

Contents

PART I INTRODUCTION

CHAPTER 1

| | |
|---|---|
| A Survey on Biological Rhythms | 3 |
| <i>Jürgen Aschoff</i> | |
| A Spectrum of Rhythms | 3 |
| The Four “Circarhythms” | 5 |
| Ultradian and Infradian Rhythms | 7 |
| Interaction among Rhythms and Their Teleonomy | 7 |
| References | 8 |

CHAPTER 2

| | |
|---|----|
| Methodology | 11 |
| <i>James Thomas Enright</i> | |
| Introduction | 11 |
| A Schematic Example | 12 |
| Complications for Interpretation | 14 |
| <i>The Search for Sustained Freerunning Rhythms</i> | 14 |
| <i>The Demonstration of Entrainment</i> | 16 |
| <i>Environmental Effects on Freerunning Period</i> | 17 |
| <i>Measurement of Phase Shift</i> | 17 |
| <i>Plasticity of Rhythm Properties</i> | 18 |
| References | 19 |

CHAPTER 3

Data Analysis 21
James Thomas Enright

 Introduction 21
 Some General Properties of the Data 21
 Descriptive versus Inferential Procedures 22
 Descriptive Statistics 22
 Objectivity in Measurement 22
 Determining Phase-Reference Points 23
 Determining Amplitude of an Oscillation 26
 Estimating the Period of a Rhythm 26
 Descriptive Statistics: An Overview 32
 Inferential Uses of Statistics 32
 The Use and Abuse of Standard Inferential Methods 32
 Rhythm-Specific Issues in Inferential Statistics 34
 Subjective Probability 37
 Summary 38
 References 38

CHAPTER 4

Mathematical Models 41
Theodosios Pavlidis

 Introduction 41
 Basic Concepts from the Theory of Oscillators 42
 Dynamic Models of the Circadian Pacemaker 44
 Review of Models Dealing with Continuous Light 47
 Instances of the Dynamic Model 49
 Population Phenomena 50
 General Features of Populations of Oscillators 50
 Concluding Remarks 52
 References 53

PART II DAILY RHYTHMS

CHAPTER 5

Circadian Systems: General Perspective 57
Colin S. Pittendrigh

 Innate Temporal Programs: Biological Clocks Measuring
 Environmental Time 57
 Clocklike Properties of the "Circa-"Oscillators 58
 Recognition of Local Time: Pacemaker Entrainment 59

| | |
|---|----|
| <i>Measurement of the Lapse of Time: Homeostasis of Pacemaker Period and Angular Velocity</i> | 60 |
| Origin and Diversification of the Pacemaker's Clock Functions | 60 |
| <i>Circadian Programs: Transition from Exogenous Temporal Order to Endogenous Temporal Organization</i> | 60 |
| <i>Pacemaker Period and Generation Time</i> | 61 |
| <i>Evolutionary Opportunism: Diversification of Pacemaker Functions</i> | 62 |
| Pacemaker versus Program | 63 |
| <i>Unicellular Systems</i> | 63 |
| <i>Pacemaker Localization in Multicellular Systems</i> | 64 |
| <i>Pacemaker Localization and Zeitgeber Pathways</i> | 65 |
| <i>Multiple Pacemakers: Mutual Coupling</i> | 66 |
| <i>Pacemaker and Slave Oscillations: Hierarchical Entrainment</i> | 68 |
| <i>Pacemaker and Slaves: The Temporal Program</i> | 68 |
| <i>Distortion of the Temporal Program by Exotic Light Cycles</i> | 71 |
| Photoperiodism: Seasonal Change in the Temporal Program | 71 |
| Convergence: Unity in the Diversity of Circadian Systems | 76 |
| References | 77 |

CHAPTER 6

| | |
|---|----|
| Freerunning and Entrained Circadian Rhythms | 81 |
| <i>Jürgen Aschoff</i> | |
| Introduction | 81 |
| Freerunning Rhythms | 81 |
| <i>Dependence of Frequency on External and Internal Factors</i> | 81 |
| <i>Variability of Frequency</i> | 84 |
| Entrained Rhythms | 86 |
| <i>Diversity of Zeitgebers</i> | 86 |
| <i>Entrainability and Phase Relationships</i> | 86 |
| <i>Phase Shift of the Zeitgeber</i> | 90 |
| Concluding Remarks | 91 |
| References | 92 |

