

**SIMPLE DIAGRAMMATIC RULES
FOR SOLVING
DENDRITIC CABLE PROBLEMS**

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Abstract

I present a set of diagrammatic rules for constructing a series solution of the linear cable equation on a dendritic tree of arbitrary geometry. The rules determine the Green's function for the time-dependent cable equation directly as a function of time and are particularly useful in the short-time limit. They can be implemented by computer algorithm and results from such a program are shown.

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1. INTRODUCTION

The computation of the potential on a highly branched, tree-like cable structure is a classic problem in mathematical biology [1, 2, 3]. This computation provides a model for the complex integration of synaptic inputs that occurs over the elaborate dendritic trees of neurons. It is the primary mathematical tool used to investigate the effects that the geometric form and electrotonic structure of a neuron have on its function. On a larger scale, properties of neuronal input integration play a key role in determining the behavior of neural networks [3-11].

Numerous cable computations for specific structures have appeared (see [1, 2, 3] for reviews and [12, 13, 14] for examples). Because these computations are often complex and difficult it is extremely useful to have diagrammatic rules to guide and assist the calculation. Diagrammatic rules for computing the Laplace transform of the cable potential have been given by Butz and Cowan [15]. The Laplace transform calculation is especially useful for computing the long-time behavior of the potential (see also [16]). The rules have been specialized to the case of a static potential by Koch and Poggio [17]. Recently E. Farhi, S. Gutmann and I have shown how the path integral formalism can be applied to the cable problem [18]. During the course of this work, we discovered a set of simple diagrammatic rules for computing the potential on a cable of arbitrary geometry directly as a function of time. This eliminates the need to perform an inverse Laplace transform and is particularly useful for investigating the short-time behavior of a dendritic tree.

2. Cable Theory

The basic problem of cable theory is to determine how the potential across the cell membrane of a neuron is affected by the current entering through synaptic input sites (in a natural setting) or through an electrode (in a laboratory setup). In mathematical terms, the problem is to solve for the potential on a branched structure like that shown in figure 1 given the initial value of the potential and the distribution of current being injected into the tree. Figure 1 introduces the naming and labeling conventions I will use. The tree consists of a number of segments that meet at nodes and end at terminals. Because the segments of a neuronal dendritic tree are long and narrow, they are represented in cable theory as one-dimensional structures. The segments are identified by an integer label and position along segment i is given by a coordinate x satisfying $0 \leq x \leq L_i$ where L_i is the length of segment i . The potential at position x on segment i at time t measured relative to the resting potential of the neuron is denoted by $v_i(x, t)$. The potential satisfies the cable equation

$$\frac{\partial v_i}{\partial t} = \frac{\partial^2 v_i}{\partial x^2} - v_i + I_i(x, t) \quad (2.1)$$

where $I_i(x, t)$ is the current being injected on segment i at the point x at time t .

Equation (2.1) is just an expression of the conservation of electric charge. The time derivative on the left side is proportional to the current leaving the region of segment i around the point x to charge the capacitance of the membrane. The second spatial derivative is the gradient of the current flowing longitudinally down the segment and thus is related to the net longitudinal current entering this region. The term $-v_i$ represents the Ohmic leakage of current out of the segment through the membrane. Thus, equation (2.1) equates the inward and outward currents (including the injected current I_i) so that the total current

sums to zero. The resistance per unit length of a segment of radius a_i is $r/(\pi a_i^2)$ where r is the intracellular resistivity. Typically, r is in the range $50 - 200 \Omega - cm$. The resistivity of the cell membrane, denoted by R , is typically in the range $10 - 100 k\Omega - cm^2$. The capacitance per unit area of membrane is $C \approx 1 - 2 \mu F/cm^2$. All these parameters have been eliminated from equation (2.1) by measuring time in units of the membrane time constant RC and the coordinate x and length L_i on segment i in units of the length constant $(Ra_i/2r)^{1/2}$.

