J. theor. Biol. (1989) **141**, 159–179

A Non-uniform Equivalent Cable Model of Membrane Voltage Changes in a Passive Dendritic Tree

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(*Received* 6 *April* 1988, *and accepted in revised form* 29 *March* 1989)

A non-uniform equivalent cable model of membrane voltage changes in a passive dendritic tree extending Rall's equivalent cylinder model is presented. It is obtained from a combination of cable theory with the continuum approach. Replacing the fine structure of the branching dendrites by an equivalent, conductive medium characterized by averaged electrical parameters, the one-dimensional cable equations with spatially varying parameters are derived. While these equations can be solved in general only numerically, we were able to formulate a general branching condition (comprising Rall's 3/2 power relationship as a special case) under which analytical solutions can be deduced from those of the equivalent cylinder model. This model allows dendritic trees with a greater variety of branching patterns than before to be analytically treated.

1. Introduction

Most neurons of the vertebrate central nervous system (CNS) possess widely branched dendritic trees. Despite recent advances in intracellular recording and staining techniques, both *in vivo* and *in vitro* (e.g. Kater & Nicholson, 1973; Sakman & Neher, 1983; Dingledine, 1984; Bottenstein & Sato, 1985), the role of dendritic geometry in neuronal information processing has been difficult to assess. In this situation, mathematical modelling proves to be an essential tool in addressing conceptual questions arising there.

The usual mathematical description of the integrative function of a neuron with passive dendritic trees proceeds from the application of one-dimensional cable theory to approximate the potential distribution in a neuronal process. Representing the cable by an RC ladder network, the cable equations for membrane voltage $V = V(x, t)$ and longitudinal (axial) current $i_a = i_a(x, t)$ in a cylindric segment of length l and diameter d are as follows (x represents distance in the axial direction, $0 \leq x \leq l$, and t is time):

$$\frac{\partial V}{\partial x} = -R \,.\, i_a, \qquad \frac{\partial i_a}{\partial x} = -i_m$$

with

$$i_m = C \,.\, \frac{\partial V}{\partial t} + G \,.\, V$$

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0022-5193/89/220159+21 $03.00/0 © 1989 Academic Press Limited

where $i_m = i_m(x, t)$ denotes membrane current consisting of a capactive component and a resistive one (Fig. 1). $R = 4R_i/(\pi d^2)$ is axial resistance, $C = C_m \cdot \pi \cdot d$ is membrane capacitance, and $G = G_m \cdot \pi \cdot d$ is membrane conductance (all quantities per unit length). Combining these equations we obtain

$$\tau_m \frac{\partial V}{\partial t} - \lambda^2 \frac{\partial^2 V}{\partial x^2} + V = 0 \tag{1}$$

where $\lambda = (GR)^{-1/2}$ is the length constant and $\tau_m = C/G$ denotes the membrane time constant (R_i, C_m and G_m are the specific parameters intracellular (axial) resistivity, membrane capacitance and membrane conductance; see Table 1 for the notation used).

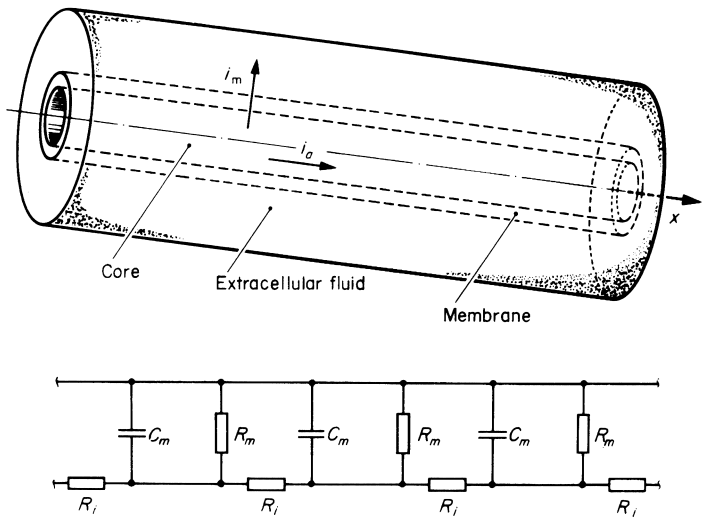

FIG. 1. Scheme of a membrane cylinder (above) and its equivalent electrical circuit (below).

The cable eqn (1) can be solved for many relevant boundary conditions. Its applicability, however, is restricted to the assumed simple geometry of a cylindric process. In the case of branching structures as dendrites, the situation becomes much more complex. One has to include boundary conditions at each branch point and terminal, resulting in very complicated expressions for the corresponding solutions. To cope with the problems, models of different complexity degree have been developed (for review, see, e.g. Schierwagen, 1988).

A frequently applied model in neurophysiology is the Rall model of the nerve cell (Rall, 1962). In short, it can be characterized as follows: if G_m, C_m and R_i are assumed to be uniform all over the neuron, the cell soma is represented by an isopotential sphere, and each dendritic tree is treated as an "equivalent cylinder".

