



## Modeling dendritic morphological complexity of deep layer cat superior colliculus neurons

Jaap van Pelt<sup>a,\*</sup>, Andreas Schierwagen<sup>b</sup>, Harry B.M. Uylings<sup>a</sup>

<sup>a</sup>*Graduate School Neurosciences Amsterdam, Netherlands Institute for Brain Research, Meibergdreef 33, 1105 AZ Amsterdam, Netherlands*

<sup>b</sup>*Institute for Computer Science, University of Leipzig, D-04107 Leipzig, Germany*

---

### Abstract

Dendritic complexity of deep layer cat superior colliculus neurons has been studied by means of a stochastic model for dendritic outgrowth with randomly branching and elongating neurites. Branching probabilities are assumed to depend on the position and the number of segments in the growing tree. It is demonstrated that the shape properties of model generated dendrites conform closely to those of the observed trees. These findings make plausible that (i) dendritic development proceeds following a first phase of elongation and branching, and a second phase of elongation only, and (ii) newly formed segments after a branching event have a short initial length. © 2001 Elsevier Science B.V. All rights reserved.

*Keywords:* Stochastic growth model; Dendritic trees; Cat superior colliculus neurons; Dendritic development; Morphology

---

### 1. Introduction

Dendritic branching patterns are complex structures with large variations in their shapes within and between different classes of neurons. Recent modeling studies have demonstrated that typical shape properties may arise naturally from differences in neurite outgrowth and branching during dendritic development [7–10]. These studies of rat cortical layer 2/3 and layer 5 pyramidal basal dendrites and guinea pig cerebellar Purkinje cell dendritic trees have shown that the observed variation in morphological shapes was accurately reproduced by a stochastic process of neuritic

---

\* Corresponding author. Tel.: + 31-20-5665481; fax: + 31-20-6961006.  
*E-mail address:* j.van.pelt@nih.knaw.nl (J. van Pelt).

elongation and branching. Branching probabilities of terminal segments were made dependent on their location, as well as on the total number of segments in the tree. For matching finer details of the intermediate segment length distribution it was additionally needed to assume that newly formed segments after a branching event had a (short) initial length [10]. Then, the model accounts for the observation that very short segments are much less abundant than expected from a random branching and elongation process. The present study was undertaken to analyse dendritic complexity of deep layer cat superior colliculus neurons and to identify the characteristics of these dendrites in terms of growth model parameters emphasizing the finer details of the segment length distributions.

## 2. Materials and methods

### 2.1. Deep layer cat superior colliculus neurons

Detailed morphological reconstructions were obtained from cat deep layer superior colliculus neurons stained with HRP [2,3,5]. A typical example of such a neuron is given in Fig. 1.

The morphology of these neurones was analyzed quantitatively for the shape parameters total dendritic length, number and lengths of intermediate and terminal segments, pathlengths, centrifugal order of the segments, and the tree-asymmetry

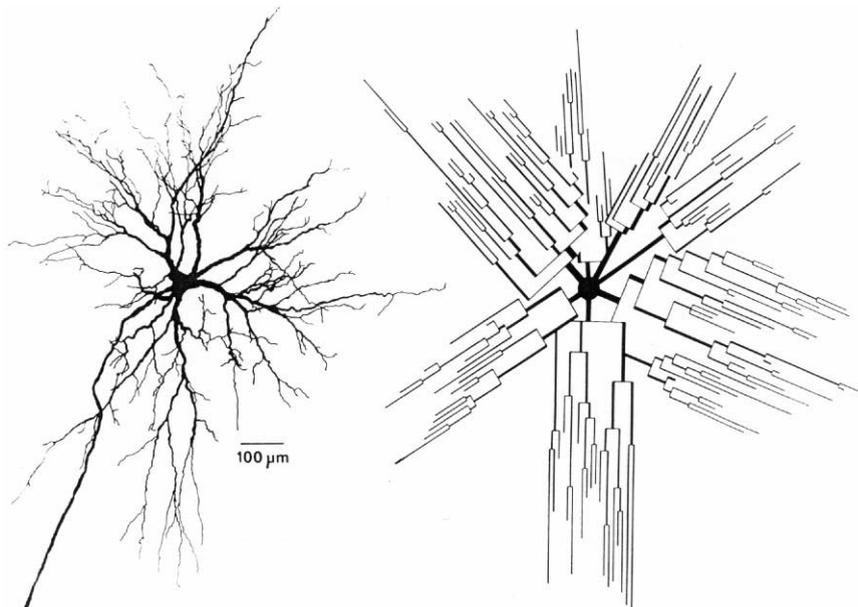


Fig. 1. Projected image (left) and dendrogram representation (right) of an HRP stained deep layer cat superior colliculus neuron (from [2] with permission).

