THE PATH INTEGRAL FOR DENDRITIC TREES

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Abstract

We construct the path integral for determining the potential at any point on a dendritic tree of arbitrary geometry described by a linear cable equation. This is done by generalizing Brownian motion from a line to a tree. The path integral allows novel computational techniques to be applied to cable problems. Using the path integral, we have discovered simple diagrammatic rules for obtaining Green's functions on dendritic trees of arbitrary geometry. We also consider arbitrary dendritic structures with spatially-varying membrane conductivities and indicate how the membrane potential can be determined by numerical computation of the path integral. In addition, we show how the path integral can be used to treat the time-dependent conductance changes that occur at synapses. Finally, we give a Feynman-type formula for the path integral and discuss Monte Carlo methods of computation.

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1. Introduction

To understand the behavior of a network of neurons it is essential to understand the input-output characteristics of a single neuron. In particular, we want to know whether a given set of synaptic inputs will cause a neuron to fire action potentials and if so at what rate. Linear cable theory [for reviews see Rall 1977, Tuckwell 1988] provides a first approximation for modeling the complex integration of synaptic inputs that occurs on neuronal dendritic trees. Although linear cable theory considers only passive conductances, it does allow a complete description of the effects of complex dendritic geometries on input signal integration.

A solution to the linear cable problem is provided by the Green's function for a given dendritic geometry. The Green's function is, up to an exponential factor, the membrane potential arising from an instantaneous injection of a unit spike (delta-function) of current at a given point on the tree. Once the Green's function is known the membrane potential at any point on a dendritic tree at any time is given in terms of the initial membrane potential and the current being injected into the tree.

In the conventional approach to the cable problem, the Green's function is obtained by solving a partial differential equation and imposing the appropriate boundary conditions using classical mathematical techniques such as separation of variables, Laplace transforms and series solutions. Similar techniques are used to solve similar equations in quantum mechanics and statistical physics. However, in these fields an alternative formulation is often used allowing a complementary assortment of mathematical techniques and numerical approximations to be applied to difficult problems. This alternative formulation is the path integral. Here, we construct the path integral for the Green's function on a dendritic tree of arbitrary geometry. By 'arbitrary' we mean a tree with any number of nodes and any number of branches having any pattern of connectivity and unrestricted radii. Ultimaly, our analysis of the path integral leads to a set of simple diagrammatic rules for generating an exact expression for the Green's function on any dendritic structure. These rules provide a fast and efficient method for solving complex cable problems.

In the path integral approach, the Green's function $G(x, y, t)$ is expressed as an integral of a certain measure over all paths connecting the point x to the point y in time t. To define the integral we must specify the measure for the paths being summed. For the Green's function on a single, infinite line, $-\infty < x < \infty$, the usual Brownian motion measure [Wiener 1923] is used to obtain the Feynman path integral [Feynman and Hibbs 1965]. In this paper, we generalize the Brownian motion measure to the case of an arbitrary branched structure. In general, different boundary conditions require different definitions of the measure. (The measures corresponding to semi-infinite and finite line segments with boundary conditions appropriate for quantum mechanics have been discussed by Clark et al. [1980], Farhi and Gutmann [1990] and Carreau et al. [1990].) To apply the path integral to the problem of general dendritic trees we must consider the measure for paths on an arbitrary branched structure with the usual boundary conditions of cable theory imposed on the membrane potential at the terminals and branching nodes.

To discuss the measure for paths on a dendritic tree we will use a heuristic approach that simplifies the discussion. We break the time interval t into N equal-sized pieces and consider paths as random walks consisting of N steps. (Ultimately we take the limit $N \to \infty$ although, of course, in numerical work a large but finite N value must be used.) In the following, we specify rules for generating random paths corresponding to a given set of boundary conditions. We do this in Secs. 3-5 for a series of cable structures of increasing complexity leading ultimately to general dendritic trees. The heuristic definition of the path integral for an arbitrary tree is given in Sec. 6. In Secs. 6 and 7 we also define the path integral for a more complicated situation than is normally considered in cable theory, dendritic trees with spatially-varying and/or time-dependent conductivities. Membrane conductivity (conductance per unit area) may vary as a function of position along a cable. In particular, synaptic inputs cause localized, time-dependent conductance changes at various points along a dendritic cable. Both spatially-varying and time-dependent conductivities can be incorporated quite simply into the path integral because the basic measure derived for the constant conductivity case can still be used.

Our work with the path integral has lead us to discover a simple set of diagrammatic rules for generating the exact Green's function on any dendritic tree. These rules are given in Sec. 8. Our diagrammatic rules generate an infinite series for the Green's function in terms of the Gaussian Green's function for a single, infinite cable. By truncating the infinite series, the rules we give can be used to generate Green's functions with any desired degree of accuracy. No restrictions are made on the segment radii for the tree. Tapering cables can be treated by introducing a sequence of non-branching nodes at which the cable radius changes. Although the rules can be used for dendritic trees with any geometric structure they require the constant membrane conductivity normally assumed in cable theory. We are hopeful that the path integral approach will provide useful methods for solving cable problems with spatially-varying and time-dependent conductivities as well. This is the subject of current research on numerical methods arising from the path integral approach.

Dendritic trees of arbitrary geometry and constant conductivity have been discussed using the conventional approach to cable theory. In certain cases, a restriction on cable diameters is used to simplify the problem [Rinzel and Rall 1974]. The most general previous result is a set of rules for constructing the Laplace transform of the potential on any tree with constant conductivity given by Butz and Cowan [1974]. The rules of Sec. 8 generate the Green's function directly as a function of time, not as a Laplace transform, and are thus complementary to those of Butz and Cowan. For numerical calculation this has the advantage that no Laplace transforms or their inverses need to be computed.

The path integral is used extensively in quantum mechanics and in statistical physics. In these fields a formula for the path integral due to Feynman [Feynman and Hibbs 1965] is frequently used. For completeness, we derive in the Appendix a Feynman-type formula for the path integral on an arbitrary tree with or without spatially-varying and time-dependent conductivity. However, this formulation will not be directly used in the body of the paper.

Because the path integral relies on the superposition principle, it can only be used in cases where the cable membrane current is a linear function of the membrane potential. However, it should be possible to treat linearized, active conductances [Koch 1984] using the path integral approach. In this paper we restrict our attention to passive cables.

2. Linear Cable Theory

The basic equation of linear cable theory expresses conservation of electrical current in an infinitesimal cylindrical element of cable. Let $v(x,t)$ be the membrane potential at position x along a cable at time t measured relative to the resting potential of the membrane (so that the resting potential is $v = 0$). We will measure the distance x in units of the membrane length constant $(Ra/2r)^{1/2}$ and time in units of the membrane time constant RC. Here C is the capacitance per unit area of the cell membrane, r is the resistivity of the intracellular fluid (in units of resistance times length), the conductivity of the membrane is $1/R$ (R has units of resistance times area) and a is the cable radius. In terms of these variables the basic cable equation is

$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} - v + I(x,t) \tag{2.1}$$

where we include the source term $I(x,t)$ corresponding to external current injected into the cable.

We are interested in solving Eq. (2.1) on a dendritic tree like that shown in Fig. 1. To do this we must give the boundary conditions for v at the nodes where branching occurs and at the terminals of the cable. We will label the various segments of a given dendritic tree with an index i running from one to the total number of segments in the tree. Along each segment we label position with the coordinate x satisfying $0 \leq x \leq L_i$ where L_i is the (dimensionless) length of the i^{th} segment. We denote the potential on segment i by v_i. Consider a branching node with a number of segments radiating from it as in Fig. 2. For convenience we will choose coordinates which place the node at the coordinate value zero for all the segments emerging from the node. The boundary conditions are continuity of the potential

$$v_i(0,t) = v_k(0,t) \tag{2.2}$$

for all values i and k corresponding to segments emerging from the node at $x = 0$, and conservation of the current flowing through the node

$$\sum_i a_i^{3/2} \left. \frac{\partial v_i(x,t)}{\partial x} \right|_{x=0} = 0. \tag{2.3}$$

Here, a_i is the radius of the i^{th} segment and the sum is over values of i corresponding to segments connected at the node. This expression is derived by noting that the longitudinal current flowing down a cable is given according to Ohms law by $\pi a^2/r$ divided by the length constant times the spatial derivative of the potential.

