

Part One Introduction 1

Chapter 1 Psychobiology: Philosophy and Techniques 2

- Philosophy of Psychobiology 2
 - The Mind and the Brain 3*
 - Philosophy and Methods of Studying the Brain 4*
- Overview of the Book 6
- The Mind–Body Problem 6
 - Definitions of Mind, of Body, and of the Problem 6*
 - Suggested Solutions to the Mind–Body Problem 7*
 - Implications for Research 9*
 - Summary of the Mind–Body Problem 11*
- Methods for Studying the Brain 11
 - Physiological Methods 11*
 - Psychological Methods 16*
 - Summary of Methods 18*
- Chapter Summary: The Mind, the Body, and Research 18

Chapter 2 Back to the Basics 19

- Basic Anatomic Principles 19
 - Organization of the Nervous System 19*
 - Anatomy of Cells in the Nervous System 23*
 - Gross CNS Anatomy 29*
 - The Cortex of the Cerebral Hemispheres 30*
 - Sensory Pathways 33*
 - Motor Systems and Control of Movement 33*
 - The Limbic and Reticular Systems 35*
 - Summary of Anatomy 37*

| | |
|--|----|
| Chemical and Electrical Forces | 37 |
| <i>Molecules of Matter</i> | 37 |
| <i>Electrical Forces</i> | 38 |
| <i>Chemical Forces</i> | 40 |
| <i>Ions and Semipermeable Membranes</i> | 40 |
| <i>Summary of Basic Forces</i> | 41 |
| Chapter Summary: Implications for Information Processing | 41 |

Part Two The Communication Function of Nerve Cells 43

Chapter 3 The Nerve Membrane 44

| | |
|---|----|
| Overview | 44 |
| <i>Essential Elements</i> | 45 |
| <i>Resting Membrane</i> | 45 |
| <i>Action Potentials</i> | 46 |
| Properties of the Resting Nerve Membrane | 46 |
| <i>The Nernst Equation and Differences in Concentration</i> | 47 |
| <i>Permeabilities: Resting Potentials and Current Flows</i> | 48 |
| <i>Types of Membrane Channels</i> | 49 |
| <i>The Na-K Pump</i> | 50 |
| <i>The Resting Membrane as a K⁺ Membrane</i> | 51 |
| <i>Capacitance of Nerve Membranes</i> | 51 |
| <i>Summary of the Resting Membrane</i> | 52 |
| Properties of the Active Nerve Membrane | 52 |
| <i>Techniques of Study</i> | 52 |
| <i>A Detailed Description of Ion Movements</i> | 57 |
| <i>Action Potentials in Other Types of Membranes</i> | 59 |

| | |
|---|-----------|
| <i>Changing Ideas about the Electrically Gated Ionic Channels</i> | 60 |
| <i>Summary of the Active Membrane</i> | 62 |
| Propagation of Action Potentials | 62 |
| <i>The Nature of Propagation</i> | 62 |
| <i>Factors Affecting the Rate of Propagation</i> | 62 |
| <i>Summary of Propagation</i> | 65 |
| Chapter Summary: The Resting and Active Nerve Membrane | 65 |
| | |
| Chapter 4 The Nerve-Cell Synapse | 67 |
| Overview | 68 |
| <i>Synaptic Events</i> | 68 |
| <i>Comparisons among Synaptic and Action Potentials</i> | 68 |
| <i>Types of Effects of Transmitter Substances</i> | 70 |
| <i>Techniques of Study</i> | 70 |
| <i>Summary of Overview</i> | 71 |
| Presynaptic Events | 72 |
| <i>Molecular Events Preceding Transmitter Release</i> | 72 |
| <i>Vesicles and Quanta</i> | 72 |
| <i>Nonvesicular Release?</i> | 74 |
| <i>Summary of Presynaptic Events</i> | 76 |
| Postsynaptic Events at Fast Synapses | 76 |
| <i>Excitatory Synapses</i> | 76 |
| <i>Inhibitory Synapses</i> | 80 |
| <i>Synaptic Inactivation</i> | 85 |
| <i>Summary of Fast Postsynaptic Events</i> | 85 |
| Postsynaptic Events at Slow Synapses | 86 |
| <i>Cyclase Receptors and Enzymatic Reactions</i> | 86 |
| <i>Decreases in Membrane Permeability</i> | 88 |
| <i>Increases in Membrane Permeability</i> | 89 |
| <i>Possible Effects on the Na-K Pump</i> | 89 |
| <i>Interactions of Fast and Slow Synapses</i> | 89 |
| <i>Comparisons between Fast and Slow Synapses</i> | 91 |
| <i>Summary of Slow Postsynaptic Events</i> | 92 |
| Transmitter Substances: Location, Function, and Metabolism | 92 |
| <i>General Principles</i> | 93 |
| <i>The Transmitters and Neuromodulators</i> | 93 |
| <i>Summary of Types of Transmitter Substances</i> | 99 |

