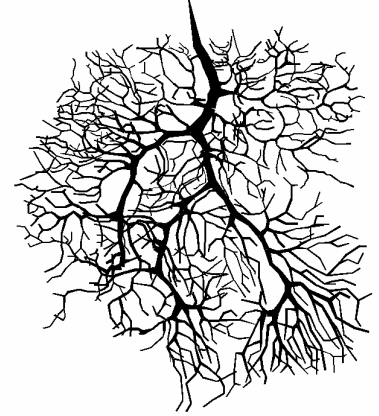


School of Mathematical Sciences

G14TNS Theoretical Neuroscience

Resonant Dendrites

Dendrites form the major components of neurons. They are complex branching structures that receive and process thousands of synaptic inputs from other neurons. It is well known that dendritic morphology plays an important role in the function of dendrites. Another important contribution to the response characteristics of a single neuron comes from the intrinsic resonant properties of dendritic membrane.



Visit NeuroMorpho.Org to see a repository of digitally reconstructed neurons. On the left is an example of a digitally reconstructed Purkinje cell.

Quasi-active membrane

Here we describe the theory of quasi-active membrane and show how it may be interpreted in the language of 'LRC' circuits, i.e. circuits with a resistor, capacitor and inductance in parallel. To start with consider a generic ionic membrane current of the form

$$I = I(V, w_1, \dots, w_N),$$

where V is a voltage and the w_k are gating variables that satisfy

$$\tau_k(V) \dot{w}_k = w_{k,\infty}(V) - w_k, \quad k = 1, \dots, N. \quad (1)$$

It is traditional to write $\tau_k(V) = (\alpha_k(V) + \beta_k(V))^{-1}$, where $w_{k,\infty}(V) = \alpha_k(V) \tau_k(V)$. Now consider variations around some fixed point

$(V, w_1, \dots, w_N) = (V_{ss}, w_{1,\infty}(V_{ss}), \dots, w_{N,\infty}(V_{ss}))$, so that

$$\delta I = \frac{\delta V}{R} + \sum_{k=1}^N \left. \frac{\partial I}{\partial w_k} \right|_{ss} \delta w_k, \quad (2)$$

where we introduce the resistance R defined by $R^{-1} = \partial I / \partial V|_{ss}$, and the subscript ss denotes that quantities are evaluated at steady state. Using (1) we can write the evolution of the perturbations in the gating variable as

$$\left(\frac{d}{dt} + \alpha_k + \beta_k \right) \delta w_k = \left[\frac{d\alpha_k}{dV} - w_{k,\infty} \frac{d(\alpha_k + \beta_k)}{dV} \right] \delta V.$$

We may now write (2) in the form

$$\delta I = \frac{\delta V}{R} + \sum_{k=1}^N \delta I_k,$$

where

$$\left(r_k + L_k \frac{d}{dt} \right) \delta I_k = \delta V.$$

Here

$$r_k^{-1} = \tau_k \frac{\partial I}{\partial w_k} \left[\frac{d\alpha_k}{dV} - w_{k,\infty} \frac{d(\alpha_k + \beta_k)}{dV} \right] \Bigg|_{ss},$$

$$L_k = \tau_k r_k.$$

Hence, for a small perturbation around the steady state, the current I responds as though the resistance R is in parallel with N impedance lines. Each of these is a resistance r_k that is itself in series with an inductance L_k . Such inductive terms account for the oscillatory overshoot commonly seen in response to depolarising current steps or even after the firing of an action potential. This form of equivalent linear membrane circuit is called quasi-active to distinguish it from a truly active (i.e. nonlinear) membrane.

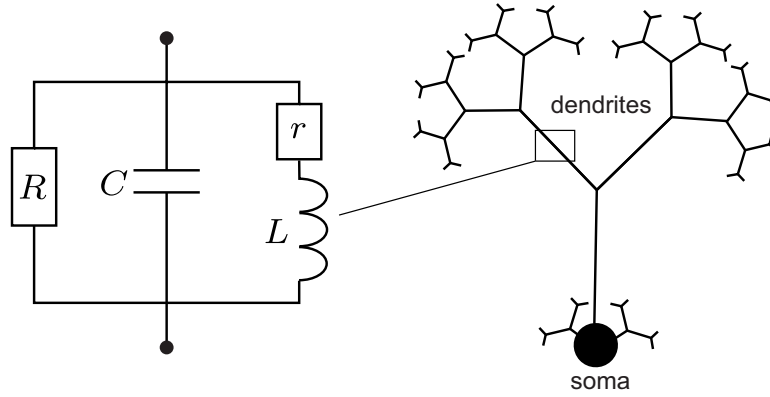


Figure 1: A caricature of a branched dendritic tree with resonant membrane. Each segment of the tree has its own resonant dynamics described by an 'LRC' circuit. The soma is regarded as a special node of the graph describing the dendritic tree.

