Biol. Cybern. 68, 15–21 (1992)

Biological Cybernetics

A simple vector implementation of the Laplace-transformed cable equations in passive dendritic trees

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Received February 6, 1992/Accepted June 2, 1992

Abstract. Transient potentials in dendritic trees can be calculated by approximating the dendrite by a set of connected cylinders. The profiles for the currents and potentials in the whole system can then be obtained by imposing the proper boundary conditions and calculating these profiles along each individual cylinder. An elegant implementation of this method has been described by Holmes (1986), and is based on the Laplace transform of the cable equation. By calculating the currents and potentials only at the ends of the cylinders, the whole system of connected cylinders can be described by a set of n equations, where n denotes the number of internal and external nodes (points of connection and endpoints of the cylinders). The present study shows that the set of equations can be formulated by a simple vector equation which is essentially a generalization of Ohm's law for the whole system. The current and potential n-vectors are coupled by a $n \times n$ conductance matrix whose structure immediately reflects the connectivity pattern of the connected cylinders. The vector equation accounts for conductances, associated with driving potentials, which may be local or distributed over the membrane. It is shown that the vector equation can easily be adapted for the calculation of transients over a period in which stepwise changes in system parameters have occurred. In this adaptation it is assumed that the initial conditions for the potential profiles at the start of a new period after a stepwise change can be approximated by steady-state solutions. The vector representation of the Laplace-transformed equations is attractive because of its simplicity and because the structure of the conductance matrix directly corresponds to the connectivity pattern of the dendritic tree. Therefore it will facilitate the automatic generation of the equations once the geometry of the branching structure is known.

1 Introduction

To calculate the transient current and potential profiles in branching dendrites one has to reduce the irregular natural structure of such trees into a mathematically manageable form. Two different approaches are generally used (Holmes 1986). In the 'compartmental approach' the structure is approximated by a series of coupled compartments and the potential is assumed to be constant within a compartment. In the 'continuous-cable approach' the system is approximated by a set of connected cylinders in which the potential profile is governed by the cable equation. In the former approach one obtains a 'piecewise constant' approximation of the potential profile over the whole structure while in the latter approach the potential can be calculated for any point in the branching structure. A new implementation of the continuous-cable approach has recently been developed by Holmes (1986) on the basis of the Laplace transform of the cable equation. The main advantages of this approach are its accuracy, its ease of implementation and its moderate computational load, while the potential can conveniently be monitored at any desired, but finite, spatial and temporal resolution. According to this method, the potential profile along the cylinder can be related to the currents and potentials at both ends of the cylinder. When cylinders are connected to each other only additional boundary conditions are imposed. This means that a branching system, being a system of connected cylinders, is fully described by the currents and potentials at the ends (nodes) of all the cylinders. Holmes (1986) showed that transients in a branching system with n nodes can be calculated by means of a set of n equations and he described how to construct the equation at each node. In the following it will be shown that, by reformulating the equations and using a vector representation of the potentials and currents at all the nodes, one simple-structured Laplace-transformed vector equation is obtained for the whole branching system. This vector equation unifies the conditions at all the nodes and essentially reflects Ohm's law for the current-voltage relations in the whole system. The current and potential n-vectors are coupled by a conductance matrix whose structure results from a one-to-one mapping of the connectivity pattern of the cylinders. In Sect. 2, the solutions of the cable equation are given and the current-voltage relations are formulated in four specific examples. A generalization of the structure of the current-voltage relation is given in Sect. 3 and several computational aspects are discussed in Sect. 4.

2 Cable equations

The general form of the cable equation for a cylinder with passive conductive membrane is given by

$$\lambda^2 \frac{\partial^2 v}{\partial x^2} - v - \tau \frac{\partial v}{\partial t} = 0 \tag{1}$$

(e.g. Rall (1959, 1977), Jack et al. (1975)) with $v(x, t)$ the transmembrane potential, $\lambda = \sqrt{dR_m/4R_i}$ the space constant, $\tau = R_m C_m$ the membrane time constant and d the diameter of the cylinder. The material constants R_m, C_m and R_i denote the specific membrane resistance and capacitance and the specific axial resistance, respectively. If a fraction f_a of the membrane conductance G_m (with $G_m = 1/R_m$) is associated with a driving potential v_a we obtain the augmented cable equation (e.g. Rall 1977)

$$\lambda^2 \frac{\partial^2 v}{\partial x^2} - v - \tau \frac{\partial v}{\partial t} + f_a v_a = 0\,. \tag{2}$$