Information Processing and Types of Synaptic
Circuits 100

Interaction of Graded Synaptic Potentials 100
*Convergence, Divergence, and Synaptic
Efficacy* 101

Presynaptic Inhibition and Facilitation 103
*Synaptic Interactions without Action
Potentials* 104

Summary: One Type of Microcircuit 104

Some Mechanisms of Synaptic Modulation 106

*Availability of Inactivating and Synthesizing
Enzymes* 106

Active Transport 107

Presynaptic Receptors and Autoreceptors 107

*Changes in Postsynaptic Receptor Availability
or Sensitivity* 107

*Prostaglandins, Neuromodulators, and
Hormones* 108

*Other Changes That Depend on the Frequency
of Synaptic Activity* 109

Summary of Synaptic Modulation 110

Chapter Summary: The Synapse and Transmission of
Information 110

Chapter 5 Genetics and the Nerve Cell 111

Overview 112

Human Chromosomes 112

*Effects of Genes on the Brain and
Behavior* 113

Genetic Types of Research 113

Purposes of Genetic Research 113

Research Techniques 115

Summary of Types of Genetic Research 118

Basic Genetic Principles 118

Genes, Chromosomes, and Proteins 118

Genetic Interactions 120

Genetic Variability 123

Genetic Regulation 125

Summary of Genetic Principles 126

Effects of Genes on Neurons 126

Indirect Effects 127

*Genetic Effects on the Structure of the Axonal
Membrane* 127

Genetic Effects on Synaptic Activity 129

*Genetic Effects on Neural Structure and
Patterns of Interconnections* 129

*Summary of the Effects of Genes on Nerve
Cells* 130

Chapter Summary: Genes and Communication of
Information 130

***Part Three The Coding Function of Nerve
Cells*** 131

Chapter 6 Principles of Sensory Coding 133

Overview 133

Principles of Coding and Transduction 134

Experimental Problems 135

Psychophysics 135

The Physics of Sensory Stimuli 135

Absolute Thresholds 137

*Difference Thresholds and Estimations of
Magnitude* 138

Judged Similarities among Stimuli 139

Psychophysics in Lower Animals 140

Summary of Psychophysics 141

Transduction by Receptors 141

Anatomy of Receptors 142

Concepts of Transduction 149

Transduction in Chemoreceptors 150

Transduction in Mechanoreceptors 152

Summary of Transduction 154

Coding Principles 154

The Concept of Coding 154

Anatomy of Coding 155

Types of Code 157

*Codes for Quality of Stimulus within a
Modality* 160

Common Codes for Intensity of Stimulus 167

Receptive Fields and Lateral Inhibition 169

*Coding for Spatial Location of the
Stimulus* 170

*Columnar Organization and Feature
Detectors* 171

*Illusions (or Hallucinations) because of Coding
Mechanisms* 172

*Summary and Implications of Coding
Principles* 172

Adaptation and Centrifugal Control 173

Rapidly and Slowly Adapting Receptors 173

Mechanisms of Adaptation 174

| | |
|---|-----|
| <i>Centrifugal Systems</i> | 174 |
| <i>Outflow Monitoring</i> | 176 |
| <i>Summary and Implications for Coding and Perception</i> | 177 |
| Chapter Summary: The Codes of the Brain | 177 |

