Signal transfer in passive dendrites with non-uniform membrane conductance: Appendix

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A Electrotonic properties of non-uniform dendrites

A.1 Heterogeneities in the specific membrane conductance

Consider an heterogeneous cylinder of constant diameter and introduce the dimensionless conductance $\gamma_m(x) = G_m(x)/\overline{G}_m$. The generalized electrotonic length (Rall, 1962) is then,

$$L = \frac{1}{\lambda^u} \int_0^\ell \sqrt{\gamma_m(x)} dx$$

We use Cauchy-Schwartz inequality (Spiegel, 1968):

$$\left[\int_a^b f(x)\, g(x)\, dx\right]^2 \leq \{\int_a^b [f(x)]^2\, dx\}\{\int_a^b [g(x)]^2\, dx\} \tag{A1}$$

with $f(x) = \sqrt{\gamma_m(x)}$ and $g(x) = 1/\ell$. Because the average of $G_m(x)$ is $\overline{G}_m$, the definition of $\gamma_m(x)$ above implies that,

$$\frac{1}{\ell} \int_0^\ell \gamma_m(x) dx = 1$$

Cauchy-Schwartz inequality then reads,

$$\left[\int_0^\ell \sqrt{\gamma_m(x)}\, dx\right] \leq \ell$$

and thus,

$$L \leq \frac{\ell}{\lambda^u} \; = \; L^u$$

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The Cauchy-Schwartz inequality (A1) becomes an equality if, and only if, $f(x)$ and $g(x)$ are linearly dependent. In our case, in which $g(x)$ is constant, this implies that $f(x)$ is also a constant, and as the average of γ_m is equal to 1, $f(x) \equiv 1$. This is, of course, the *uniform* case. Thus, for a cylinder of given physical length, constant diameter and average membrane conductance, *any* spatial heterogeneity of the membrane conductance strictly decreases the electrotonic length with respect to the *uniform* case.

Moreover, the electrotonic length can be made as small as wanted by appropriate conductance heterogeneities. Indeed, assume that the conductance is equal to $\overline{G}_m/\epsilon$ on a region of length $\epsilon\ell$ and vanishes on the rest of the cylinder, L is then equal to $L^u\sqrt{\epsilon}$.

The previous result can be derived in another way that is less direct but more enlightening. Starting from the *uniform* case with conductance $\overline{G}_m$, let us construct a sequence of piecewise uniform functions that converges to the prescribed non-uniform conductance. In the process, one modifies at step n the membrane conductance on an interval, $[x_0, x_2]$, while keeping the average conductance constant. Before this modification (i.e., at step $n-1$), the conductance on this interval is uniform and equal to $G_m^{(0)}$. After the modification it becomes a step function,

$$G_m(x) = G_m^{(1)} \qquad (x_0 \le x < x_1), \qquad\qquad G_m(x) = G_m^{(2)} \qquad (x_1 < x \le x_2)$$

where x_1 is some point in the interval. As the average conductance is not modified,

$$G_m^{(0)} = \alpha G_m^{(1)} + (1-\alpha) G_m^{(2)}$$

where $\alpha = (x_1 - x_0)/(x_2 - x_0)$. The resulting change, at step n, in the electrotonic length is,

$$\sqrt{\frac{4\pi R_i}{d}} \left(\alpha\sqrt{G_m^{(1)}} + (1-\alpha)\sqrt{G_m^{(2)}} - \sqrt{G_m^{(0)}} \right)$$

which is negative, as $\sqrt{x}$ is a *convex* function. This is sufficient to prove, by induction, that the electrotonic length is smaller than in the corresponding *uniform* case. Moreover, it is obvious that the electrotonic length can be made arbitrarily small by appropriate spatial variations of the conductance (e.g., if the cable incorporates short very leaky portions). The opposite result holds for heterogeneities in the diameter, that preserve the average diameter, because the space constant λ is a *concave* function of the cable diameter. Namely, the case where the cable has the same diameter everywhere, corresponds to a *global minimum* of the electronic length and the electrotonic length can be made arbitrarily large by appropriate variations in the diameter (e.g., if the cable incorporate very thin portions).

A.2 Branched structures

The electrotonic properties of branched structures can be fully analyzed when the membrane conductance linearly varies with the physical distance. Consider a simple branched dendrite, consisting of a father branch (diameter d_0, length ℓ_0) and two daughter branches (diameters d_1 and d_2, lengths ℓ_1 and ℓ_2), branch number 1 being the longer. Assume that the specific membrane conductance linearly increases with the same slope along all the branches. Then $G_m(x) = \overline{G}_m \alpha x$ where,

$$\alpha = \frac{1}{2} \frac{d_0\ell_0 + d_1\ell_1 + d_2\ell_2}{d_0\ell_0^2 + d_1\ell_1^2 + d_2\ell_2^2 + 2\ell_0\left(d_1\ell_1 + d_2\ell_2\right)}$$

The specific conductance is larger at the distal end of the longer branch than at the distal end of the smaller branch, $\overline{G}_m\alpha(\ell_0 + \ell_1)$ versus $\overline{G}_m\alpha(\ell_0 + \ell_2)$. The electrotonic length of the father branch is now,

$$L_0 = \frac{2}{3} L_0^u \sqrt{\alpha \ell_0}$$

while the electrotonic lengths L_j, $j = 1, 2$, of the daughter branches now read,

$$L_j = L_j^u \frac{2}{3} \sqrt{\alpha} \frac{(\ell_0 + \ell_j)^{3/2} - \ell_0^{3/2}}{\ell_j} \tag{A2}$$

where L_j^u denotes the electronic length of the j-th branch in the *uniform* case. The electrotonic lengths L_j, of the jth branch depends on the physical lengths of the three branches. The total membrane conductance of the father branch is now $g_0 = g_0^u \, \alpha \, \ell_0/2$, where g_0^u denotes the total conductance of this branch in the *uniform* case. Similarly, the total conductances of the daughter branches is $g_j = g_j^u \alpha \left(\ell_j + 2\ell_0\right)/2$. This shows that, as expected, membrane conductance is reallocated to the daughter branches at the expense of the father branch, and that the larger reallocation of membrane conductance occurs for the longer daughter branch.