CHAPTER 7

| | |
|---|-----|
| Circadian Systems: Entrainment | 95 |
| <i>Colin S. Pittendrigh</i> | |
| Introduction | 95 |
| Entrainment: General Features | 95 |
| Discrete versus Continuous Entrainment Mechanisms | 96 |
| The Phase-Response Curves (PRCs) of Circadian Pacemakers | 98 |
| Kinetics of Pacemaker Phase Shifts: Limit-Cycle Behavior | 103 |
| Discrete Entrainment of the Pacemaker by Exotic Light Cycles | 104 |
| <i>The Phase Relation, ψ, of Pacemaker and Zeitgeber in Entrained Steady States</i> | 104 |

| | |
|---|-----|
| <i>The Limits of Entrainment: Frequency Following</i> | 106 |
| <i>Frequency Demultiplication</i> | 106 |
| Entrainment by "Skeleton" Photoperiods | 106 |
| Entrainment by "Complete" Photoperiods | 110 |
| The Stability of Entrained Steady States | 114 |
| <i>Skeleton Photoperiods</i> | 114 |
| <i>Complete Photoperiods</i> | 117 |
| Seasonal Change in the External Day: τ and PRC Shape | 117 |
| Seasonal Change in the External Day: Complex Pacemakers | 119 |
| System Entrainment versus Pacemaker Entrainment | 121 |
| Perspective | 122 |
| References | 123 |

CHAPTER 8

| | |
|--|-----|
| Behavioral Rhythms in Invertebrates | 125 |
| <i>John Brady</i> | |
| Introduction | 125 |
| Locomotor Activity Rhythms | 126 |
| Feeding Rhythms | 130 |
| Mating Rhythms | 130 |
| Rhythms in Reproductive Behavior | 132 |
| Gated Behavior | 133 |
| Rhythms in Orientation Behavior | 134 |
| Time Sense | 135 |
| Rhythmicity in Learning | 136 |
| Rhythmic Changes in Responsiveness | 136 |
| Overall Circadian Organization of Behavior | 137 |
| References | 140 |

CHAPTER 9

| | |
|--|-----|
| Neural and Endocrine Control of Circadian Rhythmicity in Invertebrates | 145 |
| <i>Terry L. Page</i> | |
| Introduction | 145 |
| Circadian Pacemakers in the Nervous System | 146 |
| <i>Pacemakers in Vitro</i> | 146 |
| <i>Localization via Transplantation</i> | 148 |
| <i>Localization via Lesions</i> | 150 |
| <i>Multiple Pacemakers</i> | 155 |
| Circadian Rhythmicity and Sensorimotor Integration | 159 |
| <i>Circadian Modulation of CNS and Neurosecretory Activity</i> | 159 |
| <i>Circadian Modulation of Sensory Input</i> | 162 |

| | |
|--|-----|
| Photoreception and Entrainment | 163 |
| <i>Photoreceptor Localization</i> | 163 |
| <i>Neural Mechanisms in Entrainment</i> | 168 |
| References | 169 |
| | |
| CHAPTER 10 | |
| Genetics and Development of Circadian Rhythms in Invertebrates | 173 |
| <i>Ronald J. Konopka</i> | |
| Developmental Ontogeny of the Pacemaker and Overt Rhythms | 173 |
| Genetics of the Pacemaker and Overt Rhythms | 177 |
| <i>Multigene Analysis</i> | 177 |
| <i>Single-Gene Analysis</i> | 178 |
| References | 180 |
| | |
| CHAPTER 11 | |
| Vertebrate Behavioral Rhythms | 183 |
| <i>Benjamin Rusak</i> | |
| Introduction | 183 |
| Mammals | 185 |
| <i>Activity</i> | 185 |
| <i>Learning and Memory</i> | 193 |
| Birds | 194 |
| <i>Introduction</i> | 194 |
| <i>Activity</i> | 196 |
| Reptiles | 198 |
| Amphibians | 200 |
| Fish | 201 |
| <i>Introduction</i> | 201 |
| <i>Activity</i> | 201 |
| Conclusion | 204 |
| References | 205 |
| | |
| CHAPTER 12 | |
| Internal Temporal Order | 215 |
| <i>Martin C. Moore-Ede and Frank M. Sulzman</i> | |
| Internal Temporal Order in Steady-State-Entrained Conditions | 215 |
| <i>Determinants of Rhythm Waveform</i> | 216 |
| <i>Phase Maps of the Circadian System</i> | 217 |
| <i>Inherited Features of Internal Temporal Order</i> | 219 |

| | |
|---|-----|
| <i>Plasticity of Phase</i> | 220 |
| <i>Coupling Strength</i> | 220 |
| Temporal Order in the Absence of Environmental Time Cues | 221 |
| <i>Internal Synchrony between Rhythms</i> | 221 |
| <i>Internal Phase-Angle Shifts</i> | 222 |
| <i>Alterations in Circadian Waveform</i> | 222 |
| <i>Increased Plasticity of Phase</i> | 223 |
| Anatomical and Physiological Basis of Internal Temporal Order | 223 |
| <i>Abstract Models of Internal Organization</i> | 224 |
| <i>Qualitative Models of the Circadian Timing System</i> | 231 |
| Importance of Internal Temporal Order | 235 |
| <i>Advantages of a Periodic Internal System</i> | 236 |
| <i>Consequences of Failures in Strict Internal Temporal Order</i> | 236 |
| References | 238 |