The cable equation is, of course, a very familiar partial differential equation encountered in diffusion and heat flow problems and in quantum mechanics when an imaginary time formalism is used. Solving cable problems is particularly difficult because of the complex topological structure of the manifold on which this equation must be solved. As well as solving equation (2.1), the potential must satisfy boundary conditions at all the nodes and terminals of the tree. Consider a node where a number of segments meet as in figure 2a. The boundary conditions at such a node are continuity of the potential and conservation of charge. If we choose the coordinates on all of the radiating branches so that the node is at the point $x = 0$, then continuity of the potential requires that

$$v_k(0, t) = v_m(0, t) \quad (2.2)$$

for all values k and m corresponding to segments radiating from the node. Conservation of charge requires the sum of all longitudinal currents leaving the node to vanish which implies that

$$\sum_k a_k^{3/2} \left. \frac{\partial v_k(x, t)}{\partial x} \right|_{x=0} = 0. \quad (2.3)$$

The sum is over all k values corresponding to segments radiating from the node in question. The factor of $a_k^{3/2}$ in this boundary condition is due to the choice of dimensionless coordinates on the various radiating segments.

At a terminal like that shown in figure 2b, one of two possible boundary conditions will be imposed. If segment k terminates at $x = L_k$ then we require either that the potential vanishes at this point,

$$v_k(L_k, t) = 0 \quad (2.4)$$

or that the longitudinal current vanishes

$$\left. \frac{\partial v_k(x, t)}{\partial x} \right|_{x=L_k} = 0. \quad (2.5)$$

The first condition corresponds to an open end and the second to a closed end.

Equation (2.1) and the boundary conditions (2.2), (2.3), (2.4) and (2.5) completely specify the mathematics problem of cable theory. The solution can be written in terms of a Green's function,

$$v_i(x, t) = \sum_j \left[\int_0^{L_j} dy G_{ij}(x, y, t) e^{-t} v_j(y, 0) + \int_0^t ds \int_0^{L_j} dy G_{ij}(x, y, t-s) e^{s-t} I_j(y, s) \right] \quad (2.6)$$

where the sum on j is over all segments of the tree. I have included the exponential factors in equation (2.6) to simplify the definition of the Green's function $G_{ij}(x, y, t)$. If the tree

is initially at its resting potential, $v_i(x, 0) = 0$ for all i , the first term in equation (2.6) can be ignored. In this case, $G_{ij}(x, y, t)e^{-t}$ is the potential measured at time t at the point x on segment i in response to a delta-function spike of current injected at the point y on segment j at time zero. This provides a physical interpretation of the meaning of the Green's function. Once G_{ij} is known, equation (2.6) allows the potential to be constructed for any initial condition and distribution of currents.

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

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

for $t > 0$ and the initial condition

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

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

$$G_{kj}(0, y, t) = G_{mj}(0, y, t) \quad (2.9)$$

for all k and m corresponding to segments radiating from 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

$$\sum_k a_k^{3/2} \frac{\partial G_{kj}(x, y, t)}{\partial x} \Big|_{x=0} = 0 \quad (2.10)$$

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

$$G_{kj}(L_k, y, t) = 0 \quad (2.11)$$

for an open end (2.4) or

$$\frac{\partial G_{kj}(x, y, t)}{\partial x} \Big|_{x=L_k} = 0 \quad (2.12)$$

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

3. The Rules

The Green's function for a single segment of infinite length,

$$G_0(x - y, t) = \frac{1}{\sqrt{4\pi t}} \exp \left[-\frac{(x - y)^2}{4t} \right] \quad (3.1)$$

plays an important role in the rules I will now give for solving the general cable problem. The Green's function on any tree with any number of segments and any geometry can be written as a sum of terms involving the function (3.1). This is the basis for the well-known technique for solving (2.1) by images or by reflections. The rules listed below allow this series of terms to be constructed extremely easily using diagrammatic techniques.

The basic idea is to represent the Green's function as a sum over 'trips'. Each trip represents one term in a series giving the exact Green's function. Specifically, for any tree-like structure

$$G_{ij}(x, y, t) = \sum_{trips} A_{trip} G_0(L_{trip}, t) \quad (3.2)$$

where the sum is over all possible trips constructed using the rules given below. Also given below are the rules for determining the coefficients A_{trip} which depend on the particular trip being summed. G_0 is the function given by equation (3.1) and L_{trip} is the length of the trip being summed.