Note, that by including driven conductances as a fraction of the total conductance, the space and time constants implicitly take these driven conductances into account. The Laplace transform of this equation is given by

$$\frac{\partial^2 V}{\partial x^2} = \gamma^2 V - \frac{f_a v_a}{\lambda^2 s} \tag{3}$$

with $\gamma = \sqrt{1 + \tau s}/\lambda$ and $V(x, s)$ being the Laplace transform of the function $v(x, t)$. The general solution of this equation is given by

$$V(x, s) = A(s) \cosh \gamma x + B(s) \sinh \gamma x + C(s) \tag{4}$$

with $C(s) = f_a v_a/[s(1 + \tau s)]$ and the coefficients $A(s)$ and $B(s)$, being functions of the Laplace variable s, determined by the boundary conditions. For a single cylinder the potential profile can be expressed in terms of the potentials at both ends, $V_1 = V(x_1, s)$ and $V_2 = V(x_2, s)$ as

$$V(x, s) - C(s) = \frac{[V_1 - C(s)] \sinh \gamma(x_2 - x) + [V_2 - C(s)] \sinh \gamma(x - x_1)}{\sinh \gamma l} \tag{5}$$

with $l = x_2 - x_1$ being the length of the cylinder. Note, that in this and following equations both nodes of the cylinder will be treated symmetrically. The current profile in the cylinder can be calculated via $i(x, t) = -(1/r)(\partial v(x, t)/\partial x)$ and in Laplace domain $J(x, s) = -(1/r)(\partial V(x, s)/\partial x)$ with r the axial (core) resistance per unit length ($r = 4R_i/\pi d^2$). Using (5) we obtain for the current $J(x, s)$

$$J(x, s) = \frac{\gamma}{r}\left[[V_1 - C(s)] \frac{\cosh \gamma(x_2 - x)}{\sinh \gamma l} - [V_2 - C(s)] \frac{\cosh \gamma(x - x_1)}{\sinh \gamma l}\right]. \tag{6}$$

For the current at both ends of the cylinder we obtain

$$\begin{aligned} J_1 = J(x_1, s) &= \frac{\gamma}{r}\left[\frac{V_1 - C(s)}{\tanh \gamma l} - \frac{V_2 - C(s)}{\sinh \gamma l}\right] \\ J_2 = J(x_2, s) &= \frac{\gamma}{r}\left[\frac{V_1 - C(s)}{\sinh \gamma l} - \frac{V_2 - C(s)}{\tanh \gamma l}\right]. \end{aligned} \tag{7}$$

Let us define σ_{12} and τ_{12} as functions of the cylinder geometry, material constants and Laplace variable s as

$$\sigma_{12} = \frac{\gamma}{r} \frac{1}{\sinh \gamma l} \quad \text{and} \quad \tau_{12} = \frac{\gamma}{r} \frac{1}{\tanh \gamma l} \tag{8}$$

and let the function μ_{12} also include driven conductances

$$\mu_{12} = C(s)(\tau_{12} - \sigma_{12})\,. \tag{9}$$

Let us additionally define the current $I(x, s)$ such that $|I(x, s)| = |J(x, s)|$ and $I(x, s) > 0$, if flowing out of the cylinder and $I(x, s) < 0$ if flowing into the cylinder. Then we have $I_1 = J_1$ and $I_2 = -J_2$ if $x_2 > x_1$. Now we obtain simple expressions for the currents I_1 and I_2 in terms of V_1 and V_2

$$\begin{aligned} I_1 &= \tau_{12} V_1 - \sigma_{12} V_2 - \mu_{12} \\ I_2 &= \tau_{12} V_2 - \sigma_{12} V_1 - \mu_{12} \end{aligned} \tag{10}$$

or as

$$\begin{pmatrix} I_1 \\ I_2 \end{pmatrix} + \begin{pmatrix} \mu_{12} \\ \mu_{12} \end{pmatrix} = \begin{pmatrix} \tau_{12} & -\sigma_{12} \\ -\sigma_{12} & \tau_{12} \end{pmatrix} \begin{pmatrix} V_1 \\ V_2 \end{pmatrix} \tag{11}$$

or as

$$\mathbf{I} + \mathbf{S} = \mathrm{G}\mathbf{V}\,. \tag{12}$$

The vectors **I** and **V** contain the currents and the potentials at the two ends of the cylinder. The vector **S** contains the current contributions at the ends from the driven conductances along the cylinder. The matrix G relates the currents to the potentials at the ends. Note, that both the vector **S** and the matrix G depend on the geometry and material constants of the cylinder. For the inverse equation we get

$$\mathbf{V} = \mathrm{G}^{-1}[\mathbf{I} + \mathbf{S}]\,. \tag{13}$$

If it is assumed that the membrane has no driven conductances ($f_a = 0$), we have $\mathbf{S} = 0$ and (12) reduces to

