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A Quantitative Dendritic Analysis of Four Functionally Distinct Areas of Human Cerebral Cortex

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Abstract

Recent investigations have begun to elucidate the function of dendritic arbors, revealing that the geometry of dendrites and the presence of dendritic spines play important roles in both simulated and actual dendritic function (Midtgaard, 1994). The present study attempts to correlate dendritic complexity with cortical function under the assumption that connectivity in a local cortical area may determine its more holistic functional properties. Two human brains (ages: 23 and 69 years) were used for the present study. Four cortical areas (Brodmann's [1908] areas 3, 1, and 2; area 22; area 44; and area 10), respectively representing Benson's four levels of cortical function (primary, unimodal, heteromodal, and supramodal; 1993, 1994), were stained with the modified rapid Golgi technique (Scheibel & Scheibel, 1978). Twenty supragranular pyramidal cells per cortical level were selected (N = 80). Basilar dendritic systems were analyzed using the Neurolucida computer/microscope interface system (Microbrightfield, Inc.). Dendritic measures, which included total dendritic length (TDL), mean dendritic length (MDL), dendritic segment count (DSC), dendritic spine number (DSN), and dendritic spine density (DSD), were used to determine dendritic complexity. All dendritic measures, with the exception of MDL, increased from primary to supramodal cortex. The present findings are consistent with previous research correlating dendritic measures and cortical function (Larsen, Wainwright, Swanson, & Jacobs, 1994; Scheibel, Conrad, Perdue, Tomiyasu, & Wechsler, 1990; Scheibel et al., 1985) and suggest that

dendritic extent is related to the functional capabilities of human cerebral cortex.

The endless plurifomity of neocortical neurons...and the limited opportunities to study the way they are integrated into the circuitry of the neocortex is inaccessible to morphological research. Would such a conclusion be justified? By no means! Neurons are now mere configurations, they are discrete living structures, which may be assumed to subserve discrete functions. Not what is configurationally possible, but what is functionally required determines their shape. (Nieuwenhuys, 1994, p. 307)

The belief that learning and environment alter the morphology, physiology, and function of cerebral cortex (Darwin, 1874; Ramón y Cajal, 1894) has found support in documented differences between the cortices of rats raised in enriched and impoverished environments. Findings include increases in cortical thickness (Diamond, Krech, & Rosenzweig, 1964; Ferchmin, Bennett, & Rosenzweig, 1975; Rosenzweig, Krech, Bennett, & Diamond, 1962), enzymatic activity (Rosenzweig et al., 1962), capillary blood flow (Carughi, Carpenter, & Diamond, 1989), and increases in the complexity of dendritic neuropil in enriched rats (Bennett, Diamond, Krech, & Rosenzweig, 1964; Diamond, Rosenzweig, Bennett, Lindner, & Lyon, 1972; Globus, Rosenzweig, Bennett, & Diamond, 1973; Green, Greenough, & Schlumpf, 1983; Holloway, 1966; Uylings, Kuypers, Diamond, & Veltman, 1978; Volkmar & Greenough, 1972). Rearing conditions also affect spine morphology in male zebra finches (Rollerhagen & Bischof, 1994), and, in primates, the complexity of dendritic neuropil has also been correlated with environmental factors, including education level (Bryan & Riesen, 1989; Jacobs, Schall, & Scheibel, 1992).

At the microanatomical level,

dendritic complexity may reflect or be the causal substrate for a neuron's computational potential in terms of its ability to integrate converging information (Coss & Perkel, 1985; Crick, 1982; Greenough, Black, & Wallace, 1987; Scheibel, 1988; Scheibel, 1990; Swindale, 1981). It is known that longer dendrites increase possible interneuronal connectivity by creating larger receptive fields. The distal:proximal segment ratio might also be an important factor in information processing because distal segments (fourth order and higher) develop postnatally (Conel, 1939-67; Ramón y Cajal, 1906) and exhibit greater sensitivity to environmental variations (Carughi et al., 1989).