There are also boundary conditions at the terminals of the dendritic tree. For example if a given segment i terminates at the point $x = L_i$ we may impose one of two conditions on $v_i(L_i,t)$. The open-end condition requires that

$$v_i(L_i,t) = 0 \tag{2.4}$$

while the closed-end condition is

$$\left. \frac{\partial v_i(x,t)}{\partial x} \right|_{x=L_i} = 0 \tag{2.5}$$

for all t values. We will consider both of these cases. (Techniques for handling the more general boundary condition $\partial v/\partial x$ = constant $\times v$ are discussed in Farhi and Gutmann [1990].)

The potential at any point on any segment of a general tree can be determined if the Green's function for the particular dendritic structure is known. If $v_i(x,t)$ is the potential on segment i and the current injected per unit area at point y on segment j at time s is given by $I_j(y,s)$ then

$$v_i(x,t) \;=\; \sum_j \left[\int_0^{L_j} dy\, G_{ij}(x,y,t) e^{-t} v_j(y,0) \right. \tag{2.6}$$

$$+\int_0^t ds \int_0^{L_j} dy\, G_{ij}(x,y,t-s) e^{s-t} I_j(y,s)\Bigg]$$

where the sum on j is over all segments of the tree. We have included the exponential factors in this formula to simplify the definition of the Green's function.

In order for $v_i(x,t)$ given by (2.6) to satisfy the cable equation (2.1), $G_{ij}(x,y,t)$ must satisfy

$$\frac{\partial G_{ij}(x,y,t)}{\partial t} = \frac{\partial^2 G_{ij}(x,y,t)}{\partial x^2} \tag{2.7}$$

for $t > 0$ with the initial condition

$$G_{ij}(x,y,0) = \delta_{ij}\delta(x-y). \tag{2.8}$$

In addition, the Green's function must satisfy boundary conditions similar to those given above for v. Specifically, at a branching node located at $x = 0$ where the condition (2.2) is imposed we require

$$G_{ij}(0,y,t) = G_{kj}(0,y,t) \tag{2.9}$$

for all i and k connected to the node in question and for all values of j, y and t. Likewise for (2.3) to be satisfied at this node we must have

$$\sum_i a_i^{3/2} \left.\frac{\partial G_{ij}(x,y,t)}{\partial x}\right|_{x=0} = 0 \tag{2.10}$$

for all j, y and t values, with the sum over segments radiating from the node. At a terminal on segment i at position L_i we require either

$$G_{ij}(L_i,y,t) = 0 \tag{2.11}$$

for an open end (2.4) or

$$\left.\frac{\partial G_{ij}(x,y,t)}{\partial x}\right|_{x=L_i} = 0 \tag{2.12}$$

for a closed end (2.5) again for all j, y and t.

Green's functions obey a convolution identity that will be useful for subsequent discussions. For any s in the range $0 < s < t$ the Green's function satisfies

$$G_{ij}(x,y,t) = \sum_k \int_0^{L_k} dz\, G_{ik}(x,z,s)\, G_{kj}(z,y,t-s) \tag{2.13}$$

where the sum on k is over all segments of the tree.

The generalization to a membrane conductivity which depends on position involves introducing a varying conductivity factor $U(x)$ into the basic cable equation so that

$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} - [1 + U(x)]v + I(x,t). \tag{2.14}$$

Specifically, if the membrane conductivity at position x on segment i is $[1 + U_i(x)]/R$ then the Green's function satisfies the differential equation

$$\frac{\partial G_{ij}(x,y,t)}{\partial t} = \frac{\partial^2 G_{ij}(x,y,t)}{\partial x^2} - U_i(x)G_{ij}(x,y,t). \tag{2.15}$$

as well as the usual initial and boundary conditions. We will provide a path integral prescription and formula for this Green's function in Sec. 6.

The current injected at a synapse takes the form $g(x,t)[v(x,t) - v_r]$ where v_r is a fixed reversal potential. The cable equation with such synaptic conductance changes included can be expressed in the form (2.14) by incorporating the first term, $g(x,t)v(x,t)$, into a time-dependent U factor, $U(x,t)$, and the second term, $-g(x,t)v_r$, into the current factor $I(x,t)$. Although treating a time-dependent U involves no additional complications in the path integral approach, it does introduce some notational complexity so we will wait until Sec. 7 before discussing this case.

3. A Single Infinite Cable

As a first example we consider a single, non-branching, infinite cable for which the Green's function is Gaussian,

$$G_0(x-y,t) = \frac{1}{\sqrt{4\pi t}} \exp - \frac{(x-y)^2}{4t}. \tag{3.1}$$

The path integral for this case is widely discussed [Feynman and Hibbs 1965, Nelson 1964] but we will review some key features which will be needed for our generalization to the case of trees. The heuristic description of the path integral is based on a rule for generating random walks. Paths are defined by dividing the time t into N equal intervals of size t/N. We generate paths by starting at the point x and taking N steps of length $(2t/N)^{1/2}$ choosing at each step to move in the positive or negative direction along the cable with equal probability 1/2. The normalized distribution of final points y achieved in this manner will give the Green's function (3.1) in the limit $N \to \infty$. If we independently generate P paths of N steps all starting from the point x then

$$G_0(x-y,t) = \lim_{N\to\infty} \lim_{P\to\infty} \frac{1}{P} \sum_{from\ x\ to\ y}^{Paths} 1 \tag{3.2}$$

where the sum is over all of the generated paths with final point y so that the sum is equal to the number of generated paths that happen to end at y.

The power of the path integral for the single, infinite cable becomes apparent when we consider the case of a spatially-varying conductivity $[1+U(x)]/R$ as in Eq. (2.14) and (2.15). To compute the Green's function for this case we generate paths as before but now introduce an additional weighting factor in the sum over paths. For a path that passes through the sequence of points $x \to z_1 \to z_2 \to \ldots \to z_{N-1} \to z_N = y$ the weighting factor is

$$\exp - \frac{t}{N}\left[\frac{1}{2}U(x) + U(z_1) + \ldots + U(z_{N-1}) + \frac{1}{2}U(y)\right]. \tag{3.3}$$

If we generate P random N-step paths starting at x then

$$G(x,y,t) = \lim_{N\to\infty} \lim_{P\to\infty} \frac{1}{P} \sum_{from\ x\ to\ y}^{Paths} \exp - \frac{t}{N}\left[\frac{1}{2}U(x)\right. \tag{3.4}$$

$$\left. + U(z_1) + U(z_2) + \ldots + U(z_{N-1}) + \frac{1}{2}U(y)\right].$$

Again the sum is over those paths among the P independent paths generated by the above rule that have their final point at position y. It can be shown [Feynman and Hibbs 1965, Nelson 1964] that Eq. (3.4) does indeed give the Green's function satisfying (2.15).

4. A Single Semi-Infinite Cable

We consider next a single, semi-infinite cable (the positive real axis, $x \geq 0$) with either an open or closed terminal at the origin, $x = 0$. The Green's functions for these cases are given by,

$$G_{\pm}(x, y, t) = G_0(x - y, t) \pm G_0(x + y, t) \tag{4.1}$$

where the minus sign is for an open end and the plus sign for a closed end. We will now show how these results can be obtained from a sum over Brownian paths.

The existence of a terminal at the origin of a semi-infinite cable modifies the rules for generating the paths whose distribution determines the Green's function. As before we divide the time interval into N pieces and take spatial steps of length $(2t/N)^{1/2}$. To simplify the discussion we consider a lattice of points $n(2t/N)^{1/2}$, $n = 0, 1, 2, \ldots$ and restrict the initial point x to lie on this lattice.