TABLE 1

Notation and definitions used

V	transmembrane voltage relative to resting potential (mV)
d	diameter of dendritic branch (cm)
l	length of dendritic branch (cm)
x	distance along uniform cable (cm)
R_m	specific membrane resistance (kΩ cm^2)
G_m	specific (resting) membrane conductance (mS cm^{-2}). $G_m = 1/R_m$
R_i	specific axial resistivity (kΩ cm)
C_m	specific membrane capacitance (μF cm^{-2})
λ	length constant (cm) . $\lambda = [(R_m/R_i)(d/4)]^{1/2}$
τ_m	time constant (ms) . $\tau_m = R_m C_m$
t	time (ms)
O	origin of spherical co-ordinate system
r	distance co-ordinate (cm)
ϑ	angle co-ordinate. $\vartheta = (\vartheta_1, \vartheta_2)$ with $0 \leq \vartheta_1 < 2\pi$, $0 \leq \vartheta_2 \leq \pi$.
Θ	space angle containing a given dendritic tree
$n_\Theta(\cdot)$	number of dendritic branches as function of distance variable (related to Θ)
$d_i(\cdot)$	diameter of ith branch as function of distance variable (cm)
$\bar{d}_\Theta(\cdot)$	arithmetical mean of branch diameters as function of distance variable (cm). $$\bar{d}_\Theta(\cdot) = \frac{1}{n_\Theta(\cdot)} \sum_{i=1}^{n_\Theta(\cdot)} d_i(\cdot).$$ Same as $\bar{d}(\cdot)$.
$\tilde{d}_\Theta(\cdot)$	square mean of branch diameters as function of distance variable (cm). $$\tilde{d}_\Theta(\cdot) = \left[\frac{1}{n_\Theta(\cdot)} \sum_{i=1}^{n_\Theta(\cdot)} d_i(\cdot)^2\right]^{1/2}.$$ Same as $\tilde{d}(\cdot)$.
$\mathcal{V}$	volume element of space angle Θ
$I(r, t)$	current (related to unit space angle) at distance r and time t (μA)
$V(r, t)$	voltage (related to unit space angle) at distance r and time t (mV)
$P(r)$	summed perimeter of all dendritic branches at distance r (related to unit space angle) (cm)
$A(r)$	total cross sectional area of all dendritic branches at distance r (related to unit space angle) (cm^2)
$G(r)$	leak conductance per unit length (related to unit space angle) (mS cm^{-1}) . $G(r) = G_m . P(r)$
$C(r)$	capacitance per unit length (related to unit space angle) (μF cm^{-1}). $C(r) = C_m . P(r)$
$R(r)$	axial resistance per unit length (related to unit space angle) (kΩ cm^{-1}). $R(r) = R_i/A(r)$
$\lambda(r)$	length parameter of non-uniform cable (cm). $\lambda(r) = [G(r)R(r)]^{-1/2}$
Z	generalized distance variable (dimensionless). $Z(r) = \int_0^r ds/\lambda(s)$
τ	time constant of non-uniform cable (ms). $\tau = C(r)/G(r) = C_m/G_m$
T	dimensionless time variable. $T = t/\tau$
d_j	diameter of branches at generation j (common to all branches) (cm)
l_j	length of branches at generation j (common to all branches) (cm)
n_j	number of branches at generation j (related to Θ)
λ_j	length constant for the jth generation of branches (cm). $\lambda_j = [(R_m/R_i)(d_j/4)]^{1/2}$
γ_1	particular, stationary solution of the special Riccati differential equation $\gamma' + \gamma^2/2 = A$. $\gamma_1 = \pm\sqrt{2A}\,(A > 0)$

Provided some conditions given below are fulfilled, a further simplification can be made: they can be treated collectively as a single equivalent cylinder.

The symmetry requirements for the equivalent cylinder transformation are:

(i) all dendritic terminals are the same electrotonic distance from the soma;

(ii) the boundary conditions at all the terminals are the same;

(iii) at branch points the 3/2 power relation holds, i.e. $d_0^{3/2} = d_1^{3/2} + d_2^{3/2}$ where d_0 and d_1, d_2 are the diameters of the parent and the daughter cylinders, respectively.

The Rall model has significantly advanced our understanding of neuronal behaviour (Jack *et al.*, 1975; Redman, 1976; Rall, 1977). At its prime, this model provided the kind of compromise between available experimental facts and analytical tractability that is the philosophical goal of any modeller.

However, there is increasing evidence that some of the assumptions listed do not hold in many real dendritic trees. For example, though some nerve cells e.g. spinal motoneurons (Rall, 1977) and superior colliculus output neurons (Schierwagen & Grantyn, 1986) have been found to obey assumption (iii), many others do not (Hillman, 1979). The assumption (i) that all electrotonic path lengths in a dendritic tree are equal has also been questioned recently (Schierwagen, 1986; Fleshman *et al.*, 1988). Hence, it is necessary to develop models which allow the relaxation of some or all of the assumptions listed above.

The morphology-based branching cable model (Rall, 1959; Barrett & Crill, 1974; Koch *et al.*, 1982; Turner & Schwartzkroin, 1983; Turner, 1984; Schierwagen, 1986) assumes no constraints on dendritic branching structure, i.e. only condition (ii) is supposed to hold. The neuron is modelled by a number of individual cable segments, the dimensions of which are based on anatomical reconstructions of the cell. In this way, each dendritic tree is represented as a network of smooth, cylindrical cable segments, and either steady state or transient calculations can be performed with especially developed computer programs employing the analytical solutions of the cable eqn (1). A major advantage of this electrical description is that it enables one to calculate signal transfer between any two sites of a neuron. However, the considerable expense of labour in constructing a detailed segmental representation of a neuron is a serious drawback of this modelling approach. This is also true for the compartmental description of a neuron introduced by Rall (1964) and later adopted by others (e.g. Perkel & Mulloney, 1978; Edwards & Mulloney, 1984; Segev *et al.*, 1985; Shelton, 1985; van Hateren, 1986; Carnevale & Lebeda, 1987). In addition, both the branching cable models and the compartmental models suffer from the impossibility of exploring analytically the effects of parameter changes.

On the other hand, Rall mentioned that his theory can be applied to more general dendritic geometries than that of the equivalent cylinder class (Rall, 1962). However, this has been performed only in part. Goldstein & Rall (1974) studied changes of action potential shape and velocity for non-uniform core conductor geometry by numerical means. Strain & Brockman (1975) considered steady state membrane voltage distribution in a cable model approximating typical neuron geometries. Again, numerical methods had been used since analytical solutions were not available.

Very recently, several authors have constructed equivalent cable models with varying diameters that were based on the actual dendritic morphology (Clements & Redman, 1989; Fleshman *et al.*, 1988; Rose & Dagum, 1988). Common to those studies is the employment of exclusively numerical integration methods for determining the solutions to the differential equations.

Thus, a favourable mathematical description of a neuron would be as analytical as possible while at the same time taking its morphology sufficiently into account. The model presented here has been developed to approach these requirements. Starting from the standard assumptions of cable theory, a new model for the distribution of subthreshold membrane potential in branching dendritic trees is derived. The method is a simple variant of the continuum approach which has been used in many areas (Sanchez-Palencia, 1980; Bachmat & Bear, 1986), among them current flow and diffusion in the extracellular space of the brain (Nicholson, 1973; Nicholson & Phillips, 1982). Strictly speaking, the model results from a linear theory of wave processes in branching cable structures of the tree type developed elsewhere (Franců & Schierwagen, 1989). In the present case, the fine structure of the branching dendrites is replaced by an equivalent, conductive medium characterized by averaged electrical quantities. For potential and current in this equivalent medium, equations are derived which turn out to be generalizations of the simple case of a uniform cable.

Analysis of these equations reveals that analytical solutions can be deduced from those of the equivalent cylinder model, provided some geometrical-topological conditions hold for the dendritic tree modelled. These result from the solution of a special Riccati differential equation which comprises the 3/2 power relation (iii) of the equivalent cylinder model.

2. Assumptions and Notation

An illustration of the three-dimensional geometry of a multipolar neuron is given in Fig. 2. In these neurons dendrites are relatively straight, and they radiate in all directions [cf. Ramón-Moliner (1962) for a classification of neurons according to a qualitative description of their dendritic patterns, and Schierwagen (1987) for a quantitative one using their fractal dimension]. Hence, the use of a system of spherical co-ordinates (O, r, ϑ) seems most appropriate to the present problem. As usual, O denotes the origin, r is the distance co-ordinate and $\vartheta = (\vartheta_1, \vartheta_2)$ the angle co-ordinate (Fig. 3).

