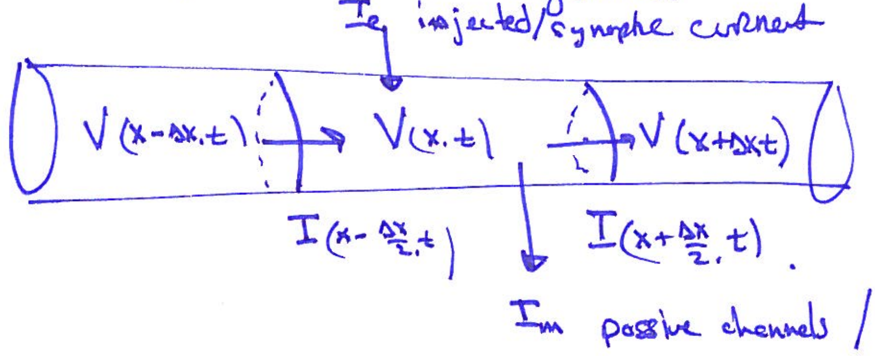
Dendrites: The Passive Cable Equation



$$C\frac{dV}{dt} = I(x-\tfrac{\Delta x}{2}, t) - I(x+\tfrac{\Delta x}{2}, t) + I_e + I_m$$

C is membrane conductance (surface property)

$$\therefore \quad C = 2\pi a \Delta x \underbrace{C_m}_{\text{per unit area capacitance.}}$$

$$\boxed{\Delta V = IR} \quad \text{or} \quad I = \Delta V/R.$$

Resistance is proportional to the ~~length~~ distance the current must travel divided by the number of path's the current can take. (Area of cross section)

$$R = \frac{R_L \Delta x}{\pi a^2}$$

$$\therefore \quad I(x-\Delta x/2, t) = \frac{\left(-V(x,t) + V(x-\Delta x, t)\right)}{\Delta x}\frac{\pi a_2}{R_L}$$

$$\Rightarrow \quad C\frac{\partial V}{\partial t} = 2\pi a \Delta x C_m \frac{\partial V}{\partial t} = \frac{\pi a^2}{R_L}\left(\frac{V(x+\Delta x, t) - 2V(x,t) + V(x-\Delta x, t)}{\Delta x}\right)$$

$$+ \underbrace{I_m + I_e}$$

I_m, I_e come in through the surface $\therefore$ $I_m = 2\pi a \Delta x\, i_m$
$I_e = 2\pi a \Delta x\, i_e$

$$\therefore \cancel{2\pi a \Delta x}\, C_m \frac{dV}{dt} = \frac{\pi a^{\cancel{2}}}{2r_L}\left(\frac{V(x+\Delta x,t) - 2V(x,t) + V(x-\Delta x,t)}{\Delta x^2}\right)$$

$$+ \cancel{2\pi a \Delta x}\left(i_e + i_m\right).$$

$$\Rightarrow C_m \frac{dV}{dt} = \frac{a}{2r_L}\frac{d^2V}{dx^2} + i_e + i_m$$

Leak : $i_m = -\dfrac{V - E_L}{r_m}$

Non-Dimensionalize

let $V = V - E_L$

$$C_m \frac{dV}{dt} = \frac{a}{2r_L}\frac{d^2V}{dx^2} - \frac{V}{r_m} + i_e$$

$$r_m C_m \frac{dV}{dt} = \frac{a r_m}{2r_L}\frac{d^2V}{dx^2} - V + r_m i_e.$$

$$\tau = r_m C_m \quad , \quad \lambda^2 = \left(\frac{a r_m}{2r_L}\right) \sim [\lambda] = d^2$$

since $r_m = R_m \cdot \text{Area}$

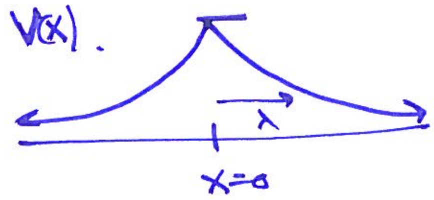
$r_L = R_L \cdot \frac{\text{Length}}{\text{Area}}$

Linear Cable Equation in Canonical form.

$$\tau \frac{dV}{dt} = \lambda^2 \frac{d^2V}{dx^2} - V + r_m i_e.$$

2 Solutions to the Linear Cable Equation.

1) Steady State w/ constant current injection at $x=0$.