To construct paths we start at the (lattice) point x and use the following probabilistic rules to construct N-step paths, $x \to z_1 \to z_2 \to \ldots \to z_{N-1} \to z_N = y$:

- As we proceed along the sequence of points, if a given z_a is not equal to zero we generate the next point in the sequence, z_{a+1}, by taking a step of one lattice length with probability 1/2 in either the positive or negative direction.

- If $z_a = 0$ so that we are at the terminal, a different rule is applied. For a closed-end boundary condition a path that hits the origin is reflected back in the positive direction with probability 1. For an open-end boundary condition, any path that touches the origin is not counted as a path going from x to y, although it is included in the total number of paths P.

To determine what we get when we sum over paths using this modified rule it is helpful to re-examine paths on an infinite cable. Consider Brownian paths going from a positive value of x to a positive value of y on an infinite cable. These paths can be broken up into two classes, those that touch the origin and those that do not. Paths that touch the origin may do so an arbitrary number of times. In the sequence of points from x to y there must be a last time that the path touches the origin before proceeding to y. Imagine that we take the portion of the total path that goes from this last contact with the origin to y and reflect it about the origin. We have now generated a path that connects the point x not to the point y but to the point $-y$. Since we can perform such a reflection for every path connecting x and y that touches the origin and since all paths going from x to $-y$ must touch (and in fact cross) the origin, we see that there is a one-to-one correspondence between paths connecting x to $-y$ and paths connecting x to y that touch the origin. Therefore, the result of summing over all Brownian paths connecting x to $-y$, $G_0(x + y, t)$, must be equal to the sum over all paths connecting x to y that touch the origin.

If we have an open-end boundary condition at the origin we do not allow paths that touch the origin. Thus, for the open-end condition we must subtract from the sum over all paths on the whole line, $G_0(x - y, t)$, all paths that touch the origin. Since paths that touch the origin generate the distribution $G_0(x+y,t)$, the result of applying the open-end rule for Brownian paths is the Green's function $G_-(x,y,t) = G_0(x-y,t) - G_0(x+y,t)$.

The rule for generating paths in the closed-end case reflects all paths that touch the origin back in the positive x direction. Consider again paths on an infinite cable. All paths from positive x to positive y on an infinite cable have analogs on a semi-infinite cable with a closed end where any excursions into the negative x region for paths on the infinite cable are reflected about the origin back to the positive x side of the semi-infinite cable. The sum of these paths produces a factor $G_0(x-y,t)$. In addition, paths that go from x to $-y$ on an infinite cable have corresponding partners on the semi-infinite cable that are reflected over to y. These sum to give a factor $G_0(x+y,t)$. Adding these two contributions gives the closed-end Green's function $G_+(x,y,t) = G_0(x-y,t) + G_0(x+y,t)$.

The discussion in the previous three paragraphs involved reflection arguments on an infinite cable. These arguments are made to demonstrate that the results we obtain using our rules for random paths on the semi-infinite cable are correct. We remind the reader that the rules given in this section involve paths which move exclusively on the semi-infinite cable.

Once we know the rule for generating random paths it is trivial to extend the path integral to the case of a semi-infinite cable with spatially-varying conductivity. The appropriate weighting factor is once again (3.3) and Eq. (3.4) for the Green's function applies in this case as well if we use the rules given in this section to generate the P random N-step paths.

5. A Single Branching Node

We now consider the Green's function for a single branching node with an arbitrary number of semi-infinite segments radiating from it as shown in Fig. 2. This can be obtained from reasoning similar to that used in the last section. As in Sec. 2 we define the branching node to be the origin for coordinates on all of the segments radiating from it. The Brownian paths that generate the appropriate Green's function run from x to y in N steps of size $(2t/N)^{1/2}$ and the spatial coordinates are latticized with a lattice spacing of $(2t/N)^{1/2}$ as before. The sequence of points $x \to z_1 \to z_2 \to \ldots \to z_{N-1} \to z_N = y$ is generated using the following probabilistic rules:

- For z_a on a given segment but not at a node, the next point in the path sequence, z_{a+1}, is obtained by moving one step in either direction along that segment with probability $1/2$.
- When z_a is at the node, we choose the next point to lie one step away on segment k with probability p_k. The new segment k can be any one of the segments attached to the node including the original segment itself. The p_k values are given in terms of the segment radii a_k by

$$p_k = \frac{a_k^{3/2}}{\sum\limits_{m\ on\ node} a_m^{3/2}} \tag{5.1}$$

  where the sum is over all segments m attached to the node.

It is interesting to note that if $p_k = 1/2$ for a certain segment k then the reflection and transmission probabilities from segment k through the node are both $1/2$ just as they are for any point on the segment away from the node. In this case, the node in some sense acts no differently than an ordinary point on a single cable. In the path integral language, this is the basis of Rall's [see Rall 1977] equivalent cable concept.

We can evaluate the path integral given by the above rules to determine the Green's function and show that it obeys the correct equations and boundary conditions. Let the point x lie on branch i and the point y on branch j. If $i = j$ there is a contribution to the Green's function from paths that do not touch the node. As in the last section the sum over paths that do not touch the node gives the contribution $G_0(x - y, t) - G_0(x + y, t)$. Since these paths do not touch the node there is no p_k dependence in this term.

Now consider paths that do touch the node. Each time these paths hit the node they proceed down segment k with probability p_k. The key feature for these paths is that no matter how many times a path touches or crosses the node the only weighting factor that actual matters is the one arising from the last time the path touches the node before proceeding to y. To see this, consider a path that somewhere in its travels makes an excursion from the node down one of the segments and then returns to the node. The sum over all paths will receive contributions from paths with similar excursions going down all the different segments connected to the node. The probability connected with an excursion going down the segment k is p_k. However, when we sum over all paths we sum the probability p_k over all k, which gives one. Thus, the probability factors associated with node-to-node excursions are irrelevant in the sum over paths. The only probability factor that does not sum in this way is the one associated with the last time the path leaves the node to go to the point y.

Because of the elimination of all but the last probability factor, the only difference between paths that go from x on segment i to y on different segments j is the particular value of p_j determined by the last section of the path. Otherwise, the paths are all in direct correspondence with paths on an infinite cable going from x to $-y$ through the origin (which is equivalent to going through the node). The factor of p_j associated with the final segment j has the effect of multiplying the distribution obtained from summing these paths by a factor $2p_j$. (The factor is $2p_j$ not p_j because analogous paths on an infinite cable going from x to y and from x to $-y$ are both included with probability p_j.)

To obtain the Green's function for a single branching node we must add the contribution $\delta_{ij}(G_0(x-y,t) - G_0(x+y,t))$ from paths that do not touch the node to that from paths that do touch the node, $2p_j G_0(x + y, t)$, to obtain

$$G_{ij}(x, y, t) = \delta_{ij} G_0(x - y, t) + (2p_j - \delta_{ij}) G_0(x + y, t). \tag{5.2}$$

To show that this Green's function obeys the correct boundary conditions (2.9) and (2.10) we note that

$$G_0(y, t) = G_0(-y, t) \tag{5.3}$$

and

$$\left.\frac{\partial G_0(x - y, t)}{\partial x}\right|_{x=0} = -\left.\frac{\partial G_0(x + y, t)}{\partial x}\right|_{x=0}. \tag{5.4}$$

As a result

$$G_{ij}(0, y, t) = 2p_j G_0(y, t) \tag{5.5}$$

which satisfies the boundary condition (2.9) because it is independent of i. Likewise

$$\left.\frac{\partial G_{ij}(x, y, t)}{\partial x}\right|_{x=0} = 2\,(\delta_{ij} - p_j)\left.\frac{\partial G_0(x - y, t)}{\partial x}\right|_{x=0} \tag{5.6}$$

which satisfies

$$\sum_i p_i \left.\frac{\partial G_{ij}(x,y,t)}{\partial x}\right|_{x=0} = 0 \tag{5.7}$$

because the p_i's sum to one. Since the p_i's are proportional to $a_i^{3/2}$ this is equivalent to the boundary condition (2.10). The reader can check that the Green's function (5.2) obeys the initial condition (2.8).