A trip is a path along the tree that starts at the point x on segment i and ends at the point y on segment j . Trips are constructed in accordance with the following rules:

- A trip may start out from x by traveling in either direction along segment i , but it may subsequently change direction only at a node or a terminal. A trip may pass through the points x and y an arbitrary number of times but must begin at x on segment i and end at y on segment j .
- When a trip arrives at a node, it may pass through the node to any other segment radiating from the node or it may reflect from the node back along the same segment on which it entered (see figure 2a).
- When it reaches a terminal, a trip always reflects back, reversing its direction (see figure 2b).

Every trip generates a term in the sum (3.2) for the Green's function. The length L_{trip} is obtained by summing the lengths (in units of the electrotonic length constant) of all the steps taken along the course of the trip.

To compute the coefficient A_{trip} we must introduce a set of factors p_k . At each node there is a p factor for each radiating segment. The factor for a segment labelled by k is given in terms of its radius a_k by

$$p_k = \frac{a_k^{3/2}}{\sum_{m \text{ on node}} a_m^{3/2}} \quad (3.3)$$

where the sum in the denominator is over all the segments radiating from the node being considered including k itself. Note that the sum of all the p_k corresponding to segments radiating from any given node is one. A particular p_k refers to both a specific segment and a specific node. A segment with a node at either end may have a different p_k associated with each of its ends because the denominator in equation (3.3) will in general be different for the two ends. Using these factors, the coefficient A_{trip} is computed from the following rules:

- Initially when the trip starts out from the point x , $A_{trip} = 1$.
- As the trip progresses from x to y , A_{trip} is multiplied by $2p_m$ every time the trip crosses a node by entering along a segment k and leaving along a different segment m with $m \neq k$ (see figure 2a).
- Every time the trip enters a node along a segment k and then reflects off the node back along the same segment k , A_{trip} is multiplied by $2p_k - 1$ (see figure 2a).

- When the trip reflects off a closed terminal, A_{trip} remains unchanged (see figure 2b).
- When the trip reflects off an open terminal, A_{trip} is multiplied by -1 so that it changes sign (see figure 2b).

As stated, the rules require that the trips be generated starting at the point x and ending at the point y . If reversed trips going from y to x are used instead, the result of summing the trips will be $G_{ji}(y, x, t)$. However, the simple identity

$$G_{ij}(x, y, t) = \left(\frac{a_j}{a_i}\right)^{3/2} G_{ji}(y, x, t) \quad (3.4)$$

allows the properly ordered Green's function to be computed using reversed trips and in some cases this is more convenient.

4. Proof that the Rules Work

It is remarkably simple to show that the above rules produce the correct Green's function satisfying 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. It is clear that the Green's function (3.2) satisfies the basic cable equation because it is the sum of terms that individually satisfy this equation. As $t \rightarrow 0$ the only term in the sum that can be non-zero is one corresponding to a trip of zero length because $G_0(L, 0) = 0$ unless $L = 0$. The zero length trip has weight $A_{trip} = 1$ giving the correct initial condition $G_{ij}(x, y, 0) = \delta_{ij}G_0(x - y, 0) = \delta_{ij}\delta(x - y)$.

To check the boundary condition at a given node, we need to examine the Green's function with x located near the node being checked, on one of its radiating segments. Let x denote the distance away from the node along segment k (see figure 3). The position of y , the segment number j and the time t are all arbitrary. The trips we must sum to compute the Green's function start at the point x and end at the point y . However, suppose that we summed all the trips ending at point y on segment j but starting from the node itself rather than from the point x . Trips departing from the node must leave by traveling out along one of the radiating segments. We denote the result of summing equation (3.2) over all trips that initially leave the node along segment k by $F_{kj}(0; y, t)$ and similarly the sum of all trips that leave the node along other segments m by $F_{mj}(0; y, t)$. The zero argument of $F_{kj}(0; y, t)$ and $F_{mj}(0; y, t)$ indicates that these trips start right at the node.

