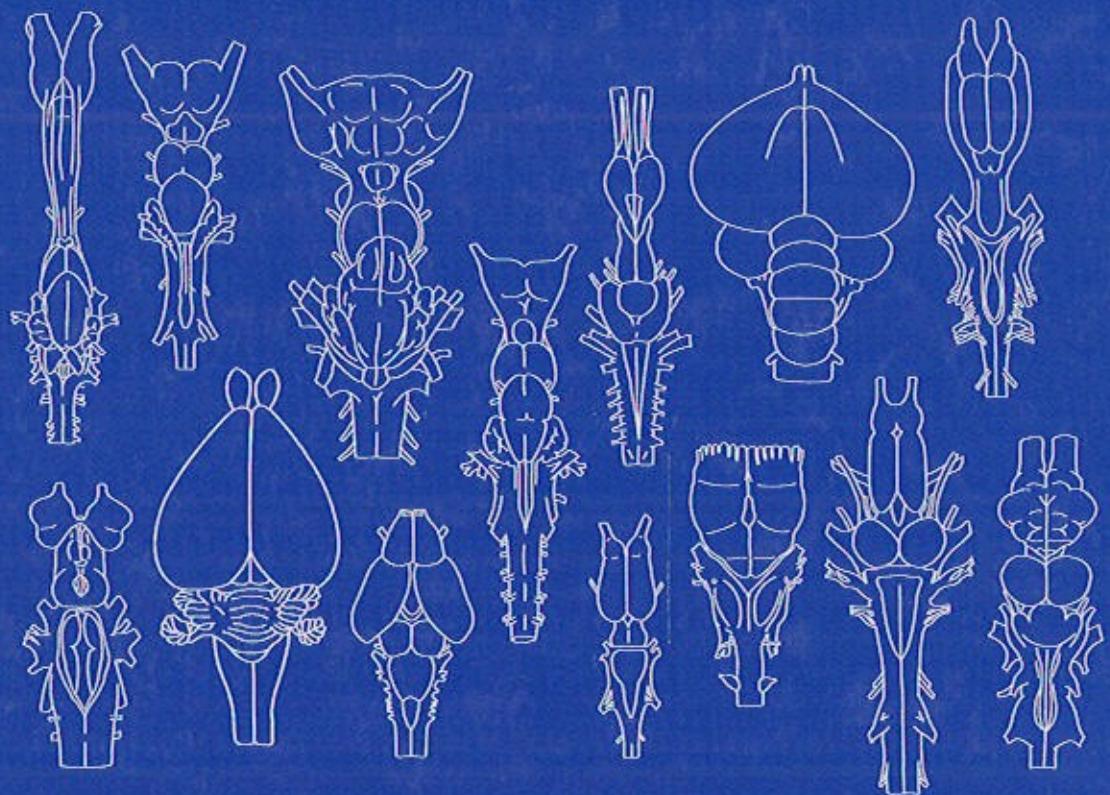


 WILEY



SECOND EDITION

**COMPARATIVE
VERTEBRATE
NEUROANATOMY**

Evolution and Adaptation

ANN B. BUTLER • WILLIAM HODOS

Contents

Preface	xv	Dendrites, 21																														
Acknowledgments	xix	Axons, 23																														
List of Boxes	xxi	Synapses, 23																														
Part One																																
EVOLUTION AND THE ORGANIZATION OF THE CENTRAL NERVOUS SYSTEM																																
1 Evolution and Variation	3	Chemical Synapses, 23																														
Introduction, 3		Neuroactive Substances, 24																														
Diversity Over Time, 4		Electrical Synapses, 26																														
Evolutionary Mechanisms, 5		Volume Transmission, 26																														
Genetic Factors, 5		Neuronal Populations, 26																														
Natural Selection, 5		Golgi Type I and II Cells, 26																														
Evolution of the Vertebrate Central Nervous System, 7		Nuclei and Planes of Section, 27																														
Sameness and Its Biological Significance, 8		Techniques for Tracing Connections Between Nuclei, 27																														
Analogy, 8		Receptors and Senses, 28																														
Historical Homology, 8		How Many Senses? 29																														
Homoplasy, 9		Receptors and Awareness, 29																														
Biological Homology, 11		Sensory Experience as a Private Mental Event, 30																														
Generative Homology or Syngeny, 12		Sensory Adaptation, 30																														
Analysis of Variation, 13		Receptor Types, 30																														
Cladistic Analysis, 13		Mechanoreceptors, 31																														
Parsimony, 14		Radiant-Energy Receptors, 34																														
Tests of Homology, 15		Chemoreceptors, 37																														
A Word of Caution, 15		Nervus Terminalis: An Unclassified Receptor, 41																														
Reconstructing Evolution, 16		Electroreceptors, 41																														
2 Neurons and Sensory Receptors	19	Nociceptors, 42		Nociceptors, 42	Magnetoreceptors, 43		Magnetoreceptors, 43	Topographic Organization, 43		Topographic Organization, 43	Receptive Fields, 46		Receptive Fields, 46	The Senses and Evolution of the Central Nervous System, 46		The Senses and Evolution of the Central Nervous System, 46	3 The Vertebrate Central Nervous System	49	Introduction, 49		Development of the Brain, 49		Segmental Development of the Vertebrate Brain, 50		Neurogenesis and Migration of Neurons, 54		Cortices and Nuclei, 55		Differing Patterns of Development, 57		Ontogeny and Recapitulation, 60	
Nociceptors, 42		Nociceptors, 42																														
Magnetoreceptors, 43		Magnetoreceptors, 43																														
Topographic Organization, 43		Topographic Organization, 43																														
Receptive Fields, 46		Receptive Fields, 46																														
The Senses and Evolution of the Central Nervous System, 46		The Senses and Evolution of the Central Nervous System, 46																														
3 The Vertebrate Central Nervous System	49																															