$$\mathbf{I} = \mathrm{G}\mathbf{V}\,. \tag{14}$$

In the branching-cable model of a dendritic tree each segment is approximated by one or more connected cylinders. In such a branching system we distinguish the root point, terminal tips, branch points and points along a dendritic segment. We shall refer to these points as nodes, and distinguish external nodes (terminal tips) and internal nodes (points where two or more cylinders are connected). The nodes at both ends of a cylinder are directly connected and are called a node pair. For each node pair the potentials and currents are related via (12) while at internal nodes the connection of cylinders introduce additional boundary conditions. To describe the current-voltage relation at all the nodes in such a branching system the current and potential vectors get as many entries as there are nodes. The conductance matrix, relating these vectors, gets a structure which is directly determined by the connectivity pattern of the cylinders. This will be shown for some simple but characteristic geometries in the following examples.

2.1 Example 1 – Internal node with two connected cylinders

A cylinder with current input somewhere along the cylinder can be regarded as two cylinders in line with a node at the site of the current input (Fig. 1a). For the two cylinders 12 and 23 the currents and potentials at their ends are related according to (12) as

$$\begin{aligned} I_1 &= \tau_{12} V_1 - \sigma_{12} V_2 - \mu_{12} \\ I_3 &= \tau_{23} V_3 - \sigma_{23} V_2 - \mu_{23} \\ I_2^{(1)} &= \tau_{12} V_2 - \sigma_{12} V_1 - \mu_{12} \\ I_2^{(3)} &= \tau_{23} V_2 - \sigma_{23} V_3 - \mu_{23} \end{aligned} \tag{15}$$

Here, $I_2^{(1)}$ and $I_2^{(3)}$ denote the currents injected at node 2 and flowing into cylinder 21 and 23, respectively. Conservation of current implies

$$\begin{aligned} I_2 &= I_2^{(1)} + I_2^{(3)} \\ &= (\tau_{12} + \tau_{23}) V_2 - \sigma_{12} V_1 - \sigma_{23} V_3 - (\mu_{12} + \mu_{23}) \end{aligned}$$

and the set of equations can be written in matrix form as

$$\begin{pmatrix} I_1 \\ I_2 \\ I_3 \end{pmatrix} + \begin{pmatrix} \mu_{12} \\ \mu_{12} + \mu_{23} \\ \mu_{23} \end{pmatrix} = \begin{pmatrix} \tau_{12} & -\sigma_{12} & 0 \\ -\sigma_{12} & \tau_{12} + \tau_{23} & -\sigma_{23} \\ 0 & -\sigma_{23} & \tau_{23} \end{pmatrix} \begin{pmatrix} V_1 \\ V_2 \\ V_3 \end{pmatrix}. \tag{16}$$

2.2 Example 2 – Internal node with three connected cylinders

A simple branching structure can be considered as three cylinders connected at a single point (Fig. 1b). For the three cylinders we can write down the six equations describing the current-voltage relationships at their ends as

$$\begin{aligned} I_1 &= \tau_{12} V_1 - \sigma_{12} V_2 - \mu_{12} \\ I_3 &= \tau_{23} V_3 - \sigma_{23} V_2 - \mu_{23} \\ I_4 &= \tau_{24} V_4 - \sigma_{24} V_2 - \mu_{24} \\ I_2^{(1)} &= \tau_{12} V_2 - \sigma_{12} V_1 - \mu_{12} \\ I_2^{(3)} &= \tau_{23} V_2 - \sigma_{23} V_3 - \mu_{23} \\ I_2^{(4)} &= \tau_{24} V_2 - \sigma_{24} V_4 - \mu_{24} \end{aligned} \tag{17}$$

Again, $I_2^{(1)}$, $I_2^{(3)}$ and $I_2^{(4)}$ denote the currents injected at node 2 and flowing into cylinder 21, 23 and 24, respectively. Current conservation at the branch point implies that

$$\begin{aligned} I_2 &= I_2^{(1)} + I_2^{(3)} + I_2^{(4)} \\ &= (\tau_{12} + \tau_{23} + \tau_{24}) V_2 - \sigma_{12} V_1 - \sigma_{23} V_3 - \sigma_{24} V_4 \\ &\quad - (\mu_{12} + \mu_{23} + \mu_{24}) \end{aligned} \tag{18}$$

and the set of equations can be written in matrix form as

$$\begin{pmatrix} I_1 \\ I_2 \\ I_3 \\ I_4 \end{pmatrix} + \begin{pmatrix} \mu_{12} \\ \mu_{12} + \mu_{23} + \mu_{24} \\ \mu_{23} \\ \mu_{24} \end{pmatrix} = \begin{pmatrix} \tau_{12} & -\sigma_{12} & 0 & 0 \\ -\sigma_{12} & \tau_{12} + \tau_{23} + \tau_{24} & -\sigma_{23} & -\sigma_{24} \\ 0 & -\sigma_{23} & \tau_{23} & 0 \\ 0 & -\sigma_{24} & 0 & \tau_{24} \end{pmatrix} \begin{pmatrix} V_1 \\ V_2 \\ V_3 \\ V_4 \end{pmatrix}. \tag{19}$$

