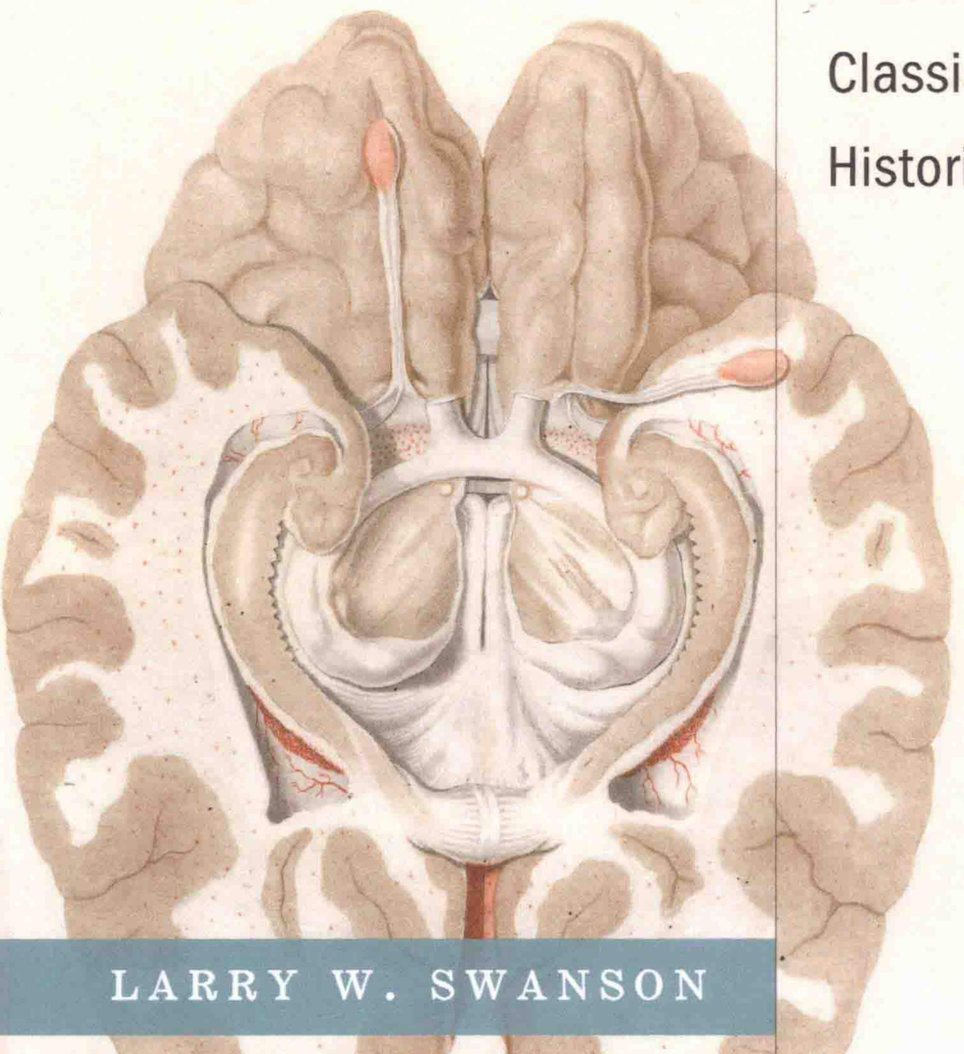
NEUROANATOMICAL TERMINOLOGY

A Lexicon of Classical Origins and Historical Foundations



LARRY W. SWANSON

OXFORD

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A LEXICON OF CLASSICAL ORIGINS AND HISTORICAL FOUNDATIONS

LARRY W. SWANSON, PhD

University Professor and
Appleman Professor of Biological Sciences
University of Southern California
Los Angeles

