Adding an impulse to the stationary solution causes an exponential decay with respect to x (3). Green's function was used to solve the general stationary solution and the partial differential equation. The general stationary solution (4) shows that the voltage at unit length x and with time independence is a convolution of a decaying exponential and the inward applied current per unit length. The partial differential equation solution of the full time-dependent equation is a decaying time exponential multiplied by the step function and normal distribution (5). The step function causes time to only be positive. The partial differential equation is modeled with different initial values. The initial values determine where the location of the peak voltage is at time zero. As time goes on, those peak values decay exponentially to zero for any type of initial condition. Matlab code was written to display the decaying voltage.