

Neuron Developmental Modeling and Structural Representation: The Statistical Model

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1 Abstract

This is the second in a series of papers describing a set of tools for the developmental modeling, visualization, and statistical analysis of neuron populations. Paper two covers the statistical model used by the N++ tools and the probability density functions which accompany it. The statistical model is described as a an essential set of properties describing neuron morphology, auxiliary properties which derive from the essential properties, and a simple indexed “flat file” organization suitable for import into a spreadsheet or similar statistical analysis package. Probability density functions are described both in terms of the properties they relate to and the parametric statistical forms used in the N++ stochastic neuron generation process.

2 Introduction

2.1 Purpose

The purpose of the statistical model is to create a framework for the description and statistical analysis of neurons and neuron populations. The statistical model specifies an indexed flat file organization suitable for import into a spreadsheet or other statistical analysis tool. The purpose of such analysis is twofold:

1. To derive probability density functions for neuron morphological properties.
2. To distinguish between different types of neurons or between variant types of neuron within an inhomogeneous neuronal population.

The probability density functions for neuron properties are of interest because they allow for the statistical description of neuron properties and for the synthetic generation of neuron populations through the stochastic modeling tools of N++. Our objective here is to stochastically generate neuron populations which are visually and statistically indistinguishable in morphology from the modeled neuron database.

2.2 Document Structure

This document is based on the N++ nneuron anatomical model, as described in the first paper in this series, *An Introduction to the N++ Language, an Open Stochastic L-System*. In this model a neuron is subdivided into a soma, one or more dendritic arbors, and one or possibly two axonal arbors. Arbors are subdivided into junctions and segments. Segments are subdivided into generalized cylinders (which will be referred to simply as “segments”) and spines, which are small, regularly spaced protrusions on the sides of the segment.

In each of the following sections a subdivision of the neuron morphological model is described. Section 3 deals with somata, Section 4 with arbors, Section 5 with segments, Section 6 with spines, and Section 7 deals with junctions. Each section is divided into a Properties subsection and Probability Density Functions subsection. Auxiliary properties are discussed in Section 8.

Description	Symbol	Type	Representation
A position property	P_1	\mathfrak{R}^3	$(p_1 \ p_2 \ p_3) \in \mathfrak{R}^3$
An orientation property	P_2	Q_{unit}	$(q_0 \ q_1 \ q_2 \ q_3) \in \mathfrak{R}^4$

Table 1: Schematic properties

2.2.1 Properties

The term *property* roughly corresponds to Mulchandani’s[2] “morphological variable” except that a distinction is made between *properties*, which provide a primary or essential representation, and *auxiliary properties* which are derived properties. Auxiliary properties are given their own treatment in Section 8¹.

The term property is also used to refer to “synthetic” values (such as an ID number) which are essential to the organization of the statistical data in a flat file but which do not have a direct anatomical basis.

Associated with each Properties subsection is a table summarizing the properties, a schematic representation of which is found in Table 1. Note that a distinction is made between the property and its representation. In Table 1 P_1 is a vector but its representation is as three scalar values. Likewise, P_2 is a quaternion but it is represented as four scalars. This distinction is important for representing data in a spreadsheet or other application which may not directly support data types like vectors or quaternions.

2.2.2 Probability Density Functions

A probability density function describes the statistical distribution of a property. All properties meaningful to the stochastic generation of neurons have associated probability density functions.

Each Probability Density Functions subsection contains a brief description of the probability density functions associated with each non-synthetic property. These are summarized in a table like Table 2.

¹In many cases there is a direct correspondence between one of Mulchandani’s morphological variables and a given property, but in a few cases there are significant differences. In every case the morphological variable can be reconstructed as an auxiliary property.

