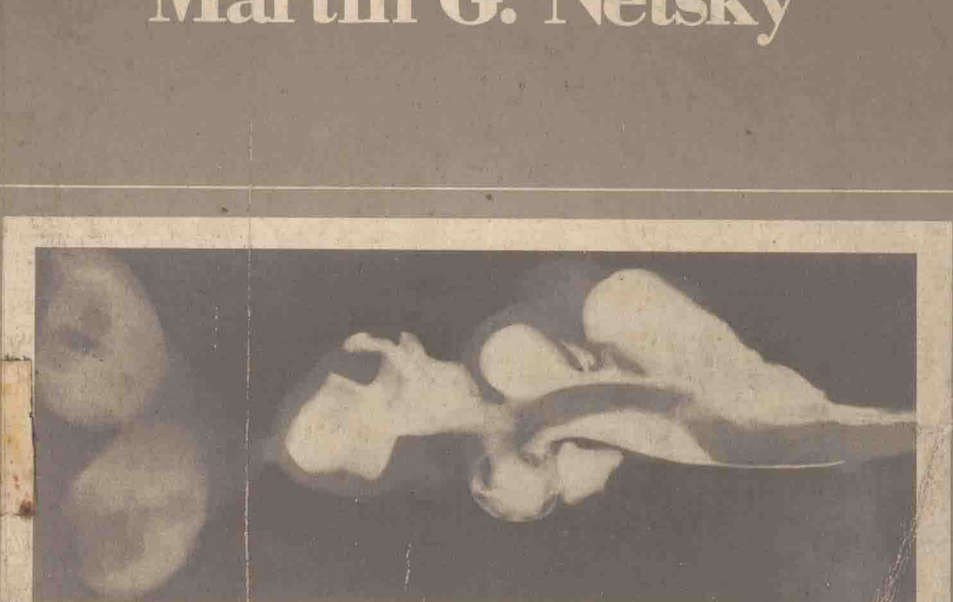
Evolution of the Nervous System

Second Edition

Harvey B. Sarnat
Martin G. Netsky



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Second Edition

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Evolution of the Nervous System

To our wives

Preface

The structure of the human nervous system may be approached in at least three ways. The first is to study the spatial relations of fiber tracts and other structures in the mature human brain. This method is the only one to which most students of the neurosciences are exposed.

The second approach is to study embryonic development and cerebral maturation after birth. This analysis of ontogenesis is particularly important to those persons concerned with the problems of anomalous development of the nervous system.

The third way of exploring neuroanatomy is through the dimension of time as revealed by analysis of evolution. The millions of years required for the evolution of species make direct experimental studies difficult. This method is the most abstract because the processes usually cannot be observed directly. In addition, much data must be inferred from the comparative study of species evolving along lines different from man, and arising from common ancestral forms now extinct. The study of comparative anatomy, however, provides a background for understanding the development of complex nervous systems. The functional capabilities of phylogenetically older systems are demonstrated in lower vertebrates, as well as their inadequacies for increasing the range of functions needed by evolving species, including man. Numerous laboratory experiments have the goal of studying isolated functional systems by creating lesions in the brains of experimental animals. Nature, however, has segregated these systems in simple species lacking the later modifications.

The rapid expansion of information on the nervous system of fossilized and existing species stimulated the preparation of a second edition of "Evolution of the Nervous System." New data have come from studies involving histochemistry, biochemistry, neurophysiology, pharmacology, electron microscopy, excavations of fossils, and analysis of invertebrates.

The influx of fresh material required updating the entire text and introducing two new chapters. One of these chapters, written by Robert B. Ramsey, describes the evolutionary changes in myelin, glia, and neurons, and the remarkable generality of known neurotransmitters. In the other new chapter, we consider the enlargement of the brain from protochordates to man and the relation of various functional systems to behavior. The chapter on the spinal cord and motor unit has been broadened to include development of neuromuscular control, including recently discovered specializations of skeletal muscle.

New discussions of topics such as thermoregulation and bioluminescence have been included, as well as additional material on sleep, the place of dinosaurs in evolution, the ventricular system and blood supply of the brain, neuromelanin, the origin of speech, and numerous other subjects. Many illustrations have been added. The bibliography has been expanded from approximately 500 to 1,500 items. Most of the newly cited papers were published after our first edition in 1974. The index also has been expanded in an effort to increase the usefulness of the book.