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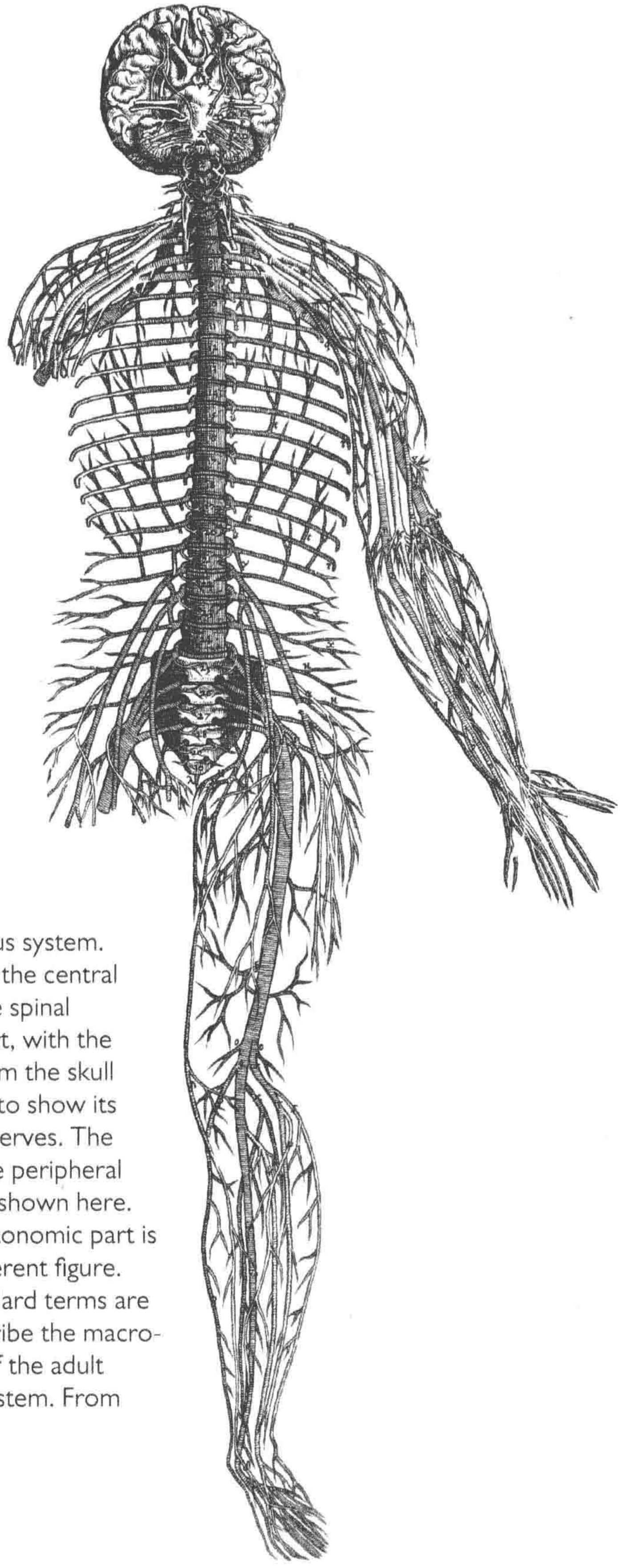

The human nervous system. The spinal cord of the central part remains in the spinal column for support, with the brain removed from the skull and tilted upward to show its base with cranial nerves. The somatic part of the peripheral nervous system is shown here. The visceral or autonomic part is illustrated in a different figure. About 1,300 standard terms are used now to describe the macroscopic structure of the adult human nervous system. From Vesalius (1543a).

Preface

Work on this book coincided with the explosive creation of the Internet and the rather more difficult birth of neuroinformatics toward the end of the 20th century. Without the former it probably could not have been finished in its present form during my lifetime, and without the latter it probably would not have been started at all.