Such a non-uniform branched structure may be equivalent, in some cases, to a single non-uniform cylinder. To determine the conditions for such an equivalence, we rewrite the cable equation in terms of the dimensionless variables $T = t/\tau_m(x)$ and $X = \int_0^x dz/\lambda(z)$. The former is time expressed in units of the local passive membrane time constant, whereas the latter is the electrotonic distance to the soma. The cable equation on the branched structure can then be written on every branch under the general form (Ohme and Schierwagen, 1998),

$$\frac{\partial^2 V}{\partial X^2} + Q(X)\frac{\partial V}{\partial X} - \frac{\partial V}{\partial T} + \frac{2}{\pi C_m}\sqrt{\frac{R_i}{d}}\frac{I(X,T)}{d^{3/2}} = 0$$

where $I(X,T)$ is the injected current density, $d(X)$ is the diameter of the branch, and $Q(X)$ characterizes the (geometric and electric) heterogeneity of the cable. Here we assume that every branch has a constant diameter. Then $Q(X)$ is just the logarithmic derivative of the specific conductance,

$$Q(X) = \frac{1}{G_m(X)} \frac{dG_m(X)}{dX}$$

and in the *maximal slope* case it is equal to $1/(3(1+X))$ for all three branches. Three conditions must be satisfied for the whole structure to be equivalent to a cylinder, as in the usual *uniform* case (Rall, 1959),

- The generalized electrotonic lengths of the two daughter branches must be equal.
- The two daughter branches must terminate with the same boundary conditions (e.g., "sealed end").
- The local condition $d_0^{3/2} = d_1^{3/2} + d_2^{3/2}$ must be satisfied at the branch point.

For fixed parameters of the father branch, the electrotonic structures satisfying these conditions constitute a two-parameters family, indexed by the common electrotonic length of the two daughter branches and by any parameter that characterizes the degree of asymmetry between the two branches. A convenient choice for that parameter is the relative difference in the physical length of the two branches $(\ell_2 - \ell_1)/\ell_1$.

When the branched structure is equivalent to a cylinder in the *uniform* case, it is no longer so in the *slope* case, except in the trivial case where the two daughter branches are identical. Indeed, if the electrotonic lengths of the two daughter branches were still equal, this would entail, in view of equation (A2) that the function,

$$f(z) = \frac{(\ell_0 + z)^{3/2} - \ell_0^{3/2}}{z}$$

takes identical values for $z = \ell_1$ and $z = \ell_2$, which is impossible as $f(z)$ is strictly monotonic. One also easily shows, with a similar argument, that in that case the total membrane conductance of the longer daughter branch is always larger than the total conductance of its sibling.

To investigate how conductance is reallocated in a neuron (rather than in a dendritic tree), consider the simple case where two cylinders emerge from a soma. The membrane conductance of the cylinders are still given by $G_m(x) = \overline{G}_m \alpha x$, where,

$$\alpha = \frac{1}{2} \frac{d_1 \ell_1 + d_2 \ell_2}{d_1 \ell_1^2 + d_2 \ell_2^2}$$

Their total membrane conductances are equal to $\overline{G}_m \pi d_j \alpha \ell_j^2 / 2$. Their ratio is equal to $d_1 \ell_1^2 / d_2 \ell_2^2$, versus $d_1 \ell_1 / d_2 \ell_2$ (which is just the ratio of the membrane area) in the *uniform* case. As a consequence, the asymmetry in the conductance distribution between the two cylinders is enhanced in the *slope* case by a factor equal to the ratio of their physical length. More generally, it can be shown that if the function $G_m(x)$ increases as a power law of the distance from the soma with integer exponent p, the asymmetry is enhanced by a factor of $(\ell_1/\ell_2)^p$. On these grounds it is clear that, for neurons possessing dendritic trees with very different morphologies (e.g. apical vs. basal), the constraint of fixed total dendritic conductance leads, in the non-uniform case, to the reallocation of the conductance (compared to the *uniform* case) to the most extensive dendritic trees at the expense of the other trees.

B Steady state solutions for cables with non-uniform membrane conductance

For all the conductance profiles discussed in this Appendix, two linearly independent analytical solutions of the steady-state cable equation are available. The potential $V(x)$ can then be computed explicitly for "sealed end" or "killed end" boundary conditions, and constant current injection at any point along the cylinder. In these cases, the input resistance, the transfer resistance, etc. can be analytically computed and there is no need to rely on numerical methods.

B.1 Piecewise uniform membrane conductance

In the case of a *uniform* cylinder with "sealed end" at $x = 0$ and an injection of a constant current I at $x = \ell$, the solution of the steady state cable equation (4) is (Rall, 1959),

$$V(x) = \frac{4I\lambda^u \cosh\left(\frac{x}{\lambda^u}\right)}{\pi R_i d^2 \sinh\left(\frac{\ell}{\lambda^u}\right)} = \frac{I\cosh(X^u)}{G^u_\infty \sinh(L^u)} \tag{B3}$$

When the specific conductance is piecewise uniform, the solution takes the form of $C_i \exp(x/\lambda^u_i) + D_i \exp(-x/\lambda^u_i)$ on the i-th interval, where the local space constant is λ^u_i. The potential profile on the cable is then derived by writing down Kirchoff's laws at the boundary points between the uniform intervals, and solving the resulting linear system to obtain the coefficients C_i and D_i (Rall, 1962).

B.2 Power law profiles

When the specific conductance is a linear function of x ($G^s_m(x) = ax + b$), the corresponding steady-state cable equation (4) has an explicit solution. Indeed, using the dimensionless variable, $y = x/\ell$, the steady state cable equation becomes,

$$\frac{1}{(L^u)^2}\frac{d^2V}{dy^2} - (1 - \alpha + 2\alpha y)\, V = 0$$

It can be transformed, through the change of space coordinate,

$$z = \left(2\alpha (L^u)^2\right)^{\frac{1}{3}} \left(y + \frac{(1-\alpha)}{2\alpha}\right)$$

to the *Airy equation* (Abramowitz and Stegun, 1970),

$$\frac{d^2V}{dz^2}(z) - zV(z) = 0 \tag{B4}$$

The general solution of this equation is $V(z) = C_1 A_i(z) + C_2 B_i(z)$, where the *Airy functions* A_i and B_i are two linearly independent solutions of the equation, and C_1 and C_2 are constants dictated by the boundary conditions. For "sealed end" at $x = 0$ and constant current injection at $x = \ell$, the appropriate boundary conditions at $z_0 = z|_{x=0} = (1-\alpha)(L^u/(2\alpha))^{2/3}$ and $z_\ell = z|_{x=\ell} = (1+\alpha)(L^u/(2\alpha))^{2/3}$ are,

$$\frac{dV}{dz}(z_0) = 0, \qquad \frac{dV}{dz}(z_\ell) = \frac{4I\ell}{\pi R_i d^2 \left(2\alpha\left(L^u\right)^2\right)^{\frac{1}{3}}}$$

One then obtains,

$$V(z) = KI\frac{B'_i(z_0)A_i(z) - A'_i(z_0)B_i(z)}{A'_i(z_\ell)B'_i(z_0) - A'_i(z_0)B'_i(z_\ell)}; \qquad K = \frac{4R_i\ell}{\pi d^2\left(2\alpha\left(L^u\right)^2\right)^{\frac{1}{3}}} \tag{B5}$$

where A'_i and B'_i denote the first order derivatives of A_i and B_i. Similarly, an explicit solution, now involving parabolic cylinder functions, is obtained when $G_m(x) = ax^2 + bx + c$ (result not shown).