6. Path Integral for an Arbitrary Tree

The rules for generating the random paths needed to compute the Green's function on an arbitrary dendritic tree are essentially identical to those given in Secs. 4 and 5. We construct a spatial lattice with spacing $(2t/N)^{1/2}$ and require for simplicity that the initial point x and all the nodes and terminals lie on the lattice. We generate the sequence of points $x \to z_1 \to z_2 \to \ldots \to z_{N-1} \to z_N = y$ defining the path by stepping from a point z_a anywhere in the sequence to the next point in the sequence, z_{a+1}, with a probability determined by the position of z_a:

- If z_a lies on segment k and is not at a node or terminal, we step in either direction along that segment with probability 1/2.
- If z_a is at a node point, we take one step onto any segment k connected to that node with probability p_k given by Eq. (5.1).
- If z_a is at a terminal which is a closed end, we take the next step away from the terminal with probability 1. If the terminal is an open end the path is not counted as a path going from x to y although it is included in the total number of paths P.

Once again the Green's function is obtained by summing over paths going from x to y in time t as in Eq. (3.2).

Note that for non-terminating segments there are two probability factors associated with each segment k, one for each end. In Eq. (5.1) we have labeled p with a single subscript. In most cases it will be clear which end of the segment k we are referring to, but when a possible confusion might arise we use p_k to denote the probability for the end at $x = 0$ and q_k for the end at $x = L_k$.

We now show that the Green's function obtained from these Brownian paths satisfies the correct boundary conditions at all the branching nodes and terminals of the tree. The rules we have given are Markov, that is, the rule for moving from one point to the next is independent of the past history of the path. This guarantees that the convolution identity (2.13) is satisfied. Using the convolution property we can write

$$G_{ij}(x,y,t) = \sum_k \int_0^{L_k} dz\, G_{ik}(x,z,\epsilon) G_{kj}(z,y,t-\epsilon). \tag{6.1}$$

with ϵ as small as we like. Consider a branching node at $x = 0$. To investigate the boundary conditions at this node we need to study the Green's function near $x = 0$. In evaluating $G_{ik}(x,z,\epsilon)$ we see that paths which move away from x by more than $\epsilon^{1/2}$ are exponentially suppressed. In the limit $\epsilon \to 0$, the paths contributing to $G_{ik}(x,z,\epsilon)$ do not touch or cross any other nodes or terminals on the tree other than the one in question. In this case, the rules we have given above are identical to those of Sec. 5 and it follows from the arguments of that section that our rules generate a $G_{ik}(x, z, \epsilon)$ that obeys the correct boundary conditions. The above convolution identity then indicates that the full Green's function also satisfies the boundary conditions. An identical argument shows that our rules produce a Green's function that satisfies the boundary condition at a terminal.

Now that we know the rules for generating random paths on an arbitrary tree we can easily write down the path integral for an arbitrary tree with a spatially-varying conductivity. Of the P paths generated, those with final point y are summed with an appropriate U-dependent weighting factor. Specifying a path by the sequence of points $x \to z_1 \to z_2 \to \ldots \to z_{N-1} \to z_N = y$, the path integral formula for the Green's function is

$$G(x, y, t) = \lim_{N\to\infty} \lim_{P\to\infty} \frac{1}{P} \sum_{from\ x\ to\ y}^{Paths} \exp -\frac{t}{N}\left[\frac{1}{2}U_i(x) \right. \tag{6.2}$$

$$\left. +U_{k_1}(z_1) + U_{k_2}(z_2) + \ldots + U_{k_{N-1}}(z_{N-1}) + \frac{1}{2}U_j(y)\right].$$

If the point z_a is on segment k_a then U_{k_a} is the varying conductivity factor on that segment. If z_a is at a node, U_{k_a} is the conductivity factor for the node. A numerical approximation of the Green's function can be obtained by performing this weighted sum using large but finite P and N.

7. An Arbitrary Tree with Synaptic Inputs

To include both the spatial and temporal variations of the conductivity required for realistic synaptic inputs we must let the factor U in Eq, (2.14) depend on both space and time,

$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} - [1 + U(x, t)]v + I(x, t). \tag{7.1}$$

In this case the membrane potential can still be written in terms of a Green's function

$$v_i(x, t) = \sum_j \left[\int_0^{L_j} dy\, G_{ij}(x, y, t, 0)e^{-t}v_j(y, 0) \right. \tag{7.2}$$

$$\left. + \int_0^t ds \int_0^{L_j} dy\, G_{ij}(x, y, t, s)e^{s-t}I_j(y, s)\right]$$

but now the Green's function depends on s and t independently, not just on their difference. This Green's function satisfies the equation

$$\frac{\partial G_{ij}(x, y, t, s)}{\partial t} = \frac{\partial^2 G_{ij}(x, y, t, s)}{\partial x^2} - U_i(x, t)G_{ij}(x, y, t, s) \tag{7.3}$$

for $t > s$ and the initial condition

$$G_{ij}(x, y, s, s) = \delta_{ij}\delta(x - y). \tag{7.4}$$

Although the extra s dependence complicates the notation somewhat, it is trivial to extend the formula (6.2) to the time-dependent case. The key is that the same rules used to generate random paths in Sec. 6 can be used here. The effect of the time-dependent conductivity only appears in the weighting factor for the sum over paths. Again specifying a path by the sequence of points $x \to z_1 \to z_2 \to \ldots \to z_{N-1} \to z_N = y$ the Green's function is given by

$$G(x, y, t, s) = \lim_{N\to\infty} \lim_{P\to\infty} \frac{1}{P} \sum_{from\ x\ to\ y}^{Paths} \exp - \frac{t}{N} \left[\frac{1}{2} U_i(x, t) \right. \tag{7.5}$$

$$\left. + U_{k_1}(z_1, t - \Delta t) + \ldots + U_{k_{N-1}}(z_{N-1}, t - (N-1)\Delta t) + \frac{1}{2} U_j(y, s) \right]$$

where

$$\Delta t = \frac{t - s}{N}. \tag{7.6}$$

Once again this can be evaluated for large P and N to obtain an approximate Green's function.

8. The Exact Green's Function for an Arbitrary Tree

The results and discussion of Sec. 5 and results derived for other simple structures suggested to us some simple rules for constructing an exact expression for the Green's function on an arbitrary tree with constant conductivity. We now present these rules and show that they do, in fact, generate the correct Green's function. The idea is to express the Green's function for an arbitrary tree as a sum of terms involving the Green's function for an infinite cable, G_0. We could in principle obtain the exact Green's function for any tree by generalizing the reflection arguments of Secs. 4 and 5, but this is more cumbersome than just presenting the rules and showing that they work.

The Green's function $G_{ij}(x, y, t)$ for an arbitrary tree is obtained by summing terms that arise from all possible 'trips' from x on segment i to y on segment j. We use the word 'trip' specifically to avoid confusion with the 'paths' of the path integral. A trip is a path, but a highly restricted one. Typical paths in the path integral make frequent changes of direction while trips may only change direction at a node or terminal. The trips are a diagrammatic device for constructing terms in the expression for the desired Green's function. To construct trips we start at the point x and proceed to the point y along any path obeying the following rules:

- A trip may start out from x in either direction on segment i but it may subsequently change direction only at a node or terminal. A trip may pass through the points x and y an arbitrary number of times but must begin at x and end at y.
- At a node a trip may pass through to any other segment connected to the node or it may reflect from the node back along the same segment on which it entered.
- At a terminal the trip always reflects back, reversing its direction.

Every trip generates a term in the sum for the Green's function. For a trip of length (distance along the cable) L this term is $AG_0(L, t)$ where A is a product of factors for each node or terminal either touched or passed through along the trip. Specifically A consists of:

- A factor of $2p_m$ for every node at which the trip passes from an initial, entering segment k to a different segment m ($m \neq k$) with p_m given by Eq. (5.1) applied to that node.

