

STEADY_STATE SOLUTIONS TO THE CABLE EQUATION

3-1. We have seen how to go from the conceptual model of a membrane segment to the cable equation, and today we will discuss steady-state solutions of the cable equation. What do we mean by steady-state? Steady-state means no change with time. How does this affect the cable equation? What it does is it eliminates the derivative with respect to time.

Consequently the cable equation, $\tau \frac{\partial V}{\partial t} = \lambda^2 \frac{\partial^2 V}{\partial x^2} - V$ or in non-dimensional form,

$$\frac{\partial V}{\partial T} = \frac{\partial^2 V}{\partial X^2} - V \text{ becomes just } \lambda^2 \frac{d^2 V}{dx^2} - V = 0 \text{ or } \frac{d^2 V}{dX^2} - V = 0 \text{ where } T=t/\tau \text{ and } X=x/\lambda.$$

This latter equation is similar to saying that the second derivative of a function equals the function, or $f''(x) = f(x)$. To solve we just integrate twice or $f(x) = \iint f(x) dx$. It is well-known that the exponential function is a function whose 2nd derivative equals itself. If we consider the non-dimensional form $d^2V/dX^2 = 0$, with $X=x/\lambda$ and $L=l/\lambda$, then we can construct 3 equivalent forms of the solution to the steady-state cable equation:

$$V(X) = A_1 e^X + A_2 e^{-X}$$

$$V(X) = B_1 \cosh(X) + B_2 \sinh(X)$$

$$V(X) = C_1 \cosh(L-X) + C_2 \sinh(L-X)$$

where the A_i , B_i , and C_i are constants to be determined by the boundary conditions. \cosh and \sinh are the hyperbolic cosine and hyperbolic sine functions. We will discuss what they are and what plots of these functions look like shortly. I will leave it to a homework problem for you to convince yourself that these three solutions are identical.

3-2. To determine values for the arbitrary constants, we must use “Boundary conditions”. What are boundary conditions? If we are considering solutions for a finite length cable, the boundaries are at the ends represented by $X=0$ and $X=L$. We can impose conditions on these boundaries. Most typically we impose either voltage conditions or current conditions at the boundaries.

For voltage boundary conditions, consider clamping the voltage at one end or the other to a specific value. For example:

$$V(X=0) \text{ or } V(0) = V_0 \quad \text{and} \quad V(X=L) \text{ or } V(L) = V_L$$

These conditions clamp the voltage at the ends of the cable to V_0 and V_L . Note, $V=0$ is usually called a “short circuit” by the electrical engineers, but here a short circuit implies that $V_i=V_e$. Given how we have defined V , $V=0$ would be clamping the voltage to the resting potential.

For current boundary conditions, consider applying a current at one end or the other. Then (from Ohm's law) $i=V/R$ we have

$$i_i = 1/r_i (-dV/dx)$$

which is evaluated either at $x=0$ or $x=\ell$, depending on which end we know the current. Recall current is positive going to the right and we have defined $\Delta V = V_2 - V_1$ where $x_2 > x_1$. If $V_2 > V_1$ then ΔV is positive, but the current is negative (current flows from high voltage to low voltage) and so we get the minus sign in the above equation. Alternatively, if $V_2 < V_1$, then ΔV is negative (giving us the minus sign) but current is positive. Note in both cases Δx is positive.

In non-dimensional form the equation is a little bit different. We have

$$i_i = 1/(\lambda r_i) (-dV/dX)$$

Recall that $dV/dx = dV/dX \cdot dx/dx = dV/dX \cdot 1/\lambda$. This is where the extra $1/\lambda$ comes from (because $X=x/\lambda$).

In these equations $r_i = R_a/4/(\pi d^2)$ as we saw earlier. Recall that r_i has dimensions of ohm/cm (this makes the equations correct dimensionally) and R_a has dimensions of ohm-cm. the factor $4/(\pi d^2)$ is the inverse of the cross-sectional area.

Usually we write these boundary conditions in terms of dV/dx (or dV/dX)

$$dV/dx = -i_i r_i \quad \text{or} \quad dV/dX = -i_i r_i \lambda$$

and evaluate $dV(x=0)/dx$ or $dV(x=\ell)/dx$ or $dV/dX(X=0)$ or $dV/dX(X=L)$ accordingly.

3-3. Let's look at some typical boundary conditions

If no current exits at a boundary we call this a "sealed end" boundary condition. In the EE world we would call this an "open circuit". A "sealed end" boundary condition can be expressed as

$$-\frac{1}{r_i} \frac{dV}{dx} \Big|_{x=\ell} = 0 \quad \text{this notation means the derivative of } V \text{ with respect to } x \text{ is evaluated at } x=\ell$$

You can think of the left hand side as V/R in Ohm's law and the 0 on the right hand side means that the current $I=0$. There is no current flow because we have a sealed end.