Introduction, 49																																
Development of the Brain, 49																																
Segmental Development of the Vertebrate Brain, 50																																
Neurogenesis and Migration of Neurons, 54																																
Cortices and Nuclei, 55																																
Differing Patterns of Development, 57																																
Ontogeny and Recapitulation, 60																																

The Brain and Spinal Cord, 61		Previous Theories of Vertebrate Brain Evolution: Addition of Structures or Areas, 114
Cellular Organization of the Central Nervous System, 61		MacLean, 114
Regional Organization of the Nervous System, 63		Flechsig and Campbell, 114
The Spinal Cord, 63		Sanides, 115
The Brain, 63		Previous Theories of Vertebrate Brain Organization: New Formation and Reorganization of Circuits, 115
The Meninges and the Ventricular System, 66		Herrick, 115
Major Systems of the Brain, 67		Bishop, 115
Sensory Systems, 68		Ariëns Kappers, 115
Motor Systems, 68		Bowsher, 115
Nomenclature of the Brain, 69		Diamond and Hall, 116
4 Vertebrate Phylogeny and Diversity in Brain Organization	73	Critique of Previous Theories of Vertebrate Brain Evolution, 116
Introduction, 73		Parcellation Theory, 117
Vertebrate Phylogeny, 74		Ebbesson, 117
Chordate Relationships, 74		Deacon, 117
Jawless Vertebrates, 74		Current Theories of Forebrain Evolution, 117
Chondrichthyes, 76		Forebrain Evolution: Experimental Foundations, 117
Actinopterygii, 76		Karten: Equivalent Cell Hypothesis, 118
Sarcopterygii, 76		Other Theories of Pallial Evolution, 119
The Big Picture of Vertebrate Evolution, 84		Perspective, 121
Two Types of Brain Organization, 84		
Laminar Brains (Group I), 86		
Elaborated Brains (Group II), 87		
Glia and Brain Elaboration, 89		
Laminar and Elaborated Brains across Evolution, 89		
5 Evolution and Adaptation of the Brain, Behavior, and Intelligence	93	Part Two
Phylogeny and Adaptation, 93		THE SPINAL CORD AND HINDBRAIN
Phyletic Studies, 93		
Adaptation Studies, 94		
The Phylogenetic Scale, 95		
The Phylogenetic Tree, 95		
Complexity and Evolution, 96		7 Overview of Spinal Cord and Hindbrain 127
Anagenesis, 97		Overview of the Spinal Cord, 127
Grades of Evolutionary Advancement, 99		Segmentation Within the Spinal Cord, 127
Evolutionary Change, 99		Roots and Ganglia, 128
Brain Evolution and Behavioral Adaptation, 100		Columns of the Spinal Cord, 129
Brain Size and Brain Allometry, 100		Pathways Within the Spinal Cord, 130
Brain Size and Behavioral Adaptation, 105		Reflexes, 131
Brain Size and Intelligence, 106		Spinal Autonomy, 133
What Is Intelligence? 108		Rhythmic Movements and Central Pattern Generators, 133
Summary and Conclusions, 109		Overview of the Hindbrain, 133
6 Theories of Brain Evolution	113	The Obex and the Fourth Ventricle, 135
Introduction, 113		The Pontine Nuclei, 135
Some Common Assumptions, 113		Ganglia of the Cranial Nerves, 135
		Organization of the Cranial Nerves, 135
		Embryology of the Hindbrain and a New Classification of Cranial Nerves, 135
		Efferent Axons in Afferent Nerves, 136
		Evolutionary Perspectives on the Spinal Cord and Hindbrain, 136
		The Transition to Land, 136
		Tetrapod Locomotor Patterns, 137