- A factor $(2p_k - 1)$ for every node at which the trip enters along segment k and then reflects off the node back along segment k. The probability p_k is again given by Eq. (5.1).
- A factor $+1$ for every closed-end terminal and a factor -1 for every open-end terminal at which the trip is reflected.

The sum of contributions arising from all possible trips generated by these rules gives an exact expression for the Green's function on any dendritic structure.

To show that the above rules correctly produce the Green's function we must show that the resulting sum satisfies the differential equation (2.7), the initial condition (2.8), the boundary conditions (2.9) and (2.10) at all nodes and (2.11) or (2.12) at all terminals. Since the result of applying these rules is a sum of functions G_0 that satisfy (2.7) it is clear that this basic cable equation is satisfied. In addition, the only term that can be non-zero at $t = 0$ is one corresponding to a straight line trip from x to y when x and y are on the same segment. This has weight $A = 1$ giving the correct initial condition $G_0(x - y, 0) = \delta(x - y)$. Thus, all we need to do is to check the boundary conditions.

Consider first the boundary condition at an arbitrary node of the tree. To study the boundary condition we only need to consider points that are arbitrarily close to the node along one of its radiating segments. Suppose this point is a distance x away from the node on radiating segment i. The position of y is arbitrary as is the time t. Let us begin by considering all trips not from x to y but from the node itself to y. These trips may begin by leaving the node along any one of its radiating segments k. Let the function $F_k(0, t)$ represent the result of summing contributions from all trips that initially leave the node along the segment k. No p-dependent factor is include in the F's for the initial node itself. The zero argument of $F_k(0, t)$ is to remind us that this function corresponds to trips starting at the node.

Now consider trips starting at the point x on segment i rather than at the node. There are three types of trips we need to consider. First, the trip may start from the point x and initially travel away from the node in question. Such trips are identical to trips that originate at the node itself and start out along segment i except that they are shorter by the amount x. As a result they give contributions to the sum identical to those for trips from the node except that all the distance are shifted downward by an amount x. We let $F_i(-x, t)$ represent this shifted sum.

Instead of leaving x in the direction away from the node, a trip may initially proceed toward the node. When it reaches the node the trip may either reflect back along segment i or go through continuing along one of the other segment $k \neq i$. If it reflects off the node the resulting trips are again identical to those originating at the node and starting out along segment i except in this case they are longer by the amount x. In addition, according to the above rules these trips pick up a factor of $(2p_i - 1)$. Thus, the result of summing contributions generated by this class of trips is $(2p_i - 1)F_i(x, t)$. Finally, trips originating at x that start out by passing through the node and proceed out along a segment $k \neq i$ are identical to trips proceeding from the node itself out along segment k except that they are longer by an amount x. The contribution coming from these trips picks up a factor $2p_k$ from passing through the node. Summing over all nodes $k \neq i$ we find that the Green's function can be written in the form

$$G_{ij}(x,y,t) = F_i(-x,t) + (2p_i - 1)F_i(x,t) + \sum_{k\neq i} 2p_k F_k(x,t). \tag{8.1}$$

The functions F appearing in this formula correspond to complicated sums over restricted trips, but fortunately we do not need to know what they are to show that (8.1) satisfies the node boundary conditions. Immediately, we see that

$$G_{ij}(0,y,t) = \sum_k 2p_k F_k(0,t). \tag{8.2}$$

The sum is now over all k values corresponding to segments radiating from the node, including i. This obeys the boundary condition (2.9) because it does not depend on i. To check the second boundary condition we note that

$$\left.\frac{\partial G_{ij}(x,y,t)}{\partial x}\right|_{x=0} = \sum_k 2p_k \left.\frac{\partial F_k(x,t)}{\partial x}\right|_{x=0} - 2\left.\frac{\partial F_i(x,t)}{\partial x}\right|_{x=0}. \tag{8.3}$$

Multiplying this result by p_i, summing over i and using the fact that the p_i's sum to one, we see that the boundary condition (2.10) is indeed satisfied.

Our rule for terminals is identical to that for nodes if we take $p_k = 0$ for $k \neq i$ and $p_i = 0$ for an open end or $p_i = 1$ for a closed end. Therefore, the above derivation can be repeated to show that the appropriate boundary conditions are also obeyed at all terminals.

The rules for computing Green's functions on arbitrary trees are remarkably simple. Of course, in all but the most trivial cases these rules result in an infinite sum for the Green's function. However for any fixed t, trips with lengths much longer than $(t)^{1/2}$ will make only small contributions and the sum can be truncated to included only thoses trips shorter than some chosen constant times $(t)^{1/2}$. Using a good algorithm for generating trips, the solution we have given should provide an extremely fast and efficient method for solving cable problems. Application of this method will be considered in a follow-up paper.

To illustrate the use of the rules we have given we consider the Green's function on a tree consisting of two nodes with an arbitrary number of semi-infinite segments radiating from them joined by a single segment (see Fig. 3). This result will be useful for constructing a Feynman-like expression for the path integral in the Appendix. We first consider the case (Fig. 3a) when x and y are both on the interconnecting segment i. Four simple trips are shown in Fig. 3a. In addition to the trips shown, there are longer trips constructed from these trips by adding on journeys up and down the interconnecting segment from one node to the other and back again. This may happen an arbitrary number of times and each round-trip excursion adds an amount $2L_i$ to the total length of the trip. We do not have to consider any trips that cross either node. Such trips will never return to the interconnecting segment because the other radiating segments have no terminals or further nodes from which reflection can occur. Using the above rules we can sum the contribution coming from the trips we have discussed. Let p_i be the reflection probability on segment i for the node at $x = 0$ and q_i the reflection probability for the node at $x = L_i$. Then,

$$\begin{aligned} G_{ii}(x,y,t) &= \sum_{n=0}^{\infty} [(2p_i - 1)^n (2q_i - 1)^n G_0(y - x + 2nL_i, t) \\ &\quad + (2p_i - 1)^n (2q_i - 1)^{n+1} G_0(2L_i - x - y + 2nL_i, t) \end{aligned} \tag{8.4}$$

$$+(2p_i-1)^{n+1}(2q_i-1)^n G_0(x+y+2nL_i,t)$$
$$+(2p_i-1)^{n+1}(2q_i-1)^{n+1} G_0(2L_i+x-y+2nL_i,t)\Big].$$

The four terms written in Eq. (8.4) correspond to the terms 1) to 4) shown in Fig. 3a plus n excursions up and down segment i between the two nodes.

Simple trips for the case when x is on the interconnecting segment i but y is on one of the semi-infinite radiating segments $j \neq i$ are shown in Fig. 3b. Here y measures the distance from the node at $x = L_i$ to the point marked on segment j in Fig. 3b. Again, we can add arbitrary numbers of journeys up and down the interconnecting segment to the trips shown. The resulting Green's function for $i \neq j$ is

$$\begin{aligned} G_{ij}(x,y,t) &= 2p_j \sum_{n=0}^{\infty} \big[(2p_i-1)^n(2q_i-1)^n G_0(L_i-x+y+2nL_i,t) \\ &\quad +(2p_i-1)^{n+1}(2q_i-1)^n G_0(L_i+x+y+2nL_i,t)\big] \end{aligned} \tag{8.5}$$

where p_j is the probability for proceeding down segment j from the node at $x = L_i$.

9. Interchange of End Points

We have given rules for computing the Green's function $G_{ij}(x,y,t)$ from paths (or trips) that begin at the point x on segment i and proceed to various points y on segments j in time t. For some purposes we may want to know the Green's function for fixed y, j and t as a function of x and i. In this case we want to generate Brownian paths that start at y on segment j and move to x on segment i. If we generate the paths in reverse order the probability factors associated with crossing a node will all be different. However as we will see, the result of summing over paths is only modified by a simple factor. We consider only the case of time-independent conductivity.