2.3 Example 3 – External node with a local conductance

For a single cylinder with a structure at one end providing an additional conductance G_0 to the outside (e.g. a somatic conductance) (Fig. 1c) we obtain

$$\begin{aligned} I_1 &= I_1^{(2)} + I_0 \\ I_1^{(2)} &= \tau_{12} V_1 - \sigma_{12} V_2 - \mu_{12} \\ I_0 &= G_0 V_1 \\ I_2 &= \tau_{12} V_2 - \sigma_{12} V_1 - \mu_{12} \end{aligned} \tag{20}$$

The matrix equation becomes

$$\begin{pmatrix} I_1 \\ I_2 \end{pmatrix} + \begin{pmatrix} \mu_{12} \\ \mu_{12} \end{pmatrix} = \begin{pmatrix} \tau_{12} + G_0 & -\sigma_{12} \\ -\sigma_{12} & \tau_{12} \end{pmatrix} \begin{pmatrix} V_1 \\ V_2 \end{pmatrix} \tag{21}$$

If the conductance at a node i to the outside consists of an ohmic and a capacitive component we can write $G_{io} = G_i + sC_i$. Note, that the equation $i(x, t) = Gv(x, t) + C[\partial v(x, t)]/\partial t$ in the time domain has the Laplace transform $I = GV + sCV = (G + sC)V$.

2.4 Example 4 – Internal node with a local conductance and a driving potential

Synaptic activity may not be homogeneously distributed along a cylinder but localized at a particular site. This can be modeled by dividing the cylinder into two parts and creating a node in between with a local conductance g_a and a driving potential v_a. The current entering the cylinder at that node is then given by $i(t) = g_a(v_a - v)$ in time domain and in Laplace domain $I = g_a(v_a/s - V)$. If in the single cylinder in Example 1 (Fig. 1a) without driven conductances, node 2 has a synaptic drive we obtain

$$I_2 = g_a\left(\frac{v_a}{s} - V_2\right) = (\tau_{12} + \tau_{23}) V_2 - \sigma_{12} V_1 - \sigma_{23} V_3$$

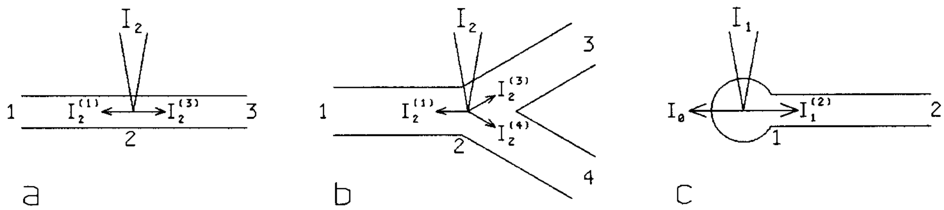

Fig. 1a–c Some simple but characteristic geometries with **a** a current injected at a point along a cylinder, **b** a current injected at a branch point and **c** a current injected at the end of a cylinder with a local conductance to the outside

or

$$g_a \frac{v_a}{s} = (\tau_{12} + \tau_{23} + g_a)V_2 - \sigma_{12} V_1 - \sigma_{23} V_3 \tag{22}$$

and the set of equations can be written in matrix form as

$$\begin{pmatrix} I_1 \\ g_a v_a / s \\ I_3 \end{pmatrix} = \begin{pmatrix} \tau_{12} & -\sigma_{12} & 0 \\ -\sigma_{12} & \tau_{12} + \tau_{23} + g_a & -\sigma_{23} \\ 0 & -\sigma_{23} & \tau_{23} \end{pmatrix} \begin{pmatrix} V_1 \\ V_2 \\ V_3 \end{pmatrix}. \tag{23}$$

The conductance g_a at node 2 is added to the diagonal term of this node in the conductance matrix (G) like in Example 3. Because of the driving potential associated with this conductance a current $g_a v_a / s$ appears in the current vector.