The early stimulus for this research was a 1989 Committee on a National Neural Circuitry Database hosted by the Institute of Medicine (IOM) of the United States National Academies (Pechura & Martin, 1991). It helped pave the way for a decade of substantial National Institutes of Health (NIH) funding of the Human Brain Project (HBP) starting in 1995 (see De Schutter, 2005). During HBP conferences in San Diego, I met regularly and informally with three participants—Douglas Bowden, Steven Koslow, and Arthur Toga—to discuss broad strategies. We eventually agreed that the chaotic state of neuroanatomical nomenclature was perhaps the single greatest impediment to developing useful neuroinformatics tools for all aspects of neuroscience. Bowden went on to implement *NeuroNames* (Bowden & Dubach, 2003), which deals with contemporary sources of terminology, and I decided to take an historical approach, following the development of neuroanatomical terminology from the beginning. This approach was orders of magnitude more difficult than I had expected, and the initial results are presented here and in our broader Foundational Model of Connectivity (Swanson & Bota, 2011; Brown & Swanson, 2013).

Neuroinformatics is based on constructing databases and knowledge management systems for the nervous system (Koslow & Huerta, 1997). To construct tables for databases and to use inference engines in knowledge management systems it is necessary to create internally consistent defined vocabularies along with sets of rules for establishing relationships between concepts and terms. In contrast, neuroanatomy—now sometimes called *structural neuroscience* or *connectomics*—is thousands of years old and its terminology remains frustratingly disorganized, unlike mathematics, physics, and chemistry, where standardized nomenclatures have long been essential for progress.

I was originally drawn into this morass in the 1970s by the tradition of citing historical precedence in my own experimental neuroanatomical research papers on axonal connections between parts of the mammalian brain. It was accepted practice to determine which available terminologies for brain parts fitted the data best, and if none were adequate it was sometimes necessary to define new parts or different borders in relation to the older views (for example, Swanson, 1976). In the *Discussion* section the earlier literature could then be viewed and interpreted in relation to the internally consistent structural nomenclature adopted and defined for the experimental results.

As the body of this work grew and expanded to include the entire central nervous system (for example, Swanson & Hartman, 1975; Swanson & McKellar, 1979), the need for a systematic atlas became apparent, and the first edition of *Brain Maps: Structure of the Rat Brain* (Swanson, 1992, 1993) eventually appeared. This work contained a traditional atlas, with a set of photomicrographs of transverse histological sections through the rat brain accompanied by a set of corresponding interpretative maps (in print and the first atlas in digital format). But perhaps more importantly it contained the first systematic, hierarchically organized Nomenclature Tables of brain parts (gray matter regions and white matter tracts) to appear in modern times, with documentation from the primary literature. This required assessing the rather extensive contemporary literature and choosing an internally consistent parceling and accompanying nomenclature that appeared to be not only best documented in terms of experimental evidence, but also most appropriate in terms of historical precedence. These Nomenclature Tables are now in their third edition (Swanson, 2004).

The experience gained by this systematic exercise was taken to another level by our translation (Swanson & Swanson, 1995) of Santiago Ramón y Cajal's masterpiece, the *Histologie du Système Nerveux de l'Homme et des Vertébrés* (Cajal, 1909–1911). This monumental work of just over 680,000 words and 1,025 original illustrations not only documented Cajal's own contributions to neuroanatomy—especially in the arenas of neuron types and connections—but also formed a critical review of most contributions to the field in the second half of the 19th century. Thus, it became necessary for us to understand clearly the state of neuroanatomical terminology at the end of the 19th century, which was presented in the translation's *Index*.

The third level of structural neuroscience nomenclature analysis presented here emerged from the needs of a new field—neuroinformatics—mentioned above. We went on to create an online Brain Architecture Knowledge Management System (Google: *BAMS*) that was based initially on our atlas, nomenclature, and experimental circuit data in the rat (Bota et al., 2003). However, the need for a comprehensive neuroanatomical nomenclature for all parts of the nervous system (central and peripheral), and in all animals, remained and led to the formulation of a Foundational Model of Connectivity (Swanson & Bota, 2010) and the work presented here. The ultimate goal is to create a language that can be used to describe clearly, accurately, and unambiguously the wiring or schematic diagram of the nervous system and that can be refined with a set of rules to accommodate new data and conceptual frameworks (see Brown & Swanson, 2013).

