A NEW METHOD FOR EXTRACTING CABLE PARAMETERS FROM INPUT IMPEDANCE DATA

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Abstract: We establish conditions under which the input impedance and its first two derivatives, evaluated at the origin, uniquely determine the axial resistance, membrane capacitance, and membrane conductance of a finite uniform cable with one sealed end. We argue that this impedance data is readily available to the experimentalist and we demonstrate the recovery of a cable's electrical parameters from synthetic noisy measurements.

1. Introduction

In the classical cable model of a dendritic neuron, see, e.g., Rall [R1–2], one assumes that the potential difference, v, across the surface (membrane) of the neuron and the current, i, traveling along the neuron's axis satisfy

$$v_x(x,t) = -Ri(x,t) \tag{1.1}$$

$$i_x(x,t) = -Cv_t(x,t) - Gv(x,t) \tag{1.2}$$

where $0 < x < \ell$, the length (cm) of the cylinder, and the coefficients are

$$R = \frac{4R_a}{\pi d^2}, \quad C = C_m \pi d, \quad \text{and} \quad G = G_m \pi d.$$

Here d is the diameter (cm) of the cylinder, R_a is the axial resistance $(\Omega\, cm)$, C_m is the membrane capacitance (F/cm^2), and G_m is the membrane conductance $(1/(\Omega\, cm^2))$.

Assuming the cable to be quiet at $t = 0$, i.e.,

$$i(x,0) = v(x,0) = 0, \qquad 0 < x < \ell, \tag{1.3}$$

one then simultaneously applies current and measures voltage at the soma, $x = 0$, while assuming a known termination at the far end. Lumping together the soma and dendrite and sealing the far end we arrive at

$$i(0,t) = i_0(t), \quad i(\ell,t) = 0, \quad t > 0. \tag{1.4}$$

The parameter identification problem consists in extracting all or some combination of R, C, and G from measurement of the input voltage, $v_0(t) \equiv v(0,t)$, resulting from the prescribed input current, $i_0(t)$. The sought after combinations in the neurophysiological literature are the electrotonic length,

$$L \equiv \ell\sqrt{RG},$$

and the membrane time constant,

$$\tau \equiv C/G.$$

Prior attempts at extracting L and τ from $v_0(t)$ consist of variations on Rall's peeling method and numerical implementations of output least squares, see, e.g., D'Aguanno et al. [D], White et al. [W], and Holmes and Rall [H]. Although these techniques are widely used they come with no guarantees. More precisely, there has yet to appear a proof that v_0 indeed uniquely determines L and τ. The aim of this paper is to prove and apply such a result. We prove in fact that three weighted integrals of v_0 and i_0 contain enough information to uniquely determine L and τ. If, in addition, one knows the physical length, ℓ, then in fact the same data uniquely determines R, C, and G.

We state and prove these results in §2. We condense our findings into a simple algorithm whose sensitivity to errors in measured v_0 and i_0 we test in §3. We close in §4 with comments on the limitations and possible extensions of our method.

2. Uniqueness

The weights alluded to above are dictated by considering the Laplace transform, with respect to time, of v and i. It is not difficult to show that if i_0 is bounded and vanishes for large time then there exist constants $K > 0$ and $\sigma < 0$ such that

$$|v(x,t)| \le K\mathrm{e}^{\sigma t} \quad \text{and} \quad |i(x,t)| \le K\mathrm{e}^{\sigma t}, \quad 0 \le x \le \ell,\ 0 \le t. \tag{2.1}$$

In particular, solving for v in in (1.2) yields

$$v(x,t) = -C^{-1}\mathrm{e}^{-Gt/C}\int_0^t \mathrm{e}^{Gr/C} i_x(x,r)\,dr.$$

As this function may decay no faster than $\mathrm{e}^{-Gt/C}$ it follows that

$$\sigma > -G/C. \tag{2.2}$$

Given (2.1) we may speak of their respective Laplace transforms, $\hat{v}(x,s)$ and $\hat{i}(x,s)$, when $\Re s > \sigma$ where $\Re$ denotes 'real part of.' In particular, we may form the input impedance

$$z_0(s) \equiv \frac{\hat{v}_0(s)}{\hat{i}_0(s)}, \quad \Re s > \sigma. \tag{2.3}$$

