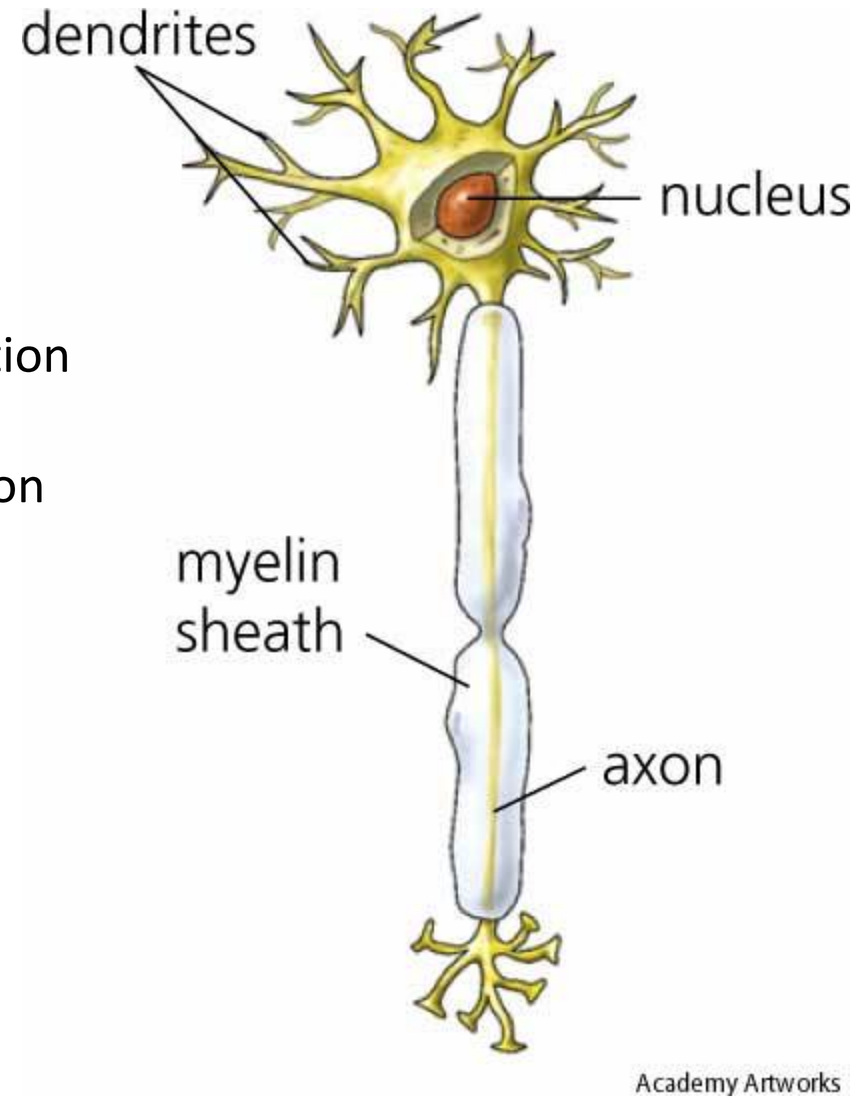
Dendritic computation

Dendrites as computational elements:

Passive contributions to computation

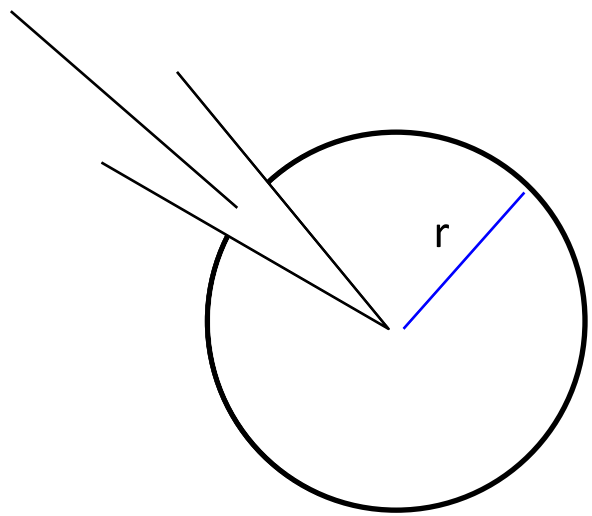
Active contributions to computation

Examples



Geometry matters: the isopotential cell

Injecting current I_0



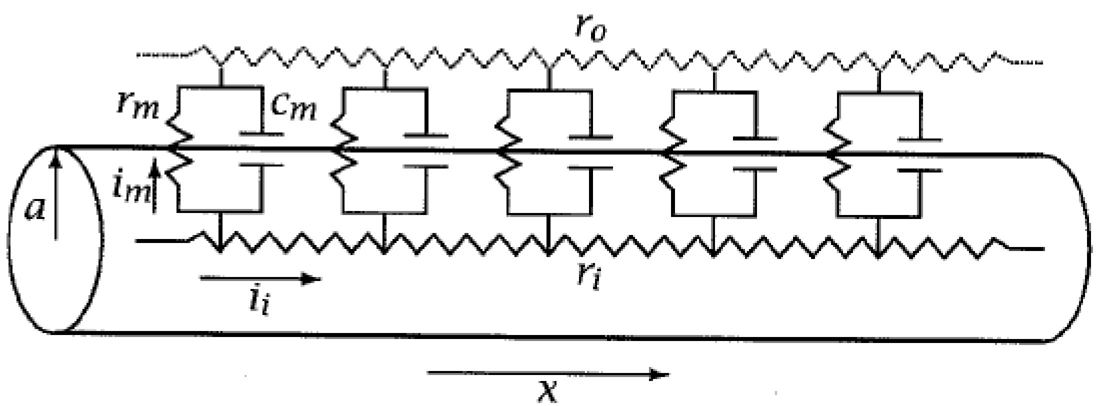
$$V_m = I_m R_m$$

Current flows uniformly out through the cell: $I_m = I_0/4\pi r^2$

Input resistance is defined as $R_N = V_m(t \rightarrow \infty)/I_0$

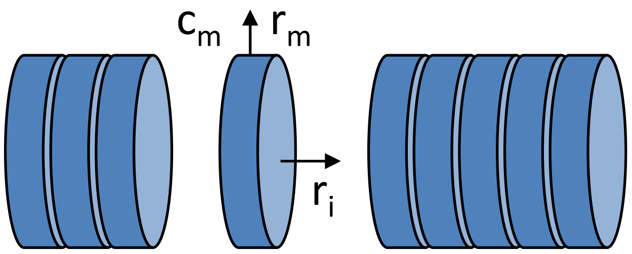
$$= R_m/4\pi r^2$$

Linear cable theory



r_m and r_i are the membrane and axial resistances, i.e. the resistances of a thin slice of the cylinder

Axial and membrane resistance



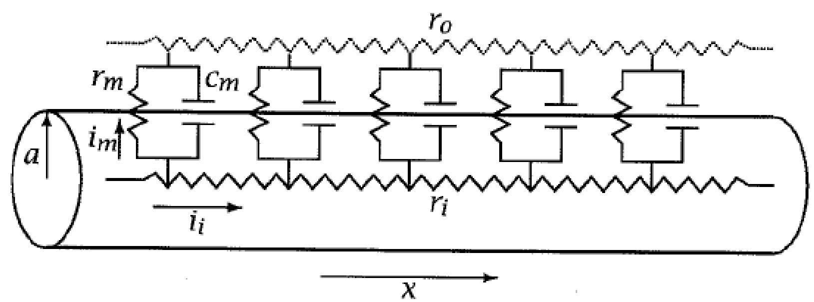
For a length L of membrane cable:

$r_i \rightarrow r_i L$
$r_m \rightarrow r_m / L$
$c_m \rightarrow c_m L$

The cable equation

(1) $$\frac{\partial V_m}{\partial x} = -r_i i_i$$

(2) $$\frac{\partial i_i(x)}{\partial x} = -i_m$$



$\frac{\partial}{\partial x}$ (1) → $$\frac{\partial^2 V_m}{\partial x^2} = -r_i \frac{\partial i_i}{\partial x} = r_i i_m.$$

$$i_m = i_C + i_{\text{ionic}} = c_m \frac{\partial V_m}{\partial t} + \frac{V_m}{r_m}$$

$$\frac{1}{r_i} \frac{\partial^2 V_m(x,t)}{\partial x^2} = c_m \frac{\partial V}{\partial t} + \frac{V_m}{r_m}.$$

or

$$\lambda^2 \frac{\partial^2 V_m}{\partial x^2} = \tau_m \frac{\partial V_m}{\partial t} + V_m$$

where

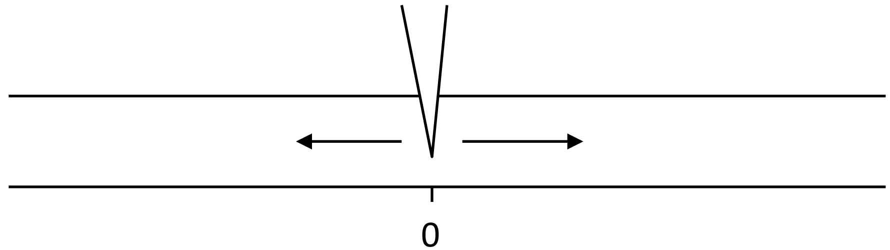
$\tau_m = r_m c_m$ Time constant

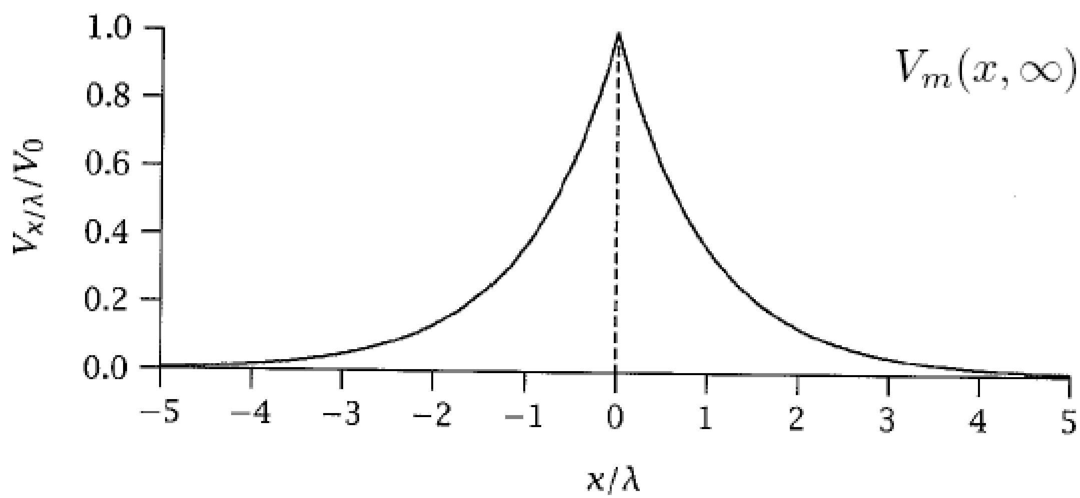
$\lambda = \sqrt{\frac{r_m}{r_i}}$ Space constant