The Green's function $G_{kj}(x, y, t)$ is obtained by summing trips that start from the point x not from the node. However, there is a relation between the Green's function and the partial sums $F_{kj}(0; y, t)$. As shown in figure 3, when a trip leaves the point x it can either start by traveling away from the node, by traveling toward the node and reflecting off it or by traveling toward the node and passing through it. There is a one-to-one correspondence between trips that start out from x in each of these directions and trips that start out from the node itself.

Trips that start out from x moving away from the node are identical to trips that start out from the node itself along segment k except that they are shorter by an amount x . We denote the sum of such shortened trips by $F_{kj}(-x; y, t)$. In the function F , the argument $-x$ does not mean that the trips used to determine F start at the point $-x$, it means that a distance x has been subtracted from the length of each trip summed to compute F . Except

for this shortening of the length, the trips used to compute $F_{kj}(-x; y, t)$ are identical to those used to compute $F_{kj}(0; y, t)$.

Trips that start out from x by moving toward the node and then reflecting off it back out along segment k (see figure 3) are also identical to trips that start out from the node along segment k except that these are longer by an amount x . In addition, when these trips reflect off the node back out along segment k they pick up a factor $2p_k - 1$ according to the rules of section 3. Therefore, the contribution to the Green's function from trips that start out from x by moving toward the node and then reflecting off it is $(2p_k - 1)F_{kj}(x; y, t)$. Here the x in the argument of F indicates that all the trips in this partial sum have been lengthened by an amount x .

Finally, trips in the sum for the Green's function may start at x , move toward the node along segment k and then cross it leaving by moving out another radiating segment m (see figure 3). The segment m can be any of the radiating segments except for the segment k . These trips can be equated to the trips used to compute $F_{mj}(0; y, t)$ except that they are longer by an amount x . Furthermore, crossing the node introduces a factor $2p_m$. Thus, the sum of such trips is given by $2p_m F_{mj}(x; y, t)$.

The full Green's function is obtained by summing the contributions from all the different types of trips we have been discussing,

$$G_{kj}(x, y, t) = F_{kj}(-x; y, t) + (2p_k - 1)F_{kj}(x; y, t) + \sum_{m \neq k} 2p_m F_{mj}(x; y, t). \quad (4.1)$$

In general, the F functions in this formula are given by infinite sums over trips but fortunately we do not need to know what they are to show that (4.1) satisfies the node boundary conditions. For example,

$$G_{kj}(0, y, t) = \sum_m 2p_m F_{mj}(0; y, t). \quad (4.2)$$

Since the sum in this formula is over all m values corresponding to segments radiating from the node including k , the Green's function at the point $x = 0$ is independent of k . This means that it automatically obeys the boundary condition (2.9). In addition,

$$\left. \frac{\partial G_{kj}(x, y, t)}{\partial x} \right|_{x=0} = \sum_m 2p_m \left. \frac{\partial F_{mj}(x; y, t)}{\partial x} \right|_{x=0} - 2 \left. \frac{\partial F_{kj}(x; y, t)}{\partial x} \right|_{x=0}. \quad (4.3)$$

If we multiply this result by p_k , sum over k and use the fact that the p_k sum to one, we see that

$$\sum_k p_k \left. \frac{\partial G_{kj}(x, y, t)}{\partial x} \right|_{x=0} = 0. \quad (4.4)$$

Since the p_k are proportional to $a_k^{3/2}$ this is equivalent to the boundary condition (2.10).

Our rules for terminals are identical to those for nodes if we take $p_m = 0$ for $m \neq k$ and $p_k = 0$ for an open end or $p_k = 1$ for a closed end. Therefore, equations (4.2) and (4.4) indicate that the boundary conditions (2.11) or (2.12) are obeyed at all terminals. The formula (4.1) used to prove that our rules generate the correct answer is also useful in computations since it allows the Green's function to be computed from the partial sums F .

