Neuronal Response to Stochastic Stimulation

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Abstract—A complete binary dendritic tree is considered in which each branch (cylinder) receives random input. The depolarization on each cylinder satisfies a stochastic cable equation. The Laplace transform of the solution can be found by solving a linear system of $2[2^{n+1}-1]$ equations when there are n orders of branching. The Laplace transform method is shown to yield the exact solution for a single cylinder with white noise current injection. A tree with n branches emanating from a common origin (soma) is then considered. With each branch electrotonic length the same, the depolarization at the soma may be found exactly and expressions may be obtained for its mean and variance.

I. Introduction

THEORIES of the deterministic spread of voltage and current in branched cablelike structures are reviewed in Jack, Noble, and Tsien [4] and Rall [7]. Models of the stochastic activity of neurons, however, have primarily collapsed the whole neuron to a single point and represented its depolarization as a single random process in time. Reviews of such models can be found in Holden [2], Yang and Chen [14], and Lee [5], further recent studies being those of Ricciardi and Sacerdote [8], Tuckwell and Cope [9], and Wan and Tuckwell [13].

In addition, some attempts have been made to take into account the spatial extent of the nerve cell. Here single nerve cylinders with inputs of white noise type have been studied ([10], [11], [12]) and the depolarization found as infinite series of Ornstein–Uhlenbeck processes.

The single cylinder studies are not without some usefulness in studying the stochastic stimulation of dendritic trees, mainly due to Rall's [6] equivalent cylinder concept. However, there are several conditions which must be satisfied for the equivalent cylinder concept to be applied. These are as follows:

1) the terminals are all the same electrotonic distance from the origin;
2) the boundary conditions at all the terminals are the same;
3) at branch points, if the diameter of the parent cylinder is d_0 and the diameters of the daughter cylinders are d_1 and d_2, then $d_0^{3/2} = d_1^{3/2} + d_2^{3/2}$;
4) the input "current densities" at all points on the dendritic tree that are the same electrotonic distance from the origin are the same.

Some nerve cells (e.g., mammalian spinal motoneurons) have been found to approximately satisfy the branch constraint 3), and condition 2) is expected to nearly always apply. However, condition 1) is highly restrictive and condition 4) will rarely, if ever, be satisfied in reality. There have been deterministic studies of neuronal stimulation when the equivalent cylinder constraints are relaxed (Butz and Cowan [1]; Horwitz [3]) and it is of interest to see what progress can be made for the corresponding problem with random inputs. It will be seen that the resulting boundary value problems are extremely difficult but when there are n branches emanating from a common soma, the depolarization can sometimes be found exactly in terms of known processes.

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II. The Boundary Value Problem with Stochastic Stimulation

Fig. 1 shows the notation to be employed. Here a *complete binary tree* with $n = 2$ orders of branching is shown. The left terminal is called the *origin*, 0, usually the location of the soma. The *primary cylinder* is called cylinder (1,1) and terminates at the *node* N_{11}. In general, at node N_{jk} the parent cylinder is (j,k) and the two daughter cylinders are $(j+1, 2k-1)$ and $(j+1, 2k)$, where $j = 1, 2, \cdots, 2^{n+1}$ and the corresponding values of k are $1, 2, \cdots, 2^{j-1}$. The right terminals are thus $N_{n+1,1}, \cdots, N_{n+1,2^n}$.

On cylinder (j,k) we let the depolarization be $V_{jk}(x_{jk}, t)$ at time t where $0 \leqslant x_{jk} \leqslant L_{jk}$, with L_{jk} the corresponding length in units of the characteristic length λ_{jk}. Time is in units of the membrane time constant. With this choice of variables we have, on cylinder (j,k),

$$\frac{\partial V_{jk}}{\partial t} = -V_{jk} + \frac{\partial^2 V_{jk}}{\partial x_{jk}^2} + I_{jk}/c_{jk}, 0 < x_{jk} < L_{jk}, t > 0 \tag{1}$$

where $I_{jk}(x_{jk}, t)$ is the applied current density and c_{jk} is the membrane capacity of a characteristic length. To avoid carrying c_{jk} along in the calculations we set $\bar{I}_{jk} = I_{jk}/c_{jk}$ and then drop the bar for convenience. Since we are concerned with random stimulation, I_{jk} and V_{jk} are random processes in space time, but we suppress the sample space variable.