Dendritic spines, which increase a cell's receptive surface (Ramón y Cajal, 1894), also play an important role in information processing. Theoretical work has supported the possibility of electrotonic modulation of whole neurons by dendritic spines (Coss & Perkel, 1985), and other models have revealed pseudosaltatory conduction mechanisms that propagate a current from spine to spine, thus increasing the signal strength of distal synaptic inputs (Shepherd et al., 1985). Models of sensory interneurons have revealed that individual cells are capable of filtering temporal frequencies and increasing the signal to noise ratio based solely on *passive* dendritic properties (Borst & Egelhaaf, 1994). The growth and production of spines after one minute training intervals has also been documented (Scheibel & Scheibel, 1976), further supporting the ability of dendritic spines to respond to information processing demands.

In addition to extrinsic factors such as environmental complexity, intrinsic demands may also shape dendritic neuropil. Based on clinical investigations, Benson (1993, 1994) has proposed four hierarchical levels of cortical function: (a) Sensory and motor *primary cortex* (PC) receives external stimuli and transfers this information to either transhemispheric primary homologues or to unimodal association cortex; (b) *Unimodal cortex* (UC) processes single modality input

(e.g., visual, auditory, somesthetic, or kinetic) into a sensory percept before the information is relayed to heteromodal cortex; (c) *Heteromodal cortex* (HC) consists of complex cognitive networks that further integrate different unimodal information into polymodal complexes; (d) Overseeing such functions, *supramodal cortex* (SC) is involved in executive control, self-analysis, and planning. The present study uses Benson's schema to predict which cortical areas should exhibit higher dendritic measures. Because the pyramidal cells in neocortex communicate primarily with each other (Nieuwenhuys, 1994), and because certain functions have been localized, we expected dendritic system complexity to correlate with Benson's hierarchical schema.

Preliminary findings suggest that such a hierarchical structuring of human cerebral cortex may exist in terms of dendritic complexity. Larsen et al. (1994) found substantial differences in dendritic complexity between unimodal occipital (area 18) and supramodal prefrontal (area 10) cortex. Partial support for the relationship between dendrite complexity and function has also been found in areas of the postcentral gyrus (Scheibel et al., 1990). These quantitative findings, coupled with the relationship between dendritic complexity and differential environments, suggest a causal relationship between dendritic complexity and the levels of information convergence and integration that occur in discrete cortical areas. The present study analyzes primary (areas 3, 1, 2), unimodal (area 22), heteromodal (area 44), and supramodal (area 10; Brodmann, 1908) cortical regions along several parameters to determine whether there is a continuum of increasing dendritic complexity from primary to supramodal cortex.

Method

Subjects

Cortical tissue was obtained from two neurologically normal, Caucasian males (autolysis time = 12 hr and 7 hr). Cause of death for the 23-year-old was a

motor vehicle accident resulting in massive blunt chest trauma; the 69-year-old died of prostate cancer. Tissue was provided by Dr. David Bowerman, the El Paso County Coroner. The research protocol was approved by The Colorado College Human Subjects Institutional Review Board (H94-004).

Apparatus

All quantification was performed on the Neurolucida computer/microscope interface system (Microbrightfield, Inc.) with an Olympus BH-2 microscope, under a 40X (.70) dry objective.

Histological Techniques.

Tissue was fixed in 10% formalin for at least one month before processing. For each brain, one 3-5 mm tissue block was removed from the following areas of the lateral aspect of the left hemisphere: Brodmann's areas 3, 1, 2 (PC), 22 (UC), 44 (HC), and 10 (SC). The postcentral gyrus block was removed from the region associated with the arm representation.

Before staining, blocks were coded to avoid experimenter bias. With the pial surface removed, tissue blocks were immediately stained using a modified rapid Golgi technique (Scheibel & Scheibel, 1978). Blocks were sectioned on a vibratome at 120 μm . Tissue sections were vertical to the pial surface and perpendicular to the long axis of the gyrus. Adjacent cortical blocks, sectioned at 50 μm , were stained with a cresyl echt violet technique (Gridley, 1960) to determine laminar depth and to provide further control for cell selection.

