

Linear Electrical Circuit Theory

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(Modified from *Electrical Current Flow in Excitable Cells* by Jack, Noble and Tsien, Oxford University Press, 1975)

We model the cell membrane as a resistor in series with a capacitor as the diagram below illustrates.

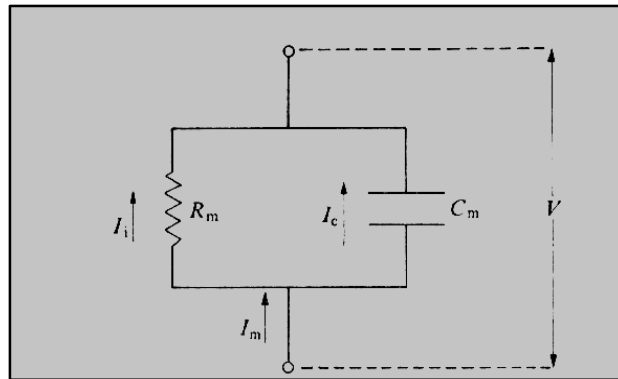


Figure 1 Model of Cell Membrane

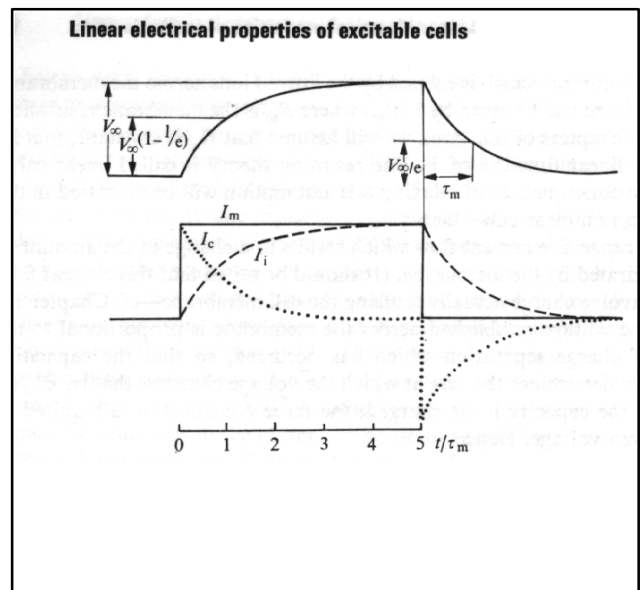
When a voltage is applied as illustrated, a current will flow through this circuit and partition itself into two components,

$$I_m = I_c + I_i \tag{1}$$

I_i is the ionic current across the resistor and I_c is the current which flows through the capacitor. For the ionic current,

$$I_i = V / R_m,$$

where R_m is the membrane resistance. The capacitive current is proportional to the *rate* at which the voltage changes and is proportional to $\partial V / \partial t$. This,



$$I_m = C_m \cdot \dot{V} + V / R_m. \quad (3)$$

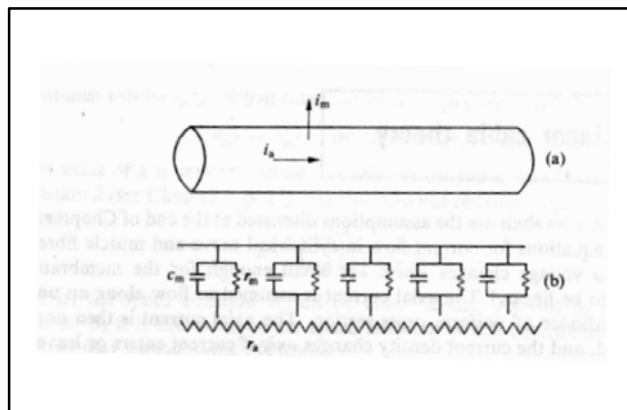
When a sudden step of current is applied across this circuit,

$$V = I_m \cdot R_m \{1 - e^{(-t/\tau_m)}\}, \quad (4)$$

where $\tau_m = R_m C_m$ and τ_m is referred to as the membrane time constant.

Linear Cable Theory

We can think of a length of dendrite or axon to be a stretch of linear cable, visualized as a cylinder made up of cell membrane as the surface of the cylinder and axoplasm (or dendroplasm/cytosol) as the internal medium. If this process is removed and placed in a bath of Ringer or oil, we can think of this cylinder with a small external resistance compared to the resistance of the cell membrane. The figure below illustrates this one-dimensional cable model and its electrical equivalent circuit.



