

**BASIC
LIMBIC SYSTEM
ANATOMY OF
THE RAT**

BASIC LIMBIC SYSTEM ANATOMY OF THE RAT

Leonard W. Hamilton

*Rutgers University
New Brunswick, New Jersey*

PLENUM PRESS · NEW YORK AND LONDON

Library of Congress Cataloging in Publication Data

Hamilton, Leonard W

Basic limbic system anatomy of the rat.

Bibliography: p.

Includes index.

1. Limbic system — Anatomy. 2. Rats — Anatomy. I. Title. [DNLM: 1. Limbic system — Anatomy and histology. WL307 H218b]

QL938.L55H35

599'.3233

76-46401

ISBN-13: 978-1-4684-2249-8

e-ISBN-13: 978-1-4684-2247-4

DOI: 10.1007/978-1-4684-2247-4

©1976 Plenum Press, New York

Softcover reprint of the hardcover 1st edition 1976

A Division of Plenum Publishing Corporation
227 West 17th Street, New York, N.Y. 10011

All rights reserved

No part of this book may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, microfilming, recording, or otherwise, without written permission from the Publisher

To Claudia and Erika

*. . . But, as the world, harmoniously confused:
Where order in variety we see,
And where, though all things differ,
all agree.*

– Pope

Preface

If this were a traditional textbook of neuroanatomy, many pages would be devoted to a description of the ascending and descending pathways of the spinal cord and several chapters to the organization of the sensory and motor systems, and, perhaps, a detailed discussion of the neurological deficits that follow various types of damage to the nervous system would also be included. But in the first draft of this book, the spinal cord was mentioned only once (in a figure caption of Chapter 2) in order to illustrate the meaning of longitudinal and cross sections. Later, it was decided that even this cursory treatment of the spinal cord went beyond the scope of this text, and a carrot was substituted as the model. The organization of the sensory and motor systems and of the peripheral nervous system have received similar coverage. Thus, this is not a traditional text, and as a potential reader, you may be led to ask, “What’s in this book for me?”

This book is directed primarily toward those students of behavior who are either bored or frightened by the medically oriented texts that are replete with clinical signs, confusing terminology, and prolix descriptions of the human brain, an organ which is never actually seen in their laboratories. I should hasten to add, however, that this text may also serve some purpose for those who read and perhaps even enjoy the traditional texts. Briefly stated, this book is designed to take the reader step-by-step through the structures and interconnections of the limbic system (broadly defined to include the olfactory system, the hypothalamus, and parts of the cortex and midbrain).

The decision to prepare a textbook of anatomy devoted strictly to the limbic system was spawned by frustration and sustained by hope. The frustration arose from students who had just earned As in their anatomy course but could not tell a septal lesion from the lateral ventricle and did not know whether the fasciculus retroflexus was a type of camera or a part of the cerebellum. Worse still was the discovery that there were no books to which I could refer them that answer their questions. As an illustration, one of the most respected and widely used textbooks of anatomy (Ranson and Clark, 1959) devotes only 11 out of more than 600 pages to the anatomy of the limbic system. Most of the currently available descriptions of the limbic system are available only in technical articles which are at best tedious and at worst incomprehensible to the novice.

The hope that the need for a fundamental textbook could be met arose from a graduate seminar which I developed in an attempt to acquaint the students of our psychobiology program with the essential aspects of the limbic system anatomy. I discovered that with the proper sequence of models, stained sections, and line drawings, it was possible for students to become conversant with the anatomy of the limbic system and to actually begin to make serious use of known anatomical connections in the design of their research projects. The same strategy has been adopted in the format of this text.

In most cases, the system being described is first outlined in general terms with several accompanying photomicrographs to familiarize the reader with the topographical characteristics of the area. The more detailed descriptions of the fiber projections are presented in line drawings that maintain a superficial similarity to the actual structures but are schematically simplified to allow the student to easily redraw them for study purposes. It is strongly suggested that the student reorganize the material in ways other than those presented as an aid to thoroughly understanding the various interconnections. Furthermore, it is suggested that the text be used in conjunction with a photographic atlas such as that of König and Klippel (1967) and, if possible, in conjunction with stained sections of the rat brain.