Description	Representation
Distribution of positions	$p(P_1)$
Distribution of orientations, conditional on P_1	$p(P_2 P_1)$

Table 2: Schematic probability density functions

Description	Symbol	Type	Representation
cell ID	ID_{cell}	$I \geq 100,000$	I
soma position	P_{soma}	\mathfrak{R}^3	$(p_1 \ p_2 \ p_3) \in \mathfrak{R}^3$
soma orientation	O_{soma}	Q_{unit}	$(q_0 \ q_1 \ q_2 \ q_3) \in \mathfrak{R}^4$
soma diameter	D_{soma}	\mathfrak{R}	\mathfrak{R}

Table 3: Somata properties

3 Somata

3.1 Properties

The soma is the root of the dendritic and axonal arbors. For the purposes of the neuron morphology model the soma is a three-dimensional solid positioned and oriented in anatomical space. As such the soma has three important properties:

cell ID A unique identifier which distinguishes one neuron cell from every other neuron cell in a population. Since there is only one soma per cell, this also uniquely identifies each soma. Cell ID is represented as a six digit integer counting upwards from 100,000.

soma position The soma’s position in anatomical (rostral \times lateral \times dorsal) space. Position is represented by a \mathfrak{R}^3 position vector.

soma orientation The soma’s orientation in anatomical space. The soma’s orientation is represented by a unit quaternion relative to the anatomical space.

soma diameter The diameter of a circle with the same cross sectional area as a 2D projection of the soma onto the sagittal plane. Soma diameter is represented as a real number.

These properties are summarized in Table 3.

3.2 Probability Density Functions

In order to statistically model somata the following probability density functions are necessary:

- $p(P_{soma})$ — A probability density function for the position of somata in anatomical space.

Description	Representation
distribution of soma positions	$p(P_{soma})$
distribution of soma orientations	$p(O_{soma} P_{soma})$
distribution of soma diameters	$p(D_{soma} P_{soma})$

Table 4: Soma probability density functions

- $p(O_{soma} | P_{soma})$ — A probability density function for the orientation of somata in anatomical space, conditional on soma position.
- $p(D_{soma} | P_{soma})$ — A probability density function for the diameter of somata, conditional on soma position.

These are summarized in Table 4.

Description	Symbol	Type	Representation
arbor ID	ID_{arbor}	$I \geq 1$	I
cell ID	ID_{cell}	$I \geq 100,000$	I
arbor type	T	$\{dendritic, axonal\}$	$\{dendritic, axonal\}$
number of segments	N_{seg}	$I \geq 1$	I
number of junctions	$N_{junction}$	$I \geq 1$	I
arbor depth	D	$I \geq 1$	I

Table 5: Arbor properties

4 Arbors

4.1 Properties

An arbor is a collection of dendritic or axonal segments which share a common predecessor segment. Arbors have the following properties:

arbor ID An identifier which distinguishes one arbor from every other arbor belonging to the same cell. This is represented as an integer value counting upwards from 1.

cell ID The identifier of the neuron to which the arbor belongs.

arbor type A symbolic designator for the type of arbor, $s \in \{dendritic, axonal\}$.

number of segments The number of segments in the arbor.

number of junctions The number of junctions in the arbor.

arbor depth The maximum junction order of the arbor. The root Soma-Arbor junction is order 0.

These properties are summarized in Table 5.

4.2 Probability Density Functions

None.

5 Segments

5.1 Properties

Segments are modeled as a trajectory in space and a diameter which may change as a function of length. Empirically measured segment trajectory data is usually in the form of a series of sampled points, which may or may not be regularly spaced. For the purposes of statistical modeling such data is re-sampled at a user-specified resolution. This results in a set of uniformly spaced data points representing the segment trajectory.

