Propagation of voltage in a neuron: the cable equation

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Abstract

We derive, solve, and analyze the cable equation to model how action potentials propagate from a neuron's main body (soma) down an axon. First, we consider a passive membrane, where ions simply "leak" out of a cell if a voltage gradient is present. Then, we consider a nonlinear model, which accounts for the "two state" nature of some neural ion channels. We solve the resulting equation for traveling wave solutions, given appropriate boundary conditions. We find the speed of the traveling wave and then prove that our solution is asymptotically stable.

Key Words: PDE, cable equation, action potential, heat equation

1 Introduction

1.1 Background

A.L. Hodgkin and A.F. Huxley received the 1963 Nobel Prize in Physiology/ Medicine for their groundbreaking work describing the initiation and propagation of action potentials in the squid giant axon [1]. They observed that each part of the axonal membrane could be analogized as part of an electric circuit, and therefore, the dynamics could be modeled using an ordinary differential equation.

Action potentials, which manifest as spikes in the voltage of a neuron, allow for communication between neural cells via synapses. They are primary units of information in the brain. We are concerned with how these spikes propagate from a neuron's main body (soma) down an axon.

1.2 The Cable Equation

In this paper, we derive a partial differential equation (PDE) model describing the propagation of potential along the length of the neuronal membrane. Then, for simplicity, we first consider a passive membrane, where ions leak out of a cell if a voltage gradient is present (i.e. current flows according to Ohm's law). Finally, we consider a nonlinear model, which accounts for the nonlinear effects that arise in the dynamics of ion currents that control and are controlled by the local voltage of the neural membrane. We choose a function that makes the membrane bistable, giving a simple model of the activation of the neural membrane; with no input, the membrane exhibits a low baseline potential, but given enough input, the membrane becomes "active" and ion channels along the membrane reinforce the potential excursion of the current input. We consider the inactive state at v=0 and the active state at v=1. By projecting the PDE down to a system of ODEs, we can derive traveling wave solutions (and set appropriate boundary conditions) which we solve analytically.

2 Derivation

The current per unit length J_m passing through the membrane of a neuron is given in terms of voltage v by the heat equation:

$$J_m(x) = \frac{\partial}{\partial x}(\frac{1}{R}\frac{\partial v}{\partial x}) \tag{1}$$

The neural membrane as a whole behaves like a resistor-capacitor (RC) circuit and the non linear properties of the resistor-like ion channels yield a nonlinear differential equation for the evolution of the transmembrane voltage v in time t. Considering the time variable now, the current across the membrane per unit length $J_m(x,t)$ is given by the sum of the capacitive current $J_C(x,t) = C\frac{\partial^2 v}{\partial t}$, the outward ionic current $J_{ION}(v(x,t),t)$, and the inward applied current $J_A(x,t)$ per unit length [1]:

$$J_m(x,t) = J_C(x,t) + J_{ION}(v(x,t),t) - J_A(x,t) \tag{2}$$

Thus, solving for the capacitive current and plugging into corresponding terms gives:

$$C\frac{\partial v(x,t)}{\partial t} = -J_{ION}(v(x,t),t) + \frac{1}{R}\frac{\partial^2 v(x,t)}{\partial x^2} + J_A(x,t) \tag{3}$$

Using a change of variables $x \mapsto y/\sqrt{(}R)$ and $t \mapsto Cs$ cancels out the capacitance C and resistance R parameters. We assume the ionic currents are given by a nonlinear function $f(v(y,s)))$. This yields the *cable equation.*

$$\frac{\partial v(y,s)}{\partial s} = \frac{\partial^2 v(y,s)}{\partial y^2} + f(v(y,s)) + J_{ext}(y,s) \tag{4}$$

We then write Equation (4) in terms of the original variables (x,t), for familiarity's sake:

$$\frac{\partial v(x,t)}{\partial t} = \frac{\partial^2 v(x,t)}{\partial x^2} + f(v(x,t)) + J_{ext}(x,t) \tag{5}$$

3 Passive Membrane

We consider the inhomogeneous PDE:

$$\frac{\partial v(x,t)}{\partial t} = \frac{\partial^2 v(x,t)}{\partial x^2} - v(x,t) + J_{ext}(x,t) \tag{6}$$

3.1 Homogeneous Time-Independent Solution

To understand the behavior of the cable equation for the passive membrane, we first examine stationary solutions for which $v_t(x,t) = 0$. First we solve the homogeneous case (where $J_{ext}(x,t) \equiv 0$).

If $v_t(x,t) = 0$, we have

$$\frac{\partial^2 v_h(x,t)}{\partial x^2} - v_h(x,t) = 0 \tag{7}$$

Since the stationary solutions $v_h(x,t) = V_0(x)$ will be only functions of x, the above equation becomes

$$\frac{\partial^2 V_0(x)}{\partial x^2} + V_0(x) = 0 \tag{8}$$

Letting $V_0(x) = e^{kx}$, we have

$$\begin{aligned} k^2 e^{kx} - e^{kx} &= 0 \\ e^{kx}(k^2 - 1) &= 0 \\ \Rightarrow k^2 &= 1 \\ \Rightarrow k &= \pm 1 \end{aligned}$$

Thus, we have a basis of solutions $\{e^{-x}, e^{x}\}$.

$$V_0 = v_h(x,t) = c_1 e^{-x} + c_2 e^{x}, \text{where } x \in (-\infty, \infty) \text{ and } c1, c2 \in \mathbb{R} \tag{9}$$

3.2 Particular Time-Independent Solution

Now, we consider the particular solution for which $J_{ext} = \delta(x)$ with boundary conditions $\lim_{x \to \pm\infty} v(x,t) = 0$ for a stationary input current located at x=0.

$$v(x,t) = V_F(x) = v_h + v_p = V_0 + v_p \tag{10}$$

We have the equation:

$$\begin{aligned} \frac{\partial^2 v_p(x)}{\partial x^2} - v_p(x) + \delta(x) = 0 \\ \frac{\partial^2 v_p(x)}{\partial x^2} - v_p(x) = -\delta(x) \end{aligned} \tag{11}$$

Because the Fourier transform is a linear operation, we can take the Fourier transform of the entire equation (and we assume that the Fourier transform exists). Note the the Fourier transform of the Dirac delta function, $\mathcal{F}[\delta](x) = 1$, for an input current located at x=0. Also, let $\hat{f}(m)$ denote the Fourier transform of $f(x)$. We obtain:

$$\begin{aligned} \mathcal{F}[\frac{\partial^2 v_p}{\partial x^2}](x) - \mathcal{F}[v_p](x) = \mathcal{F}[-\delta](x) \\ \mathcal{F}[\frac{\partial^2 v_p}{\partial x^2}](x) - \hat{v}_p(m) = -\hat{\delta}(m) = -1 \end{aligned} \tag{12}$$

Using the derivative property of the Fourier Transform:
$\mathcal{F}[\frac{\partial^2 f}{\partial x^2}](x) = (2\pi i m)^2 * \mathcal{F}[f](x)$. Thus,

$$\mathcal{F}[\frac{\partial^2 v_p}{\partial x^2}](x) = (2\pi i m)^2 * \mathcal{F}[v_p](x) = -(2\pi m)^2 * \hat{v}_p(m) \tag{13}$$

and plugging back into Equation (7), we have

$$-(2\pi m)^2 * \hat{v}_p(m) - \hat{v}_p(m) = -1 \tag{14}$$

Algebraically, we can now solve for $\hat{v}_p(m)$.