If a current is applied across the cell membrane and if no current leaks through the membrane, then the relationship between the axial current I_a and the intracellular voltage V_i is given by Ohm's law,

$$\Delta V_i / \Delta x = -r_i A i_a, \quad (5)$$

where x is the distance along the cable and r_a is the intracellular resistance per unit length of cable. This equation applies only when the membrane resistance is infinite and no current leaks through the membrane. Of course, in reality, membranes have a finite resistance and this parameter has a lot to say about how membrane current is distributed along any cell process and cannot be ignored. This implies that i_a will not be constant over any finite length. If we then consider an infinitesimal distance ∂x , across which a voltage difference ∂V occurs, then the

differential form of eqn (5) becomes,

$$(\partial V_i / \partial x)_x = -r_i (i_a)_x, \quad (6)$$

where the suffixes are meant to indicate that $\partial V_i / \partial x$ and i_a are measured at the same point. If we assume that the cylinder is immersed in a large volume, then the extracellular resistance can usually be neglected and the transmembrane voltage V is identified with V_i .

When an axial current flows along the interior of the cell, it should be apparent that the rate of change of the axial current (i_a) along the cable must be equal and opposite to the density of the membrane current I_m ,

$$\partial i_a / \partial x = -i_m. \quad (7)$$

We can combine eqns (5) and (6) by differentiating eqn (5) to give

$$\partial^2 V / \partial x^2 = -r_i \cdot \partial i_a / \partial x \quad (8)$$

Substituting eqn (7) in eqn (8),

$$(1/r_i) (\partial^2 V / \partial x^2) = i_m, \quad (9)$$

which provides an expression for the membrane current. We can also rewrite eqn (3), expressed as unit length quantities rather than units of membrane area to obtain

$$(1/r_i) (\partial^2 V / \partial x^2) = c_m \cdot \partial V / \partial t + V / r_m. \quad (10)$$

This is the basic differential equation of linear cable theory. The constants r_m , c_m and r_i are related to C_m , R_m and R_i by the equations

$$r_m = R_m / 2\pi a, \quad (11)$$

$$r_i = R_i / \pi a^2, \quad (12)$$

and

$$c_m = C_m \cdot 2\pi a, \quad (13)$$

where a is the cable radius. Hence eqn (10) can also be rewritten as

$$(a/2R_i) \partial^2 V / \partial x^2 = C_m \cdot \partial V / \partial t + V / R_m. \quad (14)$$

By further rearranging the constants in eqn (10), we obtain

$$\lambda^2 = \partial^2 V / \partial x^2 = \tau_m \cdot \partial V / \partial t + V, \quad (15)$$

where $\lambda = \sqrt{(r_m/r_i)}$ and $\tau_m = r_m \cdot c_m$. τ_m is the membrane *time constant*. λ has the dimensions of distance and is known as the *space constant*; it depends on the ratio of membrane resistance to intracellular resistance and therefore determines how current will spread along the cable. It is worth mentioning that the longitudinal spread of current also depends on the extracellular resistance and, when this cannot be neglected,

$$\lambda = \sqrt{(r_m/r_i + r_o)}, \quad (16)$$

where r_o is the external resistance per unit length. Normally this factor is neglected, but there are examples in the nervous system of high external resistivity providing an important function, such as electrical inhibition in the Mauthner cell.

Equations (14) and (15) apply to linear cables, in which r_m , c_m and r_i are independent of V , x and t . Outside a small range of potential excursions near the resting membrane potential, neurons typically show that r_m is often strongly dependent on V and t . In these situations, eqn (10) becomes,

$$(a/2R_i) \partial^2 V / \partial x^2 = c_m \cdot (\partial V / \partial t) + i_i(V, t) \quad (17)$$

or,

$$(a/2R_i) \partial^2 V / \partial x^2 = C_m \cdot (\partial V / \partial t) + I_i(V, t) \quad (18)$$

where i_i is the membrane ionic current density for a membrane area enclosing a unit length of cable and I_i is the ionic current density of a unit area of membrane. $I_i(V, t)$ is a nonlinear function of voltage and time. Equations (17) and (18) must be used for the applications of cable theory to nonlinear membrane.

It is often useful for solving and expressing the cable equation to use dimensionless variables, where $X = x/\lambda$ and $T = t/\tau$, in which case,

$$\lambda^2 \cdot \partial^2 V / \partial X^2 - V - \partial V / \partial T = 0 \quad (19)$$

For steady-state conditions, we are interested in DC voltages only, in which case V depends on x but not on t ; also $\partial V / \partial T = 0$ and eqn (19) reduces to

$$\lambda^2 \cdot \partial^2 V / \partial X^2 - V = 0$$

The solution to this equation, taking into consideration numerous boundary conditions for different physical and anatomical constraints can be used to derive many useful expressions about the electrical properties of neurons. The general solution of eqn (19) can be expressed in many alternate, but equivalent forms, one of which is

$$V = B_1 \cosh(x/\lambda) + B_2 \sinh(x/\lambda) \quad (20)$$

and

$$V = C_1 \cosh (L - X) + C_2 \sinh (L - X) \quad (21)$$

and L is another dimensionless variable $= l/\lambda$ where l is the real length of the process under consideration. These latter equations will be used to derive important relationships for understanding the input resistance of a neuron, as well as the distribution of current in complex branching tree structures.