In principle, one may evaluate $z_0(s)$ from experimental data at each admissible s. As we seek to determine only three constants, R, C, and G, it seems prudent to derive three independent quantities from z_0. Denoting d/ds by $'$, we shall argue that one such set is comprised of the first few Taylor coefficients of z_0 at the origin,

$$z_0(0), \quad z_0'(0), \quad \text{and} \quad z_0''(0). \tag{2.4}$$

We shall refer to these three numbers as our *Input Impedance Data.* Our main result establishes conditions under which this data determines the cable's electrical parameters.

Proposition 2.1. *If the Input Impedance Data satisfies*

$$z_0(0)z_0''(0) \le 3(z_0'(0))^2$$

then it uniquely determines L and τ. In this case, the Input Impedance Data together with the physical length, ℓ, uniquely determine R, C, and G.

Before proving this we wish to stress that the Input Impedance Data is readily computable from experimental measurements of i_0 and v_0. To be precise, we note that if f is a function which enjoys exponential decay then its Laplace transform

$$\hat{f}(s) = \int_0^\infty f(t)\mathrm{e}^{-st}\,dt$$

is a smooth function of s in a neighborhood of $s = 0$ and we may differentiate under the integral sign, finding

$$\hat{f}'(s) = -\int_0^\infty tf(t)\mathrm{e}^{-st}\,dt \quad \text{and} \quad \hat{f}''(s) = \int_0^\infty t^2 f(t)\mathrm{e}^{-st}\,dt.$$

Evaluating the above at $s = 0$, we arrive at

$$\hat{f}(0) = \int_0^\infty f(t)\,dt, \quad \hat{f}'(0) = -\int_0^\infty tf(t)\,dt \quad \text{and} \quad \hat{f}''(0) = \int_0^\infty t^2 f(t)\,dt,$$

the first three *moments* of f. This remark, together with the quotient rule for the derivative, permits us to conclude that our Input Impedance Data is composed of nothing more than rational combinations of the first three moments of the applied input current, i_0, and the measured input voltage, v_0. In particular, defining the nth moment of f by

$$M_n(f) \equiv \int_0^\infty t^n f(t)\,dt$$

we record

$$\begin{aligned}
z_0(0) &= \frac{M_0(v_0)}{M_0(i_0)} \\
z_0'(0) &= \frac{M_0(v_0)M_1(i_0) - M_0(i_0)M_1(v_0)}{M_0^2(i_0)} \\
z_0''(0) &= \frac{M_2(v_0)M_0(i_0) - M_2(i_0)M_0(v_0) - 2M_1(v_0)M_1(i_0) + 2M_1^2(i_0)z_0(0)}{M_0^2(i_0)}.
\end{aligned} \tag{2.5}$$

Let us now embark on the proof of our Proposition. The Laplace transform of (1.1)–(1.2) produces

$$\begin{aligned}
\hat{v}_x(x,s) &= -R\hat{i}(x,s) \\
\hat{i}_x(x,s) &= -(Cs+G)\hat{v}(x,s)
\end{aligned} \qquad 0 < x < \ell, \quad \Re s > \sigma. \tag{2.6}$$

Differentiating the latter with respect to x and then using the former we arrive at an equation for $\hat{\imath}$,

$$\hat{\imath}_{xx}(x,s) = R(Cs+G)\hat{\imath}(x,s), \quad 0 < x < \ell \quad \Re s > \sigma. \tag{2.7}$$

To this we append the Laplace transform of (1.4), i.e.,

$$\hat{\imath}(0,s) = \hat{\imath}_0(s) \quad \hat{\imath}(\ell,s) = 0, \quad \Re s > \sigma. \tag{2.8}$$

The solution of (2.7) subject to (2.8) is

$$\hat{\imath}(x,s) = \frac{\hat{\imath}_0(s)\sinh(\sqrt{R(Cs+G)}(\ell - x))}{\sinh(\sqrt{R(Cs+G)}\ell)}, \quad 0 < x < \ell \quad \Re s > \sigma.$$

