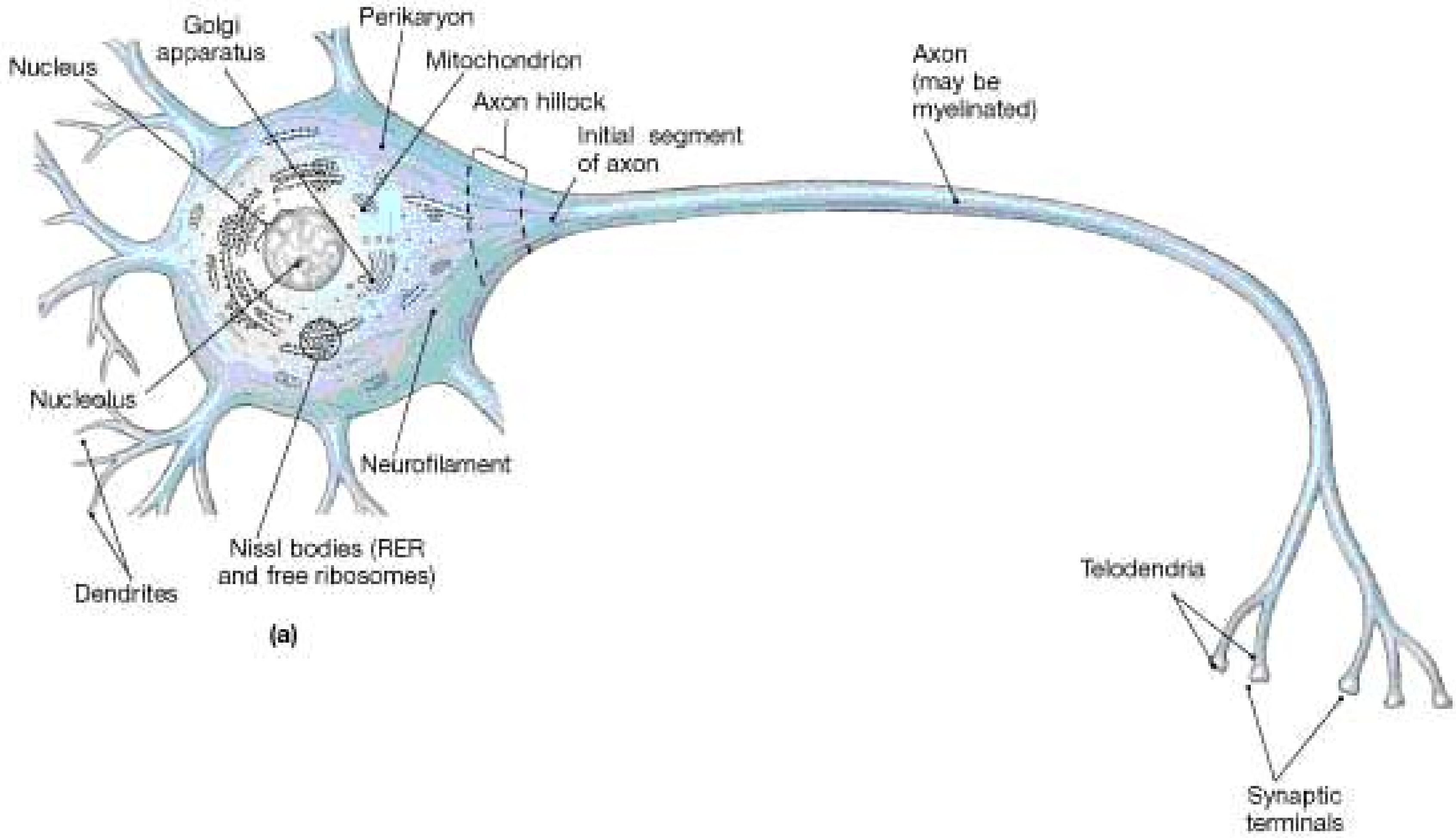
Rutgers 642:613 - Fall 2003

Instructor: Eduardo D. Sontag

Section 8.1, Cable Equation

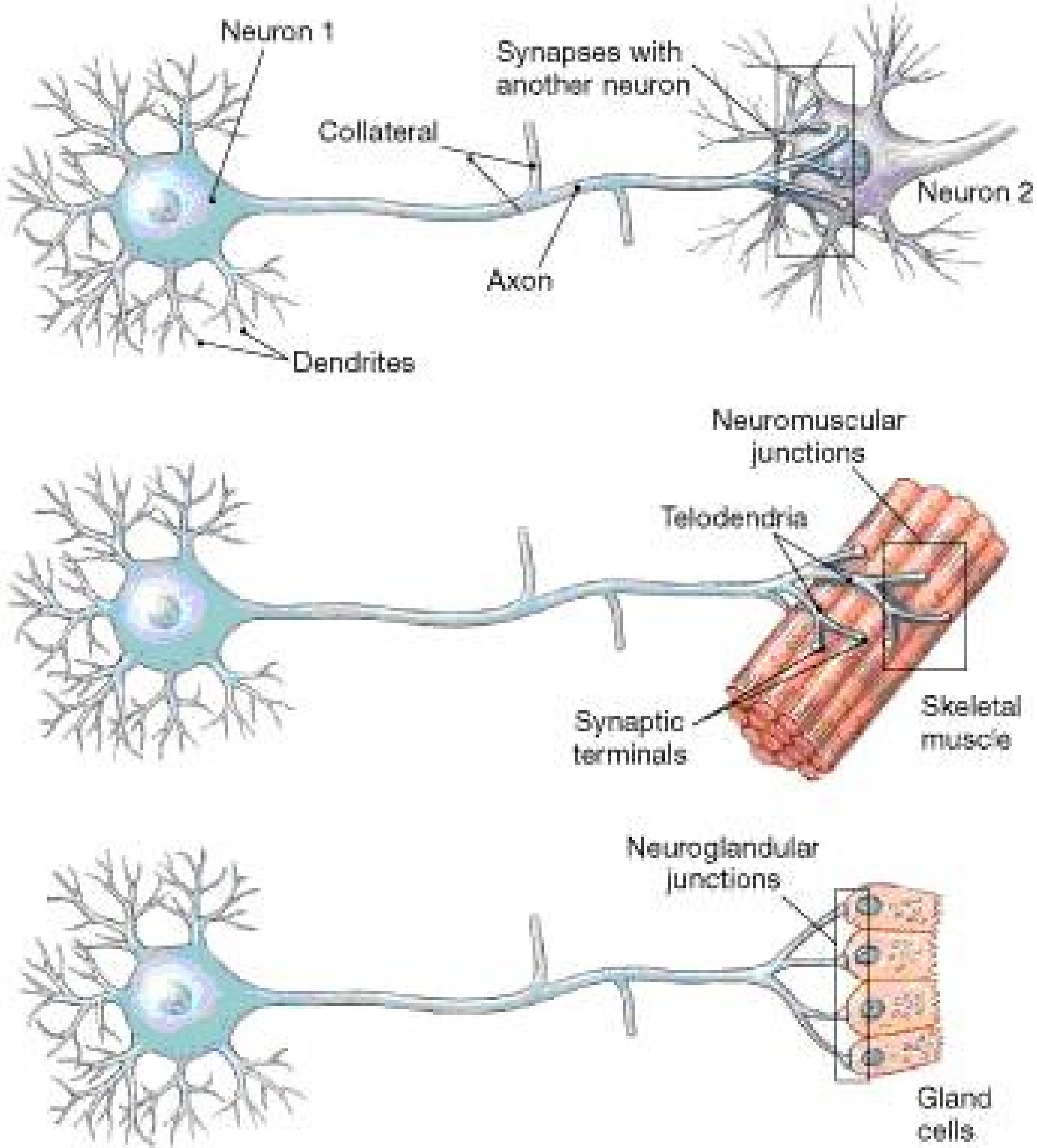
http://www.math.rutgers.edu/~sontag/613.html

Neurons



http://student.biology.arizona.edu/honors99/group6/intro.html

They transmit info (to other neurons, to musces, to glands)



http://student.biology.arizona.edu/honors99/group6/intro.html

Dendrites: Passive Conduction (Cable Equation)