CONTENTS

8 The Spinal Cord	139	Efferent Columns of the Brainstem, 179 Five Cranial Nerves Rostral to the Brainstem, 180 General Considerations, 181
The Spinal Cords of Nontetrapods, 139 Muscles and Locomotion, 139 Cell and Fiber Columns, 139 Giant Axons and Escape, 141 Electromotor Neurons, 144 The Curious Spinal Cords of Sharks, 144 Ascending and Descending Pathways, 144 Reissner's Fiber, 145 The Organization of the Tetrapod Spinal Cord, 145 Locomotor Patterns and Spinal Cord Organization, 145 The Curious Spinal Cords of Birds, 146 Segmental Organization, 147 Lamination, 147 Intrinsic Spinal Neurons, 148 Somatotopic Organization of the Ventral Horns, 148 Renshaw Cells, 149 Axon Columns and Cell Columns, 149 Marginal Cells, 150 Accessory Lobes, 150 Ascending Spinal Pathways, 150 Descending Spinal Pathways, 150 Tetrapod Central Pattern Generators, 152 Evolutionary Perspective, 152		
9 Segmental Organization of the Head, Brain, and Cranial Nerves	157	"Twelve" Cranial Nerves, 157 The Vertebrate Head: Segmental Organization, 158 Head Skeleton, 159 The Striated Musculature of the Head, 159 Neural Crest and Placodes, 162 Segmentation of the Head, 164 Theoretical Head Segments, 165 Segmental Organization of the Individual Cranial Nerves, 166 The Forebrain, 168 The First Head Segment, 168 The Second Head Segment, 169 The Third Head Segment, 169 The Fourth Head Segment, 169 The Fifth Head Segment, 170
10 Functional Organization of the Cranial Nerves	173	Introduction, 173 The Cranial Nerves and the Spinal Cord, 173 The Organization of Sensory and Motor Columns of the Caudal Brainstem, 176 Afferent Columns of the Brainstem, 177
11 Sensory Cranial Nerves of the Brainstem	183	Introduction, 183 Dorsal Cranial Nerves: Sensory Components for General Somatosensory Sensation, 183 Somatosensory Innervation of the Head, 184 Central Terminations of the Trigeminal Nerve, 185 The Mesencephalic Division of the Trigeminal System, 185 Secondary Connections of the Trigeminal Nuclei, 186 Ventrolateral Placodal Cranial Nerves: Taste, 189 The Gustatory System, 190 The Gustatory Nerves and the Nucleus Solitarius, 190 Secondary Connections of the Gustatory Nucleus and Nucleus Solitarius, 190 Cyprinid and Silurid Gustatory Specializations, 192 Dorsolateral Cranial Nerves: Lateral Line and Octaval Systems, 194 The Lateral Line System, 195 The Octaval System, 196
12 Motor Cranial Nerves	205	Introduction, 205 Feeding and Swallowing, 207 The Neural Control of Feeding and Swallowing, 209 The Communication Systems of Fishes, 211 The Acoustic Reflex, 213 Motor Control of Eye Muscles, 214 The Extraocular Muscles in Jawless Vertebrates, 214 The Extraocular Muscles in Jawed Vertebrates, 214 The Intraocular Muscles, 215 Central Control of the Eye Muscles, 215 The Oculomotor Complex, 217 Coordination of Eye Muscle Action, 218 Evolutionary Perspective on the Hindbrain and Midbrain Cranial Nerves, 218
13 The Reticular Formation	221	Introduction, 221 The Organization of the Reticular Formation, 222 Neurons of the Reticular Formation, 222 Giant Reticulospinal Neurons, 223 Nomenclature of the Reticular Formation, 224 The Reticular Formation of the Medulla, Pons, and Midbrain, 225 The Reticular Formation of the Diencephalon, 228 Pathways of the Reticular Formation, 230 Chemical Pathways of the Reticular Formation, 232