The sampled data points are referred to as $P_i, 1 \leq i \leq n$. By linearly interpolating between these points, a piecewise linear representation of the trajectory may be constructed. Each linear portion of the piecewise trajectory is referred to as a section, and is defined as:

$$s_i = P_{i+1} - P_i \mid 1 \leq i < n \quad (1)$$

5.1.1 Segment Trajectory

The Frenet Frame To statistically model the segment trajectory, it is useful to introduce the Frenet frame of the trajectory at each sampled data point $P_i \mid 1 \leq i < n$. The Frenet frame of a parametric curve $x = f(s), x \in \mathbb{R}^3$ provides a local frame of reference defined by the direction and curvature of f at s . The Frenet frame is defined as the triplet of orthonormal vectors $(t \ m \ b)$

$$t = \frac{\dot{x}}{\|\dot{x}\|}, \quad m = b \wedge t, \quad b = \frac{\dot{x} \wedge \ddot{x}}{\|\dot{x} \wedge \ddot{x}\|} \quad (2)$$

where \dot{x} is the first derivative of x with respect to s , and \ddot{x} is the second derivative of x with respect to s , and both of these derivatives exist and are non-zero[1, 2].

The Discrete Frenet Frame Since sampled data points themselves are not a continuous curve, it is necessary to use other information to approximate the true Frenet frame at a sampled data point. One way of doing this would be to refer to the Frenet frame of an interpolating spline constructed through the data points. However, this would require the use of a C2 continuous interpolating spline so that the required derivatives exist.

There is no *a priori* reason to believe that real segment trajectories are C2 continuous. Further, the curvature of an interpolating spline depends on a number of factors other than the data points. Thus it is desirable to find

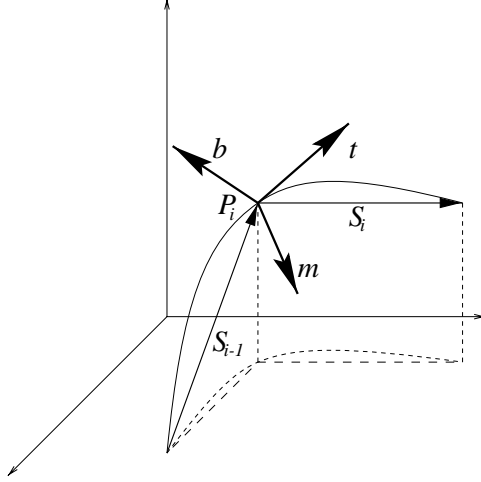


Figure 1: The discrete Frenet frame at P_i , with interpolating spline.

a representation which approximates the true Frenet frame of the trajectory but is discrete and depends only on the sampled data points.

To accomplish this, the discrete Frenet frame (Figure 1) at $P_i \mid 1 < i < n$ is defined as:

$$t = \frac{s_{i-1} + s_i}{\|s_{i-1} + s_i\|}, \quad m = b \times t, \quad b = \frac{s_i \times s_{i-1}}{\|s_i \times s_{i-1}\|} \quad (3)$$

For the special case of P_1 the discrete Frenet frame is defined as:

$$t = \frac{RF_t + s_1}{\|RF_t + s_1\|}, \quad m = b \times t, \quad b = \frac{s_1 \times RF_t}{\|s_1 \times RF_t\|} \quad (4)$$

where RF_t is the t vector of the initial segment reference frame. A succession of discrete Frenet frames may be described in terms of a series of rotations of the initial segment coordinate frame.

A Continuous Reconstruction A continuous reconstruction of the segment trajectory may occasionally be useful for resampling or visualization. Using an interpolating spline with a Catmull-Rom interpolant results in curvature at the control points which matches the discrete Frenet frame at that point.