The references to individual articles are frequently of little direct importance for a general summary of the anatomical connections but become critical for the reader who wants to study a particular system in detail. With this in mind, the number of references within the text have been kept to a minimum and a more complete annotated bibliography for each chapter appears in the appendix.

Lest the reader gain the mistaken impression that I am in basic disagreement with the format of traditional texts, I should point out that the rationale of the present text is quite similar; it represents an attempt to provide a structural framework that will foster a better understanding of function. The major difference is that this text provides a structural framework that is aimed more toward molar behavior rather than to reflexive behavior, sensory systems, etc. During the past three or four decades, experimental studies have demonstrated that the structures of the limbic system play important roles in the mediation of such complex behaviors as feeding and drinking, sexual behavior, emotional behavior, and learning and memory. Accordingly, it has become increasingly important for those who are interested in these behaviors to have a concise description of the anatomy of the limbic system. This text is intended to provide such a description. Owing to the fact that virtually all of the behavioral experimentation being carried out has utilized the rat as a subject, this text is restricted almost exclusively to the rat brain. Although it would be desirable to provide a detailed treatment of the known functional relationships, the volume of such a treatment would likely conceal the anatomy without, I fear, shedding too much light. The last chapter, however, is devoted to a brief summary of functions to at least introduce the reader to the relevant literature.

It is an unfortunate fact that anatomical terminology and interconnections are sometimes difficult to learn and always easy to forget. One of the major reasons for this is the terminology. There are frequently multiple names for the same structure as well as multiple opinions as to what constitutes a particular structure. Consequently, there have been attempts to standardize the nomenclature (e.g., International Anatomical Nomenclature Committee). Unfortunately, the resulting standardized terminology is tedious and not

in common usage. I have often pointed out to students that the drawings in the König and Klippel (1967) atlas provide an excellent study guide because it is easier to learn to recognize the structures than it is to learn the abbreviations of the Latin terminology. This is quite appropriate for an atlas, but it is probably not the best way to be introduced to an anatomical system. For more than a decade, I have been engaged in research projects involving the septal region, and I have yet to hear a colleague refer to the nucleus septi lateralis. This structure is, quite simply, the lateral septum. In view of this chasm between the appropriate terminology and that which is in common usage, I have chosen to use the more readily understood anglicized terminology at the risk of occasionally oversimplifying. Once the major structures have been learned, the need for more detailed terminology and subtle distinctions of substructures will be more readily appreciated. By the time the student has reached this level of sophistication, it will be a relatively simple matter to supplement this basic knowledge via the more precise experimental literature.

Finally, I should point out that I am not now, have never been, and almost certainly never will be a neuroanatomist. I am a biopsychologist with an almost insatiable desire to determine relationships between the brain and behavior. In most cases, I use anatomical manipulations in an attempt to learn something about behavior. In other cases, I use behavioral approaches to learn something about anatomy. Because of my bias toward the behavioral aspects, I may sometimes oversimplify or even overlook some of the nuances of anatomical connections. Hopefully, these shortcomings will be outweighed by my being able to present an understandable, yet fairly complete account of the anatomical systems that are of especial interest to behavioral researchers.

LEONARD W. HAMILTON

Acknowledgments

This book did not arise from any specific suggestion, nor was it the fulfillment of some long-term ambition. It is rather a spontaneous development of two forces that exert more control over my life than I sometimes care to admit: One of these is the inexplicable lure of trying to understand the brain and behavior; the other is my unabashed eagerness to teach others what little is known about this topic. Accordingly, I am indebted to those who have contributed to these forces.