$$\hat{v}_p(m) = \frac{1}{1 + 4\pi^2 m^2} \tag{15}$$

Now, we can simply take the inverse Fourier transform to recover $v_p(x)$.

$$v_p(x) = \mathcal{F}^{-1}[\hat{v}_p](m) = \mathcal{F}^{-1}[\frac{1}{1 + 4\pi^2 m^2}] \tag{16}$$

Now note that $\frac{1}{2} * \mathcal{F}[e^{-|x|}] = \frac{1}{1+4\pi^2 m^2}$ where $e^{-|x|}$ is the two-sided decaying exponential function. This result can be derived using the linearity property of Fourier transforms on the sum of the right-sided decaying exponential and the left-sided decaying exponential. So $\mathcal{F}^{-1}[\frac{1}{1+4\pi^2 m^2}] = \frac{1}{2} * e^{-|x|}$. Therefore,

$$v_p(x) = \frac{e^{-|x|}}{2} \tag{17}$$

Thus, from Equation (5),

$$\begin{gathered} v(x,t) = V_F(x) = v_h + v_p = c_1 e^{-x} + c_2 e^{x} + \frac{e^{-|x|}}{2} \\ \text{where } x \in (-\infty, \infty) \text{ and } c_1, c_2 \in \mathbb{R} \end{gathered} \tag{18}$$

3.3 Generalized Time-Independent Solution

Now, we derive the formula for a stationary solution $v(x,t) = V_A(x)$ given an arbitrary stationary input $J_{ext}(x)$.

$$v(x,t) = V_A(x) = v_h + v_p = V_0 + v_p \tag{19}$$

We have the equation:

$$\begin{aligned} \frac{\partial^2 v_p(x)}{\partial x^2} - v_p(x) + J_{ext}(x) = 0 \\ \frac{\partial^2 v_p(x)}{\partial x^2} - v_p(x) = -J_{ext}(x) \end{aligned} \tag{20}$$

Once again, we can take the Fourier transform of the entire equation. We obtain:

$$\begin{aligned} \mathcal{F}[\frac{\partial^2 v_p}{\partial x^2}](x) - \mathcal{F}[v_p](x) = \mathcal{F}[-J_{ext}](x) \\ \mathcal{F}[\frac{\partial^2 v_p}{\partial x^2}](x) - \hat{v}_p(m) = -\hat{J}_{ext}(m) \end{aligned} \tag{21}$$

As above, $\mathcal{F}[\frac{\partial^2 v_p}{\partial x^2}](x) = -(2\pi m)^2 * \hat{v}_p(m)$ and plugging back into Equation (16), we have

$$-(2\pi m)^2 * \hat{v}_p(m) - \hat{v}_p(m) = -\hat{J}_{ext}(m) \tag{22}$$

Algebraically solving for $\hat{v}_p(m)$,

$$\hat{v}_p(m) = \frac{\hat{J}_{ext}(m)}{1 + 4\pi^2 m^2} \tag{23}$$

Now, we can simply take the inverse Fourier transform to recover $v_p(x)$.

$$\begin{aligned} v_p(x) = \mathcal{F}^{-1}[\hat{v}](m) &= \mathcal{F}^{-1}[\frac{1}{1 + 4\pi^2 m^2} * \hat{J}_{ext}(m)] \\ &= \mathcal{F}^{-1}[\frac{1}{1 + 4\pi^2 m^2}] * \mathcal{F}^{-1}[\hat{J}_{ext}(m)] \end{aligned} \tag{24}$$

Since $\mathcal{F}^{-1}[\frac{1}{1+4\pi^2 m^2}] = \frac{e^{-|x|}}{2}$,

$$v_p(x) = \frac{e^{-|x|}}{2} * J_{ext}(x) \tag{25}$$

Using the convolution property of Fourier transforms, we obtain:

$$v_p(x) = \frac{e^{-|x|}}{2} * J_{ext}(x) = \frac{1}{2}\int_{-\infty}^{\infty} e^{-|x-\xi|} J_{ext}(\xi) d\xi \tag{26}$$

Thus, from Equation (14),

$$\begin{aligned} v(x,t) = V_A(x) = c_1 e^{-x} + c_2 e^{x} + \frac{1}{2}\int_{-\infty}^{\infty} e^{-|x-\xi|} J_{ext}(\xi) d\xi \\ \text{where } x \in (-\infty, \infty) \text{ and } c_1, c_2 \in \mathbb{R} \end{aligned} \tag{27}$$

3.4 Fundamental Solution with Time Dependence

The Fundamental solution to the Heat Equation is Denoted by:

$$u(x,t) = \frac{1}{\sqrt{4\pi kt}} e^{\frac{-x^2}{4kt}} \tag{28}$$

PDE with Time Dependence:

$$\begin{cases} \text{PDE: } \frac{\partial v(x,t)}{\partial t} = \frac{\partial^2 v(x,t)}{\partial x^2} - v(x,t) + \delta(t)\delta(x) \\ \text{"BC": } u(x,t) \text{is bounded for all} x, andt > 0 \end{cases} \tag{29}$$

This solution can be used for the heat equation with boundary conditions at $-\infty < x < \infty$. With a different PDE, it is necessary to consider both homogeneous and particular solutions to the PDE. To start, the homogeneous solution comes from the Fourier transform:

$$\begin{aligned} \mathcal{F}\left[\frac{\partial v}{\partial t}\right] &= \mathcal{F}\left[\frac{\partial^2 v}{\partial x^2}\right] - \mathcal{F}[v] \\ \Rightarrow \frac{\partial \bar{U}}{\partial t} &= -k\omega^2 \bar{U} - \bar{U} \end{aligned} \tag{30}$$

This solution comes from completing this ODE, and the following formula is for the particular solution. This

$$\begin{aligned} \bar{U}(\omega,t) &= C(\omega)e^{-(k\omega^2+1)t} \\ \bar{U}(\omega,t) &= C(t)e^{-(k\omega^2+1)t} \end{aligned} \tag{31}$$

Homogeneous solution to PDE:

$$\begin{aligned} v_h(x,t) &= e^{-t}\mathcal{F}^{-1}[F(w)] * \mathcal{F}^{-1}\left[e^{-k\omega^2 t}\right] \\ v_h(x,t) &= \frac{e^{-t}}{\sqrt{4\pi t}} \int_{-\infty}^{\infty} \delta(\bar{x}) e^{\frac{-(x-\bar{x})^2}{4t}} d\bar{x} \end{aligned} \tag{32}$$

Fundamental Solution to homogeneous solution:

$$v_h(x,t) = \frac{e^{-t}}{\sqrt{4\pi t}} \delta(\bar{x}) e^{\frac{-x^2}{4t}} \tag{33}$$

The particular form follows from solving a second ODE. Here we have the first form, and the end produce, of our calculations.

$$\begin{aligned} \frac{dC(t)}{dt} &= \bar{Q}(\omega,t)e^{k\omega^2 t} \\ \frac{1}{2\pi}\int_0^t \int_{-\infty}^{\infty} \delta(\bar{x})\delta(\tau) &\sqrt{\frac{\pi}{\tau - t}} e^{-t} e^{\frac{-(x-\bar{x})^2}{4(\tau-t)}} d\bar{x} d\tau \end{aligned} \tag{34}$$

This homogeneous and partial solution added together give a whole solution, as follows:

$$v(x,t) = \frac{e^{-t}}{\sqrt{4\pi t}} \int_{-\infty}^{\infty} \delta(\bar{x}) e^{\frac{-(x-\bar{x})^2}{4t}} d\bar{x} + \frac{1}{2\pi} \int_0^t \int_{-\infty}^{\infty} \delta(\bar{x})\delta(\tau) \sqrt{\frac{\pi}{\tau - t}} e^{-t} e^{\frac{-(x-\bar{x})^2}{4(\tau - t)}} d\bar{x} d\tau \tag{35}$$

This solution means that we have a formula that develops as time goes to infinity, and as the distance from our delta function increases in magnitude. The next graphs are shown numerical solutions with time dependence set to constant values of t = 0 and t = 1.