5. Short-Time Behavior

For all but the simplest trees, there are an infinite number of trips in the sum (3.2). However, the Green's function can be approximated by keeping only a finite number of terms. This is because long trips are exponentially suppressed by the factor $\exp(-L_{trip}^2/4t)$ in the function G_0 of equation (3.1). At very short times, this factor will suppress all but the shortest trip. Thus, the short-time limit of the Green's function is given by a single term

$$G_{ij}(x, y, t) = A_{min}G_0(L_{min}, t) \quad (5.1)$$

where *min* means the shortest trip between the points x and y . This is an interesting result - the short time behavior is determined solely by properties of the dendritic tree located on the shortest path between the points x and y . The structure of the tree away from the shortest path has no effect on the short-time behavior. Thus, for example, the rise time (measured in units of the membrane time constant) in response to a sudden input current depends primarily on the distance (measured in units of the electrotonic length constants for each intervening segment) between the synapse and the point where the response is measured. Furthermore, the response time is proportional to the square of this electronic distance because the exponential factor in equation (5.1) depends on the ratio of the length squared to the time. The membrane time constant is proportional to the membrane resistance while the length constant that determines the units of electrotonic distance is proportional to the square root of the membrane resistance. This means that as well as being independent of the global structure of the tree, rise times do not depend strongly on the value of the membrane resistance.

6. Convergence of the Sum Over Trips

In the long-time limit, the exponential suppression of long trips becomes less pronounced because the square of the trip length is divided by $4t$ in the exponential factor appearing in G_0 (3.1). The number of possible trips grows exponential with the length of the trip, so we might worry about the convergence of the sum over trips at long times. Since trips always reflect back when they hit terminals, we will think of a trip as stepping from node to node. At each node a decision must be made whether to reflect back from the node along the same segment or to proceed onward down one of the other radiating segments. Consider trips consisting of N node-to-node steps. The length of such a trip is roughly proportional to N , so the exponential factor in G_0 will go like $\exp(-\alpha N^2)$ where α is a constant. In the sum over trips this exponential factor is multiplied by a coefficient which is the sum of all the A_{trip} factors for all N step trips. I will now show (at least for a restricted set of trees) that the sum of A_{trip} factors does not grow with N despite the fact that the number of trips grows exponentially with N .

To compute the sum of A_{trip} factors over all N -step trips, I will require that all the segments of the tree have the same radius. In addition, I will consider only binary trees with closed end terminals. Otherwise, the structure of the tree is arbitrary. The restriction to binary trees is not essential but simplifies the discussion. An N -step trip can be characterized by the action taken at each of the N nodes encountered during the trip. Because I have required all the segments to have the same radius, all of the p factors for the tree are equal to $1/3$. If a trip reflects back off a node, A_{trip} will be multiplied by $2/3 - 1 = -1/3$ while if it passes through a node, A_{trip} will be multiplied by $2/3$. Consider an N -step trip consisting

of n reflections off nodes and $N - n$ transmissions through nodes. Such a trip will have

$$A_{trip} = \left(\frac{2}{3}\right)^{N-n} \left(-\frac{1}{3}\right)^n. \quad (6.1)$$

How many such trips are there? First there are $N!/(n!(N-n)!)$ ways of choosing which of the N steps correspond to the n reflections. Furthermore, each time a trip goes through a node without reflecting there are two ways it can proceed (since we are considering a binary tree). This means that the total number of N -step trips with n reflections off nodes is $2^{N-n}N!/(n!(N-n)!)$. The number of reflections can be any integer from zero to N . The total number of trips is then

$$\sum_{n=0}^N \frac{2^{N-n}N!}{n!(N-n)!} = 3^N \quad (6.2)$$

which grows exponentially with N . However, the sum of A_{trip} over all the N -step trips is

$$\sum_{n=0}^N \frac{2^{N-n}N!}{n!(N-n)!} \left(\frac{2}{3}\right)^{N-n} \left(-\frac{1}{3}\right)^n = \left(\frac{4}{3} - \frac{1}{3}\right)^N = 1. \quad (6.3)$$

Thus, the sum of trip weights does not grow with N and the exponential suppression factor coming from the trip length is not overwhelmed by a growth in the sum over trips, at least for the special case considered here. Of course, for longer times it will be necessary to include more trips in the sum to maintain the accuracy of the computation. However, since the Green's function enters equation (2.6) multiplied by e^{-t} and at sufficiently long times the product Ge^{-t} goes to zero, an accurate result for G itself is not needed in this limit.