We assume that at the origin is a general unmixed homogeneous boundary condition,

$$\alpha_{11} V_{11}(0,t) + \beta_{11} V_{11}'(0,t) = 0 \tag{2}$$

and similar boundary conditions apply at the terminals,

$$\alpha_{n+1,k} V_{n+1,k}(L_{n+1,k}, t) + \beta_{n+1,k} V_{n+1,k}'(L_{n+1,k}, t) = 0, \tag{3}$$

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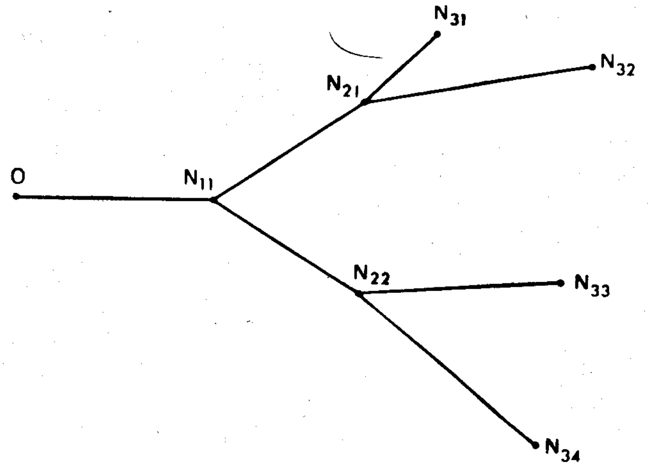

Fig. 1. Illustrating the notation employed in the case of a binary dendritic tree with two orders of branching.

where $k = 1, 2, \cdots, 2^{n+1}$. Thus if $\alpha_{jk} = 0$ and $\beta_{jk} = 1$, the condition is that for a sealed end, whereas if $\alpha_{jk} = 1$ and $\beta_{jk} = 0$, the condition is that of a killed end.

In addition there are boundary conditions at the branch points due to continuity of electric potential and conservation of axial current. At the node N_{jk} the first constraint yields

$$V_{jk}(L_{jk}, t) = V_{j+1,2k-1}(0, t), \tag{4}$$

$$V_{jk}(L_{jk}, t) = V_{j+1,2k}(0, t) \tag{5}$$

where $j = 1, 2, \cdots, n$; $k = 1, 2, \cdots, 2^{j-1}$. The second condition yields

$$\frac{1}{r_{jk}} \frac{\partial V_{jk}}{\partial x_{jk}}\bigg|_{x_{jk}=L_{jk}} = \frac{1}{r_{j+1,2k-1}} \frac{\partial V_{j+1,2k-1}}{\partial x_{j+1,2k-1}}\bigg|_{x_{j+1,2k-1}=L_{j+1,2k-1}} + \frac{1}{r_{j+1,2k}} \frac{\partial V_{j+1,2k}}{\partial x_{j+1,2k}}\bigg|_{x_{j+1,2k}=L_{j+1,2k}} \tag{6}$$

where r_{jk} is the internal resistance of a characteristic length of cylinder (j, k).

The first step is to Laplace transform the equations and boundary conditions. Define the transforms

$$V_{jk}^*(x_{jk}, s) = \int_0^\infty e^{-st} V_{jk}(x_{jk}, t)\, dt, \tag{7}$$

$$I_{jk}^*(x_{jk}, s) = \int_0^\infty e^{-st} I_{jk}(x_{jk}, t)\, dt. \tag{8}$$

If the V_{jk}'s satisfy the initial conditions

$$V_{jk}(x_{jk}, 0) = 0, \qquad 0 \leqslant x_{jk} \leqslant L_{jk} \tag{9}$$

then the transforms of $\partial V_{jk}/\partial t$ are sV_{jk}^*, so V_{jk}^* satisfies the ordinary differential equation

$$-\frac{d^2 V_{jk}^*}{dx_{jk}^2} + (s+1) V_{jk}^* = I_{jk}^*, \qquad 0 < x_{jk} < L_{jk}. \tag{10}$$

The boundary conditions (2), (3), (4), (5), and (6) remain the same in form with the partial derivatives replaced by ordinary derivatives and the V_{jk}'s replaced by the V_{jk}^*'s.