Any given dendritic tree of a neuron a space angle Θ can be assigned to in such a way that the tree is completely contained in Θ, whereas the top of the cone Θ is in the origin O, and the stem of the dendritic tree emanates from O. This situation of a single dendritic tree contained in a space angle Θ will be dealt with in this paper (Fig. 4).

We will consider a dendritic tree composed of branches each of which is assumed to be circular in cross-section. The theory also includes branches which taper (or flare) at a steady rate. The geometry of any dendritic tree is characterized by metrical (e.g. diameters and lengths of branches) as well as topological (i.e. the connectivity pattern of the branches) properties. These properties can be quantified by two

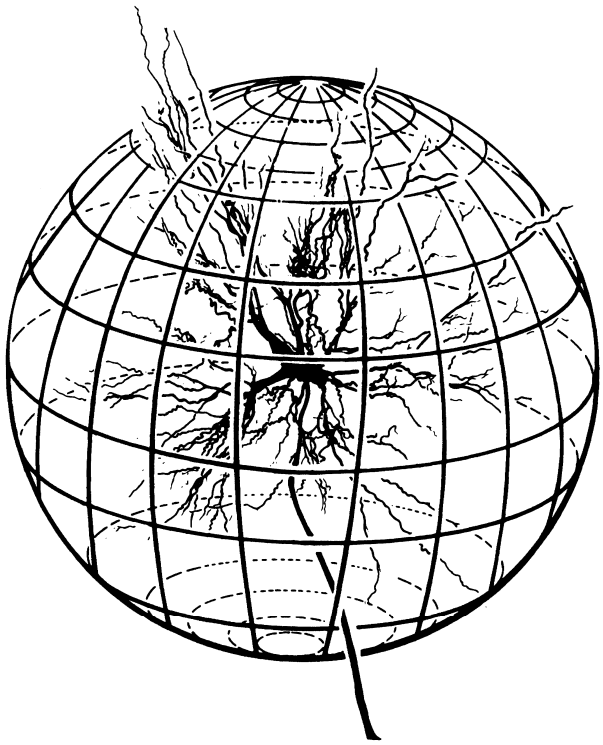

FIG. 2. Three-dimensional plot of a multipolar neuron with soma in the centre of a sphere. The nerve cell represented belongs to cat superior colliculus output neurons studied in Schierwagen & Grantyn (1986) and Schierwagen (1986).

functions of the co-ordinates r, ϑ: one is the diameter d of any individual branch (different for each branch at distance r), the other is the number n of these branches present at distance r. We suppose in the following that both branch number and diameters are equally distributed in the space angle Θ, i.e. these functions are assumed as independent on direction $\vartheta \in \Theta$. If we denote by $n_\Theta(r)$ the total branch number at distance r related to Θ, we can define the arithmetical mean $\bar{d}_\Theta(r)$ and the square mean $\tilde{d}_\Theta(r)$ of the diameters $d_i(r)$ $[i = 1, \ldots, n_\Theta(r)]$ of the $n_\Theta(r)$ branches as follows:

$$\bar{d}_\Theta(r) = \frac{1}{n_\Theta(r)} \sum_{i=1}^{n_\Theta(r)} d_i(r), \tag{2}$$

$$\tilde{d}_\Theta(r) = \left[\frac{1}{n_\Theta(r)} \sum_{i=1}^{n_\Theta(r)} d_i(r)^2\right]^{1/2}. \tag{3}$$

Because of the assumed direction independence, these mean values will be also related to the unit space angle. We then simply omit the index Θ and write $\bar{d}(r)$ and $\tilde{d}(r)$.

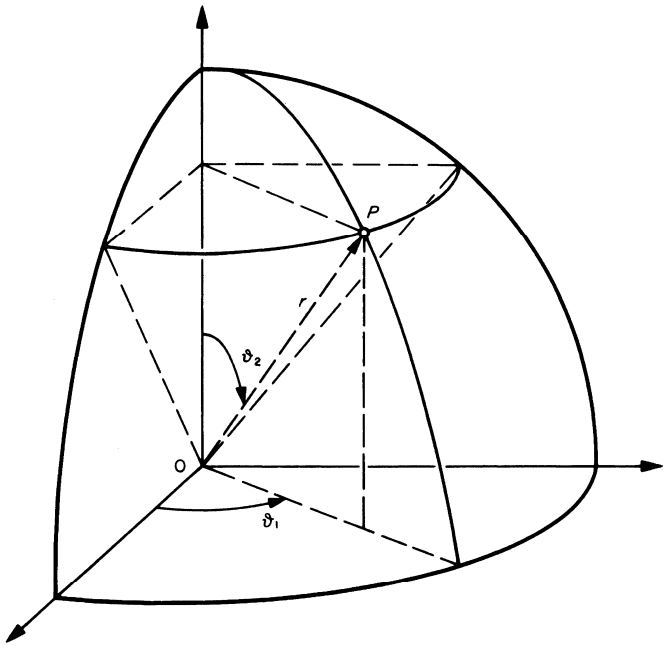

FIG. 3. System of spherical co-ordinates used in this paper. Co-ordinate surfaces are (1) spheres r = constant with origin O as centre, (2) half-planes ϑ_1 = const., and (3) cones with top in O and opening angle ϑ_2 = const. The position of any point P is determined by the parameter values of the three co-ordinate surfaces intersecting each other in P. For $0 \leq r < +\infty$, $0 \leq \vartheta_1 < 2\pi$, $0 \leq \vartheta_2 \leq \pi$ a unique mapping of all space points is realized.

Below we define particular classes of dendritic trees (including the equivalent cylinder class) by deriving some constraints upon the relation between d and n.

