Functionally relevant measures of spatial complexity in neuronal dendritic arbors

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Abstract

We introduce a set of scaling exponents for characterizing global 3D morphologic properties of mass distribution, branching and taper in neuronal dendritic arbors, capable of distinguishing functionally relevant changes in dendritic complexity that standard Sholl analysis and fractal analysis cannot. We demonstrate that the scaling exponent for mass distribution, \( d_M \), comprises a sum of independent scaling exponents for branching, \( d_N \), and taper, \( d_T \). The accuracy of experimental measurements of the scaling exponents was verified using computer generated self-similar binary trees of known fractal dimension, and with prescribed amounts of branching and taper. The theory was applied to measuring 3D spatial complexity in the apical and basal dendritic trees of two functionally distinct types of macaque monkey neocortical pyramidal neurons: long corticocortical projection neurons from superior temporal cortex to area 46 of the prefrontal cortex (PFC), and local projection neurons within area 46 of the PFC. Two distinct scaling subregions (proximal and medial) were identified in both apical and basal trees of the two neuron types, and scaling exponents were fitted. A small but significant difference in mass scaling in the proximal region distinguished long from local projection neurons. Interestingly, both classes of neuron exhibited a homeostatic pattern of mass distribution across the two regions: despite large differences between proximal and medial regions in branching and tapering exponents, these effects were compensatory, resulting in a uniform, slow reduction of mass with distance from the soma, over both scaling regions of the apical and basal trees. Given a uniformly excitable membrane, the electrotonic properties of dendritic arbors depend entirely upon mass distribution, and its relative contributions from dendritic branching and taper. By capturing each of these complex morphologic properties in a single, globally descriptive parameter, the new 3D scaling exponents introduced in this study permit efficient morphometric characterization of complex dendritic arbors in the fewest possible parameters, that can be directly related to their electrotonic properties, and hence to neuronal function.

Keywords: Three-dimensional; Dendritic morphometry; Spatial complexity; Sholl analysis

1. Introduction

Recent advances in computer-assisted methods of acquiring digitized neuronal morphology in 3D now enable precise quantitative measurements of dendritic complexity. The availability of these data has led to a renewed interest in attempts to identify morphologic parameters necessary to address questions of how dendritic structure affects neuronal function. Sholl analysis (Sholl, 1953) is amongst the most widely used methods for determining the global spatial complexity of dendritic arbors. In his original study, Sholl quantified the branching structure of neocortical pyramidal neurons by measuring the number of
intersections between dendritic branches and concentric circles with origins at either the soma for basal dendrites, or the first branch point in the apical tree for apical dendrites (Sholl, 1953). Sholl found that the number of intersections per unit annular area (between concentric circles) decreased exponentially with distance from the origin in the case of basal dendrites, but as a power function of distance from the origin in the case of apical dendrites, indicating a more rapid reduction in branching complexity in basal, relative to apical, trees. More recently, fractal analysis has been applied in neuronal morphometry to provide a global estimate of dendritic complexity (Smith et al., 1989, 1996; Caserta et al., 1990, 1995; Henry et al., 2002). Lacking the tools to reconstruct neurons in true 3D (i.e. as a set of points in $\mathbb{R}^3$ with an accompanying diameter, $[x, y, z, d]$), early analyses measured fractal dimensions in 2D, as the complexity of the cell’s border or coastline, using techniques such as 2D box-counting (Morigawa et al., 1989) or the 2D dilation method (Smith et al., 1989; Flook, 1978; Jelinek and Elston, 2001, 2003). Such 2D methods, which are perform length-related rather than mass-related, can underestimate the true 3D complexity (Caserta et al., 1995; Mandelbrot, 1982) and cannot be directly related to standard electrotonic measures such as the space constant of cable theory (Rall, 1959, 1989), which combines measures of branch length and diameter to estimate passive decay rates of membrane potential in a neural cable.

Like Sholl analysis, fractal analysis has proven useful in discriminating between certain functionally different neuronal types that are visually similar (Caserta et al., 1995; Henry et al., 2002; Jelinek and Elston, 2003). However both these forms of analysis average over multiple morphologic features, only some of which are directly relevant to the electrotonic properties of dendritic arbors, and hence to neuronal firing patterns. The mass fractal dimension, for example, which measures the scaling exponent for dendritic mass with Euclidean distance, depends upon the combined effects of dendritic branching and die-off, dendritic taper, and tortuosity. Traditional Sholl analysis depends upon the combined effects of dendritic branching, die-off and tortuosity, while ignoring dendritic taper.

### 1.1. Functional significance of dendritic mass distribution

Neurons exhibit a wide variety of dendritic morphologies, and a correspondingly diverse range of intrinsic firing patterns. Using compartmental models of reconstructed cortical neurons (Mainen and Sejnowski, 1996; Krichmar et al., 2002), and model neurons (van Ooyen et al., 2002), recent simulation studies have demonstrated that the full spectrum of experimentally observed firing patterns can be reproduced in a range of neuronal morphologies with common ion channel distributions, differing only in the extent of arborization of their dendritic geometries. Such modeling studies suggest a causal relationship for the observed correlations between dendritic geometry and neural firing properties (Franceschetti et al., 1995; Connors and Gutnick, 1990; Mason and Larkman, 1990; Yang et al., 1996). Recent experimental work has highlighted the role of dendritic action potential backpropagation in neuronal plasticity (Johnston et al., 1996; Linden, 1999), where it acts as a coincidence detecting mechanism between presynaptic activity and postsynaptic action potentials. Backpropagating action potentials signal the occurrence of neuronal output to dendritic synapses, allowing selective up or downweighting of concurrently active synapses (Stuart et al., 1997; Haussler et al., 2000). Simulation studies (Vetter et al., 2001; Schaefler et al., 2003; Kabaso et al., 2003) have demonstrated that marked differences in the efficacy of backpropagation in different neuron types (see for review Stuart et al., 1997; Segev and London, 2000; Euler and Denk, 2001) are attributable in large part to variations in dendritic morphology. In particular, the number of dendritic branchpoints, and hence the complexity of branching are important predictors of the extent of backpropagation through the dendritic arbor (Vetter et al., 2001; Callaway and Ross, 1995; Spruston et al., 1995). Taken together, these studies demonstrate the crucial role of dendritic mass distribution and branching complexity in determining neural integration, synaptic plasticity, and the firing patterns that define neuronal function.

### 1.2. Representation in dendrogram space

The electrotonic properties of morphologically characterized neurons can be simulated with computational models, using cable theory (Rall, 1989) and modern compartmental modeling techniques (Hines, 1994; Koch, 1999; Koch and Segev, 1998; Jaffe and Carnevale, 1999). The relevant morphologic parameters in these models are lengths, diameters and branching of cable segments. These parameters can be distilled in a schematic dendrogram of the neuronal morphology as a binary tree, as shown for example in Fig. 4B. The arc length of the root branch is represented as a length along a primary axis. The arc lengths of progeny branches are shown as lengths in a direction parallel to the same primary axis, with their starting positions given by the arc length from the root to their branch points of origin. The progeny branches may be displaced in the orthogonal direction by arbitrary amounts to aid visualization and the branch diameters can be represented visually as scaled cylinders (Fig. 4B), or numerically, as associated parameters. An important feature of the representation in dendrogram space is that the distance metric is proportional to the arc length along dendritic branches, which determines their cable properties. In this paper we introduce and implement...
global scaling measurements on dendrogram representations of neurons. Our scaling exponents are related to mass fractal scaling measurements. However, by performing scaling measurements in dendrogram space we are able to isolate independent global parameters related to tapering and branching, which affect the cable properties of dendritic trees in different but complementary ways. Scaling measurements of neuronal dendritic arbors could also be studied in other metric spaces such as electrotonic space where the distance metric characterizes the attenuation of membrane potential (Rall, 1989; Carnevale et al., 1995; Zador et al., 1995). An approximate mapping from dendrogram space to electrotonic space can be achieved by first introducing renormalized electrotonic branch lengths proportional to the anatomical branch length divided by the square root of the diameter (Rall, 1989). Although we have not pursued electrotonic space scaling measurements in this paper, this remains an important direction for future research.

In order to characterize the spatial complexity of neuronal dendritic arbors, we first introduce an appropriate branch labeling scheme (Horton, 1945; Strahler, 1957; Tokunaga, 1984; Tarboton et al., 1988; Peckham, 1995; Turcotte et al., 1998). Such labeling schemes were originally applied to river networks (Horton, 1945; Strahler, 1957; Tokunaga, 1984; Tarboton et al., 1988) but have since been used to characterize bronchial systems (Horsfield, 1980), cardiovascular systems (West, 1990), and diffusion limited aggregation clusters (Vannimenus and Viennot, 1989; Halsey, 1997). We have not applied these schemes directly to neuronal dendritic arbors in this paper, however we have utilized the labeling schemes to construct "toy neurons": prefractal dendritic branching structures (DBS) with prescribed global mass scaling and prescribed amounts of branching and taper. These toy neuronal dendritic arbors are then used to guide and test the implementation of the global scaling measurements on neurons represented in dendrogram space.

In Section 2, we define scaling exponents that measure the global spatial complexity of an arbitrary DBS. We first consider scaling exponents for the anatomical space representation of the DBS. We derive a relationship between the mass fractal dimension and a power law exponent from Sholl analysis, by considering the scaling of the average area of intersection between dendritic branches and spherical shells of increasing radius. While this result is of theoretical interest, it does not isolate the individual effects of branching, tapering and tortuosity that contribute to the global mass scaling. Next we consider analogous scaling exponents derived from the dendrogram representation of the DBS. We show that these scaling exponents, when measured in dendrogram space, effectively distinguish the independent contributions of branching and tapering to global dendritic mass distribution.