Equation (B5) can be simplified in the *maximum slope* case (i.e., $\alpha = 1$), where the conductance increases from 0 at $x = 0$ to $2\overline{G}_m$ at $x = \ell$. Using one form of the *hypergeometric function*, ${}_0F_1$ and the Euler Gamma function (Abramowitz and Stegun, 1970), we get the following solution,

$$V(x) = \frac{6R_iI\ell}{\pi d^2\left(L^u\right)^2}\frac{\Gamma(\frac{5}{3})}{\Gamma(\frac{2}{3})}\frac{{}_0F_1\left(\frac{2}{3}, \frac{2x^3}{9\ell\lambda^{u2}}\right)}{{}_0F_1\left(\frac{5}{3}, \frac{2\ell^2}{9\lambda^{u2}}\right)} \tag{B6}$$

More generally, the solution of the steady state cable equation can be explicitly written when the specific membrane conductance increases along the cylinder, from 0 at $x = 0$, to its maximal value at $x = \ell$, as a power law,

$$G_m(x) = \overline{G}_m(p+1)\left(\frac{x}{\ell}\right)^p$$

in which p is a positive integer. Using the dimensionless variable, $y = x/\ell$, the steady state equation is

$$\frac{1}{\left(L^u\right)^2}\frac{d^2V}{dy^2} - (p+1)y^pV = 0$$

Two independent solutions of this equation are given by

$$\sqrt{y}I_{\pm\frac{1}{p+2}}\left(\frac{\sqrt{p+1}L^u}{1+\frac{p}{2}}y^{1+\frac{p}{2}}\right)$$

where I_ν is the modified Bessel function of order ν. Note that $p = 1$ corresponds to the *maximum slope* case.

B.3 Other solvable cases

An explicit solution is also available when the membrane conductance exponentially increases with distance, $G_m(x) = \overline{G}_m\left(a + b\exp(cx)\right)$. Two independent solutions of the steady state equation are in this case

$$I_{\pm\nu}\left(\mu\exp\left(\frac{cx}{2}\right)\right); \qquad \mu = \frac{2\sqrt{b}}{c\lambda^u\overline{G}_m}\ , \qquad \nu = \frac{2}{c\lambda^u}\sqrt{1 - \frac{b}{c\,\ell\overline{G}_m}\left(\exp(c\,\ell) - 1\right)}$$

Finally, the steady state cable equation can be analytically solved when the specific membrane *resistance*, $R_m(x)$, increases or decreases linearly ($R_m(x) = ax + b$). Defining a slope parameter α, like we have done in equation (3), and denoting here again by $\overline{G}_m$ the spatial average of the membrane conductance $G_m(x) = 1/R_m(x)$ (note that in this case we still require that the total membrane *conductance* is conserved), we get,

$$R_m(x) = \frac{1}{2\alpha\overline{G}_m} \ln\left(\frac{1+\alpha}{1-\alpha}\right)\left(1 + 2\alpha\frac{x - \ell/2}{\ell}\right)$$

Introducing the dimensionless variable z such that $R_m(x) = \left(z/\overline{G}_m\right) \ln^2\left((1+\alpha)/(1-\alpha)\right)$, the steady state equation can be written, in this case, as

$$\frac{1}{(L^u)^2}\frac{d^2V}{dz^2} - \frac{V}{z} = 0$$

Independent solutions are then $\sqrt{z}I_{\pm 1}\left(2L^u\sqrt{z}\right)$.

C Transfer resistance

C.1 Uniform case versus Slope case

We can use equations (B3) and (B6), respectively, to calculate the transfer resistance $R_{\ell,0}$ between the cable ends, in the *uniform* case,

$$R^u_{\ell,0} = \frac{1}{G^u_\infty \sinh L^u}$$

and in the *maximal slope* case ($\alpha = 1$), assuming "sealed end" boundary conditions,

$$R^s_{\ell,0} = \frac{1}{G^u_\infty \, {}_0F_1(\frac{5}{3}, \frac{2}{9}{L^u}^2)L^u}$$

The ratio between these two quantities is,

$$\frac{R^s_{\ell,0}}{R^u_{\ell,0}} = \frac{\sinh L^u}{{}_0F_1(\frac{5}{3}, \frac{2}{9}(L^u)^2)L^u} \tag{C7}$$

and is only a function of the electrotonic length L^u. When L^u goes to 0, the hypergeometric function goes to 1 (Abramowitz and Stegun, 1970) and so does the ratio. Moreover, the hypergeometric function is less than 1 in modulus, which implies that the ratio is bounded from below by $\sinh\left(L^u\right)/L^u \geq 1$. The transfer resistance, $R_{\ell,0}$, is thus always larger in the *maximum slope* case than in the *uniform* case.

C.2 Steady State Synaptic input

The transfer resistance $R_{x,0} = V(0)/I_x$, defined for constant *current* injection, also enables us to compute the steady state voltage at the cable end $x = 0$ in response to a steady state synaptic *conductance* change, g_{syn}, at location x, that is associated with reversal potential E_{syn}. Indeed, the steady state voltage at x is then given by,

$$V(x) = \frac{g_{syn}}{g_{syn} + G_{in}(x)} E_{syn}$$

where $G_{in}(x)$ denotes the input conductance of the cable at point x. The steady state synaptic current is,

$$\begin{aligned} I_{syn} &= g_{syn}(V(x) - E_{syn}) \\ &= -E_{syn} g_{syn} \left(\frac{G_{in}(x)}{g_{syn} + G_{in}(x)} \right) \end{aligned}$$

Noting the convention that inward synaptic current is negative, the voltage response at $x = 0$ is given by,

$$\begin{aligned} V(0) &= -I_{syn} R_{x,0} \\ &= E_{syn} g_{syn} \left(\frac{G_{in}(x)}{g_{syn} + G_{in}(x)} \right) R_{x,0} \end{aligned}$$