Let us now consider a small volume $\mathcal{V}$ of the space angle Θ, i.e. an obtuse cone bounded by the mantle surface $\mathcal{M}$ and the spherical caps $\mathcal{B}_1$, $\mathcal{B}_2$ (see Fig. 5). We conceptionally can divide $\mathcal{V}$ into three components: (a) the intracellular space (cytoplasm) of the dendritic branches contained in $\mathcal{V}$, (b) the dendritic membrane surrounding the cytoplasm and separating it from (c) the extracellular space. We aim for a description of current flow in the conductive medium represented by the components (a) and (b). Employing the standard assumptions of linear cable theory (see Jack *et al.*, 1975; Rall, 1977 for discussion), the physical model situation can be characterized as follows: the dendritic tree is embedded in a large, isopotential extracellular space. Hence, orientation effects of the dendritic branches (i.e. angles between branches) can be neglected, and the axes of all branches are assumed to be aligned radially. The cytoplasm provides a simple ohmic resistance to current flow, and for all directions $\vartheta \in \Theta$ voltage gradients are supposed as completely radial. Thus, any angular dependence of current flow as well as of geometrical neuron parameters can be ignored, so that the angle co-ordinate ϑ will be omitted. The passive membrane properties are represented as a resistance in parallel with a

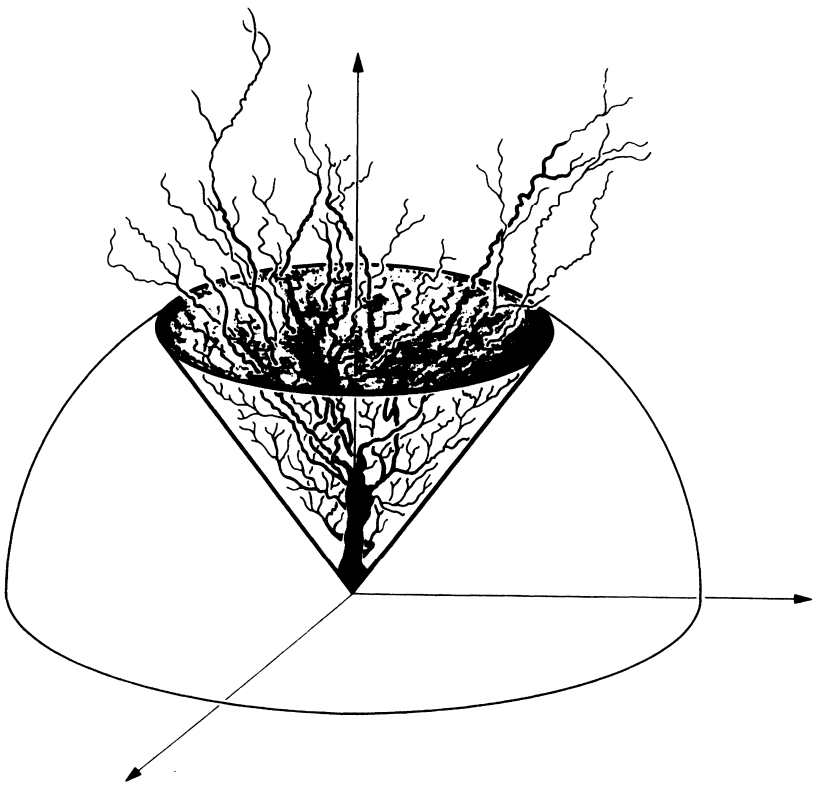

FIG. 4. Illustration of the model situation assumed. A single dendritic tree is completely contained in space angle Θ.

capacitance which are both uniformly distributed throughout the dendritic tree. Table 1 summarizes the notation used in this paper.

3. Derivation of the Model Equations

Let $i(r, t)$ be the total current (related to the unit space angle) at distance r and time t in the conductive medium consisting of the dendritic branches, and let $V(r, t)$ be the corresponding voltage measured relative to the resting potential. A positive sign for $I(r, t)$ denotes current flow directed centrifugally, i.e. towards increasing r. As usual, $I(r, t)$ and $V(r, t)$ are assumed to be continuous functions of both variables r and t. According to the physical model described above, current flow is confined to the space angle Θ, i.e. there are no intersections of branches with the boundary $\mathscr{M}$ (Fig. 5). Therefore, current can enter or leave $\mathscr{V}$ only via the boundaries $\mathscr{B}_1$, $\mathscr{B}_2$. On the other hand, conservation of current implies that excess current must flow out through the membrane of the dendritic branches. Thus, the following

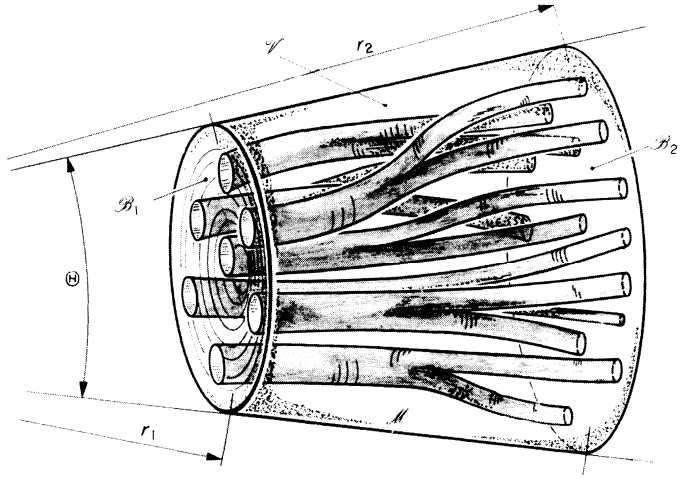

FIG. 5. Volume $\mathscr{V}$ of space angle Θ with the components involved. $\mathscr{V}$ is an obtuse cone bounded by surface $\mathscr{M}$ and spherical caps $\mathscr{B}_1$, $\mathscr{B}_2$.

currents have to be taken into account: (a) the centripetal current $H - I_1$ at $\mathscr{B}_1$, (b) the centrifugal current I_2 at $\mathscr{B}_2$, and (c) the membrane current I_m (see Fig. 6).

Applying Kirchhoff's law, we find

$$I_1 + I_2 + I_m = 0. \tag{4}$$

The membrane current I_m can be split into resistive and capacitive components I_G, I_C, due to the passive membrane properties assumed. Thus, $I_m = I_G + I_C$.

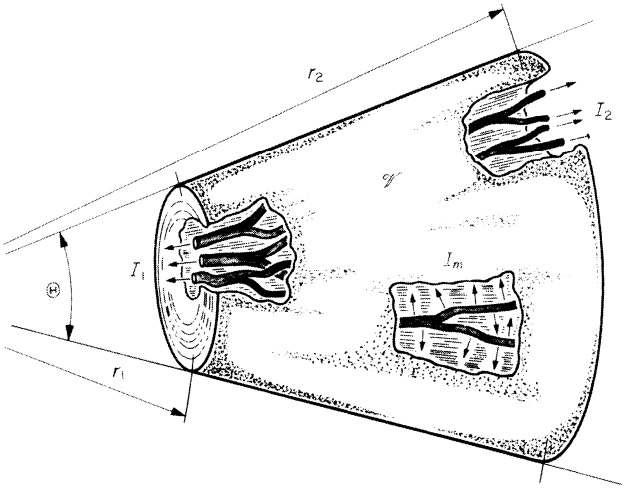

FIG. 6. Sketch of portion currents to be considered. Because of the purely ohmic axial resistance assumed, conservation of current is equivalent to $I_1 + I_2 + I_m = 0$ where membrane current I_m consists of a resistive and a capacitive component (see text).