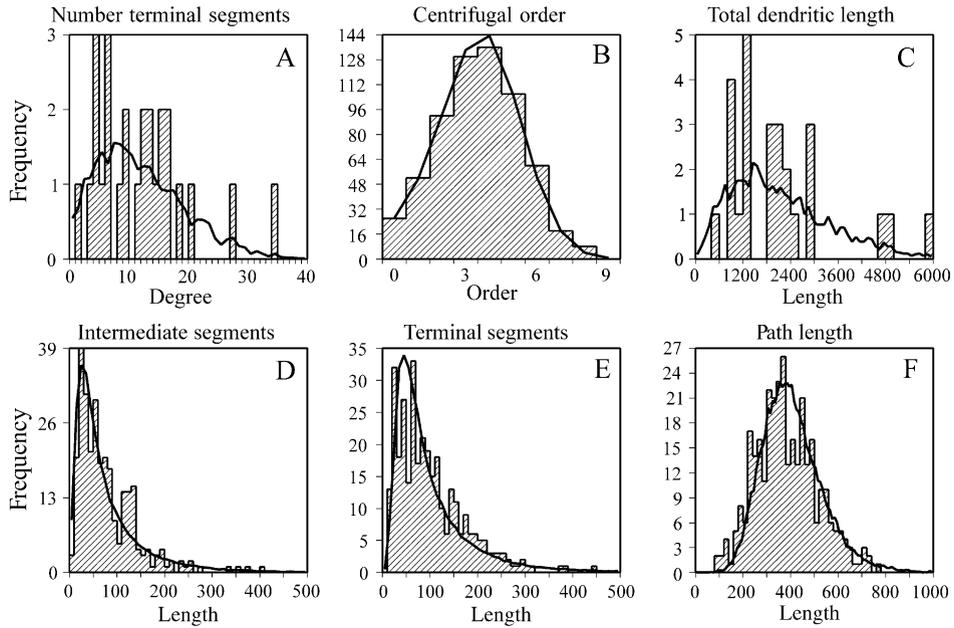


Fig. 2. Frequency distributions of dendritic tree shape parameters of deep layer cat superior colliculus neurons (dashed histograms) and of model generated trees (continuous thick lines), using the optimized parameter values given in Table 2. The panels show the frequency distributions for (A) the number of terminal segments, (B) centrifugal order of the segments, (C) total dendritic length, (D) intermediate segment length, (E) terminal segment length and (F) pathlength, with length in  $\mu\text{m}$ . The frequency scales refer to the observed distributions. The model distributions have been normalized accordingly.

index as a measure for the topological structure (connectivity pattern of the segments). The mean and SD values are given in Table 2. The frequency distributions for the different shape parameters are shown in Fig. 2 as dashed histograms.

### 2.2. Growth model

The dendritic growth model has recently been discussed in [8,10]. Briefly, the branching probability of a terminal segment is given by  $p_i = C2^{-S\gamma}B/Nn_i^E$ , with  $N$  denoting the total number of time bins in the full period of development and  $n_i$  denoting the actual number of terminal segments in the tree at time bin  $i$ . Parameter  $B$  denotes the expected number of branching events at an isolated segment in the full period, while parameter  $E$  determines how strong the branching probability of a terminal segment depends on the actual number of terminal segments in the tree. Parameter  $\gamma$  denotes the centrifugal order of the terminal segment and  $C = n_i / \sum_{j=1}^{n_i} 2^{-S\gamma_j}$  is a normalization constant, with a summation over all  $n_i$  terminal segments. Parameter  $S$  determines how strong the branching probability of a terminal segment depends on the proximal-distal location of the segment in the tree. The