The solutions of (10) can be written as

$$V_{jk}^*(x_{jk}, s) = c_{jk} \cosh\sqrt{(1+s)}\, x_{jk} + d_{jk} \sinh\sqrt{(1+s)}\, x_{jk} + P_{jk}(x_{jk}, s) \tag{11}$$

where the c_{jk}'s and d_{jk}'s are constants and the P_{jk}'s are particular solutions that can be expressed as

$$P_{jk}(x_{jk}, s) = \frac{1}{2\sqrt{1+s)}} \left[e^{-\sqrt{1+s}\, x_{jk}} \int^{x_{jk}} e^{\sqrt{1+s}\, y} I_{jk}^*(y, s)\, dy - e^{\sqrt{1+s}\, x_{jk}} \int^{x_{jk}} e^{-\sqrt{1+s}\, y} I_{jk}^*(y, s)\, dy \right]. \tag{12}$$

We introduce the further notations

$$p_{jk} = P_{jk}(0, s) \tag{13}$$

$$\bar{p}_{jk} = P_{jk}(L_{jk}, s) \tag{14}$$

and

$$Q_{jk}(x_{jk}, s) = \frac{dP_{jk}(x_{jk}, s)}{dx_{jk}} \tag{15}$$

so that

$$\frac{dV_{jk}^*}{dx_{jk}} = \sqrt{(1+s)}\left[c_{jk} \sinh\sqrt{(1+s)}\, x_{jk} + d_{jk} \cosh\sqrt{(1+s)}\, x_{jk}\right] + Q_{jk}(x_{jk}, s). \tag{16}$$

We also define

$$q_{jk} = Q_{jk}(0, s)$$

$$\bar{q}_{jk} = Q_{jk}(L_{jk}, s). \tag{17}$$

The boundary conditions may now be applied. At the origin we get, from the transform of (2),

$$\alpha_{11} c_{11} + \beta_{11} d_{11} = -(\alpha_{11} p_{11} + \beta_{11} q_{11}) \tag{18}$$

and from the transforms of the terminal boundary conditions (3)

$$\alpha_{n+1,k}^* c_{n+1,k} + \beta_{n+1,k}^* d_{n+1,k} = -(\alpha_{n+1,k} \bar{p}_{n+1,k} + \beta_{n+1,k} \bar{q}_{n+1,k}) \tag{19}$$

where $k = 1, 2, \cdots, 2^n$ and where

$$\alpha_{n+1,k}^* = \alpha_{n+1,k} \cosh L_{n+1,k} + \beta_{n+1,k} \sinh L_{n+1,k},$$

$$\beta_{n+1,k}^* = \alpha_{n+1,k} \sinh L_{n+1,k} + \beta_{n+1,k} \cosh L_{n+1,k}. \tag{20}$$

The boundary conditions at the branch points yield, first from continuity of potential,

$$C_{jk} c_{jk} + S_{jk} d_{jk} - c_{j+1,2k-1} = p_{j+1,2k-1} - \bar{p}_{jk}$$

$$C_{jk} c_{jk} + S_{jk} d_{jk} - c_{j+1,2k} = p_{j+1,2k} - \bar{p}_{jk} \tag{21}$$

where we have used the abbreviations

$$C_{jk} = \cosh\sqrt{(1+s)}\, L_{jk}$$

$$S_{jk} = \sinh\sqrt{(1+s)}\, L_{jk}. \tag{22}$$

Second, the conservation of current conditions yields

$$S'_{jk}c_{jk} + C'_{jk}d_{jk} - \gamma_{j+1,2k-1}d_{j+1,2k-1} - \gamma_{j+1,2k}d_{j+1,2k} = \frac{q_{j+1,2k-1}}{r_{j+1,2k-1}} + \frac{q_{j+1,2k}}{r_{j+1,2k}} - \frac{\bar{q}_{jk}}{r_{jk}} \quad (23)$$

where

$$C'_{jk} = \frac{\sqrt{(1+s)}\cosh\sqrt{(1+s)}\,L_{jk}}{r_{jk}}$$

$$S'_{jk} = \frac{\sqrt{(1+s)}\sinh\sqrt{(1+s)}\,L_{jk}}{r_{jk}}$$

$$\gamma_{jk} = \sqrt{(1+s)}/r_{jk}. \quad (24)$$

The equations (18), (19), (21), and (23) constitute a linear system of $N = 2[2^{n+1} - 1]$ independent equations for the N constants, c_{jk} and d_{jk}. As such it may be solved by elimination or iterative methods in some cases to yield the Laplace transform of the depolarization over the entire dendritic tree. The system has the same form whether the inputs are deterministic or random and in most cases of interest is extremely complicated. Hence the great utility, despite its limited practical application, of the equivalent cylinder concept that reduces the number of unknown constants to two.