C.3 Spatially decreasing conductance profiles

Symmetry properties can be used to study the case of a linearly decreasing conductance with a slope parameter of $-1 \le \alpha^- \le 0$. Let us denote by $R^{-s}_{x,y}$ the transfer resistance in such a case. Due to the linearity of the cable equation (Koch, 1999), $R^{-s}_{\ell,0} = R^{-s}_{0,\ell}$, and by symmetry, $R^{-s}_{0,\ell} = R^{s}_{\ell,0}$ where $R^{s}_{x_1,x_2}$ is the transfer resistance for an *increasing* conductance with slope parameter $\alpha^+ = -\alpha^-$ (note that this holds only when the "correct" boundary conditions are assumed). Consequently, $R^{-s}_{\ell,0} = R^{s}_{\ell,0}$. This shows that for *both* increasing and decreasing membrane conductance, the transfer resistance between the end points of the cylinder is larger in the *slope* case compared to the *uniform* case. In addition, the transfer resistance, $R^{-s}_{0,0} = R^{-s}_{in}(0)$, is equal, by symmetry, to $R^{s}_{in}(\ell)$ which is smaller than the value of the input resistance $R^{u}_{in}(\ell)$ in the *uniform* case. Together with the first result above, this implies that the transfer resistance curves $R^{-s}_{x,0}$ (linearly decreasing conductance) and $R^{u}_{x,0}$ (*uniform* case) cross each other, for any value of the slope parameter α^-. More generally, these symmetry considerations apply to any monotonically increasing membrane conductance (power law, exponential etc.), leading to results similar to those we derived here for the *slope* case.

D Transient solutions: general results

D.1 The Schrödinger eigenvalue problem

The motion of a particle of mass m is described by its (complex) wave function $\psi(x,t)$, the square modulus of which gives the probability of finding the particle at x, when testing for its location at time t. $\psi(x,t)$ is solution of the Schrödinger equation,

$$i\hbar\frac{\partial\psi(x,t)}{\partial t} = -\frac{\hbar^2}{2m}\frac{\partial^2\psi(x,t)}{\partial x^2} + W(x)\psi(x,t)$$

where $\hbar$ is the Planck constant h divided by 2π. At variance with classical mechanics, a stationary state of motion is possible in the quantum case only for discrete values E_j of the energy. The corresponding wave functions can be written, with variables x and t separated, as,

$$\exp\left(-i\frac{E_j t}{\hbar}\right)\psi_j(x)$$

where $\psi_j(x)$ is real. The E_j and $\psi_j(x)$ are obtained by solving,

$$-\frac{\hbar^2}{2m}\frac{d^2\psi_j(x)}{dx^2} + \left(W(x) - E_j\right)\psi_j(x) = 0 \tag{D8}$$

This equation can be written,

$$-\frac{\hbar^2}{2m\overline{W}}\frac{d^2\psi_j(x)}{dx^2} + \left(\frac{W(x)}{\overline{W}} - \frac{E_j}{\overline{W}}\right)\psi_j(x) = 0 \tag{D9}$$

where $\overline{W}$ is the spatial average $\int_0^\ell W(x)dx/\ell$. Comparing this equation with equation (5) shows that determining the fundamental energy level E_0 and the excited energy levels E_j ($j \geq 1$) in the well $W(x)$, and determining the system time constant, τ_0, and the equalizing time constants, τ_j ($j \geq 1$), for an heterogeneous cable of conductance, $G_m(x)$ are actually the same problem, provided that three conditions are satisfied:

- the dimensionless conductance $\gamma_m(x)$ and the dimensionless potential $W(x)/\overline{W}$ must have the same spatial variations.
- the characteristic diffusion lengths λ^u and $\hbar/\left(\sqrt{2m\overline{W}}\right)$ must be equal. The latter diffusion length can be interpreted as the wavelength of the wave function associated to the particle. It is obtained by requiring that the average kinetic and potential energies of the quantum particle be equal.
- identical boundary conditions must be imposed at $x = 0$ and $x = \ell$ in equations (5) and (D9).

In the quantum problems, "killed end" boundary conditions (which correspond to infinite potential barriers) are generally used. However, a "sealed end" is easily introduced: to impose such a condition at $x = \ell$, one defines a well on $[0, 2\ell]$ by reflection of $W(x)$ with respect to $x = \ell$. The eigenfunctions for the "sealed end" problem are then given by the restriction to $[0, \ell]$ of the eigenfunctions of the new problem, that are *even* with respect to $x = \ell$. This way of introducing a sealed end is equivalent to the reflection of paths reaching the end of the cable in Abbott et al. (1991); Bressloff and Taylor (1993).

D.2 System time constant

We can use the usual variational method of quantum mechanics to show that, for "sealed end" boundary conditions, the system time constant, τ_0, is always larger in the non-uniform case than in the corresponding *uniform* case. Indeed, let us rewrite equation (5) as $H\mathcal{G}_j(x) + (\tau_m^u/\tau_j)\,\mathcal{G}_j(x) = 0$ where H is the linear operator $-(\lambda^u)^2 \frac{d^2}{dx^2} + G_m(x)/\overline{G}_m$. Then (τ_m^u/τ_0) is equal to the average value of H in the state $\mathcal{G}_0(x)$,

$$\frac{\tau_m^u}{\tau_0} = \langle \mathcal{G}_0 H \mathcal{G}_0 \rangle = \int_0^\ell \mathcal{G}_\prime(x) H[\mathcal{G}_0](x) dx$$

since $H\mathcal{G}_0 = (\tau_m^u/\tau_0)\,\mathcal{G}_0$. Because the $\mathcal{G}_j$ are eigenfunctions of H and they form a complete orthonormal basis, and because (τ_m^u/τ_0) is the smallest eigenvalue of H,

$$\frac{\tau_m^u}{\tau_0} = \min \langle \phi H \phi \rangle = \min \int_0^\ell \left(-(\lambda^u)^2 \phi(x) \frac{d^2\phi}{dx^2} + \gamma_m(x)\phi(x)^2 \right) dx \tag{D10}$$

the minimum being taken over all real square integrable functions $\phi(x)$ defined on $[0, \ell]$ and of norm unity $\left(\int_0^\ell \phi(x)^2 dx = 1\right)$. In particular, (τ_m^u/τ_0) is smaller than $\langle \phi^* H \phi^* \rangle$ where ϕ^* is the constant function $1/\sqrt{\ell}$. This shows that (τ_m^u/τ_0) is smaller than the average value of $\gamma_m(x)$, which is equal to 1, and thus $\tau_0 > \tau_m^u$. Because for the *uniform* case with "sealed ends" $\tau_0 = \tau_m^u$, this result can be reformulated as $\tau_0 > \tau_0^u$.