Suppose we were to assume that the end of the cable was composed of the same material as the membrane and that current could leak out of the end of the cable through this membrane. We would call this a “leaky end” boundary condition. By Ohm’s law, $I=V/R$ or in terms of conductance $I=VG$, where G is the leak conductance. We can compute the leak conductance through an end cap of membrane. The area of this end cap is $\pi d^2/4$. If we know R_m , which has units of ohm-cm² then this leak conductance would be $G_\ell = \pi d^2/(4R_m)$. Then we can express our “leaky end” boundary condition as

$$-\frac{1}{r_i} \frac{dV}{dx} \Big|_{x=\ell} = V \left(\frac{\pi d^2}{4R_m} \right).$$

Note that both dV/dx and V are evaluated at the boundary in this expression.

In models we usually assume that the terminal ends have a “sealed end” boundary condition rather than the more correct leaky end. If we substitute in a diameter of 1 μm and an R_m of 10000 ohm-cm² for example, we see that the leak conductance is on the order of 10^{-12} S. This is small so we typically neglect it.

Suppose we inject current into one end of the cable (soma end, for example). Then the “current input” boundary condition would be:

$$-\frac{1}{r_i} \frac{dV}{dx} \Big|_{x=0} = I_0 \quad \text{where } I_0 \text{ is the current that we inject.}$$

3-4. Earlier we gave solutions to the non-dimensional steady-state cable equation as

$$V(X) = A_1 e^X + A_2 e^{-X}$$

$$V(X) = B_1 \cosh(X) + B_2 \sinh(X)$$

$$V(X) = C_1 \cosh(L-X) + C_2 \sinh(L-X)$$

If we represent these solutions not in non-dimensional form we have:

$$V(x) = A_1 e^{x/\lambda} + A_2 e^{-x/\lambda}$$

$$V(x) = B_1 \cosh(x/\lambda) + B_2 \sinh(x/\lambda)$$

$$V(x) = C_1 \cosh((\ell-x)/\lambda) + C_2 \sinh((\ell-x)/\lambda)$$

Let’s review some properties of these functions.

Recall that $\exp(0) = 1$, $\exp(-\infty) = 0$, $\exp(\infty) = \infty$

$$\cosh(x) = 0.5*(\exp(x) + \exp(-x)) \quad \text{so } \cosh(0) = 1 \quad \cosh(-\infty) = \infty \quad \cosh(\infty) = \infty$$

$$\sinh(x) = 0.5*(\exp(x) - \exp(-x)) \quad \text{so } \sinh(0) = 0 \quad \sinh(-\infty) = -\infty \quad \sinh(\infty) = \infty$$

$$\tanh(x) = \sinh(x)/\cosh(x) \quad \text{so } \tanh(0) = 0 \quad \tanh(-\infty) = -1 \quad \tanh(\infty) = 1$$

$$d/dx \cosh(x) = \sinh(x) dx$$

$$d/dx \sinh(x) = \cosh(x) dx$$

Try plotting these functions so that you have some idea what they look like. We will use our knowledge of these functions to solve the steady-state cable equation for particular boundary conditions.

3-5. Consider the solution of the steady-state cable equation for a semi-infinite cylinder. For boundary conditions let's take:

$$V(0) = V_0 \quad \text{and} \\ V(\infty) \text{ is bounded (meaning } V \text{ is not } \infty)$$

Of the three forms of the solution given above, the first form is the easiest to use for this example

$$V(x) = A_1 \exp(x/\lambda) + A_2 \exp(-x/\lambda)$$

Then $V(0) = V_0$ implies that $V(0) = A_1 \exp(0) + A_2 \exp(0) = V_0$ or $A_1 + A_2 = V_0$

$V(\infty)$ is bounded implies that $V(\infty) = A_1 \exp(\infty) + A_2 \exp(-\infty)$ is bounded or $A_1 = 0$

Therefore $A_2 = V_0$ and $A_1 = 0$ and the solution is $V(x) = V_0 \exp(-x/\lambda)$

What this says is that the voltage in the cylinder will drop to V_0/e at distance $x = \lambda$ and will drop to V_0/e^2 at $x = 2\lambda$, etc.

What is the significance of the space constant λ ?

λ is a measure of voltage decay with distance

The voltage drops $1/e$ for each λ distance. Although textbooks often use this feature as part of the definition of λ , it strictly applies only for a semi-infinite cylinder.