Full solution for current step in infinite cable

$$V_m(t,x) = \frac{r_i I_0 \lambda}{4}\left[e^{-x/\lambda}\mathrm{erfc}\left(\frac{x/\lambda}{2\sqrt{t/\tau_m}} - \sqrt{t/\tau_m}\right) - e^{x/\lambda}\mathrm{erfc}\left(\frac{x/\lambda}{2\sqrt{t/\tau_m}} + \sqrt{t/\tau_m}\right)\right]$$

Decay of voltage in space for current injection at x = 0, T → ∞



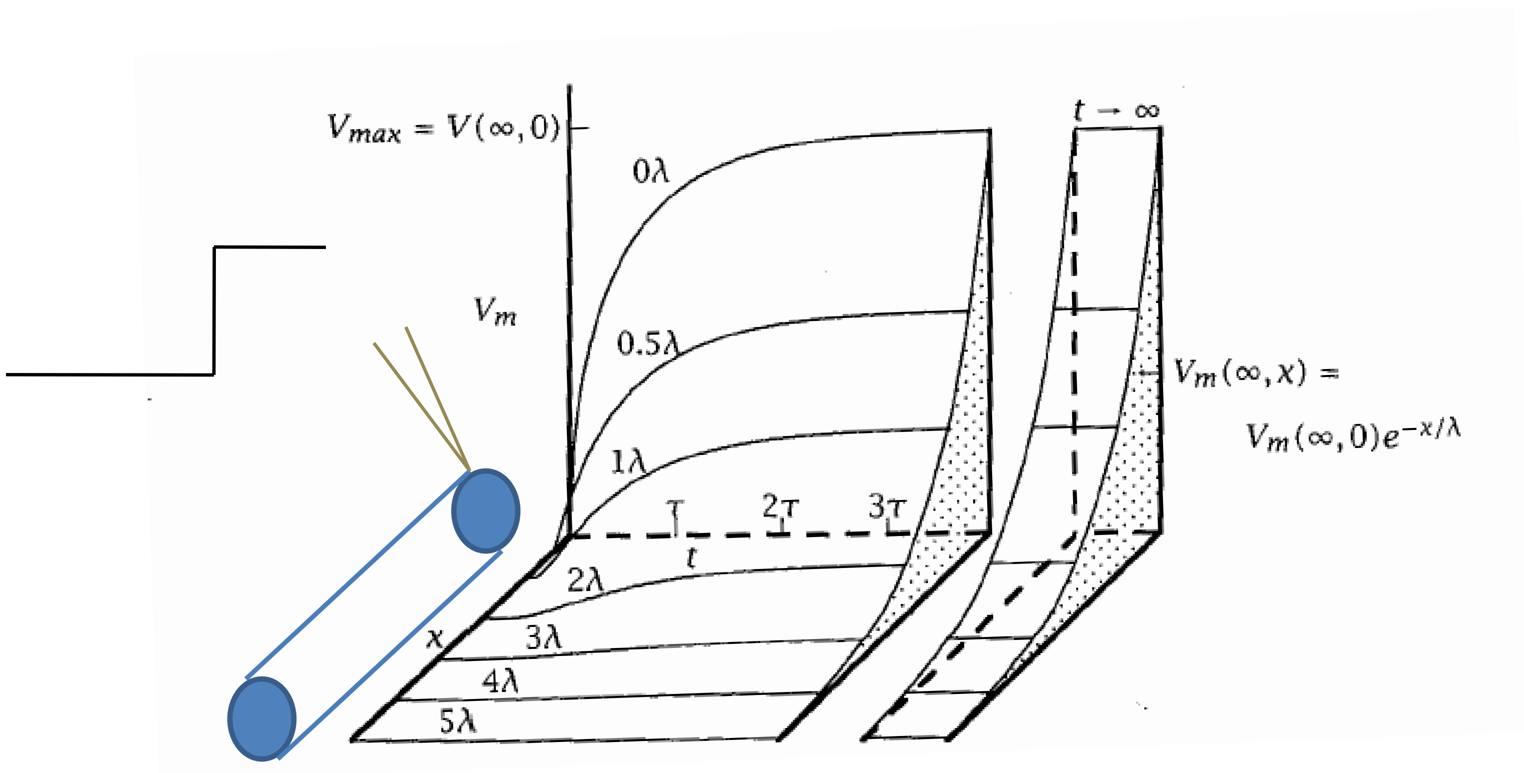


$$V_m(x, \infty) = \frac{r_i I_0 \lambda}{2} e^{-x/\lambda}$$

Properties of passive cables

→ Electrotonic length $\lambda = \sqrt{\frac{r_m}{r_i}}$

Electrotonic length

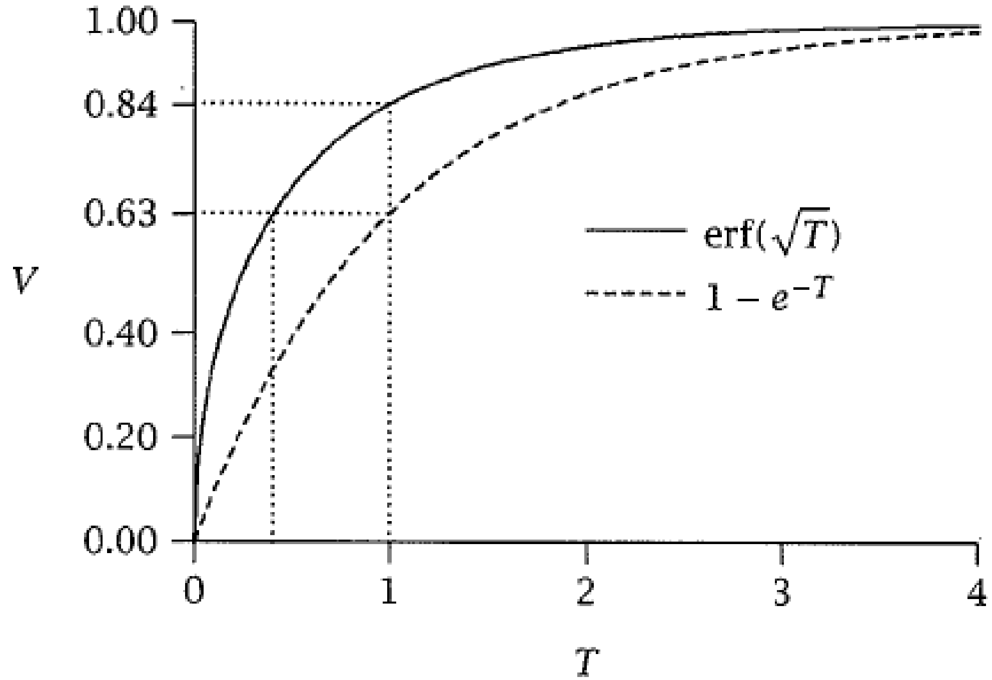


Johnson and Wu

Properties of passive cables

→ Electrotonic length $$\lambda = \sqrt{\frac{r_m}{r_i}}$$

→ Current can escape through additional pathways: speeds up decay

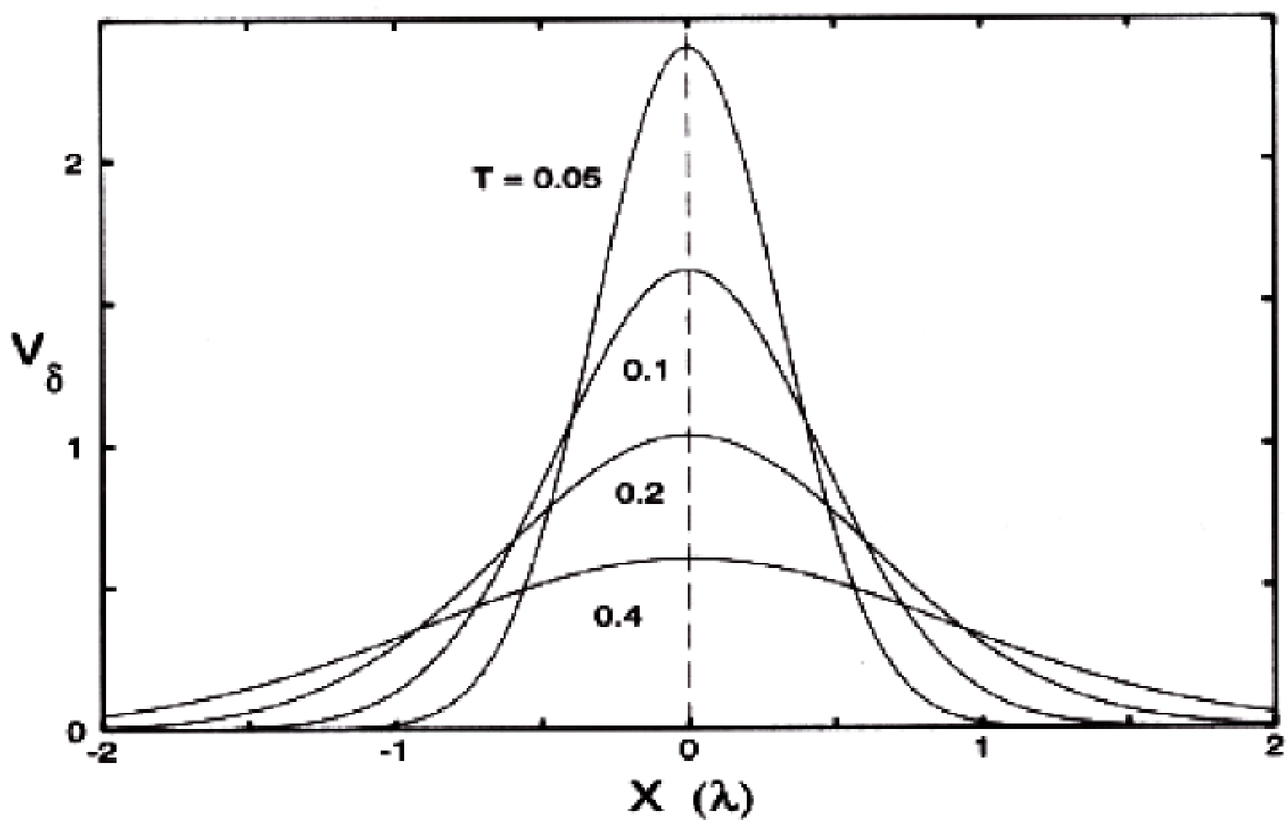


Johnson and Wu

Pulse response

$$V(x,t) \propto \sqrt{\frac{\tau}{4\pi\lambda^2 t}} e^{-\frac{t}{\tau} - \frac{\tau x^2}{4\lambda^2 t}}$$