III. Laplace Transform Method of Solution for a Single Nerve Cylinder with White Noise Inputs

In a previous paper (Wan and Tuckwell [12]) we considered a nerve cylinder with white noise current injection at a single point. In that case the depolarization $V(x,t)$ was assumed to satisfy

$$\frac{\partial V}{\partial t} = -V + \frac{\partial^2 V}{\partial x^2} + \delta(x-y)\left[a + b\frac{dW}{dt}\right], \quad 0 < x < L, \quad t > 0 \quad (25)$$

where $0 < y < L$ and a and b are constants and W is a standard Wiener process. The initial condition was $V(x,0) = 0$, $0 < x < L$, and homogeneous unmixed boundary conditions in V and its derivative were imposed at $x = 0$ and $x = L$. Here we will find the solution of (25) by first taking Laplace transforms. Before proceeding we need a preliminary result.

Laplace Transform of an Ornstein–Uhlenbeck Process

An Ornstein–Uhlenbeck process $X(t;\alpha,\beta,\sigma,W)$ may be defined by its stochastic differential equation

$$dX = (\alpha X + \beta)\,dt + \sigma\,dW, \qquad X(0) = 0 \quad (26)$$

where α, β, and σ are constants with α negative. We define the Laplace transforms as

$$\bar{X}(s) = \int_0^\infty e^{-st}X(t)\,dt \quad (27)$$

$$\bar{W}(s) = \int_0^\infty e^{-st}W(t)\,dt. \quad (28)$$

Then, taking transforms in (26) gives, on rearranging,

$$\bar{X}(s) = \frac{\frac{\beta}{s} + \sigma s\bar{W}(s)}{s-\alpha}. \quad (29)$$

Without a rigorous proof, we may assert that the inverse transform of the right side of (29) is in fact an Ornstein–Uhlenbeck process $X(t;\alpha,\beta,\sigma,W)$. Thus if L^{-1} denotes the inverse Laplace transform, then

$$L^{-1}\left[\frac{\frac{\beta}{s} + \sigma s\bar{W}(s)}{s-\alpha}\right] = X(t;\alpha,\beta,\sigma,W). \quad (30)$$

Solution Using Laplace Transform

Let the normalized spatial eigenfunctions be $\phi_n(x)$, $n = 0,1,2,\cdots$. That is, the ϕ_n's satisfy

$$-\frac{d^2\phi_n}{dx^2} + \mu_n^2\phi_n = 0, \qquad 0 < x < L \quad (31)$$

where μ_n^2 are the eigenvalues for the given boundary conditions, and

$$\int_0^L \phi_n^2(x)\,dx = 1. \quad (32)$$

Then we may write

$$\delta(x-y) = \sum_n \phi_n(x)\phi_n(y) \quad (33)$$

which may be substituted in (25). On taking transforms and letting $V^*(x,s)$ be the transform of $V(x,t)$ we get

$$-\frac{d^2V^*}{dx^2} + (s+1)V^* = \sum_n \phi_n(x)\phi_n(y)\left[\frac{a}{s} + bs\bar{W}(s)\right]. \quad (34)$$

The general solution of this equation is

$$V^*(x,s) = c\cosh\sqrt{(s+1)}\,x + d\sinh\sqrt{(s+1)}\,x + \left[\frac{a}{s} + bs\bar{W}(s)\right]\sum_n \frac{\phi_n(x)\phi_n(y)}{\mu_n^2 + s + 1} \quad (35)$$

and its spatial derivative is

$$\frac{dV^*(x,s)}{dx} = \sqrt{(s+1)}\left[c\sinh\sqrt{(s+1)}\,x + d\cosh\sqrt{(s+1)}\,x\right] + \left[\frac{a}{s} + bs\bar{W}(s)\right]\sum_n \frac{\phi'_n(x)\phi_n(y)}{\mu_n^2 + s + 1}. \quad (36)$$

If there are unmixed linear homogeneous boundary conditions in V and its space derivative at $x = 0$ and $x = L$, then it follows, since the ϕ_n's already satisfy these conditions that $c = d = 0$. Hence the Laplace transform of the solution is

$$V^*(x,s) = \left[\frac{a}{s} + bs\bar{W}(s)\right]\sum_n \frac{\phi_n(x)\phi_n(y)}{\mu_n^2 + s + 1}. \quad (37)$$