We expect that $\tau_0 > \tau_0^u$ for any boundary condition and any non-uniform membrane conductance $G_m(x)$, but we could not prove this general result. However, we can show that this result remains valid for "killed ends" at both boundaries in the *slope* case, and more generally, for all cases in which the departure of the membrane conductance from its mean value is odd with respect to the mid-point, namely,

$$G_m\left(\frac{\ell}{2} + x\right) - G_m\left(\frac{\ell}{2}\right) = -\left(G_m\left(\frac{\ell}{2} - x\right) - G_m\left(\frac{\ell}{2}\right)\right)$$

(Note that in such a case, $G_m(\ell/2) = \overline{G}_m$). Indeed, integrating by parts the first term on the right-hand-side of equation (D10) and then taking into account the boundary condition $\phi(x) = 0$ at $x = 0$ and at $x = \ell$, one obtains,

$$\frac{\tau_m^u}{\tau_0} = \min \int_0^\ell \left((\lambda^u)^2 \frac{d\phi}{dx}^2 + \gamma_m(x)\phi(x)^2 \right) dx \leq \int_0^\ell \left((\lambda^u)^2 \frac{d\mathcal{G}_0^u}{dx}^2 + \gamma_m(x)\mathcal{G}_0^u(x)^2 \right) dx$$

where $\mathcal{G}_0^u$ is the first eigenfunction in the *uniform* conductance case (for which $\gamma_m(x) \equiv 1$). Therefore,

$$\frac{\tau_m^u}{\tau_0} \leq \int_0^\ell \left((\lambda^u)^2 \frac{d\mathcal{G}_0^u}{dx}^2 + \mathcal{G}_0^u(x)^2 \right) dx + \int_0^\ell (\gamma_m(x) - 1)\, \mathcal{G}_0^u(x)^2 dx$$

The first integral, which corresponds to the *uniform* case, is equal to (τ_m^u/τ_0^u). The second integral vanishes as $\gamma_m(x)$ is odd with respect to the mid-point $x = \ell/2$, while $\mathcal{G}_0^u$ is even with respect $\ell/2$ (more generally $\mathcal{G}_n^u(x) = \sqrt{2/\ell}\sin([n+1]\pi x/\ell)$). Consequently, $\tau_0 > \tau_0^u$. Note that, for these boundary conditions, τ_0 is larger than τ_0^u but may still be smaller than τ_m^u, as $\tau_0^u < \tau_m^u$. This happens, for instance, in the *slope* case when the slope parameter α is small enough, as τ_0 is a smooth function of α that converges to τ_0^u when α goes to 0.

Note also that the first eigenvalue, τ_m^u/τ_0, of the eigenvalue problem (5) is always larger than the minimum of the function $G_m(x)/\overline{G}_m$ (in the corresponding quantum problem, the ground state is necessarily above the minimum of the potential well). As a consequence, the opposite bound $\tau_0 < C_m/\min(G_m(x))$ always holds.

D.3 Localization of eigenfunctions

As shown in section 2.4 for the *slope* case, the time constants as well as the eigenfunctions depend on the electrotonic length of the cable. Moreover, the larger time constants are more sensitive to the value of L^u and the associated eigenfunctions become localized in the low conductance region for smaller values of L^u compared to smaller time constants. The quantum analogy is useful to understand that behavior. Energy levels are always discrete as motion takes place in a finite domain $[0, \ell]$. However, two types of energy levels can still be distinguished by considering the limit of large ℓ. Bound states are located inside the potential well and remain discrete in that limit, while free states, that are located above it, tend to form a continuum in that same limit. Bound states are sensitive to the shape of the potential well and display some spatial localization, while free states are little affected by the potential well and are close to the eigenfunctions of the *uniform* case. In the *maximal slope* case, for instance, the dimensionless conductance is $\gamma_m(x) = 2x/\ell$ and grows from 0, at $x = 0$, to 2 at $x = \ell$. Bound states correspond to time constants larger than $\tau_m^u/2$. It can be seen in figure 9A and in section 2.4 that the equalizing time constants become sensitive to the conductance non-uniformity only when they get close to $\tau_m^u/2$. On the opposite, the fundamental state is always bound (the system time constant is equal to τ_m^u in the limit of vanishing L^u and increases with L^u). As a consequence, the system time constant is affected by the conductance non-uniformity even when the cable is electrotonically very compact. The same behavior is observed on the eigenfunctions (see Figs. 9B and C). The eigenfunction $\mathcal{G}_0(x)$ becomes non-uniform in the *slope* case, while $\mathcal{G}_1(x)$ is delocalized on the whole interval $[0, \ell]$ as long as τ_1 does not approach $\tau_m^u/2$. This explains why the slow relaxation is much more sensitive to conductance non-uniformities than the faster equalizing process.

When the particle wavelength goes to 0 in the quantum problem (D9) (for instance, when the mass of the particle gets large), the predictions of classical mechanics describe more and more accurately the behavior of the particle. The energy spectrum tends to a continuum, the fundamental energy level E_0 becomes equal to the global minimum $W(x_0) = \min(W(x))$ of the potential well $W(x)$ on $[0, \ell]$ and the associated eigenfunction $\psi_0(x)$ becomes localized at the corresponding location x_0. This is the so-called semi-classical limit of the quantum problem. The same behavior is observed in the cable problem, in the limit where the electrotonic length L^u of the *uniform* cable goes to infinity. In this limit, voltage relaxation is governed by the minimum of the conductance: the system and equalizing time constants go to $C_m/min(G_m(x))$ and the associated eigenfunctions become localized at the location where $G_m(x)$ is minimum. In section 2.4 this can be seen in the *maximal slope* case, for which the $G_m(x)$ takes its minimum value, 0, at $x = 0$. The time constants all increase with L^u (see Fig. 9A), that is, when λ^u decreases . The corresponding quantities τ_m^u/τ_j decrease and get bound in the potential well. Of course this occurs first for the lower levels. For instance, the state, $\mathcal{G}_1$, gets bound for $L^u \simeq 3.5$ while for the state, $\mathcal{G}_2$, this only happens for $L^u \simeq 7$ (see Fig. 9). In the limit of large L^u, all time constants increase without bound, which corresponds to discrete levels closely packed near 0, where the potential reaches its minimum.