Chapter 7 Vision 178

| | |
|---|-----|
| Overview | 178 |
| The Psychophysics of Light | 179 |
| <i>Nature of Light</i> | 179 |
| <i>Psychophysics of Detection and Brightness</i> | 179 |
| <i>Psychophysics of Color</i> | 181 |
| <i>Summary of Psychophysics</i> | 182 |
| Anatomy of the Visual System | 182 |
| <i>Retinal Anatomy</i> | 182 |
| <i>Central Pathways</i> | 186 |
| <i>X-, Y-, and W-Cells in Cat Visual Systems</i> | 188 |
| <i>Summary of Anatomy</i> | 188 |
| Transduction | 189 |
| <i>Overview</i> | 189 |
| <i>Phase I: Nonneural Changes</i> | 190 |
| <i>Phase II: Changes in Receptor Permeability</i> | 190 |
| <i>Phase III: Changes in Membrane Potentials</i> | 194 |
| <i>Summary of Transduction</i> | 198 |
| Subcortical Coding | 199 |
| <i>Brightness Coding in the Retina and Geniculate</i> | 199 |
| <i>Coding of Spatial Location and Lateral Inhibition</i> | 199 |
| <i>Wavelength Coding in the Retina and Geniculate</i> | 202 |
| <i>Summary of Subcortical Coding</i> | 205 |
| Cortical Coding Mechanisms and Feature Detectors | 205 |
| <i>Receptive Field Characteristics</i> | 206 |
| <i>Spatial Frequency Detectors</i> | 212 |
| <i>Binocularity and Perception in Three-Dimensional Space</i> | 214 |
| <i>Color Coding</i> | 214 |
| <i>Some Higher-Level Feature Detectors</i> | 216 |
| <i>Summary of Cortical Coding</i> | 217 |

| | |
|--|-----|
| Adaptation and Centrifugal Control | 217 |
| <i>Stabilized Retinal Images</i> | 217 |
| <i>Light and Dark Adaptation</i> | 218 |
| <i>Centrifugal Connections and Effects</i> | 221 |
| <i>Summary of Adaptation and Centrifugal Control</i> | 222 |
| Chapter Summary: Visual Codes | 222 |

Part Four The Coding of Internal Motivational and Emotional States 225

Chapter 8 Effects of Hunger, Thirst, and Arousal on Nerve Cells 228

| | |
|--|-----|
| Overview | 229 |
| Command Cells and Motives | 229 |
| <i>Invertebrate Command Cells</i> | 229 |
| <i>Possible Command Systems in Primates</i> | 230 |
| <i>Summary of Command Cells</i> | 231 |
| Effects of Level of Nonspecific Arousal on Neural Responses | 231 |
| <i>Stages of Sleep</i> | 232 |
| <i>Single-Unit Recordings during Sleep and Arousal</i> | 235 |
| <i>Arousal and Responses in the Sensory Systems</i> | 239 |
| <i>Summary of Arousal Effects</i> | 240 |
| Basic Physiology of Two Homeostatic Motives | 241 |
| <i>Hunger</i> | 241 |
| <i>Thirst</i> | 249 |
| <i>Summary of Physiology</i> | 250 |
| Genetics of Hunger | 250 |
| <i>The Genetics of Overeating</i> | 250 |
| <i>Taste Preferences</i> | 252 |
| <i>Summary of Genetics</i> | 253 |
| Neural Coding of Hunger, Thirst, and Motivationally Relevant Stimuli | 253 |
| <i>Neurons outside the Hypothalamus</i> | 254 |
| <i>Thirst Stimuli and Neural Responses</i> | 254 |
| <i>Hunger Stimuli and Hypothalamic Neural Responses</i> | 255 |
| <i>Summary of Neural Coding</i> | 261 |
| Effects of Motivational States on Reinforcement | 262 |
| <i>Hunger and Sensory Coding</i> | 264 |
| <i>Motives and Self-Stimulation</i> | 264 |
| <i>Neural Responses to Self-Stimulation</i> | 266 |
| <i>Summary of Motives and Reinforcement</i> | 268 |