Cell selection criteria & quantification techniques. Ten supragranular pyramidal cells per tissue block were selected according to previously established criteria (Jacobs & Scheibel, 1993): (a) The soma-apical dendrite orientation is perpendicular to the pial surface. (b) The soma is located centrally within the 120 μm section depth. (c) The apical shaft is at least 100 μm in length. (d) At least three primary basilar dendritic shafts are present, each with at least two secondary branches and their consequent branch systems. (e) Neurons

show no obvious evidence of incomplete impregnation. (f) Cells are relatively unobscured by adjacent neuronal structures. (g) Higher order branches should have natural terminations, either characterized by naturally tapered ends, growth cone-bearing tips, or by terminal clusters of dendritic spines. For the present study, the last criterion was the most difficult to meet, but cells having incomplete branches were included to prevent biasing the sample towards smaller, less complex cells. Because deeper situated neurons tend to have more extensive branching patterns in rodents (Clendinnen & Eayrs, 1961), a running average of soma depth was kept to ensure that soma depth averages from each block were similar.

The first 10 cells in each block ($N = 80$) meeting criteria and soma depth requirements were traced. Somata were traced at their widest points to give a rough estimate of cross sectional area. The apical shaft was then traced in order to confirm cell orientation. Basilar dendrites were subsequently traced in their entirety, and their endings were designated as complete or incomplete. After all cells were drawn, the tracings were independently examined to ensure that they met the selection criteria.

Independent measures

Functional complexity, as determined by Benson's schema (1993, 1994), provided the independent measure for the present study.

Dependent measures

Total dendritic length (TDL), mean dendritic length (MDL), dendritic segment count (DSC), dendritic spine number (DSN), and dendritic spine density (DSD) were the dependent measures. Using a centrifugal nomenclature (Uylings, Ruiz-Marcos, & van Pelt, 1986; Uylings, Smit, & Veltman, 1975), dendritic measures were further analyzed by segment order to determine what part of the dendritic arbor was most responsible for the differences between cortical areas. First to third order segments were considered proximal, while

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fourth order and higher segments were considered distal.

Intra- and Inter-rater reliability

Two raters traced all cells: SB = 70 cells; Lori Larsen = 10 cells. Intrarater reliability was determined by having each rater trace the same dendritic system, including somata and dendritic spines, 10 times. The average coefficient of variation across both raters for TDL, soma size, and DSN, was 0.036, indicating little variation in tracings. The first 5 tracings were compared with the second 5 tracings in a split plot design ($\alpha = 0.5$). There was no significant difference within raters for any of these measures. Both raters were normed before quantification to maximize interrater reliability. In tracings of 10 different dendritic systems, Pearson product correlations across TDL, soma size, and DSN averaged 0.97, indicating high agreement between raters. An ANOVA ($\alpha = 0.5$) indicated no significant difference between raters on these measures.

Statistical techniques. Only descriptive statistics were used because the limited sample size and insufficient degrees of freedom prohibited a repeated measures MANOVA.

Results

Neuronal Population

Average soma depth was recorded for sampled cells, while laminar thickness

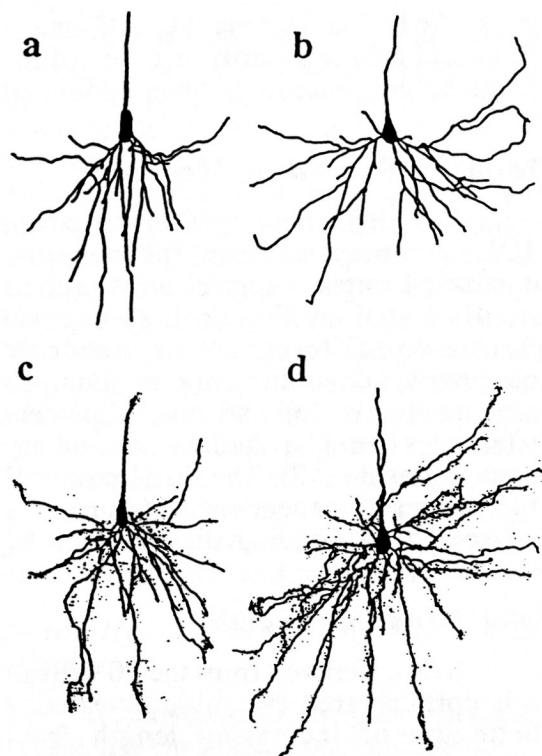


Figure 1. Representative supragranular pyramidal cells from primary (A), unimodal (B), heteromodal (C), and supramodal cortex (D). There is a general increase in dendritic complexity from primary to supramodal cortical areas.