Description	Symbol	Type	Representation
segment ID	$ID_{segment}$	$I \geq 200,000$	I
cell ID	ID_{cell}	$I \geq 100,000$	I
arbor ID	ID_{arbor}	$I \geq 1$	I
segment type	t	$\{nonterminal, terminal\}$	$\{nonterminal, terminal\}$
parent junction ID	ID_{j0}	$I \geq 300,000$	I
daughter junction ID	ID_{j1}	$I \geq 300,000$	I
initial diameter	d_i	$\mathbb{R} > 0$	\mathbb{R}
initial taper	$-d'_i$	$\mathbb{R} > 0$	\mathbb{R}
final diameter	d_f	$\mathbb{R} > 0$	\mathbb{R}
final taper	$-d'_f$	$\mathbb{R} > 0$	\mathbb{R}
diameter interpolation method	I_{method}	$\{linear, Hermite\}$	$\{linear, Hermite\}$
segment arc length	l_{arc}	$\mathbb{R} > 0$	\mathbb{R}
segment electrotonic length	l_e	$\mathbb{R} > 0$	\mathbb{R}
total rotation	R_{total}	Q_{unit}	$(q_0 \ q_1 \ q_2 \ q_3) \in \mathbb{R}^4$
number of sampled data points	n	$I \geq 2$	I
sampling interval	l_s	$L_{arc} \geq l_s > 0$	\mathbb{R}
trajectory	T	$(P_1 \ P_2 \ \dots \ P_n)$	$P_i = (p_{i0} \ p_{i1} \ p_{i2}) \in \mathbb{R}^3$
discrete Frenet frames	D	$(Q_{P_1} \ Q_{P_2} \ \dots \ Q_{P_n})$	$Q_{P_i} = (q_{P_{i0}} \ q_{P_{i1}} \ q_{P_{i2}} \ q_{P_{i3}}) \in \mathbb{R}^4$
segment growth force field	$-\nabla\phi$	$(-\nabla\phi_{P_1} \ -\nabla\phi_{P_2} \ \dots \ -\nabla\phi_{P_n})$	$-\nabla\phi_{P_i} = (\frac{-\partial\phi}{\partial t} \ \frac{-\partial\phi}{\partial m} \ \frac{-\partial\phi}{\partial b}) \in \mathbb{R}^3$

Table 6: Segment properties

5.1.2 Force Fields

To model the growth of neuron segments it is necessary to take into account the effects of chemical “force fields” which attract or repel the neuron growth cone. The statistical model assumes that such a field can be approximated as a constant gradient with respect to the growth of a single section, but can vary over the length of the segment. The further assumption is that the field effects segment growth by applying a torque to the Frenet frame of the growth tip equal to the cross product of the t vector and the gradient. The presence of such a field is therefor detectable through analysis of the discrete Frenet frame data.

5.1.3 Properties list

Segments have the following properties:

segment ID A unique identifier which distinguishes one segment from ev-

ery other segment in a neuron. Segment ID is represented as a six digit integer counting upwards from 200,000.

cell ID The identifier of the cell in which the segment resides.

arbor ID The identifier of the arbor in which the segment resides.

segment type There are two types of segments, nonterminal and terminal. Nonterminal segments have daughter junctions; terminal segments do not.

parent junction ID The identifier of the parent junction of the segment.

daughter junction ID The identifier of the daughter junction of the segment.

initial diameter The initial diameter of the segment.

initial taper The negative slope of the diameter as a function of length at the beginning of the segment. This is used as the initial tangent for cubic Hermitian diameter interpolation.

final diameter The final diameter of the segment.

final taper The negative slope of the diameter as a function of length at the end of the segment. This is used as the final tangent for cubic Hermitian diameter interpolation.

diameter interpolation method The method used to interpolate between the initial and final diameter. The choices are *linear* and *hermite*.

segment arc length The path length of the trajectory of segment.

segment electrotonic length The electrotonic length of the segment.

total rotation The rotation of the final reference frame of the trajectory with respect to the initial reference frame, i.e. $RF_{initial} \Rightarrow RF_{final}$

number of sampled data points The number of data points in the trajectory.

sampling interval The sampling interval for the data points.

Description	Representation
Distribution of nonterminal segments	$p(t)$
Distribution of initial segment diameter	$p(d_i)$
Distribution of initial segment taper	$p(-d'_i)$
Distribution of final segment diameter	$p(d_f)$
Distribution of final segment taper	$p(-d'_f)$
Distribution of segment arc length	$p(l_{arc})$
Distribution of segment electrotonic length	$p(l_e l_{arc} d_i d_f)$
Distribution of successive discrete Frenet frame rotations	$p(Q_P)$
Distribution of segment growth force field	$p(-\nabla\phi)$

Table 7: Segment probability density functions

trajectory A sequence of sampled data points representing the segment trajectory. These are \mathfrak{R}^3 vectors relative to the initial reference frame of the segment.

discrete Frenet frames The discrete Frenet frames at points $P_i | 1 \leq i \leq n$ expressed as a series of successive rotations of the initial segment reference frame.

segment growth force field The negative gradient of the chemical concentration effecting the growth of the segment, as measured at each sampled data point.