*Chapter 9 Sex Hormones: Reproductive
Motives and Behaviors 270*

- Overview 270
- Types of Sex Hormone and Effects 271
 - Types of Sex Hormone and Metabolic Pathways 271*
 - Hormones and Sexual Development 273*
 - Organizational versus Activational Effects of Sex Hormones 276*
 - Cellular Actions of Sex Hormones 278*
 - Summary of Cellular Effects 279*
- Hormone Receptors in the Brain 280
 - Receptors and Sexual Behavior 280*
 - Estrogen Receptors 281*
 - Androgen Receptors 283*
 - Progesterone Receptors 285*
 - Summary of Hormone Receptors 285*
- The Genetics of Sexual Differentiation and Reproductive Behaviors 286
 - Genes That Cause Testes 286*
 - X-Inactivation 287*
 - Androgen-Insensitivity Syndrome 287*
 - Enzyme Deficits 288*
 - Behavioral Sensitivity to Sex Hormones 288*
 - Summary of Genetics 289*
- The Hormone-Sensitive, Sexually Dimorphic Behaviors 290
 - Techniques and Problems 290*
 - Sexual Behaviors 293*
 - Social Motives and Emotions 293*
 - Responses to Sensory Stimuli 294*
 - Hunger and Food Intake 294*
 - Learning: Motives and Emotions? 294*
 - Summary of Sexually Dimorphic, Hormone-Sensitive Behaviors 295*
- Organizational Effects on the Brain 295
 - Mechanisms and Locations of Effects 295*
 - Biochemical Effects of Sex Hormones 297*
 - Morphological Effects of Sex Hormones: Sex Differences in Neuron Structure 298*
 - Summary of Organizational Effects 305*
- Activational Effects on Neural Activity 306
 - Mechanisms of Effects 306*
 - Sex Hormones and Transmitter*

| | |
|---|-----|
| Substances | 308 |
| Single-Unit Recording: Effects of Sex Hormones on Neural Activity | 311 |
| A Paradigmatic Research Program: Pfaff and Lordosis | 315 |
| Neural Activity during Sexual Behavior | 318 |
| Summary of Activational Effects | 318 |
| Chapter Summary: Neural Coding of Sexually Dimorphic Behaviors | 319 |

Chapter 10 The Psychobiology of Emotions and Curiosity 320

| | |
|---|-----|
| Overview | 321 |
| The Biology of Emotions: A Survey | 321 |
| The Issue of Specificity and the Role of Visceral Afferents | 321 |
| The Autonomic Nervous System | 323 |
| The Adrenal Glands | 323 |
| Limbic System | 324 |
| Summary of Biology | 325 |
| Genetics of Emotions | 325 |
| Inheritance of Temperament and Emotionality | 325 |
| Schizophrenia and Affective Disorders | 327 |
| A Link with Genes: Dopamine Neurons, "Curiosity," and Schizophrenia | 329 |
| Summary of Genetics | 329 |
| Effects of Stress on Brain Transmitter Levels | 330 |
| Background and a Model | 330 |
| Stress-Induced Changes in Brain Transmitters | 331 |
| Factors Affecting Stress Responses | 335 |
| Stress: A Model for Depression | 337 |
| Stress: A Model for Schizophrenia | 338 |
| Summary of Stress Effects | 338 |
| The Biochemistry of Some Emotions | 338 |
| Aggression and Anger | 339 |
| Platelet MAO Activity and Emotions | 341 |
| Anxiety | 341 |
| Schizophrenia | 344 |
| Affective Disorders | 347 |
| Summary of the Biochemistry of Emotions | 351 |
| Single-Unit Studies | 353 |
| Limbic-System Activity | 353 |
| The Locus Coeruleus and Anxiety | 355 |
| Drug Effects | 355 |
| Effects of the Glucocorticoids | 358 |

