



# **Brain Structure and Its Origins**

in Development and in Evolution of Behavior and the Mind

**Gerald E. Schneider**

## Brain Structure and Its Origins



# **Brain Structure and Its Origins**

**in Development and in Evolution of Behavior and the Mind**

**Gerald E. Schneider**

The MIT Press  
Cambridge, Massachusetts  
London, England

© 2014 Massachusetts Institute of Technology

All rights reserved. No part of this book may be reproduced in any form by any electronic or mechanical means (including photocopying, recording, or information storage and retrieval) without permission in writing from the publisher.

MIT Press books may be purchased at special quantity discounts for business or sales promotional use. For information, please email [special\\_sales@mitpress.mit.edu](mailto:special_sales@mitpress.mit.edu).

This book was set in Syntax LT Std and Times Ten LT Std by Toppan Best-set Premedia Limited, Hong Kong. Printed and bound in the United States of America.

Library of Congress Cataloging-in-Publication Data

Schneider, Gerald E.

Brain structure and its origins : in development and in evolution of behavior and the mind / Gerald E. Schneider.

pages cm

Includes bibliographical references and index.

ISBN 978-0-262-02673-4 (hardcover : alk. paper) 1. Brain. 2. Brain—Evolution. I. Title.

QP376.S348 2014

612.8'2—cd23

2013023059

10 9 8 7 6 5 4 3 2 1

This book is dedicated to the memory of my mother and father and my youngest sister, Linda Jean. Their enthusiastic support is always with me.



# Contents

Detailed contents	xi
Preface	xxiii

## **PART I: INTRODUCTORY ORIENTATION 1**

- 1 Getting Ready for a Brain Structure Primer 3**
- 2 Methods for Mapping Pathways and Interconnections That Enable the Integrative Activity of the CNS 29**

## **PART II: THE CENTRAL NERVOUS SYSTEM, FROM INITIAL STEPS TO ADVANCED CHORDATES 53**

- 3 Evolution of Multicellular Organisms with Neuron-Based Coordination 55**
- 4 Expansions of the Neuronal Apparatus of Success 67**

## **PART III: INTRODUCTION TO CONNECTION PATTERNS AND SPECIALIZATIONS IN THE EVOLVING CNS 87**

- 5 The Ancestors of Mammals: Sketch of a Pre-mammalian Brain 89**
- 6 Some Specializations Involving Head Receptors and Brain Expansions 107**
- 7 The Components of the Forebrain Including the Specialty of the Mammals: The Neocortex 117**

## **PART IV: DEVELOPMENT AND DIFFERENTIATION: SPINAL LEVEL 137**

- 8 The Neural Tube Forms in the Embryo, and CNS Development Begins 139**
- 9 The Lower Levels of Background Support: Spinal Cord and the Innervation of the Viscera 153**
- Intermission: The Ventricular System, the Meninges, and the Glial Cells 175**



<b>PART V: DIFFERENTIATION OF THE BRAIN VESICLES</b>	<b>179</b>
10 Hindbrain Organization, Specializations, and Distortions	181
11 Why a Midbrain? Notes on Evolution, Structure, and Functions	205
12 Picturing the Forebrain with a Focus on Mammals	217
13 Growth of the Great Networks of Nervous Systems	235
<b>PART VI: A BRIEF STUDY OF MOTOR SYSTEMS</b>	<b>263</b>
14 Overview of Motor System Structure	265
15 Descending Pathways and Evolution	283
16 The Temporal Patterns of Movements	299
<b>PART VII: BRAIN STATES</b>	<b>309</b>
17 Widespread Changes in Brain State	311
<b>PART VIII: SENSORY SYSTEMS</b>	<b>323</b>
18 Taste	325
19 Olfaction	333
20 Visual Systems: Origins and Functions	355
21 Visual Systems: The Retinal Projections	371
22 The Visual Endbrain Structures	393
23 Auditory Systems	417
<b>PART IX: THE FOREBRAIN AND ITS ADAPTIVE PRIZES: A SNAPSHOT</b>	<b>447</b>
24 Forebrain Origins: From Primitive Appendage to Modern Dominance	449
<b>PART X: THE HYPOTHALAMUS AND LIMBIC SYSTEM</b>	<b>465</b>
25 Regulating the Internal Milieu and the Basic Instincts	467
26 Core Pathways of the Limbic System, with Memory for Meaningful Places	483
27 Hormones and the Shaping of Brain Structures	501
28 The Medial Pallium Becomes the Hippocampus	513
29 The Limbic Striatum and Its Outpost in the Temporal Lobe	537