A revolution in scholarly research methodology took place literally during the course of this investigation. I began in 1998 the traditional, time-honored way: reading books in a library and taking notes. Shortly thereafter, catalogs of most of the world's most important libraries came online, massive union catalogs like WorldCat and Karlsruher Virtueller Katalog (KVK) were created, and librarians could be contacted easily by email for more detailed information about individual holdings. The vast majority of Western literature from the 15th century on was digitized and made available by keyword searches online, often in text searchable format. And word processing software made note taking, file searching, and text organization much more convenient and efficient than ever before. Today there is no excuse but laziness for not examining the earlier literature on any topic, including the history of neuroscience, which goes back to the Smith Papyrus of about 1700 BC.

Aside from my personal library, the most useful by far has been the Louise M. Darling Biomedical Library at the University of California, Los Angeles, and the exceptionally knowledgeable and helpful staff in the History and Special Collections for the Sciences Division, including especially Katherine Donahue, Russell Johnson, and Teresa Johnson. Marie-Françoise Chesselet, Chair of the Neurobiology Department at UCLA at the time, also made the research go much more smoothly by arranging a Visiting Scholar appointment for me. The second most useful resource was the incomparable collection and staff at the U.S. National Library of Medicine in Bethesda, Maryland. Here I want especially to thank those in the History of Medicine Division who helped the most: Stephen Greenberg, Crystal Smith, Anne Rothfeld, and Karen Pitts. Other valuable resources in California included the Huntington Library and its Dibner Senior Curator Daniel Lewis, the William Andrews Clark Library of UCLA and its then Head Librarian Bruce Whiteman, the Arts Library of UCLA, the Charles E. Young Research Library of UCLA, and the Lane Medical Library of Stanford and its Historical Curator Drew Bourn. In New York City I especially thank Arlene Shaner at the superb New York Academy of Medicine Library, and Stephen Novak and Jennifer McGillan at the Archives and Special Collections of the Augustus C. Long Health Sciences Library of Columbia University. Exceptionally rare material was also examined at the Francis A. Countway Library of Medicine of Harvard University and the Bancroft Library and Marian Koshland Biosciences and Natural Resources Library of the University of California, Berkeley. This research was supported in part by NIH Grant R01NS050792.

Readers will understand that no undertaking like this by one individual in a limited time frame can be regarded as anything but a preliminary guide to the vast, multilingual literature and part of a never ending revision of nomenclature tables.

AUGUST 15, 2013
LOS ANGELES

Quotations

"He who can properly define and divide is to be considered a god."

Plato (quoted in Mackay, 1977, p. 119)

"For in order that nothing I say be misunderstood and that precision and clarity be everywhere present, it is most essential that the meaning of every term be accurately defined."

Galen (*On the Doctrines of Hippocrates and Plato*; De Lacy, 1980, p. 361)

"Truth is the daughter of Time and not of authority."

Leonardo da Vinci (quoted in Garrison, 1929, p. 14)

"I cannot set bounds to my astonishment at my own stupidity and excessive trust in the writings of Galen and other anatomists. I was so besotted by Galen that I had never undertaken to demonstrate a human head without the head of a lamb or ox at my public dissections; I was so keen not to gain the reputation of having been unable to find the plexus [rete mirable (Herophilus, c335–c280 BC)] whose name was familiar to everyone that I imposed upon my audience by demonstrating from a sheep's head something I had never found in a human one."

Andreas Vesalius (1543a; Richardson & Carman translation, 2002, p. xvii)

"I implore his Majesty the Emperor [Charles V] to punish severely, as he deserves, this monster born and reared in his own home, this most pernicious exemplar of ignorance, ingratitude, arrogance, and impiety; and to suppress him completely, lest he poison the rest of Europe with his pestilential breath. With his deadly spume, he has already infected certain Frenchmen, Germans, and Italians, but they, I believe, are ignorant of anatomy and of the other branches of medicine..."