The currents in eqn (4) can be expressed as follows. Firstly,

$$I_1 = -\int_\Theta I(r_1, t)\,\mathrm{d}\Theta$$

$$I_2 = \int_\Theta I(r_2, t)\,\mathrm{d}\Theta$$

and so

$$I_1 + I_2 = \int_\Theta [I(r_2, t) - I(r_1, t)]\,\mathrm{d}\Theta$$

$$= \int_\Theta \int_{r_1}^{r_2} \frac{\partial I(r, t)}{\partial r}\,\mathrm{d}r\,\mathrm{d}\Theta \tag{5}$$

according to the definition of the antiderivative of a function.

If we denote by $G(r)$ the membrane conductance of the branches in $\mathscr{V}$ (related to the unit space angle), then Ohm's law gives for the resistive component I_G of I_m

$$I_G = \int_\Theta \int_{r_1}^{r_2} G(r)\,.\,V(r, t)\,\mathrm{d}r\,\mathrm{d}\Theta \tag{6}$$

The change of charge Q during a short time interval $[t_1, t_2]$ due to the membrane capacitance $C(r)$ of the branches in $\mathscr{V}$ (related to the unit space angle) is

$$Q(t_2) - Q(t_1) = \int_\Theta \int_{r_1}^{r_2} C(r)[V(r, t_2) - V(r, t_1)]\,\mathrm{d}r\,\mathrm{d}\Theta$$

$$= \int_\Theta \int_{r_1}^{r_2} \int_{t_1}^{t_2} C(r) \frac{\partial V(r, t)}{\partial t}\,\mathrm{d}t\,\mathrm{d}r\,\mathrm{d}\Theta,$$

which via $\partial Q/\partial t = I_C$ implies for the capactive membrane current

$$I_C = \int_\Theta \int_{r_1}^{r_2} C(r) \frac{\partial V(r, t)}{\partial t}\,\mathrm{d}r\,\mathrm{d}\theta. \tag{7}$$

Substituting the expressions (5)-(7) in eqn (4), dividing it by $|\Theta|\,.\,|r_2 - r_1|$ and passing to the limit $|\Theta| \to 0$, $|r_2 - r_1| \to 0$, we obtain the first model equation:

$$\frac{\partial I(r, t)}{\partial r} + C(r) \frac{\partial V(r, t)}{\partial t} + G(r)\,.\,V(r, t) = 0. \tag{8}$$

On the other hand, applying Ohm's law again the voltage drop between the boundaries $\mathscr{B}_1$, $\mathscr{B}_2$ can be expressed as

$$V(r_1, t) - V(r_2, t) = -\int_{r_1}^{r_2} \frac{\partial V(r, t)}{\partial r}\,\mathrm{d}r$$

$$= \int_{r_1}^{r_2} R(r)\,.\,I(r, t)\,\mathrm{d}r$$

where $R(r)$ is the axial (cytoplasmic) resistance of the dendritic branches in $\mathcal{V}$ (related to the unit space angle). Thus, by differentiating with respect to r the second

$$\frac{\partial V(r, t)}{\partial r} + R(r) \,.\, I(r, t) = 0. \tag{9}$$

In deriving the eqns (8) and (9) the "macroscopic" parameters $R(r)$, $C(r)$ and $G(r)$ have been introduced to describe the characteristic bulk properties of the conductive medium formed by the dendritic tree. In general, "macroscopic" parameters of a composite are derived from its "microscopic" characteristics by applying specific averaging theorems (Babuška, 1976; Sanchez-Palencia, 1980; Bachmat & Bear, 1986). From the physical model assumed in the present case, the bulk parameters will depend in a simple way on the microscopic quantities describing the dendritic tree (i.e. on its electronic and geometrical-topological parameters).

According to the assumptions formulated above all branches of the tree at distance r form a population of electrically parallel cables of circular cross-section. The total cross-sectional area $A_\Theta(r)$ (related to Θ) of the dendritic branches at any distance r then is given by

$$\mathrm{A}_\Theta(r) = \pi/4 \,.\, n_\Theta(r) \,.\, \tilde{d}(r)^2$$

[cf. eqn (3)], and the corresponding quantity related to the unit space angle is

$$A(r) = \mathrm{A}_\Theta(r)/|\Theta|.$$

The total resistance to current flow (in the radial direction and related to the unit space angle) is therefore

$$R(r) = R_i/A(r) \tag{10}$$

where the axial resistivity R_i is assumed to be constant throughout the tree.

On the other hand, the capacitance $C(r)$ and conductance $G(r)$ of the equivalent conductive medium depend on the total membrane surface area of all branches at distance r, i.e. in the limit on their summed perimeter (related to the unit space angle)

$$P(r) = \mathrm{P}_\Theta(r)/|\Theta|$$

where

$$\mathrm{P}_\Theta(r) = \pi \,.\, n_\Theta(r) \,.\, \bar{d}(r)$$

is the total perimeter related to Θ [cf. eqn (2)]. For constant membrane capacity C_m and constant membrane conductivity G_m,

$$C(r) = C_m \,.\, P(r), \tag{11}$$

$$G(r) = G_m \,.\, P(r) \tag{12}$$

is obtained.

4. Transformation into Normal Form

Equations (8) and (9) are Kelvin's well-known RCG cable equations with non-constant coefficients. Physically, the situation corresponds to a non-uniform cable where the non-uniformity is due either to the electrical or the geometrical parameters, or to both. The linear, homogeneous system of partial differential eqns (8) and (9) is of the parabolic type. It can be written as a single second order equation in the transmembrane voltage $V = V(r, t)$:

$$\frac{\partial V}{\partial t} - \frac{1}{C(r)} \frac{\partial}{\partial r}\left[\frac{1}{R(r)} \cdot \frac{\partial V}{\partial r}\right] + \frac{G(r)}{C(r)} \cdot V = 0. \tag{13}$$

A non-uniform cable must be characterized by a changing length parameter, which can be defined as

$$\lambda(r) = [G(r) \,.\, R(r)]^{-1/2}. \tag{14}$$

The space variable r, then, can be transformed into dimensionless distance Z:

$$Z(r) = \int_0^r \frac{\mathrm{d}s}{\lambda(s)} \tag{15}$$

which replaces the electrotonic distance $X = r/\lambda$ used in the uniform cable case with the constant length parameter λ. If we further assume that the membrane time constant

$$\tau = C(r)/G(r) \tag{16}$$

is fixed throughout the non-uniform cable, then eqn (13) yields

$$\frac{\partial V}{\partial T} - \frac{\partial^2 V}{\partial Z^2} - \gamma \cdot \frac{\partial V}{\partial Z} + V = 0. \tag{17}$$