was recorded for cortical blocks. For cell population control, a routine Nissl stain ensured that the cells sampled came from cortical layers II and III (see Table 1). Measurements taken from the Golgi stained tissue revealed that the average soma size was similar for all cortical regions. Soma depth measurements revealed that the soma

Table 1

Cortical Layer Thickness and Soma Depths of Sampled Cells (M [\pm SD] in μ m) for Primary (areas 3, 1, 2), Unimodal (area 22), Heteromodal (area 44), and Supramodal (area 10) Cortex.

	Primary	Unimodal	Heteromodal	Supramodal
Layer I/II Junction	241 \pm 33	259 \pm 41	305 \pm 1007	305 \pm 56
Layer II/III Junction	352 \pm 58	363 \pm 95	327 \pm 88	326 \pm 73
Sampled Cells	886 \pm 150	870 \pm 123	846 \pm 129	810 \pm 154
Layer III/IV Junction	1090 \pm 225	1467 \pm 113	1030 \pm 215	1220 \pm 454
Gray/White Junction	3291 \pm 466	3816 \pm 840	3997 \pm 514	3789 \pm 1032

depth of the sampled cells increased from supramodal to primary cortex. Because

deeper lying neurons tend to have more complex dendritic neuropil (Clendinnen &

Eayrs, 1961). The fact that SC, HC, and UC all had greater dendritic measures than PC gives the present findings additional validity.

Dendritic Dependent Measures

All dependent measures, except MDL, increased from primary to supramodal cortex. Representative neurons are illustrated in Figure 1 and reveal qualitative differences in dendritic complexity across the four regions. To ease quantitative comparisons, all percent differences are in reference to primary cortex (areas 3, 1, 2). The distal:proximal ratio for each dependent measure was determined by dividing distal values by proximal values.

Total Dendritic Length

TDL, summed from the 20 cells in each cortical area (in μm), revealed a continuum of increasing length from primary to supramodal cortex. TDL was 43% higher in supramodal (84,022), 15% higher in heteromodal (67,649), and only 0.4% higher in unimodal (59,127) versus primary cortex (58,876). Figure 2 indicates

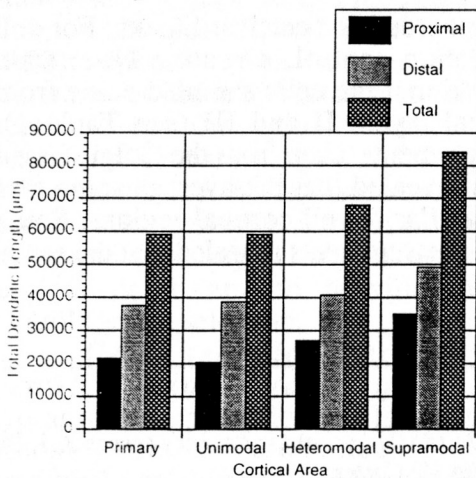


Figure 2. Total dendritic length (TDL, 20 cells per cortical area) values for primary (PC), unimodal (UC), heteromodal (HC), and supramodal (SC) cortex. Note the continuum from primary to supramodal cortex for overall TDL, and the higher distal TDL values across tissue blocks.

that distal segments contributed more to TDL than proximal segments in all four cortical blocks (PC: 1.73; UC: 1.89; HC:

1.53; SC: 141). Order by order analysis revealed TDL in all areas was highest in fourth order segments (see Figure 3). For all areas, TDL steadily increased up to the fourth and subsequently declined.