The Laplace transform of the voltage now follows from the second equation in (2.6), namely

$$\hat{v}(x,s) = -\frac{\hat{\imath}_x(x,s)}{Cs+G} = \frac{\hat{\imath}_0(s)R\cosh(\sqrt{R(Cs+G)}(\ell - x))}{\sqrt{R(Cs+G)}\sinh(\sqrt{R(Cs+G)}\ell)}, \quad 0 < x < \ell \quad \Re s > \sigma.$$

Evaluating the ratio of $\hat{v}$ to $\hat{\imath}$ at $x = 0$ we arrive at the input impedance

$$z_0(s) = \frac{\hat{v}(0,s)}{\hat{\imath}_0(s)} = \frac{R\cosh(\sqrt{R(Cs+G)}\ell)}{\sqrt{R(Cs+G)}\sinh(\sqrt{R(Cs+G)}\ell)}, \quad \Re s > \sigma. \tag{2.9}$$

The presence of R, C, and G in z_0 is clear enough, the question however is whether they may be individually coaxed from z_0. As we only seek 3 numbers it seems reasonable to search for 3 independent equations. One such set comes from evaluating z_0 and its first two derivatives at $s = 0$. We shall find it more convenient to express these equations in terms of

$$\lambda = 1/\sqrt{RG}, \quad L = \ell/\lambda, \quad \text{and} \quad \gamma = \sqrt{R/G}.$$

Differentiating (2.9) at $s = 0$ yields

$$z_0(0) = \frac{\gamma\cosh L}{\sinh L}, \tag{2.10}$$

$$z_0'(0) = -\frac{\lambda\gamma^2 C(L + \sinh L\cosh L)}{2\sinh^2 L}, \tag{2.11}$$

$$z_0''(0) = \frac{\lambda^5 R^3 C^2(3L\sinh L + 2L^2\cosh L + 3\sinh^2 L\cosh L)}{4\sinh^3 L}. \tag{2.12}$$

Recall that we have shown that the left hand sides are determined by the first three moments of the applied input current and the measured input voltage. Hence, given ℓ, they constitute three equations for our three unknown cable parameters. The first of these is well known while the latter two appear to be new. More precisely, $z_0(0)$ is commonly known as the input resistance and (2.10) is identical to [R2, eqn. 2.33].

We proceed now to derive from (2.10)–(2.12) a single equation for L. To begin, we solve (2.10) for γ,

$$\gamma = z_0(0)\frac{\sinh L}{\cosh L}. \tag{2.13}$$

Substituting this into (2.11) produces an expression for the membrane capacitance

$$C = -2\frac{z_0'(0)\cosh^2 L}{z_0^2(0)\lambda(L+\sinh L\cosh L)}. \tag{2.14}$$

Substituting (2.14) and (2.13) into (2.12) brings

$$\begin{aligned} z_0''(0) &= \frac{\gamma^3(z_0'(0))^2\cosh^4 L(3L\sinh L + 2L^2\cosh L + 3\sinh^2 L\cosh L)}{z_0^4(0)(L+\sinh L\cosh L)^2\sinh^3 L} \\ &= \frac{(z_0'(0))^2\cosh L(3L\sinh L + 2L^2\cosh L + 3\sinh^2 L\cosh L)}{z_0(0)(L+\sinh L\cosh L)^2} \end{aligned}$$

or, upon moving all measured quantities to the left hand side,

$$\frac{z_0(0)z_0''(0)}{(z_0'(0))^2} = \frac{\cosh L(3L\sinh L + 2L^2\cosh L + 3\sinh^2 L\cosh L)}{(L+\sinh L\cosh L)^2}. \tag{2.15}$$

We denote the right hand side of this equation by $F(L)$ and offer, see figure 1, the graph of F for $0 \le L \le 10$.