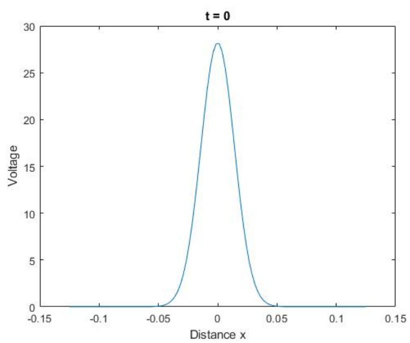

Figure 1

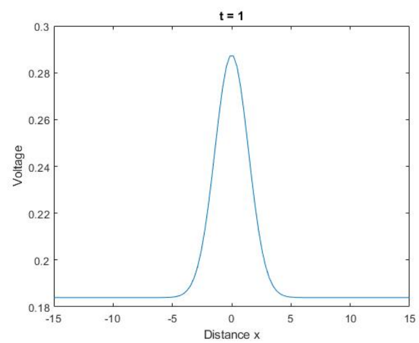

Figure 2

These graphs show a shortened time frame for how voltage propagates, but in the first time unit (Figure 2) we are able to see a massive drop in voltage from the instant the impulse is initiated, and this can be modeled further using a constant distance value.

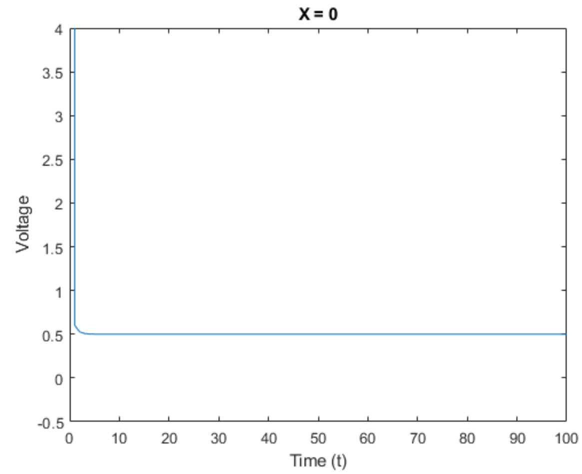

Figure 3

Figure 3 demonstrates a monotonically decreasing function at x = 0, as it is straight line that comes infinitely close to zero as t goes to infinity.

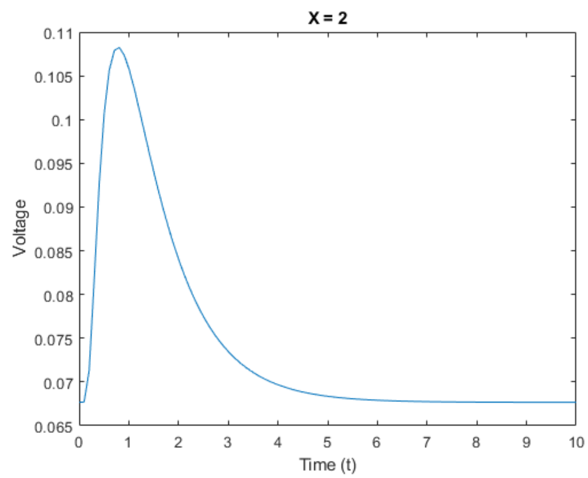

Figure 4

Figure 4 is the amount of voltage in the Neuron at a distance of 2, and this shows how our function is non-monotonic for $t \in (0, \infty)$. We can see the change in sign from the curve change near t=1.

3.5 Generalized Time-Dependent Solution

The generalized time dependent solutions follow from the principle of superposition, which says we can create more solutions for our PDE within our vector space. This idea allows us to create solutions that are linear combinations of our solution. We will mainly focus on expanding using the variable $\bar{x}$ for linear combinations.

$$v(x,t) = \frac{e^{-t}}{\sqrt{4\pi t}} \int_{-\infty}^{\infty} \delta(\bar{x}) e^{\frac{-(x-\bar{x})^2}{4t}} d\bar{x} + \frac{1}{2\pi} \int_0^t \int_{-\infty}^{\infty} J_{ext}(\bar{x},t) \sqrt{\frac{\pi}{\tau - t}} e^{-t} e^{\frac{-(x-\bar{x})^2}{4(\tau-t)}} d\bar{x} d\tau \tag{36}$$

In this full solution, the function $J_ext(\bar{x},t)$ is used as a stand in for the combinations of solutions we can have.

$$v_p = \frac{1}{2\pi} \int_0^t \int_{-\infty}^{\infty} \delta(\bar{x}-1)\delta(\tau) \sqrt{\frac{\pi}{\tau - t}} e^{-t} e^{\frac{-(x-\bar{x})^2}{4(\tau-t)}} + \delta(\bar{x}+1)\delta(\tau) \sqrt{\frac{\pi}{\tau - t}} e^{-t} e^{\frac{-(x-\bar{x})^2}{4(\tau-t)}} d\bar{x} d\tau \tag{37}$$

$$v_p = \frac{1}{2\pi} \int_0^t \int_{-\infty}^{\infty} [1] \sqrt{\frac{\pi}{\tau - t}} e^{-t} e^{\frac{-(x-\bar{x})^2}{4(\tau-t)}} d\bar{x} d\tau \tag{38}$$

$$v_p = \frac{1}{2\pi} \int_0^t \int_{-\infty}^{\infty} sin(x) \sqrt{\frac{\pi}{\tau - t}} e^{-t} e^{\frac{-(x-\bar{x})^2}{4(\tau-t)}} d\bar{x} d\tau \tag{39}$$

This is relatively easy, but we can see how these would behave in graphs similar to the section before.

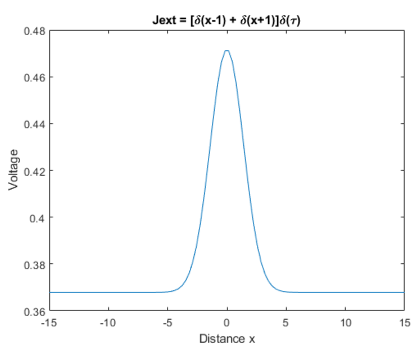

Figure 5

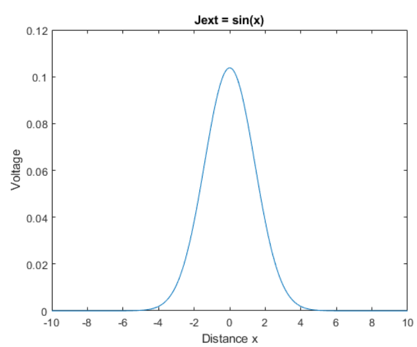

Figure 6

These solutions both show that different linear combinations have an effect on the total voltage of the Neuron, despite having very different impulse functions of δ they all show a similar shape, and in total a similar total voltage output for our PDE.