The Reticular Formation and Sleep, 234		Locus Coeruleus, 277
Evolutionary Perspective on the Reticular Formation, 236		Group I, 277
14 The Cerebellum	241	Group II, 277
Introduction, 241		Evolutionary Perspective, 278
Overview of the Cerebellum, 241		Nucleus Isthmi, 281
Cerebellar Size, 242		Group I, 281
The Various Forms of the Cerebellum, 243		Group II, 281
Corpus Cerebelli, 243		Evolutionary Perspective, 283
Electroreception and the Cerebellum, 244		Isthmo-Optic Nucleus, 283
The Cerebellar Auricle, 245		Group I, 283
Phyletic Development of the Form of the Cerebellum, 245		Group II, 283
The Cerebella of Tetrapods, 246		Evolutionary Perspective, 284
The Cerebella of Nontetrapods, 246		Midbrain Locomotor Region and Pedunculopontine Tegmental Nucleus, 284
Agnathans and Cartilaginous Fishes, 246		Group I, 284
Ray-Finned Fishes, 246		Group II, 284
The Cerebellar Cortex, 247		Evolutionary Perspective, 285
The Purkinje Cell Layer, 247		Interpeduncular Nucleus, 285
The Granule Cell Layer, 249		Group I, 285
The Molecular Layer, 253		Group II, 285
Afferent Inputs to the Cerebellar Cortex, 253		Evolutionary Perspective, 285
Interconnections Within the Cerebellar Cortex, 255		17 Tegmentum and Tori
The Precerebellar Nuclei, 256		289
Cerebelloid Structures Associated With the Cerebellum in Nontetrapods, 257		Introduction, 289
The Exceptional Cerebella of Weakly Electric Fishes, 259		Mesencephalic Nucleus of the Trigeminal Nerve, 289
Cerebellar Efferents and the Deep Cerebellar Nuclei, 260		Group I, 289
Evolutionary Perspective, 262		Group II, 290
Functions of the Cerebellum, 262		Evolutionary Perspective, 290
Part Three		Red Nucleus and Related Nuclei, 290
THE MIDBRAIN		Group I, 290
15 Overview of the Midbrain	267	Group II, 290
Introduction, 267		Evolutionary Perspective, 292
The Isthmus, 268		Substantia Nigra and Ventral Tegmental Area, 292
The Tegmentum, 273		Group I, 293
The Tectum, 273		Group II, 294
16 Isthmus	275	Evolutionary Perspective, 303
Introduction, 275		Torus Lateralis, 304
Nuclei of the Raphe, 275		Group I, 304
Group I, 275		Group II, 304
Group II, 275		Evolutionary Perspective, 304
Evolutionary Perspective, 277		Torus Semicircularis, 304
18 Optic Tectum	311	Group I, 304
Introduction, 311		Group II, 305
Overview of Tectal Organization, 311		Evolutionary Perspective, 306
Overview of Tectal Connections, 312		
The Optic Tectum in Group I Vertebrates, 315		

Lampreys, 315	21 Epithalamus	407
Squalomorph Sharks and Ratfishes, 316	Introduction, 407	
Nonteleost Ray-Finned Fishes, 316	Epiphysis, 407	
Amphibians, 319	Habenula, 409	
The Optic Tectum in Group II Vertebrates, 321	Evolutionary Perspective, 414	
Hagfishes, 321	22 Dorsal Thalamus	417
Galeomorph Sharks, Skates, and Rays, 322	Introduction, 417	
Teleosts, 322	Collothalamic Auditory System, 418	
Amniotes, 325	Group I, 418	
Evolutionary Perspective, 334	Group IIA, 418	
Part Four	Group IIB, 420	
THE FOREBRAIN: DIENCEPHALON	Collothalamic Visual and Somatosensory Systems, 426	
19 Overview of the Forebrain	Group I, 427	
Introduction, 343	Group IIA, 430	
Nomenclature of the Forebrain in Amniotes, 344	Group IIB, 430	
The Diencephalon, 344	Lemnothalamus, 432	
Prepectum, 344	Group I, 432	
Posterior Tuberculum, 344	Group IIA, 434	
Epithalamus, 345	Group IIB, 434	
Dorsal Thalamus, 346	Evolutionary Perspective, 437	
Ventral Thalamus, 347	Collothalamus, 437	
Hypothalamus and Preoptic Area, 352	Lemnothalamus, 437	
The Telencephalon: Pallium, 352	A New Definition of the Dorsal Thalamus in Vertebrates, 439	
The Telencephalic Pallium of Mammals, 353	23 The Visceral Brain: The Hypothalamus and the Autonomic Nervous System	445
The Telencephalic Pallium of Nonmammalian Amniotes, 361	Introduction, 445	
The Telencephalon: Subpallium, 364	The Hypothalamus, 445	
The Ventrolateral Telencephalon of Anamniotes, 364	The Hypothalamus and the Endocrine System, 446	
The Ventrolateral Telencephalon of Mammals, 364	Circumventricular Organs, 449	
The Ventrolateral Telencephalon of Nonmammalian Vertebrates, 368	Biological Rhythms, the Epiphysis, and the Hypothalamus, 449	
The Septum, 369	The Hypothalamus and the Limbic System, 450	
20 Prepectum, Accessory Optic System, and Migrated Posterior Tuberculum	The Preoptic Area, 450	
Introduction, 373	The Hypothalamus in Anamniotes, 451	
Prepectum, 373	Jawless Fishes, 451	
Group I, 374	Cartilaginous Fishes, 451	
Group II, 375	Actinopterygians, 451	
Accessory Optic System, 389	Sarcopterygians, 455	
Group I, 391	The Hypothalamus in Amniotes, 455	
Group II, 392	Connections of the Hypothalamus in Reptiles and Birds, 456	
Evolutionary Perspective, 394	Connections of the Hypothalamus in Mammals, 457	
Migrated Posterior Tuberculum, 396	Functions of the Hypothalamus, 460	
Group I, 396	The Autonomic Nervous System, 460	
Group II, 396	Autonomic Neurochemistry, 462	
Evolutionary Perspective, 399	Amniotes, 462	
	Anamniotes, 462	
	Evolutionary Perspective, 462	