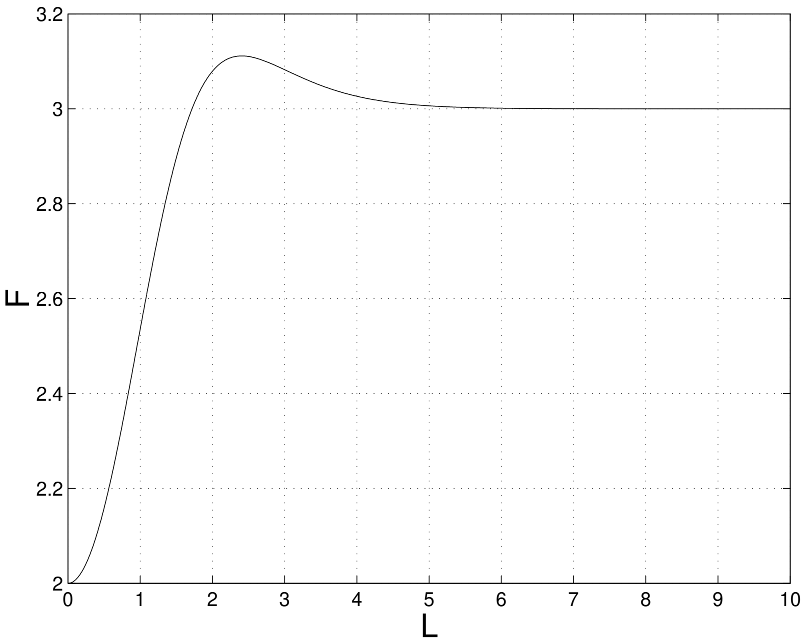

Figure 1. The graph of F.

With this figure in hand it is not difficult to show by analytical means that F is strictly increasing between the values of 2 and 3 and that once it exceeds 3 it never reaches 3 again. The upshot is that F is one–to–one when

$$\frac{z_0(0)z_0''(0)}{(z_0'(0))^2} \leq 3 \tag{2.16}$$

and hence L is uniquely determined by (2.15) is this case. Once L is determined we arrive immediately at $C\ell$ via (2.14) and γ via (2.13) and then at τ via

$$\tau = \frac{C}{G} = \frac{C\ell}{L}\gamma. \tag{2.17}$$

Finally, if ℓ is also known then one has $C = (C\ell)/\ell$ and $\lambda = \ell/L$ and, from λ and γ come

$$R = \gamma/\lambda \quad \text{and} \quad G = 1/(\gamma\lambda). \tag{2.18}$$

This completes the proof of Proposition 2.1.

An alternative interpretation of (2.16), in light of fig. 1, is that L is uniquely determined by the Input Impedance Data so long as $L \leq 1.717$. We remark that this range encompasses each of the examples considered by White et al. [W].

In those cases for which $z_0(0)z_0''(0) > 3(z_0'(0))^2$ the graph of F returns precisely two consistent values of L and further data must be gathered in order to distinguish them from one another. It appears likely that knowledge of the third derivative, $z_0'''(0)$, would suffice. Rather than pursuing that line we instead show that L may be determined by replacing $z_0''(0)$ with τ. The membrane time constant is the quantity that the peeling method returns with confidence.

Corollary 2.2. *Measurement of $z_0(0)$, $z_0'(0)$, and τ uniquely determines L.*

Proof: It follows directly from (2.17), (2.14), and (2.13) that

$$\tau = \frac{C}{G} = C\lambda\gamma = -2\frac{z_0'(0)}{z_0(0)}\frac{\sinh(2L)}{2L + \sinh(2L)}.$$

Our claim follows on noting that the right hand side is a strictly monotone function of L.
∎

Our uniqueness result was touted in the introduction as the first of its kind. In fact it can be read as a special case of a result of Vu [V]. Unfortunately, Vu's claim is false. He supposes that having measured v_0 that one can compute its Laplace transform *at every s* and hence that the input impedance, z_0, is known in the full complex plane. In particular, he supposes that one may compute its poles, i.e., the numbers s_n for which $|z_0(s_n)| = \infty$. Recalling (2.9) these poles are simply

$$s_n = -\frac{G}{C} - \frac{n^2\pi^2}{RC\ell^2}, \quad n = 0, 1, \ldots$$

Clearly, three of these are sufficient to determine R, C, and G. However, recalling (2.1) and (2.2), each of these poles lies on or to the left of the line $\Re s = \sigma$ and therefore *can not* be determined in terms of the Laplace transform of the measured input voltage, v_0. In brief, though z_0 as given by (2.9) is a meromorphic function on the full complex plane, it only represents the input impedance function of the cable for s lying in the half plane $\Re s > -G/C$.