4 Traveling Wave Solutions to the PDE

Now, we account for the nonlinear effects that arise in the dynamics of ion currents that exist due to the local voltage of the neural membrane. The impulse current to a neural membrane does not always just spread out, as in the case of a passive membrane, it tends to propagate like a wave approaching a beach. We model these "active" properties of the cell by using a simple, bistable function to account for the nonlinearity $f(v(x,t))$. Consider the Heaviside step nonlinearity:

$$f(v) = -v + H(v - \theta) \tag{40}$$

where $H(v-\theta)$ is the Heaviside step function with threshold θ. The two stable states that will be considered are the inactive state at $v = 0$ and the active state at $v = 1$.

4.1 Homogeneous Solutions

We first look at homogeneous solutions, which are constant in space and time: $v(x,t) = \bar{v}$. Thus,

$$\frac{\partial \bar{v}}{\partial t} = \frac{\partial^2 \bar{v}}{\partial x^2} + f(\bar{v}) \tag{41}$$

Becomes

$$0 = 0 + f(\bar{v}) \tag{42}$$

Solving,

$$-\bar{v} + H(\bar{v} - \theta) = 0 \tag{43}$$

we get $\bar{v}^+ = 1$ and $\bar{v}^- = 0$.
Quick check:

$$\begin{aligned} 1 &= H(1-\theta) \Rightarrow 1 = 1 \\ 0 &= H(0-\theta) \Rightarrow 0 = 0 \end{aligned}$$

We note that $\bar{v}^- < \theta < \bar{v}^+$ for both homogeneous solutions to exist.

4.2 Change of Variables

Due to the fact that neuronal axons are long compared to their diameter, they can be modeled as infinitely long cables. Thus $x \in (-\infty, \infty)$. Additionally, physically realistic solutions must obey the boundary conditions:

$$\lim_{x\to\infty} \frac{\partial v(x,t)}{\partial x} = 0 \text{ and } \lim_{x\to-\infty} \frac{\partial v(x,t)}{\partial x} = 0 \tag{44}$$

Since we are looking for traveling wave solutions $v(x,t) = V(\xi)$, we use the change of variables, $\xi = x - ct$, which is the traveling wave coordinate.

Applying the change of variables $\xi = x - ct$ and boundary conditions from Equation (44) to the cable equation in Equation (5), we get

$$\begin{aligned} \frac{\partial V(\xi)}{\partial t} &= \frac{\partial^2 V(\xi)}{\partial x^2} + f(V(\xi)) \\ \Rightarrow -c\frac{\partial V(\xi)}{\partial \xi} &= \frac{\partial^2 V(\xi)}{\partial \xi^2} - V(\xi) + H(V(\xi) - \theta) \end{aligned} \tag{45}$$

with boundary conditions

$$\lim_{\xi \to \infty} \frac{\partial V(\xi)}{\partial \xi} = 0 \text{ and } \lim_{\xi \to -\infty} \frac{\partial V(\xi)}{\partial \xi} = 0 \tag{46}$$

We now have a second order ODE.

4.3 Two Different 2nd Order ODEs

Now, we can solve for the shape of the traveling wave solution, with a couple caveats. The Heaviside step function $H(V(\xi) - \theta)$ has two possible values (0 or 1) at any point ξ. We assume a traveling front solution that decreases as ξ increases and that crosses through zero at $\xi = 0$, so that

$$V(\xi) > \theta \text{ when } \xi < 0 \tag{47}$$

$$V(\xi) < \theta \text{ when } \xi > 0 \tag{48}$$

As a result, we have two second order ODEs to solve.

$$-c\frac{\partial V_1(\xi)}{\partial \xi} = \frac{\partial^2 V_1(\xi)}{\partial \xi^2} - V_1(\xi) + 1 \text{ for } \xi < 0 \tag{49}$$

$$-c\frac{\partial V_2(\xi)}{\partial \xi} = \frac{\partial^2 V_2(\xi)}{\partial \xi^2} - V_2(\xi) \text{ for } \xi > 0 \tag{50}$$

Because the solution to the ODE must be piecewise smooth, including when the two solutions meet at $\xi = 0$, we obtain our boundary conditions:

$$\begin{aligned} \lim_{\xi \to \infty} \frac{\partial V_1(\xi)}{\partial \xi} &= 0 \\ \lim_{\xi \to -\infty} \frac{\partial V_2(\xi)}{\partial \xi} &= 0 \\ V_1(\xi^-) = V_2(\xi^+) &\text{ when } \xi = 0 \\ V_1'(\xi^-) = V_2'(\xi^+) &\text{ when } \xi = 0 \end{aligned} \tag{51}$$

4.4 Traveling Front Solutions

4.4.1 Solving ODE 1 (EQUATION(EQUATION NUMBER))

$$-c\frac{\partial V_1(\xi)}{\partial \xi} = \frac{\partial^2 V_1(\xi)}{\partial \xi^2} - V_1(\xi) + 1 \text{ for } \xi < 0$$

Let $V_1(\xi) = e^{r\xi} + 1$. We have

$$\begin{aligned} -cV_1' &= V_1'' - V_1 + 1 \\ -r^2 e^{r\xi} - cre^{r\xi} + e^{r\xi} + 1 - 1 &= 0 \\ -r^2 - cr + 1 &= 0 \\ \Rightarrow r &= \frac{c \pm \sqrt{c^2+4}}{-2} \end{aligned}$$

Thus,

$$V_1(\xi) = A_1 e^{\frac{-c+\sqrt{c^2+4}}{2}\xi} + B_1 e^{\frac{-c-\sqrt{c^2+4}}{2}\xi} + 1 \tag{52}$$

with $A_1, B_1 \in \mathbb{R}$.

4.4.2 Solving ODE 2(EQUATION(EQUATION NUMBER))

$$-c\frac{\partial V_2(\xi)}{\partial \xi} = \frac{\partial^2 V_2(\xi)}{\partial \xi^2} - V_2(\xi) \text{ for } \xi > 0$$

Let $V_2(\xi) = e^{r\xi}$. We have

$$\begin{aligned} -cV_2' &= V_2'' - V_2 \\ -r^2 e^{r\xi} - cre^{r\xi} + e^{r\xi} &= 0 \\ -r^2 - cr + 1 &= 0 \\ \Rightarrow r &= \frac{c \pm \sqrt{c^2+4}}{-2} \end{aligned}$$

Thus,

$$V_2(\xi) = A_2 e^{\frac{-c+\sqrt{c^2+4}}{2}\xi} + B_2 e^{\frac{-c-\sqrt{c^2+4}}{2}\xi} \tag{53}$$

with $A_2, B_2 \in \mathbb{R}$.