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



Koch

Pulse response

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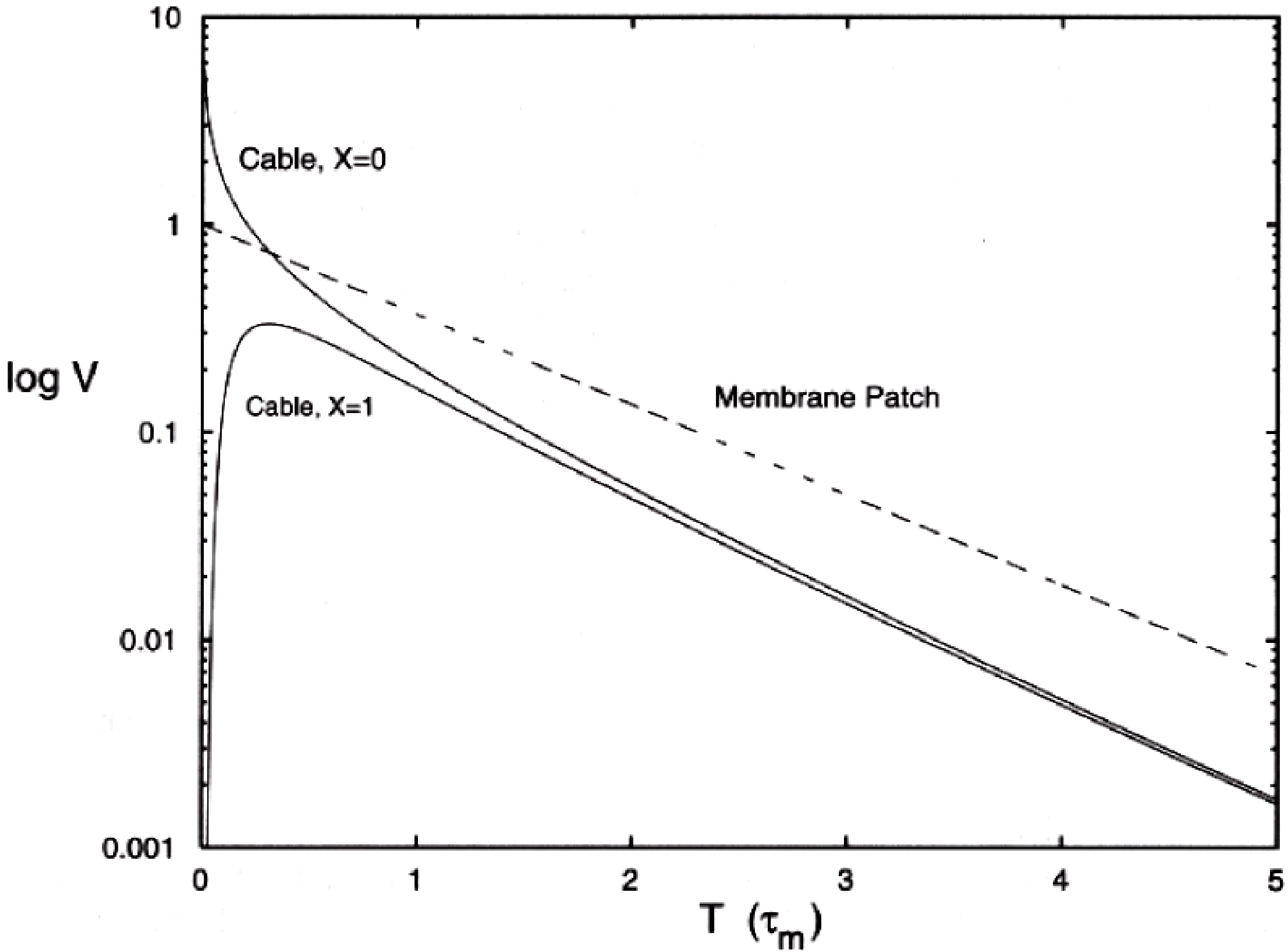
Dendrites as *filters*



10
1
0.1
0.01
0.001
log V
Cable, X=0
Cable, X=1
Membrane Patch
0
1
2
3
4
5
T (τ_m)

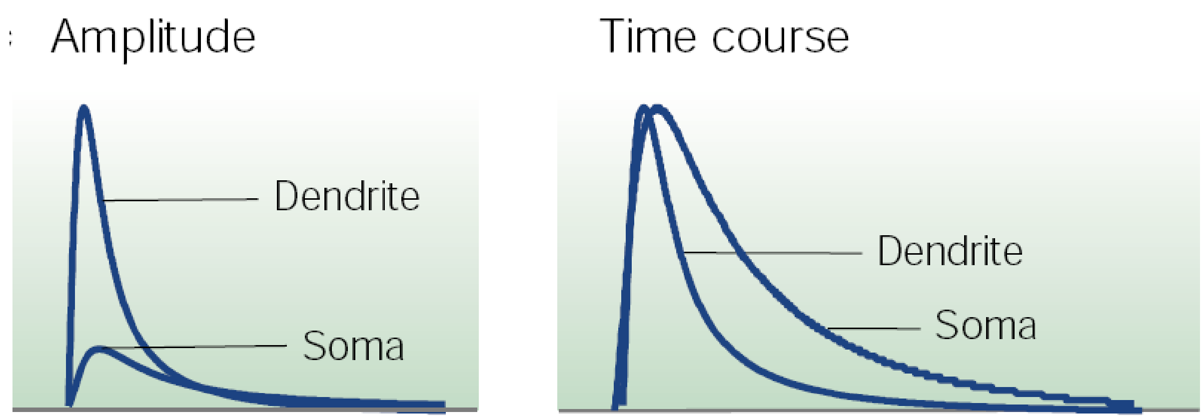
Koch

Properties of passive cables

→ Electrotonic length $\lambda = \sqrt{\frac{r_m}{r_i}}$

→ Current can escape through additional pathways: speeds up decay

→ Cable diameter affects input resistance $R_N = \frac{\sqrt{R_m R_i / 2}}{2\pi a^{3/2}}$