In Section 3, we relate the dendrogram scaling exponents to the electrotonic structure of a dendritic arbor by identifying a relation between the power exponent for diameters at branch points and the global dendrogram scaling exponents for branching and taper.

In Section 4, we describe branch labeling schemes for characterizing topologically self-similar DBS, and derive relationships between branch labels that apply to the special case of binary self-similar DBS with side branches and parent–child taper.

In Section 5, we use the branch labeling relationships introduced in Section 4 to construct binary self-similar DBS with prescribed fractal dimensions, branching ratios and parent–child tapering. In Section 6, we apply our dendrogram scaling measurements to these toy neuronal dendritic arbors, and demonstrate how independent global scaling exponents related to mass, tapering, and branching can be reliably measured.

In Section 7, we apply the dendrogram scaling exponents to characterizing the global properties of mass distribution, branching, and taper in the apical and basal trees of two functionally distinct classes of neocortical pyramidal neurons from macaque monkeys: long projection neurons, that mediate corticocortical pathways between association areas, and local projection neurons, that form local circuits within the PFC. In both apical and basal trees of long and local projection neurons we find the same two distinct scaling regions: Region I, which we designate as the proximal or "growth" region, located adjacent to the soma, and Region II, which we designate as the medial or "plateau" region, located in the middle third of apical and basal trees. The distal ends of each tree are characterized by a non-scaling region, in which end effects due to branch die-off prevent measurement of standard scaling behavior. The mass exponent is essentially uniform over the proximal and medial scaling regions, but there are dramatic differences between these two regions in the contributions of the branching and tapering exponents. In the proximal region, a large positive branching exponent is compensated by an even larger, negative tapering exponent, resulting in a slow reduction in mass as a function of distance from the origin. In the medial scaling region both branching and tapering exponents are small, resulting in a plateau region which maintains the same slow reduction in mass as occurs in the proximal region, hence preserving a uniform global mass scaling across the two regions. The robustness of this pattern of scaling behavior across both apical and basal trees, as well as across two functionally distinct classes of pyramidal neuron, suggests that the pattern may be a universal characteristic of neocortical pyramidal neurons. Superimposed upon these global trends we find small but significant differences in scaling behavior in the proximal region of the apical trees, that distinguish the two neuron types. In
particular, the rate of increase in accumulated mass, measured by $d_M$, is significantly lower in long than local projection neurons. Comparison of the individual contributions of branching and tapering exponents, $d_N$ and $d_T$, to global mass distribution, demonstrates that this difference is unrelated to branching topology, and results primarily from a higher rate of taper, measured by $d_T$, in the apical trees of long, rather than local projection neurons. Similar differences between neuron types were observed in the basal trees, although these failed to reach statistical significance.

We conclude with a summary and discussion in Sections 8 and 9.

2. Scaling exponents

2.1. Anatomical space scaling exponents

We first consider scaling exponents in physical or anatomical space, which is the 3D Euclidean space in which the DBS is embedded. If the DBS has mass fractal dimension $D_M$, then the mass, $M(R)$, of the structure contained in a ball of radius $R$ (the center of which is inside the structure) scales as (Mandelbrot, 1982; Gouyet, 1996; Meakin, 1989)

$$M(R) \sim R^{D_M},$$

where $\sim$ means that $|M(R)/R^{D_M}|$ is constant for a range of $R$. We assume that the mass per unit volume is uniform inside the DBS. Then the incremental volume, $dV(R)$, of the DBS inside a spherical shell of radius from $R$ to $R + dR$ scales as

$$dV(R) \sim R^{D_M-1} dR,$$

from which we infer that the total area of intersection between the DBS and the sphere of radius $R$, $S(R)$, scales as

$$S(R) \sim R^{D_M-1}. $$

In the above we regard $dR$ as much smaller than the smallest length scale over which the scaling relation holds. $S(R)$ can be factored as

$$S(R) = N(R) \langle S(R) \rangle,$$

where $N(R)$ is the number of branch intersections with a sphere of radius $R$ and $\langle S(R) \rangle$ is the average area of intersection of a branch with the sphere. Variations in the quantity $N(R)$ with radius depend on (i) branching, the growth of new branches on existing branches, (ii) die-off, or truncation of branches, and (iii) tortuosity, the deviation of individual branches from following a straight path. Variations in the quantity $\langle S(R) \rangle$ with radius depend on (i) tapering between branchpoints or via a reduction in branch diameter from parent to child at a branchpoint and (ii) inclination, the angle between the branch axis and the normal to the sphere.

We define the Sholl dimension, $D_N$, in anatomical space, via the scaling of the number of branch intersections with radius $R$,

$$N(R) \sim R^{D_N}. $$

Then the scaling of the average area of intersection between a branch and the sphere of radius $R$ can be written as

$$\langle S(R) \rangle \sim R^{D_M-1-D_N}. $$

Eq. (6) relates the mass fractal dimension and the Sholl dimension in anatomical or Euclidean space.

2.2. Dendrogram space scaling exponents

Consider a dendrogram representation of a DBS with $L$ measuring distance from the origin at the root, along the primary axis. We begin by defining a mass scaling exponent, $d_M$, in dendrogram space.

**Definition 1** (Mass exponent $d_M$). Let $M(L)$ denote the mass of the dendrite that extends a distance $L$ from the origin in dendrogram space. Then $d_M$ is defined by the scaling law:

$$M(L) \sim L^{d_M}. $$

Note that in the above definition it is assumed that $|M(L)/L^{d_M}|$ remains constant over a range of values of $L$. Although Eq. (7) has the same power law form as Eq. (1) there are important differences. Firstly, the scaling relation in Eq. (7) is measured only from the origin at the root, not from an arbitrary point on the tree. Secondly, the distance metric in Eq. (1) is the 3D Euclidean metric whereas the distance metric in Eq. (7) is the arc length along the branch.

The incremental volume, $dV(L)$, between planes in dendrogram space orthogonal to the primary axis at $L$ and $L + dL$ scales as

$$dV(L) \sim L^{d_M-1} dL$$

and thus the total cross-sectional area of intersection of the DBS with these planes, $S(L)$, scales as

$$S(L) \sim L^{d_A},$$

where

$$d_A = d_M - 1.$$

This relationship between scaling exponents for volume, $d_M$, and cross-sectional area, $d_A$, with distance reflects the spatial derivative relationship between the quantities $S(L)$ and $V(L)$.

The particular advantage of the dendrogram space scaling exponents over anatomical space scaling exponents...
is that the effects of branching and tapering can be uncoupled, as demonstrated in the following definitions:

**Definition 2 (Branching exponent \( d_N \)).** Let \( N(L) \) denote the number of branch intersections with sequential planes orthogonal to the primary axis, as a function of distance \( L \). Then \( d_N \) is defined by the scaling law

\[
N(L) \sim L^{d_N}. \tag{11}
\]

**Definition 3 (Tapering exponent \( d_T \)).** Let \( \langle S(L) \rangle \) denote the average area of intersection of the DBS with the sequential planes orthogonal to the primary axis, as a function of distance \( L \). Then the tapering exponent \( d_T \) is defined by the scaling law

\[
\langle S(L) \rangle \sim L^{d_T}. \tag{12}
\]

Analogous to Eqs. (4) and (6) it can be shown, in dendrogram space, that

\[
\langle S(L) \rangle \sim L^{d_M-1-d_N}, \tag{13}
\]

and thus

\[
d_T = d_M - 1 - d_N. \tag{14}
\]

The branching exponent, \( d_N \), thus corresponds to the Sholl dimension, measured in dendrogram space.

3. Relating dendrogram exponents to electrotonic structure

A well-known result used in simplifying the description of voltage spread in branching neural cables is Rall’s Law (Rall, 1962, 1964):

\[
D_0^{3/2} = D_1^{3/2} + D_2^{3/2}, \tag{15}
\]

which relates the diameter \( D_0 \) of a parent branch to the diameters \( D_1 \) and \( D_2 \) of progeny branches at a binary branch point. The exponent value 3/2 allows impedance matching at branch points so that the branched segment can be replaced by a single cable segment with the same electrotonic properties. Rall’s Law is a special case of the general power branching relation

\[
D_0^\Delta = D_1^\Delta + D_2^\Delta. \tag{16}
\]

In this relation an exponent value \( \Delta = 2 \) obtains if the cross-sectional area is conserved at branch points. The power law branching relation was also recently derived to specify the optimal diameters at branch points in axons under the dual constraints of minimizing signal propagation delays and minimizing the axonal arbor volume (Chklovskii and Stepanyants, 2003). In this work exponent values of \( \Delta = 3 \) and \( \Delta = 2.5 \) were obtained for myelinated and non-myelinated axons, respectively.

