

Comparative Neurology of the Telencephalon

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Edited by

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Ponce, Puerto Rico*

Plenum Press · New York and London

Library of Congress Cataloging in Publication Data

Main entry under title:

Comparative neurology of the telencephalon

Includes bibliographies and index.

1. Telencephalon. 2. Vertebrates -- Physiology. 3. Anatomy, Comparative.
4. Neurology. I. Ebbesson, Sven O. E. [DNLM: 1. Telencephalon. 2. Anatomy,
Comparative. 3. Physiology, Comparative. QL933 C737 (P)]

QP381.C63

596'.01'88

79-12145

ISBN-13:978-1-4613-2990-9

e-ISBN-13:978-1-4613-2988-6

DOI: 10.1007/978-1-4613-2988-6

© 1980 Plenum Press, New York

Softcover reprint of the hardcover 1st edition 1980

A Division of Plenum Publishing Corporation

227 West 17th Street, New York, N.Y. 10011

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Dedicated to Professor Horacio Vanegas and his son, Professor Horacio Vanegas Fishbach, whose kindness and generosity will never be forgotten by those who met in Caracas to exchange views on the evolution of the telencephalon.

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Foreword

When a young graduate student sat before Percival Bailey in 1960 and spoke of his longstanding interest in zoology and his recent interest in the nervous system, he asked the then Director of the Illinois Neuropsychiatric Institute if there was support in the scientific establishment for research in evolutionary comparative neurology. Bailey patted his abdomen with both hands and thought for a moment. Finally he said: "Young man, there is no place for people like you." The graduate student was crestfallen.

To a large extent what Bailey said is still true. The greater part of research in neurobiology is directed toward answering a single broad question. How do brains in general, and the human brain in particular, work? This is a legitimate and important question. It is not, however, the only question worth answering. This overweening emphasis on function, especially in regard to the human nervous system, is a result of the origins of neurology in the clinic. The professional school, site of most such research, has been remarkably well-insulated from many of the major concerns of biology.

The telencephalon has figured prominently in concepts relating to the intellectual superiority of man over the beasts. As a consequence, a great many studies have been made of the structural organization, physiological properties, and behavioral role of the cerebral hemispheres of mammalian brains. Less attention has been devoted to the telencephalon of nonmammalian vertebrates. This relative neglect was partially a result of the widespread notion that the forebrain of most nonmammalian vertebrate groups was exclusively concerned with olfaction, a sensory system with somewhat less appeal to human-oriented investigators.

As a result of pioneering experimental studies in the late 1960s and early 1970s it is now well known that there are strong organizational similarities in the forebrains of amniotes. Also, olfaction apparently does *not* dominate the forebrain of birds, reptiles, amphibians, and fishes. These findings have raised many questions. If portions of the telencephalon of nonmammalian vertebrates are "wired up" in a manner similar to the neocortex of mammals, do these cell populations perform the same functions as does neocortex? If they do, what then is the significance of the laminar organization found in mammals? If they do not, then

how is the laminar organization involved in this difference in function? What were the selection pressures involved in the evolution of neocortex? Where did this neocortex first appear in vertebrate history? It is important also to remember that a frog brain is not designed to be an intermediate brain between that of a fish and that of a man. It is designed to regulate the physiological functions and behavior of a frog living in an environment that challenges the animal to survive as a frog. The frog brain is interesting from that point of view in addition to whatever it may tell us about the brain of man.

The participants in the conference which produced this book were charged with the task of assessing what we have learned about the vertebrate telencephalon since the appearance of that burst of research activity in the 1960s which continues to this day. How well they have accomplished this task must be judged by the reader. It is nevertheless encouraging to this former graduate student that there are now more neurobiologists interested in zoology and the nervous system than there were when Percival Bailey momentarily shattered his hopes. This conference was a witness to that fact. To Bailey's everlasting credit, he did not recommend the abandonment of interest in evolutionary comparative neurology. On the contrary, he suggested that a place for this interest had to be made.

C. B. G. Campbell

Preface

The fascination of comparative neurology can be compared to the fascination experienced by those who engage in a search for their individual roots through means of genealogical studies. During a period of almost 100 years, comparative neurologists have been examining animals selected from almost all vertebrate groups in order to understand how brains evolved. The search for an understanding of the neocortical evolution has particularly captivated neurologists because they believed this would lead to a better understanding of the essence of man.

The insights obtained from most neurological studies have always been highly dependent on the technology available. As new techniques for studying brain structures became available, and were applied, more meaningful interpretations were made of the highly varied and confounding brain organizations. About 20 years ago, the development of better methods for tracing neuronal pathways revolutionized a field of exploration that had been dormant for several decades. As a result, a great number of new neuronal pathways have been traced in a broad spectrum of vertebrates. The technological breakthroughs were especially important to those researchers studying the telencephalon. All at once a completely new insight was provided into the evolution of the mammalian cerebral cortex. These data have been complemented with new exciting physiological and behavioral studies.

Recent evidence indicates that the so-called neocortex was probably formed not by an invasion of neuronal systems from caudal levels, as previously thought, but rather by differentiation and proliferation of systems already present in the brains of the earliest vertebrates. The data, at this point in time, are far from complete and provide no real insight into which selective pressures resulted in specific morphological features, although that is no doubt coming.

This book provides a review of some of the most recent data on the telencephalic structure and function in the major vertebrate groups. The focus is on the sensory systems because a great deal of factual information is already available. Other regions, such as the amygdala and the hippocampus, are not dealt with extensively because these systems, in nonmammalian vertebrates, are still not well understood and there is a scarcity of valid data.

One of the most stimulating messages that one receives, as he reads through the pages of this book, is that almost unlimited opportunities exist in comparative neurology for gaining a more complete understanding of how brains work and how each structure evolved.

The Editor

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On The Organization of the Telencephalon in Elasmobranchs

SVEN O. E. EBBESSON

I. Introduction

The interest in brain organization of elasmobranchs relates to the evolutionary history of the group. The best paleontological information suggests an origin in the early Devonian period, some 400 million years ago, or 250 million years before the African and American continents separated. The sharks evolved rapidly in Devonian times and continued their expansion through the Carboniferous and Permian periods. The available data suggest that the group was successful early and that relatively few selective pressures for structural modification have taken place since those early days.

Contrary to common belief only 10 years ago, recent studies have shown that brain organization in sharks is much more "advanced" in terms of connections than hitherto believed, that the brain size-body weight ratio in some sharks exceeds those of other anamniotes, and that some sharks are capable of learning complex visual discriminations rapidly (see Chapter 2 in this volume). These and other findings have revealed our ignorance about brain organizations of elasmobranchs and have provided new insights into brain evolution. Perhaps the most important recent revision of thought relates to the organization and functional role of the forebrain. Whereas the telencephalon has traditionally been considered an "olfactory lobe," recent experiments indicate an organization comparable to that of other vertebrates, including mammals.

This is a brief overview of telencephalic organization as we see it 12 years after the new neuroanatomical methods of Nauta (1957) were first applied to shark