$T = t/\tau$ denotes dimensionless time, and the function $\gamma = \gamma(Z)$ is defined by the expression

$$\gamma = (G'R - GR')/(2GR) \tag{18}$$

where primes denote differentiation with respect to Z. Only recently, Poznański (1988) studied eqn (17) in the case of constant γ as an equation representing an exponentially tapering equivalent cable. In the present case, however, γ is subjected to the restriction of eqn (18) which does not imply that γ must be constant (see below). Introducing the variable $W = W(Z, T)$ through the relation

$$V(Z, T) = F(Z) \,.\, W(Z, T) \tag{19}$$

where

$$F(Z) = \exp\left[-\tfrac{1}{2} \int \gamma(Z)\, \mathrm{d}Z\right]. \tag{20}$$

Equation (17) can be rearranged into normal form

$$\frac{\partial W}{\partial T} - \frac{\partial^2 W}{\partial Z^2} + \delta \,.\, W = 0. \tag{21}$$

The coefficient $\delta = \delta(Z)$ is defined by

$$\delta = \gamma^2/4 + \gamma'/2 + 1. \tag{22}$$

From the literature the following assertions on existence and unity of solutions of eqn (21) can be derived (Babitsch *et al.*, 1967: 160).

Given that $\delta = \delta(Z)$ possesses a continuous derivative, then there is a unique solution of eqn (21) which assumes (and continuously depends on) prescribed continuous intial and boundary values. These properties obviously transfer themselves to the original eqn (13).

The assumption about δ clearly holds if γ is twice continuously differentiable [see eqn (22)]. According to the definition of γ, eqn (18), this is equivalent to the property of the electrical parameters G and R being three times continuously differentiable functions of Z. This property will hold if it does for the geometrical functions, $A(\cdot)$ and $P(\cdot)$ [see eqns (10) and (12)]. Therefore, $A(\cdot)$ and $\mathrm{P}(\cdot)$ are assumed in the following to be three times continuously differentiable (with respect to r or Z), so that the existence and unity of solutions of eqn (21) are guaranteed.

5. Restriction to Constant-Coefficient Case

The determination of explicit solutions of eqn (21)—and so of eqn (13)—represents a non-trivial problem. Although one could try to solve eqn (21) directly, e.g. by adopting the classical method of separation of variables, or by applying the Laplace transform technique, neither appears promising. The difficulty is due to the non-constant coefficients in eqns (21) or (13), respectively. As Jack *et al.* (1975) mentioned, very few exact solutions have been obtained in this case. These authors, therefore, favoured an approach where combinations of parameters are determined which reduce the problem to the constant coefficient case.

Applying this strategy also to the present problem, we suppose in the following that the coefficient δ in eqn (21) is a constant.

In this case we have the usual equation of an uniform cable in normalized form (see Jack *et al.*, 1975; Rall, 1977, for review). Substituting the variable W in eqn (21) by

$$W = \exp[1-\delta)T] \,.\, U \tag{23}$$

we see that the many specific solutions derived for the uniform cable eqn

$$\frac{\partial U}{\partial T} - \frac{\partial^2 U}{\partial Z^2} + U = 0 \tag{24}$$

can be applied to the original, non-uniform cable eqn (13) through the transformations defined by eqns (15), (16), (19) and (23), provided the changed initial and boundary conditions are considered.

To put those transformations effectively into practice, the underlying assumptions must be analysed in more detail. According to eqn (22), $\delta = \text{constant}$ means that

the differential equation

$$\gamma' + \gamma^2/2 = A \tag{25}$$

can be solved for the function $\gamma(Z)$ defined in eqn (18) where A is an arbitrary real constant. Equation (25) is a special Riccati differential equation which is integrable by the separation of variables, and its solutions can be expressed by elementary functions.

Depending upon the constant A, different forms of solutions can be derived. We assume $0 < Z < +\infty$ and $A \geqslant 0$ (the case $A < 0$ leads to a solution which is incompatible with reality). Denoting by

$$\gamma(Z) = \pm\gamma_1 = \pm\sqrt{2A} \tag{26}$$

the particular, stationary solution of eqn (25) in the case $A > 0$, the solution set of eqn (25) is easily derived as

$$\gamma(Z) = \begin{cases} 0 & (A = 0) \\ 2/(Z - C) & (A = 0, Z \neq C) \\ -\gamma_1\left(1 - \dfrac{2}{1 + C\exp(-\gamma_1 Z)}\right) & (A > 0). \end{cases} \tag{27}$$

Inserting eqn (27) into eqn (19), the voltage $V(Z, T)$ which solves the non-uniform cable eqn (17) can be calculated through

$$V(Z, T) = F(Z) \,.\, W(Z, T) \tag{19}$$

where $F(Z)$ is specified by

$$F(Z) = \begin{cases} D \\ D/(Z - C) \\ D \,.\, \exp\left(-\dfrac{\gamma_1}{2} \,.\, Z\right) \Big/ [1 + C\exp(-\gamma_1 Z)] \end{cases} \tag{28}$$

[the lines in eqn (28) correspond to those in eqn (27), and C, D are any constants].

Thus, the solutions of eqn (17) can be expressed now in terms of the solutions of eqn (24), as follows:

$$V(Z, T) = \exp[(1 - \delta)T] \,.\, F(Z) \,.\, U(Z, T) \tag{29}$$

where eqns (19), (20) and (23) have been comprised into one.

This relationship shows that the deviations from the uniform cable case described by eqn (24) are mirrored by certain "correction factors" which take into account the particular non-uniformity of the cable characterized by eqns (13), (17) and (21). Depending upon the value of δ and the course of $F(Z)$, various situations of locally different amplification or attenuation of the uniform cable solutions are possible.

Two examples are given here. The general steady-state solution of the normal

(21) can be applied to derive that of the non-uniform cable eqn (17). For $\partial W/\partial T = 0$, (21) reads

$$\frac{d^2 W}{dZ^2} - \delta \,.\, W = 0, \tag{30a}$$

the general solution of which is

$$W(Z) = \begin{cases} A_1 Z + A_2 & \text{for } \delta = 0 \\ A_1 \exp(\sqrt{\delta} Z) + A_2 \exp(-\sqrt{\delta} Z) & \text{for } \delta < 0 \\ A_1 \sin(\sqrt{-\delta} Z) + A_2 \cos(\sqrt{-\delta} Z) & \text{for } \delta < 0 \end{cases} \tag{30b}$$

(the two arbitrary constants A_1, A_2 must be determined from the boundary conditions belonging to any specific problem).

Using (30b) in (19), the general steady-state solution of (14) is obtained:

$$V(Z) = F(Z) \,.\, W(Z) \tag{30c}$$

where $F(Z)$ is specified as in (28).

In a similar manner, the basic transient solution of (17) in separable form may be calculated from that of (24):

$$V(Z, T) = F(Z) \,.\, [B_1 \sin(\alpha Z + B_2 \cos(\alpha Z)] \,.\, \exp[-(\delta + \alpha^2) T] \tag{30d}$$

where B_1, B_2 and α depend on the boundary and initial conditions [cf. Rall, 1977 (1.15)].