In this section we identify a relation between the power exponent \( \Delta \) and the dendritic scaling exponents \( d_T, d_N \) for dendritic trees whose diameters at branch points satisfy the power branching relation of Eq. (16). Consider a dendrogram representation of a DBS with \( l_k \) denoting the dendrogram distance from the origin at the root to the \( k \)th branch point. Let \( n_k \) denote the number of branches at a distance \( l \) where \( l_{k-1} < l < l_k \) so that we have \( n_k \) branches immediately before the \( k \)th branch point and \( n_{k+1} \) branches immediately after. The branch diameters are labeled \( D_{k,i} \) where \( i = 1, 2, \ldots, n_k \) immediately before a branch point and \( D_{k+1,i} \) where \( i = 1, 2, \ldots, n_{k+1} \) immediately after. Now if a branch \( i \) does not bifurcate at the \( k \)th branch point then \( D_{k,i} = D_{k+1,i} \) and \( D_{k,i} = D_{k+1,i}^A \) whereas if a branch \( i_0 \) bifurcates into two branches \( i_1 \) and \( i_2 \) at the \( k \)th branch point then assuming the power branching relation, Eq. (16), holds we have

\[
D_{k,i_0}^A = D_{k+1,i_1}^A + D_{k+1,i_2}^A. \tag{17}
\]

Thus if we consider all branches before and after the \( k \)th branch point and we assume power branching relations at all binary branch points then by summing over all possibilities we have

\[
[D_k(\Delta)]^A = \sum_{j=1}^{n_k} [D_{k,i_j}(\Delta)]^A. \tag{18}
\]

We now define the power mean of the branch diameters at distance \( l_k \) by

\[
\langle D_k(\Delta) \rangle = \left[ \frac{1}{n_k} \sum_{j=1}^{n_k} [D_{k,i_j}(\Delta)]^A \right]^{1/\Delta}. \tag{19}
\]

Then Eq. (17) can be rewritten as

\[
n_k \langle D_k(\Delta) \rangle^\Delta = n_{k+1} \langle D_{k+1}(\Delta) \rangle^\Delta. \tag{20}
\]

Using the scaling relation for the dendrogram branching exponent, \( d_N \) (Eq. (11)), we obtain

\[
\frac{[D_{k+1}(\Delta)]^A}{[D_k(\Delta)]^A} = \left( \frac{l_{k+1}}{l_k} \right)^{d_N}. \tag{21}
\]

The average area of intersection of the dendritic branches with sequential planes orthogonal to the primary axis can also be represented using power means. Explicitly at distance \( l_k \) we have

\[
\langle S_k \rangle = \frac{1}{n_k} \sum_{j=1}^{n_k} S_{k,i_j} \tag{22}
\]

\[
= \frac{1}{n_k} \sum_{j=1}^{n_k} \pi \left( \frac{D_{k,i_j}}{2} \right)^2 \tag{23}
\]

\[
= \frac{\pi}{4} [D_k(2)]^2. \tag{24}
\]

Using the scaling result for the tapering exponent, \( d_T \) (Eq. (12)), we can now write

\[
\frac{[D_{k+1}(2)]^2}{[D_k(2)]^2} = \left( \frac{l_{k+1}}{l_k} \right)^{d_T}. \tag{25}
\]
Finally, we eliminate \( \frac{I_{k+1}}{I_k} \) from Eqs. (20) and (24) to write

\[
\left( \frac{[D_{k+1}(\Delta)]}{[D_{k}(\Delta)]} \right)^\Delta = \left( \frac{[D_{k+1}(2)]}{[D_{k}(2)]} \right)^{-2d_k/d_T}.
\]

(25)

The above equation thus relates the power exponent \( \Delta \) to the two scaling exponents \( d_T \) and \( d_N \). Whilst we are not aware of any methods that can be used to solve this equation explicitly for \( \Delta \) we note the following: (i) The special case where \( d_N = -d_T \) is consistent with a power exponent \( \Delta = 2 \) at binary branching points. (ii) If \( D_{ij} \approx D_i \), for all \( i,j \) and if \( n_i \approx n_{i+1} \) then using the properties of power means we have \( [D_i(\Delta)] \approx [D_i(2)] \) and from Eq. (25) we deduce \( \Delta \approx -2d_N/d_T \). From this result we can use the measured values of the exponents \( d_N \) and \( d_T \) to infer \( \Delta \). For example, if \( \Delta = 3/2 \) and the above approximations were valid then \( d_N = -3d_T/4 \).

The importance of the relation Eq. (25) is not so much the possibility of deducing \( \Delta \) from \( d_N \) and \( d_T \) as it is the significance of the exponents \( d_N \) and \( d_T \) for predicting global electrotonic properties of a dendritic tree. Whereas \( \Delta \) measures electrotonic properties locally, across an individual branchpoint, \( d_N \) and \( d_T \) measure aspects of branching and tapering that are relatively uniform within a particular scaling region, and that predict a relatively uniform value of \( \Delta \) within that same region.

4. Classification of self-similar branching structures

We now consider the special case of self-similar DBS for which the property \( P \) of the object on one length scale, \( R \) say, is similar to a number of copies, \( b \), of itself on a smaller length scale, \( R/a \), i.e.

\[
P(aR) = bP(R).
\]

(26)

Without loss of generality we write, \( b = a^\Delta \), and the exponent \( \Delta \) is called the similarity dimension. The solution of the functional equation, Eq. (26), is given by

\[
P(R) = cR^\Delta,
\]

where \( c \) is arbitrary. If the property \( P \) is mass then the similarity dimension is equivalent to the mass fractal dimension. The morphology of a self-similar DBS can be characterized in detail using branch labeling schemes, which we now consider.

4.1. Horton–Strahler scheme

In the simpler Strahler scheme (Strahler, 1957; Meakin, 1989) we first label all terminal branches as order “1”. Proceeding downstream towards the root branch, the following rules are progressively applied. If a single upstream branch contacts a node the downstream unlabeled branch is assigned the same label as the upstream unlabeled branch. If more than one labeled branch meets a node then the downstream unlabeled branch is assigned the label max\( \{i\} \) if max\( \{i\} \) is unique, otherwise max\( \{i\} + 1 \). After all branch labels are assigned, the order of the network is max\( \{i\} \). Let \( N_i \) denote the number of branches of order \( i \). Let \( L_i \) denote the (average) length of a branch of order \( i \). See Fig. 1(A) for an example.

The Horton labeling (Horton, 1945) can be implemented by first applying the Strahler labeling scheme. Starting at the root of the highest order branch, the Strahler label assigned to this branch replaces all lower order labels out to the terminal of the longest continuation of this branch. The algorithm is applied consecutively to branches of successively lower orders. See Fig. 1(B) for an example.

The sequences \( N_i \) and \( L_i \) are not the same in the Horton and Strahler labeling scheme, nevertheless for a self-similar DBS, Horton’s laws for the branching ratio

\[
R_B = \frac{N_i}{N_{i+1}}
\]

(27)

and for the length ratio

\[
R_L = \frac{L_{i+1}}{L_i}
\]

(28)

hold; approximately for Strahler labeling (Fig. 1A) and exactly for Horton labeling (Fig. 1B). The similarity dimension for a network obeying Horton’s laws is given by (Tarboton et al., 1988)

\[
D_s = \frac{\log R_B}{\log R_L}.
\]

(29)

Fig. 1. Comparison of Strahler and Horton branch order labeling schemes for a dendritic branching structure (DBS). The branching tree shown in Fig. 1 is a Mandelbrot–Vicsek prefractal toy neuron of order 4, with branch orders labeled according to the Strahler labeling scheme (A) and according to the Horton scheme (B). \( N_{i} \) denotes the number of branches of order \( i \). \( L_{i} \) denotes the average length of a branch of order \( i \).
Eq. (29) can be justified as follows. Consider a DBS that obeys Horton’s laws and let $M(L_i)$ denote the mass of that part of the structure emerging from a branch of length $L_i$. Assuming that individual branches have constant diameter and density then the branching ratio, Eq. (27), can be expressed equivalently as a mass ratio:

$$R_B = \frac{M(L_{i+1})}{M(L_i)}.$$  \hspace{1cm} (30)

Using Eq. (28), it now follows that

$$R_B M(L_i) = M(R_L L_i).$$  \hspace{1cm} (31)

This functional equation is a defining equation for self-similarity: it shows that the structure on one scale ($R_L L_i$) is identical to having a number of copies ($R_B$) of the structure on a smaller scale ($L_i$). The solution of the functional equation is a power law, i.e.

$$M(L_i) = a L_i^\Delta$$  \hspace{1cm} (32)

for some constant $a$ and some exponent $\Delta$. The constant $a$ is arbitrary but the exponent $\Delta$ is found by substitution, viz.

$$R_B c L_i^\Delta = c (R_L^2 L_i^\Delta)$$

and thus,

$$R_B = R_L^\Delta$$  \hspace{1cm} (33)

or equivalently,

$$\Delta = \log \frac{R_B}{\log R_L}.$$  \hspace{1cm} (34)

From Eqs. (31) and (33) we have

$$M(a L) = a^\Delta M(L),$$

where $a$ is a constant, which defines $\Delta$ as a similarity dimension. Note however that $M(L_i)$ as defined above is not necessarily the same as the mass of that part of the structure contained in a ball of size $L_i$ and thus we cannot deduce that the similarity dimension given by Eq. (29) will be equivalent to the mass fractal dimension defined in Eq. (1).

4.2. Self-similar binary trees with side branching

We now consider Tokunaga labeling (Tokunaga, 1984) and ramification labeling (Vannimenus and Viennot, 1989; Halsey, 1997) for specific parent–progeny relationships. The Tokunaga scheme (Tokunaga, 1984; Peckham, 1995; Turcotte et al., 1998) records the average number of lateral side branches of order $j$ for a branch of order $i$. We will follow the notation of Peckham (1995) and denote this number by $T_{ij}$. Note that if $\Omega$ is the order of the network then $2 \leq i \leq \Omega$ and $1 \leq j \leq i - 1$.