The initial kindling of my interests in the neurosciences is easy to pinpoint. It was Professor S. P. Grossman's undergraduate course in physiological psychology at the University of Iowa. I am grateful not only for this initial exposure, but also for his patient guidance of my graduate training at the University of Chicago. He afforded me the opportunity to learn that research is fun.

I am also grateful to the students who have worked in my laboratory at Rutgers University, sharing the labors of my joys. In particular, Sal Capobianco, Tom Schoenfeld, Robin Timmons, Fred vom Saal, and Liz Worsham have contributed their energies, their ideas, and their enthusiasm to the research that indirectly led to the writing of this text. I am especially grateful to Robin Timmons for the numerous ideas relating to style, format, and organization that have improved the quality of communication in this text.

Throughout the years, my research projects have been supported by the U.S. Public Health Service, the Rutgers Research Council, Biological Sciences Support Grants, and, most recently, the Weight Watchers Foundation, Inc.

An author is always indebted to a typist who can turn a rough copy into flawless black and white. This is especially true if the manuscript contains strange vocabulary and is constantly interrupted by figures and italicizing. My appreciation goes to Libby Brusca.

Finally, I am grateful to my wife, Claudia, for her understanding of my commitments to the laboratory, and to my daughter, Erika, for the laughter in her eyes. It would be dishonest to say that the preparation of this book resulted in lost evenings, weekends, and vacations. These were, in fact, lost, but, in the absence of this project, they would as likely have been lost to other manuscripts or other experiments.

L.W.H.

Contents

1	A BRIEF HISTORY OF THE STUDY OF NEUROANATOMY .	1
	The Early Anatomists	1
	Twentieth Century Advances	3
	Theoretical Approaches	5
	The Scope of This Volume	6
2	NEUROANATOMICAL PROCEDURES AND TERMINOLOGY	7
	Introduction	7
	Neuroanatomical Procedures	8
	Gross Observation	9
	Microscopic Observation	10
	Cell Body Stains	10
	The Golgi Stain	10
	The Cresylviolet Stain	11
	Fiber Stains	12
	Luxol Blue	12
	Iron Hematoxylin	12
	Silver Stains	12
	Specialized Fiber Stains	13
	Stains for Degenerating Fibers	13
	Histochemical Methods	16
	Chemically Specific Stains	16
	Axoplasmic Transport Methods	17
	Electrophysiological Methods	17

	Summary of Anatomical Terms	19
	Terms Defining Spatial Relationships	19
	Terms Defining Planes of Sections	20
	Terms Defining Lateral Positions	20
	Terms Defining Units of the Nervous System	21
	Terms Defining Pathways of Fibers and Impulses	22
3	THE LIMBIC SYSTEM DEFINED	25
	Introduction	25
	Ontogenetic and Phylogenetic Development	27
	Phylogeny	27
	Ontogeny	28
	Some Concluding Remarks	31
4	GENERAL TOPOGRAPHY OF THE LIMBIC SYSTEM	33
	Introduction	33
	The Hippocampus	34
	The Hypothalamus	39
	The Amygdaloid Complex	41
	The Olfactory System	44
	Cortical Structures	46
	Areas Related to the Limbic System	49
	The Thalamus	49
	The Tegmentum	51
5	THE FORNIX SYSTEM AND RELATED HIPPOCAMPAL CONNECTIONS	53
	Introduction	53
	Organizational Criteria	55
	The Dorsal Fornix System	56
	The Fimbrial System	57
	Other Hippocampal Connections	58
	Connections with Entorhinal Cortex	58
	Hippocampal Association Connections	59
	Hippocampal Commissures	59
	Summary	62