S.S. $\Rightarrow \frac{\partial V}{\partial t} = 0.$

point current injection $\Rightarrow$ $i_e = \frac{I_e}{2\pi a \Delta x} \rightarrow \frac{I_e}{2\pi a}\delta(x).$

at $x=0$
0 otherwise

Solution Method ① Find solutions for $i_e = 0$ which will work for $x \neq 0$,
② Determine Solution at $x=0$.
③ Stitch Solution for $x \gtrless 0$ together using 2-

$i_e = 0. \Rightarrow \quad \lambda^2 \frac{\partial^2 V}{\partial x^2} = V \quad \Rightarrow \quad V = Ae^{-x/\lambda} + Be^{x/\lambda}.$

Boundary conditions at $x \to \pm\infty \Rightarrow$.
with continuity at $x=0$

$$V(x) = Ae^{-|x|/\lambda}$$

2) The Jump condition at $x=0$.

$$\lim_{\varepsilon \to 0} \int_{-\varepsilon}^{\varepsilon} \lambda^2 \frac{\partial^2 V}{\partial x^2} = V - \left(\frac{r_m}{2\pi a} I_e\right)\delta(x).\ dx$$

$$= \lim_{\varepsilon \to 0} \lambda^2\left(\frac{\partial V}{\partial x}\Big|_{x=\varepsilon} - \frac{\partial V}{\partial x}\Big|_{x=-\varepsilon}\right) = 2\varepsilon \bar{V} - \frac{r_m I_e}{2\pi a}$$

$$= \lambda^2\left(\frac{\partial V}{\partial x}\Big|_{x=0^+} - \frac{\partial V}{\partial x}\Big|_{x=0^-}\right) = -\frac{r_m I_e}{2\pi a}.$$

$$A \cdot \lambda^2\left(-\frac{1}{\lambda} - \frac{1}{\lambda}\right) = -\frac{r_m I_e}{2\pi a}.$$

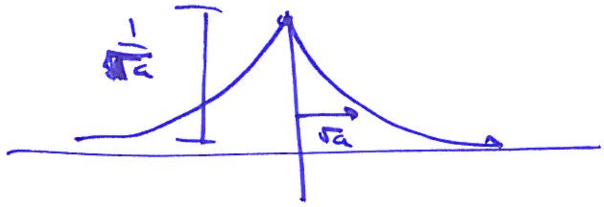
$$A = r_m I_e / 4\pi a \lambda$$

Note the $A = \frac{r_m I_L}{2\lambda} \sim I_e / \sqrt{a}$.

smaller the the the greater the voltage.

Similar the decay is $\ln \lambda$

$\sim \sqrt{a}$.



Oscillatory Input.

suppose $i_e = I_e e^{i\omega t} \delta(x)$.

Solution is just as easy.

let $V(x,t) = V(x) e^{i\omega t}$

$$\Rightarrow \therefore \tau \frac{\partial V}{\partial t} = \lambda^2 \frac{\partial^2 V}{\partial x^2} - V + i$$

$$i\omega\tau e^{i\omega t} V(x) = \lambda^2 \frac{\partial^2 V}{\partial x^2} e^{i\omega t} - V e^{i\omega t} + I_e \delta(x) e^{i\omega t}$$

$$\lambda^2 \frac{\partial^2 V}{\partial x^2} = (1 + i\omega\tau) V + I_e \delta(x).$$

$\xi_\pm = \pm \sqrt{1 + i\omega\tau}$ note $+\sqrt{1+i\omega\tau}$ has + Real part.

$$\therefore V(x) = \begin{cases} A e^{x/\xi_+} & x < 0 \\ A e^{x/\xi} & x > 0 \end{cases}$$

and $\lambda^2 \left(\frac{\partial V}{\partial x}\Big|_{x=0^+} - \frac{\partial V}{\partial x}\Big|_{x=0^-} \right) = I_e$ as before.

Arbitrary Driving (Green's Function Solution). (5)

Green's Function for Linear Equations

Linear Dynamical Systems have the superposition property.

i.e. if $U^1(x,t)$ is a solution & $U^2(x,t)$ is a solution

then $AU^1(x,t) + BU^{(2)}(x,t)$ is a solution.

when Boundary conditions are trivial i.e.

$$U(x,t) = 0 \quad \forall \; x \in \delta B \text{ - Boundary.}$$

then this also applies to driving forces, i.e.

$$\frac{\partial U_1}{\partial t} = \frac{\partial^2 U_1}{\partial x^2} - U_1 + f_1(x,t) \quad \leftarrow \text{driving force}$$

$$\frac{\partial U_2}{\partial t} = \frac{\partial^2 U_2}{\partial x^2} - U_2 + f_2(x,t)$$

then $U = U_1 + U_2$

satisfies. $$\frac{\partial U}{\partial t} = \frac{\partial^2 U}{\partial x^2} - U + f_1(x,t) + f_2(x,t).$$

With this in mind consider the heat equation OR the case for which Leak is zero.

hard. $\rightarrow$ $$\frac{\partial V}{\partial t} = \frac{\partial^2 V}{\partial x^2} + I(x,t).$$

but $$I(x,t) = \int \delta(x-x_0)\,\delta(t-t_0)\, I(x_0,t_0)\, dx_0\, dt_0.$$

$\therefore$ if we could find $G(x,t|x_0,t_0)$.