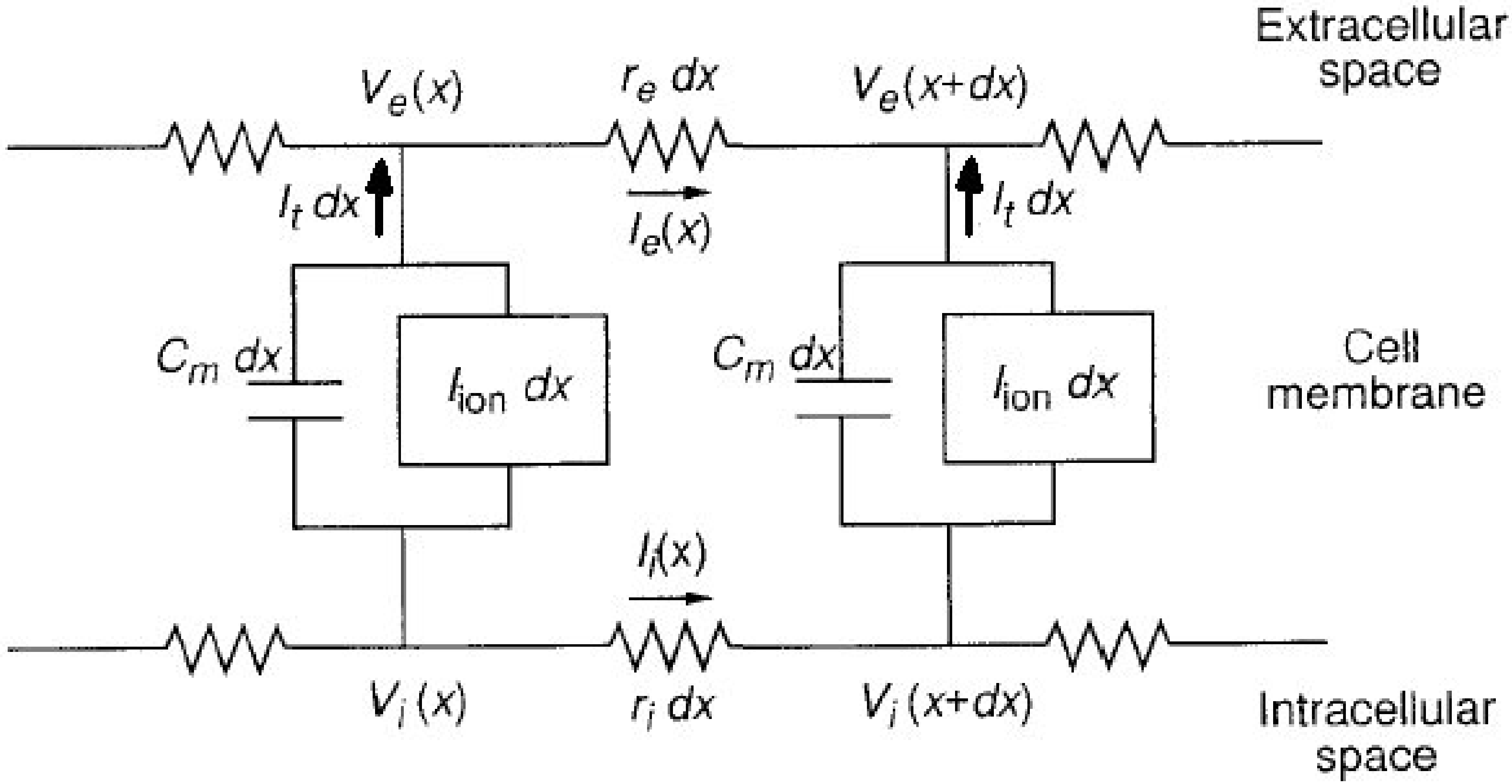
cable equation **(Lord Kelvin 1855)**
first proposed for flow of electricity on leaky cable
Hodgkin-Rushton 1946, Rall 1957: application to neurons

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:

$I_i(x)$: ***internal axial*****, oriented left to right**
$I_e(x)$: ***external axial*****, oriented left to right**
$I_t(x)$: ***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_{ion} in curent/unit area of membrane, same for capacitance, so multiply by perimiter in LHS; intuitively: I_{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 $dx \to 0$:

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

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

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

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

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

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

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

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

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

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

$X(0) = A + B = 0 \Rightarrow X(x) = A(e^{ax} - e^{-bx})$ so
$X'(1) = A(ae^{a} + be^{-b}) = 0 \Rightarrow$
(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)...