3. **Sensitivity**

Given exact measurement of i_0 and v_0 Prop. 2.1 provides conditions sufficient to guarantee the exact recovery of R, C, and G. Moreover, the proof of the proposition is constructive. More precisely, it gives rise to the simple

<u>Inverse Impedance Algorithm</u>

I. Inject $i_0(t)$ at $x = 0$ and record $v_0(t)$ for all $0 \le t$,
II. Compute $z_0(0)$, $z_0'(0)$, and $z_0''(0)$ per (2.5).
III. Solve (2.15) for L.
IV. Express $\lambda = \ell/L$ and compute C per (2.14).
V. Compute γ per (2.13) and then R and G per (2.18).

Steps II,IV, and V entail explicit calculations. It is only in step III that one must solve an implicit equation. So long as the data meets the requirement (2.16) this equation possesses a unique solution that may be ascertained by, say, Newton's method.

We shall now investigate the degree to which steps II–V are sensitive to errors made in the recording of i_0 and v_0. Laboratory tests on RC compartmental circuit models will be reported under separate cover. We content ourselves here with synthetic determination of the effect of ignoring the first few milliseconds of i_0 and v_0. This early response is commonly presumed, see, e.g., Jack et al. [J, p. 105], to be tainted by residual potential shed by the membrane capacitance.

For the injected current we have followed [J, p. 47] and chosen Rall's α function

$$i_0(t) = \alpha^2 t e^{-\alpha t}.$$

Its moments are simply $M_0(i_0) = 1$, $M_1(i_0) = 2/\alpha$, and $M_2(i_0) = 6/\alpha^2$. Upon ignoring i_0 up to time ε we arrive at the adulterated moments

$$\begin{aligned}
M_0(i_0, \varepsilon) &\equiv \int_\varepsilon^\infty i_0(t)\, dt = e^{-\varepsilon\alpha}(1 + \varepsilon\alpha), \\
M_1(i_0, \varepsilon) &\equiv \int_\varepsilon^\infty t i_0(t)\, dt = e^{-\varepsilon\alpha}(2 + 2\varepsilon\alpha + \varepsilon^2\alpha^2)/\alpha, \quad \text{and} \\
M_2(i_0, \varepsilon) &\equiv \int_\varepsilon^\infty t^2 i_0(t)\, dt = e^{-\varepsilon\alpha}(6 + 6\varepsilon\alpha + 3\varepsilon^2\alpha^2 + \varepsilon^3\alpha^3)/\alpha^2.
\end{aligned}$$

With regard to the associated moments of the voltage at the soma we first note that the voltage satisfies

$$\begin{aligned} v_{xx}(x,t) - RCv_t(x,t) - RGv(x,t) = 0 \quad 0 < t,\ 0 < x < \ell, \\ v(x,0) = 0, \quad 0 < x < \ell, \\ v_x(0,t) = -Ri_0(t), \quad 0 < t, \\ v_x(\ell,t) = 0, \quad 0 < t, \end{aligned}$$

and, as such, has the series representation

$$v(x,t) = R\sum_{n=0}^{\infty} \phi_n(0)\phi_n(x) \int_0^t \mathrm{e}^{-\mu_n(t-r)} i_0(r)\,dr$$

where μ_n and ϕ_n are the eigenpairs of the associated eigenvalue problem

$$\begin{aligned} -\phi_n'' + RG\phi_n = \mu_n RC\phi_n, \quad 0 < x < \ell, \\ \phi_n'(0) = \phi_n'(\ell) = 0, \end{aligned}$$

namely

$$\mu_n = \frac{n^2\pi^2}{\ell^2 RC} + \frac{G}{C} \quad \text{and} \quad \phi_n(x) = \frac{1}{\sqrt{RC\ell}} \begin{cases} 1 & \text{if } n = 0, \\ \sqrt{2}\cos(n\pi x/\ell) & \text{if } n = 1, 2, \ldots \end{cases}$$