$I(x,t)$.

sum of delta fns

s.t. $$\frac{\partial G}{\partial t} = \frac{\partial^2 G}{\partial x^2} + \delta(x-x_0)\,\delta(t-t_0)$$

then $$V(x,t) = \int G(x,t|x_0,t_0)\, I(x_0,t_0)\, dx_0\, dt_0$$

Green's functions for the Free space Heat Equation.

suppose $V \to 0$ as $x \to \pm\infty$.

~~By symm~~ By symmetry $G(x,t \mid x_0, t_0) = G(x-x_0, t-t_0 \mid 0,0)$

$\therefore$ seek soln to

$$\frac{\partial G}{\partial t} = \frac{\partial^2 G}{\partial x^2} + \delta(x)\delta(t) \quad \text{wt} \quad G \to 0 \text{ as } x \to \pm\infty$$

Solution is a standard gaussian but one particular derivation (the self similar derivation) for

For $t>0$ ~~this is easy~~ $\frac{\partial G}{\partial t} = \frac{\partial^2 G}{\partial x^2}$ $\leftarrow$ Homogeneous (no driving)

For $t=0$ it is easy to show that $G(x, t=0 \mid 0,0) = \delta(x)$.

So lets try to find a self-similar solution st.

$$\lim_{t\to 0^+} G(x,t) = \delta(x).$$

Self similar solutions to homogeneous ~~equations~~ P.D.E.'s often exist.

and take the form $G(x,t) = t^\alpha U(xt^\beta)$

for some funct $U(\eta)$ wh $\eta = xt^\beta$

Heat Eq. $\Rightarrow$ $$t^\alpha U'(\eta)\beta \underbrace{xt^{\beta-1}}_{\eta/t} + \alpha t^{\alpha-1}U(\eta) = t^\alpha t^{2\beta} U''(\eta).$$

$\therefore$ a self similar soln exists when exponents match

$$\alpha - 1 = \alpha - 1 = \alpha + 2\beta.$$

$\therefore$ $\alpha = ?$ $\beta = -\tfrac{1}{2}$.

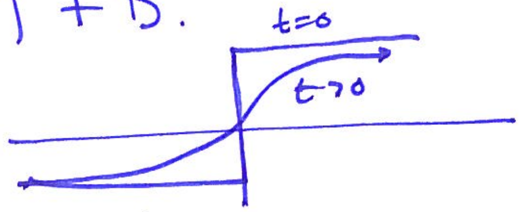
Suppose! let $\alpha = 0$ $\therefore$ $-\frac{1}{2}U'(\eta)\eta = U''(\eta)$.

OR $U''/U' = -\frac{1}{2}\eta \Rightarrow \ln U' = -\eta^2/4 + \text{Const}$

$U' = Ae^{-\eta^2/4}$

$\Rightarrow \quad U(\eta) = A\,\mathrm{erf}(\eta/2) + B$ ✓.

$$U(x,t) = A\,\mathrm{erf}\left(x/2\sqrt{t}\right) + B.$$



Super A self-similar solutn. too bad its a step functn and doesn satisfy our boundary conditn

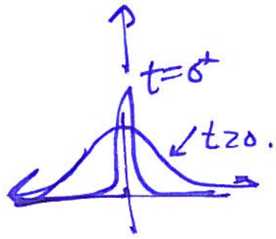
$$U(x,t) = \delta(x) \quad \text{as} \quad t \to 0^+$$

Fortunately if $U(x,t)$ satisfies the homogeneous Heat Eq. so does $\frac{\partial U}{\partial x}$.

so $$\frac{\partial}{\partial x}\left(\frac{\partial U}{\partial t} = \frac{\partial^2 U}{\partial x^2}\right)$$

$$\Rightarrow \frac{\partial}{\partial t}\left(\frac{\partial U}{\partial x}\right) = \frac{\partial^2}{\partial x^2}\left(\frac{\partial U}{\partial x}\right).$$ ✓.

$$\therefore \quad U^{(a)}(x,t) = \frac{\partial U}{\partial x} = \frac{A}{\sqrt{t}}\,e^{-x^2/2t}$$ ✓.



to find A we just note that ✓.