**PART XI: CORPUS STRIATUM 559**

- 30 The Major Subpallial Structure of the Endbrain 561
- 31 Lost Dopamine Axons: Consequences and Remedies 583
  - Intermission: Neurogenesis in Mature Brains 589

**PART XII: THE CROWN OF THE MAMMALIAN CNS: THE NEOCORTEX 593**

- 32 Structural Origins of Object Cognition, Place Cognition, Dexterity, and Planning 595
- 33 Basic Neocortical Organization: Cells, Modules, and Connections 617
- 34 Structural Change in Development and in Maturity 645

Figure Credits 669

Index 679



# Detailed Contents

Preface xxiii

## **PART I: INTRODUCTORY ORIENTATION 1**

### **1 Getting Ready for a Brain Structure Primer 3**

- The Nature of This Book 3
- Brain Space: Specifying Directions and Major Regions 5
- CNS Tissue 9
- Primitive Cellular Mechanisms 12
- Irritability and Conduction 13
- The Specialized Membrane of the Axon 15
- Specializations for Irritability 19
- Movement 19
- Secretion 20
- Synaptic Morphology and Types 21
- Related Cellular Dynamics 23
- Parallel Channels of Information Flow and Integrative Activity 25
- Endogenous Activity 25
- Readings 27

### **2 Methods for Mapping Pathways and Interconnections That Enable the Integrative Activity of the CNS 29**

- Histology and Brain Architecture 29
- What Is Connected to What? 35
- Tracing a Pathway from Sensory Input to the Response (S to R) 38
- Pathways Seen as Bundles and Ribbons of Fibers 41
- Experimental Studies Needed to Trace Connections in the Brain 41
- Experimental Neuroanatomy: Tract-Tracing Methods 42
- Readings 51

## **PART II: THE CENTRAL NERVOUS SYSTEM, FROM INITIAL STEPS TO ADVANCED CHORDATES 53**

### **3 Evolution of Multicellular Organisms with Neuron-Based Coordination 55**

- Basic Survival Skills 55
- The First Neurons and Nerve Networks 56
- The Nervous System in Basic Concept 58
- Some Terminology for Brain Talk 59
- Introducing the Simplest Chordates 60
- Natural Selection and the Logic of Evolution 63
- The Behavioral Demands That Changed the Neural Tube 63
- Readings 65

### **4 Expansions of the Neuronal Apparatus of Success 67**

- Why We Can Talk about Broad Aspects of Brain Evolution with Some Confidence 67
- Three Enlargements Formed the Primitive Brain 67
- Expansions of the Hindbrain 69
- Early Forebrain Expansion Served Olfactory Functions 72
- Midbrain Expansions, Distance Receptors, and Decussations 75
- A Second Expansion of the Forebrain with Invasion of Non-olfactory Inputs 77
- Concurrent Evolutionary Changes: Motor Control and Plasticity 79
- Concurrent Evolutionary Changes: Motivational States 80
- A Third Expansion of the Forebrain: Anticipating Events and Planning Actions 81
- Brain Sizes Relative to Body Weight Compared for Present-Day Animals 81
- Where We Stand in the Path to Our Goal 83
- Readings 84

## **PART III: INTRODUCTION TO CONNECTION PATTERNS AND SPECIALIZATIONS IN THE EVOLVING CNS 87**

### **5 The Ancestors of Mammals: Sketch of a Pre-mammalian Brain 89**

- The "Old Chassis" for the Building of Further Additions 90
- Subdividing the CNS 94
- The Basic Setup: Major Types of Neurons 96
- Sensory Channels of Conduction: Local Reflex, and Not so Local 97
- Old Ribbons to the Brain 101
- Ribbons to the Little Brain: The Cerebellum 103
- Readings 106