From the result (30) we see that

$$L^{-1}\left\{\frac{\left[\frac{a}{s}+bs\overline{W}(s)\right]}{\mu_n^2+s+1}\right\}=X_n\left(t;-\left(1+\mu_n^2\right),a,b,W\right), \tag{38}$$

so that the inverse transform of each term is an Ornstein–Uhlenbeck process. Thus the solution is

$$V(x,t)=\sum_n \phi_n(x)\phi_n(y)X_n(t) \tag{39}$$

where the x_n's satisfy

$$dX_n=\left[-\left(1+\mu_n^2\right)X_n+a\right]dt+b\,dW, \qquad X_n(0)=0. \tag{40}$$

For example, if there are zero derivative conditions at $x=0$ and $x=L$, we have

$$\phi_n(x)=\begin{cases}1/\sqrt{L}, & n=0,\\ \sqrt{2/L}\cos(n\pi x/L), & n=1,2,\cdots\end{cases} \tag{41}$$

$$\mu_n^2=n^2\pi^2/L^2, \qquad n=0,1,2,\cdots. \tag{42}$$

The solution we have obtained by Laplace transform is the same as that obtained using the Green's function and indicates that the transform method is useful for random inputs.

IV. Solution for a Dendritic Tree with a Single Branch Point—Exact Solution at the Origin (SOMA).

In this section an expression will be obtained for the depolarization over a dendritic tree as sketched in Fig. 2. Here only three cylinders are considered (the case of $n>3$ being considered later), C_1, C_2, and C_3, all of the same electrotonic length L, originating from the soma. On cylinder C_i the space coordinate is x_i, the depolarization is $V_i(x_i,t)$ and there is white noise current $a_i+b_i dW_i/dt$ at a distance y_i from $x_i=0$. Thus

$$\mathscr{D}_i V_i(x_i,t) \doteq \left\{\frac{\partial}{\partial t}+1-\frac{\partial^2}{\partial x_i^2}\right\}V_i(x_i,t)$$
$$=\delta(x_i-y_i)\left[a_i+b_i\,dW_i/dt\right] \tag{43}$$

$0<x_i<L$, $t>0$, which defines the differential operators $\mathscr{D}_i$. There may be multiple current sources on each cylinder but for now to avoid an extra index and summation we assume there is only one on each cylinder.

To be specific we impose the initial conditions

$$V_i(x_i,t)=0, \qquad 0<x_i<L \tag{44}$$

and suppose that all the ends at $x_i=0$ are sealed so that

$$\left.\frac{\partial V_i}{\partial x_i}\right|_{x_i=0}=0. \tag{45}$$

The boundary conditions at the branch point are

$$V_1(L,t)=V_2(L,t)=V_3(L,t) \tag{46}$$

and

$$-\frac{1}{r_i}\left.\frac{\partial V_1}{\partial x_1}\right|_{x_1=L}=\frac{1}{r_2}\left.\frac{\partial V_2}{\partial x_2}\right|_{x_2=L}+\frac{1}{r_3}\left.\frac{\partial V_3}{\partial x_3}\right|_{x_3=L}. \tag{47}$$

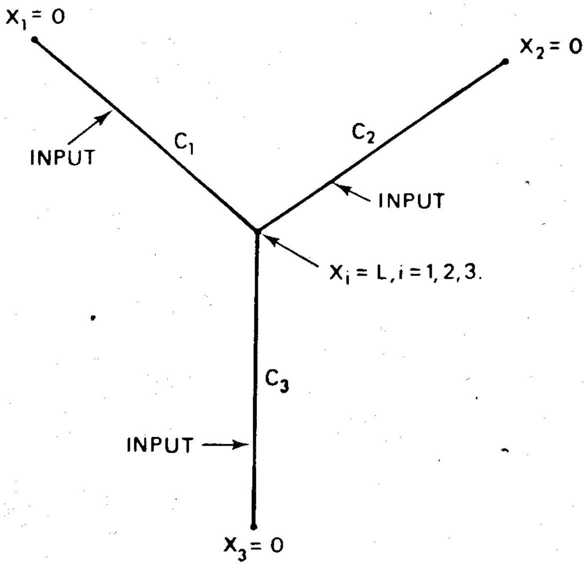

Fig. 2. Schematic representation of a neuron with inputs on each of its dendritic cylinders.