Mean Dendritic Length

MDL, (20 cells per cortical area; in μm), tended to increase from unimodal to supramodal cortex although the MDL of primary cortex fell between hetero- and

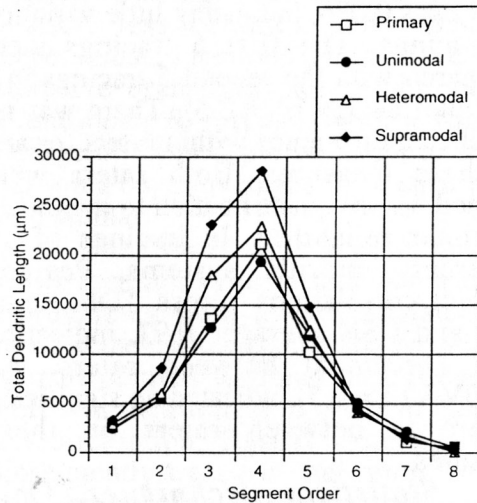


Figure 3. Order by order analysis of TDL (20 cells per cortical area). Note that TDL in supramodal cortex is substantially higher than in the functionally "lower" regions.

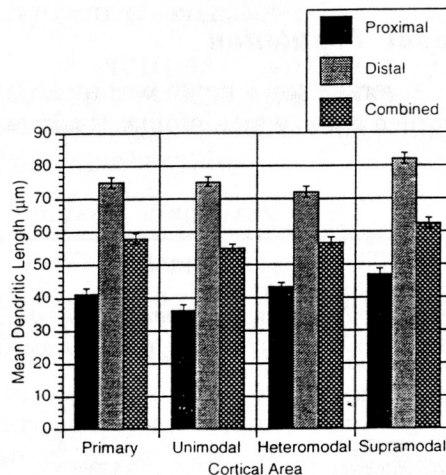


Figure 4. Mean dendritic length (MDL, 20 cells per cortical area) values for primary (PC), unimodal (UC), heteromodal (HC), and supramodal (SC) cortex. Distal segments in all cortical blocks had higher MDL values than proximal segments.

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supramodal values (*Mean ±SEM*: PC: 57.8, ±1.7; UC: 54.7, ±1.6; HC: 56.6, ±1.6; SC: 62.5, ±1.7; see Figure 4). Distal segments contributed more to overall MDL than the proximal segments across cortical areas (PC: 1.83; UC: 2.08; HC: 1.67; SC: 1.74). An order by order analysis of MDL revealed that MDL tended to increase until the 7th order before decreasing (see Figure 5).

Dendritic Segment Count

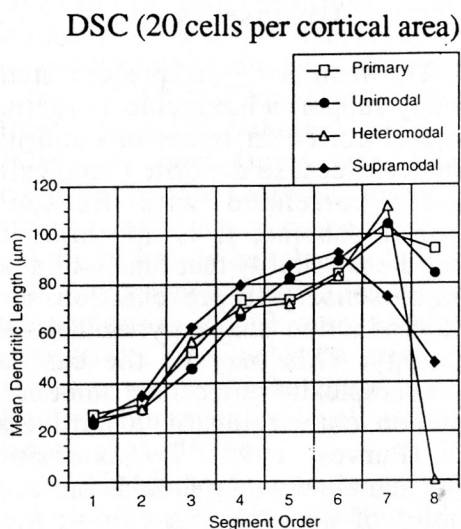


Figure 5. Order by order analysis of MDL (20 cells per cortical area). Note the steady increase in MDL from proximal to distal segments.

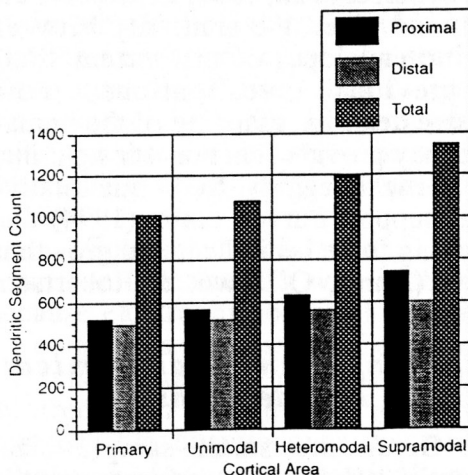


Figure 6. Dendritic segment count (DSC, 20 cells per cortical area) for primary (PC), unimodal (UC), heteromodal (HC), and supramodal (SC) cortex. The continuum of increasing DSC from PC to SC reflects more extensive branching in the functionally "higher" regions.

increased from primary to supramodal cortical areas. DSC was 32% higher in supramodal (1,344), 17% higher in heteromodal (1,194), and 6% higher in unimodal cortex (1,081) than in the primary region (1,018; see Figure 6). As illustrated in Figure 7, order by order analysis of DSC revealed peak values in third and fourth order segments, which subsequently declined. Proximal and distal DSC values were close to equivalent in all regions except supramodal cortex (PC: 0.95, UC: 0.91, HC: 0.9, SC: 0.8). It is noteworthy that both proximal and distal DSC values increased from primary to supramodal cortices, suggesting that "higher" areas contain more dendritic segments both pre- and postnatally.