4.4.3 Boundary Conditions

Applying boundary conditions:

BC:

$$\lim_{\xi \to \infty} \frac{\partial V_1(\xi)}{\partial \xi} = 0$$

$$\lim_{\xi\to\infty}(A_1(\frac{-c+\sqrt{c^2+4}}{2})e^{\frac{-c+\sqrt{c^2+4}}{2}\xi}+B_1(\frac{-c-\sqrt{c^2+4}}{2})e^{\frac{-c-\sqrt{c^2+4}}{2}\xi})=0$$

$$\Rightarrow \lim_{\xi\to\infty}(A_1e^{\frac{-c+\sqrt{c^2+4}}{2}\xi}+B_1e^{\frac{-c-\sqrt{c^2+4}}{2}\xi})=0$$

$$\Rightarrow B_1=0$$

BC:

$$\lim_{\xi\to-\infty}\frac{\partial V_2(\xi)}{\partial\xi}=0$$

$$\lim_{\xi\to\infty}(A_2(\frac{-c+\sqrt{c^2+4}}{2})e^{\frac{-c+\sqrt{c^2+4}}{2}\xi}+B_2(\frac{-c-\sqrt{c^2+4}}{2})e^{\frac{-c-\sqrt{c^2+4}}{2}\xi})=0$$

$$\Rightarrow \lim_{\xi\to\infty}(A_2e^{\frac{-c+\sqrt{c^2+4}}{2}\xi}+B_2e^{\frac{-c-\sqrt{c^2+4}}{2}\xi})=0$$

$$\Rightarrow A_2=0$$

BC:

$$V_1(0)=V_2(0)$$

$$A_1e^{\frac{-c+\sqrt{c^2+4}}{2}(0)}+1=B_2e^{\frac{-c-\sqrt{c^2+4}}{2}(0)}$$

$$\Rightarrow A_1+1=B_2$$

BC:

$$V_1'(0)=V_2'(0)$$

$$A_1(\frac{-c+\sqrt{c^2+4}}{2})e^{\frac{-c+\sqrt{c^2+4}}{2}(0)}=b_2(\frac{-c-\sqrt{c^2+4}}{2})e^{\frac{-c-\sqrt{c^2+4}}{2}(0)}$$

$$\Rightarrow A_1(\frac{-c+\sqrt{c^2+4}}{2})=B_2(\frac{-c-\sqrt{c^2+4}}{2})$$

$$\Rightarrow A_1(-c+\sqrt{c^2+4})=(A_1+1)(-c-\sqrt{c^2+4})$$

$$\Rightarrow -cA_1+A_1\sqrt{c^2+4}=-cA_1-A_1\sqrt{c^2+4}-c-\sqrt{c^2+4}$$

$$\Rightarrow A_1=\frac{-c-\sqrt{c^2+4}}{2\sqrt{c^2+4}}$$

$$\Rightarrow B_2=1-\frac{c+\sqrt{c^2+4}}{2\sqrt{c^2+4}}$$

4.4.4 Solution

Putting it all together, we have

$$V_1(\xi)=1-\frac{c+\sqrt{c^2+4}}{2\sqrt{c^2+4}}e^{\frac{-c-\sqrt{c^2+4}}{2}\xi},\ \text{for } \xi<0 \tag{54}$$

$$V_2(\xi)=(1-\frac{c+\sqrt{c^2+4}}{2\sqrt{c^2+4}})e^{\frac{-c+\sqrt{c^2+4}}{2}\xi},\ \text{for } \xi>0 \tag{55}$$

4.5 Speed of Traveling Front

Finally, we specify the speed c of the traveling wave front by applying the threshold condition $V(0) = \theta$ and solving for c.

When $\xi = 0$, V(0) $= \theta$. Thus,

$$V_1(0) = V_2(0) = \theta \tag{56}$$

Solving for $V_1(0)$ and $V_2(0)$, we have

$$\begin{aligned} 1 - \frac{c + \sqrt{c^2+4}}{2\sqrt{c^2+4}} = 1 - \frac{c + \sqrt{c^2+4}}{2\sqrt{c^2+4}} &= \theta \\ \Rightarrow \frac{c + \sqrt{c^2+4}}{2\sqrt{c^2+4}} &= 1 - \theta \\ \Rightarrow c = \sqrt{c^2+4} - 2\theta\sqrt{c^2+4} \\ \Rightarrow c^2 = (1-2\theta)^2(c^2+4) \\ \Rightarrow (1-(1-2\theta)^2)c^2 = 4(1-2\theta)^2 \\ c = \pm\frac{(1-2\theta)}{\sqrt{\theta-\theta^2}} \end{aligned}$$

But since c is a speed, it must be real and positive. Thus,

$$c = \frac{(1-2\theta)}{\sqrt{\theta-\theta^2}} \tag{57}$$

The threshold θ represents how "active" the axon is, with a smaller θ representing a more active (faster) moving wave-front. For our result for c, as θ becomes smaller, the magnitude of c increases, aligning with the physical interpretation of the model.

$$\lim_{\theta\to 0^+} c = \lim_{\theta\to 0^+} \left(\frac{(1-2\theta)}{\sqrt{\theta-\theta^2}}\right) = \infty$$

4.6 Asymptotic Stability of Solutions

We prove that our solution is asymptotically stable using linear stability analysis.

First, we add a perturbation $\epsilon\psi(\xi, t)$ to the traveling wave solution by plugging the solution $v(x,t) = V(\xi) + \epsilon\psi(\xi,t)$ into Equation (5).

$$\frac{\partial(V(\xi) + \epsilon\psi(\xi,t))}{\partial t} = \frac{\partial^2(V(\xi) + \epsilon\psi(\xi,t))}{\partial x^2} + f(V(\xi) + \epsilon\psi(\xi,t))$$

Taylor expanding $f(V + \epsilon\psi)$ using the fact that ϵ is small and linearize by eliminating terms that are not on the order of ϵ, we get

$$\begin{aligned} \text{T.E. } [f(V(\xi) + \epsilon\psi(\xi,t)(\xi,t))] &= f|(\epsilon\psi = 0) + f'|(\epsilon\psi = 0) \\ &\Rightarrow f(V) + \epsilon\psi f'(V) \end{aligned}$$

Since $f(V(\xi)) = -V(\xi)+H(V(\xi)-\theta)$ and $\epsilon\psi f'(V(\xi)) = \epsilon\psi(-1+\delta(V(\xi)-\theta)) = \epsilon\psi(-1+\delta(\xi))$, the equation becomes

$$\text{T.E. } [f(V(\xi)+\epsilon\psi(\xi,t))] = -V(\xi)+H(V(\xi)-\theta)) - \epsilon\psi(\xi,t)+\epsilon\psi(\xi,t)\delta(\xi) \tag{58}$$

The derivatives are found using the chain rule.

$$\begin{aligned} \frac{\partial(V(\xi)+\epsilon\psi(\xi,t))}{\partial t} &= -cV'(\xi) + \epsilon(\partial_\xi\psi(\xi,t)\frac{\partial\xi}{\partial t} + \partial_t\psi\frac{\partial\xi}{\partial\xi} \\ &= -cV'(\xi) - c\epsilon\partial_\xi\psi(\xi,t) + \epsilon\partial_t\psi \end{aligned} \tag{59}$$

$$\begin{aligned} \frac{\partial^2(V(\xi)+\epsilon\psi(\xi,t))}{\partial x^2} &= \frac{\partial}{\partial x}(V'(\xi) + \epsilon\partial_\xi\psi(\xi,t)) \\ &= V''(\xi) + \epsilon\partial_{\xi^2}\psi(\xi,t)) \end{aligned} \tag{60}$$