Denoting $v(0,t)$ by $v_0(t)$ it follows that

$$\begin{aligned} M_0(v_0,\varepsilon) &= R\sum_{n=0}^{\infty} \frac{\phi_n^2(0)}{\mu_n} \left\{ \int_0^{\varepsilon} \mathrm{e}^{-\mu_n(\varepsilon-t)} i_0(t)\,dt + \int_{\varepsilon}^{\infty} i_0(t)\,dt \right\}, \\ M_1(v_0,\varepsilon) &= R\sum_{n=0}^{\infty} \frac{\phi_n^2(0)}{\mu_n^2} \left\{ (1+\mu_n\varepsilon) \int_0^{\varepsilon} \mathrm{e}^{-\mu_n(\varepsilon-t)} i_0(t)\,dt + \int_{\varepsilon}^{\infty} (1+\mu_n t) i_0(t)\,dt \right\}, \\ M_2(v_0,\varepsilon) &= R\sum_{n=0}^{\infty} \frac{\phi_n^2(0)}{\mu_n^3} \Big\{ (2 + 2\mu_n\varepsilon + \mu_n^2\varepsilon^2) \int_0^{\varepsilon} \mathrm{e}^{-\mu_n(\varepsilon-t)} i_0(t)\,dt + \\ &\qquad \int_{\varepsilon}^{\infty} (2 + 2\mu_n t + \mu_n^2 t^2) i_0(t)\,dt \Big\}. \end{aligned}$$

As a concrete instance let us identify the electrical parameters of a 1 cm length of a squid giant axon. With reference to the first column of table 1 in [R1] we take

$$R = 15.279\ k\Omega/cm, \quad C = 0.15708\ \mu F/cm, \quad \text{and} \quad G = 0.15708\ 1/(k\Omega cm).$$

This results in an electrotonic length $L = 1.55$ and a membrane time constant $\tau = 1$ (ms). Regarding the current pulse, we take $\alpha = 0.1$, and proceed to compute the tainted moments for ε ranging from 0 to 0.4 milliseconds. With regard to the $M_j(i_0,\varepsilon)$ this, of course, was a simple matter. Regarding the $M_j(v_0,\varepsilon)$ however we were obliged to apply a low–pass filter to v_0. More precisely, in evaluating the infinite sums we accounted only for the first 500 terms.

We next combined the $M_j(i_0,\varepsilon)$ and $M_j(v_0,\varepsilon)$ as in (2.5) and so arrived at the tainted input impedance data $\{z_0(0,\varepsilon),\ z_0'(0,\varepsilon),\ z_0''(0,\varepsilon)\}$. Using this data in steps II–V of our algorithm gave rise to the tainted electrotonic $\{L(\varepsilon),\ \tau(\varepsilon)\}$ and electrical $\{R(\varepsilon),\ C(\varepsilon),\ G(\varepsilon)\}$ parameters. We quantify the respective average relative misfits in

$$E_1(\varepsilon) \equiv \frac{|L(\varepsilon)-L|}{2L} + \frac{|\tau(\varepsilon)-\tau|}{2\tau} \quad \text{and} \quad E_2(\varepsilon) \equiv \frac{|R(\varepsilon)-R|}{3R} + \frac{|C(\varepsilon)-C|}{3C} + \frac{|G(\varepsilon)-G|}{3G}.$$

From the graph of these functions, see Fig. 2, we see that ignoring the first 0.4 milliseconds of i_0 and v_0 allows us to estimate the axon's true electrotonic parameters to within 12% and its electrical parameters to within 18%. The fact that $E_j(0) \neq 0$ derives from our truncation of the sums representing the moments of v_0.