Let us begin by generating a random path in the normal way from x on segment i to y segment j. Suppose that somewhere in its travels this path goes from a segment k through a node that we will label node 1, onto another segement k'. When the path leaves segment k' it passes through another node, node 2, to yet another segment k''. The probability factor associated with this particular portion of the total path involves the product of probabilities for crossing each node. Written in terms of the radius variables using (5.1) this factor is

$$\frac{a_{k'}^{3/2}}{\sum\limits_{m \text{ on node } 1} a_m^{3/2}} \frac{a_{k''}^{3/2}}{\sum\limits_{m \text{ on node } 2} a_m^{3/2}}. \tag{9.1}$$

If we had generated this path in the reverse order, $k'' \to k' \to k$, then the factor would be instead

$$\frac{a_{k'}^{3/2}}{\sum\limits_{m \text{ on node } 2} a_m^{3/2}} \frac{a_{k}^{3/2}}{\sum\limits_{m \text{ on node } 1} a_m^{3/2}} \tag{9.2}$$

because the probability factors are associated with the final segment in a node crossing. In terms of the original probability variables, (9.1) and (9.2) are completely different. However written as above in terms of the radii, a cancellation takes place and the ratio of (9.2) to (9.1) is just $(a_k/a_{k''})^{3/2}$. We can repeat this argument for arbitrary numbers of node crossings and we find that the ratio between the results obtained by using paths from y to x compared with paths from x to y is just the ratio of the radii of the initial and final segments raised to the 3/2 power. As a result,

$$G_{ij}(x,y,t) = \left(\frac{a_j}{a_i}\right)^{3/2} G_{ji}(y,x,t). \tag{9.3}$$

The result (9.3) is rather remarkable because the multiplicative factor only depends on the radii of segments i and j and not on the radii of intermediate segments. As we have noted, this simplification is due to the particular relation between the probabilities p_k and the radii a_k given by Eq. (5.1).

10. Structures with Loops

Neuronal dendritic trees do not loop. Nevertheless, it is interesting to note that all the results we have discussed are completely applicable to structures containing loops. The rules we have given for generating random paths, the exact results for constant conductivity, the weighted sum formulas for spatially-varying and time-dependent conductivities and the interchange formula (9.3) all hold for dendritic structures with loops.

All of the results we have given are expressed in terms of the probability factors p_k given by Eq. (5.1). However, the basic parameters characterizing a dendritic structure are the radii a_k. Recall that there are two probability factors associated with each non-terminating segment, but such a segment has of course only one radius. Despite this, there are still the same number of relevant radius parameters as free probabilities for a structure without loops. However, when loops are present this is no longer true. To derive these results, consider a structure with S segments, V nodes and T terminals. There are S radius variables for such a structure. However, it is clear from the basic cable equations that an overall scaling of all segment radii has no effect, so among the S radii there are $S-1$ relevant free parameters. The number of probability factors p_k can be counted as follows. There is a probability associated with each end of a segment that connects to a node. Since there are twice as many segment ends as segments there are $2S - T$ node probability factors. At each node the sum of the probabilities is constrained to be one, so there are $2S - T - V$ free parameters among the probabilities. From the Euler relation ($L = S - T - V + 1$) for a structure with L loops, we find that

$$2S - T - V = (S - 1) + L \tag{10.1}$$

where L is the number of loops in the structure. If $L = 0$, as it does for neuronal trees, the number of free parameters in terms of radii or probabilities matches and there is no restriction introduced by the relation (5.1). However, if there are loops in the structure there are more free probabilities than radii and (5.1) is a genuine constraint. If the probabilities satisfy (5.1) then (9.3) is still valid for structures with loops.

11. Discussion

We see three main applications of our results. First, the formal methods used here may be helpful for deriving useful identities and explicit results in special cases of interest. Second, the rules of Sec. 8 for obtaining the exact Green's function provide an extremely fast and efficient method for solving cable problems either analytically or numerically. The interchange formula, (9.3), is useful in cases where the x dependence of the Green's function for fixed y is needed.

Finally, the path integral formula for the Green's function, as well as the exact expression given by the rules of Sec. 8, allows a novel form of analysis to be applied to the characterization of the cable properties of large populations of neurons. It is unlikely that detailed structural information will be available for large numbers of neurons in a biological neural network of interest, or that such information could be used even if it were available. However, it may be possible to obtain statistical information like the distributions of segment lengths or numbers of nodes for dendritic trees in a large population of cells. This information cannot simply or directly be incorporated into an analysis based directly on the cable differential equation. However, the path integral expression for the Green's function (or our exact expression) can be averaged over the statistical distribution of cable structures to obtain an average Green's function for the neuronal population. Such averaging of the path integral is used extensively in statistical physics. Applied to dendritic structures, this approach should be extremely helpful for determining what statistical properties are important for characterizing the cable properties of a neuronal population as well as for evaluating the average dendritic response of neurons in the population. Work on these ideas is currently in progress.

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Appendix: Feynman Formula for the Path Integral

In the body of this paper, we defined the path integral in terms of Brownian paths approximated by random walks. For completeness, we now consider an alternate way of summing over paths, Feynman's approach, which is more commonly used in physics applications. As before, paths are specified by the sequence $x \to z_1 \to z_2 \to \ldots \to z_{N-1} \to z_N = y$ but now the coordinates will be allowed any values on the tree and the sum over paths will be performed by integrating over all values of the z_a. In the limit $N \to \infty$ both methods converge to the same path integral.

The Feynman formula is based on an N-fold convolution identity for the Green's function. By repeatedly applying the convolution identity (2.13) we can write the Green's function as a convolution of an arbitrary number of terms,

$$G_{ij}(x,y,t) = \sum_{k_1,\ldots k_{N-1}} \prod_{a=1}^{N-1} \int_0^{L_{k_a}} dz_a \; \Big[G_{ik_1}(x,z_1,t/N) \times G_{k_1k_2}(z_1,z_2,t/N) \times \ldots \times G_{k_{N-1}j}(z_{N-1},y,t/N)\Big] \tag{A.1}$$

for any N. We have used a compact product notation to denote the $N-1$ nested integrals in this and the following expressions. This formula holds for spatially-varying conductivity as well as in the time-dependent case. The basic idea is that for large N, Eq. (A.1) gives the Green's function for an arbitrary time interval t in terms of an N-fold convolution of Green's functions for short time intervals t/N. The path integral expression is constructed by using an approximate formula for $G_{k_ak_{a+1}}(z_a, z_{a+1}, t/N)$ valid in the limit $N \to \infty$ inside the integral of Eq. (A.1) to obtain a formula for the unknown Green's function.

We consider first the case of a single, semi-infinite cable with spatially-varying conductivity $[1 + U(x)]/R$ and either an open or closed end at $x = 0$. To make use of Eq. (A.1) we need an approximate expression for the unknown Green's function $G(z_a, z_{a+1}, t/N)$ that becomes exact in the limit $N \to \infty$. $G(z_a, z_{a+1}, t/N)$ has the property that it vanishes exponentially for separations $(z_a - z_{a+1})^2 \gg t/N$. As a result, paths with such large single-step separations contribute a negligible amount to the convolution integral (A.1) and it is sufficient to use an approximate expression for G valid for $(z_a - z_{a+1})^2$ of order t/N. For large enough N, the varying conductivity factor U is approximately constant over a distance of order $(t/N)^{1/2}$ so we can replace it on the spatial interval between z_a and z_{a+1} by its average value $[U(z_a) + U(z_{a+1})]/2$. Recall that $G(x, y, t)$ satisfies the differential equation (2.15). For constant U, Eq. (2.15) can easily be solved to get the approximation for large N

$$G(z_a, z_{a+1}, t/N) \approx G_\pm(z_a, z_{a+1}, t/N) e^{-\frac{t}{2N}[U(z_a)+U(z_{a+1})]} \tag{A.2}$$

where the Green's function $G_\pm$ is used so that the appropriate boundary condition is satisfied at $x = 0$. Substituting this into Eq. (A.1) and taking the limit $N \to \infty$ gives the result we seek,

$$\begin{aligned} G(x, y, t) = \lim_{N\to\infty} \prod_{a=1}^{N-1} \int_0^\infty dz_a \, \Big[& e^{-\frac{t}{2N}U(x)} G_\pm(x, z_1, t/N) \\ & \times e^{-\frac{t}{N}U(z_1)} G_\pm(z_1, z_2, t/N) e^{-\frac{t}{N}U(z_2)} \times \ldots \times G_\pm(z_{N-1}, y, t/N) e^{-\frac{t}{2N}U(y)} \Big]. \end{aligned} \tag{A.3}$$

The techniques required to rigorously establish this result are given in Nelson [1964].