These properties are summarized in Table 6.

5.2 Probability Density Functions

A segment may be statistically modeled using the following probability density functions:

- $p(t)$ — A probability density function for the distribution of nonterminal segments.
- $p(d_i)$ — A probability density function for the distribution of initial segment diameter.
- $p(-d'_i)$ — A probability density function for the distribution of initial segment taper.

- $p(d_f)$ — A probability density function for the distribution of final segment diameter.
- $p(-d'_f)$ — A probability density function for the distribution of final segment taper.
- $p(l_{arc})$ — A probability density function for the distribution of segment arc length.
- $p(l_e)$ — A probability density function for the distribution of segment electrotonic length. It is assumed that electrotonic length can be computed from l_{arc} , d_i , and d_f , and for segments adjacent to the soma, additionally from $-d'_i$ and $-d'_f$.
- $p(Q_P)$ — A probability density function for the distribution of successive discrete Frenet frame rotations independent of segment growth force field.
- $p(-\nabla\phi)$ — A probability density function for the distribution of segment growth force field.

These probability density functions are summarized in Table 7.

Description	Symbol	Type	Representation
segment ID	$ID_{segment}$	$I \geq 200,000$	I
cell ID	ID_{cell}	$I \geq 100,000$	I
number of spines	n_{spine}	$I \geq 0$	I
spine distances	d_{spines}	$(d_1 \ d_2 \ \dots \ d_{n_{spine}})$	$d_i \in \mathfrak{R}$
spine rotations	θ_{spines}	$(\theta_1 \ \theta_2 \ \dots \ \theta_{n_{spine}})$	$\theta_i \in \mathfrak{R}$

Table 8: Spine properties

6 Spines

6.1 Properties

Spines are small protrusions found on the sides of segments. The precise measurement of individual spines is difficult and time consuming given their small scale — these structures are barely visible at the limit of optical resolution. However, an attempt must be made to accurately measure the position and orientation of individual spines on at least some segments for statistical modeling purposes. Spines have the following properties:

segment ID The ID of the segment being described.

cell ID The identifier of the cell in which the segment resides.

number of spines The observed number of spines on the segment.

spine distances A list of the distances of each spine from the parent junction.

spine rotations A list of the rotations of each spine (in radians) relative to the b vector of the Frenet frame.

These properties are summarized in Table 8.

6.2 Probability Density Functions

Spines may be statistically modeled using the following probability density functions:

- $p(n_{spine} | l_{arc})$ — a probability density function for the distribution of the number of spines, conditional on segment length.

Description	Representation
Distribution of number of spines	$p(n_{spine} l_{arc})$
Distribution of spine distances	$p(d_{spines} n_{spine} l_{arc})$
Distribution of spine rotations	$p(\theta_{spines})$

Table 9: spine probability density functions

- $p(d_{spines})$ — a probability density function for the distribution of the distance of spines from the segment junction.
- $p(\theta_{spines})$ — a probability density function for the distribution of spine rotations relative to the b vector of the local Frenet frame.

These probability density functions are summarized in Table 9.

7 Junctions

7.1 Properties

A junction is a branch point in an axon or dendrite. A single segment, referred to as the parent, branches into two or more daughter segments. In the case where there are two daughter segments the junction is termed a bifurcation, otherwise it is called a multifurcation. The statistical model directly accommodates bifurcations and multifurcations of three daughter segments. For multifurcations of more than three daughter segments, additional junctions may be used.

Junctions are defined by the intersection of parent and daughter segments. The parent segment is referred to as S_0 and the daughter segments as $S_1 \dots S_n$, $n \in \{2, 3\}$. Daughter segments are designated S_1, S_2 , etc. in order of decreasing diameter, unless dependency relationships dictate otherwise (see below).