CHAPTER 13

| | |
|--|-----|
| Neural and Endocrine Control of Circadian Rhythms in the Vertebrates | 243 |
| <i>Michael Menaker and Sue Binkley</i> | |
| Introduction | 243 |
| Perception of Entraining Signals | 244 |
| Primary Pacemaking Structures | 247 |
| <i>The Avian Pineal Organ</i> | 247 |
| <i>The Mammalian Suprachiasmatic Nuclei</i> | 252 |
| Damped Oscillators and Driven Rhythms | 253 |
| References | 253 |

CHAPTER 14

| | |
|--|-----|
| Ontogeny of Circadian Rhythms | 257 |
| <i>Fred C. Davis</i> | |
| Introduction | 257 |
| Emergence of Organization | 258 |
| <i>Measurement of Developing Rhythms</i> | 258 |
| <i>Development of Overt Rhythmicity in Humans</i> | 260 |
| <i>Physiology of Emerging Rhythmicity in the Rat</i> | 262 |
| <i>Development of the Circadian System</i> | 265 |
| Role of the Environment in the Ontogeny of Rhythms | 266 |
| <i>Light-Dark Cycles</i> | 266 |
| <i>The Mother as a Zeitgeber</i> | 267 |
| <i>The Internal Environment</i> | 268 |
| Aging | 268 |
| Prospectus | 270 |
| References | 270 |

CHAPTER 15

| | |
|---|-----|
| Adaptive Daily Strategies in Behavior | 275 |
| <i>Serge Daan</i> | |
| Introduction: Selection Pressures for Daily Rhythms | 275 |
| The Community: Nocturnal and Diurnal Ways of Life | 279 |
| <i>Night and Day in Evolutionary Radiation</i> | 280 |
| <i>Temporal Specialization</i> | 280 |
| <i>Temporal Segregation</i> | 281 |
| <i>Temporal Niche Shifts</i> | 282 |
| The Species: Daily Allocation of Time and Energy | 283 |
| <i>Foraging and Food Intake</i> | 285 |
| <i>Daily Movements and Migration</i> | 287 |
| <i>Reproduction and Life History</i> | 289 |
| The Individual: Daily Habits | 291 |
| <i>Time Memory in Honeybees</i> | 291 |
| <i>The Anticipation of Periodic Food</i> | 293 |
| <i>The Strategy of Habits</i> | 294 |
| References | 296 |

CHAPTER 16

| | |
|---|-----|
| Clock-Controlled Orientation in Space | 299 |
| <i>Hans G. Wallraff</i> | |
| Introduction | 299 |
| Biological Clocks in Astro-Orientation | 299 |
| <i>The Sun as an Orientational Cue</i> | 300 |
| <i>The Moon as an Orientational Cue</i> | 305 |
| <i>The Stars as Orientational Cues</i> | 306 |
| Other Aspects of Periodic Change of Oriented Activities | 306 |
| <i>Periodic Change of Direction</i> | 306 |
| <i>Periodic Change of Locomotion</i> | 307 |
| References | 307 |

CHAPTER 17

| | |
|---|-----|
| The Circadian System of Man | 311 |
| <i>Jürgen Aschoff and Rütger Wever</i> | |
| Patterns of Rhythms: Reproducibility and Dependence on Conditions | 311 |
| Freerunning Rhythms | 315 |
| Entrainment by Artificial Zeitgebers | 317 |
| Internal Desynchronization and Partial Entrainment | 319 |
| Shift Experiments and Flights | 325 |
| Application to Problems in Medicine | 327 |
| References | 329 |

CHAPTER 18

| | |
|---|-----|
| Rhythms in Performance | 333 |
| <i>Peter Colquhoun</i> | |
| Introduction: The Measurement of Performance Rhythms | 333 |
| Time-of-Day Effects | 335 |
| Round-the-Clock Studies | 338 |
| Effects of Phase Shifts of the Zeitgeber | 340 |
| Motivation, Situational Factors, and Individual Differences | 343 |
| Concluding Remarks | 346 |
| References | 347 |