$$\int U(x,t)\,dx = 1 \quad \forall \quad t \geq 0.$$

$$\therefore \quad A = \frac{1}{\sqrt{2\pi}}$$ ✓

Why did you solve the heat equation we need to solve

$$\tau \frac{\partial V}{\partial t} = \lambda^2 \frac{\partial^2 V}{\partial x^2} - r_m V + \delta(x)\delta(t) \, . I_e$$

no worries if you can solve.

$$\cancel{\frac{\partial U}{\partial t} = bU} \qquad \frac{\partial U}{\partial t} = L_x U$$

the

$$V = e^{\alpha t} U(x,t).$$

sch.

$$\tau \frac{\partial V}{\partial t} = \tau \alpha e^{\alpha t} U(x,t) + e^{\alpha t} \tau \frac{\partial U}{\partial t}$$

$$= \alpha V + L_x U e^{\alpha t}$$

$$= \alpha V + L_x V$$

$$\therefore \quad \boxed{V = I_e e^{-r_m t/\tau} \frac{e^{-\tau x^2/\lambda^2 t}}{\lambda\sqrt{2\pi t/\tau}}}$$

Fun question to ask, at a given distance from the source x, at what time does x reach its maximum value.

$$\frac{d}{dt} \ln V = -r_m t/\tau - \tau x^2/\lambda^2 t - \tfrac{1}{2} \ln t = 0.$$

$$-r_m/\tau + \tau x^2/\lambda^2 t^2 - \tfrac{1}{2} \tfrac{1}{t} = 0.$$

$$t^2 - \tau^2/\lambda^2 r_m + t/2 = 0.$$

Actively Propogated Spikes (Axons).

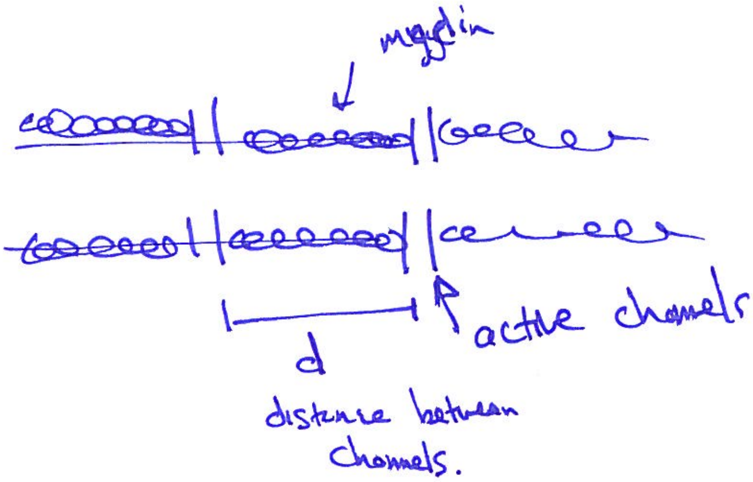
unlike passive dendrites axons have 2 property.

1) Myelinated Sheath
2) Voltage gated chanels.

insulating myelin. Reduces Leak to Something small. given by the ratio of a_1/a_2+a ??

Voltage Gated chanels

- Individual Chanels will be modeled later but we can use a Simple threshold model to estimate the speed of a propogatin action potential.



Chanels are modeled as non-linear sources.

$$\frac{\partial V}{\partial t} = \frac{\partial^2 V}{\partial x^2} + I_e \delta(x - nd) \cancel{\delta(V(nd,t) - \theta)}$$
$$\times \delta(t - t_n).$$

where $t_n = \inf_{t_n} V(nd, t_n) = \theta$ ← firing threshold

$t_n =$ first time $V(nd, t) = \theta$.

Suppose the axon is infinitely long and a traveling wave with velocity V has been propagating

that is $t_n = \frac{nd}{V}$ for $n = -\infty \dots -1$

~~Such a wave can exist~~

this means for $-\frac{d}{V} < t < 0$ we know that

$$V(x,t) = I_e \sum_{n=-\infty}^{-1} G\left(x,t \mid nd, \frac{nd}{V}\right).$$

Such a wave can propagate (But might not be stable).
When threshold is reached at $x=0$ at $t=0$.

$$\Theta = V(0,0) = I_e \sum_{n=-\infty}^{-1} \frac{1}{\sqrt{2\pi(-nd/V)}} e^{-(nd)^2/2\left(\frac{-dn}{V}\right)}$$

$$\Theta/I_e = \sum_{k=1}^{\infty} \sqrt{\frac{V}{2\pi k d}} \cdot e^{-kVd/2}$$

$$= \sum_{k=1}^{\infty} \sqrt{\frac{V\tau}{2\pi d}}\, k^{-1/2} e^{-k\left(\frac{\tau V d}{2\lambda^2}\right)}$$

$V \sim \lambda/\tau$ for $\lambda/\tau < 1$