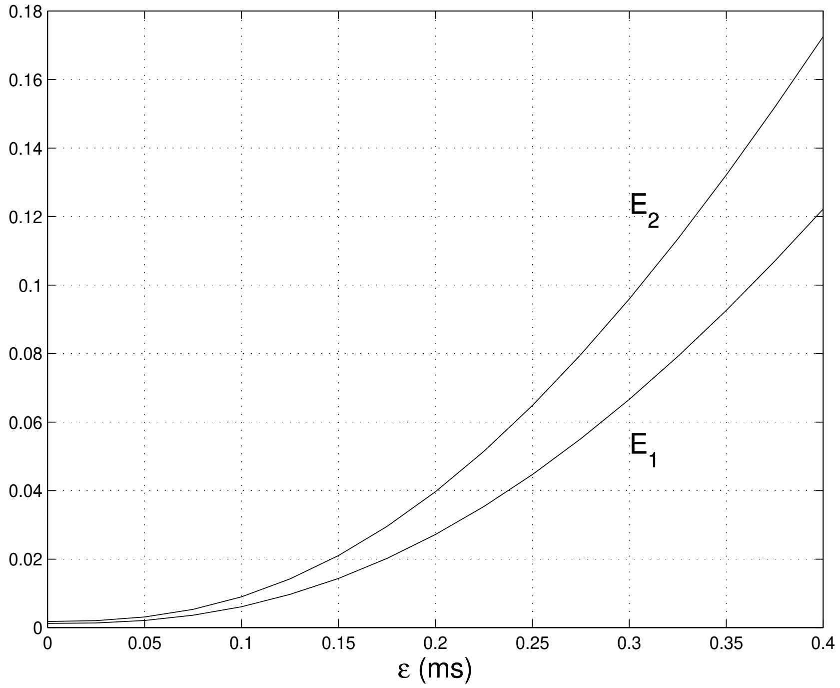

Figure 2. Reconstruction error as a function of delay.

One expects that this error could be diminished by filtering rather than ignoring the first ε milliseconds of data. Such a claim is however best tested on real rather than synthetic measurements. We should also mention that we have ignored errors arising from the finite resolution of actual current and voltage sensors as well as the aliasing that occurs in the discrete sampling of their values. Supposing the sensor noise to be additive, its contribution to errors in the reconstruction of R, C, and G could be accounted for by a simple calibration in which the first three moments of a known reference signal are recorded. Regarding sampling error, we note that most data acquisition systems typically precondition the signal with an anti–aliasing filter.

4. **Conclusions**

The precision of our result and the robustness of its implementation come at a price. Namely, it applies only to the most naive model of a biological cell. More precisely, we have lumped the soma in with the cell and assumed that any dendritic structure could be averaged onto a uniform equivalent cylinder.

With regard to distinguishing the soma one typically places a soma capacitance, C_s, and soma conductance, G_s, in parallel with the current source. The upshot is that the boundary condition $i(0,t) = i_0(t)$ then takes the form

$$i(0,t) = i_0(t) - C_s v_t(0,t) - G_s v(0,t), \quad 0 < t.$$

The experiment remains the same, i.e., inject i_0 and measure v_0, however two 2 additional parameters are now to be identified. Proceeding as above we find that the input impedance now takes the form

$$z_0(s) = \frac{R\cosh(\sqrt{R(Cs+G)}\ell)}{R(C_s s + G_s)\cosh(\sqrt{R(Cs+G)}\ell) + \sqrt{R(Cs+G)}\sinh(\sqrt{R(Cs+G)}\ell)},$$

for $\Re s > \sigma$. It remains to be seen whether z_0 and its first four derivatives at the origin indeed determine the three cable parameters and the two soma parameters. Assuming such to be the case we would then be in a position to test whether or not our data is less sensitive to measurement error than the peeled data adopted by White et al. [W] and Holmes and Rall [H].

Regarding nonuniform/nonequivalent cylinder models we recall that the starting point of our analysis was the *closed form* expression, (2.9), for the input impedance, $z_0(s)$. Poznanski [P] has indicated that such expressions may be obtained for a large class of tapering neurons. More generally, it would be odd if the existence of such closed form expressions turned out to be a necessary condition for identifiability of the cable properties. Along such lines, it appears that one should be able to check the invertibility of the mapping from $\{R, C, G\}$ to $\{z_0(0), z_0'(0), z_0''(0)\}$ for an arbitrary taper.

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6. **References**

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