The technique used in quantum mechanics to investigate the semi-classical limit can also be applied to the steady state cable equation for large but finite L^u. Let us define the small dimensionless parameter $\epsilon = 1/L^u$. Using the dimensionless space variable $y = x/\ell$, the equation for the j-th eigenvalue reads,

$$-\epsilon^2 \frac{d^2\mathcal{G}_j(y)}{dy^2} + \left(\gamma_m(y) - \frac{\tau_m^u}{\tau_j}\right) \mathcal{G}_j(y) = 0 \tag{D11}$$

Consider a monotonically increasing conductance $\gamma_m(y)$ and assume the equalizing time constant τ_j is known. Let $p(y) = \sqrt{\tau_m^u/\tau_j - \gamma_m(y)}$ and define the turning point y^* by $p(y^*) = 0$. Using the ansatz $\mathcal{G}_j(y) = \exp(i\sigma(y)/\epsilon)$, equation (D11) becomes,

$$-\left(\frac{d\sigma}{dy}\right)^2 + i\epsilon\frac{d^2\sigma}{dy^2} - \gamma_m(y) + \frac{\tau_m^u}{\tau_j} = 0$$

Expanding σ as a power series in ϵ, and solving the above equation order by order, one obtains on the interval $[y^*, \infty($, where $p(y)$ is imaginary,

$$\mathcal{G}_j(y) = \frac{C_2}{\sqrt{|p(y)|}} \exp\left(-\frac{1}{\epsilon}\int_{y^*}^{y} |p(y)|dy\right)$$

This is interpreted as follows in quantum mechanics. The motion of the particle remains confined in the region $[0, y^*]$ allowed by the laws of classical mechanics (the kinetic energy must be positive), except for an exponentially small probability to visit the "classically forbidden" region ($y > y^*$). For the cable problem this means that though the support of $\mathcal{G}_j$ is the whole interval $[0, \ell]$, nearly all the weight is in the low conductance region, defined by $G_m(x) < \overline{G}_m\tau_m^u/\tau_j$, except for an exponential tail in the higher conductance region. Such an exponential tail is clearly visible when $L^u = 10$ (and even for $L^u = 2$) in figure 9B, which displays the spatial variations of $\mathcal{G}_0$ for several values of L^u. In that case, the classical region extends only to $y \simeq 0.18$ while the exponential tail covers the rest of the domain. Both the width of the classical region and the weight of the exponential tail, that can be characterized by the "penetration factor" $\exp\left(-\int_{y^*}^1 |p(y)|dy/\epsilon\right)$, increase with j, because y^* increases with j. As a consequence, the functions $\mathcal{G}_j(x)$ become less and less localized as their order, j, increases. In the case of $\mathcal{G}_1$ for instance, the classical region extends to $y \simeq 0.56$ for $L^u = 10$, three times more than for for $\mathcal{G}_0$ (see Fig. 9C).

On the other hand, by solving equation (D11) on the interval $[0, y^*]$ (the "classical" region) in the same way as above one obtains

$$\mathcal{G}_j(y) = \frac{C_1^+}{\sqrt{p(y)}} \exp\left(\frac{i}{\epsilon}\int_{y^*}^y p(y)dy\right) + \frac{C_1^-}{\sqrt{p(y)}} \exp\left(-\frac{i}{\epsilon}\int_{y^*}^y p(y)dy\right)$$

up to corrections of order ϵ in the pre-exponential factors. The continuity of the analytic continuation of $\mathcal{G}_j(y)$ to complex values of the argument y implies that these two forms of $\mathcal{G}$ must smoothly transform one into the other, when one follows a path in the complex plane avoiding the turning point y^* (Landau and Lifschitz, 1997). This entails that,

$$\mathcal{G}_j(y) = \frac{C}{\sqrt{p(y)}} \sin\left(\frac{1}{\epsilon}\int_{y^*}^y p(y)dy + \frac{\pi}{4}\right)$$

In addition $G_j(y)$ must satisfy the imposed boundary condition at $x = 0$ (in the limit of large electrotonic length the results no longer depend on the boundary condition at $x = \ell$), which gives

$$\frac{1}{\epsilon}\int_0^{y^*} p(y)dy + \frac{\pi}{4} = (j+1)\pi \tag{D12}$$

for a killed end at $x = 0$. The case of a sealed end boundary condition at $x = 0$ is handled in a similar way : the "quantization" condition (D12) then reads,

$$\frac{1}{\epsilon}\int_0^{y^*} p(y)dy + \frac{\pi}{4} = \left(j + \frac{1}{2}\right)\pi \tag{D13}$$

These formulas, which give approximate expressions of the time constants for large values of L^u, are applied in the next section to the *slope* case (see Appendix E.2).

The picture, grounded on the quantum analogy, presented in this section also helps to understand how the voltage relaxation depends on the steepness of the conductance profile. For sigmoid profiles displaying an abrupt transition or power-laws profiles with a large exponent, the contrast between the low conductance proximal and the high conductance distal region is much sharper than in the *slope* case . Time constants, τ_n, are then close to $C_m/\overline{G}_m^{(low)}$, where $\overline{G}_m^{(low)}$ is the average conductance of the low conductance region. Only higher order time constants significantly depart from this behavior. As a consequence, both the ultimate relaxation of voltage transients and the faster "equalization" process are slowed down in a similar way. Only the fastest transients can be affected by the presence of the high conductance distal region. Note that the transient behavior depends much less on the distal boundary condition for such steep profiles than in the *slope* case, because the leaky distal region acts as a potential barrier for motion in the low conductance region. Consequently, low order eigenfunctions are close to sine functions in the low conductance region, and just present an exponential tail in the high conductance region if the electrotonic length L^u is not too small. Note also that the generalized electrotonic length, L, can be drastically reduced in such cases as compared to the electrotonic length, L^u, of the corresponding *uniform* case.