As in the first edition, we have surveyed comparative anatomy and trends in the evolution of the central nervous system of vertebrates. It has at times been necessary to speculate on some aspects of development but such speculations are clearly indicated. Applications to human issues are made as often as possible in the hope that they will help neuroscientists to understand these problems of the brain and spinal cord. We have strived to maintain narrative flow and to avoid encyclopedic detail. Our purpose has been to provide a means, not otherwise readily available in one publication, to achieve better comprehension of the evolutionary aspects of the nervous system in our own species.

June 1980

H.B.S.
M.G.N.

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Evolution of the Nervous System

1

Evolution and neurology

Evolution

Evolution is change. The constant features of the nervous system of vertebrates are structures that have failed to evolve or change appreciably. They offer insight into the *origin* of the brain, but the differences among species denote *evolution.* The limited range of function available to animals using simple nervous systems affords an understanding of their limitations, and an appreciation of refinement and supplementation in more complex species. The observation of simple vertebrates also brings an awareness that the brain of man resembles the brains of "lower" animals more than it differs from them.

Comparative neurology reveals a flexibility of cerebral organization necessary for evolution. For example, the laminar arrangement of cerebral cortex in mammals is not the only means of achieving complex functions of the forebrain. The nonlaminar organization of the avian telencephalon gives some birds an ability to learn and to solve problems equal to many mammals and superior to some. Each vertebrate has distinctive neuroanatomic features ultimately expressed in its relation to the environment and its use of ecologic resources.

It is frequently suggested that high intelligence, from the evolutionary standpoint, may be equated with superiority. In his essay "The evolutionary advantages of being stupid," Robin (1973) proposed that in some circumstances a small cerebral mass may be more advantageous than a large one. For example, the freshwater turtle survives prolonged underwater dives of more than a week. The small brain requires relatively little energy and is capable of functioning normally with zero oxygen tensions in the blood, meeting energy requirements entirely from anerobic glycolysis. Diving iguana lizards may remain submerged for as long as 4½ hours, during which time they withstand blood lactate levels of 320 mg. per 100 ml. and severe acidosis as low as pH 6.9 (Moberly, 1968). Other diving animals with progressively larger brains tolerate lack of oxygen for shorter periods. The bottle-nosed porpoise, a highly intelligent mammal, has a maximal diving time of only five minutes. The turtle has survived largely unchanged for more than 200 million years; it can hardly be regarded as an unsuccessful animal. If oxygen supply in the ambient environment should ever become limited, the turtle, with its small, slowly functioning brain would probably survive longer than man. The line of evolution leading to man is not necessarily the best for all animals, and each path of specialization offers both advantages and liabilities.

The sequential evolution of the various classes of vertebrates has been reconstructed primarily by examining skeletal structure of living and fossilized species. The comparative anatomy of the heart, kidneys, and other organs of contemporary vertebrates provides another, although inferred, basis for understanding progressive phylogenetic development. The central nervous system has been studied less and only recently from the perspective of confirming the sequence of evolution, not only because of the complexity of this organ even in the simplest species, but also because more variations and divergence in structure are found in the brains of living vertebrates than in any other organ system.

Differences in opinion regarding the phylogenetic relations of various species of vertebrates are minor problems in contrast to the great question of the origin of vertebrates from an invertebrate ancestor. This enigma, second in importance in evolutionary theory only to the more fundamental question of the origin of life, has generated many hypotheses ranging from fanciful to plausible. No single theory yet proposed explains all features of vertebrate evolution. We favor the nemertine hypothesis, explained in a following section of this chapter, because it accounts for more features of the vertebrate body than any other, even though the nervous system ironically may be one of the weakest aspects of its explanation of vertebrate evolution.

Phylogeny

Phylogeny refers to the relation of individual species of vertebrates to all other species, living or extinct, with respect to their place in evolution. These relations are schematically illustrated in Figures 1-1 and 1-2. It is technically inaccurate to speak of "lower" and "higher" vertebrates, because all contemporary species have evolved, each along a different path of specialization or generalization. The arbitrary place that each class of vertebrates and each species occupies on the phylogenetic scale is based on many anatomic features of body and brain. Some vertebrates lower in this scale have particular structures better developed than in other animals considered higher, including man. Many exam-

Figure 1-1 Simplified scheme of vertebrate evolution. (Modified from Romer, 1970)