Jacques Dubois (1551; from *A Repudiation of the Calumnies of a Certain Madman [Vesalius] Concerning Hippocratic and Galenic Anatomy by Jacobus Sylvius, the Royal Interpreter of Things Medical at Paris*; see Cushing translation, 1943, p. xxx)

"Among the parts of an animated Body, which are subject to Anatomical disquisition, none is presumed to be easier or better known than the brain; yet in the meantime, there is none less or more imperfectly understood."

Thomas Willis (1664; Pordage translation, 1681, p. 55)

"To examine each part [of the brain] thoroughly requires so much time and such application of mind that it would be necessary to give up all other labors and all other considerations on that particular task."

Nicolaus Steno (1669; see translation, 1965, p. 141)

"When a committee is made up of five or six people, one of them is reading, another is delivering his opinion, two are gossiping together, one is asleep, and one is diverting himself by leafing through one of the Dictionaries on the table."

Antoine Furetière (1688. A member of *l'Académie française*, founded in 1635 to produce a dictionary of the French language; quoted in Hitching, 2005, p. 51)

"Dictionaries are like watches. The worst is better than none, and the best cannot be expected to go quite true."

Samuel Johnson (shortly before his death in 1784, quoted in Hitching, 2005, p. 179)

"We shall provisionally adopt the more rational language which C. Chaussier has substituted for the whimsical and ridiculous names employed by the ancients to denote the different parts of the encephalic organ. But, it must be confessed, that zootomy will never be in possession of a nomenclature completely satisfactory, and susceptible of being generally adopted, until intelligent anatomists employ themselves, as the modern chemists [Antoine Lavoisier in particular] have done, to reform the language of their science; and until, after adopting a method of nomenclature, they shall have given to the different parts names suited not only to the organs of man, but also to the similar or analogous parts in animals, so as to connect by language two branches of natural history, which ought never to be separated."

Jean Burdin (1803 translation, Vol. 1, pp. 156–157)

"Anatomy may be likened to a harvest field. First come the reapers who, entering on untrodden ground, cut down great store of corn from all sides of them. These were the earliest anatomists of modern Europe, such as Vesalius, Fallopius, Malpighi, and Harvey. Then come the gleaners, all gather up ears enough from the bare ridges to make a few loaves of bread. Such were the anatomists of the last century—Winslow, Vicq d'Azyr, Camper, Hunter, and the two Monroes. Last of all come the geese, who still contrive to pick up a few grains scattered here and there among the stubble, and waddle home in the evening, poor things, cackling with joy because of their success. Gentlemen, we are the geese."

John Barclay (1758–1826; from a warning to his students, as quoted in Sinclair and Robb-Smith, 1950, p. 74)

"It is not a little remarkable that what is definitely known regarding the special functions of the nervous system has been ascertained within the last thirty years."

British and Foreign Medical Review (1840, Vol. 9, p. 98)

"The best workman uses the best tools. Terms are the tools of the teacher; and only an inferior hand persists in toiling with a clumsy instrument when a better one lies within his reach. But 'he has been used to the other.' No doubt; and some

extra practice is necessary to acquire the knack of applying the new tool. But in this acquisition a small capital of trouble will have been invested with a sure return of large profits. A single substantive term is a better instrument of thought than a paraphrase. But the substitution of such terms for definitions is still more advantageous when they are susceptible of becoming adjectives by inflection..."

Richard Owen (1866, p. xiii–xiv)

"Faced with an anatomical fact proven beyond doubt, any physiological result that stands in contradiction to it loses all its meaning... So, first anatomy and then physiology; but if first physiology, then not without anatomy"

Bernard von Gudden (quoted in Brodmann, 1909; Garey translation, 1994, p. 267)

"'A well-chosen word can save an enormous amount of thought,' because to name is to classify, to establish ideal affiliations—analogous relationships—between little-known phenomena, and to identify the general idea or principle wherein they lie latent, like the tree within its seed."

Santiago Ramón y Cajal (1999, p. 54)

"The terminology of the brain is in great confusion. Most of the more obvious parts were named before their functions were known, and the same part often receiving many different names, and sometimes the same name being applied to very different parts."

