Section 8.1, Cable Equation

http://www.math.rutgers.edu/~sontag/613.html
Neurons

http://student.biology.arizona.edu/honors99/group6/intro.html
They transmit info (to other neurons, to muscles, to glands)

http://student.biology.arizona.edu/honors99/group6/intro.html
Dendrites: Passive Conduction (Cable Equation)

*cable equation* (Lord Kelvin 1855)
first proposed for flow of electricity on leaky cable
Hodgkin-Rushton 1946, Rall 1957: application to neurons

assume one-dimensional flow (“core conductor assumption”)

divide cable into short pieces of isopotential membrane
of length \( dx \)
each piece is like before (capacitance, current components)
assume only two types of current:

\[ I_i(x) : \text{internal axial, oriented left to right} \]
\[ I_e(x) : \text{external axial, oriented left to right} \]
\[ I_t(x) : \text{transmembrane per unit length} \] (so \( I_t(x)dx \) is current through any given small patch), oriented inside/out,
also: \( r_e, r_i \) resistances per unit of length

\[ V_i(x), V_e(x) \] potentials inside, exterior
\[ V_i(x + dx) - V_i(x) = -I_i(x) r_i dx \]
\[ V_e(x + dx) - V_e(x) = -I_e(x) r_e dx \]
\[ I_i(x) = I_t(x + dx) dx + I_i(x + dx) \]
\[ I_e(x) + I_t(x + dx) dx = I_e(x + dx) \]
\[
C \dot{V} + I_{\text{ion}} = I_t
\]

actually, book: \( I_{\text{ion}} \) in current/unit area of membrane, same for capacitance, so multiply by perimeter in LHS; intuitively: \( I_{\text{ion}} \) is total current, of which part \( I_{\text{ion}} - I_t \) that stays in that area contributes to increasing charge across membrane, and hence to potential difference via \( C \dot{V} = -(I_{\text{ion}} - I_t) \) (negative sign as earlier)
so, taking limits as $dx \to 0$:

$$\frac{\partial V_i}{\partial x} = -I_i r_i, \quad \frac{\partial V_e}{\partial x} = -I_e r_e$$

$$I_i(x) - I_i(x + dx) = I_t(x + dx) dx$$

$$I_t(x + dx) dx = I_e(x + dx) - I_e(x)$$

so, taking limits as $dx \to 0$ (argument of $I_t$ just goes to $x$):

$$I_t = -\frac{\partial I_i}{\partial x}, \quad I_t = \frac{\partial I_e}{\partial x}$$

total axial current: $I_T = I_i + I_e$, so:

$$-I_T = -I_i - I_e = (1/r_i) \frac{\partial V_i}{\partial x} + (1/r_e) \frac{\partial V_e}{\partial x}$$

$$-I_T = \frac{r_i + r_e V_i}{r_i r_e x} - \frac{1}{r_e} \frac{\partial V}{\partial x}$$

where $V = V_i - V_e$, so (algebra):

$$\frac{1}{r_i} \frac{\partial V_i}{\partial x} = \frac{1}{r_i + r_e} \frac{\partial V}{\partial x} - \frac{r_e}{r_i + r_e} I_T$$
and now use \( (1/r_i) \frac{\partial V_i}{\partial x} = -I_i \),
take \( \frac{\partial}{\partial x} \),
and use \( \frac{\partial I_i}{\partial x} = -I_t \) to get:

\[
I_t = \frac{\partial}{\partial x} \left( \frac{1}{r_i + r_e \frac{\partial V}{\partial x}} \right) + 0
\]

where the last term vanishes because \( \frac{\partial I_T}{\partial x} \equiv 0 \)
(current conserved along axis)

\[
C \dot{V} + I_{\text{ion}} = \frac{\partial}{\partial x} \left( \frac{1}{r_i + r_e \frac{\partial V}{\partial x}} \right)
\]

leads, for constant resistances,
to a reaction-diffusion equation of the form

\[
\frac{\partial V}{\partial t} = D \frac{\partial^2 V}{\partial x^2} + F(V, t)
\]

where \( F \) gives the currents in terms of voltage and
(time varying, possibly) conductances
Example of Solution

Passive case when $f = -V$, i.e. membrane is Ohmic resistor
good approximations for dendritic networks

e.g. of typical boundary/initial conditions on $V(x, t)$:
$V(x, 0) = 0$ if starts at rest
$\frac{\partial V}{\partial x}(0, 0) = 0$ if no current at left endpoint

Let us just solve an example using separation of variables:

$$\frac{\partial V}{\partial t} = \frac{\partial^2 V}{\partial x^2} - V, \; 0 < x < 1; \; V(0, 0) = 0, \; \frac{\partial V}{\partial x}(1, 0) = 0$$
separation of variables try solution of form $V = X(x)T(t)$ for $V_t = V_{xx} - V$:

$$\frac{XT'}{XT} = \frac{X''T}{XT} - \frac{XT}{XT}$$

so there is some number $\lambda$ such that

$$\lambda = \frac{T'}{T} = \frac{X''}{X} - 1$$

i.e. $T(t) = e^{\lambda t}T(0)$, $X'' = (\lambda + 1)X$

if $\mu = \lambda + 1 > 0$, then look at

$X'' - \mu X = 0$, $X(0) = X'(1) = 0$, $\mu > 0$:

$$\Rightarrow X(x) = Ae^{ax} + Be^{-bx}, \ ab = \mu \text{ both positive or negative}$$

$X(0) = A + B = 0 \Rightarrow X(x) = A(e^{ax} - e^{-bx})$ so

$X'(1) = A(\alpha e^{ax} + \beta e^{-bx}) = 0 \Rightarrow$

(asuming nontrivial solution: $A \neq 0$) $ae^a + be^{-b} = 0$, which contradicts that $a, b$ have same sign and nonzero
if $\mu = \lambda + 1 = 0$ then $X'' = 0 \Rightarrow X = A + Bx$, and bdry conds $\Rightarrow A = B = 0$

so $\lambda + 1 < 0$, write $\mu^2 = -(1 + \lambda)$,

$X(x) = A \cos \mu x + B \sin \mu x$

first boundary condition forces $A = 0$,

so $\mu \cos \mu = 0$ implies $\mu = \pi/2 + k\pi$

$$V(x, t) = \sum_{k \geq 0} A_k e^{(-1-(\pi/2+k\pi)^2)t} \sin(\pi/2 + k\pi)x$$

(w.l.o.g. $k \geq 0$ using sin odd)

now fit initial condition using Fourier series decomposition

note that $V \to 0$ as $t \to +\infty$

can compute current at endpoint by calculating $V_x(0, t)$, etc

far more interesting: nonlinear $f(V)$ (active, like axons)\ldots