3 General structure of the Laplace-transformed current-voltage equation

Generalizing the findings in the previous examples the current-voltage (c-v) equation $\mathbf{I} + \mathbf{S} = \mathrm{G}\mathbf{V}$ can be constructed for any system of connected cylinders in any arrangement. Actually, this relation reflects Ohm's law for the whole system. An external node i has only one directly-connected node k and we obtain $I_i + \mu_{ik} = \tau_{ik} V_i - \sigma_{ik} V_k$. An internal node i has two or more directly connected nodes and for the current-voltage relation we obtain $I_i + \Sigma_j \mu_{ij} = V_i \Sigma_j \tau_{ij} - \Sigma_j V_j \sigma_{ij}$ with j denoting all directly connected nodes to i.

The general structure of the conductance matrix G for a system of connected cylinders can now be defined by the following two rules for the calculation of the matrix elements G_{ij}:

- node i has a diagonal term $G_{ii} = \Sigma_j \tau_{ij} + G_{io}$ with j running over all nodes directly connected to node i and G_{io} indicating the additional conductance to the outside at node i.
- node i has an off-diagonal term $G_{ij} = -\sigma_{ij}$ for any node $j (j \neq i)$ directly connected to node i. All other off-diagonal matrix elements in row i (i.e. from all nodes not directly connected to node i) are zero.

The diagonal terms in G (i.e. the τ's) relate the current at a node with the local potential. The off-diagonal terms (i.e. the σ's) relate the current at a node with the potential at a directly connected node. Because the σ's depend only on the cylinder, this relation is symmetric such that also matrix G is a symmetric one.

The general structure of the vector **S** is defined by a third rule:

- node i has an entry $S_i = \Sigma_j \mu_{ij}$ with j running over all nodes directly connected to node i.

Remember that σ_{ij}, τ_{ij}, μ_{ij} and therefore the conductance matrix G are functions of the geometry and material constants of the cylinder connecting node i and j, while μ_{ij} additionally contains a conductance associated with a driving potential. All may be different for any cylinder in the network.

3.1 Sparsity of G

The two nodes in a node pair are directly connected by a link (cylinder). The number of nonzero off-diagonal matrix elements is twice the number of node pairs and thus equal to $2k$, with k denoting the number of links. For a tree-like structure (i.e., without closed loops) the number of links k and the number of nodes n are related as $k = n - 1$. The nonzero matrix elements G comprise $2k = 2n - 2$ off-diagonal terms and n diagonal terms, in total $3n - 2$ terms. The fraction of zero matrix elements in G is then given by $[n^2 - 3n + 2]/n^2 = (1 - 2/n)(1 - 1/n)$. For large n this fraction approaches one, indicating that G becomes increasingly sparser for larger n.

4 Solving the equations

4.1 Boundary conditions

The variables in the c-v equation $\mathbf{I} + \mathbf{S} = \mathrm{G}\mathbf{V}$ are the currents I_i and the potentials V_i at all the nodes $i = 1, \ldots, n$ in the system. Thus for a system with n nodes we have $2n$ variables while the vector equation incorporates n equations. This system can be solved only if n out of the $2n$ variables are known (conditioned). Examples of boundary conditions are

- a 'sealed' node i, at which no current can flow to the outside and $I_i = 0$,
- an 'injured' or open node i, at which the potential is equal to that on the outside, that can be zero with $V_i = 0$,
- a voltage or current stimulus, given at a node,
- a driving potential, associated with a conductance to the outside at a node.

For instance, using the branching system of Example 2 (Fig. 1b) without driven conductances, the response to a stimulus with a current I_4 at node 4, with sealed conditions at the other three nodes is obtained by solving the equation

$$\begin{pmatrix} 0 \\ 0 \\ 0 \\ I_4 \end{pmatrix} = \mathsf{G} \begin{pmatrix} V_1 \\ V_2 \\ V_3 \\ V_4 \end{pmatrix} \tag{24}$$

with G equal to the conductance matrix in (19).

4.2 Stimulus-response equation

In the previous examples the currents were conditioned while the potentials at all the nodes were the unknown variables. The *c-v* equation can also be used if the potentials are conditioned and the current responses have to be calculated. However, if both current and voltage conditions are imposed the *c-v* equation should be transformed into a stimulus-response equation $\mathbf{S} = \mathsf{M}\mathbf{R}$ with the conditions (voltage and current) put in the vector **S** and the unknown response in the vector **R**. Such a transformation implies the exchange of current and voltage variables and the transformation of the matrix G into the matrix M. A procedure for such an exchange of variables is described in Bartsch (1985). The exchange of variables means that the matrix loses its symmetry, that the sparsity changes and that the matrix is no longer pure conductive.

