3 Cables: Electrotonic Length, Attenuation, and Filtering

We consider, briefly, the behavior of the transmembrane potential across a long process. The cytoplasm acts as one conductor and the extracellular space acts as the second. Let's assume, as is often but not always the case, that the conductance of the extracellular space may be taken as infinite. Then a signal that flows down the center will be attenuated over a length of axon such that the cytoplasmic and membrane impedances (don't forget the capacitance of the membrane) are about equal, i.e., over the length required to form a voltage divider.

FIGURE - chapt-5-dendrites.eps

3.1 Basic Scales

For an axon of radius a with membrane thickness L, we can estimate this length by equating the cytoplasmic and membrane resistances, i.e.,

$$\rho_c \frac{\lambda}{\pi a^2} \approx \rho_m \frac{L}{2\pi a \lambda} \tag{3.101}$$

or

$$\lambda = \sqrt{\frac{\rho_m}{\rho_c}\frac{aL}{2}} \tag{3.102}$$

Usually the product

$$r_m = \rho_m L \tag{3.103}$$

is denoted as the specific membrane resistance It has typical values of r_m =1 to 100 kΩcm^2, while the cytoplasm has resistances of order ρ_c = 30 to 300 Ωcm. The spatial attenuation length λ is seen to vary as $\lambda \propto a^{1/2}$.

3.2 Cable Equation

We can now just consider a model with resistances and capacitances (inductance is negligable at the ¡10 kHz frequencies of neuronal operation) and write down a lumped parameter model for a lossy cable. The exact equation for a cable can be considered by writing the circuit equations for a segment of length Δx and letting $\Delta x \to 0$. We get

$$\tau \frac{\partial V(x,t)}{\partial t} + V(x,t) - \lambda^2 \frac{\partial^2 V(x,t)}{\partial x^2} = \frac{r_m}{2\pi a} I_m(x,t) \tag{3.104}$$

We have included the possibility of additional membrane currents, denoted I_m in units of Amperes per unit length; these will become evident when we study action potential propagation.

FIGURE - chapt-5-linear-cable.eps

3.2.1 Steady State Response

A particularly simple case to consider is the steady state response to the continuous injection of current at a point. The cable equation turns into Helmholtz's equation (λ plays the role of 'k'), i.e.,

$$V(x) - \lambda^2 \frac{\partial^2 V(x)}{\partial x^2} = \frac{r_m}{2\pi a} I_m(x) \tag{3.105}$$

and we know that the solutions are of the form

$$V(x) = Ae^{\frac{x}{\lambda}} + Be^{-\frac{x}{\lambda}} + C \tag{3.106}$$

where here the A, B, Cs are constants. For the case of current injected at a spot into an infinitely long uniform cable, , i.e, $I_m(x) = I_o \delta(x)$, the change in voltage is

$$V(x) = \frac{I_o}{2\lambda} \frac{r_m}{2\pi a} e^{-\frac{|x|}{\lambda}} + V(\infty) \tag{3.107}$$

FIGURE - chapt-5-steady-state-dc.eps

Thus, as we claimed above, we see directly that λ scales the length of the electrical disturbance. We also see that the input resistance scales as

$$R = \frac{V(0)}{I_o} = \frac{\sqrt{2}}{4\pi} \sqrt{\rho_c r_m}\; a^{-3/2} \tag{3.108}$$

Thus the resistance goes up faster than linear as the radius of the process decreases. To the extent that large resistances are a good thing, as least as far as not loading down the soma, one cannot be too thin ... .

We can push this result into the frequency domain to see what the low pass filtering characteristics of the cable look like. The simplest way to do this is to take the Fourier transform, with respect to time, of the original cable equation. We get

$$i\tau\omega \tilde{V}(x,\omega) + \tilde{V}(x,\omega) - \lambda^2 \frac{\partial^2 \tilde{V}(x,\omega)}{\partial x^2} = \frac{r_m}{2\pi a} \tilde{I}_m(x,\omega) \tag{3.109}$$

or

$$(1 + i\omega\tau)\tilde{V}(x,\omega) - \lambda^2 \frac{\partial^2 \tilde{V}(x,\omega)}{\partial x^2} = \frac{r_m}{2\pi a} \tilde{I}_m(x,\omega) \tag{3.110}$$

This looks exactly like the Helmholtz equation if we make the substitutions

$$r_m \leftarrow \frac{r_m}{1 + i\omega\tau} \tag{3.111}$$

$$\lambda \leftarrow \frac{r_m}{\sqrt{1 + i\omega\tau}} \tag{3.112}$$

The resistance is generalized to a steady-state impedance with

$$Z(\omega) = R\frac{1}{\sqrt{1 + i\omega\tau}} = R\frac{e^{-\frac{i}{2}tan^{-1}(\omega\tau)}}{(1 + (\omega\tau)^2)^{\frac{1}{4}}} \tag{3.113}$$

It is interesting that the impedance varies as $Z \sim R/\sqrt{\omega\tau}$, in contrast to the $Z \sim R/(\omega\tau)$ dependence for a lumped RC circuit. This was recently seen in motoneurons. Thus long cables provide a very soft filtering effect.

FIGURE - chapt-5-facial-motoneurons.eps

3.2.2 General Response

The full cable equation is simple to evaluate once you realize that this is really the diffusion equation in terms of the function $U(x,t)$, with

$$V(x,t) = e^{-\frac{t}{\tau}}U(x,t) \tag{3.114}$$

where $\frac{\lambda^2}{\tau} = \frac{a}{\rho_c c_m}$ plays the role of the diffusion constant. The homogeneous part of the cable equation becomes

$$\lambda^2 \frac{\partial^2 U(x,t)}{\partial x^2} - \tau\frac{\partial U(x,t)}{\partial t} = 0 \tag{3.115}$$

We can write down the delta function response directly. That is, for an impulse of charge so that $I_m(x,t) = Q_o\delta(x)\delta(t)$, the voltage evolves as

$$V(x,t) = \frac{Q_o}{\tau}\frac{r_m}{2\pi a}\sqrt{\frac{\tau}{4\pi\lambda^2 t}}\; e^{-\frac{t}{\tau} - \frac{x^2\tau}{4\lambda^2 t}} \tag{3.116}$$

There are two essential aspects of the response to consider. The first is that the voltage at the injection site initially decay faster than τ_m as current flows into the cable and and charge it. At later times all locations of the cable essentially discharge together and the decay is exponential. This behavior can be seen from plots of the calculated response at various distances from the origin, and in the data of Rall, who spent much effort on the issue of cables.

FIGURE - chapt-5-cable-solutions.eps

FIGURE - chapt-5-cable-decay.eps

The second point is that the pulse is decaying as it spreads, and thus has the appearance of a front. We can ask where the front of the pulse is by calculating $\frac{\partial V(x,t)}{\partial t} = 0$. We rewrite our solution of the cable equation with all of the time and space dependent terms in the exponent, so that

$$V(x,t) = V(0)e^{-\frac{1}{2}ln\frac{t}{\tau} - \frac{t}{\tau} - \frac{x^2\tau}{4\lambda^2 t}} \tag{3.117}$$

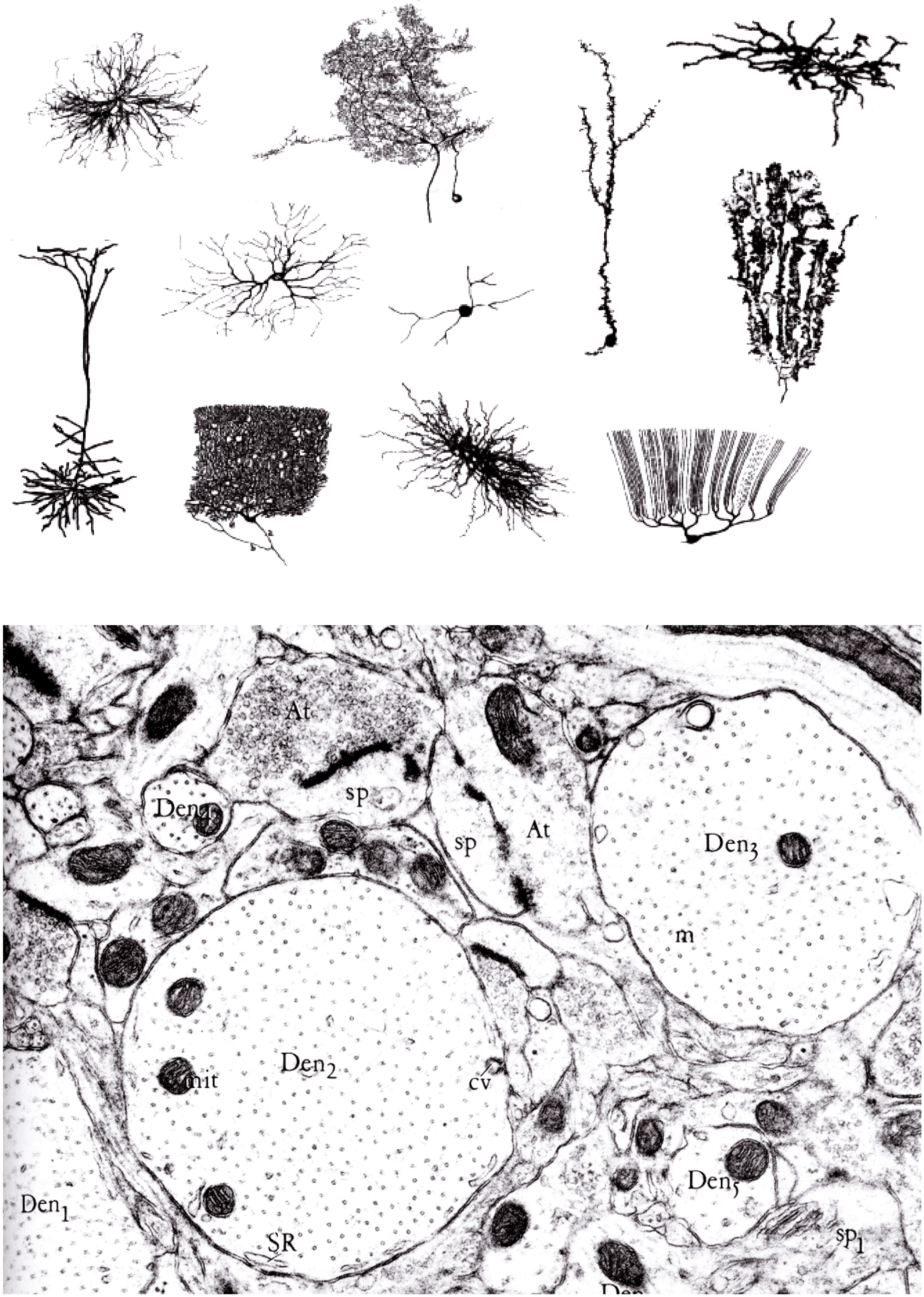
Thus $\frac{\partial V(x,t)}{\partial t} = \frac{\partial V_o e^{f(x,t)}}{\partial t} = V_o e^{f(x,t)} \frac{\partial f(x,t)}{\partial t} = 0$ implies

$$
\begin{aligned}
\frac{d\left(\frac{1}{2} ln \frac{t}{\tau} + \frac{t}{\tau} + \frac{x^2\tau}{4\lambda^2 t}\right)}{dt} &= 0 \qquad (3.118) \\
t\frac{\tau}{2} + t^2 - \frac{x^2\tau^2}{4\lambda^2} &= 0 \qquad (3.119)
\end{aligned}
$$

which gives

$$
t_{max} = \frac{\tau}{2}\left(\sqrt{\frac{1}{4} + \frac{x^2}{\lambda^2}} - \frac{1}{2}\right) \approx \frac{\tau}{2}\frac{|x|}{\lambda} \qquad (3.120)
$$

The ratio $\frac{|x|}{t_{max}} = \frac{2\lambda}{\tau}$ is the speed of the peak of the voltage pulse.



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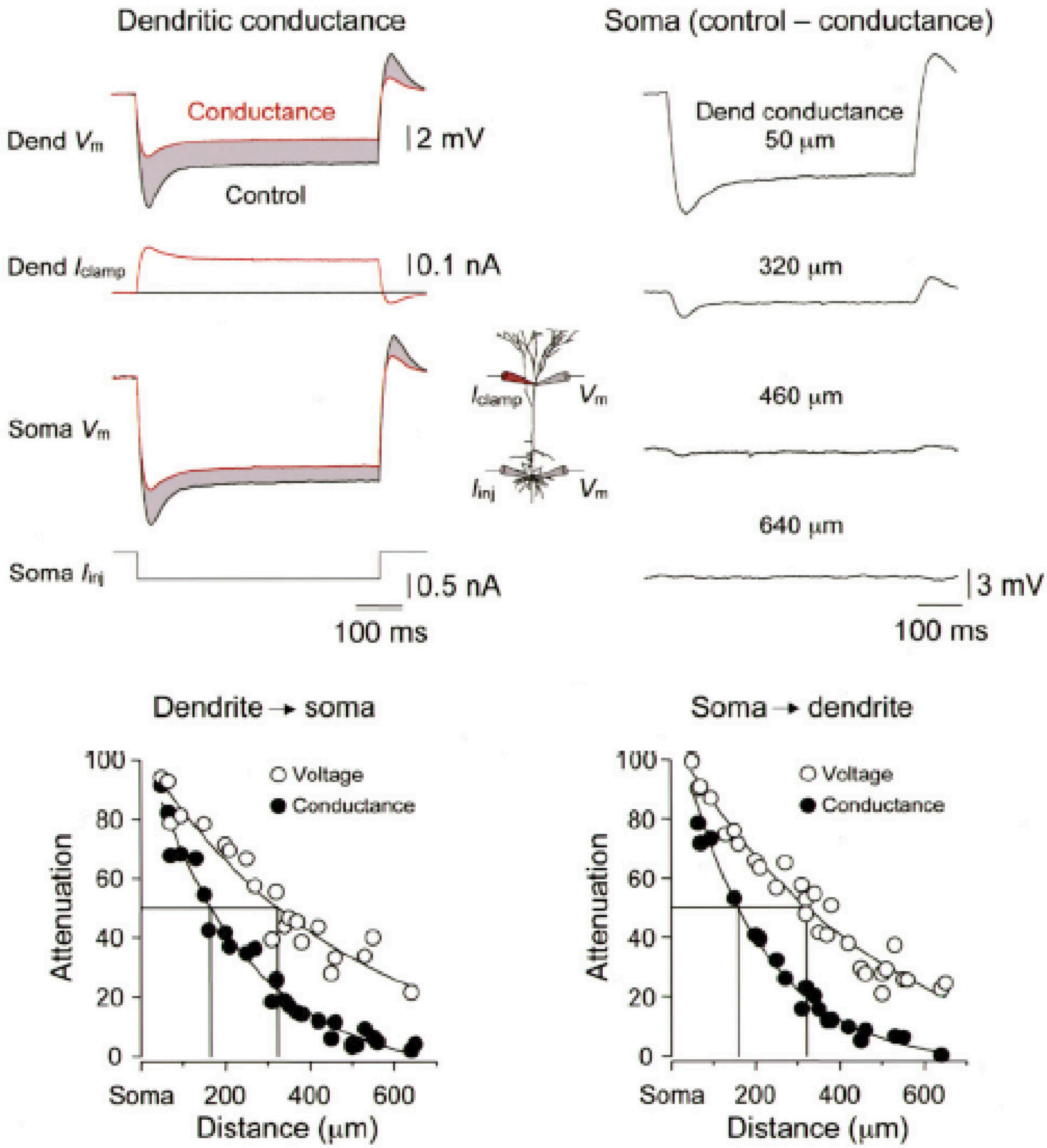

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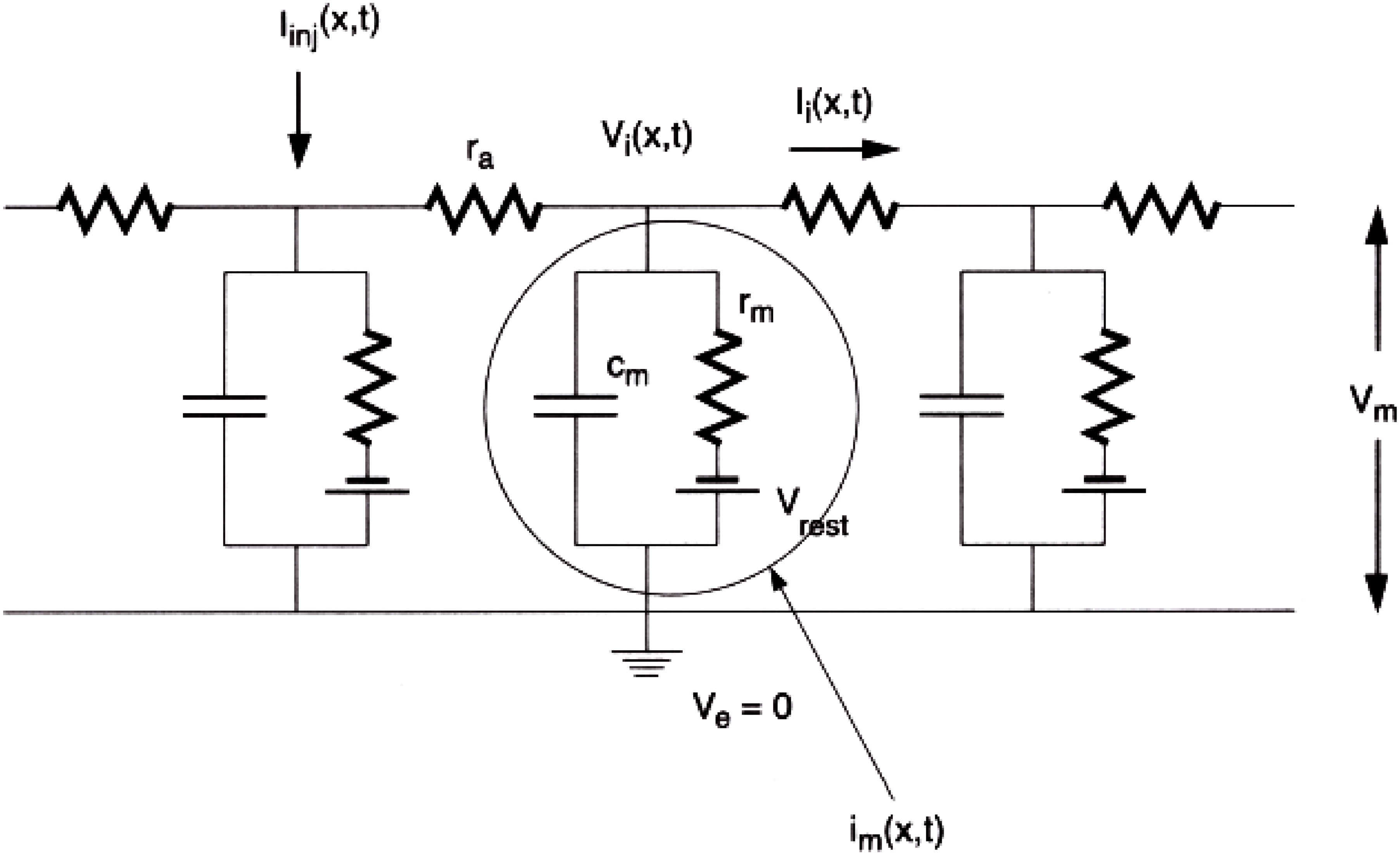

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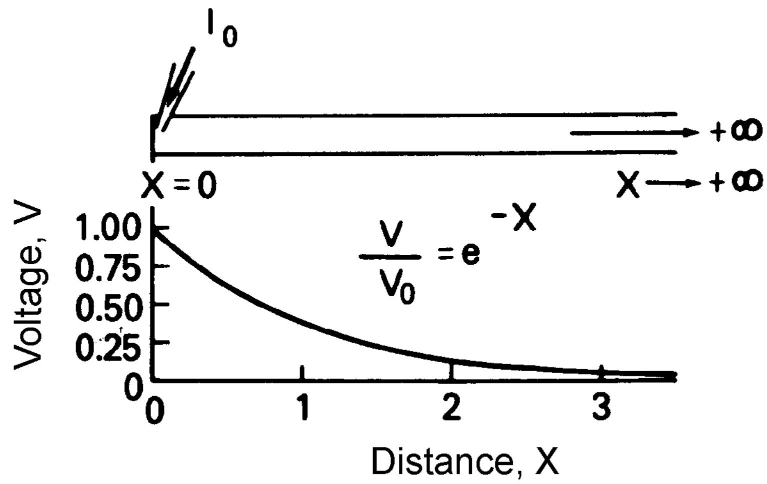

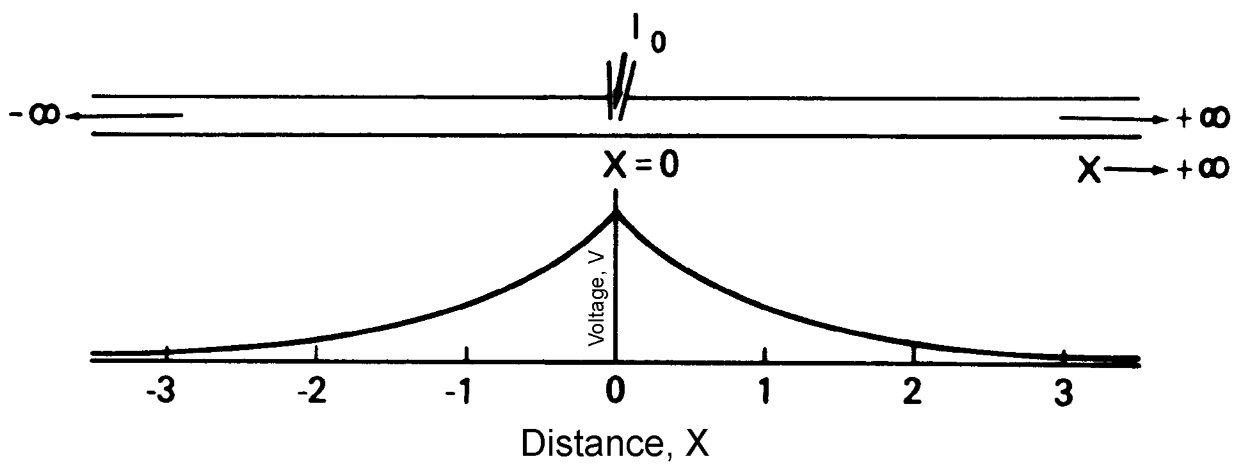

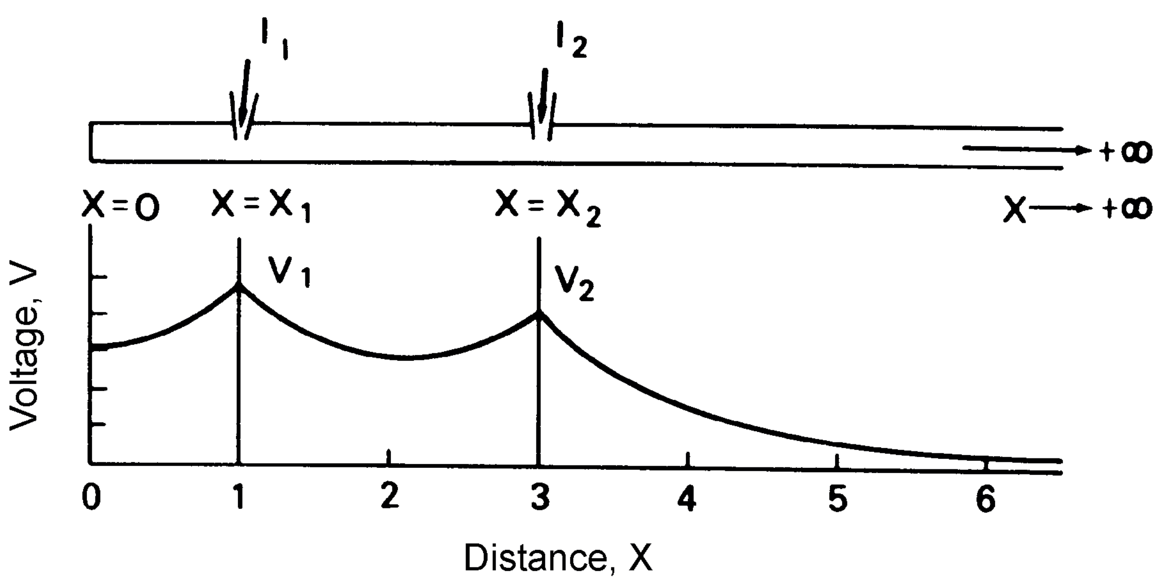

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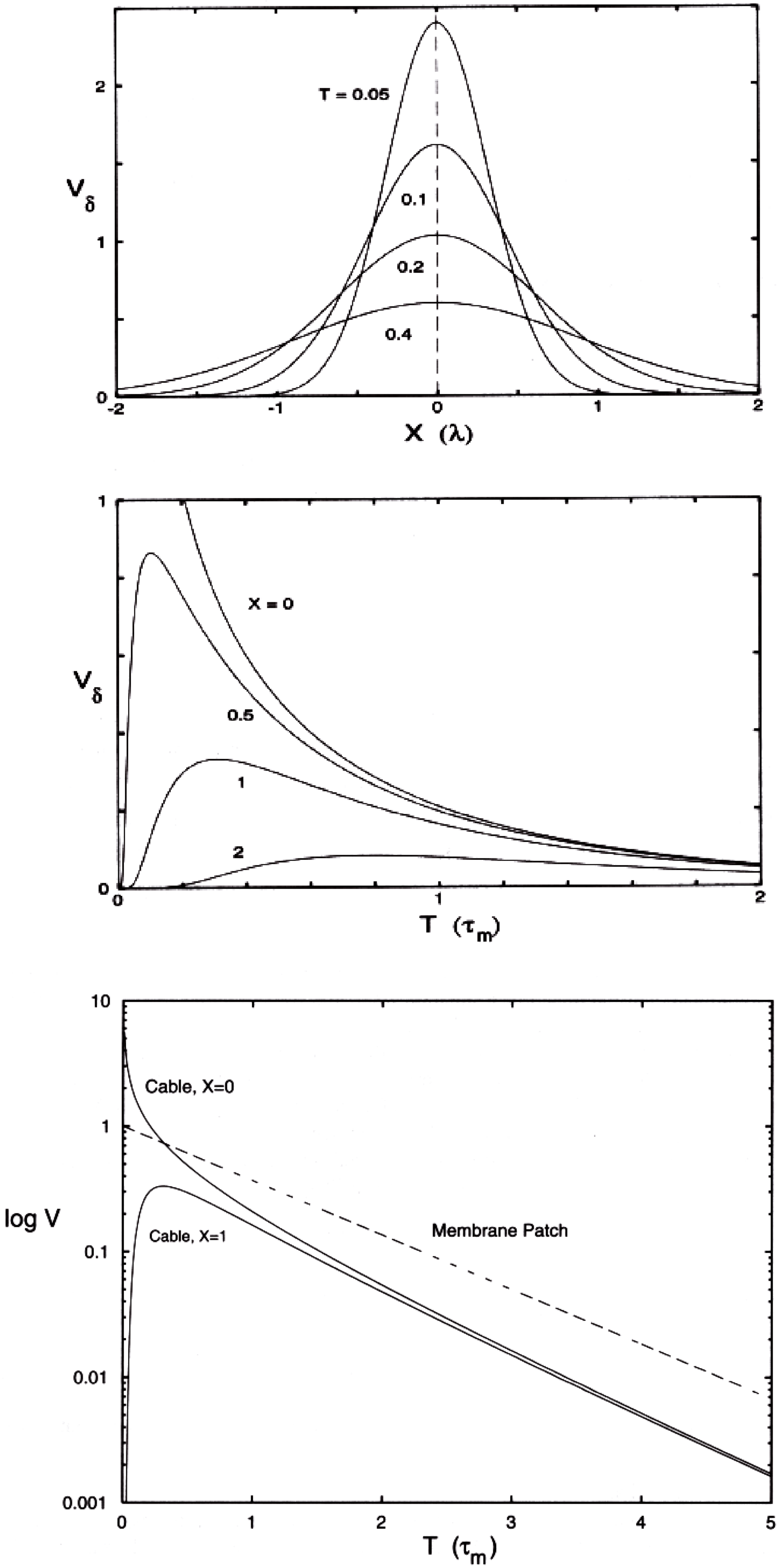

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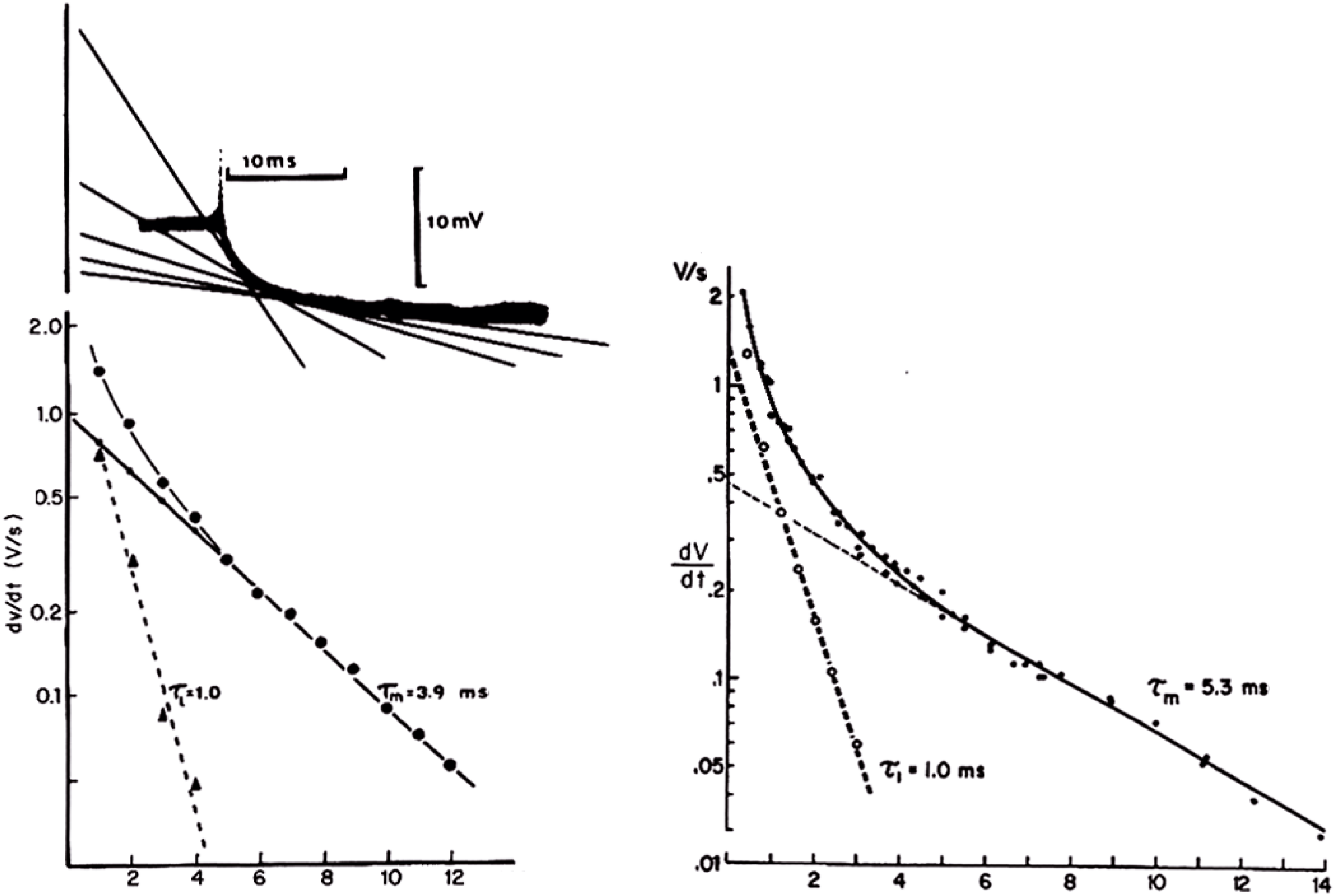

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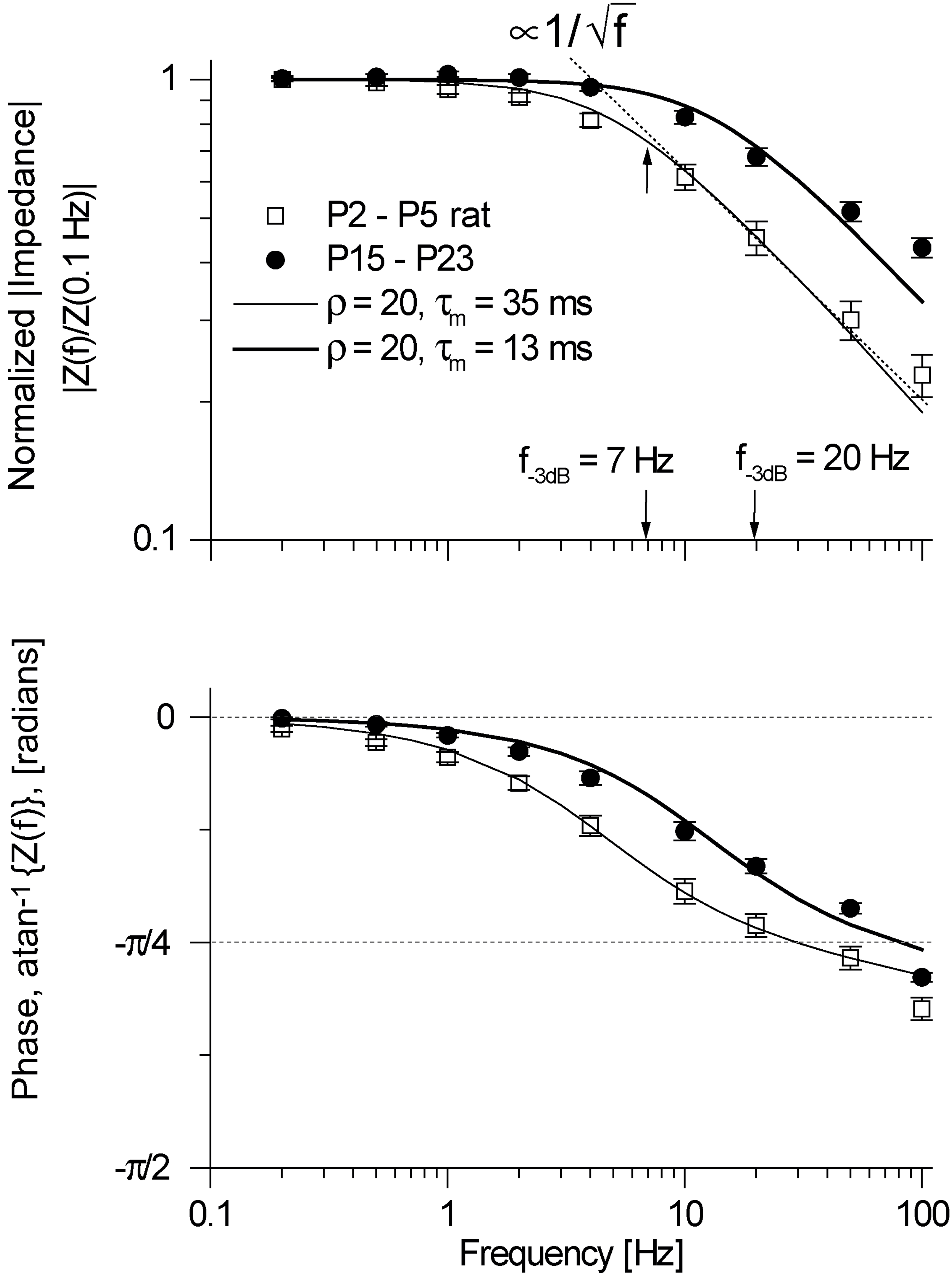

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