7.1.1 Relative Angle Junction Geometry Representation

Mulchandani[2] describes bifurcation junction geometry in terms of three relative angles (θ_{01} , θ_{02} , and θ_{12}) and a chirality factor which indicates the “handedness” of the structure. Unfortunately this is adequate only for a bifurcation. For a trifurcation the number of relative angles needed increases to six (θ_{01} , θ_{02} , θ_{03} , θ_{12} , θ_{13} , and θ_{23} .) Further, an additional “twist” angle must be calculated for each daughter segment trajectory to orient the initial reference frame of the daughter segment.

7.1.2 Quaternion Junction Rotation Representation

The relative angle representation treats the junction as a rigid body. More generally, the neuron morphology model treats the junction as a set of branching trajectories, each with its own reference frame. This means that the initial trajectory of each S_i , $1 \leq i \leq n$ may be described in terms of a rotation of the final trajectory reference frame of S_0 . This junction rotation may be conveniently represented as a unit quaternion q_i . The quaternion representation has several advantages:

1. A quaternion completely specifies the initial reference frame of a daughter segment trajectory. Additional factors such as chirality and “twist” are derived attributes.

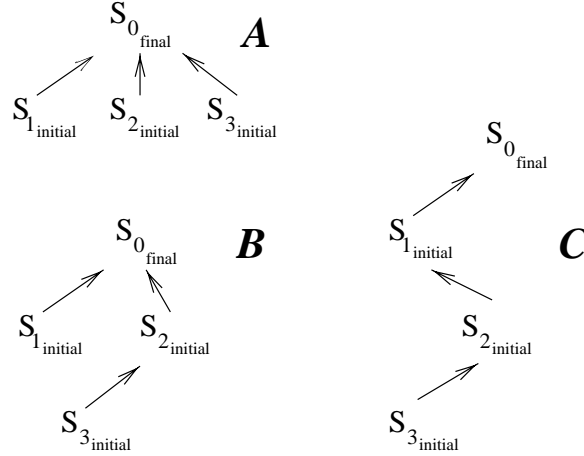


Figure 2: Example hierarchical dependency relationships

2. The quaternion representation allows junction branch angles to be easily decoupled or made dependent. (See below.)
3. The quaternion representation supports the neuron morphology model paradigm of treating junctions as branching segment trajectories, each with its own coordinate frame. This paradigm is not supported by using relative angles.
4. Figuring out “twist” angles in the relative angle approach requires analyzing a junction in terms of segment trajectories and reference frames anyway. Thus, no work is saved by using this representation.

7.1.3 Hierarchical Daughter Segment Dependency

In the simplest case the initial frame of reference and the trajectory of daughter segment S_n depends only on the final reference frame of S_0 . In other words, the initial trajectories of all daughter segments are influenced only by the final trajectory of the parent. There is no *a priori* reason to believe that this is true in every case; it is possible that the initial trajectory of daughter segments could influence each other. Leaving aside the problem of detecting such influences, it is possible to represent this kind of complex trajectory dependency in the statistical model through hierarchical daughter dependency relationships.

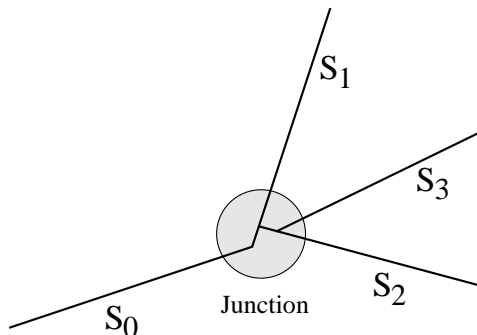


Figure 3: Dendritic branching with three levels of daughter dependency

Figure 2 graphically represents three possible dependency relationships. In *A*, all daughter segments depend only on the parent segment — the simplest case. The junction rotations of each daughter segment are specified relative to the final reference frame of S_0 . In *B*, the initial trajectory (junction rotation) of daughter segment S_2 depends on the junction rotation of daughter segment S_1 , which in turn depends on the final trajectory of S_0 . The dependency relationship in *C* is a three level hierarchy, and is geometrically illustrated in Figure 3.