E Transient solutions: the slope case

E.1 Solving the eigenvalue problem

In the *slope* case, the system time constant and all equalizing time constants, together with the associated eigenfunctions $\mathcal{G}_j(x)$, can be analytically derived. The j-th equalizing time constant τ_j satisfies the equation

$$-(\lambda^u)^2 \frac{d^2\mathcal{G}_j(x)}{dx^2} + \left(1 - \alpha + 2\alpha\frac{x}{\ell} - \frac{\tau_m^u}{\tau_j}\right)\mathcal{G}_j(x) = 0$$

which is derived from equation (5). This equation can be recast into the standard Airy equation (B5) through the change of variable,

$$z[x] = \left(2\alpha(L^u)^2\right)^{\frac{1}{3}}\left(\frac{x}{\ell} + \frac{(1-\alpha)}{2\alpha} - \frac{\tau_m^u}{2\alpha\tau_j}\right)$$

that *involves* τ_j itself. The eigenfunction, $\mathcal{G}_j(x) = a_j A_i(z[x]) + b_j B_i(z[x])$, is then a linear combination of the Airy functions A_i and B_i. We shall consider from now on sealed-end boundary conditions, but the computations are quite similar for killed ends: the corresponding equations can be formally obtained by replacing, everywhere in the formula, the derivatives of Airy functions by the Airy functions themselves. For these "sealed end" conditions, the derivative of $\mathcal{G}_j$ vanishes at the points $z^{\pm}$, that respectively correspond to $x = \ell$ and $x = 0$,

$$z^{\pm} = \left(\frac{L^u}{2\alpha}\right)^{2/3}\left(1 \pm \alpha - \frac{\tau_m^u}{\tau_j}\right)$$

This implies that $b_j = -a_j A_i'(z^-)/B_i'(z^-)$ and $A_i'(z^+)B_i'(z^-) - B_i'(z^+)A_i'(z^-) = 0$. Therefore, to determine the time constants it is enough to compute all the roots T_j on the real positive axis of the transcendental equation,

$$A_i'\left(z^+(T)\right)B_i'\left(z^-(T)\right) - A_i'\left(z^-(T)\right)B_i'\left(z^+(T)\right) = 0 \qquad \text{(E14)}$$

where $z^{\pm} = (L^u/2\alpha)^{2/3}(1 \pm \alpha - T)$ are now considered as functions of the unknown quantity $T = \tau_m^u/\tau_0$. The j-th equalizing time constant is then given by $\tau_j = \tau_m^u/T_j$ and the associated eigenfunction by,

$$\mathcal{G}_j(x) = a_j \left(A_i(z[x]) - \frac{A_i'\left(z^-\left(T_j\right)\right)}{B_i'\left(z^-\left(T_j\right)\right)} B_i(z[x]) \right)$$

where the value of the remaining coefficient a_j is set by the normalization condition that the integral of $\mathcal{G}_j^2(x)$ on $[0, \ell]$ be unity. Equivalently, equation (E14) can be put under the form,

$$f'\left(z^+(T)\right) g'\left(z^-(T)\right) - f'\left(z^-(T)\right) g'\left(z^+(T)\right) = 0 \qquad \text{(E15)}$$

where the functions f and g (Abramowitz and Stegun, 1970) are defined by,

$$\begin{aligned} f(z) &= \frac{3^{2/3}\Gamma(2/3)}{2} \left(\frac{B_i(z)}{\sqrt{3}} + A_i(z) \right) \\ g(z) &= \frac{3^{1/3}\Gamma(1/3)}{2} \left(\frac{B_i(z)}{\sqrt{3}} - A_i(z) \right) \end{aligned}$$

Equations (E14) or (E15) can be numerically solved to determine all the time constants τ_j.

Note that a similar procedure can be used to determine the eigenvalues and eigenfunctions, when the membrane conductance is a second degree polynomial or an exponential function. In those cases, one is also led to solve a transcendental equation. This equation involves parabolic cylinder functions in the former case and modified Bessel functions in the latter.

E.2 Approximate expressions of the time constants

Approximate expressions of the time constants can be derived in certain limiting cases. For compact cables, one proceeds as follows. When the electrotonic length L^u goes to 0, the system time constant τ_0 goes to τ_m^u, as in the *uniform* case. Introducing the small parameter $\epsilon = \left(\left(L^u\right)^2 \alpha/4\right)^{1/3}$ and using the ansatz $X = 1 - \alpha\epsilon^\beta Y$, equation (E15) can be rewritten as,

$$f'\left(\epsilon\left(\epsilon^\beta Y + 1\right)\right) g'\left(\epsilon\left(\epsilon^\beta Y - 1\right)\right) - f'\left(\epsilon\left(\epsilon^\beta Y - 1\right)\right) g'\left(\epsilon\left(\epsilon^\beta Y + 1\right)\right) = 0$$

Replacing the functions f' and g' by their Taylor series (Abramowitz and Stegun, 1970), one easily shows that $\beta = 3$, and $Y = 2/15 + \mathcal{O}\left(\epsilon^6\right)$, so that

$$\tau_0 = \frac{\tau_m^u}{1 - \frac{\alpha^2 (L^u)^2}{30}} \qquad \text{(E16)}$$

at leading correction order in L^u. This shows that the conductance gradient increases the system time constant with respect to the *uniform* case, for small electrotonic length L^u, in agreement with the general result previously established. The slope parameter appears in equation E16 with an even exponent, as the system time constant does not depend on the sign of the gradient but only on its magnitude; this explains why the next correction to the system time constant is of order $\mathcal{O}\left(\alpha^4 \left(L^u\right)^6\right)$.

The situation is different for the equalizing time constants τ_j ($j \geq 1$), because they go to 0 as $\tau_m^u (L^u)^2 / (j^2\pi^2)$ in the limit of vanishing electrotonic length, in the *uniform* case. The arguments $z^{\pm} (\tau_m^u/\tau_j))$ of A_i' and B_i' go to $-\infty$ as $(L^u)^{-4/3}$ in equation (E14), so that we can use the asymptotic forms of these functions (Abramowitz and Stegun, 1970)

$$\begin{aligned} A_i'(-z) &\sim -\frac{1}{\sqrt{\pi}} z^{1/4} \exp(-\zeta) \left(\sin\left(\zeta + \frac{\pi}{4}\right) h\left(\frac{1}{\zeta}\right) - \cos\left(\zeta + \frac{\pi}{4}\right) k\left(\frac{1}{\zeta}\right) \right) \\ B_i'(-z) &\sim -\frac{1}{\sqrt{\pi}} z^{1/4} \exp(\zeta) \left(\cos\left(\zeta + \frac{\pi}{4}\right) h\left(\frac{1}{\zeta}\right) + \cos\left(\zeta + \frac{\pi}{4}\right) k\left(\frac{1}{\zeta}\right) \right) \end{aligned}$$

where $\zeta = 2z^{3/2}/3$ and the analytical functions $h(x)$ and $k(x)$ are respectively even and odd, and can be expanded for small values of their argument as $h(x) = 1 + \mathcal{O}(x^2)$ and $k(x) = 1 - 21x/216 + \mathcal{O}(x^3)$. Equation (E14) can then be rewritten as