Dendritic Spine Number and Density

Relative to DSN (20 cells per cortical area) in primary cortex (8,204),

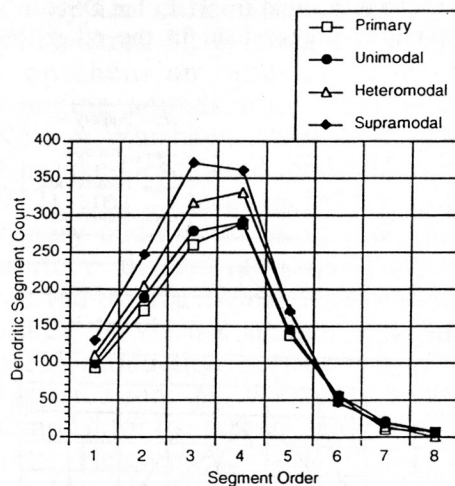


Figure 7. Order by order analysis of DSC (20 cells per cortical area). Although SC had the highest overall DSC, all regions are characterized by a similar dendritic envelope.

DSN was 16% higher (9,498) in unimodal, 32% higher in heteromodal (10,762), and 196% higher in supramodal cortex (24,317; see Figure 8). Order by order analysis revealed an envelope similar to TDL and DSC although DSN was substantially higher in supramodal cortex for segment orders two through six (see

Figure 9). DSN was higher in distal segments for all cortical blocks (PC: 2.61; UC: 2.95; HC: 1.96; SC: 1.69).

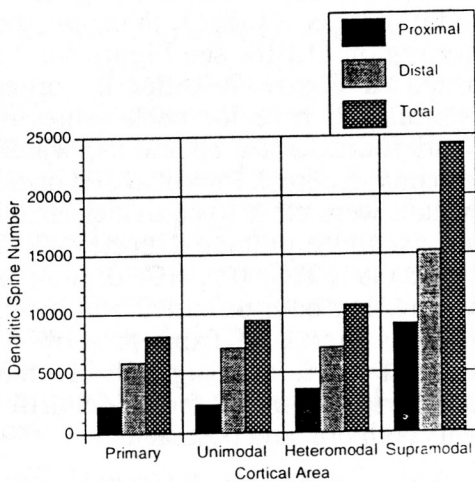


Figure 8. Dendritic spine number (DSN, 20 cells per cortical area) values for primary (PC), unimodal (UC), heteromodal (HC), and supramodal (SC) cortex. The continuum from PC to SC is similar to the one found from TDL, but DSN in SC is substantially higher than in the other three regions.

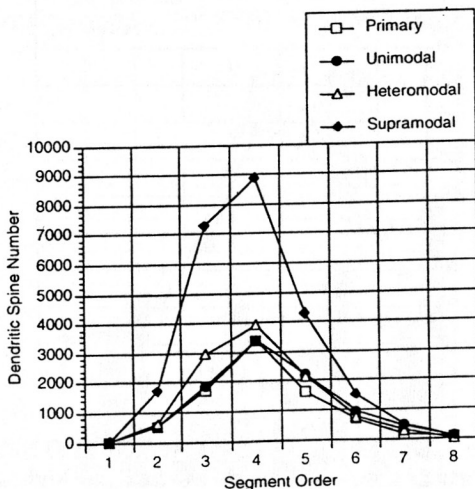


Figure 9. Order by order analysis of DSN (20 cells per cortical area). Although absolute values differ appreciably, the qualitative picture is similar for the four regions.