Note that minus sign appears on the left because the longitudinal current is in the direction of increasing distance on C_1 but in the direction of decreasing distance on C_2 and C_3.

We now write each $V_i(x,t)$ as the sum of a part which is known and a part which is to be determined. We put

$$V_i(x_i,t)=U_i(x_i,t)+Y_i(x_i,t), \qquad 0<x_i<L, \qquad t>0, \qquad i=1,2,3, \tag{48}$$

where $U_i(x_i,t)$ is the solution of the cable equation with white noise input at y_i and with *both* ends sealed. Thus U_i satisfies

$$\mathscr{D}_i U_i(x_i,t)=\delta(x_i-y_i)\left[a_i+b_i\,dW_i/dt\right], \qquad 0<x_i<L, \qquad t>0 \tag{49}$$

with initial condition

$$U_i(x_i,0)=0, \qquad 0<x_i<L, \tag{50}$$

and with boundary conditions

$$\left.\frac{\partial U_i}{\partial x_i}\right|_{x_i=0}=\left.\frac{\partial U_i}{\partial x_i}\right|_{x_i=L}=0. \tag{51}$$

Thus U_i is known from the results of Section III.

We now consider the unknown parts of the solution $Y_i(x,t)$. These satisfy the homogeneous equations

$$\mathscr{D}_i Y_i(x_i,t)=0, \tag{52}$$

with initial conditions

$$Y_i(x_i,0)=0, \qquad 0<x_i<L, \tag{53}$$

and sealed end boundary conditions at $x_i=0$.

$$\left.\frac{\partial Y_i}{\partial x_i}\right|_{x_i=0}=0, \qquad i=1,2,3. \tag{54}$$

From the boundary conditions at the branch point we get

$$-\frac{1}{r_1}\left.\frac{\partial Y_1}{\partial x_1}\right|_{x_1=L}=\frac{1}{r_2}\left.\frac{\partial Y_2}{\partial x_2}\right|_{x_2=L}+\frac{1}{r_3}\left.\frac{\partial Y_3}{\partial x_3}\right|_{x_3=L} \tag{55}$$

and

$$U_1(L,t) + Y_1(L,t) = U_2(L,t) + Y_2(L,t) = U_3(L,t) + Y_3(L,t). \quad (56)$$

We now introduce the Laplace transforms $Y_i^*(x_i, s), i = 1, 2, 3$. These are given by

$$Y_i^*(x_i, s) = c_i \cosh\sqrt{1+s}\,x_i + d_i \sinh\sqrt{1+s}\,x_i \quad (57)$$

so that

$$\frac{dY_i^*}{dx_i} = \sqrt{1+s}\left[c_i \sinh\sqrt{1+s}\,x_i + d_i \cosh\sqrt{1+s}\,x_i\right] \quad (58)$$

where the c_i's and d_i's are constants.

We have immediately from (54), $d_i = 0, i = 1, 2, 3$. Hence

$$Y_i^*(x_i, s) = c_i \cosh\sqrt{1+s}\,x_i, \qquad i = 1, 2, 3. \quad (59)$$

Applying the remaining boundary condition (55) at $x_i = L$ we get

$$\frac{c_1}{r_1} + \frac{c_2}{r_2} + \frac{c_3}{r_3} = 0, \quad (60)$$

which is one relation between the c_i's. Denoting the (known) Laplace transforms of the U_i's by U_i^*, we also have from (56)

$$c_1 - c_2 = \frac{U_2^*(L,s) - U_1^*(L,s)}{\cosh\sqrt{1+s}\,L}, \quad (61)$$

$$c_1 - c_3 = \frac{U_3^*(L,s) - U_1^*(L,s)}{\cosh\sqrt{1+s}\,L}. \quad (62)$$

Solving (60), (61), and (62) for c_1 we obtain

$$c_1 = \frac{\dfrac{U_2^*(L,s) - U_1^*(L,s)}{r_2} + \dfrac{U_3^*(L,s) - U_1^*(L,s)}{r_3}}{[1/r_1 + 1/r_2 + 1/r_3]\cosh\sqrt{(1+s)}\,L} \quad (63)$$

and c_2 and c_3 can be found from (61) and (62).