If consecutive points z_a and z_{a+1} in (A.3) are not too near the origin we can use the Green's function $G_0(z_a - z_{a+1}, t/N)$ rather than $G_\pm(z_a, z_{a+1}, t/N)$. The Green's function for a time step t/N is exponentially small outside an effective range of order $(t/N)^{1/2}$. If z_a and z_{a+1} are much further away from the origin than this effective range then the boundary condition at the origin has no appreciable effect on the Green's function and we can use the Green's function for an infinite cable. We can easily evaluate the error introduced by using the Green's function G_0 rather than $G_\pm$. Note that

$$G_\pm(z_a, z_{a+1}, t/N) = G_0(z_a - z_{a+1}, t/N)[1 \pm \exp -(N z_a z_{a+1}/t)]. \tag{A.4}$$

Suppose we use G_0 instead of $G_\pm$ for all steps in the path integral for which z_a and z_{a+1} are both greater than some Δ. The maximum error in the resulting path integral occurs when all N steps of the path have $z_a = z_{a+1} = \Delta$. Use of G_0 instead of $G_\pm$ will in this worst case multiply the path integral by a factor

$$[1 \pm \exp -(N\Delta^2/t)]^N \tag{A.5}$$

which goes to one in the limit $N \to \infty$ provided that

$$\Delta > (1 + \epsilon)\sqrt{\frac{t \ln N}{N}} \tag{A.6}$$

for any $\epsilon > 0$. This means that in order to obtain the correct expression for the path integral with non-trivial boundary conditions we only need to worry about incorporating the boundary condition corrections to the Green's function in a region close to the boundary whose size goes to zero as $N \to \infty$. In the present case, we might as well use $G_\pm$ in the path integral for all path steps, but for cable segments with boundaries on both ends it will be important that we can treat each node independently using the above argument.

To write a Feynman-like expression for the path integral on a general tree we write the N-fold convolution formula (A.1) and again use an approximate expression, valid for large N, for the Green's function appearing inside the convolution integral. For the case of a semi-infinite cable, the approximate expression (A.2) turned out to be an exponential involving the factor U times the exact Green's function for the semi-infinite cable with $U = 0$. The same result applies here. However, the exact Green's function for an arbitrary tree is expressed as an infinite series even when $U = 0$ and we need to approximate this function as well.

The argument given above shows that it is sufficient if the approximate formula for the $U = 0$ Green's function reduces to G_0 away from a node or terminal and satisfies the correct boundary condition if z_a or z_{a+1} is within a distance of order $(t \ln N/N)^{1/2}$ of a node or terminal. The results of Sec. 8 provide the exact Green's function for $U = 0$. The appropriate expression for the infinitesimal Green's function is obtained by taking the limit of (8.4) and (8.5) for short times. Rather than using the notation z_a, z_{a+1}, k_a and k_{a+1} we will use the notation of Fig. 3. In this case we should imagine that Fig. 3 is part of a larger structure that does not have to be specified because we only want the Green's function for short times. To obtain the short-time Green's function we only need to include the contribution from the shortest possible trip. However, because we want an expression valid no matter where x and y are located relative to the nodes there are several terms. Specifically, in the N-fold convolution formula if x and y are on the same segment or separated by at most one node we will use the approximate Green's function

$$\begin{aligned}\tilde{G}_{ij}(x,y,t/N) = \delta_{ij}\,[G_0(x-y,t/N) + (2p_i-1)G_0(x+y,t/N) \\ +(2q_i-1)G_0(x+y-2L_i,t/N)] + 2p_j(1-\delta_{ij})G_0(d(x,y),t/N).\end{aligned} \tag{A.7}$$

If x and y are separated by more than one node we take $\tilde{G} = 0$. The function $d(x,y)$ is just the distance along the cable between the two points that are its arguments. The explicit formula for this distance depends on how coordinates are defined on the different segments and so is not given. Of course inside the convolution integral the variables x, y, i, and j in Eq. (A.7) must be replace by the appropriate z_a,z_{a+1},k_a and k_{a+1}.

An expression for the Green's function on an arbitrary tree with spatially-varying conductance is obtained by using (A.7) in the path convolution formula,

$$\begin{aligned}G_{ij}(x,y,t) = \lim_{N\to\infty} \sum_{k_1,\ldots k_{N-1}} \prod_{a=1}^{N-1} \int_0^{L_{k_a}} dz_a\; e^{-\frac{t}{N}U_i(x)}\tilde{G}_{ik_1}(x,z_1,t/N) \\ \times e^{-\frac{t}{N}U_{k_1}(z_1)}\tilde{G}_{k_1k_2}(z_1,z_2,t/N)e^{-\frac{t}{N}U_{k_2}(z_2)} \times \ldots \\ \times e^{-\frac{t}{N}U_{k_{N-1}}(z_{N-1})}\tilde{G}_{k_{N-1}j}(z_{N-1},y,t/N)e^{-\frac{t}{2N}U_j(y)}.\end{aligned} \tag{A.8}$$

Again we could use the Green's function G_0 instead of $\tilde{G}$ in this formula if z_a and z_{a+1} are sufficiently far from any nodes or terminals but there is no real advantage in doing this.

For the case of a time-dependent conductivity, the Feynman formula for the path integral is obtained directly from (A.8) with the simple modification that the time-dependence of U is included,

$$G_{ij}(x,y,t) = \lim_{N\to\infty} \sum_{k_1,\ldots k_{N-1}} \prod_{a=1}^{N-1} \int_0^{L_{k_a}} dz_a\; e^{-\frac{t}{N}U_i(x,t)}\tilde{G}_{ik_1}(x,z_1,t/N)$$

$$\times e^{-\frac{t}{N}U_{k_1}(z_1,t-\Delta t)}\tilde{G}_{k_1k_2}(z_1,z_2,t/N)e^{-\frac{t}{N}U_{k_2}(z_2,t-2\Delta t)}\times\ldots \tag{A.9}$$
$$\times e^{-\frac{t}{N}U_{k_{N-1}}(z_{N-1},t-(N-1)\Delta t)}\tilde{G}_{k_{N-1}j}(z_{N-1},y,t/N)e^{-\frac{t}{2N}U_j(y,s)}.$$