7. Computer Computations

Junchu Cao and I have developed a computer program that performs the sum over trips to any desired degree of accuracy. Of course, the more accuracy required, the more trips must be summed and this requires more computer time. However, as the following example shows, quite accurate results can be obtained by summing a reasonable number of trips. Details of the program will be presented elsewhere. Here, I will concentrate on results from a sample tree structure.

Figure 4 show the example used here to illustrate how the sum over trips can be used to compute the Green's function. Figure 5 shows results of the program that performs this sum. The points x and y have been chosen as shown in figure 4. The results of summing 1, 4, 40, 276, 1664 and 9460 trips are shown in figure 5. In this figure we have plotted e^{-t} times the Green's function since this is the response to a delta-function input current. The curves for 1664 and 9460 trips are practically indistinguishable (although a small separation between the curves can be seen for $x > 0.4$). This indicates that the sum over trips has very nearly converged to the exact answer by 9460 trips. The sum over one trip is correct only at very short times. A surprising result is the accuracy of the curve summing only 4 trips. We have noticed in other examples as well that a sum of only four trips often gives a remarkable good approximation of the correct answer. The four trips used are: 1) the shortest trip between x and y , 2) a trip that starts from x moving away from y , reflects back off the first node it encounters and then proceeds directly to y , 3) a trip that proceeds directly to y but passes through y to the next node it hits and then reverses back to y and 4) a trip that starts from

x moving away from y , reverses direction at the first node it encounters, proceeds directly to y , passes through to the next node it hits and then reverses back to y .

8. Discussion

The sum over trips is a simple way to evaluate Green's functions for arbitrary dendritic trees. It is particularly useful for deriving exact expressions for relatively simple trees and for determining the short-time behavior on more complex trees. Results from computer calculations indicate that summing trips provides a practical method for numerical computation as well. There are some definite limitations to the method. The most important of these is that the method only works for linear cables. Nonlinear voltage dependences would eliminate the superposition principle on which the sum is based. As given here, the rules only apply to current injection along a tree and not to the conductance changes produced by real synapses. However, it should be possible to treat such conductance changes perturbatively and to incorporate them into the sum over trips.

The diagrammatic rules given here and the proof that they work were developed in collaboration with E. Farhi and S. Gutmann [18]. The program used to generate computer results was developed with Junchu Cao.

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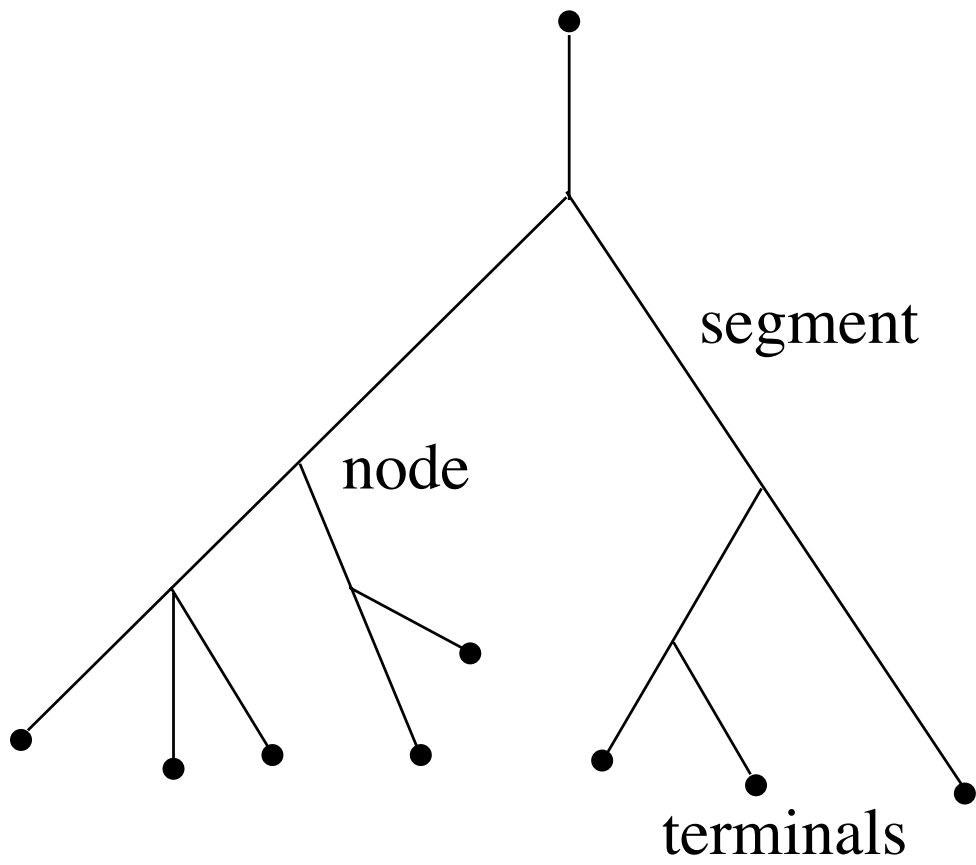