Dendritic spine densities (DSD = DSN/TDL) increased from primary to supramodal cortical regions although the differences from primary to heteromodal cortex were small. Relative to primary

cortex (0.14), DSD was 14% higher in unimodal (0.16), 14% higher in heteromodal (0.16); and 107% higher in supramodal cortex (0.29). Distal segments had greater spine density values across cortical blocks (PC: 1.5; UC: 1.5; HC: 1.2; SC: 1.2). Order by order analysis of DSD failed to differentiate between the four cortical regions. DSD was fairly constant in all cortical regions in orders three through eight.

Discussion

The results of the present study tentatively support a hierarchical ordering of cerebral cortex in terms of dendritic complexity. Because dendrite complexity positively correlated with Benson's *functional* schema, it is appealing to consider the possibility that functions such as somatosensory representation and speech production shape pyramidal cell morphology. This may be the case as dendrite complexity reflects the amount of information converging on a particular neuron (Purves, 1994). By extension, complex neural networks should consist of ensembles of neurons that exhibit high dendritic measures. Given previous correlations of dendritic extent with cortical function (Larsen et al., 1994; Scheibel, 1988; Scheibel et al., 1990; Scheibel et al., 1985), and given the similarity between dendritic envelopes of the current study and previous investigations, more extensive dendritic mapping of the human cortex may provide functional insight into other cortical regions. Such quantitative studies support Purves' claim (1994) that the driving force behind cortical growth is activity (Annis, O'Dowd, & Robertson, 1994).

Limitations and anatomical/functional considerations

Given the small sample size, differential staining between areas was the most problematic aspect of the present study. The rapid Golgi technique has produced mixed results with both disparate and consistent staining reported (Buell, 1982; Williams, Ferrante, & Caviness,

1977). In the present study, one block of SC stained extremely well, whereas the other regions exhibited somewhat poorer impregnation. This differential staining may have increased the values for DSN and DSD for the 23-year-old brain,

especially in the supramodal cortical region, but it is noteworthy that the overall trends in dendritic measures were the same for both brains when analyzed independently. Although several studies have found that prolonged formalin fixation (6 months or longer) is *desired* for the rapid Golgi technique (Davenport & Coombs, 1954; Fox, Ubeda, Ihrig, & Biagioli, 1951; Scheibel & Scheibel, 1978), our own Golgi work does not support this. The variable impregnation may be a reflection of tissue fixation time, or it might simply be inherent in the Golgi stain. A constant tissue fixation time for the four regions in the 23 year-old brain was not possible. Nonetheless, a strict protocol was observed to minimize other artifacts affecting homogeneous cell populations (Jacobs et al., 1993).

The truncation of dendritic arbors was an unavoidable methodological constraint because light microscopes lose their resolving abilities when rapid Golgi stained sections are too thick. Although the dependent measures are therefore estimates of dendritic complexity, it should be noted that the truncations caused by sectioning were equal for all tissue blocks, and that these truncations did not produce any ceiling or basement effects in the dependent measures (Shaughnessy & Zechmeister, 1990).

Cortical block selection along functional parameters was problematic because electrophysiological mapping of the cortex was not possible. Consequently, the function of each cortical region was inferred from anatomical location. The considerable dispute over the range of functions for each cortical region (Carpenter, 1991; Zilles, 1990), and the large variability in human tissue, makes absolute functional localizations untenable.

Despite functional inferences, the distinctive anatomy and cytoarchitectonics of the four cortical regions, as determined

by Nissl stains (Gridley, 1960) and *in situ* hybridization techniques (Garrett, Finsen, & Wree, 1994), warrants the attempt to delineate the regions by dendritic complexity level. Primary somesthetic cortex (areas 3, 1, 2), which is considered koniocortex (Bailey & von Bonin, 1951), receives sensory input from the periphery and then transfers this information to adjacent, unimodal areas (Carpenter, 1991; Zilles, 1990). Primary cortex is lowest on Benson's functional hierarchical schema for three reasons: (a) information from the external world is first received in primary cortex; (b) brain activation studies show little or no activity in primary cortex during "cognitive" tasks (Roland, 1993); (c) its connections are limited to transhemispheric homologues, adjacent unimodal areas, and the external sensory systems (Benson, 1994).