Putting it all together, the PDE becomes

$$\frac{\partial(V(\xi)+\epsilon\psi(\xi,t))}{\partial t} = \frac{\partial^2(V(\xi)+\epsilon\psi(\xi,t))}{\partial x^2} + f(V(\xi)+\epsilon\psi(\xi,t))$$

$$\begin{aligned} &\Rightarrow -cV'(\xi) - c\epsilon\partial_\xi\psi(\xi,t) + \epsilon\partial_t\psi = \\ &\qquad V''(\xi) + \epsilon\partial_{\xi^2}\psi(\xi,t)) - V(\xi) + H(V(\xi)-\theta)) - \epsilon\psi(\xi,t) + \epsilon\psi(\xi,t)\delta(\xi) \end{aligned}$$

$$\begin{aligned} &\Rightarrow (-cV'(\xi) - V''(\xi) + V(\xi) - H(V(\xi)-\theta)) - c\epsilon\partial_\xi\psi(\xi,t) + \epsilon\partial_t\psi = \\ &\qquad\qquad \epsilon\partial_{\xi^2}\psi(\xi,t)) - \epsilon\psi(\xi,t) + \epsilon\psi(\xi,t)\delta(\xi) \end{aligned}$$

$$\Rightarrow (0) - c\epsilon\partial_\xi\psi(\xi,t) + \epsilon\partial_t\psi = \epsilon\partial_{\xi^2}\psi(\xi,t)) - \epsilon\psi(\xi,t) + \epsilon\psi(\xi,t)\delta(\xi)$$

$$\Rightarrow -c\partial_\xi\psi(\xi,t) + \partial_t\psi = \partial_{\xi^2}\psi(\xi,t)) - \psi(\xi,t) + \psi(\xi,t)\delta(\xi) \tag{61}$$

Now we have a linear PDE. Let $\psi(\xi,t) = h(t)f(\xi)$.

$$
\begin{aligned}
h'(t)f(\xi) = ch(t)f'(\xi) + h(t)f''(\xi) - h(t)f(\xi) + h(t)f(xi)\delta(\xi)\\
\Rightarrow \frac{h'}{h} = \frac{cf'}{f} + \frac{f''}{f} - 1 + \delta(\xi) = \lambda\\
\Rightarrow \frac{h'}{h} = \lambda \Rightarrow h(t) = e^{\lambda t}\\
\Rightarrow \frac{cf'}{f} + \frac{f''}{f} - 1 + \delta(\xi) = \lambda\\
\Rightarrow cf' + f'' - f + f\delta(\xi) = \lambda f\\
\lambda = 0, \psi(\xi, t) = V'(\xi)\\
\Rightarrow cV''(\xi) + V'''(\xi) - V'(\xi) + V'(\xi)\delta(\xi) = 0\\
\Rightarrow \frac{\partial}{\partial \xi}(V''(\xi) + cV'(\xi) - V(\xi)) + V'(\xi)\delta(\xi) = 0\\
\Rightarrow \frac{\partial}{\partial \xi}(-H(V(\xi) - \theta)) + V'(\xi)\delta(\xi) = 0\\
\Rightarrow -\delta(V(\xi) - \theta)V'(\xi) + V'(\xi)\delta(\xi) = 0\\
\Rightarrow -\delta(\xi)V'(\xi) + V'(\xi)\delta(\xi) = 0
\end{aligned}
$$

Our derived equation for the evolution of ϵ has three possible forms, depending on the sign of λ.

Case 1: $\lambda = 0$

When $\lambda = 0$,

$$\psi(\xi, t) = V'(\xi) \tag{62}$$

Case 2: $\lambda > 0$

If $\lambda > 0$, and since $h(t) = e^{\lambda t}$,

$$
\begin{aligned}
\psi(\xi, t) = e^{\lambda t} f(\xi)\\
\lim_{\lambda \to \infty} (\psi(\xi, t)) = \lim_{\lambda \to \infty} (e^{\lambda t} f(\xi)) = \infty
\end{aligned} \tag{63}
$$

Therefore, there are no solutions when $\lambda > 0$.

Case 3: $\lambda < 0$

When $\lambda < 0$,

$$
\begin{aligned}
\lim_{\lambda \to -\infty} \psi(\xi, t) = \lim_{\lambda \to -\infty} e^{\lambda t} f(\xi) = 0\\
cf' + f'' - f + f\delta(\xi) = \lambda f
\end{aligned} \tag{64}
$$

Therefore, solutions exist when $\lambda < 0$.

A solution exists for $\lambda \leq 0$ (and there are no solutions with $\lambda > 0$). Because the equation decays in time, the solutions in the vicinity of the wave will tend to be attracted to it. Thus, our solution is asymptotically stable.

4.7 Comparison to Numerical Simulations

4.7.1 Cable Equation with the Heaviside step nonlinearity

We numerically simulate Equation (5) given Equation (40) by using a finite difference approximation using $x = -10$, $x = 10$, and $t = 50$ as the stopping time and compute the speed of the wave for different values of θ. The speed of the traveling wave was numerically computed by finding the speed for each value of x_i and then averaging. Changing the timestep δt and the stepsize δx does not dramatically change the result, but does make it less accurate. The speeds of the traveling wave for $\theta = [0.5, 0.3, 0.1]$ are $[0, 0.87, 2.67]$ m/s.

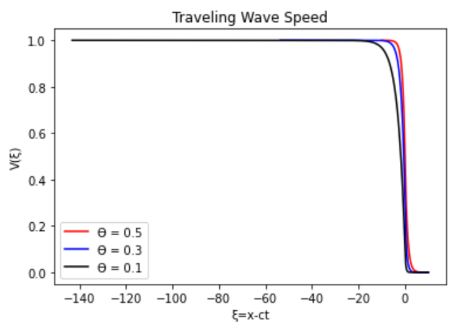

Figure 7

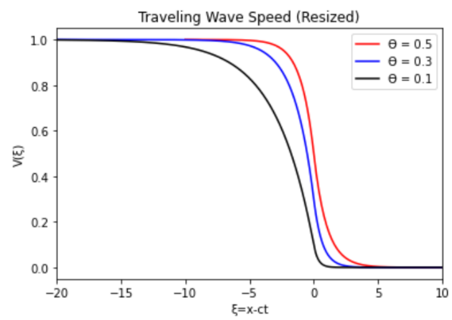

Figure 8

4.7.2 Changing the Heaviside step function

We now simulate the system again numerically using

$$f(v, x) = -v + H(v - \theta(1 + 0.5cos(x)))$$

The average speeds of the traveling wave when the constant in front of $\cos(x) = [0, 0.3, 0.5, 0.9]$ are $[0, 0.41, 0.72, 1.96]$. As this constant increases, the average speed of the wavefront increases. The speed of the front approaches zero as $\theta \to 0$ and is equal to 0 when $\theta = 0$ and when the constant in front of $\cos(x) = 0$.

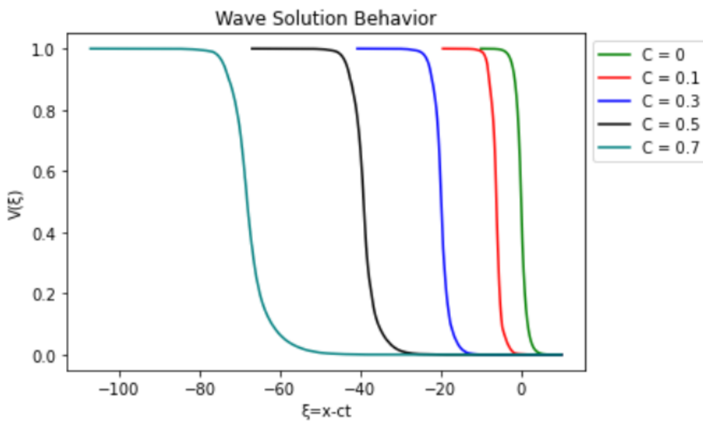

Figure 9

5 Conclusion

In this project, we model how action potentials propagate down the body of a neuron by considering the passive case and a nonlinear case using the Heaviside step function. Our traveling wave solution consists of two parts. We solve for the speed constant c and demonstrate numerical simulations. We show our solution to be asymptotically stable, by using linear stability analysis. Our result requires that the $lim_{x\to\pm\infty} v(x,t) = 0$ as a condition. This is a potential downside, because we will not have a solution if $v(x,t)$ is not bounded. We would also consider using a different equation other than the Heaviside step function as our nonlinearity to improve our model, as the bistable system is a simple model of the activation of a neural membrane.