Fig. 1

Fig 1: A dendritic tree with labelled node, segment and terminals. Terminals are marked with dots.

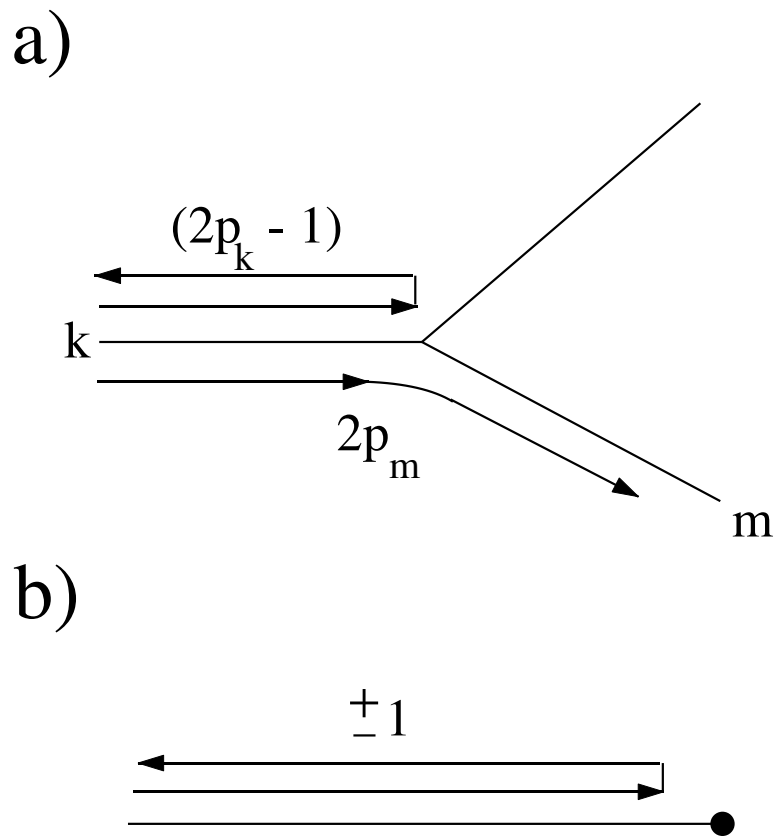


Fig. 2

Fig. 2: The rules for trips. a) At a node a trip may reflect back along the same segment on which it entered (in this case segment k). When this happens the coefficient A_{trip} is multiplied by $2p_k - 1$. A trip may also cross a node and leave along any of the other segments m with $m \neq k$. In this case A_{trip} is multiplied by $2p_m$. b) At a terminal the trip always reflects back the way it came. A_{trip} is either multiplied by $+1$ or -1 depending on whether the terminal is a closed end or an open end.

