

Preface

The present monograph explores the prenatal development of the human brain motor cortex from its emergence in the undifferentiated neuroepithelium, through the establishment of its primordial organization and the subsequent ascending and stratified cytoarchitectural and functional organizations. The prenatal development of the motor cortex basic neuronal, fibrillar, synaptic, microvascular, and neuroglial systems follows a concomitant, ascending and stratified progression from lower (older) to upper (younger) cortical strata. The monograph introduces new developmental data that explain, for the first time, why, how, and in what order the mammalian cerebral cortex becomes stratified (laminated) as well as the number of pyramidal cells strata that characterizes each mammalian species. It represents the first systematic exploration and description of the prenatal development maturations of the human motor cortex recorder. The rapid Golgi procedure has been used primarily in this developmental study with some additional staining procedures (Chapter 12). The monograph reassembles, organizes by age, discusses, and illustrates lifelong rapid Golgi studies of the developing brains of humans, cats, hamsters, and mice embryos and fetuses. New insights into the mammalian cerebral cortex developmental strategy and progressive ascending stratification (laminations) are discussed. A new developmental cytoarchitectonics theory and a new nomenclature, applicable to all mammalian species, are introduced. The new cytoarchitectonics theory proposes that the structural and functional maturations of the mammalian cerebral cortex are ascending and stratified processes that concomitantly involve its essential systems. The new theory challenges the current and universally held conception of descending (Layers I, II, III, IV, V, VI, VII) cortical laminations. To best describe some of the mammalian cerebral cortex developing fundamental features, new terms are introduced that should replace the less-specific ones currently used.

In separate chapters, the monograph describes and illustrates the following topics: Chapter 2, Mammalian Cerebral Cortex: Embryonic Development and Cytoarchitecture; Chapter 3, Human Motor Cortex: Development and Cytoarchitecture; Chapter 4, The Mammalian Pyramidal Neuron: Development, Structure and Function; Chapter 5, Human Motor Cortex First Lamina: Development and Cytoarchitecture; Chapter 6, Human Motor Cortex Excitatory–Inhibitory Neuronal Systems: Development and Cytoarchitecture; Chapter 7, Human Cerebral Cortex Intrinsic Microvascular System: Development and Cytoarchitecture; Chapter 8, Human Motor Cortex First Lamina and Gray Matter Special Astrocytes: Development and Cytoarchitecture; Chapter 9: New Developmental Cytoarchitectonics Theory and Nomenclature; Chapter 10, Epilogue; Chapter 11, Cat Motor Cortex: Development and Cytoarchitecture (that corroborates many aspects of the developing human motor cortex).

The monograph Epilogue recapitulates the major developmental observations, explores their significance and implications, and introduces some personal insights into the possible anatomical substrate for those attributes that are uniquely human. The monograph emphasizes that in the course of mammalian ontogeny and phylogeny the number of cortical strata increases by adding new ones to those previously established. The number of cortical strata reflects the motor capabilities of each mammalian species. A separate appendix is dedicated to an analysis of the rapid Golgi procedure, from a personal perspective of many a year of using it (Chapter 12). This section aims at clarifying some of the misconceptions that surround this classic staining procedure and explains its capricious nature, extraordinary revealing capabilities, universal applicability, and authenticity. It emphasizes that to learn the rapid Golgi procedure and use it successfully requires perseverance and many years of dedication.

The monograph color illustrations celebrate the rapid Golgi procedure revealing potentials, beauty, clarity, and authenticity. Also its capability of staining neurons, fibers, synapses, blood capillaries (and growing capillaries), and glial elements, thus permitting to explore their variable morphologies and spatial (three-dimensional) interrelationships. The rapid Golgi color illustrations selected and reassembled in this monograph, reproduced herein for the first time, are unique and unavailable in either classic and/or current scientific literature. The monograph hopes to revive interest in this classic procedure and encourage young neuroscientists to learn and apply it in their studies.

Because of its enormous functional size, Golgi studies of the entire cerebral cortex are presently impossible. For such a study we will need: (a) a Brain Institute with dozen of committed investigators prepared to study the various regions of each brain received; (b) satellite Medical Centers to gather fresh (unspoiled) postmortem brains specimen; and (c) a system for bringing the material to the Brain Institute for processing and study, something similar to transporting fresh donor organs. Lacking these options, the best alternative – perhaps the only one – is to study a selected region of young brains, accumulate the data, make it available to guide additional studies of the same and/or other cortical areas. A single investigator, even if he/she devotes their entire life to it, can only study a small cortical area, preferably the same one and from different aged brains. Which I have done throughout my entire academic life and the observations made are reassembled and presented in this monograph.