Table 1

Optimized values for growth parameters to match the statistical shape properties of deep layer cat superior colliculus neurons, given in Table 2

$B$	$E$	$S$	$\overline{l_{in}}$ ( $\mu\text{m}$ )	$\sigma_{l_{in}}$	$T_{be}$ ( $\Delta t$ )	$\overline{v_{be}}$ ( $\mu\text{m}/\Delta t$ )	$T_e$ ( $\Delta t$ )	$\overline{v_e}$ ( $\mu\text{m}/\Delta t$ )	$cv_v$
3.89	0.285	0.4	17	12	500	0.6	25	0.6	0.7

number of time bins  $N$  can be chosen arbitrarily but such that the branching probability per time bin remains much smaller than one, making the probability of more than one branching event per time bin negligibly small. Newly formed daughter segments after a branching event are given a gamma-distributed, randomly chosen initial length with mean  $\overline{l_{in}}$  and standard deviation  $\sigma_{l_{in}}$ , and a gamma-distributed, randomly chosen elongation rate. The developmental period is assumed to consist of a first phase of elongation and branching, and a subsequent phase of elongation only, with elongation rates  $\overline{v_{be}}$  and  $\overline{v_e}$ , respectively, both with a coefficient of variation  $cv_v$ . The gamma-distributions, characterized by their mean and SD, are assumed to have a zero value for their offset.

### 2.3. Parameter optimization

The modular structure of the model helps in finding optimal parameter values as is explained in detail in [10]. Briefly, parameter  $S$  can be estimated from the topological structure by the mean value of the tree-asymmetry index, and parameters  $B$  and  $E$  from the segment number distribution [7,10]. The segment length parameters have been optimized using the procedures and considerations in [10].

## 3. Results

The optimization process resulted in parameter values given in Table 1. Because of lack of data on the developmental period it has been taken equal to  $T_{be} = 500\Delta t$  for the branching-elongation phase, with  $\Delta t$  denoting an arbitrary length of time. Elongation rates are consequently expressed in terms of the relative quantity  $\mu\text{m}/\Delta t$ . Assuming an equal elongation rate in the elongation phase, a duration of this phase of  $T_e = 25\Delta t$  was needed for further optimization.

The model trees for these parameter values have shape properties that conform closely to the observed ones, as is shown in Table 2. A detailed comparison can be made in Fig. 2, displaying the observed (dashed histograms) and the model predicted (thick continuous lines) frequency distributions of different shape properties.

Table 2

Mean and SD of shape properties of observed and modeled dendrites of deep layer cat superior colliculus neurons, with  $N_{\text{obs}}$  denoting the number of experimental observations

Shape variable	Observations			Model outcomes	
	$N_{\text{obs}}$	Mean	SD	Mean	SD
Degree (# terminal segments)	26	12.58	7.46	12.49	7.39
Tree symmetry	26	0.41	0.15	0.41	0.14
Centrifugal order	628	3.58	1.74	3.53	1.70
Total dendritic length ( $\mu\text{m}$ )	26	2115	1198	2156	1289
Terminal segment length ( $\mu\text{m}$ )	327	101.7	71.8	100.8	86.5
Intermediate segment length ( $\mu\text{m}$ )	290	78.7	62.8	78.0	77.5
Pathlength ( $\mu\text{m}$ )	327	382.7	130.0	406.8	128.2

#### 4. Discussion

The growth model is based on the assumption that dendritic complexity can be described by a stochastic growth process of branching and elongation, with order- and size dependent branching probabilities. The correspondence between the frequency distributions of observed and model generated trees demonstrates that these stochasticity assumptions are successful in explaining the variation in dendritic trees. Experimental data on the developmental period is needed for making absolute estimates of the elongation rates.

The segment length distributions for the superior colliculus neurons have a modal shape (Fig. 2(D), (E)). Similar modal shapes have earlier been reported in studies of cat dorsal horn cells [1] and of rat cortical pyramidal neurons and guinea pig cerebellar Purkinje cells [10]. Such a modal shape was not expected from a random branching and elongation process. The shortage of short segments may arise when, at a branching event, the newly formed segments have experienced a short phase of elongation without branching. In our model this assumption is implemented by assigning an initial length to newly formed segments after a branching event, followed by a process of sustained elongation. An alternative implementation was made by [1] who included a transient suppression of the branching probability in newly formed segments.