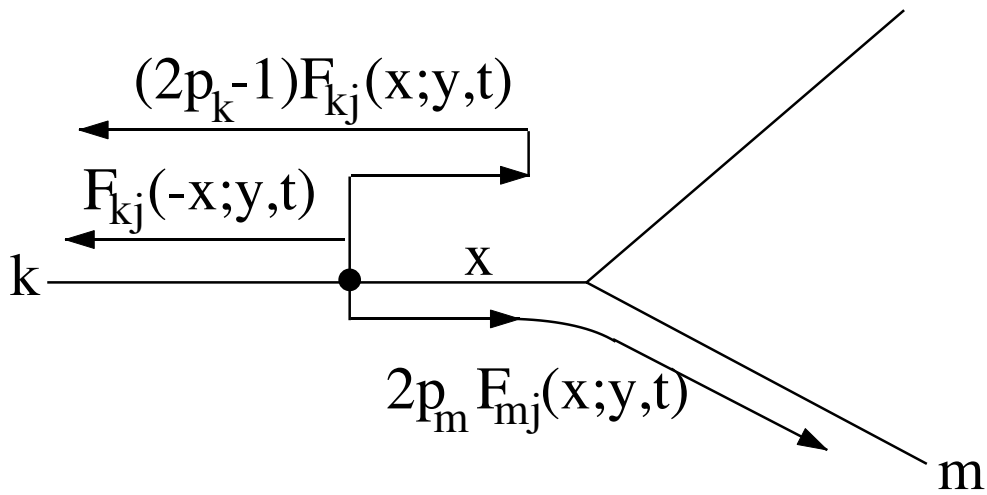


Fig. 3

Fig. 3: Proof that the sum over trips satisfies the node boundary condition. Trips from the point x represented by the dot can either leave by moving away from the node, by moving toward the node and reflecting off it or by moving toward the node and crossing it. As explained in the text, these three sets of trips give the terms indicated in the figure. The Green's function is the sum of all such terms.

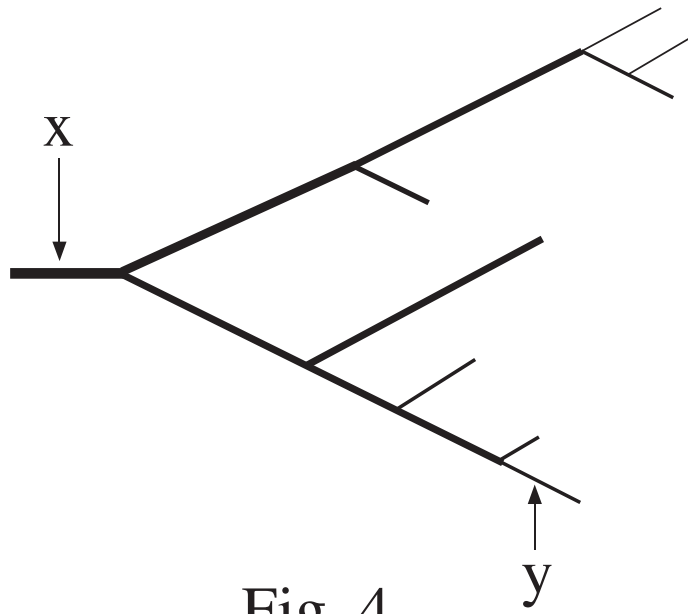


Fig. 4

Fig. 4: Sample dendritic tree. The potential measured at the point marked x in response to a delta-function of current injected at the point y at time zero is shown in figure 5. All terminals are closed ends.

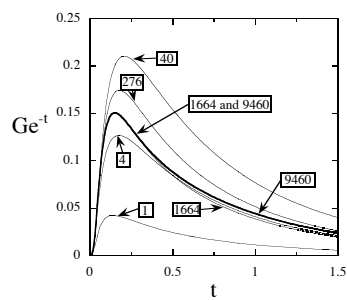


Fig. 5: Results for the tree of figure 4. The numbers in the boxes give the number of trips summed to produce each curve. The sum of 9460 terms is a very good approximation of the exact answer and is drawn thicker than the other curves. The result of 1664 terms is quite close to the thicker curve as is the sum of just four terms. The sum of a single term is only accurate in the short-time limit.