The vertebrate central nervous system (CNS) might be conceived as a stratified series of nuclei composed of neurons that receive sensory information from the animal surroundings and transmit the information to motor neurons for controlling the animal motor activities in the searching for food, mate, and/or avoiding danger. In the course of vertebrate evolution, as new adaptations and novel motor activities emerge, new nuclei are established for their control. The new nuclei are added to previously established ones, in a caudal–cephalad progression along the animal neural axis (Llinás 2003). Each nucleus is also a stratified system composed of neurons that received sensory information from the animal surrounding, of neurons for controlling its motor activities, and of interneurons that interconnect sensory and motor neurons. Each nucleus develops its own intrinsic microvascular and neuroglial systems. During vertebrate evolution, the number of added nuclei increases progressively as well as their cytoarchitectural complexity. In the course of mammalian evolution, the cytoarchitectural complexity achieved by the added nuclei increases exponentially and, in general, remains poorly understood.

The last nucleus added to the vertebrate CNS is the mammalian cerebral cortex or neocortex. Throughout mammalian evolution, the neocortex remains a single, stratified and biologically open nucleus capable of further expansion by increasing the number of additional pyramidal cell strata. Understanding the neuronal, fibrillar, synaptic, microvascular, and neuroglial cytoarchitectural organization and composition of the entire cerebral cortex of any mammal is, at present, beyond our possibilities. Even understanding the organization of a single cortical region from an adult animal brain may be beyond our present resources. Consequently, the only option – as Cajal recommended – is to study the developing cerebral cortex with an appropriate neuro-histological staining procedure capable of staining all of its elements. In the developing cerebral cortex, the basic elements are fewer, smaller, and easier to visualize, interpret, and understand. Even, a developmental study of a single cortical region will require a life-long dedication, accepting the impossibility of understanding its complete cytoarchitectural and functional organizations and much less that of proximal and distal cortical regions functionally interconnected with it. Despite these shortcomings, the basic neuronal, fibrillar, synaptic, microvascular, and glial systems of a single cortical area can be studied, though partially, with the rapid Golgi procedure, if sufficient amount of time and perseverance are dedicated to it, as the present monograph hopes to prove.

The information presented in the monograph pertains almost exclusively to the prenatal development of the human motor cortex. Despite 36 years of studying this relatively small area and over 4,000 preparations, what I have been able to observe and learn is merely a fraction of its overall cytoarchitectural organization. Despite its incompleteness, the developmental rapid Golgi observations, presented in this monograph, should provide a general view of the developing human motor cortex basic components and of their interrelationships. Comparative developmental Golgi studies of the motor cortex of cats, hamsters, and mice embryos and fetuses provide additional and corroborating information concerning the mammalian cerebral cortex developmental strategy. The monograph introduces three basic propositions: (a) The mammalian cerebral cortex prenatal development and functional maturation is an ascending, progressive and stratified process from lower (older) to upper (younger) strata that concomitantly involve all its essential components; (b) The number of pyramidal cells strata established in the cerebral cortex varies among different mammalian species; and (c) The number of pyramidal cell functional strata formed in the cerebral cortex reflects the animal motor capabilities and may distinguish the motor cortex of each mammalian species.

Since what the brain actually does is to move things, essentially muscles, the following working hypothesis was considered in selecting the study of the human brain primary motor cortex. Information from different cortical regions is channeled to the motor cortex for action or execution. The mammalian cerebral cortex essential functional outlet is through the motor cortex large pyramidal neurons. The assumption was that the motor capabilities of any mammalian species should be reflected on the cytoarchitectural organization and complexity of its primary motor cortex, such that the mouse motor cortex cytoarchitectural organization should be simpler (quantitatively and qualitatively) than that of humans and that the organization of the cat motor cortex should lie somewhere between them. In other words, a mouse, to accomplish all its motor needs, will need a cytoarchitectural organization in its motor cortex that should reflect its inherent and/or acquired motor capabilities. Similarly, the cytoarchitectural organization of a cat motor cortex should reflect its motor capabilities

and should be more complex than that of a mouse and simpler than that of a primate motor cortex. Consequently, the cytoarchitectural organization of the human motor cortex should reflect his extraordinary – inherent and learned – motor capabilities (including motor creativity) and should be more complex than that of other primates. These differences might be expressed in the number of functional pyramidal cell strata established in the motor cortex of each mammalian species. The present monograph explores and reaffirms these assumptions. If this working hypothesis turns out to be correct, the universally held idea (since Darwin and classic neuroanatomical studies) that the only cytoarchitectural differences in the cerebral cortex among mammals is one of degree and not of kind should be reevaluated.

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