### **6 Some Specializations Involving Head Receptors and Brain Expansions 107**

- Electroreception and the Cerebellum 107
- Infrared Sensors in Pit Vipers 109
- Echolocation and the Auditory System 110
- The Visual Systems of Primates 111
- Whisker Fields and Barrel Fields 111
- Other Behavioral Specializations with Corresponding Enlargements of Brain Parts 112
- Readings 116

## **7 The Components of the Forebrain Including the Specialty of the Mammals: The Neocortex 117**

Forebrain Removal Experiments	117
Cat Behavior after Forebrain Removal	117
Rat Behavior Is Less Drastically Affected by Forebrain Removal	118
Pigeons after Forebrain Removal, Sparing the Optic Tracts	119
Forebrain Function: A Conclusion	120
The Problem of Species Differences in Brain Lesion Effects	120
The Phenomena of Diaschisis: An Answer to the Problem	120
What Can We Conclude about Interpreting Effects of Brain Lesions?	123
Role of the Corpus Striatum	123
The Rostral End of the Brainstem Located between the Hemispheres ('Tweenbrain)	124
Limbic System of the Forebrain	125
Olfactory System Origins of Major Functions of the Limbic Endbrain	126
Overview of the Roles of Corpus Striatum and Limbic Forebrain	128
Neocortex, the Grand Innovation of the Mammals: Appearance of New Pathways	128
But What Does It Do? Why Did Neocortex Evolve?	134
Taking Stock	134
Readings	135

## **PART IV: DEVELOPMENT AND DIFFERENTIATION: SPINAL LEVEL 137**

### **8 The Neural Tube Forms in the Embryo, and CNS Development Begins 139**

Before There Is Any CNS	139
The Onset of a Nervous System	140
Molecules from the Notochord Induce the Formation of the Nervous System	141
The Neural Crest Gives Rise to the PNS	142
Cell Proliferation in the Early Neural Tube	143
Diversity in Neuronal Migration	145
Differentiation of the Neurons Begins	149
Notes	150
Readings	150

### **9 The Lower Levels of Background Support: Spinal Cord and the Innervation of the Viscera 153**

Major Features of Cord Structure	153
Questions from Comparing Different Species	156
The Local Reflex Channel and the Older Lemniscal Channels	158
The Mammalian Highway for Ascending Somatosensory Information	161
Cerebellar Channel	162
The Pathways of Regulation within the Spinal Cord Itself	163
The Pathways of Influence and Control from the Brain	164
A Reminder	165
Maintaining Stability of the Internal Environment: The Autonomic Nervous System	166
Three Major Divisions of the Motor System	166
A Sketch of the Autonomic Nervous System	167
Chemical Mediation at Autonomic Nervous System Synapses	171

The Enteric Nervous System	171
Levels of Control of the Internal Environment	173
Readings	173

### **Intermission: The Ventricular System, the Meninges, and the Glial Cells 175**

Readings	178
----------	-----

## **PART V: DIFFERENTIATION OF THE BRAIN VESICLES 179**

### **10 Hindbrain Organization, Specializations, and Distortions 181**

A Glamorized Spinal Cord	181
Vital Functions of the Hindbrain	183
Routine Maintenance Services	184
Hindbrain Participation in Mammalian Higher Functions	184
The Isodendritic Core of the Brainstem	185
Segmentation of the Hindbrain	186
Columns and Cranial Nerves	188
The Adult Hindbrain: Cell Groups and Axons of Passage	192
Somatosensory Inputs from the Face	193
The Evolution of Crossed Projections	194
Hindbrain Sensory Channels in Mammals	197
Hindbrain Specializations and Mosaic Evolution	199
Readings	204

### **11 Why a Midbrain? Notes on Evolution, Structure, and Functions 205**

Primitive Vision	206
Primitive Olfaction	206
A Structural Consequence of the Priority of Escape Behavior for Survival	207
The Midbrain Correlation Centers	208
Outputs of Midbrain for Motor Control	210
Mosaic Evolution of Midbrain	212
Long Axons Passing through the Midbrain	212
Readings	216