7.1.4 Properties List

A junction has the following properties:

junction ID Junction ID is a unique identifier which distinguishes one junction from every other junction in a neuron. Junction ID is represented as a six digit integer counting upwards from 300,000.

cell ID The identifier of the cell in which the junction resides.

arbor ID The identifier of the arbor in which the junction resides.

junction order The order of the junction.

path length The total length of the shortest path from the branch point of the junction back to the root of the arbor.

electrotonic path length The total electrotonic length of the shortest path from the branch point of the junction back to the root of the arbor.

Description	Symbol	Type	Representation
junction ID	$ID_{junction}$	$I \geq 300,000$	I
cell ID	ID_{cell}	$I \geq 100,000$	I
arbor ID	ID_{arbor}	$I \geq 1$	I
junction order	O	$I \geq 1$	I
path length	l_{path}	$\Re > 0$	\Re
electrotonic path length	l_e	$\Re > 0$	\Re
number of segments	N_{seg}	$\{3,4\}$	I
parent segment ID	ID_{S_0}	$I \geq 200,000$	I
S_1 ID	ID_{S_1}	$I \geq 200,000$	I
S_2 ID	ID_{S_2}	$I \geq 200,000$	I
S_3 ID	ID_{S_3}	$I \geq 200,000$	I
S_1 rotation dependency	D_{S_1}	$\{0\}$	I
S_2 rotation dependency	D_{S_2}	$\{0, 1\}$	I
S_3 rotation dependency	D_{S_3}	$\{0, 1, 2\}$	I
S_1 junction rotation	R_{S_1}	Q_{unit}	$(q_0 \ q_1 \ q_2 \ q_3) \in \Re^4$
S_2 junction rotation	R_{S_2}	Q_{unit}	$(q_0 \ q_1 \ q_2 \ q_3) \in \Re^4$
S_3 junction rotation	R_{S_3}	Q_{unit}	$(q_0 \ q_1 \ q_2 \ q_3) \in \Re^4$

Table 10: Junction properties

Description	Representation
Distribution of S_1 junction rotations.	$p(R_{S_1})$
Distribution of S_2 dependencies.	$p(D_{S_2})$
Distribution of S_2 junction rotations dependent on S_0 .	$p(R_{S_2} D_{S_2} = 0)$
Distribution of S_2 junction rotations dependent on S_1 .	$p(R_{S_2} D_{S_2} = 1)$
Distribution of S_3 dependencies.	$p(D_{S_2})$
Distribution of S_3 junction rotations dependent on S_0 .	$p(R_{S_3} D_{S_3} = 0)$
Distribution of S_3 junction rotations dependent on S_1 .	$p(R_{S_3} D_{S_3} = 1)$
Distribution of S_3 junction rotations dependent on S_2 .	$p(R_{S_3} D_{S_3} = 2)$

Table 11: Junction probability density functions

number of segments The number of segments intersecting at the junction.

parent ID The identifier of the S_0 (parent) segment.

S_i ID Three segment identifiers corresponding to daughter segments S_1 , S_2 , and S_3 . For a bifurcation only S_1 and S_2 will be non-zero.

S_i rotation dependency Three dependency identifiers designating the rotation dependencies of the daughter segments S_1 , S_2 , and S_3 respectively.

S_i junction rotation Three rotations specified as unit quaternions representing the junction rotations of the daughter segments S_1 , S_2 , and S_3 respectively.

These properties are summarized in Table 10.

7.2 Probability Density Functions

The probability density functions which govern the junction all relate to the initial junction rotation and hierarchical dependency relationships of the daughter segments. Separate probability density functions for junction rotation are specified for each daughter segment dependency case.

A junction may be statistically modeled using the following probability density functions:

- $p(R_{S_1})$ — A probability density function for the junction rotation of S_1 . By definition, S_1 always depends on S_0 .