Part Five**THE FOREBRAIN: TELENCEPHALON**

24 Basal Telencephalon	471	Somatosensory Lemnothalamus, 548 Somatosensory Collothalamus, 548 Motor Lemnothalamus, 548 Afferents to Somatosensory Cortex, 549 Efferents of Somatosensory Cortex, 549 Pain Pathways, 549 Somatotopic Organization, 552 Motor Cortex, 557 Multiple Motor Representations of the Body, 558 The Cortical Eye Fields, 558 Afferents and Efferents of the Motor Cortex, 558 The Somatosensory and Motor Forebrain of Nonmammalian Amniotes, 559 Somatosensory System, 559 Motor System, 564 Evolutionary Perspective, 566
25 Nonlimbic Pallium	495	28 Auditory and Vocal Forebrain in Amniotes 571 Introduction, 571 Location of Sound Sources, 571 Echolocation, 572 Auditory Channels for Time and Intensity, 573 Design Features of the Auditory System, 574 Topographic Organization, 574 Bilateral Interaction in the Auditory Pathway, 574 Descending Auditory Pathways, 574 Auditory Pathways in Tetrapods, 574 Auditory Telencephalon, 577 Columnar Organization, 577 Mammals, 577 Reptiles and Birds, 579 Vocal Telencephalon, 580 Vocalization and Hearing, 581 Anurans, 582 Reptiles and Birds, 583 Mammals, 587 Evolutionary Perspective, 589
26 Visual Forebrain in Amniotes	523	29 Terminal Nerve and Olfactory Forebrain 593 Introduction, 593 Olfactory System, 593 Group I, 594 Group II, 595 Vomeronasal System, 601 Terminal Nerve, 605 Evolutionary Perspective, 606
27 Somatosensory and Motor Forebrain in Amniotes	547	30 Limbic Telencephalon 611 Introduction, 611 The Limbic Pallium in Anamniotes, 612
Introduction, 547 The Somatosensory and Motor Forebrain of Mammals, 547 The Ventral Tier Nuclei of the Dorsal Thalamus, 548		

CONTENTS

Group I, 612		
Group IIA, 613		
The Limbic Pallium in Amniotes (Group IIB), 617		
Limbic Pallium of Mammals, 619		
Limbic Pallium in Nonmammalian Amniotes, 623		
Limbic Subpallium: Septum, 628		
Evolutionary Perspective, 629		
Part Six		
CONCLUSION		
31 Evolution of Brains: A Bilaterian View	637	
Introduction, 637		
Invertebrate Brains and the Inversion Hypothesis, 638		
Insect Brain Organization, 639		
Urbilateria and the Ancestral Condition of Bilaterian Brains, 641		
Deuterostomes and Dorsoventral Inversion, 641		
Brain Evolution within Chordates, 644		
The Origin of Vertebrates, 649		
Haikouella, 650		
Sensory System Evolution in the Vertebrate Lineage, 652		
Organization of the Vertebrate Brain, 653		
The Advent of Jaws, 655		
Onto the Land and Into the Air, 656		
Theories of Vertebrate Brain Evolution, 657		
How Vertebrate Brains Evolve, 657		
Appendix: Terms Used in Neuroanatomy	665	
Introduction, 665		
Direction and Location Terms, 665		
Planes of Section, 666		
Neuroanatomical Names, 668		
Derivation of Terms, 668		
Glossary	671	
Index	679	