C. Judson Herrick (1915, p. 115)

"It is almost unbelievable how many people are unable to copy a name correctly, and once a mistake gets into print or into an official document it is difficult to eradicate."

Henry E. Sigerist (1960, p. 292)

"Regardless of how terms are defined by lexicographers or committees of experts, terms cannot be used outside a theory. That is true even when terms are contingent—'given so-and-so, that is a neuron'—or hedged with observational restrictions—'that is an object at this time and place which has observable properties a, b, ... n.' The principal reason for the frequent disputes over terminology is not so much about whether a new term muddles Greek with Latin. It is really about whether the term is biased toward their theory rather than ours."

Marcus Jacobson (1993, p. 16)

"Without the belief in some principle of organization of the nervous system there can be no science of the nervous system."

Marcus Jacobson (1993, p. 23)

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Chapter I

LEXICON OF NERVOUS SYSTEM PARTS

Understanding how any system works requires four things: a general understanding of what the system does, a parts list, an account of how each part works, and knowledge of how the parts are interconnected to function as a whole. For the ***nervous system (Monro, 1783)*** in particular, there is a basic understanding of its role as a biological computer in controlling and coordinating both the internal physiological state of the body and behavioral interactions of the body with the external environment. However, a fundamental block to understanding mechanisms underlying this integration is the lack of a comprehensive, systematic, and widely accepted parts list for the ***nervous system (Monro, 1783)***.

A standard parts list is important for at least three main reasons. First, effective scientific communication requires an accurate, clearly defined vocabulary of technical terms. Second, a global parts list allows global analysis at the systems level. What is the internal configuration of each part and how does it work, how are the parts interconnected to function as a whole, and how does activity in one part or node influence activity in other parts or nodes of the network? And third, knowledge management systems that use inference engines with associated databases require unambiguous, systematic defined vocabularies of terms and relationships between terms.

Connectomes are one way to organize information about the wiring diagram of the ***nervous system (Monro, 1783)***. As originally conceived, a connectome is a global table of connections between ***nervous system (Monro, 1783)*** parts—a "from-to" lookup table or matrix (Sporns et al., 2005). Obviously, a comprehensive, internally consistent set of defined terms for parts that are connected is required for such a connectome (Bota et al., 2003; Bota & Swanson, 2010).

Foundational Model of Connectivity

Because the ***nervous system (Monro, 1783)*** is a biological computer, the "wiring" or schematic diagram of its structural connectivity provides one obligatory foundational model for understanding functional localization and mechanisms at all levels of organization from molecules to behavior and cognition. To facilitate accurate and clear scientific communication, global analysis of neural networks, and network modeling in knowledge management systems, a Foundational Model of Connectivity was formulated (Swanson & Bota, 2010). It is a high-level, downwardly extendible conceptual framework that applies to all animals with a ***nervous system (Monro, 1783)***, invertebrates and vertebrates alike, at all levels of analysis or resolution.

Any system or network has nodes and connections between nodes (see next section). This book has two major, interrelated parts: a Lexicon of defined terms and a set of 10 Nomenclature Tables. Fundamentally, they deal with the identity and location of nodes and connections within the ***nervous system (Monro, 1783)*** and are developed within the framework of the Foundational Model of Connectivity.

Location or position within the ***nervous system (Monro, 1783)***, and within the body as a whole, is described for any and all animals with a standard set of terms defined in the Foundational Model of Connectivity (Figure 1). This is a common approach in comparative anatomy, but for historical reasons it has been a major problem in human anatomy, where an idiosyncratic and deeply rooted set of positional terms is commonly used, especially in medical contexts. Nevertheless, the Foundational Model of Connectivity terms for positional information are used here as much as is practical for describing human ***nervous system (Monro, 1783)*** parts in the Lexicon (Figure 2).

Macrolevel, Mesolevel, and Microlevel of Analysis

An important feature of the Foundational Model of Connectivity is the precise definition for the ***nervous system (Monro, 1783)*** of three nested levels of analysis, resolution, granularity, and description (Swanson & Bota, 2010; Brown & Swanson, 2013). This approach (Figure 3) provides a strategy for attacking the well-known complexity of the ***nervous system (Monro, 1783)***, either from the top down (simple to complex) or bottom up (complex to simple).