6 References

[1] A.L. Hodgkin and A.F. Huxley, *A quantitative description of membrane current and its application to conduction and excitation in nerve*, The Journal of Physiology, 117(1952), p, 500
[2] J.P. Keener and J. Sneyd, *Mathematical physiology*, vol. 1, Springer, 1998
[3] R. Haberman, *Applied Partial Differential Equations*, vol. 5, Pearson, 2004

7 Appendix

```
%Plot of X-0

syms n t

K = int((sqrt(pi/(t))*exp(-t)), 0, inf);

J = exp(-t)/sqrt(4*pi*t) + 1/(2*pi)*K;
t = linspace(0.000001, 2);
VOLT = subs(J);
%plot(t,VOLT)
%ylim([-.5 4])
%title('X = 0')
%xlabel('Time (t)')
%ylabel('Voltage')
```

```
%Plot of X=2
syms n t
K = int((sqrt(pi/t))*exp(-t)*exp(-1/(t)), 0, inf);

J = exp(-t)/sqrt(4*pi*t)*exp(-1/t) + 1/(2*pi)*K;
t = linspace(0.000001, 10);
VOLT = subs(J);
%plot(t,VOLT)
%title('X = 2')
%xlabel('Time (t)')
%ylabel('Voltage')
```

```
%e^t or Ginf
syms x t
K = int((sqrt(pi/t))*exp(-t)*exp(-x^2/(4*t)), 't', 0, inf);

H = int(exp(-t)/sqrt(4*pi*t)*exp(-x^2/(4*t)), 'x', -inf, inf);

P = int(H + K, 'x', -inf, inf);

t = linspace(0, 100, 100);
sol = subs(H);
%plot(t, 2*sol)
```

```
%Jext of Sin
syms x t

g = 1/(2*pi)*sin(x)*sqrt(pi/(t))*exp(-t)*exp((-x.^2./(4*t)));

a = int(g, -inf, inf);

x = linspace(-10, 10, 1000);
t = 1;


y = exp(-t)/(sqrt(4*pi*t))*exp(-x.^2/(4*t))+ a;

m = subs(y);
%plot(x,m)
```

```
%title('Jext = sin(x)')
%xlabel('Distance x')
%ylabel('Voltage')
```

```
%T=0
syms m y t_0
%Plot t = .0001
g = exp(-t_0)*(sqrt(pi./(m-t_0))*exp((-y.^2./(4*(m-t_0)))));

part = int(g, 'm',0, .0002);

m = .0002;
t_0 = .0001;
y = linspace(-.125, .125, 100);

h = exp(-t_0)/(sqrt(4*pi*t_0))*exp(-y.^2/(4*t_0)) + (1/(2*pi))*part;

fin = subs(h);

%figure(1)
%plot(y,fin)
%title('t = 0')
%xlabel('Distance x')
%ylabel('Voltage')
```

```
%T=1
syms n x t_1

%Plot t = 1
g = exp(-t_1)*(sqrt(pi./(n-t_1))*exp((-x.^2./(4*(n-t_1)))));

part = int(g, 0, 1.0002);

n = 1.0001;
t_1 = 1;
x = linspace(-15, 15, 100);

h = exp(-t_1)/(sqrt(4*pi*t_1))*exp(-x.^2/(4*t_1)) + 2*(1/(2*pi))*part;

Fin = subs(h);

%figure(2)
%plot(x,Fin)

%title('Jext = [\delta(x-1) + \delta(x+1)]\delta(\tau)')
%xlabel('Distance x')
%ylabel('Voltage')
```

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In [2]:
```
%matplotlib inline

import numpy as np
import matplotlib.pyplot as plt
```

In [3]:
```
# part 2 g
```

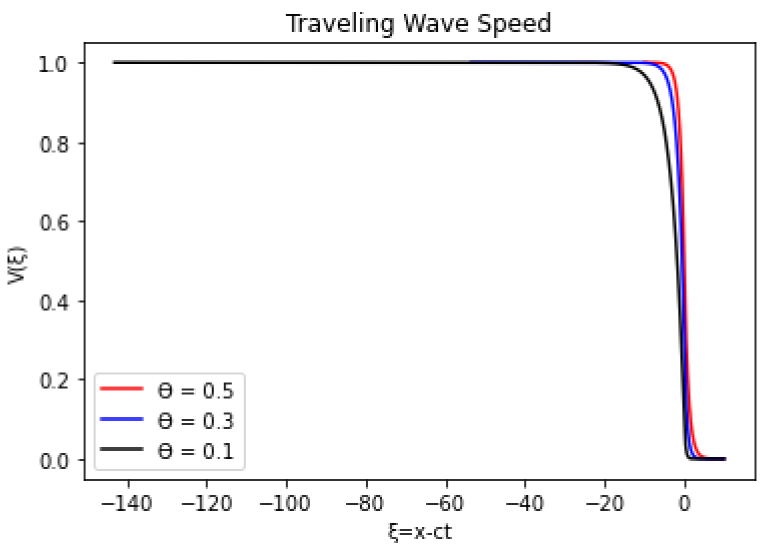
In [13]:
```
def funk(lx,hx,dx,ht,dt,th):

    x = np.arange(lx,(hx+dx),dx)
    t = np.arange(0,ht,dt)
    c = ((4*th**2-4*th+1)/(th-th**2))**(1/2)
    v = np.zeros(len(x)*len(t))
    s = (c+(c**2+4)**(1/2))/(2*(c**2+4)**(1/2))

    i = 0
    k = 0

    while i < len(x):
        j = 0
        while j < len(t):
            v[k] = x[i]-c*t[j]
            j+=1
            k+=1
        i+=1

    e = sorted(v)

    k = 0

    while k < len(e):

        lowv = 1 - s*np.exp(((-c+(c**2+4)**(1/2))/2)*e[k])
        highv = (1 - s)*np.exp(((-c-(c**2+4)**(1/2))/2)*e[k])

        if lowv > th:
            v[k] = lowv
        if highv < th:
            v[k] = highv

        k+=1

    return [e,v,c]
```

In [14]:
```
[x1,y1,c1] = funk(-10,10,0.1,50,0.1,0.5)
[x2,y2,c2] = funk(-10,10,0.1,50,0.1,0.3)
[x3,y3,c3] = funk(-10,10,0.1,50,0.1,0.1)

print("The speed of the front when theta = 0.5 is", c1)
print("The speed of the front when theta = 0.3 is", c2)
print("The speed of the front when theta = 0.1 is", c3)
```

```
The speed of the front when theta = 0.5 is 0.0
The speed of the front when theta = 0.3 is 0.8728715609439697
The speed of the front when theta = 0.1 is 2.666666666666667
```