### **12 Picturing the Forebrain with a Focus on Mammals 217**

Pictures of Ancestral and Modern Endbrain	218
Words for Forebrain Parts	220
Major Structural and Functional Subdivisions of the 'Tweenbrain	220
Major Parts of the Telencephalon of Mammals	222
Origins and Course of Two Major Pathways of the Forebrain	222
The Neocortex Is Involved in Both Major Systems	224
Interim Review of Neuroanatomy	226
Segmentation of the Forebrain	227
Notes on Neocortical Origins	227
Readings	232

<b>13</b>	<b>Growth of the Great Networks of Nervous Systems</b>	<b>235</b>
	The Axonal Growth Cone	235
	Signals That Shape the Development of Neuronal Circuits	239
	Four Types of Chemical Guidance	244
	Two Modes of Axon Growth	247
	Formation of Maps in the Brain	247
	Plasticity in Brain Maps	249
	More Plasticity in the CNS: Collateral Sprouting	252
	Modulation of Competitive Axonal Growth Vigor	255
	Rules of Sprouting Apply to Development, with Implications for Evolutionary Change	256
	Plasticity in the Small Interneurons of the Adult Brain	256
	Structural Regression during Development and Its Purposes	257
	Axon Loss in the Damaged CNS: Is Regeneration Possible?	258
	Readings	259
	<b>PART VI: A BRIEF STUDY OF MOTOR SYSTEMS</b>	<b>263</b>
<b>14</b>	<b>Overview of Motor System Structure</b>	<b>265</b>
	A Functional Starting Point for the Study: Three Major Types of Movement Critical for Survival	265
	Midbrain Control of the Three Types of General-Purpose Movement	266
	The Midbrain Was the Connecting Link between the Primitive Forebrain and Motor Systems	267
	Head Receptors and Locomotor Approach and Avoidance	268
	Initiation of Foraging by Activity Intrinsic to the Brain	268
	The Motor System Hierarchy	269
	Locomotor Pattern Generation and Its Adjustments by Vestibular and Cerebellar Systems	269
	Orienting of Head and Body	272
	Grasping: The Third Major Type of Movement Controlled by the Midbrain	275
	Comparative Anatomy of the Red Nucleus and Its Projection to the Spinal Cord	275
	A Structural Approach to Understanding Motor Control: Begin with the Motor Neurons	277
	The Spatial Arrangements of Somatic Motor Neurons in the Spinal Cord	278
	Readings	281
<b>15</b>	<b>Descending Pathways and Evolution</b>	<b>283</b>
	Axons Descending from Brain to Spinal Cord: Functional Groupings	283
	Functions of the Descending Pathways: The Corticospinal Tract	286
	Functions of the Descending Pathways: The Medial Hindbrain Tracks	287
	Functions of the Descending Pathways: The Lateral Brainstem Tracks	287
	A Conclusion with Application to Humans	289
	The Brain Disconnected from the Motor Pattern Generators	289
	Importance of the Corticospinal Tract for Innate and Learned Movements That Require Special Dexterity	290
	The Nature of the Spinal Motor Pattern Generators	291
	Motor Cortex in Phylogeny	291
	Corticospinal Projections in Phylogeny	293
	The Highest Levels of Motor Control	296
	Readings	296



**16 The Temporal Patterns of Movements 299**

- Three Types of Mechanism 299
- Explaining Movement Dynamics in Terms of S-R Circuits 300
- Central Programs Rather than Reflex Chaining 302
- Many Fixed Action Patterns Are Centrally Generated 302
- Reverberating Circuits within the Brain and Spinal Cord 303
- Endogenous Activity of Single CNS Neurons 304
- The Endogenous Clock 304
- How It All Works at the Circuit Level 305
- The Circuits Are Not Always Fixed 305
- How Adequate Are These Concepts? 306
- Readings 306

**PART VII: BRAIN STATES 309****17 Widespread Changes in Brain State 311**

- Brain States Influenced by Widely Projecting Axon Systems 311
- Cholinergic Systems 312
- The Monoamine-Containing Systems 313
- Serotonin, Another Monoamine Neurotransmitter Influencing Behavioral State 315
- Diencephalic Origins of Other Widely Projecting Axon Systems 316
- How Many Different Brain States? 318
- Readings 320