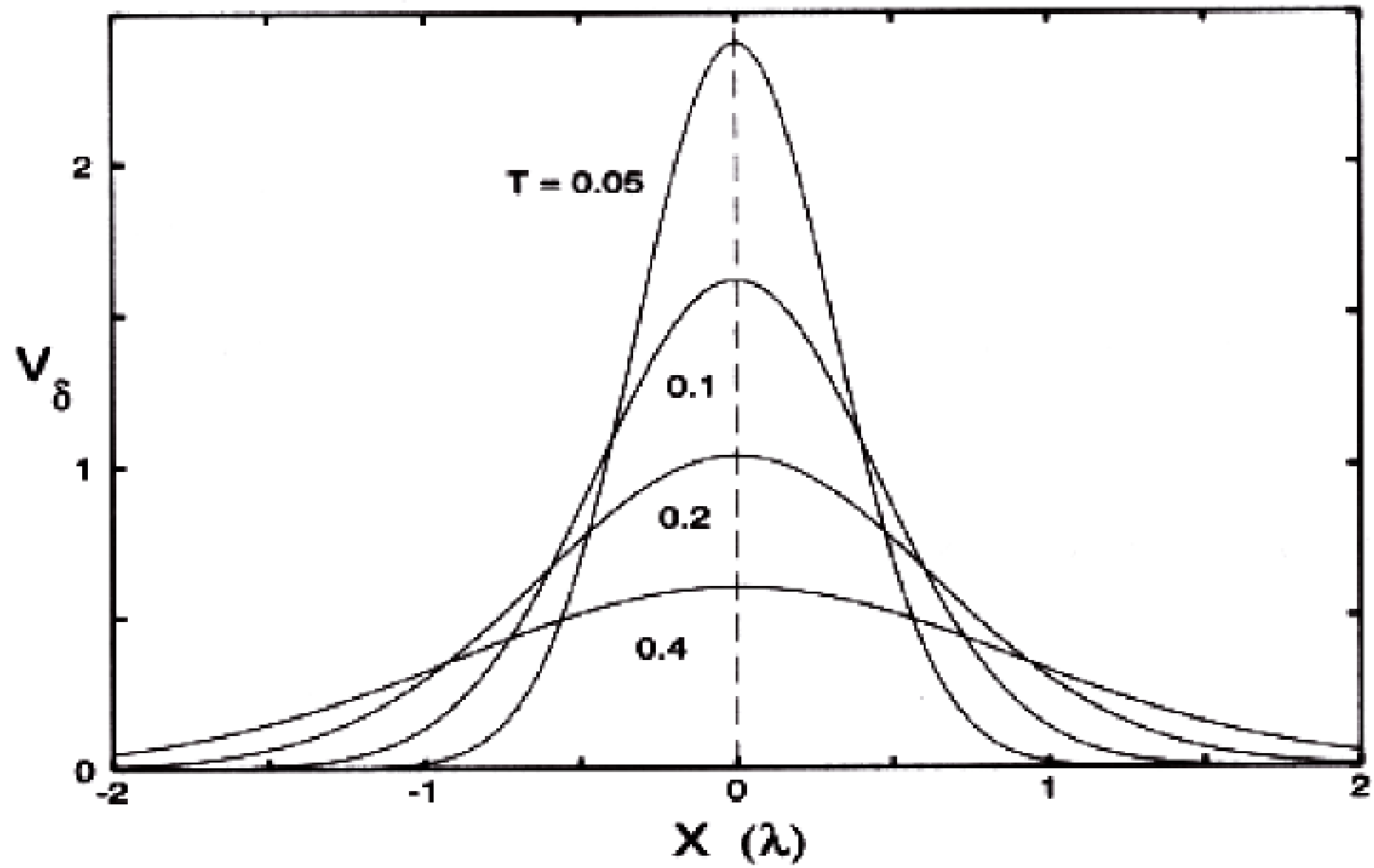
Properties of passive cables

→ Electrotonic length $\lambda = \sqrt{\frac{r_m}{r_i}}$

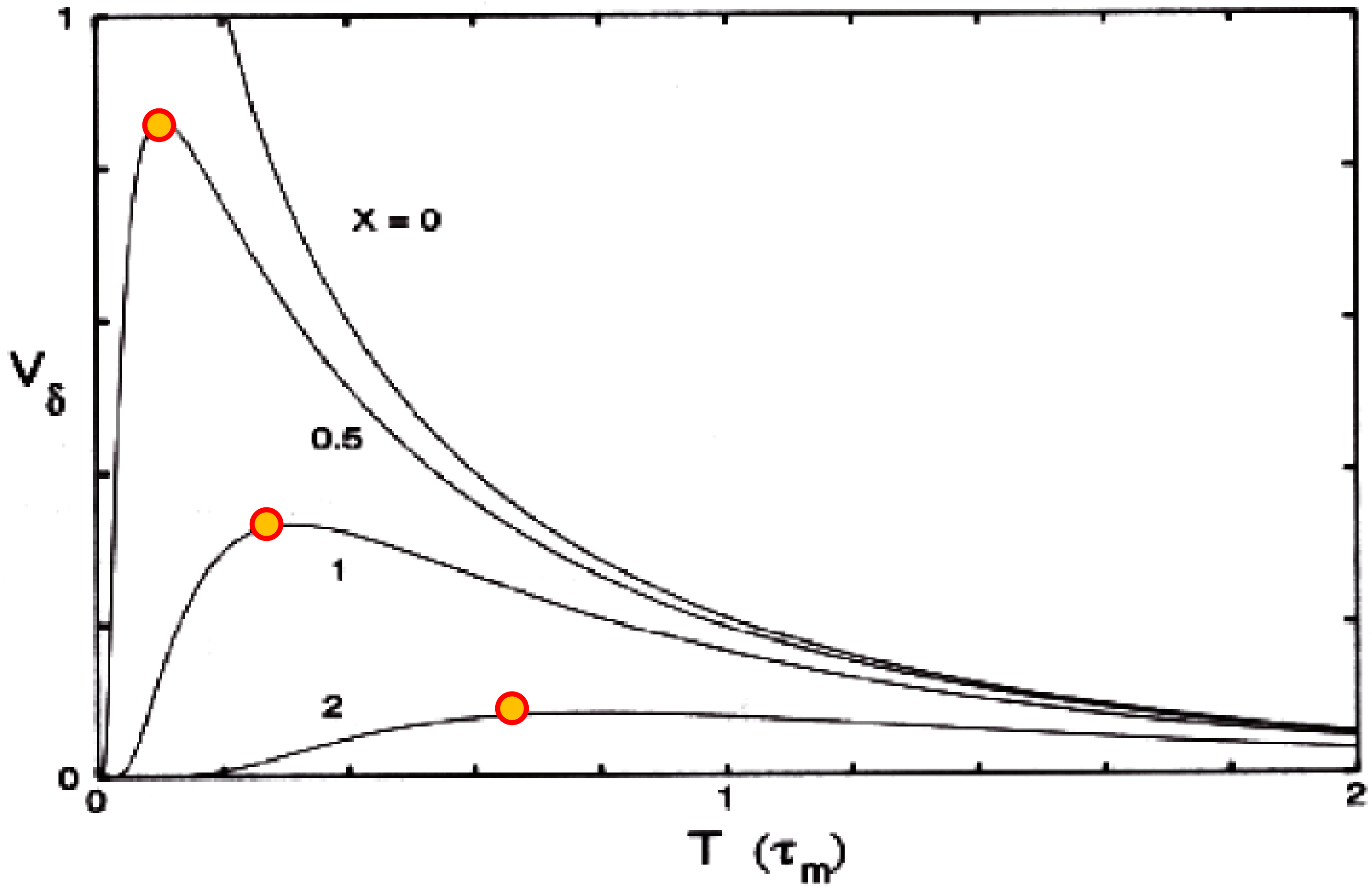
→ Current can escape through additional pathways: speeds up decay

→ Cable diameter affects input resistance $R_N = \frac{\sqrt{R_m R_i / 2}}{2\pi a^{3/2}}$

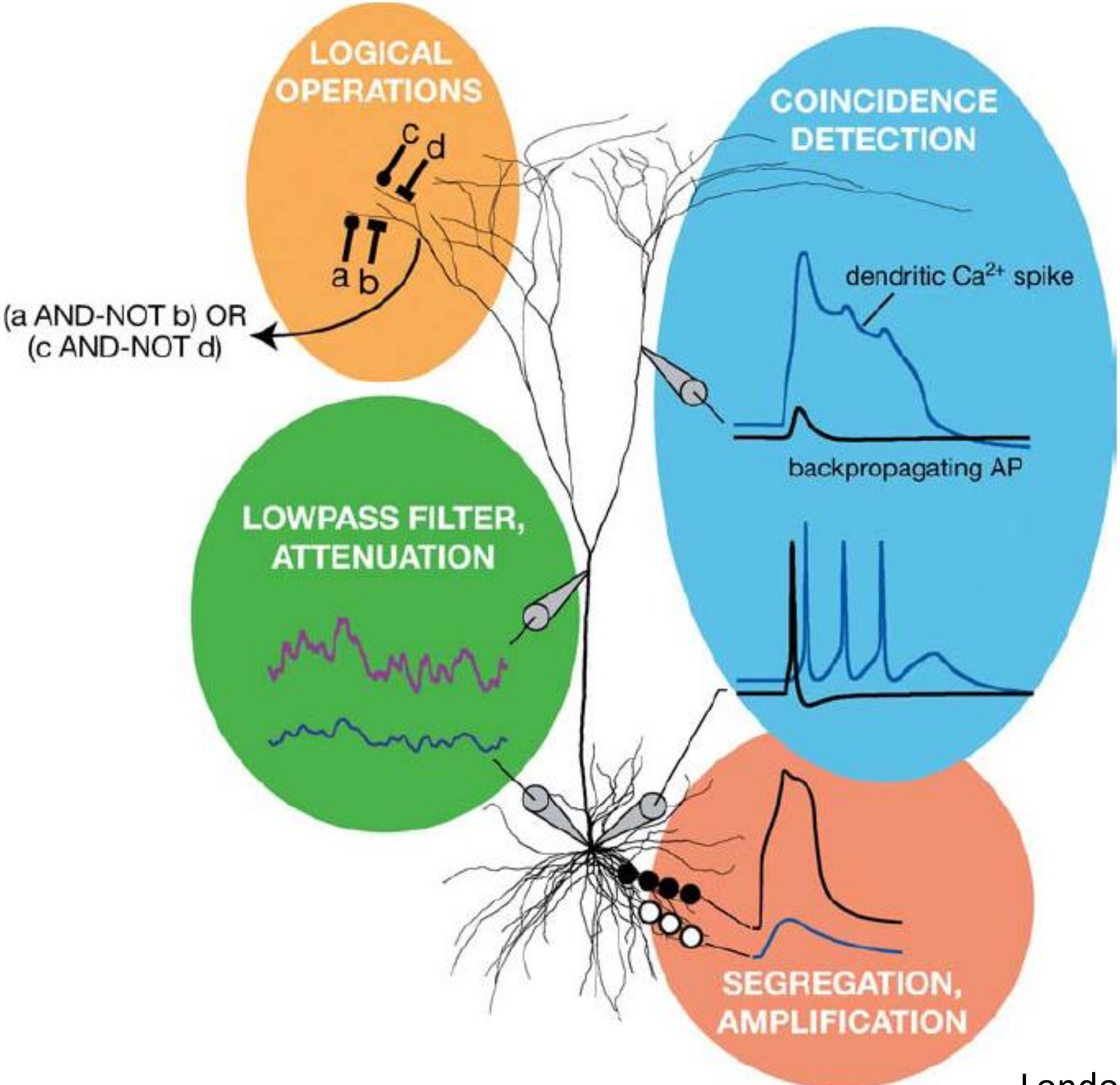
→ Cable diameter affects transmission velocity



T = 0.05
0.1
0.2
0.4
V_δ
X (λ)
0
1
2
-2
-1
0
1
2



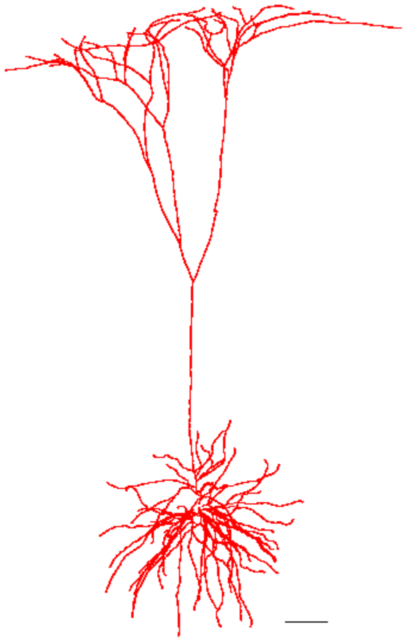
$$\theta = \frac{2\lambda}{\tau_m} = \sqrt{\frac{2a}{R_m R_i C_m^2}}$$



London and Hausser, 2005

Passive computations

Linear filtering:



→ Inputs from dendrites are broadened and delayed

→ Alters summation properties..
coincidence detection to temporal integration

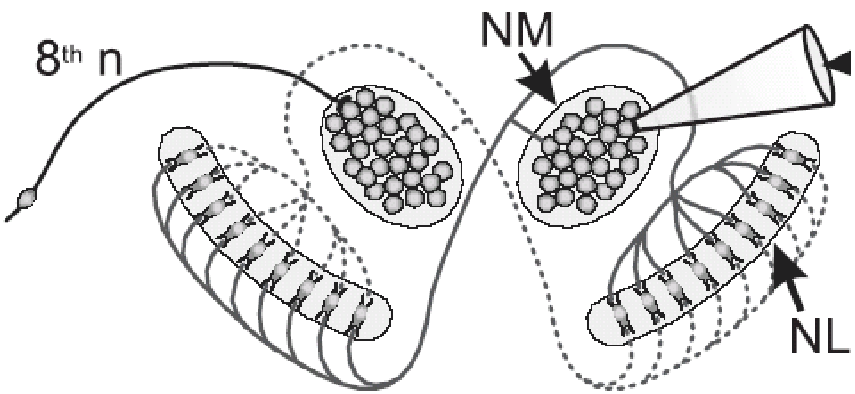
→ Delay lines

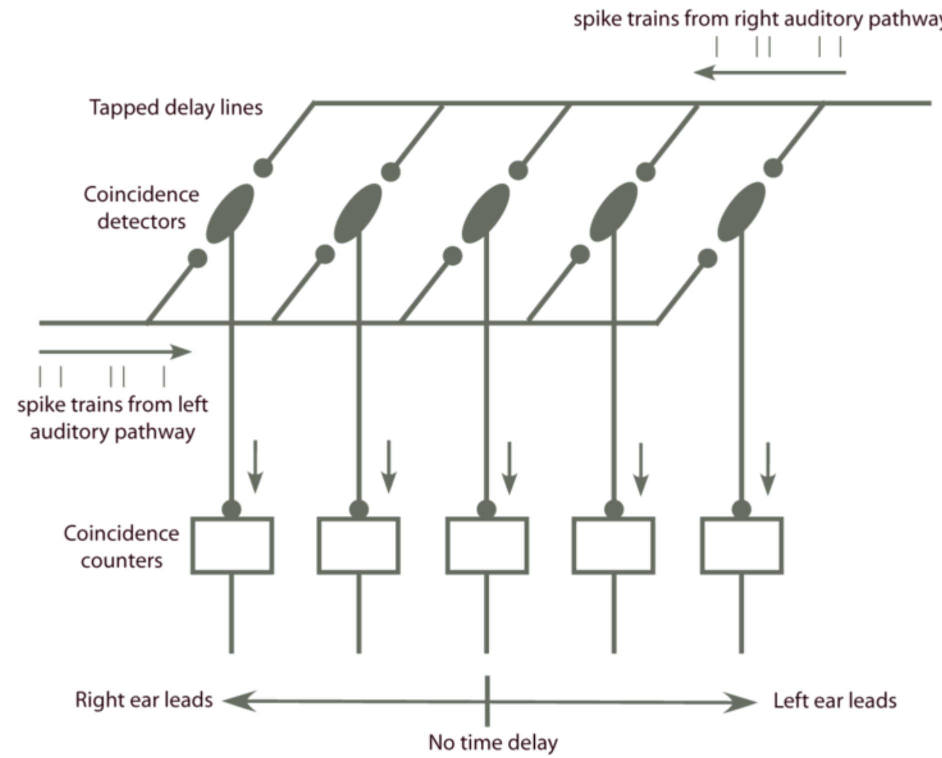
→ Segregation of inputs

→ Nonlinear interactions within a dendrite
-- sublinear summation
-- shunting inhibition