If the length of the cylinder is $> 4\lambda$, then $\exp(-x/\lambda)$ is a good approximation to the solution.

3-6. Consider the case where there is a voltage clamp at $x=0$ and a sealed end at $x=\ell$.

Boundary conditions are $V(0) = V_0$ and $-1/r_i \, dV/dx(x=\ell) = 0$.

In this case the third form of the solution is the easiest one to use.

$$V(x) = C_1 \cosh((\ell - x)/\lambda) + C_2 \sinh((\ell - x)/\lambda)$$

$V(0) = V_0$ implies that $V(0) = C_1 \cosh(\ell/\lambda) + C_2 \sinh(\ell/\lambda) = V_0$

To apply the sealed end condition we must take the derivative of $V(x)$ and multiply by $-1/r_i$

$$dV/dx = C_1 \sinh((\ell - x)/\lambda) (-1/\lambda) + C_2 \cosh((\ell - x)/\lambda) (-1/\lambda)$$

Note d/dx of $(\ell - x)/\lambda = d/dx (\ell/\lambda - x/\lambda) = 0 - 1/\lambda = -1/\lambda$

So at $x = \ell$, $dV/dx = C_1 \sinh(0) (-1/\lambda) + C_2 \cosh(0) (-1/\lambda) = C_2 (-1/\lambda)$

So $-1/r_i \, dV/dx(x=\ell) = -1/\lambda r_i C_2$. For this to be 0 means that C_2 must be 0.

Therefore $C_1 = V_0 / \cosh(\ell/\lambda)$ and our solution is $V(x) = V_0 \frac{\cosh((\ell - x)/\lambda)}{\cosh(\ell/\lambda)}$

3-7. Suppose we voltage clamp at both ends.

Suppose boundary conditions are $V(0)=V_0$ and $V(\ell)=0$.

Which form of the solution should we use? Again the third form is the easiest to work with.

$$V(x) = C_1 \cosh((\ell - x)/\lambda) + C_2 \sinh((\ell - x)/\lambda)$$

$V(\ell) = 0$ implies that $C_1 = 0$. (Check this for yourself) and

$$V(0) = V_0 \text{ implies that } C_2 \sinh(\ell/\lambda) = V_0$$

$$\text{The final solution is } V(x) = V_0 \frac{\sinh((\ell - x)/\lambda)}{\sinh(\ell/\lambda)}$$

3-8. On this overhead we have plotted solutions of the steady-state cable equation for a variety of boundary conditions. Regardless of the boundary condition at $x=0$, the voltage in all cases is plotted relative to the value at $x=0$ which is called V_0 .

Lines A, B and D are solutions where the end at $x=\ell$ is clamped to 0. Examples are for three different cables having electrotonic length $L=\ell/\lambda = 0.5, 1.0$ and 2.0 .

Lines I and K are solutions where the end at $x=\ell$ is clamped to either $0.9V_0$ or $1.1V_0$. In both cases $L=1.0$.

Lines F, H and J are solutions where the $x=\ell$ boundary condition is a sealed end and L is $0.5, 1.0$ and 2.0 .

Lines C and G are solutions where the $x=\ell$ boundary condition is a leaky end. For C the leak is equivalent to a leak 4 times larger than the conductance of an infinite cylinder of the same diameter attached at the end. For G the leak is equivalent to a leak $\frac{1}{4}$ that of the conductance of an infinite cylinder of the same diameter attached at the end.

Line E is the solution for a semi-infinite cylinder.

Why is the voltage higher when there is a sealed end instead of an infinite cylinder? Intuitively, current is dammed up at the end and has no place to go except through the membrane. In the infinite cylinder, the current can proceed down the cylinder.

In the leaky end cases (C and G) the size of the leak is expressed in terms of the conductance of an attached infinite cylinder G_∞ . In C the leak is $G_L/G_\infty = 4$ which is a substantial leak, but still not quite large enough to be the same as clamping to 0. In G, the leak is $G_L/G_\infty = 0.25$, which is small, but not as small as a sealed end ($=0$). This explains the relative positioning of these lines in the plot. For E, the "leak" is $G_L/G_\infty = 1$, or the same as attaching an infinite cylinder, which is what this case represents.

3-9. Input resistance is a parameter often measured and is an important characteristic of the cell. Why so we measure input resistance? Input resistance is a measure of how excitable a cell is. A large R_N means a cell is very excitable whereas a small R_N means the cell is less excitable. You can see this from Ohm's law $V=IR$. A large R will produce a large V for a given I .