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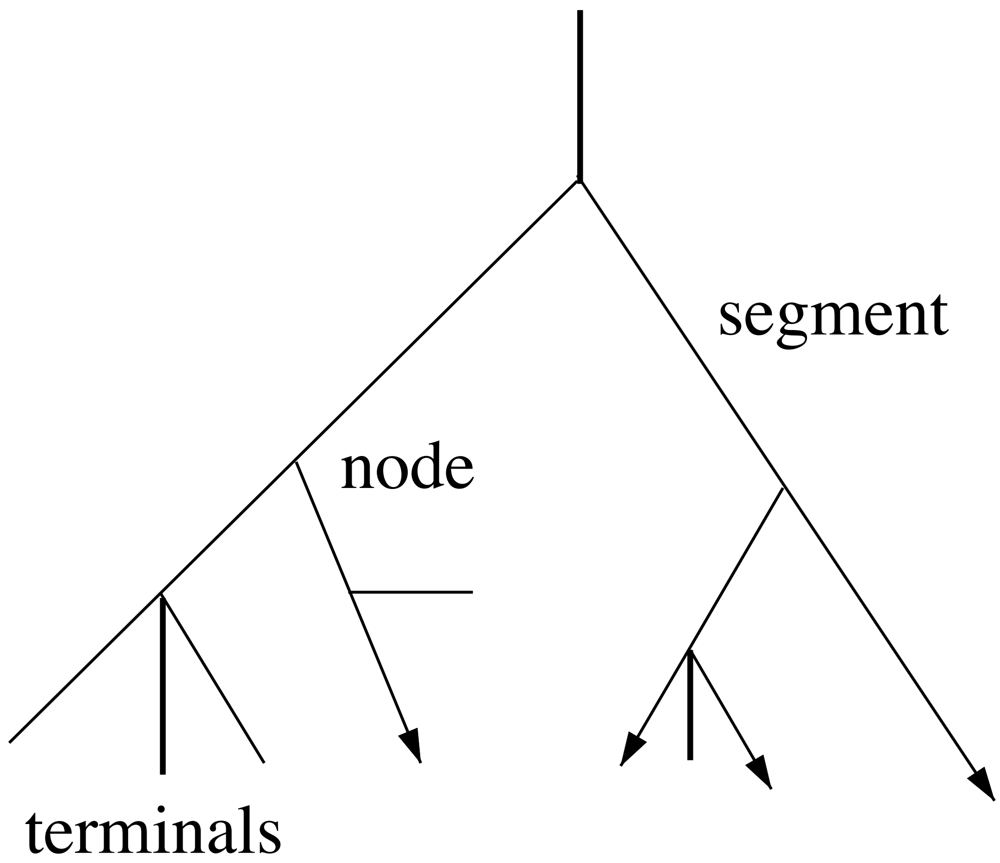

Fig. 1

Fig. 1: A typical dendritic tree with labeled segment, node and terminals. In this and the other figures, lines ending in arrows denote semi-infinite segments .

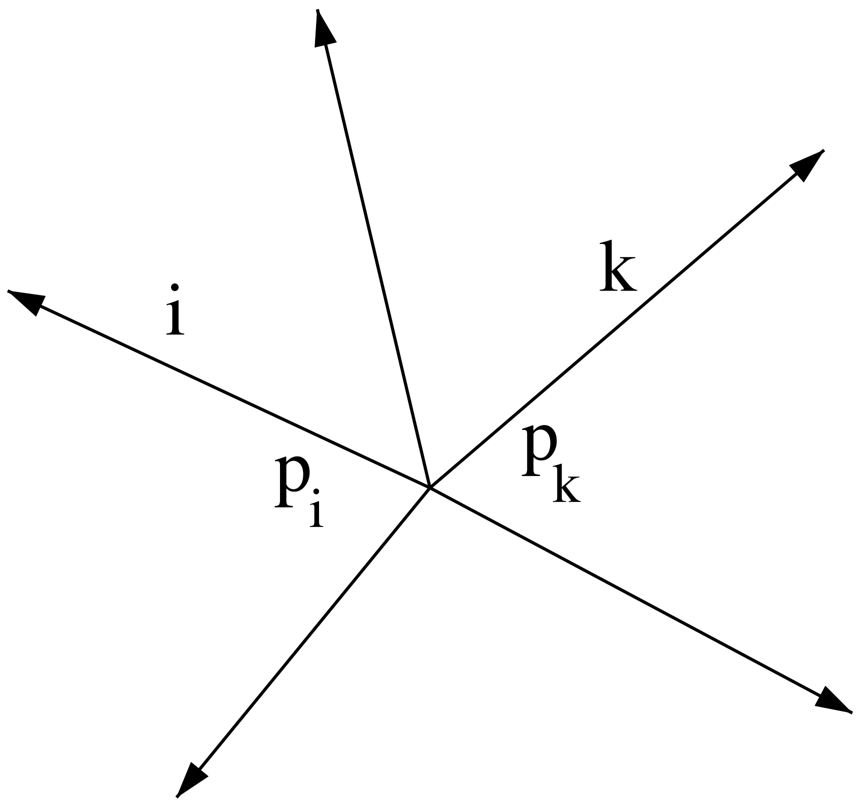

Fig. 2

Fig. 2: A single branching node. Two segments are labeled and their radius-dependent probability factors are indicated. All segments are semi-infinite.

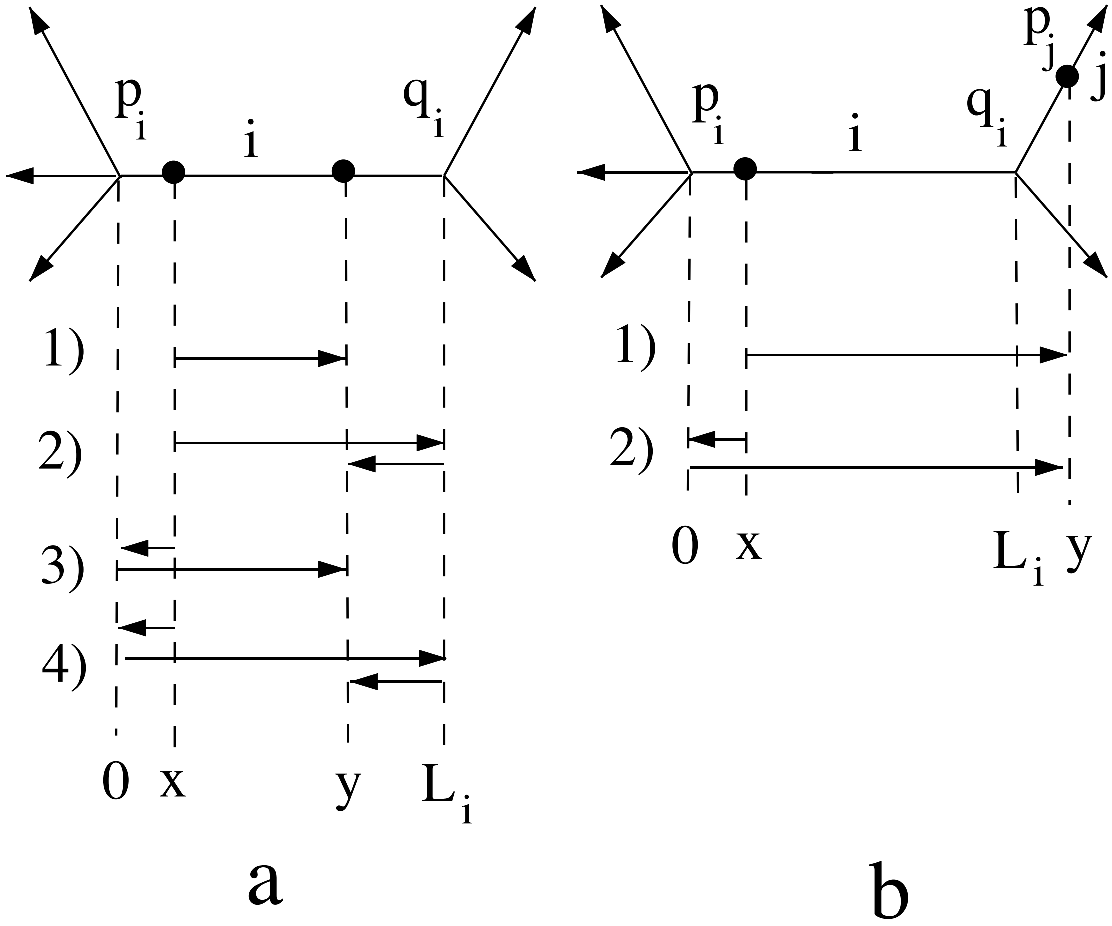

Fig. 3

Fig. 3: A two-node tree. In a) x and y are both located on segment i while in b) y is on another segment, j. In b), y measures the distance from the right-hand node to the point indicated on segment j. Beneath each figure, we show some of the trips used to compute the Green's function.