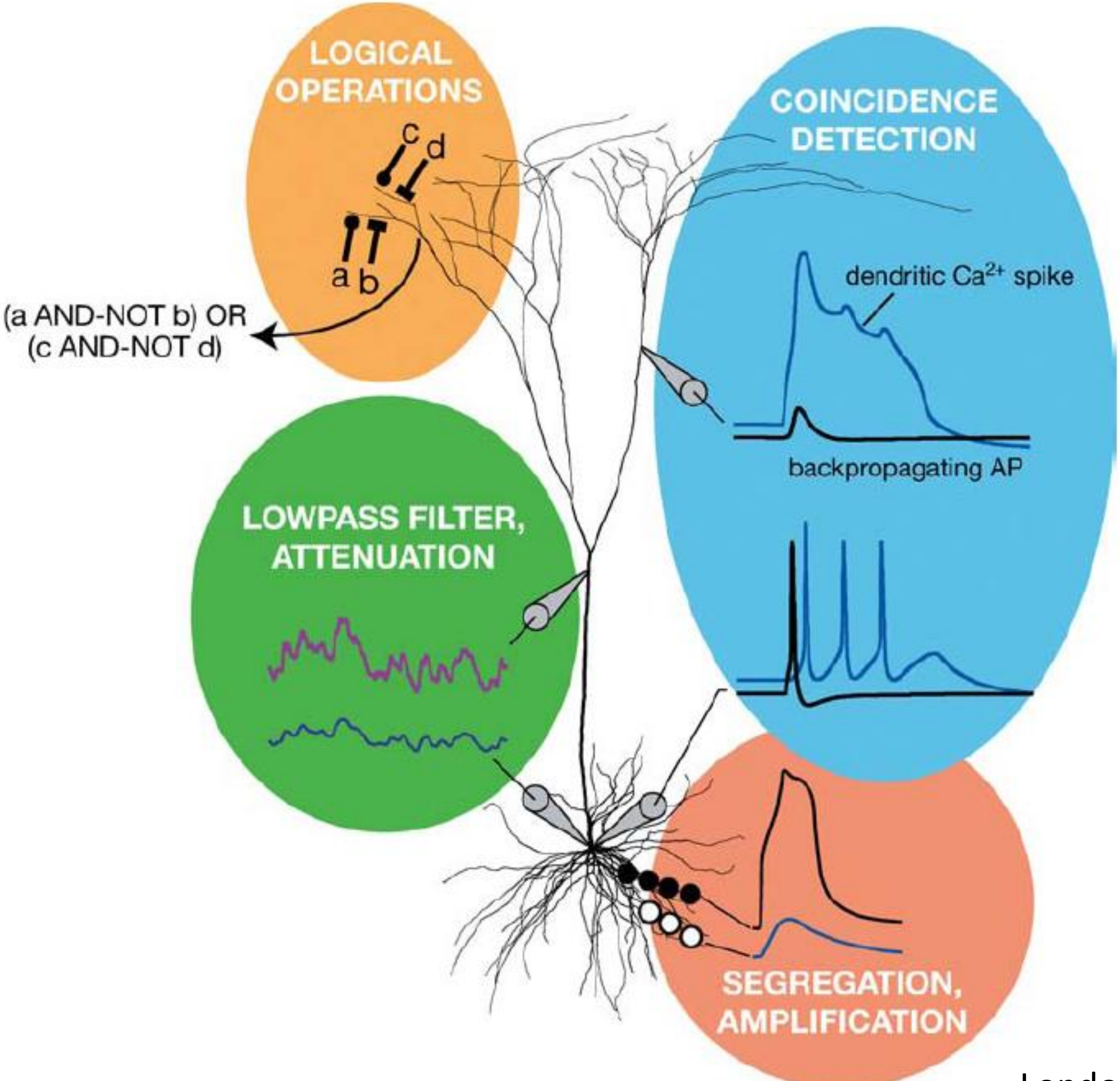
→ Dendritic inputs "labelled"

Delay lines: the sound localization circuit





Spain; Scholarpedia



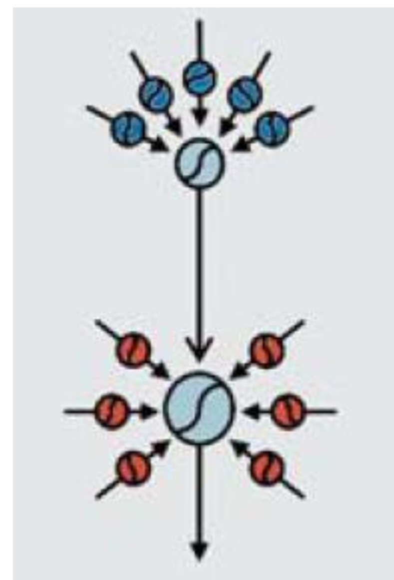
London and Hausser, 2005

Active dendrites

Mechanisms to deal with the distance dependence of PSP size

→ Subthreshold boosting: inward currents with reversal near rest
Eg persistent Na^+