Another way to quantify side-branch statistics in a DBS is through ramification numbers, $N_{ij}$, which denote the number of branches of order $i$ that have parents of order $j$ (Vannimenus and Viennot, 1989; Halsey, 1997). The DBS can be labeled using ramification labeling with two indices $i, j$ for each branch; the first index $i$ is the Strahler index of the branch and the second $j$ is the Strahler index of its upstream parent. Fig. 2 shows an example of a DBS labeled by ramification labels. Note that the ramification numbers, which are only defined for $j > i$, are related to the Strahler numbers by

$$N_i = \sum_{j=i+1}^{\Omega} N_{ij}.$$  \hspace{1cm} (35)

In a topologically self-similar DBS the relationship of second-order side-branches to first-order branches is (statistically) the same as the relationship of third-order side-branches to second-order branches, etc. This can be expressed mathematically by Tokunaga’s self-similarity condition (Tokunaga, 1984)

$$T_k = T_{jj-k}.$$  \hspace{1cm} (36)

This self-similarity condition can be used to derive a consistency relation governing the Strahler numbers in any self-similar DBS (Turcotte et al., 1998). In a binary DBS, each branch of order $i + 1$ that is not a terminal branch bifurcates into two branches of order $i$. By also considering the number of lateral side branches we find that the total number of branches of order $i$ is given by

$$N_i = 2N_{i+1} + \sum_{j=i+1}^{\Omega} N_j T_{ij}.$$  \hspace{1cm} (37)

Fig. 2. Order 4 Mandelbrot–Vicsek prefractal tree labeled by ramification labels. Each branch has two indices, $(i, j)$. The first index $i$ is the Strahler index of the branch, the second index $j$ is the Strahler index of its upstream parent.
Thus for a self-similar binary DBS we have
\[ N_i = 2N_{i+1} + \sum_{j=i+1}^{\Omega} N_jT_{j-i} \]
which follows using Tokunaga’s self-similarity condition, Eq. (36). After re-labeling the index of the sum with \( k = j - i \) we can write
\[ N_i = 2N_{i+1} + \sum_{k=1}^{\Omega-i} N_{k+i}T_k. \]
This consistency relation can be used to determine the branching ratio, \( R_B \), for a self-similar binary DBS, which is then only dependent on the side branch statistics embodied in \( T_k \) (Peckham, 1995; Turcotte et al., 1998).

4.3. Self-similar binary tree with tapering

We now devise a method for introducing parent–progeny taper in a binary topologically self-similar DBS with side branches. Our method is based on the following parent–progeny taper ansatz:
\[ N_iD_i^z = \sum_{j=1}^{i-1} N_{j,i}D_j^z, \]
which equates the diameter, \( D_i \), of a parent branch \( i \) raised to a power \( z \), with the sum of the diameters of its progeny branches each raised to the same power \( z \). This tapering ansatz does not have the functional significance of preserving impedance across a branch point as, e.g. Rall’s law for branching neuronal cables (Rall, 1989), Eq. (15). Nevertheless the ansatz in Eq. (39) is sufficient for our purposes of constructing a self-similar binary tree with prescribed branching and taper. For future reference we note that a taper that also satisfies Rall’s law could be introduced through a more elaborate labeling scheme, identifying the separate segments between branch junctions along each branch of the same Strahler order.

To introduce the tapering ansatz we first note that Eq. (37) can be rewritten as
\[ N_i = \sum_{j=i+1}^{\Omega} N_j\hat{T}_{j,i}, \]
where
\[ \hat{T}_{j,i} = \begin{cases} 2 + T_{j,i} & \text{if } j = i + 1, \\ T_{j,i} & \text{otherwise}. \end{cases} \]
Then using the result
\[ N_i = \sum_{j=i+1}^{\Omega} N_{i,j} \]
we can write
\[ N_i\hat{T}_{j,i} = N_{i,j}\hat{T}_{j,i}. \]
Our tapering ansatz can thus be rewritten as follows:
\[ N_iD_i^z = \sum_{j=1}^{i-1} N_{i,j}\hat{T}_{j,i}D_j^z, \]
which expands as
\[ D_i^z = 2D_{i-1}^z + \sum_{k=1}^{i-1} T_{k,i}D_k^z, \]
equivalent to Eq. (26) in Turcotte et al. (1998). Using a change in summation indices and the Tokunaga self-similarity condition, Eq. (36), we can write this as
\[ D_i^z = 2D_{i-1}^z + \sum_{k=1}^{i-1} T_{k,i}D_k^{z-k}. \]
Given \( T_k \), which embodies the side branch statistics, this equation can be used to determine the parent–progeny diameter ratio, \( R_D \), required for a topologically self-similar binary DBS.

5. The Mandelbrot–Vicsek prefractal tree with tapering

The consistency relations in Eqs. (38) and (40) can be used to identify the branching and tapering ratios in a binary self-similar tree. As an example we consider the binary self-similar prefractal tree introduced by Mandelbrot and Vicsek (1989). This tree is generated by an iterative process, the first few stages of which are shown in Fig. 3. It is clear from the iterative construction that after \( s \) iterations the Mandelbrot–Vicsek prefractal tree is composed of three copies of the tree at \( s-1 \) iterations, and it therefore has a branching ratio \( R_B = 3 \). Since each of the copies of the tree at stage \( s-1 \) is scaled by one-half in the tree of stage \( s \), the branch length ratio for the Mandelbrot–Vicsek tree is \( R_L = 2 \). Hence from Eq. (29) the Mandelbrot–Vicsek tree is a self-similar prefractal with similarity dimension \( \Delta = \log(3)/\log(2) \). In the absence of tapering the similarity dimension is equivalent to the mass scaling exponent in dendrogram space. The mass of the tree over a distance of \( L_{s+1} \) is three times the mass over a distance \( L_s \), and the distance \( L_{s+1} \) is twice the distance \( L_s \), from which the result immediately follows. The similarity dimension is invariant under the introduction of taper but the mass scaling exponent is a function of the taper.

The Tokunaga numbers for the Mandelbrot–Vicsek tree are given by (Peckham, 1995)
\[ T_1 = 0 \quad \text{and} \quad T_k = 2^{k-2}, \quad k \geq 2. \]
Using these numbers in Eq. (38) we obtain

\[ N_i = 2N_{i+1} + \sum_{k=2}^{\Omega_i} N_{i+k} 2^{k-2}. \]

The branching ratio \( R_B \) can now be found from the substitution

\[ N_i = R_B^{i-1}, \]

(which itself follows from \( N_i = R_B N_{i+1} \) with \( N_1 = 1 \)).

With this substitution we have

\[ R_B^{i-1} = 2R_B^{i-1} + \sum_{k=2}^{\Omega_i} 2^{k-2} R_B^{i-k-1}. \]

Hence

\[ 4 \left( 1 - \frac{2}{R_B} \right) = \sum_{k=2}^{\Omega_i} \left( \frac{2}{R_B} \right)^k. \]

In the case of an infinite order tree we can take the sum to infinity, provided \( R_B > 2 \) for convergence, and we obtain

\[ 4 \left( 1 - \frac{2}{R_B} \right) = \frac{\left( \frac{2}{R_B} \right)^2}{1 - \frac{2}{R_B}}. \]

This expands as the quadratic

\[ (R_B - 3)(R_B + 1) = 0 \]

with the allowed solution \( R_B = 3 \). This is consistent with the known value of the branching ratio for the Mandelbrot–Vicsek prefractal tree (Mandelbrot and Vicsek, 1989; Yekutieli et al., 1994).

In a similar fashion we can compute the branch order diameter ratio

\[ R_D = \frac{D_{i+1}}{D_i}. \] (42)

Substitution of

\[ D_i = D_1 R_D^{i-1} \]

into Eq. (40) yields

\[ 4 \left( 1 - \frac{2}{R_D} \right) = \sum_{k=2}^{i-1} \left( \frac{2}{R_D} \right)^k, \]

and thus, after considering the limit of infinite branch order, we have

\[ R_D^2 = R_B. \] (43)

In the appendix we provide a proof that for the Mandelbrot–Vicsek tree with parent–progeny taper governed by the tapering ansatz, Eq. (39), we have the exact result

\[ D_j = \left( \frac{3^{j-1} + 1}{2} \right) D_i \],

from which the approximation

\[ R_D = 3^{\frac{1}{j}} \]

is obtained with \( j \) large.

6. Toy neuron results

The results in the preceding section readily enable us to construct self-similar binary trees with prescribed...
amounts of branching and taper. To construct these model neurons we first generate an s-stage Mandelbrot–Vicsek tree. We then assign Strahler labels to branches and use Eq. (44) to determine their diameters. The exponent $a$ is a tapering parameter, the limit $a \to \infty$ corresponds to no taper and $d_M = \log 3/\log 2$.

In the studies below we have constructed one hundred self-similar binary trees with varying amounts of taper determined by the taper ansatz (Eq. (39)) with $a = 1, a = 2, \ldots, a = 100$. Two other parameters are adjustable, the branch diameter at the final order, and the branch length at the final order. The constructed toy neurons have $s = 5$ stages of growth, resulting in an order 6 tree, with $D_6 = 5$ and $L_6 = 250$, so that the total length of the tree is two times $L_6$, or 500 units. For consistency with the real neurons analysed in Section 7, we take these units to be micrometers. The other diameters $D_i$ are then determined by Eq. (44) and the other branch lengths $L_i$ are determined by the constant branch length ratio, $R_i = 2$. Fig. 4 shows a schematic illustration of a fourth-order tapering toy neuron in anatomical space (Fig. 4A) and in dendrogram space (Fig. 4B).