- $p(D_{S_2})$ — A probability density function for the dependency of the junction rotation of S_2 . Segment S_2 may depend on either the parent or the first daughter segment.
- $p(R_{S_2}|D_{S_2} = 0)$ — A probability density function for the junction rotation of S_2 when S_2 depends on S_0 .
- $p(R_{S_2}|D_{S_2} = 1)$ — A probability density function for the junction rotation of S_2 when S_2 depends on S_1 .
- $p(D_{S_3})$ — A probability density function for the dependency of the junction rotation of S_3 . Segment S_3 may depend on either the parent, the first, or the second daughter segment.
- $p(R_{S_3}|D_{S_3} = 0)$ — A probability density function for the junction rotation of S_3 when S_3 depends on S_0 .
- $p(R_{S_3}|D_{S_3} = 1)$ — A probability density function for the junction rotation of S_3 when S_3 depends on S_1 .
- $p(R_{S_3}|D_{S_3} = 2)$ — A probability density function for the junction rotation of S_3 when S_3 depends on S_2 .

These probability density functions are summarized in Table 11.

Description	Type	Representation
auxiliary property name	$[A \dots Z a \dots z]^n$	text string
auxiliary property type	$\{soma\ arbor\ segment\ spine\ junction\}$	$\{soma\ arbor\ segment\ spine\ junction\}$
auxiliary property description	descriptive text	text string

Table 12: Auxiliary Property Definition

8 Auxiliary Properties

8.1 Introduction

Auxiliary properties provide an alternate or elaborated representation of neuron morphology. An auxiliary property derives from one or more of the fundamental properties of a morphological element. One example of an auxiliary property is the Mulchandani relative angle representation for junction geometry.

There are two components to the N++ auxiliary property framework: an auxiliary property definition, and zero or more auxiliary property records. The auxiliary property definition provides a label for the auxiliary property and a description of how the property is calculated. An auxiliary property record is a individual instance of an auxiliary property.

8.2 Auxiliary Property Definition

In the flat file representation, auxiliary property definitions are placed after all other data except auxiliary property records. An auxiliary property definition is composed of the following elements:

auxiliary property name A unique text string identifying the property.

This string is composed of the letters A–Z and a–z.

auxiliary property type The type of morphology to which this auxiliary property relates.

auxiliary property description A text string describing the property.

This description could take the form of a symbolic expression or descriptive text. If a symbolic expression is used it should be human-readable, since the N++ model does not specify a standard for parsing such expressions and a data-set may be evaluated in a wide range of software applications.

The auxiliary property definition is summarized in Table 12.

Description	Symbol	Type	Representation
record ID	ID_{record}	$I \geq 400,000$	I
cell ID	ID_{cell}	$I \geq 100,000$	I
arbor ID	ID_{arbor}	$I \geq 1$	I
segment ID	$ID_{segment}$	$I \geq 200,000$	I
junction ID	$ID_{junction}$	$I \geq 300,000$	I
property	X_{record}	any	text string

Table 13: Auxiliary Property Record

8.3 Auxiliary Property Record

An auxiliary property record is an instance of an auxiliary property which refers to a particular soma, arbor, segment, or junction. In the flat file representation, auxiliary property records are placed after all auxiliary property definitions. An auxiliary property record is composed of the following elements:

record ID A unique identifier which distinguishes this auxiliary property record from every other auxiliary property record in the flat file. Record ID is represented as a six digit number counting upwards from 400,000.

record type The type of auxiliary property record. This string must match a defined auxiliary property name.

cell ID The ID of the neuron to which the auxiliary property record refers.

arbor ID The identifier of the arbor to which the auxiliary property record refers, if relevant. Zero otherwise.

segment ID The identifier of the segment to which the auxiliary property refers, if appropriate. Zero otherwise.

junction ID The identifier of the junction to which the auxiliary property refers, if appropriate. Zero otherwise.

property A text string representation of the value of the auxiliary property. The use of a text string representation allows the greatest flexibility for the contents of this field.

9 Literature Cited

References

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