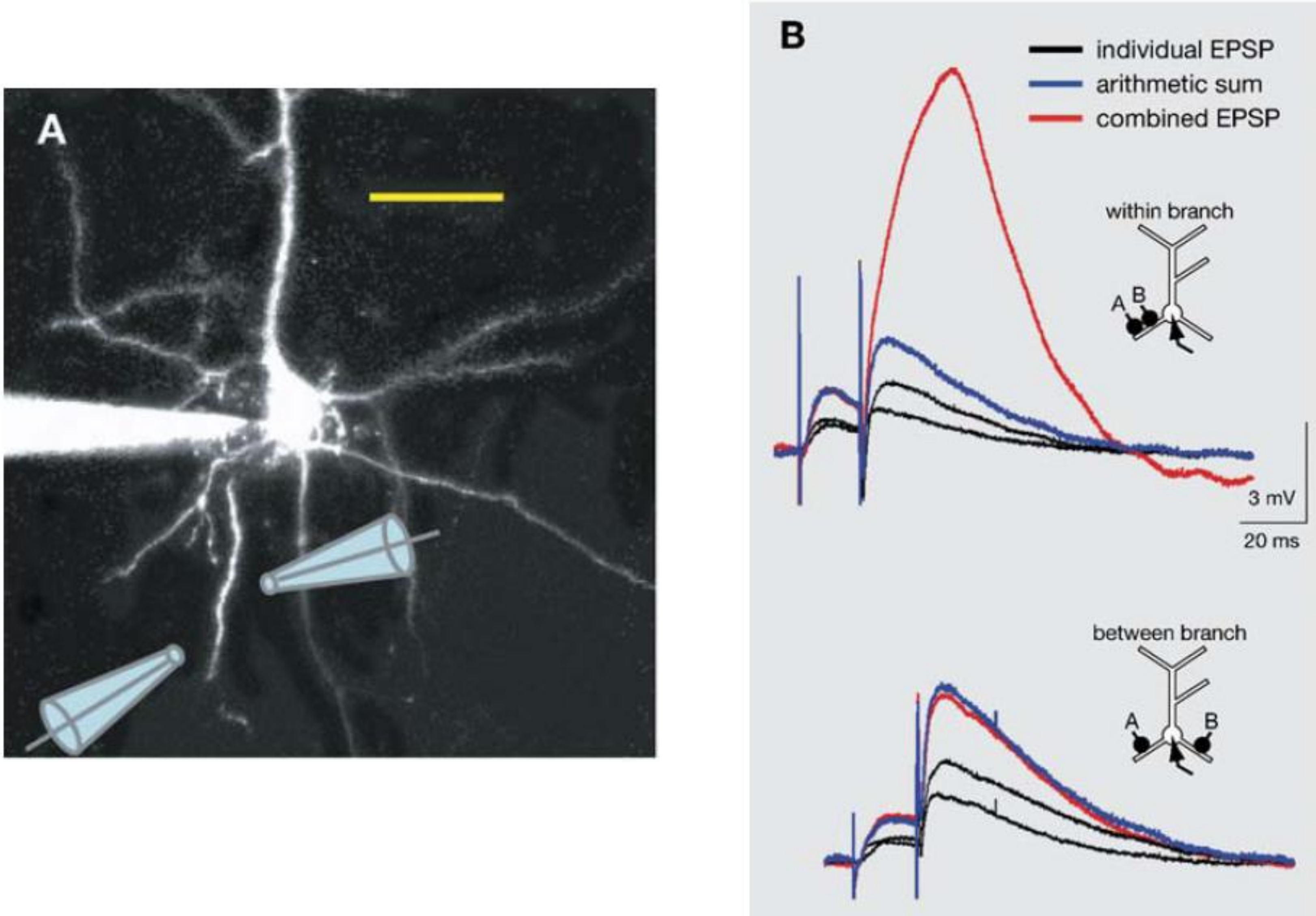
→ Synaptic scaling



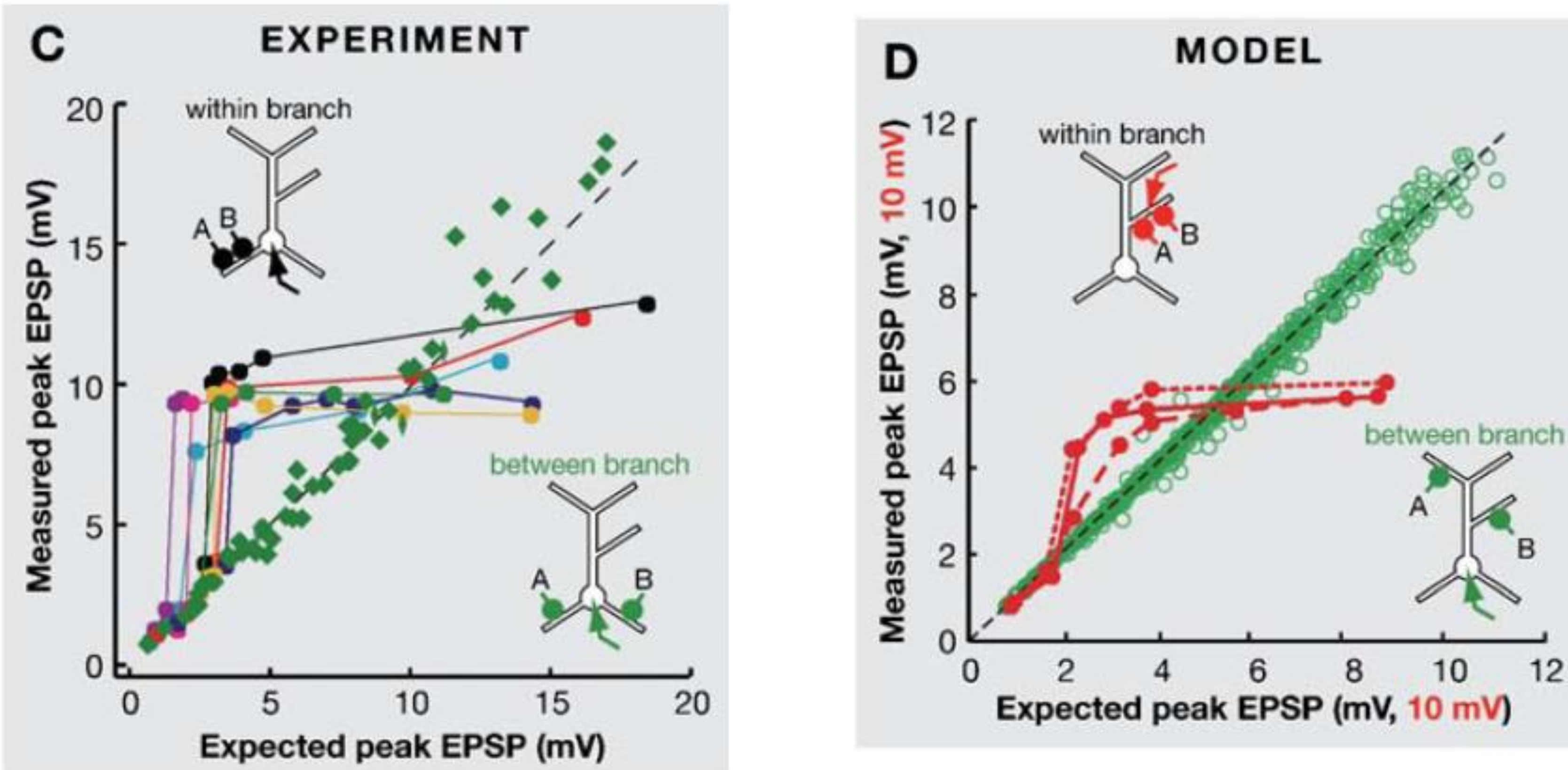
→ Dendritic spikes
Na^+, Ca^{2+} and NMDA
Dendritic branches as
mini computational units

→ backpropagation:
feedback circuit
Hebbian learning through
supralinear interaction of backprop spikes with inputs