**PART VIII: SENSORY SYSTEMS 323****18 Taste 325**

- Pre-chordate Taste and Other Chemoreceptor Systems 325
- Olfaction or Taste? 326
- Visceral and Taste Inputs to the Hindbrain 326
- Innervation of the Tongue 327
- Distribution of Mammalian Taste Receptors 327
- From Tongue to Telencephalon 328
- Purposes of Taste: Routes to Motor Control 330
- Readings 331

**19 Olfaction 333**

- Sections through the Forebrain of Vertebrates 333
- Olfactory Bulb Projections in Primitive Vertebrates 336
- Variations in Relative Size of Olfactory Systems 338
- Olfactory Bulb Projections in Mammals 339
- Human and Small Mammalian Brains 341
- Neuronal Organization as Depicted by Ramón y Cajal 341
- The Axons of the Lateral Olfactory Tract 344
- Overview 346

Spatial Organization of the Primary Sensory Neurons	347
Beyond the Mitral Cells	349
Ongoing Plasticity in the Olfactory Bulb by Cell Turnover	350
Olfaction and Behavior	351
Readings	352

## 20 Visual Systems: Origins and Functions 355

Origins of Vision, 1: Light Detection	356
Origins of Vision, 2: Image Formation	358
Predator Avoidance and Escape: A Hypothesis Concerning Evolution and the Origins of Crossed Projections	359
Orienting Toward or Around Visually Detected Objects and Other Responses	361
The Midbrain Tectum and Orienting Toward Novel Objects, Food, or Potential Mates or Rivals	363
Identifying Animals, Objects and Textures	364
The Invasion of the Endbrain by Visual Pathways: Likely Evolutionary Steps in Pre-mammalian and Mammalian Ancestors	365
More about the Third Role of Visual Images	366
Expansions and Specializations in the Visual System	367
Readings	369

## 21 Visual Systems: The Retinal Projections 371

Two Views of the Optic Tract and Its Terminations	371
Distortions in Large Primates	374
How the Optic Tract Looks in the Brain of an Adult Animal	375
Looking at the Exposed Brain from Above	380
The Embryonic Optic Tract	381
Midbrain Tectum: Species Differences	384
Lamination of the Midbrain Tectum	385
Topographic Organization of the Retinal Projection to the Midbrain Surface	385
Notes	391
Readings	392

## 22 The Visual Endbrain Structures 393

Multiple Routes from Retina to the Endbrain	393
The Visual System's Two Major Routes to the Endbrain in Phylogeny	395
The Route through the Lateral Geniculate Body	397
Early Myelination of the Optic Radiations	399
The Brain and Neocortex in Human Development and in Phylogeny	399
Evolutionary Multiplications of Cortical Representations of the Retina	404
Comparing Species: Evidence for Older and Newer Visual Cortical Areas	407
And Where Do We Go from Here?	407
Transcortical Pathways from Visual Cortex	409
Three Visual Pathways and Their Functions	411
The Third Major Transcortical Pathway	412
Comments on Transcortical Interconnections	414
Readings	415