4.3 Inverse Laplace transform

Since the solution for the response vector **R** is obtained in Laplace domain one has to apply the inverse Laplace transform to obtain the response in time domain. An efficient (Holmes 1986) procedure has been given by Stehfest (1970a, b) in which the outcome for any point in time is approximated by a linear combination of the outcomes for a limited number of solutions in Laplace domain, i.e., for a limited number of values for the variable s. The coefficients in the linear combination are functions of both t and s, and are explicitly given by Stehfest (1970a, b).

4.4 Sequence of calculations

The sequence of calculations to obtain the transient response to a stimulus pattern in time is schematically given in Figure 2. The number of time steps can be chosen and depend on the desired time span and time resolution of the response. The number of s-values depends on the precision of the arithmetic used, which turned out to be optimal in our case for $N = 14$ for double precision.

4.5 Sparse matrices

To reduce computational load one may profit from the sparsity of the matrix by (*i*) keeping only nonzero matrix elements in storage and (*ii*) solving the equation by means of an algorithm optimized for sparse systems like the one of Sherman (1977), as suggested by Holmes (1986).

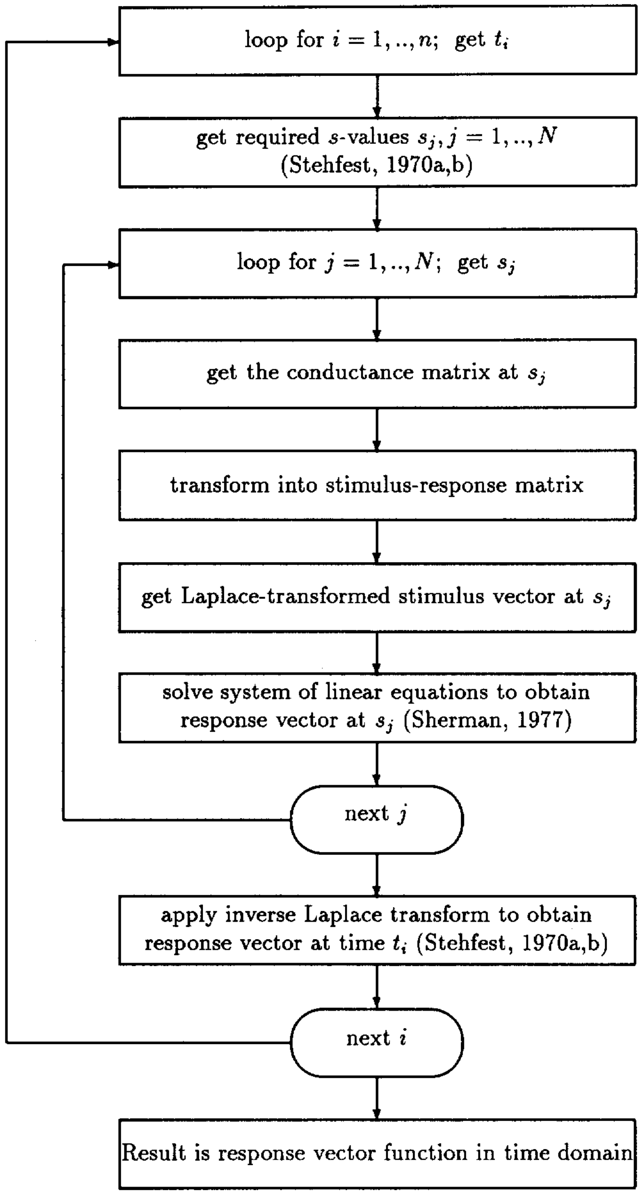

Fig. 2. Sequence of calculations to obtain the transient response in time domain at all nodes in the branching system on a time-dependent stimulus

4.6 Steady state

If a constant stimulus pattern is applied, the calculation of the (constant) response can be obtained by solving the *c-v* equation only once. A constant current $\mathring{i}$ and voltage vector $\mathring{v}$ in time domain have simple Laplace transforms $\mathring{I} = \mathring{i}/s$ and $\mathring{V} = \mathring{v}/s$, therefore we need to solve the equation $\mathring{i} = \mathring{G}\mathring{v}$ in case of a system without driven conductances. The circle above the symbols indicates the steady-state value of the variable. The steady-state matrix $\mathring{G}$ is obtained by evaluating the matrix G for $s = 0$. Then, the variable $\gamma = \sqrt{1 + \tau s/\lambda}$ reduces to $\gamma = 1/\lambda$ and the variables σ_{12} and τ_{12} reduce to $\mathring{\sigma}_{12} = (\lambda r \sinh(l/\lambda))^{-1}$ and $\mathring{\tau}_{12} = (\lambda r \tanh(l/\lambda))^{-1}$. The *c-v* equation for a single cylinder in time domain, that has to be solved once, now becomes