Unimodal cortex (Wernicke's area, area 22), which is adjacent to the primary auditory areas, is considered parakonio- or homotypical cortex (Bailey & von Bonin, 1951). Area 22 is crucial for language comprehension and is involved in arranging sounds into coherent speech (Kolb & Whishaw, 1990). In the classical Wernicke-Geschwind model (Geschwind, 1972), area 22 receives information from primary auditory areas in order to make auditory discriminations. Information received by area 22 may also be transferred to area 44 via the arcuate fasciculus for speech production, further supporting the classification of Wernicke's area as unimodal for the present study.

Heteromodal cortex (Broca's area, area 44), which is considered dysgranular (Bailey & von Bonin, 1951), is involved in speech production (Kolb & Whishaw, 1990). Its range of functions is still debatable (Ojemann & Mateer, 1979), which may account for the small differences found between Wernicke's and Broca's areas in the present study.

Supramodal cortex (area 10), which is considered isocortical, association cortex (Bailey & von Bronin, 1951), appears to be the most complex area of the brain for several reasons.

1. Highest metabolic and regional cerebral blood flow (rCBF) rates occur in

area 10 in conscious, alert, human subjects (Roland, 1993). Studies correlating metabolic activity with neuron-based electrical activity (Sokoloff, 1981) support the notion that the prefrontal cortex functions as executive control over sensory and motor activities.

2. Direct connections between prefrontal and sensorimotor areas suggest a regulatory role for area 10 (Zilles, 1990), which includes performing higher cognitive functions (e.g., discrimination, recognition, abstraction; Roland, 1993).

3. Area 10 is generally considered responsible for handling sequential contingencies and multiple information representations (Carpenter, 1991; Kolb & Wishaw, 1990; Zilles, 1990).

Different pyramidal cell populations may determine local cortical function

Pyramidal neurons are considered the workhorse of the neocortex, comprising at least 70% of the total cell population (Nieuwenhuys, 1994). The basilar dendritic systems of pyramidal cells, especially those compartments with high dendritic spine counts, comprise the major input system of the cell. By extension, pyramidal cells comprise the major input system of the neocortex, receiving up to 95% of all synapses on their dendritic spines (Nieuwenhuys, 1994). Basilar dendrites, which develop later phylo- and ontogenetically, (Sanides & Sanides, 1972) are extremely plastic. Thus suggesting, on an intrinsic level, pyramidal cell populations that differ in dendritic parameters may also be expected to differ in the complexity of information processing.

Quantitative results tentatively support a positive correlation between posited functional demands and dendritic complexity in discrete cortical regions. This is consistent with previous studies correlating dendritic complexity with function. (Jacobs et al., 1993; Scheibel et al., 1990; Scheibel, 1988; Scheibel, et al., 1985). These correlative examples are informative only if it is assumed that dendritic complexity either reflects or is the

causal substrate for neocortical information processing. Recent neo- and subcortical investigations (Midtgaard, 1994), have revealed that (a) certain electrotonic modulatory mechanisms are found primarily on the spiny dendrite compartments (e.g., regenerative Ca^{2+} responses and spikes), (b) dendritic compartments have distinct electrophysiological properties, and (c) that certain electrotonic parameters (e.g., I_A) often mediate the communication between proximal and distal dendritic segments, thus influencing synaptic integration (Midtgaard, 1994). Thus, dendritic arbors differing in geometrical complexity and spine density should be expected to process information distinctly. Because dendritic complexity is correlated with the degree of convergence on a particular cell, it may be argued that the distinguishing feature of complex dendritic systems is their ability to process more *complex* types of information.

Conclusion

Dendritic complexity, as determined by all dendritic measures except MDL, correlated positively with the putative functional complexity of different cortical areas. Distal segments in all cortical blocks had higher TDL, DSN, MDL, and DSD values relative to the proximal segments. Little or no differences in DSC values were found between proximal and distal segments. Dendritic complexity provides morphological support for Benson's (1993, 1994) functional hierarchical schema.

The present findings also tentatively support the idea that the growth and quantitative parameters of pyramidal cells are largely reflective of if not determined by the activity of a cortical region. To this end, the current study suggests that the growth and proliferation of dendritic neuropil may be a means of functionally differentiating cortical areas.

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