6. Condition for Reduction to Non-uniform Cable

In the preceding derivations the question of what classes of dendritic trees allow a reduction to a non-uniform cable according to eqn (17) has been left open. Analysis of the relationship stated between macroscopic parameters on the cable and microscopic quantities of the underlying dendritic tree (see section 3) in the light of the constant coefficient assumption of section 5 will enable us to formulate a general branching condition for those trees.

It will be remembered that all branches of a given tree at any distance from the origin are considered as electrically parallel. Therefore, if eqns (10) and (12) are transferred to Z-space we obtain

$$\begin{aligned} R(Z) &= R_i / A(Z), & A(Z) &= \mathrm{A}_\Theta(Z)/|\Theta| \\ G(Z) &= G_m \,.\, P(Z), & P(Z) &= \mathrm{P}_\Theta(Z)/|\Theta|, \end{aligned} \tag{31}$$

where the functions $\mathrm{A}_\Theta(\cdot)$, $\mathrm{P}_\Theta(\cdot)$ are defined in eqns (10) and (12). According to the definition of $\gamma(Z)$ we have

$$\gamma(Z) = \frac{G'(Z) \,.\, R(Z) - G(Z) \,.\, R'(Z)}{2G(Z)R(Z)}. \tag{18}$$

Inserting eqn (31) into eqn (18) we obtain, after some straightforward calculations,

$$\gamma(Z) = \frac{1}{2}\left[\frac{f_1'(Z)}{f_1(Z)} - \frac{f_2'(Z)}{f_2(Z)}\right] \tag{32}$$

where $f_1(Z) = P_\Theta(Z)/\pi$ and $f_2(Z) = \pi/[4A_\Theta(Z)]$. From eqn (32) it follows that

$$\exp\left[\int \gamma(Z)\,\mathrm{d}Z\right] \propto [f_1(Z)/f_2(Z)]^{1/2}$$

$$\propto \left\{\left[\sum_{i=1}^{n_\Theta(Z)} d_i(Z)\right]\left[\sum_{i=1}^{n_\Theta(Z)} d_i(Z)^2\right]\right\}^{1/2} \tag{33}$$

$$= n_\Theta(Z)\,.\,\bar{d}(Z)^{1/2}\,.\,\tilde{d}(Z)$$

where $\bar{d}(Z)$, $\tilde{d}(Z)$ denote the means defined in eqns (2) and (3). Remembering the definition of $F(Z)$ in eqn (20), we see that

$$F(Z)^{-2} \propto n_\Theta(Z)\,.\,\bar{d}(Z)^{1/2}\,.\,\tilde{d}(Z) \tag{34}$$

from which we can derive

$$n_\Theta(Z)\,.\,\bar{d}(Z)^{1/2}\,.\,\tilde{d}(Z) = \begin{cases} D \\ D(Z-C)^2 \\ D\exp(\gamma_1 Z)[1+C\exp(-\gamma_1 Z)]^2 \end{cases}$$

where the lines correspond to those in eqns (27) and (28), and C and D are any constants.

Since for $Z \approx 0$ the left-hand side of this equation must equal $d_0^{3/2}$(d_0 is the diameter of the dendritic stem), the constant D can be determined. We yield

$$n_\Theta(Z)\,.\,\bar{d}(Z)^{1/2}\,.\,\tilde{d}(Z) = \begin{cases} d_0^{3/2} \\ d_0^{3/2}\,.\,(Z/C-1)^2 \\ d_0^{3/2}\,.\,\exp(\gamma_1 Z)\,.\left(\dfrac{1+C\exp(-\gamma_1 Z)}{1+C}\right)^2. \end{cases} \tag{35}$$

Eqn (35) represents a branching condition characterizing the classes of dendritic trees which can be collapsed into a single, non-uniform cable described by eqns (17) and (21). From eqns (34) and (35) it is obvious that the particular branching pattern directly determines the factor $F(Z)$ in eqn (29) reflecting the non-uniformity of the equivalent cable. The implications of condition (35) in r-space can be deduced when the inverse transformation to

$$Z(r) = \int_0^r \mathrm{d}s/\lambda(s) \tag{15}$$

is known. Using eqns (10), (12), and (14) we find

$$\lambda(r) = [G(r)R(r)]^{-1/2} = \left[\frac{R_m}{R_i}\cdot\frac{\tilde{d}(r)^2}{4\bar{d}(r)}\right]^{1/2} \tag{36}$$

therefore

$$Z(r) = 2\sqrt{\frac{R_i}{R_m}}\int_0^r \frac{\bar{d}(s)^{1/2}}{\tilde{d}(s)}\,\mathrm{d}s. \tag{37}$$

We conclude that the application of eqns (17) or (21) to describe membrane voltage changes in an unequally branched dendritic tree described by eqn (35) is satisfied when all terminal branches terminate at the same Z value. The Z value along each branching pathway from the tree origin 0 to any particular site in the tree is defined by separate application of eqn (37) to that pathway [note that $\bar{d}(r) = \tilde{d}(r)$ holds in this case]. Analogous to the equivalent cylinder model (which is contained in the present model, see below), this considerably simplifies the mathematical treatment because the original problem which requires explicit boundary conditions for every branch point now is reduced to a problem with only two boundary conditions: one at the origin of the dendritic tree (i.e. the cell body), and the other at the terminations of the tree all of which must be of the same kind [see Schierwagen (1986) where explicit boundary conditions are used in a segmental cable model]. A limitation of the mathematical description derived above is that $n_\Theta(\cdot)$ has been assumed to vary continuously with distance (r or Z). In fact, however, it can only change in discrete steps (see Jack *et al.*, 1975, for a discussion).

7. Comparison with Other Results

It might be worth noting that eqn (35) provides a generalization of Rall's "3/2 power relationship" (Rall, 1959, 1962). To illustrate this, we remember that the conditions (i)-(iii) stated above as prerequisites for the equivalent cylinder transformation (see Introduction) imply that the sum of the 3/2 powers of the diameters of all branches at any given electrotonic distance from the soma must remain constant to the terminal points. In Rall's ideal, symmetrically branching tree (Rall, 1962) all branches of a given generation have both equal diameters and equal lengths in r-space, i.e. for $r_j \leq r \leq r_{j+1}$

$$d_i(r) = d_j \qquad (i = 1, \ldots, n_j)$$

holds where branching occurs at distances r_j $(j = 1, \ldots, k)$ with n_j branches of length $l_j = r_{j+1} - r_j$ between branch points r_j and r_{j+1}. Obviously, in this case arithmetical and square mean are equal for any generation j, $\bar{d}(r) = \tilde{d}(r) = d_j$. Thus the length parameter λ becomes a constant for generation j,

$$\lambda_j = \sqrt{\frac{R_m}{R_i}\frac{d_j}{4}}.$$

The left-hand side of eqn (35) simplifies in this case to $n_j \,.\, d_j^{3/2}$, so that for $C = 0$

$$n_j \,.\, d_j^{3/2} = d_0^{3/2} \exp(\gamma_1 Z) \tag{38}$$

follows as a special case.