The macrolevel of ***nervous system (Monro, 1783)*** connectivity is the simplest and lowest resolution. It deals with parceling ***gray matter (Meckel, 1817)*** and ***white matter (Meckel, 1817)*** into distinct ***gray matter regions (Swanson & Bota, 2010)*** and ***white matter tracts (Bell & Bell, 1826)***, respectively. At the macrolevel, ***nervous system (Monro, 1783)*** circuitry is described as ***gray matter region (Swanson & Bota, 2010)*** macronodes with ***white matter tract (Bell & Bell, 1826)*** input and output macroconnections. Before the microscope was used effectively for studying ***nervous system (Monro, 1783)*** connectivity organization in the mid 1830s, and the cell theory was introduced (Schleiden, 1838; Schwann, 1839), macrolevel examination was done with the naked eye, occasionally aided by a hand lens. Since then it has been examined predominantly with histological methods in animals and, more recently, with imaging techniques like MRI in living humans.

The mesolevel of ***nervous system (Monro, 1783)*** connectivity deals with neuron types (Bota & Swanson, 2007).

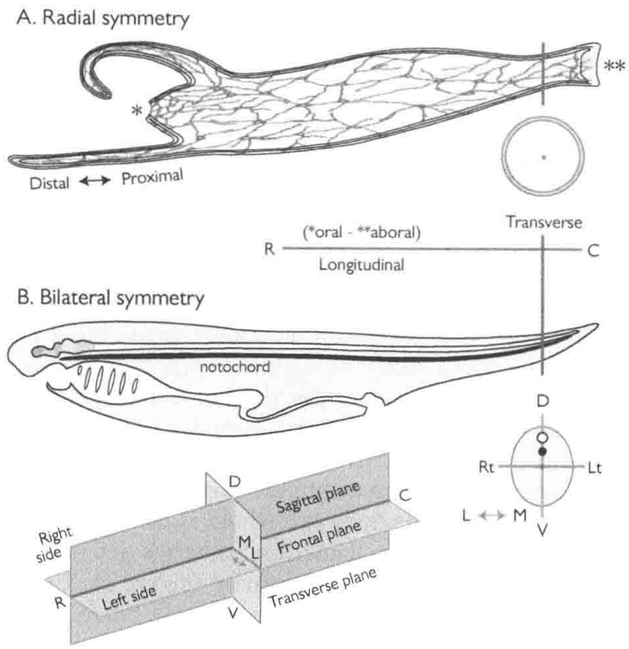

FIGURE 1. Describing position and symmetry in all animals with a ***nervous system (Monro, 1783)***. The basic assumption is that the body of all animals, whether radially or bilaterally symmetrical, has a longitudinal axis and one or two transverse axes, with the former having rostral and caudal ends. (A) Radially symmetrical animals like the hydra illustrated here have a ***nerve net (>1840)*** and two orthogonal axes, longitudinal (rostrocaudal or oral-aboral) and transverse. They also have two orthogonal planes of section, longitudinal or transverse. Relative position along body extensions, in this case tentacles, is indicated (distal or proximal to its attachment to the body). In bilaterally symmetrical animals, proximal and distal are used for extensions like fins, wings, limbs, or noses. (B) Bilaterally symmetrical invertebrates and vertebrates have three cardinal axes and three corresponding planes of section, as well as right and left halves or sides. An idealized chordate body plan is shown here. The ***central nervous system (Carus, 1814)*** lies dorsal to the notochord that in turn lies dorsal to the digestive system. A key principle in comparative schemes for indicating positional information is use of terms referring to the body itself, rather than to relationships of the body to the environment, which can change dramatically depending on behavior. Especially egregious offenders include horizontal (parallel to the horizon), superior (toward the sky, or heavens), and inferior (toward the earth). *Abbreviations*: *C*, caudal; *D*, dorsal; *L*, lateral; *Lt*, left; *M*, medial; *R*, rostral; *Rt*, right; *V*, ventral. *Reproduced with permission from Swanson & Bota (2010).*

In essence, each ***gray matter region (Swanson & Bota, 2010)*** is defined by a unique set of neuron types. At the mesolevel, ***nervous system (Monro, 1783)*** connectivity is described as neuron type mesonodes within particular macronodes that have input and output mesoconnections following specific routes though ***white matter tracts (Bell & Bell, 1826)***.