6	CONNECTIONS OF THE STRIA MEDULLARIS AND HABENULAE	63
	Introduction	63
	The Septal Contribution	63
	The Preoptic Contribution	65
	The Thalamic Contribution	67
	The Amygdaloid Contribution	68
	The Contribution of the Interpeduncular Nucleus	69
	Projections from the Medial Habenula	69
	Projections from the Lateral Habenula	70
	Summary	72
7	THE STRIA TERMINALIS, THE VENTRAL AMYGDALOID PATHWAYS, AND RELATED AMYGDALOID CONNECTIONS	73
	Introduction	73
	Dorsal Component of Stria Terminalis	75
	Ventral Component of Stria Terminalis	76
	The Ventral Amygdalofugal Pathway	77
	Olfactory Connections	77
	Summary	78
8	THE MEDIAL FOREBRAIN BUNDLE AND RELATED HYPOTHALAMIC CONNECTIONS	79
	Introduction	79
	Descending Fibers of the Medial Forebrain Bundle	81
	Ascending Component of the Medial Forebrain Bundle	84
	Summary	85
9	THE LATERAL OLFACTORY TRACT, THE ANTERIOR COMMISSURE, AND OTHER OLFACTORY CONNECTIONS	87
	Introduction	87
	Olfactory Reception	87
	The Central Olfactory Connections	90
	The Anterior Commissure	90
	The Lateral Olfactory Tract	91

	The Vomeronasal System	92
	Summary	92
10	CORTICAL EXTENSIONS OF THE LIMBIC SYSTEM	95
	Introduction	95
	Cingulate Cortex	95
	Topography	95
	Connections of the Cingulate Cortex	96
	Frontal Cortex	97
	Topography	97
	Connections of the Frontal Cortex	99
	The Entorhinal Cortex	100
	Topography	100
	Connections of the Entorhinal Cortex	101
	The Piriform Cortex	103
	Summary	103
11	HISTOCHEMICAL MAPPING OF THE LIMBIC SYSTEM	105
	Introduction	105
	Monoamines	106
	The Noradrenergic System	107
	The Serotonergic System	109
	The Dopaminergic System	110
	The Nigrostriatal System	110
	The Ventral Dopaminergic Bundle	111
	The Acetylcholine Systems	111
	Summary	114
12	SOME FUNDAMENTAL APPROACHES TO AN ANALYSIS OF LIMBIC SYSTEM FUNCTION	117
	Introduction	117
	The Structure–Function Problem	119
	Anatomical Specificity	120
	Behavioral Specificity	121
	Combining Anatomical and Behavioral Specificity	122

Pharmacological Approaches	123
Drugs That Mimic or Enhance Neurotransmitter Action ...	124
Drugs That Block or Deplete the Neurotransmitter	124
Specificity of Action	125
Phylogenetic Approaches	125
Ontogenetic Approaches	126
Conclusions	127

APPENDIX: A BIBLIOGRAPHIC GUIDE TO FURTHER STUDY
OF THE LIMBIC SYSTEM

129

Part I: References Pertaining to Individual Chapters	129
Chapter 1. A Brief History of the Study of Neuroanatomy	129
Chapter 2. Neuroanatomical Procedures and Terminology	130
Chapter 3. The Limbic System Defined	132
Chapter 4. General Topography of the Limbic System ...	134
Chapter 5. The Fornix System and Related Hippocampal Connections	135
Chapter 6. Connections of the Stria Medullaris and Habenulae	136
Chapter 7. The Stria Terminalis and Ventral Amygdaloid Pathways, and Related Amygdaloid Connections	136
Chapter 8. The Medial Forebrain Bundle and Related Hypothalamic Connections	137
Chapter 9. The Lateral Olfactory Tract, the Anterior Commissure, and Other Olfactory Connections	138
Chapter 10. Cortical Extensions of the Limbic System ...	139
Chapter 11. Histochemical Mapping of the Limbic System	139
Chapter 12. Some Fundamental Approaches to an Analysis of Limbic System Function	141
Part II: Reference Sources	143
Rat Brain Atlases	143
Textbooks of Neuroanatomy	144
Technical Journals	144

AUTHOR INDEX	145
STRUCTURE INDEX	147