How do we measure input resistance? Typically we inject current and measure the steady-state voltage change. This is done for several different current amplitudes, mostly hyperpolarizing currents. V is plotted on the x-axis and I on the y-axis and the slope of the straight line through the points is $1/R$.

How can we get an expression for input resistance from the cable equation? Mathematically we assume the cell is a cable and assume boundary conditions of current input at $x=0$ and a sealed end at $x=\ell$. These boundary conditions mathematically are:

$$-1/r_i dV/dx (x=0) = I_0 \quad \text{and} \quad -1/r_i dV/dx = 0$$

Using these boundary conditions to get the solution is left as a homework problem.

The solution is $V(x) = \frac{r_i \lambda I_0 \cosh((\ell - x)/\lambda)}{\sinh(\ell/\lambda)}$. Since the current is injected at $x=0$, we calculate

the solution at $x=0$. Then $V(0) = r_i \lambda I_0 / \tanh(\ell/\lambda)$. Then $R_N = r_i \lambda / \tanh(\ell/\lambda)$

3-10. Now we can substitute in $r_i = R_a 4 / (\pi d^2)$ and $\lambda = \sqrt{R_m d / (4 R_a)}$ and do some canceling to

get $R_N = \frac{2}{\pi} \frac{\sqrt{R_m R_a} d^{-3/2}}{\tanh(\ell/\lambda)}$. From this expression you can directly see the dependence of R_N on

the various electrotonic parameters. The only complication is that the tanh term contains a λ which contains R_m , R_a and d as well. However, for $\ell/\lambda > 1.0$, this tanh term does not vary much.

What happens if there is shrinkage during fixation in a neuron reconstruction? How will this affect the R_N estimate in a model? R_N will appear to be larger than it really is.

What happens for a semi-infinite cylinder? In this case $\ell \rightarrow \infty$ and when this happens the tanh term $\rightarrow 1$. So $R_N \rightarrow (2/\pi) \sqrt{R_m R_a} d^{-3/2}$ which is $r_i \lambda$.

We can express this a little differently as $R_m / (\pi d \lambda)$. It is left as an exercise to verify that these quantities are all equal.

We use R_∞ to mean the input resistance of a semi-infinite cylinder. Alternatively we can express the conductance of a semi-infinite cylinder as $G_\infty = 1/R_\infty = 1/(\lambda r_i)$

Given the expression above for the input resistance for a semi-infinite cylinder, what is the input resistance of a double infinite cylinder (extending from $-\infty$ to $+\infty$, input resistance measured at $x=0$)? Input resistance would be that for a semi-infinite cylinder divided by 2.

3-11. Let's look at the special case of a cell represented by a sphere, or a cell with no dendrites.

In this case the cable equation $\tau \frac{\partial V}{\partial t} = \lambda^2 \frac{\partial^2 V}{\partial x^2} - V$ is reduced to $\tau \frac{dV}{dt} = -V$ because for an isopotential cell (or sphere), there is no spatial dependence on the voltage. The second derivative term is 0.

The equation $\tau dV/dt + V = 0$ with initial condition $V(t=0)$ has the solution $V(t)=V_0 \exp(-t/\tau)$. The details of this solution are a homework problem.

What is τ ? τ is the time constant = $R_m C_m$ as we saw earlier. The voltage decays to $1/e$ of its initial value in time τ in a sphere or isopotential cell. Although this fact is often used in the definition for τ , strictly speaking it is correct only for the isopotential cell. When we consider transient solutions to the cable equation, we will revisit this issue.

What is the importance of τ ?

τ is a measure of voltage decay with time. It is a measure of the window of temporal integration of inputs (temporal summation). When τ is large, inputs sum better. When τ is small, decay is faster and there is less summation.

3-12. Let's consider input resistance in a sphere.

When current is applied the differential equation becomes

$$C dV/dt + V/R = I_0 \quad \text{or} \quad \tau dV/dt + V = I_0 R_N$$

Constant current will take the cell from its resting voltage (assumed to be 0 or V_0) to a new steady-state voltage V_∞ where $V_\infty = I_0 R_N$.

The solution is $V(t) = V_\infty - (V_\infty - V_0) \exp(-t/\tau)$ or $V(t) = V_\infty (1 - \exp(-t/\tau))$ when $V_0=0$

For a sphere input resistance is calculated directly from R_m and membrane area as $R_N = R_m/(4\pi r^2)$. Note how the units cancel correctly.

Compare this with the expression for a cable given earlier where

$$R_N = R_m/(2\pi r \lambda \tanh(\ell/\lambda))$$