This equation is identical to that formulated by Rall [1962, eqn (21)] or Jack *et al.* [1975, eqn (7.61]. It characterizes a dendritic tree for which the sum of the 3/2 powers of the branch diameters (common to all branches) at any given value of actual distance r or electrotonic distance Z either is a constant ($\gamma_1 = 0$) as in the equivalent cylinder model (Rall, 1959, 1962), or it shows exponential taper ($\gamma_1 < 0$) or flare ($\gamma_1 > 0$), see Rall (1962), Jack *et al.* (1975) and Poznański (1988). Membrane

voltage changes in such a tree then can be described by eqn (17) with $\gamma = \gamma_1$, i.e.

$$\frac{\partial V}{\partial T} - \frac{\partial^2 V}{\partial Z^2} - \gamma_1 \frac{\partial V}{\partial Z} + V = 0. \tag{39}$$

This equation also applies to dendritic trees with asymmetrical branching and taper. According to eqn (35), such a tree must obey the branching condition

$$\left[\left(\sum_{i=1}^{n_\Theta(Z)} d_i(Z)\right)\left(\sum_{i=1}^{n_\Theta(Z)} d_i(Z)^2\right)\right]^{1/2} = d_0^{3/2} \exp(\gamma_1 Z). \tag{40}$$

8. Summary and Conclusions

The aim of this study was to expand the range of application for analytical models of electrotonic current flow in branching dendritic trees. Such models have the advantage over computer models (e.g. compartmental models or branching cable models, cf. Schierwagen, 1988 for review) of giving immediate insight into how the various physical parameters describing the dendritic tree affect the solution.

In the past, several authors have tried to broaden both the classes of dendritic branching patterns and the physical situations which can be treated analytically (e.g. Butz & Cowan, 1974; Horwitz, 1983; Jack & Redman, 1971; Rall & Rinzel, 1973; Rinzel & Rall, 1974; Walsh & Tuckwell, 1983; Poznański, 1988). Rall's "equivalent cylinder" model (Rall, 1962, 1977) has been used as prototype as well as starting point in these analyses.

Following in essentials Rall's modelling philosophy, we have constructed a new model for passive membrane electrotonus. Our equations have been obtained from a combination of core conductor theory with the continuum approach. Interestingly, the method leads to natural generalization of the cable equation with constant coefficients, i.e. to such an equation with spatially varying coefficients.

While the non-uniform cable equation can be solved in general only numerically, we were able to derive a general branching condition under which analytical solutions can be deduced from those of the uniform cable equation. The method developed in the present paper for this purpose can be summarized as follows:

application of $Z(r) = \int_0 ds/\lambda(s)$ to each branching pathway of the tree] it must be proved that the tree belongs to one of the classes defined by branching condition (35),

$$n_\Theta(Z) \,.\, \bar{d}(Z)^{1/2} \,.\, \tilde{d}(Z) = \begin{cases} d_0^{3/2} \\ d_0^{3/2}(Z/C-1)^2 \\ d_0^{3/2} \exp(\gamma_1 Z)\left(\dfrac{1+C\exp(-\gamma_1 Z)}{1+C}\right)^2. \end{cases}$$

2. If so, then passive membrane electrotonus in that tree can be described by the non-uniform cable eqn (17),

$$\frac{\partial V}{\partial T} - \frac{\partial^2 V}{\partial Z^2} - \gamma \frac{\partial V}{\partial Z} + V = 0$$

the solutions of which are related to those of the uniform cable eqn (24),

$$\frac{\partial U}{\partial T}-\frac{\partial^2 U}{\partial Z^2}+U=0$$

through the "correction factors" of eqn (29),

$$V(Z, T)=\exp[(1-\delta)T] \,.\, F(Z) \,.\, U(Z, T).$$

3. Depending on the particular branching pattern of the dendritic tree under study, the "correction factors" $\exp[(1-\delta)T] \,.\, F(Z)$ for the uniform cable solutions $U(Z, T)$ are specified to give the corresponding solutions of the non-uniform cable eqn (17), i.e.

$$V(Z, T)=\begin{cases} \exp[(1-\delta)T]U(Z, T) & (A=0) \\ \dfrac{\exp[(1-\delta)T]}{Z-C} \,.\, U(Z, T) & (A=0, Z\neq C) \\ \dfrac{\exp[(1-\delta)T]\exp(-\gamma_1 Z/2)}{1-C\exp(-\gamma_1 Z)} \cdot U(Z, T) & (A>0) \end{cases}$$

4. Determination of the corresponding solutions of the original non-uniform cable eqn (13) in the r, t-domain requires that the back-transformations $Z\to r$, $T\to t$ can be carried out. While simply $t=T \,.\, \tau$, the space variables are related through eqn (37),

$$Z(r)=2\sqrt{\frac{R_i}{R_m}}\int_0^r \frac{\bar{d}(s)^{1/2}}{\tilde{d}(s)}\,ds$$

so that knowledge of the functions $\bar{d}(r)$, $\tilde{d}(r)$ from anatomical measurements is necessary.

By comparing our results with those of other models, we found that for an ideal, symmetrically branching dendritic tree obeying the "3/2 power relationship" the present model reduces to Rall's equivalent cylinder model, or, if exponential taper of the dendritic trunk parameter is considered, to Poznański's tapering equivalent cable model (see Rall, 1959, 1962; Poznański, 1988).

Since the general branching conditions derived here allows one to adjust two free parameters [γ_1 and C, see eqn (35)] a greater variety of branching patterns than those of the tapering cable class (including the equivalent cylinder class) can be analytically treated now.

A particular advantage of the present model is the possibility to use in principle all results derived so far for the equivalent cylinder model and its recent modifications [e.g. the somatic shunt cable model, see Iansek & Redman, 1973; Durand, 1984; Kawato, 1984; Poznański, 1987, or the tapering equivalent cable model of Poznański, 1988], provided the dendritic tree under study belongs to one of the model classes. This will be illustrated in a forthcoming article for several branching patterns and for various standard situations of cable modelling.

I am indebted to Dr J. Franců for fruitful collaboration which gave the impulse for this work. Thanks are due to Dr J. van Pelt for his critical reading of an earlier draft of this

paper, and for some very useful suggestions. I am also grateful to a referee for some helpful comments on this manuscript.

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