Aplysia: A Model for the Cellular Basis of Anxiety? 358

Summary of Neurons and Emotions 361

Chapter Summary: The Coding of Emotional States 361

Part Five Effects of Experience on Brain Coding Mechanisms 363

Definitions and Concepts 363

The Neuron Doctrine and Memory 364

Chapter 11 Changes in Neural Activity Associated with Learning and Memory 366

Overview 367

Conceptual and Experimental Difficulties 367

Types of Memory Research Covered 367

The Biochemistry of Learning and Memory 368

Agents That Affect Retention

Performance 368

Brain Transmitters and Learning 373

Biochemical Changes Associated with Learning 377

Genetics of Learning and Memory 378

Summary of Biochemistry 381

Single-Unit Activity during Learning 382

General Background 382

Hippocampus 384

Eyelid Conditioning 389

Summary of Learning and Neural Activity 393

Model Systems 393

Hippocampal Potentiation 393

Learning and Memory in Invertebrates 396

Summary of Model Systems 397

Chapter Summary: Neural Codes and Learning 397

Chapter 12 Effects of Developmental Experiences on Coding 399

Overview 400

Environmental Enrichment and Deprivation 400

Techniques 400

Effects on Behavior 402

Effects on Gross Anatomy and Biochemistry 404

Microanatomy: Enrichment versus Special

| | |
|---|-----|
| <i>Training</i> | 406 |
| <i>Summary of Environmental Enrichment</i> | 409 |
| Effects of Stimulation during Development | 410 |
| <i>Olfactory</i> | 410 |
| <i>Somatosensory</i> | 410 |
| <i>Auditory</i> | 413 |
| <i>Summary of Developmental Effects</i> | 413 |
| Binocular versus Monocular Visual Deprivation | 414 |
| <i>Binocular Deprivation</i> | 414 |
| <i>Monocular Deprivation</i> | 415 |
| <i>Manipulating the Magnitude of the Monocular-Deprivation Effects</i> | 419 |
| <i>Summary of Visual Deprivation</i> | 420 |
| Selective Exposure and Visual Coding | 421 |
| <i>Background and a Model</i> | 421 |
| <i>Stereoscopic Coding</i> | 423 |
| <i>Orientalional Coding</i> | 424 |
| <i>Directional Coding</i> | 429 |
| <i>Sensitivity of Coding Mechanisms</i> | 429 |
| <i>Summary of the Effects of Specialized Experiences</i> | 430 |
| Synaptogenesis in the Brain | 430 |
| <i>Changes during Development</i> | 431 |
| <i>Changes in Synaptogenesis after Lesions</i> | 433 |
| <i>Summary and Implications for the Effects of Experience on Coding</i> | 438 |
| Chapter Summary: We Learn to Perceive | 438 |

*Chapter 13 Single Cells and Mental
Events 442*

Consciousness 443

The Concept of Consciousness 443

Eccles's Evidence for a Mind 443

Two Consciousnesses? 444

Animal Work: A Dead End? 445

*Dissociations of Behavior from Reported
Awareness 445*

Single Nerve Cells and Illusions 447

Anxiety as Evidence of Human

Self-Consciousness? 448

*Summary and Implications of
Consciousness 448*

Alternatives to the Neuron Doctrine 448

*Consciousness and Global Patterns of Brain
Activity 448*

Across-Fiber Coding 449

Comparisons with the Neuron Doctrine 450

Summary of Alternatives 450

Chapter Summary: Looking to the Future 451

References 453

Index 497