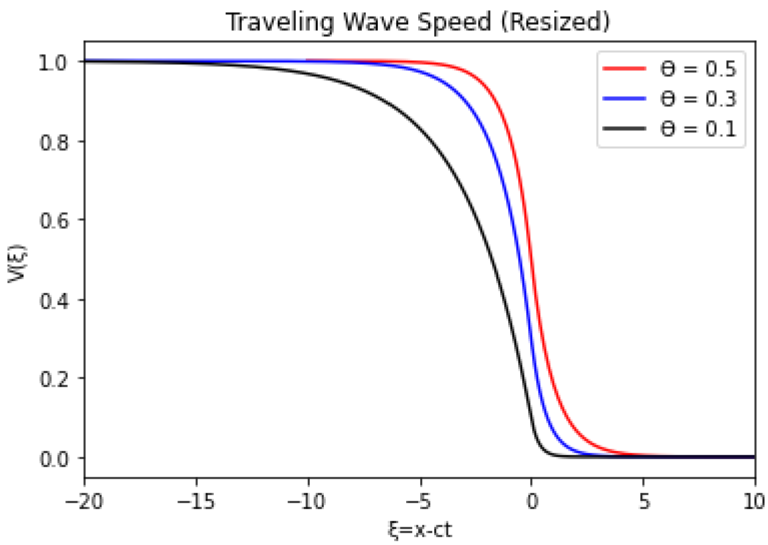
In [26]:
```
plt.plot(x1,y1, color='r', label='\u03F4 = 0.5')
plt.plot(x2,y2, color='b', label='\u03F4 = 0.3')
plt.plot(x3,y3, color='k', label='\u03F4 = 0.1')

plt.title('Traveling Wave Speed')
plt.legend()
plt.xlabel('\u03BE=x-ct')
plt.ylabel('V(\u03BE)')
```

Out[26]:
```
Text(0, 0.5, 'V(ξ)')
```



In [27]:
```
plt.plot(x1,y1, color='r', label='\u03F4 = 0.5')
plt.plot(x2,y2, color='b', label='\u03F4 = 0.3')
plt.plot(x3,y3, color='k', label='\u03F4 = 0.1')

plt.title('Traveling Wave Speed (Resized)')
plt.legend()
plt.xlim(-20,10)
plt.xlabel('\u03BE=x-ct')
plt.ylabel('V(\u03BE)')
```

Out[27]:
```
Text(0, 0.5, 'V(ξ)')
```



In [17]:
```
# part 2 vii
```

In [18]:
```
def funk_p2(lx,hx,dx,ht,dt,th,c_th):

    if c_th == 0:
        return funk(lx,hx,dx,ht,dt,th)

    x = np.arange(lx,(hx+dx),dx)
    t = np.arange(0,ht,dt)
    e = np.zeros(len(x)*len(t))
    v = np.zeros(len(e))
    c = np.zeros(len(x))
    s = np.zeros(len(x))
    new_th = np.zeros(len(x))

    i = 0
    k = 0

    while i < len(x):
        new_th[i] = th*(1+c_th*np.cos(x[i]))
        c[i] = ((4*new_th[i]**2-4*new_th[i]+1)/(new_th[i]-new_th[i]**2))**(1/2)
        s[i] = (c[i]+(c[i]**2+4)**(1/2))/(2*(c[i]**2+4)**(1/2))
        j = 0
        while j < len(t):
            e[k] = x[i]-c[i]*t[j]
            j+=1
            k+=1
        i+=1

    av_c = np.average(c)

    i = 0
    j = 0
    i_x = 0
    th = new_th[0]

    while i < len(e):

        if j == len(t):
            i_x+=1
            j = 0

        lowv = 1 - s[i_x]*np.exp(((-c[i_x]+(c[i_x]**2+4)**(1/2))/2)*e[i])
        highv = (1 - s[i_x])*np.exp(((-c[i_x]-(c[i_x]**2+4)**(1/2))/2)*e[i])

        if lowv > new_th[i_x]:
            v[i] = lowv
        if highv < new_th[i_x]:
            v[i] = highv

        i+=1
        j+=1

    e1 = sorted(e)
    v1 = sorted(v)
    v2 = np.zeros(len(e))

    i = 0
```

```
    while i < len(e):
        v2[i] = 1 - v1[i]
        i+=1


    return [e1,v2,av_c]
```

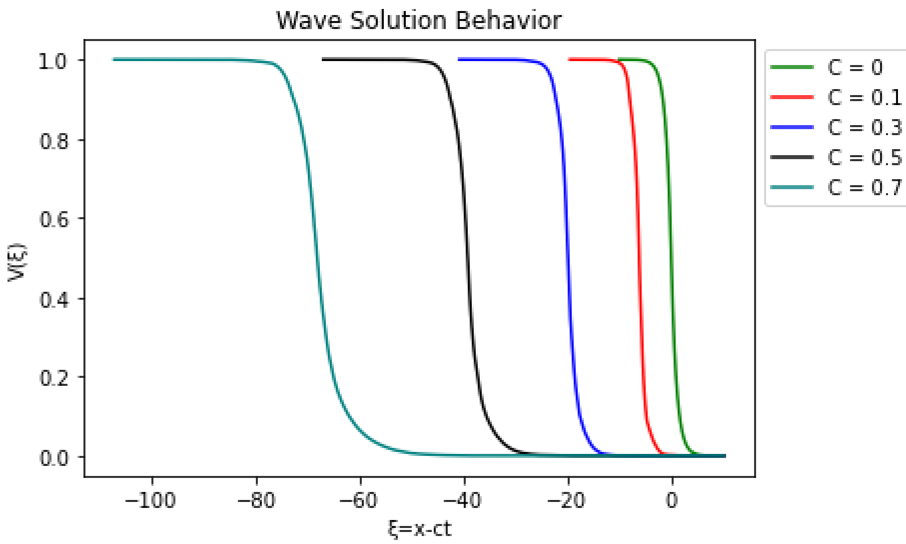
In [19]:

```
[x4,y4,av_c4] = funk_p2(-10,10,0.1,50,0.1,0.5,0)
[x5,y5,av_c5] = funk_p2(-10,10,0.1,50,0.1,0.5,0.1)
[x6,y6,av_c6] = funk_p2(-10,10,0.1,50,0.1,0.5,0.3)
[x7,y7,av_c7] = funk_p2(-10,10,0.1,50,0.1,0.5,0.5)
[x8,y8,av_c8] = funk_p2(-10,10,0.1,50,0.1,0.5,0.7)
av_c9 = funk_p2(-10,10,0.1,50,0.1,0.5,0.9)[2]

print("Average speed of the front when the constant in front of cos(x) is 0 = ",
print("Average speed of the front when the constant in front of cos(x) is 0.3 = '
print("Average speed of the front when the constant in front of cos(x) is 0.5 = '
print("Average speed of the front when the constant in front of cos(x) is 0.9 = '
```

```
<ipython-input-18-9a08324968a8>:42: RuntimeWarning: overflow encountered in exp
  highv = (1 - s[i_x])*np.exp(((-c[i_x]-(c[i_x]**2+4)**(1/2))/2)*e[i])

Average speed of the front when the constant in front of cos(x) is 0 =  0.0
Average speed of the front when the constant in front of cos(x) is 0.3 =  0.406
05501026589397
Average speed of the front when the constant in front of cos(x) is 0.5 =  0.722
0107717516927
Average speed of the front when the constant in front of cos(x) is 0.9 =  1.961
3822671976315
```

In [23]:
```
plt.plot(x4,y4, color='g', label='C = 0')
plt.plot(x5,y5, color='r', label='C = 0.1')
plt.plot(x6,y6, color='b', label='C = 0.3')
plt.plot(x7,y7, color='k', label='C = 0.5')
plt.plot(x8,y8, color='teal', label='C = 0.7')

plt.title('Wave Solution Behavior')
plt.legend(bbox_to_anchor=(1,1))
plt.xlabel('\u03BE=x-ct')
plt.ylabel('V(\u03BE)')
```

Out[23]:
```
Text(0, 0.5, 'V(ξ)')
```



In [ ]: