Physics 171/271 - David Kleinfeld - 2002/2011

1 Electrotonics

1.0.1 Parallel Capacitance

Our goal is to derive an expression for the time constant of an axon. First, we need to calculate the conductance between the inner and outer conductors, denoted G_{ab}, in terms of the voltage drop, denoted V_{ab}, and the current flow, I_{ab}, where $G_{ab} = I_{ab}/V_{ab}$. Then we need to calculate the capacitance between the inner and outer conductors, denoted C_{ab}, in terms of the voltage drop and the charge difference, Q_{ab}, where $C_{ab} = Q_{ab}/V_{ab}$. The time constant is just the ratio $\tau = C_{ab}/G_{ab}$. If we are lucky, geometrical factors will cancel and the result will be simple.

We start with an expression for membrane conductance. From $\vec{E}(\vec{r}) = -\vec{\nabla}V(\vec{r})$ the voltage from the inside, a, to the outside, b, is

$$V_{ab} = \int_a^b \vec{E}(\vec{r}) \cdot d\vec{l} \tag{1.1}$$

where $d\vec{l}$ defines a path from the inside to outside conductor (it need not follow a radius). From $\vec{\nabla} \cdot \vec{J}(\vec{r}) + \frac{\partial \rho(\vec{r})}{\partial t} = 0$, $\vec{J}(\vec{r}) = g\vec{E}(\vec{r})$, and the divergence theorem, i.e., $\int_S \vec{J}(\vec{r}) \cdot d\vec{A} = \int_V \vec{\nabla} \cdot \vec{J}(\vec{r}) d^3\vec{r} = \frac{\partial}{\partial t}\int_V \rho(\vec{r}) d^3\vec{r} = \frac{\partial Q_{ab}}{\partial t} = I_{ab}$ where ρ is the charge density (sorry for the confusion with resistivity) and $d\vec{A}$ defines a cylindrical shell that the current passes through, the current that flows between the two conductors is

$$I_{ab} = \int_S \vec{J}(\vec{r}) \cdot d\vec{A} = g\int_S \vec{E}(\vec{r}) \cdot d\vec{A} = g\oint_C \vec{E}(\vec{r}) \cdot d\vec{n} \;\; \Delta z \tag{1.2}$$

where $d\vec{n}$ is a unit vector that is normal to a closed path "around" the perimeter of the conductor that defines the shell. The conductance is just

$$G = \frac{I_{ab}}{V_{ab}} = \Delta z \frac{g\oint_C \vec{E}(\vec{r}) \cdot d\vec{n}}{\int_a^b \vec{E}(\vec{r}) \cdot d\vec{l}} \tag{1.3}$$

The final ratio is dimensionless and depends only the geometry. When the cable is a cylinder, the two integrals are equal so the ratio is just 1.

We now consider the expression for membrane capacitance. In the limit of linear response, the electric field leads to a polarization of membrane dipoles, so $\vec{P}(\vec{r}) = \epsilon_o \chi \vec{E}(\vec{r})$. We define an auxiliary, or displacement field, by $\vec{D}(\vec{r}) = \epsilon_o \vec{E}(\vec{r}) + \vec{P}(\vec{r}) = \epsilon_o(1+\chi)\vec{E}(\vec{r}) \equiv \epsilon \vec{E}(\vec{r})$. The displacement field obeys $\vec{\nabla} \cdot \vec{D}(\vec{r}) = \rho$

$$Q_{ab} = \int_V \rho(\vec{r}) d^3\vec{r} = g\int_S \vec{D}(\vec{r}) \cdot d\vec{A} = \epsilon \oint_C \vec{E}(\vec{r}) \cdot d\vec{n} \;\; \Delta z \tag{1.4}$$

The capacitance is just

$$C = \frac{Q_{ab}}{V_{ab}} = \Delta z \frac{\epsilon \oint_C \vec{E}(\vec{r}) \cdot d\vec{n}}{\int_a^b \vec{E}(\vec{r}) \cdot d\vec{l}} \tag{1.5}$$

We thus see immediately that the ratio of capacitance to conductance is independent of the geometry, i.e.,

$$\frac{C}{G} = \frac{\epsilon}{g} \tag{1.6}$$

Thus the time constant of the membrane is independent of geometry, i.e.,

$$\tau = \frac{\epsilon_m}{g_m} = \epsilon_m \rho_m = \frac{\epsilon_m}{L} \rho_m L = c_m r_m \tag{1.7}$$

where $c_m \equiv \frac{\epsilon_m}{L} \approx 1 \frac{\mu F}{cm^2}$ (L is the thickness of the membrane here). Note that we immediately see that the ratio of the resistive to the capacitive impedance is:

$$\left| \frac{Z_{C_m}}{Z_{R_m}} \right| = \left| \frac{G}{i 2\pi f C} \right| = \frac{1}{2\pi f \tau} \tag{1.8}$$

so that the time-constant of the membrane sets the scale between resistive versus capacitive current flow.

1.0.2 Series Inductance

We have one bit of business left to calculate, the series inductance. From $\vec{J}(\vec{r}) = \vec{\nabla} \otimes \vec{H}(\vec{r})$ and Strokes theorem, i.e., $\int_S \left(\vec{\nabla} \otimes \vec{H}(\vec{r}) \right) \cdot d\vec{A} = \oint_C \vec{H}(\vec{r}) \cdot d\vec{l}$, the current that flows along $\hat{z}$ in either conductor is

$$I_z = \int_S \vec{J}(\vec{r}) \cdot d\vec{A} = \oint_C \vec{H}(\vec{r}) \cdot d\vec{l} \tag{1.9}$$

We also know that the magnetic flux, ψ, that is contained within the cable is found by intergating over a cylindrical shell

$$\psi = \int_S \vec{B}(\vec{r}) \cdot d\vec{A} = \mu \int_S \vec{H}(\vec{r}) \cdot d\vec{A} = \mu \int_a^b \vec{H}(\vec{r}) \cdot d\vec{n} \;\; \Delta z \tag{1.10}$$

Thus the inductance, L, is give by

$$L = \frac{\psi}{I_z} = \Delta z \frac{\mu \int_a^b \vec{H}(\vec{r}) \cdot d\vec{n}}{\int_C \vec{H}(\vec{r}) \cdot d\vec{l}} \tag{1.11}$$

We can recast this in terms of the electric field by noting that $\vec{E}(\vec{r})$ and $\vec{H}(\vec{r})$ are orthogonal to each other, so that $\vec{H}(\vec{r}) \propto \vec{E}(\vec{r}) \otimes \hat{z}$. Then

$$\begin{aligned} L &= \Delta z \frac{\mu \int_a^b \vec{E}(\vec{r}) \otimes \hat{z} \cdot d\vec{n}}{\oint_C \vec{E}(\vec{r}) \otimes \hat{z} \cdot d\vec{l}} \\ &= \Delta z \frac{\mu \int_a^b \vec{E}(\vec{r}) \cdot \hat{z} \otimes d\vec{n}}{\oint_C \vec{E}(\vec{r}) \cdot \hat{z} \otimes d\vec{l}} \end{aligned} \tag{1.12}$$

$$= \quad \Delta z \frac{\mu \int_a^b \vec{E}(\vec{r}) \cdot d\vec{l}}{\oint_C \vec{E}(\vec{r}) \cdot d\vec{n}}$$

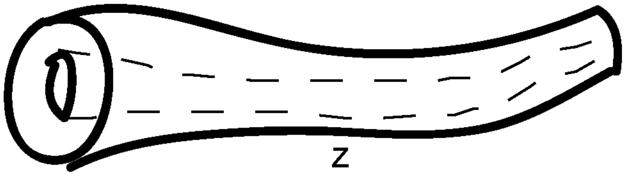
where we used $\vec{A} \cdot \vec{B} \otimes \vec{C} = \vec{B} \cdot \vec{C} \otimes \vec{A} = \vec{C} \cdot \vec{A} \otimes \vec{B}$. We now see, quite generally, that the product of the capacitance per unit length, $C/\Delta z$ and the inductance per unit length, $L/\Delta z$, is

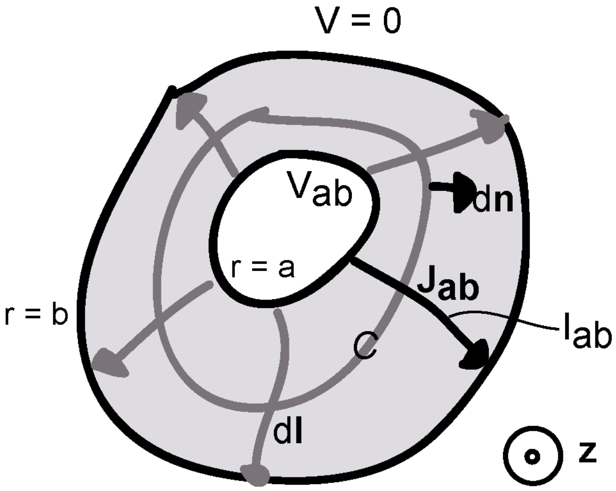
$$\frac{C}{\Delta z}\frac{L}{\Delta z} = \mu\epsilon \tag{1.13}$$

Let's compare the impedance of the series inductance with that the series resistance (we now assume a loss in the inner conductor) over a distance of one space constant, λ, i.e.,

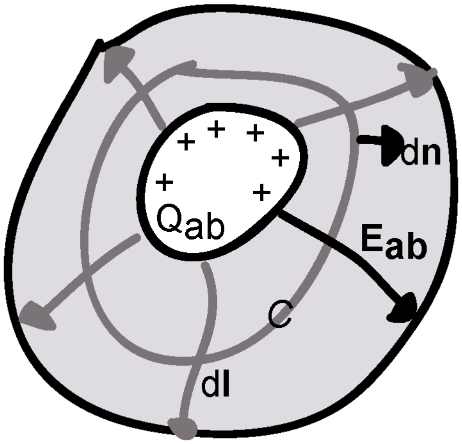
$$\begin{aligned} \left|\frac{Z_{L_s}}{Z_{R_s}}\right| &= \left|\frac{i2\pi f L}{R_s}\right| = \frac{2\pi f \mu\epsilon\lambda^2}{C R_s} = \frac{2\pi f\tau}{c^2}\frac{\lambda^2}{C R_m \tau}\frac{R_m}{R_c} \\ &= \frac{2\pi f\tau}{c^2}\left(\frac{\lambda}{\tau}\right)^2\frac{R_m}{R_c} \\ &\approx 2\pi f\tau\left(\frac{v}{c}\right)^2 \end{aligned} \tag{1.14}$$

where we used $\sqrt{\mu\epsilon} = 1/c$ where c is the speed of light, $R_m \approx R_c$ when $\Delta z = \lambda$, and $v \equiv \frac{\lambda}{\tau}$ as a measure of passive speed. The ratio of impedances is extraordinarily small, we we may safely ignore series inductance in a model of the cell.

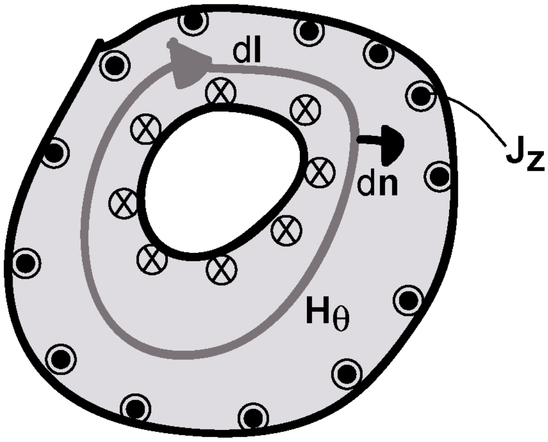




for Condutance (G)



for Capacitance (C)



for Inductance (L)

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