<b>23</b>	<b>Auditory Systems</b>	<b>417</b>
	Embryonic Placodes Give Rise to Auditory and Vestibular Nerves	417
	The Auditory Pathway (in Brief)	418
	Some Special Functions of the Auditory System: Antipredator Behaviors	418
	Aversiveness of Noise and the Role of the Limbic System	419
	Learned Fear: Importance of the Forebrain	420
	Predation Had Other Requirements: Identifying and Localizing Prey Animals	421
	Transformations of Sound Vibrations in Middle Ear and Cochlea	423
	Evolution of Jaw Bones of Ancestral Reptiles into the Ossicles of the Middle Ear in Mammals	424
	Mammalian Ear Structures and Dynamics	425
	Initial Coding of Information	426
	The Flow of Auditory Information in the CNS	428
	Terminations of the Auditory Nerve	428
	Thalamic Projections Carry Auditory Information to the Limbic System and to Neocortex	430
	Review: Multiple Routes Carrying Auditory Information to the Forebrain	430
	Distinct Pathways for Two Major Functions: Orienting and Identification	431
	Location Specificity Arises in Cells of the Hindbrain's Trapezoid Body	431
	How Direction Can Be Derived from Precise Time-of-Arrival at the Two Ears	432
	A Second Hindbrain Mechanism for Sound Localization	434
	How Did This Spatial Localization Apparatus of the Hindbrain Evolve?	434
	Judging a Sound's Direction in the Vertical Axis	434
	Location Information Reaches the Midbrain's Superior Colliculus	434
	Location Information Also Reaches the Endbrain	435
	The Second Function of Ascending Auditory Pathways: Pattern Identification	435
	Temporal Pattern Selectivity: Examples	438
	Functionally Distinct Auditory Pathways in the Neocortex	440
	Auditory System Specializations	442
	Readings	445

## **PART IX: THE FOREBRAIN AND ITS ADAPTIVE PRIZES: A SNAPSHOT 447**

<b>24</b>	<b>Forebrain Origins: From Primitive Appendage to Modern Dominance</b>	<b>449</b>
	Life without a Forebrain	449
	In Search of Ideas about Origins: Primitive Forebrains	450
	Brain Expansions in the Vertebrates	452
	More about the Early Forebrain	456
	The Scene Is Set for the Early Expansion of the Striatum	456
	Another Kind of Plasticity in the Primitive Endbrain	457
	Parallel Evolution of Pallium and Subpallium	459
	Visualizing the Early Striatum and Pallium	460
	Next Steps into the Forebrain	463
	Readings	463

**PART X: THE HYPOTHALAMUS AND LIMBIC SYSTEM 465**

- 25 Regulating the Internal Milieu and the Basic Instincts 467**
- Nature of the Hypothalamus and Affiliated Structures: The Limbic System 467
  - Approaching the Limbic System from Below: Two Kinds of Arousal from the Midbrain 468
  - Autonomic and Endocrine Functions of the Hypothalamus 470
  - Homeostatic Regulation of the Internal Milieu 472
  - Regulation of Cyclic and Episodic Behaviors 473
  - The Center of Motivational State Control 474
  - Distinguishing between Appetitive and Consummatory Behaviors Involved in a Drive 474
  - Computational Neuroethology 475
  - Hunger, Feeding, and Brain Circuits 476
  - Electrically Elicited Drive States 476
  - Connections with Other Systems 478
  - Drive and Reward Involve Distinct Axon Populations in the Medial Forebrain Bundle 479
  - Readings 479
- 26 Core Pathways of the Limbic System, with Memory for Meaningful Places 483**
- Cell Groups in the Hypothalamus 483
  - Feedback from Visceral Afferents and from Blood Chemistry 484
  - Limbic System Interconnections within the Forebrain: The Circuit of Papez 486
  - Why the Revival of Interest in This Circuit? 490
  - Visualizing the Circuit of Papez 490
  - What Is the Functional Significance of the Return Pathway? 492
  - Place Memories in the Neuronal Pathways of Feeling and Emotion 493
  - Review of Structures in the Limbic System 493
  - A Variety of Ways the Hypothalamus Sends Its Influences to the Neocortex 494
  - Mental State and the Hypothalamus 497
  - Influence of the Hypothalamus on the Brainstem and Spinal Cord 497
  - Review 498
  - Functional Specificity in the Limbic Midbrain 498
  - Readings 499
- 27 Hormones and the Shaping of Brain Structures 501**
- Sex Differences in the Human CNS: Evidence from Pathologies 502
  - What Determines an Individual's Sexual Orientation? 502
  - Hormone Peaks and Brain Differentiation 503
  - More Sex Differences in the CNS 504
  - Sexual Dimorphism Underlying Singing in the Canary and Other Songbirds 506
  - "A Brain for All Seasons" 507
  - How Many More Sex Differences in the Brain Will Be Found? 508
  - Back to the Anatomy of the Limbic System 510
  - Readings 511