The microlevel of ***nervous system (Monro, 1783)*** connectivity deals with individual neurons of a neuron type. At the microlevel, individual neurons form individual micronodes and the connection pattern of individual neurons at the level of axon branching patterns, and the distribution and size of individual synapses is accounted for.

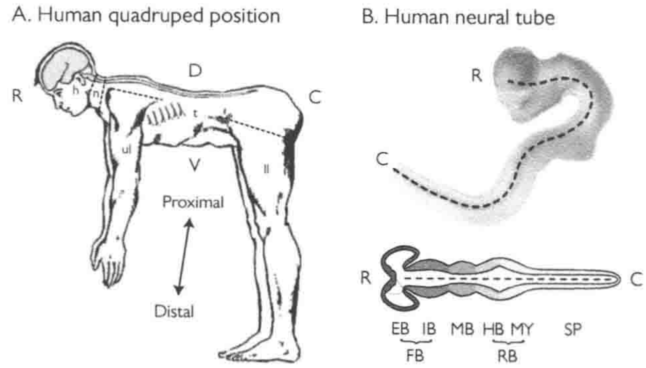

FIGURE 2. Describing position and symmetry in the developing and adult human. This problem is especially difficult because of dramatic changes in the longitudinal axis of the developing embryo, and of the adult body, which is vertical and bipedal with the palms facing forward in the standard human anatomical position. (A) Adult human in the comparative anatomical position where comparison with other bilaterally symmetrical animals (Figure 1B) is easy, and position along extensions like limbs is also easily described (compare with tentacle in Figure 1B). The body's longitudinal axis is indicated with a dashed line and has rostral (*R*) and caudal (*C*) ends. (B) ***Neural tube (Baer, 1837)*** of a one-month human embryo, with the longitudinal axis indicated by a dashed line. The ***endbrain (Kuhlenbeck, 1927)*** (*EB*) is at the rostral end and the ***spinal cord (Galen, c162–c166)*** (SP) is at the caudal end. The top part of the figure shows the right half of the ***neural tube (Baer, 1837)***, and the bottom half is a conceptualized straightened ***neural tube (Baer, 1837)*** in frontal (horizontal) section with topographic divisions listed in Appendix 2. *Other abbreviations*: *D*, dorsal; *FB*, ***forebrain (Goette, 1873)***; *HB*, ***hindbrain (Baer, 1837)***; *IB*, ***interbrain (Baer, 1837)***; *MB*, ***midbrain (Baer, 1837)***; *MY*, ***medulla (Winslow, 1733)*** or ***afterbrain (Baer, 1837)***; *RB*, ***rhombicbrain (His, 1893b)***; *V*, ventral. *Reproduced with permission from Swanson & Bota (2010).*

In general, the macrolevel and mesolevel of ***nervous system (Monro, 1783)*** organization are genetically determined, discounting injury and disease. They are still commonly treated qualitatively, although differences between individuals are often measured. In contrast, the effects of experience—which include factors like learning, pharmacological agents, and stress—are measured at the microlevel. Microlevel features are commonly treated quantitatively and change rather quickly, and often more or less continuously, in the individual.

Goals and Scope of the Book

The general goal of this book was to provide a comprehensive, systematic defined vocabulary for describing the ***nervous system (Monro, 1783)*** in general and the human ***nervous system (Monro, 1783)*** in particular. This was approached by developing two major interrelated features. The first is the Lexicon. It provides for each ***standard term*** in the defined vocabulary a literature citation for the first use of the term; a textual definition including method used to describe the part, age, species, and sex to which