We now describe methods for estimating the scaling exponents $d_M, d_A, d_N, d_T$ that characterize the morphology of the toy neurons in dendrogram space. First we consider the case without tapering, i.e. $a \to \infty$, where $d_M = \log 3/\log 2$. Note that the tapering does not affect the topological self-similarity and thus the branching exponent $d_N$ should be invariant to changes in $a$. In accordance with the theory developed in Section 2.2, the scaling exponents $d_M, d_A, d_N$ and $d_T$ can be measured experimentally as the respective slopes of log–log plots of mass ($M(L)$), total cross-sectional area ($S(L)$), numbers of intersections ($N(L)$), and average area of intersection ($S(L)$) versus distance ($L$) from the origin. In Fig. 5 we show each of these log–log plots for the two extreme cases of maximal taper ($a = 1$, left column, Fig. 5A,C,E,G), and no taper ($a = 100(\to \infty)$, right column, Fig. 5B,D,F,H). The morphology of these two toy neurons is shown in the far right column: Fig. 5I: $a = 1$, maximal taper; Fig. 5J: $a = 100(\to \infty)$, no taper. Because both toy neurons have the same branching structure, the log–log plots for number of branch intersections (Fig. 5E,F), and hence the fitted values of the branching exponent, $d_N$, are the same. However, differences in taper cause the log–log plots for mass (Fig. 5A,B), total area of intersection (Fig. 5C,D), and average area of intersection (Fig. 5G,H) to differ significantly for the two neurons. In particular, for the non-tapering neuron, the log–log curve of average area of intersection as a function of distance is constant (Fig. 5H), and hence the tapering exponent is zero, $d_T = 0$. For the highly tapering neuron ($a = 1$), by contrast, the log–log curve of average area of intersection falls off rapidly with distance in distal regions of the tree (Fig. 5G) and hence the fitted tapering exponent is negative, $d_T = -0.59$.

The trends in these plots are unmistakable but in some cases the scatter of the data makes it difficult to extract reliable slopes. A key determinant of these slopes is the scaling region over which they are measured. Determination of the appropriate scaling region, or scaling regions, is a well known problem in experimental measurements of scaling exponents (see Meakin, 1989, Chapter 2), which can be facilitated by exploiting theoretical relationships between the scaling exponents. For our four scaling exponents in dendrogram space, we utilized the theoretical relationships expressed by Eq. (10) and knowledge of the theoretical branching ratio: $d_N = (\log 3/\log 2) - 1$. Deviations from these theoretical quantities were expressed as errors:

$$e_1 = 1 - \frac{d_M}{d_A + 1}, \quad e_2 = 1 - \frac{d_N + 1}{\log 3/\log 2}.$$  

In the measurements below, for each value of $a$, the scaling exponents were measured over all possible scaling regions, with a minimum length of at least one-third of the extent of the tree in dendrogram space. This was achieved by finding the best first-order linear fit to the data points on each of the log–log plots of Fig. 5, within a sliding window of minimum length equal to one-third of the length of the tree. The sliding window moved in 5\,\mu m increments from the origin to the end of the tree, and the optimal scaling region was selected in which the total error $e_1 + e_2$ was a minimum, subject to the constraint that minimum scaling length > 167\,\mu m, (i.e. at least one-third of the total length of the tree).
optimal scaling regions are shown as gray bands superimposed on the log–log plots of Fig. 5. For the case $\alpha = 100(\to \infty)$, an optimal scaling region of length 180 units was determined with $d_M = 1.599$, $d_A = 0.593$, $d_N = 0.593$ and $d_T = 0.000$. For the case $\alpha = 1$, an optimal scaling region of length 185 units was determined with $d_M = 1.004$, $d_A = 0.006$, $d_N = 0.582$ and $d_T = -0.580$. Fig. 6 shows the distribution of scaling regions, determined in this way for $\alpha = 1, 2, \ldots, 100$. Note that the location and length of the optimal scaling region changes as the taper of the trees changes.

The fitted values of all dendrogram scaling exponents, $d_M, d_A, d_N, d_T$ are shown as functions of $\alpha$ in Fig. 7. The mass scaling exponent, $d_M$, increases monotonically with $\alpha$ from $d_M \approx 1$ at $\alpha = 1$ to $d_M \approx \log 3/\log 2 \approx 1.59$ at $\alpha = 100$. The value $d_M \approx 1$ at $\alpha = 1$ indicates that the lateral side branches contribute negligibly to the mass scaling when there is very high taper. That is, the mass dimension is approximately that of a 1D line; the side branches are relatively so thin that their contribution is insignificant. The fitted value of $d_N$ is approximately

![Fig. 5. Log–log plots showing fits of scaling exponents (black lines) and scaling regions of best linear fit (gray shaded bands) for Mandelbrot–Vicsek prefractal toy neurons with maximal taper ($\alpha = 1$, left column) and minimal taper ($\alpha = \infty$, right column). The fitted slopes give exponents $d_M$ for scaling of mass (A,B); $d_A$ for scaling of the total area of intersection (Tot. area, (C,D)); $d_N$ for the scaling of number of branch intersections (Num. inter, (E,F)) and $d_T$ for the scaling of average area of intersection (Av. area inter, (G,H)) with distance from the origin. (I,J): Schematic illustrations of the two toy neurons from which the data were measured. Both neurons have the same branching structure, and hence the same log–log plots and fitted values of the branching exponent, $d_N$, in Fig. 5(E,F). The branches of the top tree show large amounts of taper (I, $\alpha = 1$), creating a substantial drop-off in the distal regions of the log–log plots of Tot. area inter. (C,D) and Av. area inter. (G,H), while the branches of the lower tree show no taper (J, $\alpha = \infty$).]

![Fig. 6. Scaling regions found by the optimized fitting procedure, described in Section 6, for all toy neurons with values of $\alpha$ ranging from 1 to 100 on the abscissa, and the distance from the origin of the toy neurons (at 0 μm) to the tip of the tree (at 500 μm) on the ordinate. For each value of $\alpha$, optimal scaling regions covering at least one-third the length of the tree are shown as a length and distance from the origin.]
mass exponent, \( d_M \), and \( d_N \) with \( d_M \) graph of \( dN \) as a function of \( a \), the theoretical value of the branching exponent, \( d_N \), is close to unity and it increases as a saturating function of \( a \) up to \( \log(3)/\log(2) = 1.59 \) as \( a \) approaches 100. Upper right: The plot of \( d_A \) versus \( a \) is similar in shape to the plot of \( d_M \) versus \( a \), but is continuously smaller by 1 due to the theoretical constraint \( d_M = d_A + 1 \). Lower left: The plot of the branching exponent, \( d_N \) versus \( a \), is constant, and close to the theoretical value of \( d_N = 0.59 \). The size of \( d_N \) should not change with \( a \), since the branching structure, and hence the number of intersections is constant with \( a \). This is reflected in the minimal variation around the theoretical value of \( d_N = 0.59 \). Lower right: Since \( d_N \) is constant for all \( a \), the graph of \( d_T \) versus \( a \) determines the shape of the graphs \( d_A \) versus \( a \) and \( d_M \) versus \( a \). As \( a \) increases from 1 to 100, the taper decreases continuously until \( d_T \) approaches zero at \( a = 100 \).

\[
\log 3 / \log 2 - 1 \approx 0.59.
\]

The close fit of the measured value of \( d_N \) over a large scaling region and across all values of \( a \), indicates that \( d_N \) can be reliably measured using these techniques. Finally, the value of \( d_T \) increases monotonically from \( d_T \approx -0.58 \) at \( a = 1 \) to \( d_T \approx 0 \) at \( a = 100 \), mirroring the monotonic increase in \( d_M \) with \( a \). This functional behavior accurately reflects our construction of the family of Mandelbrot–Vicsek prefractal trees, such that the only source of variation in mass distribution between different trees was the degree of taper.

The jump discontinuity in the scaling exponents as functions of \( a \) that occurs at \( a \approx 40 \) in Fig. 7 is an artefact of the algorithm used to determine the optimal scaling region. This discontinuity is also apparent in the length and location of the optimal scaling region, at \( a \approx 40 \) in Fig. 6. The position of the jump can be pushed to higher values of \( a \) by decreasing the minimum allowable length of the scaling regions. Because we seek scaling exponents that are globally descriptive of complex geometric properties, we have elected to keep the minimum allowable length of the scaling region at least one-third the length of the tree, while still satisfying the theoretical constraints.

Finally, Fig. 8 demonstrates the goodness of fit to the theoretical relation of Eq. (10) (heavy dashed line, Fig. 8), by plotting the fitted values of \( d_M \) versus \( d_A \) for all tapering Mandelbrot–Vicsek prefractal trees (gray shaded circles, Fig. 8). Apart from a small discontinuity at \( d_M \approx 1.5 \) (corresponding to the jump discontinuity at \( a = 40 \) in Figs. 4 and 5), the data fit the theoretical relation

\[
d_M = d_A + 1
\]

very closely, with a slope of 1 and an intercept of (0,1).

7. Application to measuring 3D spatial complexity in neocortical pyramidal neurons

The dendrogram space scaling exponents developed in Sections 2–6 were applied to measuring the relative contributions of branching and taper to 3D spatial complexity in the apical and basal trees of neocortical pyramidal neurons from macaque monkey. We compared the scaling exponents measured for two functionally different types of pyramidal neurons distinguished by their projections: (1) long-range corticocortical projection neurons that send axons from association regions of superior temporal cortex (STC) to area 46 of the PFC, which we designate in this paper as simply “long projection neurons”; and (2) layer II–III pyramidal neurons providing local intrinsic horizontal connections between groups of pyramidal cells that contribute to local circuits within area 46 of the PFC, which we designate here as “local projection neurons”. The long projection neurons are predominantly layer III pyramidal cells (Jones, 1984; Barbas, 1986; de Lima et al., 1990; Dal cells (Jones, 1984; Barbas, 1986; de Lima et al., 1990;...
Hof et al., 1995), exhibit a different neurochemical phenotype from those providing local projections (Hof et al., 1995), and represent a particularly vulnerable class of neurons in Alzheimer’s disease (Morrison et al., 1987; Hof et al., 1990; Hof and Morrison, 2004).