Segregation and amplification

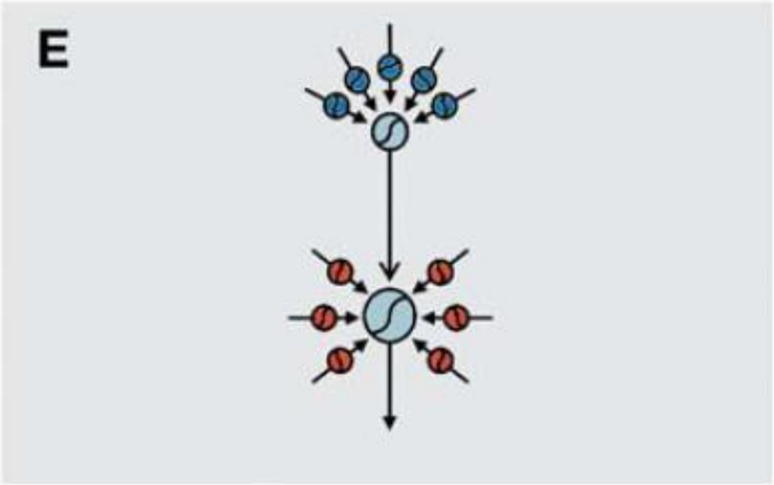


Segregation and amplification

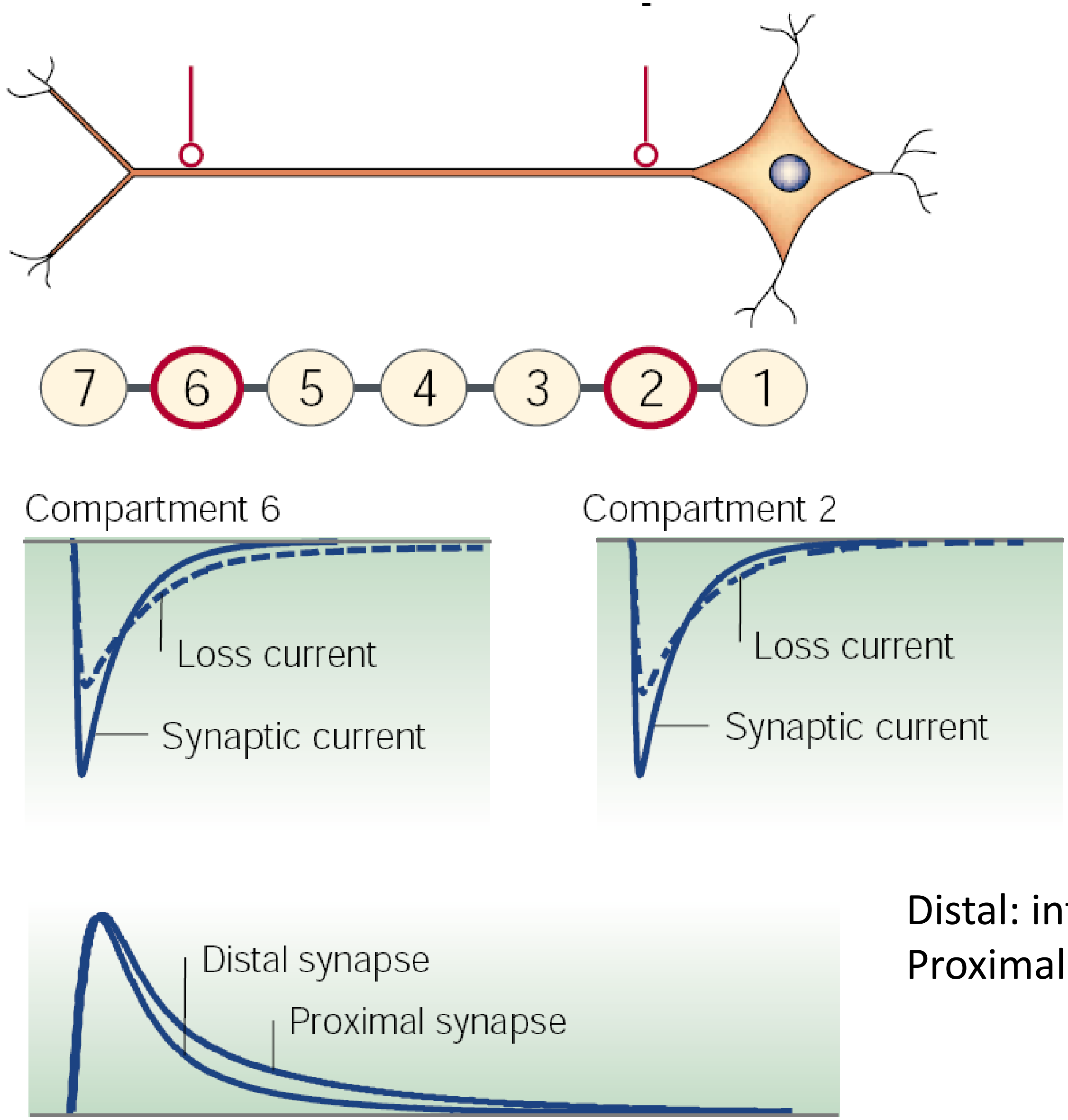


Segregation and amplification

The single neuron as a neural network



Synaptic scaling



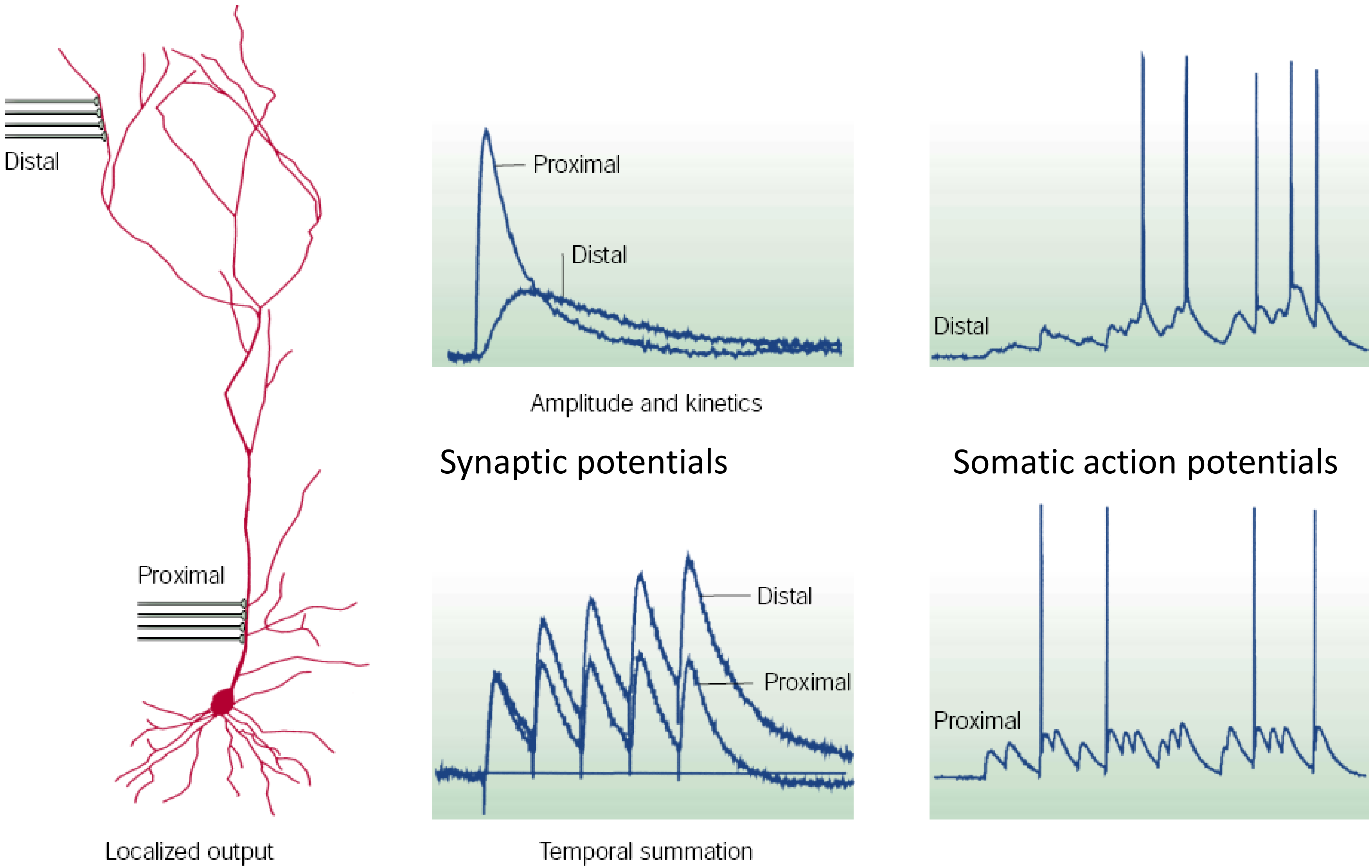
Currents

Potential

Distal: integration
Proximal: coincidence

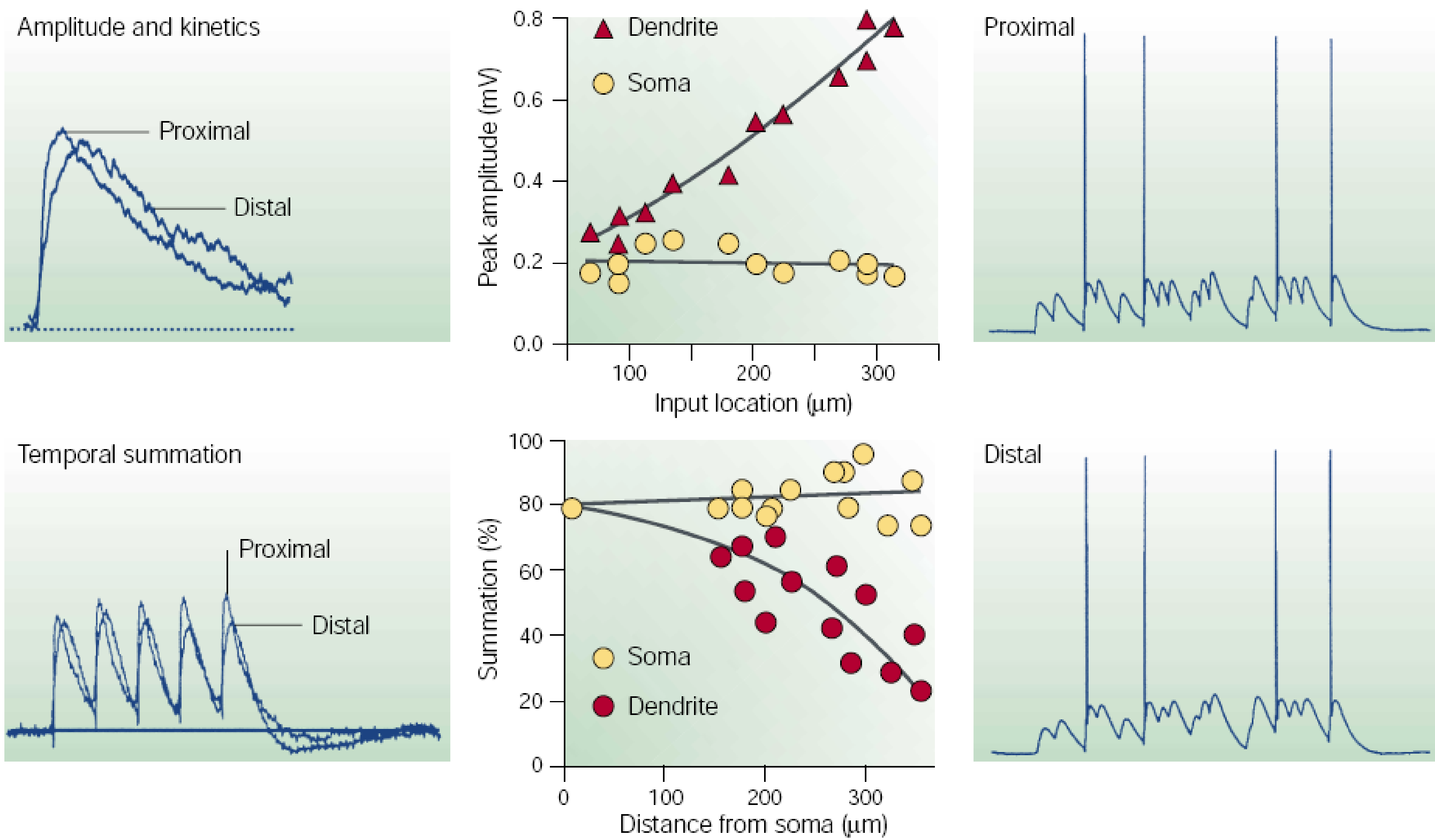
Magee, 2000

Expected distance dependence

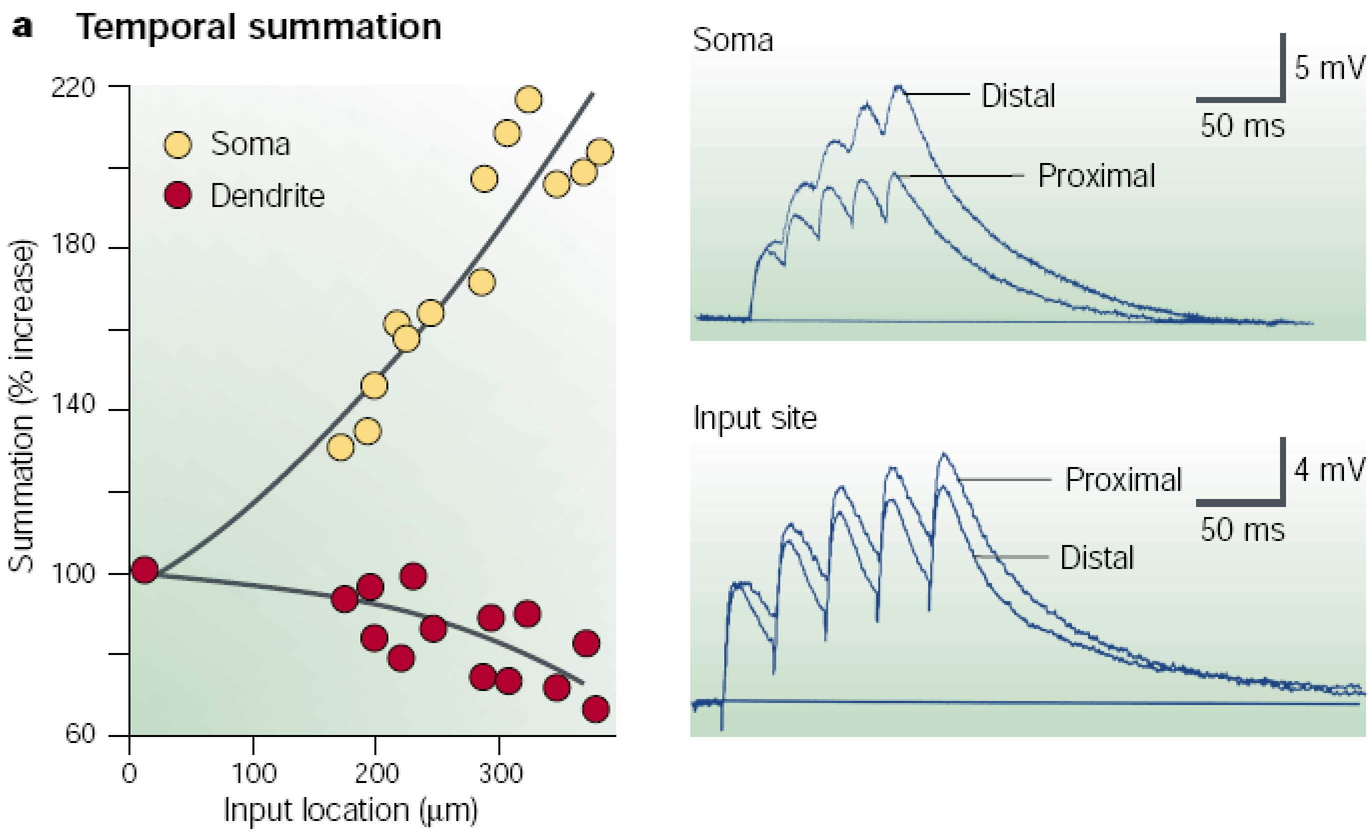


Magee, 2000

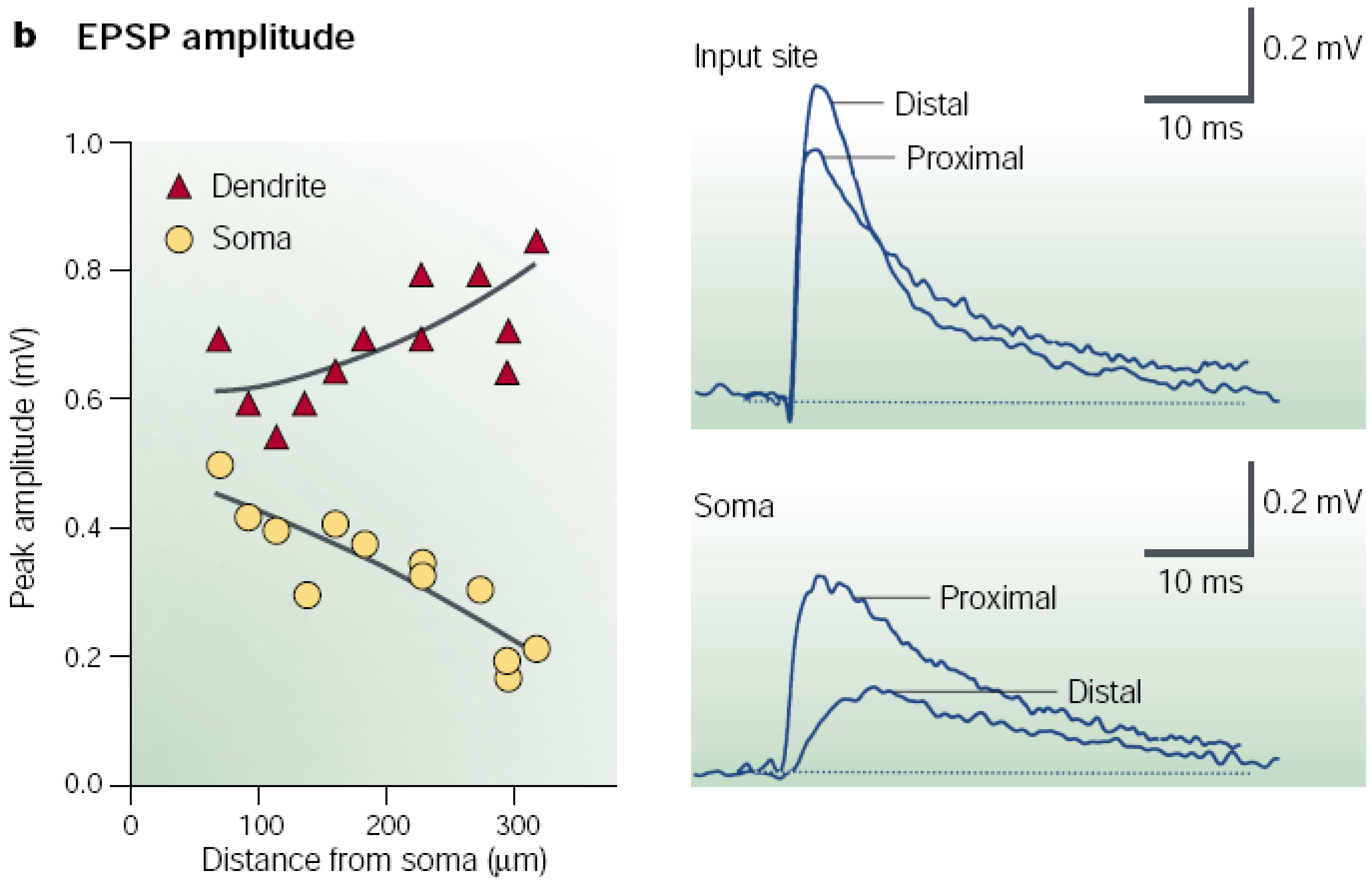
CA1 pyramidal neurons



Passive properties



Passive properties



Active properties: voltage-gated channels

For short intervals (0-5ms), summation is linear or slightly supralinear

For longer intervals (5-100ms), summation is sublinear

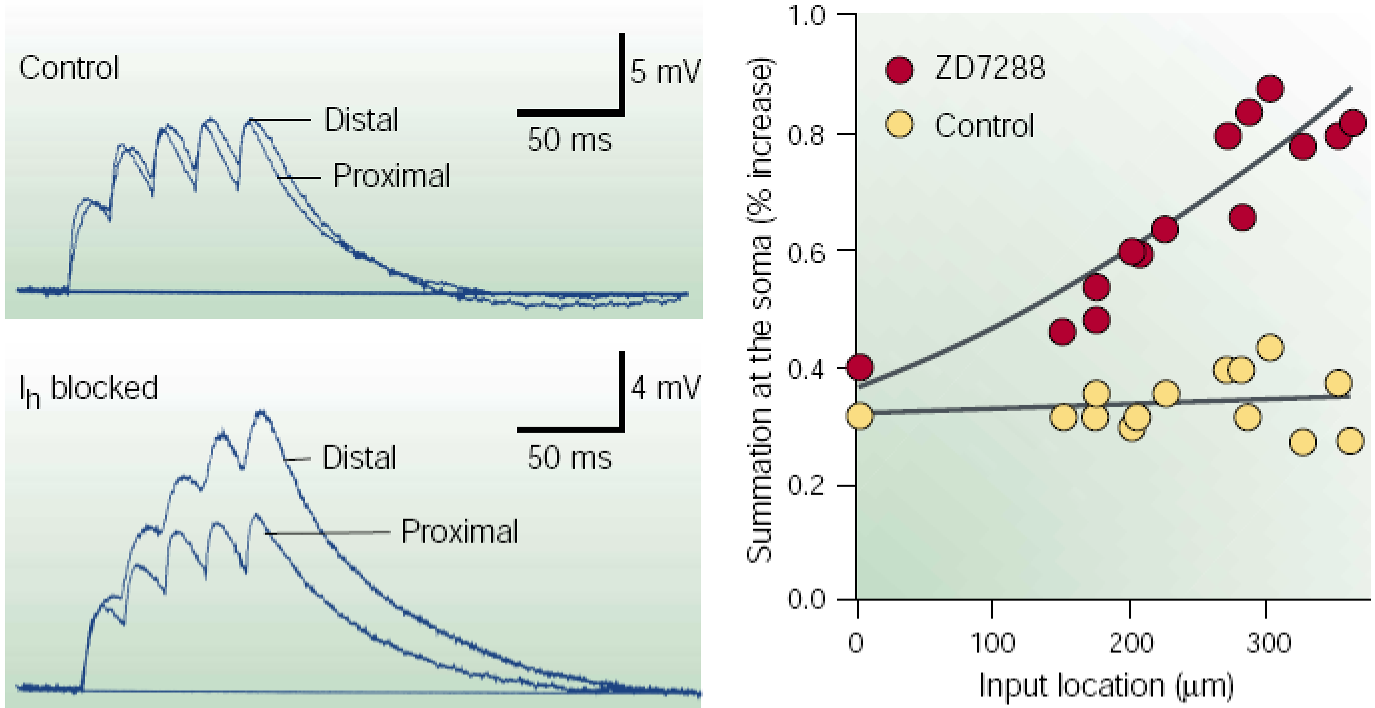
Na^+, Ca^{2+} or NDMA receptor block eliminates supralinearity

I_h and K^+ block eliminates supralinearity

Major player in synaptic scaling: hyperpolarization activated K current, I_h

Increases in density down the dendrite