$$\tan\left(\zeta^- - \zeta^+\right) = \frac{h(\zeta^+)\, k(\zeta^-) - h(\zeta^-)\, k(\zeta^+)}{h(\zeta^+)\, h(\zeta^-) - k(\zeta^-)\, k(\zeta^+)}$$

where $\zeta^{\pm} = (L^u/3\alpha)\left(\tau_m^u/\tau_j - 1 \mp \alpha\right)^{3/2}$. In the limit of vanishing electrotonic length, the right hand side goes to 0, so that $\zeta^- - \zeta^+ = j\pi$ and $\tau_j = \tau_m^u / \left(1 + j^2\pi^2/(L^u)^2\right)$; the result of the *uniform* case is thus recovered. Using the Taylor development of h and k around 0, the right hand side is then equivalent, for small values of L^u, to $21\left(\zeta^- - \zeta^+\right)/216\zeta^+\zeta^-$. One easily shows that $\zeta^- - \zeta^+ = j\pi(1+\eta)$, where, at leading order, $\eta = 189\alpha^2 (L^u)^4 / 216 j^6 \pi^6$, so that,

$$\tau_j = \frac{\tau_m^u}{1 + \frac{j^2\pi^2}{(L^u)^2} + \frac{189}{108}\frac{\alpha^2 (L^u)^2}{j^4\pi^4}}$$

This shows that, at variance with the system time constant, the equalizing time constants are *reduced* by the conductance gradient.

The opposite limit of a cable of large electrotonic length is also analytically tractable by using the formalism sketched in Appendix D.3. Applying equation (D12) to the *slope* case, where $\gamma_m(y) = 1 - \alpha + 2\alpha y$, so that $p(y) = \sqrt{2\alpha(y^* - y)}$, gives

$$\frac{2\sqrt{2\alpha}}{3\epsilon} (y^*)^{3/2} = \left(j + \frac{3}{4}\right)\pi$$

where $y^* = \left(\tau_m^u/\tau_j + \alpha - 1\right)/2\alpha$. This gives, at the leading correction order,

$$\tau_j = \frac{\tau_m^u}{1-\alpha} - \frac{\tau_m^u}{(1-\alpha)^2} \left(\frac{3\pi\alpha}{L^u}\right)^{2/3} \left(j + \frac{3}{4}\right)^{2/3}$$

All the time constants converge to the same limit $\tau_m^u/(1-\alpha)$, which corresponds to the *maximal* value of the *local* time constant $\tau_m(x)$, as the electrotonic length L^u goes to infinity. The higher the order of the equalizing time constant, the longer the cable must be to observe that asymptotic regime, as corrections to the asymptotic value of τ_n become negligible only for $L^u >> \left(3\alpha\pi/(1-\alpha)^{3/2}\right) j$.

Note also that the convergence rate to the asymptotic value is faster in the *uniform* case, where it is of order $1/\left(L^u\right)^2$, than in the *slope* case, where it is of order $1/\left(L^u\right)^{2/3}$.

Analogous results are obtained for a sealed end boundary condition at $x = 0$. The "quantization" condition (D12) then reads,

$$\frac{1}{\epsilon}\int_0^{y^*} p(y)dy + \frac{\pi}{4} = \left(j + \frac{1}{2}\right)\pi$$

which leads to,

$$\tau_j = \frac{\tau_m^u}{1-\alpha} - \frac{\tau_m^u}{(1-\alpha)^2}\left(\frac{3\pi\alpha}{L^u}\right)^{2/3}\left(j + \frac{1}{4}\right)^{2/3}$$

Finally, note that not only the *slope* case, but also power-law profiles $\gamma_m(y) = (q+1)y^q$, are easily handled. Writing $p(y)$ under the form $p(y) = \sqrt{(q+1)\left(y^{*q} - y^q\right)}$ and using the fact that $q\int_0^1 \sqrt{1-u^q}du$ is just the Beta function $B(1/q, 3/2)$, one derives, for a killed end boundary condition at $y = 0$, from equation (D12),

$$\left(\frac{\tau_m^u}{\tau_j}\right)^{\frac{1}{2}+\frac{1}{q}} = \left(j + \frac{3}{4}\right)\sqrt{\pi}\frac{2q(q+1)^{\frac{1}{q}}\Gamma\left(\frac{1}{q}+\frac{3}{2}\right)}{\Gamma\left(\frac{1}{q}\right)}\frac{1}{L^u}$$

E.3 Non-uniformity of $\mathcal{G}_0$

At large times, the voltage profile along the cable is proportional to $\exp(-t/\tau_O)\mathcal{G}_0(x)$ where $\mathcal{G}_0(x)$ is the first eigenfunction of the eigenvalue problem (5) (associated to the eigenvalue τ_m^u/τ_0). For "sealed end" boundary conditions, $\mathcal{G}_0(x)$ is a decreasing function of the physical distance x along the dendrite. This is proved as follows. Inflection points of the Airy equation (B5) occur only at $z = 0$ and wherever the solution vanishes. Therefore $\mathcal{G}_0(x)$, which is everywhere strictly positive with vanishing derivative at $x = 0$ and $x = \ell$, has exactly one inflection point, and it is located at $x = (\tau_m^u/\tau_0 - (1-\alpha))\ell/2\alpha$. If $\mathcal{G}_0$ had an extremum at some location between $x = 0$ and $x = \ell$, it would display at least two inflection points on this interval, which is impossible. On the other hand, higher order eigenfunctions $\mathcal{G}_j$, $j \geq 2$ are not monotonic, as they vanish j times on the open interval $(0, \ell)$. For killed end boundary conditions, the situation is different as $\mathcal{G}_0(x)$ vanishes at the boundaries and must present a maximum on the open interval. Note also that, for the sealed ends, the fact that $\mathcal{G}_0$ must have one inflection point at $z = 0$ entails that $z^+ > 0$ and $z^- < 0$. From this we derive the inequalities $\tau_m^u/(1+\alpha) < \tau_0 < \tau_m^u/(1-\alpha)$, and using the results from the preceding subsection, $\tau_m^u < \tau_0 < \tau_m^u/(1-\alpha)$. Similarly, the eigenfunction $\mathcal{G}_1(x)$ is monotonic when τ_1 is outside the interval $(\tau_m^u/(1+\alpha), \tau_m^u/(1-\alpha))$, as it presents otherwise two inflection points on the interval $(0, \ell)$. It is monotonic, in particular, when the cable is electrotonically compact, since τ_1 vanishes with L.

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