Anatomical studies in macaque monkey have demonstrated that local projection neurons in PFC extend horizontal axon collaterals that travel through the gray matter, parallel to the pial surface, and terminate in a regular pattern of stripes or microcolumns of 200–400 µm width, restricted to cortical layers I–III (Levitt et al., 1993; Pucak et al., 1996), see Lewis et al. (2002) for review. The cell bodies of local projection neurons are arranged in similar vertical stripes which overlap the stripes of axon terminals (Pucak, 1996), suggesting that reciprocal connections between functionally related stripes (Melchitzky et al., 1998; Kritzer and Goldman-Rakic, 1995) might provide a neural substrate for the recurrent excitatory networks believed to subserve the delay-related persistent activity (Funahashi and Kubota, 1994; Wang, 2001; Durstewitz et al., 2000; Lisman et al., 1998) that underlies working memory in the PFC (Goldman-Rakic, 1988, 1995; Miller et al., 1996; Miller and Cohen, 2001). Functionally, long corticocortical projection neurons support the transmission of increasingly complex sensory or motor information along hierarchies of organized cortical regions, linking distant and functionally different regions of the cerebral cortex, while the local projection neurons subserve lattices of connections within a given cortical region and may enable local binding of converging information within a given cortical domain (Hof et al., 1995; Barbas, 1986; Lewis et al., 2002; Goldman-Rakic, 1995). Although the neurons of origin of these functionally distinct pathways share a general pyramidal morphology and their dendritic trees are visually similar, subtle differences in the 3D complexity of their dendritic arbors are yet to be elucidated.

Using traditional 1D Sholl analysis, a recent anatomical study showed that long projection neurons have longer, more complex dendritic arbors than local projection neurons, where “complexity” was defined by traditional Sholl analysis as the number of branch intersections at a particular distance from the soma (Duan et al., 2002). Long projection neurons had a significantly higher number of branches over the middle third of both apical and basal trees (approx. 60–180 µm from the soma). By measuring rate of change of mass, branching and taper with distance from the soma, the scaling exponents developed in this study provide a different, but complementary measure of branching complexity in 3D, that can be related to the electrotonic properties of the dendritic trees (see Section 3).

In the following analysis we addressed the specific questions: (1) Do global scaling regions exist in real pyramidal neurons, in which general properties of mass distribution, branching and taper are relatively constant? (2) Do real neuronal dendritic arbors show general trends in scaling behavior that are robust across different neuron types, and across apical and basal trees? (3) Can the fitted scaling exponents be used to distinguish significant differences in 3D spatial complexity between long and local projection neurons and to what extent are such differences due to the individual contributions of branching and tapering?

7.1. Experimental procedures

Materials from six young adult long-tailed macaque monkeys (Macaca fascicularis, 7–12 years old) were used in the present study. All experimental protocols were conducted within the NIH guidelines for animal research and were approved by the Institutional Animal Care and Use Committee (IACUC) at Mount Sinai School of Medicine. These animals received intracortical injections of the retrograde tracers Fast Blue (FB, 4%; Sigma, St. Louis, MO) in area 46 of the PFC to identify long and local projection neurons as previously described (Nimchinsky et al., 1996; Duan et al., 2002, 2003). The animals were then perfused transcardially under deep anesthesia (Nimchinsky et al., 1996), with cold 1% paraformaldehyde in phosphate-buffered saline (PBS) and then for 14 min with cold 4% paraformaldehyde in PBS. Following perfusion, 4-mm-thick blocks were dissected out of prefrontal area 46 and the superior temporal cortex, postfixed for 2 h in 4% paraformaldehyde, and cut at 400 µm on a Vibratome. One block of tissue adjacent to the injection sites was used for intracellular injection. FB-labeled cells in this area form local intrinsic horizontal corticocortical projections (called local projections in this study) within area 46 (Pucak et al., 1996; Melchitzky et al., 1998). Another block of tissue used for cell loading was taken from the cortex located in the fundus of the superior temporal sulcus, corresponding to areas TPOr, IPA and TEa (de Lima et al., 1990). As described in Duan et al. (2002, 2003), the FB-labeled cells visualized in this area formed long association corticocortical projections (referred to as long projections in this study) from the temporal cortex to area 46 (de Lima et al., 1990; Hof et al., 1995). These blocks were postfixed for 2 h in 4% paraformaldehyde and cut at 400 µm on a Vibratome. FB-containing neurons were identified under epifluorescence with a UV filter, impaled, and loaded with 5% Lucifer Yellow (Molecular Probes, Eugene, OR) in dH2O under a DC current of 3–8 nA for 10–12 min. Neurons were subsequently traced and reconstructed in 3D using a computer-assisted morphometry system consisting of a Zeiss Axioshot photomicroscope equipped with a Zeiss MSP65 computer-controlled motorized stage (Zeiss, Oberkochen, Germany), a Zeiss ZVS-47E video camera system (Zeiss, Thornwood, NY), a Macintosh G3 computer, and the software NeuroLucida (MicroBrightField, Williston, VT).
437 microcomputer, and custom designed morphometry software (NeuroZoom (Young et al., 1997); NeuroGL (Rodriguez et al., 2003)).

438 The injections of FB in the ventral part of area 46 resulted in comparable numbers of retrogradely labeled local projection neurons within area 46 and the long projection neurons lining the superior temporal sulcus. Consistent with previous studies in macaque monkey PFC (Kritzer and Goldman-Rakic, 1995; Pucak et al., 1996; Melchitzky et al., 1998), the local projection neurons were located primarily in layers II and III. The long projection neurons formed two clearly defined bands, corresponding to layer III, and layers V and VI. Forty-eight local projection neurons and 55 long projection neurons in layer III were intracellularly injected with Lucifer Yellow. Of these, 44 neurons (24 long and 20 local projection neurons) all of which exhibited a typical pyramidal morphology with extensive branching and large numbers of spines, were reconstructed and used for 3D analysis. Criteria for inclusion of filled cells for 3D reconstruction are detailed in Duan et al. (2002).

446 7.2. Methods for fitting scaling exponents to real neurons

447 The technique used to fit scaling exponents to toy neurons described in Section 6, was adapted to the experimental data for long and local projection neurons. The apical and basal dendritic trees were separately converted to dendrogram space as shown in the schematics of Fig. 10E,J. The dendrogram space was then divided into 200 sections of equal thickness, separated by parallel planes. The thickness of these sections was determined by dividing the maximum length of apical or basal trees by the total number of sections. Accumulated mass, total area of intersections, number of intersections and average area of intersection (i.e. total area of intersections divided by number of intersections) were calculated for each annulus of the 200 sections and plotted versus distance from the soma in dendrogram space, on a log–log scale (Figs. 9,10).

459 Fig. 9 shows how the start and endpoints of the scaling regions were determined from the log–log plots. In most neurons two linear regimes, each approximately one-third the length of the tree (Region II, Fig. 9A,C), in which branching decayed rapidly and did not scale linearly. These natural points of inflection, marked by the open arrows and vertical dashed lines on the plots of log(number of intersections) and log(average area intersection) (Fig. 9A,C,D) were used to select initial boundary values for the proximal and medial scaling regions for all log–log plots.

469 Determination of the optimal scaling region and corresponding exponents within these visually identified boundaries was facilitated by exploiting the theoretical relation of Eq. (10). Deviation from the theoretical relation, 

471 \[ d_M = d_A - 1 \]

472 (45)

473 The best first-order linear fit within each of the proximal and medial regions was found by moving a sliding window covering at least 90% of the size of the region identified by eye, in increments of 1μm from start to end boundaries. The optimal scaling region had the minimum error, \( \varepsilon \), subject to two further constraints: (1) logarithmic plots of cumulative mass, area of intersection, number of intersections and average area of intersection versus distance were visually linear; (2) the absolute magnitude of the error \( \varepsilon \), was smaller than 0.3, which was the maximum error for these datasets that still allowed good linear fits to each of the four log–log data plots.

482 Most neurons exhibited proximal and medial regions covering approximately one-third of the length of the tree. In some trees, either the proximal or the medial region was very short. To maximize reliability of the fitted exponents, in such cases no exponents were fitted for the shorter region, and exponents for the longer region only were included in the analysis. Shorter scaling regions occurred more frequently for apical than basal trees, and reduced the effective sample size (N in Tables 1 and 2) for scaling exponents in those regions. For this reason, the numbers of exponents fitted in each region do not correspond exactly to the numbers of long and local projection neurons reconstructed in the study.

495 7.3. Existence of two distinct scaling regions in apical and basal trees of long and local projection neurons

496 Fig. 10 shows the raw data with superimposed optimized fits of scaling exponents and resulting scaling regions (gray shaded areas) superimposed upon the log–log plots (left panels) and upon a dendrogram representation of the apical (top figure) and basal (bottom figure) trees of a representative neuron used in our study.
The raw data fits in the left panels of Fig. 10 show log–log plots of mass (Fig. 10A,F), total cross-sectional intersection area (Fig. 10B,G), numbers of intersections (Fig. 10C,H) and average intersection area (Fig. 10D,I) versus distance from the soma in dendrogram space. The images in the right panels of Fig. 10 show 2D projections of the reconstructed morphology of typical neurons used in our study. Fig. 10E shows a neuron with the apical tree represented in dendrogram space (red) and the basal tree represented in anatomical space (blue). Fig. 10J shows a different neuron with the basal tree converted to dendrogram space and the apical tree in anatomical space. The shaded areas in each of these figures show two distinct scaling regions for both the apical and basal trees: a proximal region (Region I) and a medial region (Region II), that were identified by the fitting procedure. The distal region (Region III) beyond the medial region, exhibiting branch die-off, has different scaling properties which are not characterized by a power law, and hence are not investigated in this paper. The straight lines of best fit have different slopes in Regions I and II but the relation $d_M = d_A - 1$ holds to a good approximation in each of the regions.

7.4. Comparisons between long and local projection neurons

In the results summarized in Tables 1 and 2 below, data are reported as group means and standard deviations of the measured scaling exponents, with $p$-values from a Student’s $t$-test for independent samples. Scaling exponents for Region I (Proximal region) are shown in the first two rows, exponents for Region II (Medial region) are shown in the second two rows.