Effectively outward current due to deactivation during EPSP hyperpolarizes, shortens EPSP duration, reduces local summation

Active properties: voltage-gated channels



Major player in synaptic scaling: hyperpolarization activated K current, I_h

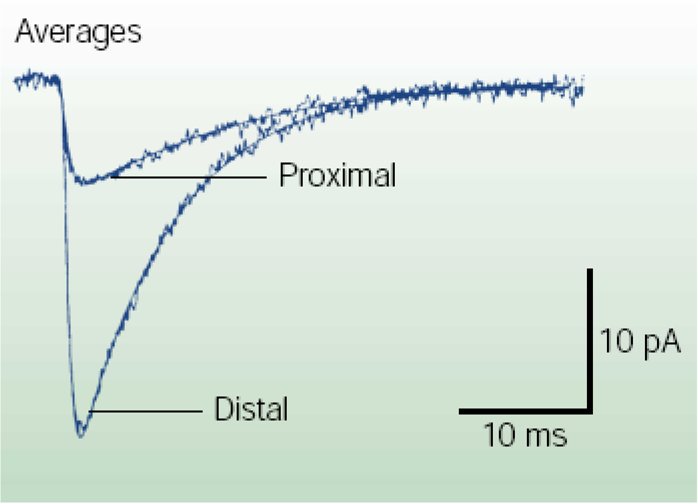
Increases in density down the dendrite
Effectively outward current due to deactivation during EPSP hyperpolarizes, shortens EPSP duration, reduces local summation

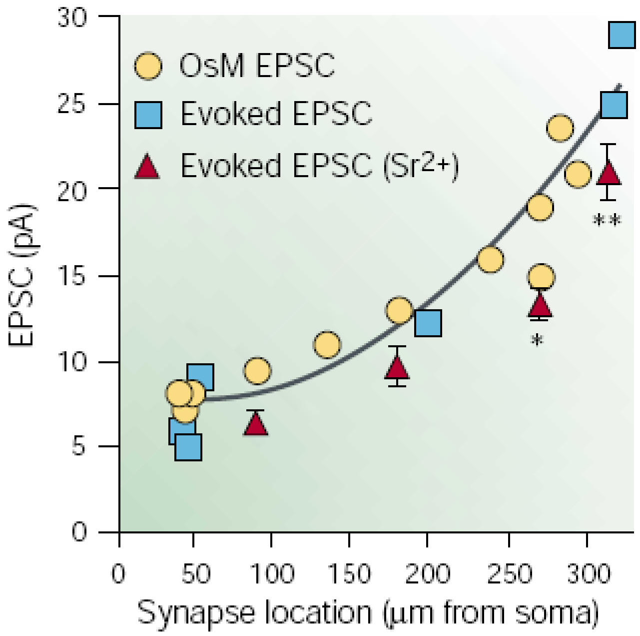
Synaptic properties

While active properties contribute to summation, don't explain normalized amplitude

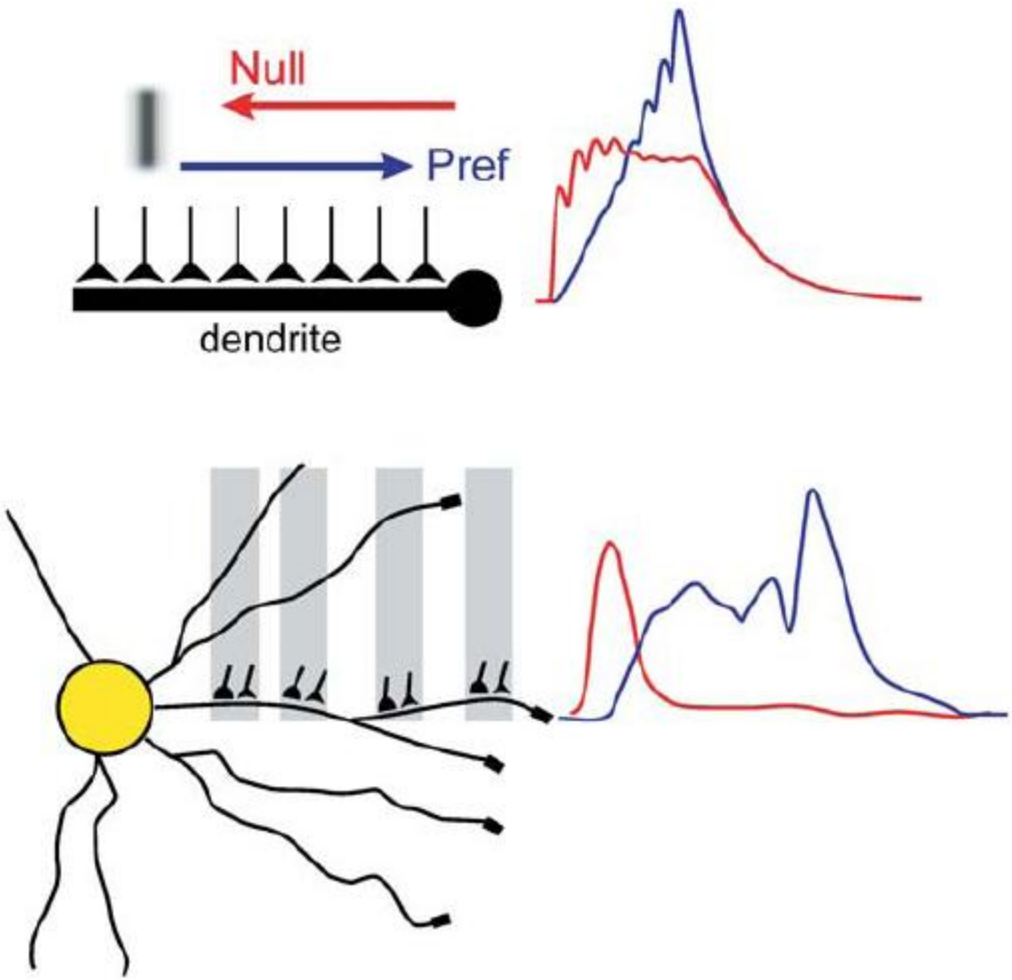
Shape of EPSC determines how it is filtered .. Adjust ratio of AMPA/NMDA receptors

Eliminate role of I_h





Direction selectivity



Rall; fig London and Hausser

References:

Johnson and Wu, *Foundations of Cellular Physiology*, Chap 4

Koch, *Biophysics of Computation*

Magee, *Dendritic integration of excitatory synaptic input*, Nature Reviews Neuroscience, 2000

London and Hausser, Dendritic Computation, Annual Reviews in Neuroscience, 2005