The developmental period has been split into a first phase of branching and elongation (500 time units) and a (short) phase of elongation only (25 time units), to account for the length difference between intermediate and terminal segments. Such a two-phase development has been observed during outgrowth of rat cortical pyramidal neurons in vivo [6], and has been used explicitly in modeling the complexity of basal dendrites in these neurons [8–10]. Thus, also for cat superior colliculus neurons we expect, albeit less pronounced, a two-phase development.

Deep layer superior colliculus neurons appear to be more compact than superficial layer neurons, with functional implications discussed in [4]. The present study contributes to a detailed morphological characterization of these neurons as well as their variability, an essential requirement for studies of neuronal structure and function.

## References

- [1] R.S. Nowakowski, N.L. Hayes, M.D. Egger, Competitive interactions during dendritic growth: a simple stochastic growth algorithm, *Brain Res.* 576 (1992) 152–156.
- [2] A. Schierwagen, Segmental cable modelling of electrotonic transfer properties of deep superior colliculus neurons in the cat, *J. Hirnforsch.* 27 (1986) 679–690.
- [3] A. Schierwagen, Dendritic anatomy and electrotonic transfer properties of cat superior colliculus neurons, *Acta Biol. Hung.* 39 (1988) 221–227.
- [4] A. Schierwagen, C. Claus, Dendritic morphology and signal delay in superior colliculus neurons, *Neurocomput.* 38–40 (2001) 343–350, this issue.
- [5] A. Schierwagen, R. Grantyn, Quantitative morphological analysis of deep superior colliculus neurons stained intracellularly with HRP in the cat, *J. Hirnforsch.* 27 (1986) 611–623.
- [6] H.B.M. Uylings, J. van Pelt, J.G. Parnavelas, A. Ruiz-Marcos, Geometrical and topological characteristics in the dendritic development of cortical pyramidal and non-pyramidal neurons, in: J. van Pelt, M.A. Corner, H.B.M. Uylings, F.H. Lopes da Silva (Eds.), *Progress in Brain Research, The Self-Organizing Brain: From Growth Cones to Functional Networks*, Vol. 102, Elsevier, Amsterdam, 1994, pp. 109–123.
- [7] J. van Pelt, A.E. Dityatev, H.B.M. Uylings, Natural variability in the number of dendritic segments: model-based inferences about branching during neurite outgrowth, *J. Comp. Neurol.* 387 (1997) 325–340.
- [8] J. van Pelt, H.B.M. Uylings, Natural variability in the geometry of dendritic branching patterns, in: R.R. Poznanski (Ed.), *Modeling in the Neurosciences: From Ionic Channels to Neural Networks*, Harwood Academic Publishers, Amsterdam, 1999, pp. 79–108.
- [9] J. van Pelt, H.B.M. Uylings, Modeling the natural variability in the shape of dendritic trees: application to basal dendrites of small rat cortical layer 5 pyramidal neurons, *Neurocomputing* 26 and 27 (1999) 305–311.
- [10] J. van Pelt, A. van Ooyen, H.B.M. Uylings, Modeling dendritic geometry and the development of nerve connections, in: E. de Schutter, R.C. Cannon (CD-ROM) (Eds.), *Computational Neuroscience: Realistic Modeling for Experimentalist*, CRC-Press, Boca Raton, FL, 2000.



**Jaap van Pelt** received his Ph.D. in Physics in 1978 at the Free University in Amsterdam, Netherlands. His research group *Neurons and Networks* at the NIBR works both experimentally and theoretically on neuronal morphology and activity-dependent mechanisms in neurite outgrowth and neuronal network formation.

**Andreas Schierwagen** See biosketch in [4].



**Harry B.M. Uylings** received his Ph.D. in Neurobiology in 1977 at the University of Amsterdam, Netherlands. His research group at the NIBR works on the functional and structural organization of the prefrontal cortex, both in animals and in humans.