7.4.1. Apical trees

Table 1 shows summary statistics for scaling exponents in Regions I and II of the apical trees of long and local projection pyramidal neurons.
(i) **Scaling Region I: proximal region**: The mass scaling exponent, $d_M$, was significantly larger for local than for long projection neurons in Region I ($p = 0.02^*$. This indicates that the rate of increase in mass with branch distance from the soma in the proximal region of the apical tree is significantly greater for local projection,
Table 1
Summary statistics for scaling exponents in Regions I (proximal) and II (medial) of apical trees

<table>
<thead>
<tr>
<th>Region</th>
<th>Type</th>
<th>Number</th>
<th>( d_M )</th>
<th>( d_A )</th>
<th>( d_N )</th>
<th>( d_T )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean s.d.</td>
<td>Mean s.d.</td>
<td>Mean s.d.</td>
<td>Mean s.d.</td>
</tr>
<tr>
<td>I</td>
<td>Long</td>
<td>17</td>
<td>0.61 0.12</td>
<td>0.32 0.20</td>
<td>0.65 0.38</td>
<td>-1.53 0.43</td>
</tr>
<tr>
<td></td>
<td>Proximal</td>
<td>11</td>
<td>0.74 0.14</td>
<td>0.16 0.22</td>
<td>1.06 0.46</td>
<td>-1.22 0.56</td>
</tr>
<tr>
<td>II</td>
<td>Long</td>
<td>16</td>
<td>0.86 0.12</td>
<td>0.25 0.17</td>
<td>0.83 0.21</td>
<td>-0.94 0.27</td>
</tr>
<tr>
<td></td>
<td>Proximal</td>
<td>12</td>
<td>0.82 0.16</td>
<td>-0.21 0.16</td>
<td>0.17 -0.12</td>
<td>0.11</td>
</tr>
</tbody>
</table>

Means and standard deviations of the scaling exponents \( d_M, d_A, d_N \) and \( d_T \) are shown for long and local projection neurons, which satisfied the constraints on minimum allowable length of scaling region, linearity of fits and maximum allowable error (Eq. (45)) described in the text. Tabulated \( p \)-values were computed for Student’s \( t \)-tests for independent samples. Asterisks indicate significance levels:

- \(*\) Significance at .05 level.

Table 2
Summary statistics for scaling exponents in Regions I (proximal) and II (medial) of basal trees.

<table>
<thead>
<tr>
<th>Region</th>
<th>Type</th>
<th>Number</th>
<th>( d_M )</th>
<th>( d_A )</th>
<th>( d_N )</th>
<th>( d_T )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean s.d.</td>
<td>Mean s.d.</td>
<td>Mean s.d.</td>
<td>Mean s.d.</td>
</tr>
<tr>
<td>I</td>
<td>Long</td>
<td>21</td>
<td>0.78 0.15</td>
<td>0.23 0.20</td>
<td>0.78 0.13</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>Proximal</td>
<td>16</td>
<td>0.86 0.12</td>
<td>-0.11 0.17</td>
<td>0.83 0.21</td>
<td>-0.94 0.27</td>
</tr>
<tr>
<td>II</td>
<td>Long</td>
<td>22</td>
<td>0.82 0.15</td>
<td>-0.25 0.17</td>
<td>-0.08 0.17</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td>Proximal</td>
<td>13</td>
<td>0.82 0.16</td>
<td>-0.21 0.16</td>
<td>-0.09 0.17</td>
<td>0.17</td>
</tr>
</tbody>
</table>

Means and standard deviations of the scaling exponents \( d_M, d_A, d_N \) and \( d_T \) are shown for long and local projection neurons, which satisfied the constraints on minimum allowable length of scaling region, linearity of fits and maximum allowable error (Eq. (45)) described in the text. Tabulated \( p \)-values were computed for Student’s \( t \)-tests for independent samples.

Compared with long projection neurons. A similar trend was found for the scaling exponent \( d_A \) \((p = 0.05^*)\), which is approximately linearly related to \( d_M \) by Eq. (10). From the theoretical relationship of Eq. (14):

\[
d_M = d_N + d_T + 1,
\]

the greater rate of increase in mass for local neurons could be produced by a greater rate of increase in branching; a lower rate of taper; or a combination of these effects. As indicated by the independent measurements of \( d_N \) and \( d_T \) listed in Table 1, no significant differences were observed in the branching exponents, \( d_N \) \((p = 0.38)\). The tapering exponent, \( d_T \), was considerably lower for local than long projection neurons, although due to the higher variability in estimating \( d_T \), this effect failed to reach significance at the 0.05 level \((p = 0.10)\). These results indicate that the significantly higher value of \( d_M \) in Region I of local projection neurons was due primarily to a slower rate of taper than in long projection neurons. Although branching tended to increase more rapidly in long than in local projection neurons, this effect was not sufficient to counterbalance the substantially higher rate of taper in long projection neurons.

(ii) Scaling Region II: medial region: The last two rows of Table 1 compare scaling exponents measured in Region II of the two classes of neurons. While a similar trend for a higher rate of increase in mass for local than long projection neurons was also found in the medial region of apical trees, this failed to reach statistical significance for either scaling exponent, \( d_M \) \((p = 0.28)\) or \( d_A \) \((p = 0.06)\). As in the proximal apical region, differences in the tapering exponent were the main contributors to this trend, with lower variability in estimates of \( d_T \) in the medial apical trees contributing to a significantly larger negative value of \( d_T \) and correspondingly greater rate of taper for long than local projection neurons \((p = 0.04^*)\). The branching exponents were not significantly different between long and local projection neurons \((p = 0.72)\).

7.4.2. Basal trees

No significant differences were found between long and local projection neurons for any of the scaling exponents in either Region I or II of the basal trees (see Table 2). Similar to the trends in the apical trees, the mass and total area exponents, \( d_M \) and \( d_A \), tended to be greater for local than long projection neurons in the proximal region, but these trends failed to reach statistical significance \((p = 0.09)\) for \( d_M \), \( p = 0.06 \) for \( d_A \). These trends were not present in the medial region, however.
7.5. General homeostatic pattern of mass distribution for long and local projection neurons

While significant differences between long and local projection neurons were found for scaling exponents in the apical trees, the global pattern of mass distribution was remarkably similar for apical and basal trees, and for both neuron types. This pattern can be characterized as a gradual decrease in the amount of dendritic mass located between equi-spaced orthogonal planes in dendrogram space at increasing distances from the soma. The scaling exponent $d_A$, which measures the rate of change of total area of intersection of all dendritic branches at a given arc length distance from the soma, is a more intuitive indicator of this trend than the scaling exponent $d_M$ which measures the rate of accumulation of total mass within the given arc length distance. As shown graphically in Fig. 11, $d_A$ maintains a constant, small negative value of between $-0.10$ and $-0.40$ in both regions I and II of apical trees (Fig. 11A, first column) and basal trees (Fig. 11B, first column), indicating that mass is slowly decreasing as a function of distance from the soma, and at an approximately uniform rate. Fig. 11 compares the contributions to this slow decrease of mass, of branching ($d_N$) and of tapering ($d_T$), in the two regions of apical and basal trees. Exponents for local neurons are shown in black, exponents for long neurons are shown in gray. Despite large differences in the magnitudes of branching and tapering exponents between Regions I and II, these differences are compensatory such that a uniform, slow rate of mass reduction is maintained across both regions. This pattern is independent of neuron type and independent of tree type (apical or basal). In Region I of the apical trees of long projection neurons, for example, a large positive branching exponent ($d_N = 1.06$) is compensated by an even larger negative tapering exponent ($d_T = -1.22$), resulting in an overall negative value of $d_A$ ($d_A = -0.16$), and hence a global decline in mass as a function of distance from the soma, and at an approximately uniform rate. This pattern is independent of neuron type and independent of tree type (apical or basal). In Region I of the apical trees is repeated for long projecting neurons (gray histograms, Fig. 11A, top row). The same pattern occurs for Region I of the basal trees of both long and local projection neurons (Fig. 11B, top row).

In Region II, the pattern of branching and tapering is very different, but again the exponents $d_N$ and $d_T$ are compensatory, such that the same slow global decline of mass with distance, indexed by $d_A$, is maintained. In the apical trees, $d_N$ in Region II is close to zero for both long and local projection neurons (Fig. 11A, 2nd row, 2nd column) and slightly negative in the basal trees (Fig. 11B, 2nd row, 2nd column), indicating no increase in branching and even a slight tendency for branches to die off. The tapering exponent is also small, indicating little change in branch diameters with distance either for

Fig. 11. Global pattern of branching and taper in apical (A) and basal (B) trees of long and local projection neurons. The two rows of (A) and (B) contrast the different branching and tapering patterns in Region I (top rows, A, B) and Region II (bottom rows, A, B). Means ± standard deviations are represented as histograms with superimposed error bars. Exponents for long projection neurons are shown as gray histograms; exponents for local projection neurons as black histograms. From the theoretical result of Eq. (10), the total area exponent $d_A$ equals the sum of the branching $d_N$ and tapering $d_T$ exponents. In both local and long projection neurons there is a slow decrease in the total area of intersection, $d_A$ with distance from the soma, at an approximately uniform rate over both proximal (I) and medial (II) regions, and in both apical and basal trees (compare column 1 of Regions I and II in (A) and (B)). This uniform rate of decrease is maintained by very different patterns of branching and taper in the two regions, however. In the proximal region, the slow decrease is achieved by large amounts of tapering $d_T$ compensating for large amounts of branching $d_N$. In the medial region by contrast, the slow decrease is maintained by a negligible amount of branching $d_N$, and a very small amount of taper $d_T$. This pattern is consistent across neuron type and across apical and basal trees. The asterisks in (A) indicate significant differences ($p < 0.05$) in scaling exponents between long and local projection neurons.
the apical trees (Fig. 11A, 2nd row, 3rd column) or the basal trees (Fig. 11B, 2nd row, 3rd column). When summed, these two contributions to global mass distribution again almost cancel, resulting in a slow, uniform global decline in mass with distance, across both Regions I and II.