$$\begin{pmatrix} \mathring{i}_1 \\ \mathring{i}_2 \end{pmatrix} = \begin{pmatrix} \mathring{\tau}_{12} & -\mathring{\sigma}_{12} \\ -\mathring{\sigma}_{12} & \mathring{\tau}_{12} \end{pmatrix} \begin{pmatrix} \mathring{v}_1 \\ \mathring{v}_2 \end{pmatrix} \tag{25}$$

while the potential profile in the cylinder (5) reduces to the steady-state profile given by

$$\mathring{v}(x) = \frac{1}{\sinh(l/\lambda)} \left(\mathring{v}_1 \sinh \frac{x_2 - x}{\lambda} + \mathring{v}_2 \sinh \frac{x - x_1}{\lambda} \right). \tag{26}$$

4.7 Changing system parameters

The Laplace-transformed cable equation (3) has been derived under the condition that the parameters of the cylinder (geometry and material constants) are constant. Holmes (1986) had indicated that changes in the membrane conductance cannot be accounted for unless these changes occur in a stepwise pattern and the system remains constant between these steps. After such a step, however, the currents and potentials are generally nonzero and these start values for the subsequent period with constant system parameters have to be incorporated in the Laplace transform of the cable equation.

For nonzero initial conditions for the potential we obtain the following Laplace-transformed cable equation

$$\frac{\partial^2 V}{\partial x^2} = \gamma^2 V - \frac{f_a v_a}{\lambda^2 s} - \frac{\tau}{\lambda^2} v(x, 0) \tag{27}$$

with $v(x, 0)$ indicating the potential profile at $t = 0$. To solve (27), Holmes (1986) assumed a linear function for $v(x, 0)$, i.e., $v(x, 0) = \mathring{v}_1 - (\mathring{v}_1 - \mathring{v}_2)x/l$. We shall, however, approximate the function $v(x, 0)$ by the steady-state solution for the potential profile in a cylinder, given by (26), assuming that such a profile is a more realistic one. Without driven conductances, the Laplace-transformed cable equation now becomes

$$\frac{\partial^2 V}{\partial x^2} = \gamma^2 V - \frac{\tau}{\lambda^2} \mathring{v}(x) = \gamma^2 V - \frac{\tau}{\lambda^2} \frac{1}{\sinh(l/\lambda)} \times \left(\mathring{v}_1 \sinh \frac{x_2 - x}{\lambda} + \mathring{v}_2 \sinh \frac{x - x_1}{\lambda} \right). \tag{28}$$

The solution of this equation is given by

$$V(x, s) = A(s) \cosh \gamma x + B(s) \sinh \gamma x + \frac{1}{s} \mathring{v}(x) \tag{29}$$

and expressing the coefficients $A(s)$ and $B(s)$ in terms of the potentials V_1 and V_2 at the ends of the cylinder we obtain

$$V(x, s) = \frac{1}{s} \mathring{v}(x) + \frac{1}{\sinh \gamma l} \left[\left(V_1 - \frac{\mathring{v}_1}{s} \right) \sinh \gamma (x_2 - x) + \left(V_2 - \frac{\mathring{v}_2}{s} \right) \sinh \gamma (x - x_1) \right]. \tag{30}$$

Calculating the currents I_1 and I_2 in analogy to the derivation of (6) – (10) we obtain

$$\begin{aligned} I_1 &= \tau_{12}\left(V_1 - \frac{\mathring{v}_1}{s} \right) - \sigma_{12}\left(V_2 - \frac{\mathring{v}_2}{s} \right) + \frac{1}{s} [\mathring{\tau}_{12} \mathring{v}_1 - \mathring{\sigma}_{12} \mathring{v}_2] \\ I_2 &= \tau_{12}\left(V_2 - \frac{\mathring{v}_2}{s} \right) - \sigma_{12}\left(V_1 - \frac{\mathring{v}_1}{s} \right) + \frac{1}{s} [-\mathring{\sigma}_{12} \mathring{v}_1 + \mathring{\tau}_{12} \mathring{v}_2] \end{aligned} \tag{31}$$

or

$$\begin{pmatrix} I_1 \\ I_2 \end{pmatrix} = \begin{pmatrix} \tau_{12} & -\sigma_{12} \\ -\sigma_{12} & \tau_{12} \end{pmatrix} \left[\begin{pmatrix} V_1 \\ V_2 \end{pmatrix} - \frac{1}{s} \begin{pmatrix} \mathring{v}_1 \\ \mathring{v}_2 \end{pmatrix} \right] + \begin{pmatrix} \mathring{\tau}_{12} & -\mathring{\sigma}_{12} \\ -\mathring{\sigma}_{12} & \mathring{\tau}_{12} \end{pmatrix} \frac{1}{s} \begin{pmatrix} \mathring{v}_1 \\ \mathring{v}_2 \end{pmatrix} \tag{32}$$

or

$$\mathbf{I} = \mathsf{G}\left[\mathbf{V} - \frac{\mathring{\mathbf{v}}}{\mathbf{s}} \right] + \mathring{\mathsf{G}} \frac{\mathring{\mathbf{v}}}{\mathbf{s}}. \tag{33}$$