Now consider a general current balance equation in the form

$$C \frac{dV}{dt} = -g_L(V - V_L) - I + I_{inj}.$$

The linearised equations will be

$$C \frac{dV}{dt} = -\frac{V}{\tilde{R}} - \sum_{k=1}^N I_k + I_{inj}, \quad \frac{1}{\tilde{R}} = g_L + \frac{1}{R},$$

$$L_k \frac{dI_k}{dt} = -r_k I_k + V.$$

The steady state voltage satisfies

$I(V_{ss}, w_{1,\infty}(V_{ss}), \dots, w_{N,\infty}(V_{ss})) + g_L(V_{ss} - V_L) = I_{inj}$. Introducing the Laplace transform (with spectral parameter ω)

$$f(\omega) = \int_0^{\infty} dt e^{-\omega t} f(t),$$

we find that $V(\omega) = K(\omega) I_{inj}(\omega)$, where

$$K(\omega) = \frac{\sum_{k=1}^N r_k + \omega L_k}{(C\omega + \tilde{R}^{-1})(\sum_{k=1}^N r_k + \omega L_k) + 1}.$$

We identify $K(\omega)$ as the impedance of the linearised system, and note that it is a ratio of two polynomials, with the denominator of order $N + 1$, and the numerator of order N (where N is the number of gating variables). For example, the linearisation of the Hodgkin-Huxley model generates a bandpass filter with optimal response around 67 Hz. The range of validity of the reductive process is limited to a few millivolts around the resting potential.

Infinite resonant cable

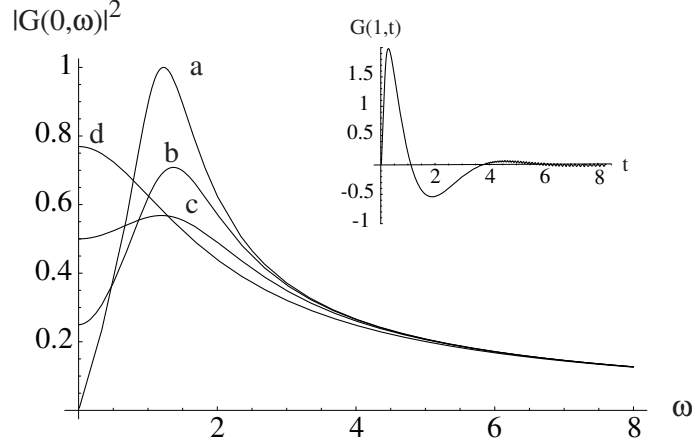


Figure 2: Modulus of transfer function $|G_\infty(0, \omega)|^2$ as a function of frequency ω for various values of inductive resistance r . A transition from band-pass to low-pass filtering can be seen as r increases. (a) $r = 0$ (b) $r = 0.1$ (c) $r = 0.3$ (d) $r = 1.0\Omega\text{m}^2$. Inset: Plot of Green's function $G_\infty(X, t)$ at $x = 1$ as a function of time t (in units of τ) for $r = 0.1\Omega\text{m}^2$.

Writing $V = V(X, t)$, $X \in \mathbb{R}$, $t \geq 0$, (with $V(X, 0) = 0 = I_k(X, 0)$) as the dendritic voltage the resonant cable equation is

$$\frac{\partial V}{\partial t} = -\frac{V}{\tau} + D \frac{\partial^2 V}{\partial X^2} - \frac{1}{C} \left[\sum_k I_k - I_{inj} \right],$$

$$L_k \frac{dI_k}{dt} = -r_k I_k + V.$$

Here D is the cable diffusion coefficient and τ the (passive) cell membrane time constant. After Laplace transforming we obtain the ODE

$$-V_{xx} + \gamma^2(\omega)V = \frac{I_{inj}}{CD},$$

$$\gamma^2(\omega) = \frac{1}{D} \left[\frac{1}{\tau} + \omega + \frac{1}{C} \sum_k \frac{1}{r_k + \omega L_k} \right],$$

where $V = V(X, \omega)$ and $I_{inj} = I_{inj}(X, \omega)$. Introducing a re-scaled space $x = \gamma(\omega)X$ gives

$$-V_{xx} + V = A, \quad A(x, \omega) = I_{inj}(x/\gamma(\omega), \omega)/(CD\gamma^2(\omega)) \quad (3)$$