8. Summary and discussion

Neuronal dendritic arbors are good examples of spatially complex structures, and attempts to relate this spatial complexity to function date back at least as far as Sholl (1953). In this paper we have introduced measures of spatial complexity that are relevant to the cable properties of neurons (Rall, 1989), and hence to their firing patterns. A fundamental parameter in this analysis is the distance metric in dendrogram space and the utility of the exponents for quantifying the independent contributions of branching and taper to 3D dendritic spatial complexity was first demonstrated on computer generated self-similar binary trees with prescribed branching and taper. We then measured dendrogram scaling exponents on the apical and basal trees of macaque monkey pyramidal neurons and found scaling behavior that discriminated long projection neurons from local projection neurons. An interesting feature of this analysis was the identification of three distinct regions, present in both apical and basal trees: proximal, medial and distal, corresponding approximately to “growth”, “plateau” and “die-off” regions, respectively. Scaling behavior that discriminated long from local projection neurons was found in both proximal and medial regions of the apical, but not the basal trees. In an earlier study, we used a cumulative mass method to compute mass fractal dimension, $D_M$, in anatomical space, in a group of 16 long and 19 local projection neocortical pyramidal neurons from macaque monkey (Henry et al., 2002). A single scaling region was found for $D_M$, which, like $d_M$ in the present analysis, was also significantly larger for local than long projection neurons. The present result for $d_M$ in dendrogram space refines and clarifies these differences in two ways: (i) the significant differences in $d_M$ between long and local neurons are restricted to the proximal third, or “growth region” of the apical trees; (ii) because $d_M$ in dendrogram space can be decoupled into independent parameters quantifying branching $d_N$ and taper $d_T$, the analysis in this paper demonstrates that global taper across the proximal region, and not branching, was the cause of the observed differences in mass distribution. Since $d_N$, equivalent to the standard Sholl exponent, did not differ significantly in either proximal or medial regions, these differences between the two classes of neuron would not be detected in a standard Sholl analysis.

Another interesting feature was that the mass exponent is conserved across both proximal and medial regions but the branching exponent and tapering exponent are not. This raises the intriguing question of whether any functional significance can be inferred from the fine balance between branching and tapering effects, such that the overall mass scaling is unchanged. We suggest that maintenance of a uniform mass scaling exponent over most of the dendritic tree may be a potentially adaptive homeostatic mechanism controlling global mass distribution.

The morphological measurements we have reported in this paper are defined by power law functions of branch distance measured from the soma. Typically we found one power law out to a distance $r_0$ and a second power law from $r_0$ to $2r_0$, where $r_0$ is approximately one-third the length of the apical or basal tree. In the apical tree of Fig. 10, for example, the first power law describes self-similar scaling over approximately a factor of ten in distance scales (e.g. 10–100 μm), whereas the second describes self-similar scaling over approximately a factor of two in distance scales (e.g. 100–200 μm). In terms of self-similar scaling, this range of scales is quite small, particularly in the second region. However the significance of the power law fits is not the extent to which we can interpret the neuronal morphology as fractal—although the power law scaling behavior is certainly consistent with that of a low order prefractal. The main significance of the power law fits is twofold: (i) the domain width ($\approx$ 100 μm in Fig. 10, Apical tree) over which each power law applies is about the same for each scaling region and it typically spans about one-third of the entire apical or basal tree in each neuron. (ii) The small range scaling laws that we measured discriminate between different, functionally relevant properties. As an aside we note that small range scaling laws have been shown to be reliable discriminants in other contexts, e.g. heartbeat time series from healthy young, healthy elderly, and heart failure subjects exhibit short-range discriminative scaling (Goldberger et al., 2002).

9. Conclusion

We have shown that the global distribution of dendritic mass, measured by the mass dimension $d_M$, can be decomposed into a sum of two independent scaling exponents representing global branching
complexity, $d_N$, and global rate of taper, $d_T$ over prescribed scaling regions of the tree. The tapering exponent $d_T$ is thus a global measure of dendritic geometry that is independent of the standard Sholl branching exponent, $d_N$, and can distinguish subtle differences in branching structure that standard Sholl analysis cannot. These new scaling exponents provide novel 3D tools with which to distinguish changes in global spatial complexity that can be related to functional changes in the electrotonic properties of single neurons.

Acknowledgements

We thank Huiling Duan for supplying the digitized macaque monkey pyramidal neurons used to test application of the scaling exponents developed in this paper. We also thank Alfredo Rodriguez, Douglas Ehlenberger and Kevin Kelhier for technical assistance, and Dr. John H. Morrison for scientific advice and support. This work was supported by NIH Grants MH58911, MH060734, AG05138, AG06649, DC04632, DC05669, RR16754, and a Discovery Grant funded by the Australian Research Council.

Appendix

In this appendix we provide a mathematical proof by induction that if the diameter of each $j$th order branch in the Mandelbrot–Vicsek tree is related to the diameter of first-order branches by

$$D_j^s = \left(\frac{3^{j-1} + 1}{2}\right) D_1^s, \quad (A.1)$$

then the taper ansatz

$$N_i D_i^s = \sum_{j=1}^{i-1} N_{ij} D_j^s \quad (A.2)$$

is satisfied at all stages of growth. The taper ansatz relates progeny branch diameters $D_j$ to parent branch diameters $D_i$ for a self-similar binary tree using the Strahler labeling for branch orders. $N_i$ is the number of branches of order $i$ and $N_{ij}$ is the number of lateral side branches of order $j$ that attach to parent branches of order $i$.

The Mandelbrot–Vicsek tree is generated in stages with branch numbers at stage $s+1$ related to branch numbers at stage $s$ as follows:

$$N_i^{(s+1)} = 3N_i^{(s)} - 1, \quad (A.3)$$

$$N_{1j}^{(s+1)} = 3N_{1j}^{(s)} - N_{1j}^{(s-1)}, \quad (A.4)$$

$$N_{i+1,j+1}^{(s+1)} = N_{ij}^{(s)}, \quad (A.5)$$

The following relations are also apparent by inspection

$$N_{s+1}^{(s)} = 1, \quad (A.6)$$

$$N_{1j}^{(s)} = 2, \quad (A.7)$$

$$N_{1j}^{(s-1)} = 2^{s-3}, \quad j \geq 3. \quad (A.8)$$

The linear recurrence relation, Eq. (A.3), that satisfies the condition, Eq. (A.6), has the solution

$$N_i^{(s)} = \frac{3^{s-i+1} + 1}{2}. \quad (A.9)$$

The linear recurrence relation, Eq. (A.4), that governs the number of lateral first-order branches joining $j$th order branches at successive stages of growth is straightforward to solve for the auxiliary conditions Eqs. (A.7) and (A.8). The result is

$$N_{1j}^{(s)} = 3^{s-j+1} + 1, \quad (A.10)$$

$$N_{1j}^{(s-j+1)} = 2^{-4}(3^{s-j+1} + 1), \quad j \geq 3. \quad (A.11)$$

The results in Eqs. (A.9), (A.10) and (A.11) now enable us to prove Eq. (A.1) by induction. First consider Eq. (A.2) with $i = 2$,

$$N_2 D_2^s = N_{12} D_1^s = N_{12} D_1^s. \quad (A.12)$$

Using the results in Eqs. (A.9) and (A.10) this simplifies to

$$D_2^s = 2D_1^s, \quad (A.12)$$

in agreement with Eq. (A.1) for $j = 2$.

Now consider Eq. (A.2) with $i = 3$. This can be rewritten as

$$N_3 D_3^s = N_{13} D_1^s + N_{12} D_2^s, \quad (A.13)$$

where we have also used Eq. (A.5) with $i = 1$ and $j = 2$. Using Eqs. (A.9), (A.10) and (A.11) this simplifies to

$$D_3^s = D_1^s + 2D_2^s, \quad (A.13)$$

and thus, from Eq. (A.12),

$$D_3^s = 3D_1^s, \quad (A.13)$$

which is in agreement with Eq. (A.1) for $j = 3$.

We now consider Eq. (A.2) with $i = k$ and assume that Eq. (A.1) holds for $j = 2, 3, \ldots, k - 1$. First we use the results of Eq. (A.5) to rewrite the taper ansatz as

$$N_k D_k^s = N_{1k} D_1^s + \sum_{j=1}^{k-1} N_{1k,j} D_j^s. \quad (A.14)$$

Now use Eq. (A.1) for $j = 2, 3, \ldots, k - 1$ to obtain

$$N_k D_k^s = N_{1k} D_1^s \left(3^{k-2} - 1\right) \frac{1}{2} + \sum_{j=1}^{k-2} N_{1k,j} \left(3^{k-j-2} - 1\right) \frac{1}{2} \left(3^{j-1} + 1\right) D_1^s. \quad (A.15)$$
With Eqs. (A.9), (A.10) and (A.11) this simplifies to

\[
D^j_k = (3^{k-2} + 1)D^1_k + \sum_{j=2}^{k-2}(3^{j-1} + 1)2^{k-j-3}D^2_j, \quad \text{(A.14)}
\]

\[
= \left( \frac{3^{k-1} + 1}{2} \right)D^1_k, \quad \text{(A.15)}
\]

in agreement with the main result in Eq. (A.1) for \( j = k \).

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