The exact solution can be found at the origin, $x_i = L$. We have

$$V_1^*(L,s) = U_1^*(L,s) + c_1\cosh\sqrt{1+s}\,L = U_1^*(L,s) + \frac{\dfrac{U_2^*(L,s) - U_1^*(L,s)}{r_2} + \dfrac{U_3^*(L,s) - U_1^*(L,s)}{r_3}}{[1/r_1 + 1/r_2 + 1/r_3]}. \quad (64)$$

Inverting the transforms gives the depolarization at $x_1 = L$

$$V_1(L,t) = \frac{\dfrac{U_1(L,t)}{r_1} + \dfrac{U_2(L,t)}{r_2} + \dfrac{U_3(L,t)}{r_3}}{[1/r_1 + 1/r_2 + 1/r_3]}. \quad (65)$$

We may generalize this result to a tree with n branches emanating from the soma with internal resistances per unit length $r_1, \cdots, r_n$, and in the case where there are m_j inputs on cylinder c_j. The depolarization satisfies

$$\frac{\partial V_j}{\partial t} = -V_j + \frac{\partial^2 V_j}{\partial x_j^2} + \sum_{i=1}^{m_j} \delta(x_j - y_{ij})\left[a_{ij} + b_{ij}\, dW_{ij/dt}\right], \quad 0 < x_j < L \quad (66)$$

with sealed end boundary conditions at the terminals. The depolarization at the soma is then

$$V(t) = \frac{\sum_{j=1}^{n}\left(\sum_{i=1}^{m_j}\dfrac{U_{ji}(t)}{r_j}\right)}{\sum_{j=1}^{n}\dfrac{1}{r_j}} \quad (67)$$

where

$$U_{ji}(t) = X_{0,ji}/L + (2/L) \cdot \sum_{n=1}^{\infty}(-1)^n \cos(n\pi y_{ij}/L) X_{n,ji}(t) \quad (68)$$

and

$$dX_{n,ji} = \left[-(1 + n^2\pi^2/L^2)X_{n,ji} + a_{ij}\right]dt + b_{ij}\,dW_{ij}. \quad (69)$$

The expectation of the somatic depolarization is, using the results from Wan and Tuckwell [12] for a single cylinder,

$$E[V(t)] = \frac{\sum_{j=1}^{n}\sum_{i=1}^{m_j}\dfrac{\left[a_{ij}\sum_{m=0}^{\infty}\dfrac{\left(1 - e^{-\lambda_m^2 t}\right)}{\lambda_m^2}(-1)^m\cos(m\pi y_{ij}/L)\right]}{r_j}}{\sum_{j=1}^{n}\dfrac{1}{r_j}} \quad (70)$$

where $\lambda_m^2 = 1 + m^2\pi^2/L^2, m = 0, 1, 2, \cdots$. Its variance is

$$\operatorname{Var}[V(t)] = \frac{\sum_{j=1}^{n} r_j^{-1}\sum_{i=1}^{m_j}\left[b_{ij}^2\sum_{l=0}^{\infty}\sum_{m=0}^{\infty}\left\{\dfrac{1 - \exp\{-(\lambda_l^2 + \lambda_m^2)t\}}{\lambda_l^2 + \lambda_m^2}\right\}(-1)^{l+m}\cos(l\pi y_{ij}/L)\cos(m\pi y_{ij}/L)\right]}{\left(\sum_{i=1}^{n}\dfrac{1}{r_j}\right)^2}. \quad (71)$$

Furthermore as $t \to \infty$, the expectation approaches

$$E[V(\infty)] = \frac{\frac{1}{\sinh L} \sum_{j=1}^{n} \sum_{i=1}^{m_j} \frac{a_{ij} \cosh(y_{ij})}{r_j}}{\sum_{j=1}^{n} \frac{1}{r_j}}. \quad (72)$$

V. Conclusion

We began by treating a general binary dendritic tree with random inputs. A linear system of equations was obtained whose solution yields the Laplace transform of the depolarization at all points on the tree. In principle the depolarization may be found by inverting the transform. In Section III we treated a single nerve cylinder with white noise current injection and found the solution using Laplace transforms. In Section IV we considered n cylinders emanating from the soma with white noise inputs on each cylinder. In the case where the cylinders have the same electrotonic length, but with no other symmetry requirements, we were able to find an exact expression for the depolarization at the soma in terms of series of Ornstein–Uhlenbeck processes. Expressions were also obtained for the mean and variance of the somatic depolarization.

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