The incorporation of nonzero initial conditions can thus elegantly be accounted for by correcting both the potential and the current vector for their initial values. On the basis of the steady-state assumption the initial potential and current vector are related by the steady-state conductance matrix $\mathring{\mathsf{G}}$. All system parameters are put into the matrix G and a series of stepwise changes in these parameters (e.g. in the conductance and/or the driving potential at a node) implies a series of matrices G_j. After a stepwise change from G_{j-1} to G_j the initial conditions for the subsequent period are nonzero and we have to solve

$$I = \mathsf{G}_j\left[V - \frac{\mathring{v}}{s} \right] + \mathring{\mathsf{G}}_j \frac{\mathring{v}}{s} \tag{34}$$

with the potential vector $\mathring{\mathbf{v}}$ taken at the time of change.

4.8 Stimulus functions

For calculating the transfer properties of dendritic trees one generally uses one of the following stimulus functions which have simple Laplace transforms.

- step-function. The step function is defined as $f(t) = a$ for $t \geqslant 0$ with amplitude a and $f(t) = 0$ for $t < 0$ and is used for steady-state stimuli. Its Laplace transform is equal to $F(s) = a/s$.
- α-function. The α-function $f(t) = \alpha\beta t \exp(1 - \alpha t)$ is generally used to mimic post-synaptic responses. The function is zero at $t = 0$, has a positive slope from $t = 0$ up to $t = 1/\alpha$ where it reaches a peak value of β and falls down asymptotically to zero for larger time values. The area underneath the function is equal to $\beta e/\alpha$. Its Laplace transform is given by $F(s) = (\alpha\beta e)/(s + \alpha)^2$.
- δ-function. The δ-function $f(t) = \delta(t)$ is used for calculating impulse responses and has the simple Laplace transform $F(s) = 1$.

5 Discussion

It is shown that the Laplace-transformed cable equations, formulated by Holmes (1986) for the calculation of transient responses in dendritic trees, can be expressed as a simple (current-voltage) matrix equation for the whole branching system. An important advantage of such a formulation is that the conductance matrix (connecting the current and voltage vectors) is a direct mapping of the tree's connectivity pattern. The diagonal matrix elements express the local relation between current and voltage, while the off-diagonal matrix elements express the current-voltage relation between different, but directly connected nodes. Only two rules are required to define the nonzero matrix elements. The current-voltage equation also accounts for conductances, associated with a driving potential, localized at a particular site or uniformly distributed along a cylinder. If transients have to be calculated for a system with step-wise changing system parameters, the equations must incorporate nonzero initial conditions for each new period. Even then, the equations remain simple in structure, if the potential profile in a cylinder at the start of a new period is approximated by the steady-state profile. The present formulation, clearly revealing its Ohmic basis, provides insight into the current-voltage relationships in a branching system. It also facilitates an automatic generation of the equations, once the geometry of a dendrite is known. This is of particular importance if one wants to study how electrical transfer properties in dendritic trees depend on dendritic morphology.

Acknowledgements. I thank Dr. A. Schierwagen for many stimulating and helpful discussions and M.P. van Veen and A. van Ooyen for critical reading of the manuscript.

References

Bartsch HJ (1985) Taschenbuch Mathematischer Formeln. Harri Deutsch, Thun Frankfurt/Main

Holmes WR (1986) A continuous cable method for determining the transient potential in passive dendritic trees of known geometry. Biol Cybern 55:115–124

Jack JJB, Noble D, Tsien RW (1975) Electric current flow in excitable cells, Oxford University Press, Oxford

Rall W (1959) Branching dendritic trees and motoneuron membrane resistivity. Exp Neurol 1:491–527

Rall W (1977) Core conductor theory and cable properties of neurons, In: Kandel ER (ed) Cellular biology of neurons, American Physiological Society, Bethesda (Handbook of Physiology, Sect. 1/I, 39–97)

Sherman AH (1977) Algorithm 533: NSPIV, a fortran subroutine for sparse gaussian elimination with partial pivoting. ACM Trans Math Software 4:391–398

Stehfest H (1970a) Algorithm 368: numerical inversion of Laplace transforms. Comm ACM 13:47–48

Stehfest H (1970b) Remark on algorithm 368. Comm ACM 13:624