The Green's function of the operator $(1 - d_{xx})$ is simply $H_\infty(x) = e^{-|x|}/2$, and we may write the general solution to (3) in the form

$$V(x, \omega) = \int_0^\infty dy H_\infty(x - y) A(y, \omega). \quad (4)$$

In original co-ordinates we have that

$$V(X, \omega) = \int_0^\infty dY G_\infty(X - Y, \omega) I(Y, \omega),$$

where $I(X, \omega) = I_{inj}(X, \omega)/C$ and

$$G_\infty(X, \omega) = \frac{H_\infty(\gamma(\omega)X)}{D\gamma(\omega)} = \frac{e^{-\gamma(\omega)|X|}}{2D\gamma(\omega)}.$$

Performing the inverse Laplace transform gives

$$V(X, t) = \int_0^t ds \int_0^\infty dY G_\infty(X - Y, t - s) I(Y, s),$$

where $G_\infty(X, t)$, is the inverse Laplace transform of $G_\infty(X, \omega)$. Note that in the limit $r_k \rightarrow \infty$ we recover the purely passive system ($\gamma^2(\omega) = (1/\tau + \omega)/D$) with Green's function

$$G_\infty(X, t) = \frac{e^{-t/\tau}}{\sqrt{4\pi Dt}} e^{-X^2/(4Dt)} \Theta(t).$$

Here $\Theta(t)$ is the Heaviside step function.

Branched structures can be treated using a “sum-over-trips” approach: S Coombes, Y Timofeeva, C-M Svensson, G J Lord, K Josic, S J Cox and C M Colbert 2007 Branching Dendrites with Resonant Membrane: A “sum-over-trips” approach, Biological Cybernetics, Vol 97, 137-149

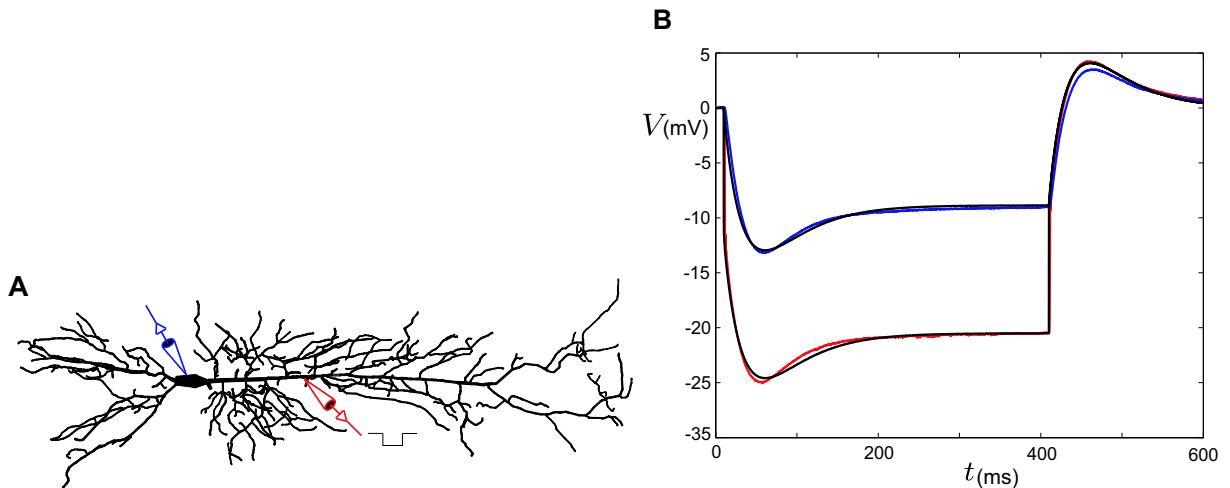


Figure 3: A: Reconstructed rat CA1 hippocampal pyramidal cell. B: An example of dendritic (red) and somatic (blue) dual simultaneous recording in response to the current injection at the dendrite trunk. A pulse current with amplitude -300 pA is applied for a duration of 400 ms starting from 10 ms. The other two curves in B are dendritic and somatic voltage responses calculated from the model of the branched cell with resonant membrane. The model cell was stimulated at the dendrite (as shown in A) with the same current used in experimental recordings.