PART III TIDAL, LUNAR, AND ANNUAL RHYTHMS

CHAPTER 19

| | |
|--|-----|
| Tidal and Lunar Rhythms | 351 |
| <i>Dietrich Neumann</i> | |
| Tidal Rhythms | 351 |
| <i>Environmental Conditions between Tidemarks</i> | 351 |
| <i>Temporal Adaptations of Behavior to Intertidal Conditions</i> | 353 |
| <i>Circatidal Rhythms</i> | 356 |
| <i>Other Mechanisms for Tidal Timing</i> | 361 |
| <i>The Modulation of Tidal Rhythms by Daily and Semimonthly Components</i> | 366 |
| Lunar Rhythms | 367 |
| <i>Environmental Conditions Related to the Phases of the Moon</i> | 367 |
| <i>Lunar-Rhythmic Adaptations of Behavior</i> | 368 |
| <i>Semimonthly and Monthly Timing of Reproductive Behavior</i> | 371 |
| References | 377 |

CHAPTER 20

| | |
|---|-----|
| Annual Rhythms: Perspective | 381 |
| <i>Eberhard Gwinner</i> | |
| The Phenomenon of Seasonality | 381 |
| Ultimate Factors Controlling Annual Rhythms | 383 |
| Proximate Factors Controlling Annual Rhythms | 384 |
| <i>Proximate Factors Identical or Closely Related to Ultimate Factors</i> | 385 |
| <i>Proximate Factors Temporally Separated from Ultimate Factors</i> | 386 |
| <i>Circannual Rhythms</i> | 386 |
| <i>Hierarchical Organization of Proximate Factors</i> | 387 |
| References | 388 |

CHAPTER 21

| | |
|--|-----|
| Circannual Systems | 391 |
| <i>Eberhard Gwinner</i> | |
| Introduction | 391 |
| Demonstration and Distribution of Circannual Rhythms | 392 |
| Properties of Circannual Rhythms under Constant Environmental Conditions | 394 |
| <i>Persistence of Circannual Rhythms</i> | 394 |
| <i>Range of Circannual Period Lengths: Transients</i> | 395 |
| <i>Dependence of τ on External Conditions</i> | 395 |
| <i>Innateness of Circannual Rhythms</i> | 396 |
| <i>Relationship between Various Circannual Functions within an Individual Organism</i> | 396 |
| Synchronization of Circannual Rhythms | 397 |
| <i>Zeitgebers</i> | 397 |
| <i>Behavior within the Range of Entrainment</i> | 399 |
| Mechanisms of Circannual Rhythms | 400 |
| <i>General Remarks</i> | 400 |
| <i>Circadian Rhythms as Possible Components of Circannual Rhythms</i> | 400 |
| <i>A Sequence of Stages? If So, at What Level?</i> | 403 |
| Adaptive Significance of Circannual Rhythms | 404 |
| <i>Timing of Seasonal Activities</i> | 404 |
| <i>Programming of Temporal Patterns</i> | 406 |
| References | 408 |

CHAPTER 22

| | |
|---|-----|
| Insect Photoperiodism | 411 |
| <i>D. S. Saunders</i> | |
| Introduction | 411 |
| The Photoperiodic Response | 412 |
| <i>Photoperiodic Response Curves</i> | 412 |
| <i>Sensitive and Responsive Stages</i> | 414 |
| <i>The Effects of Temperature on the Photoperiodic Response</i> | 415 |
| <i>The Effects of Latitude and Altitude: Geographical Populations and the Genetics of the Response</i> | 418 |
| The Physiology of Photoperiodic Induction | 419 |
| <i>Photoreception and Spectral Sensitivity of the Photoperiodic Response</i> | 419 |
| <i>Time Measurement in Insect Photoperiodism: The "Nature" of the Clock</i> | 421 |
| <i>An Attempted Rationalization of the Various Propositions to Account for Photoperiodic Induction in Insects</i> | 441 |
| References | 443 |

CHAPTER 23

| | |
|---|-----|
| Photoperiodism in Vertebrates | 449 |
| <i>Klaus Hoffmann</i> | |
| Introduction | 449 |
| Mammals | 449 |
| <i>The Photoperiodic Signal</i> | 450 |
| <i>Photoperiodic Effects on Puberty</i> | 451 |
| <i>Spontaneous Process and Photoperiodic Refractoriness</i> | 451 |
| <i>Organs and Physiological Processes Involved</i> | 452 |
| <i>Endocrine Aspects</i> | 458 |
| Birds | 461 |
| <i>The Photoperiodic Mechanism</i> | 462 |
| <i>Photoperiodic Refractoriness</i> | 463 |
| <i>Organs and Physiological Processes Involved</i> | 463 |
| <i>Endocrine Aspects</i> | 464 |
| Lower Vertebrates | 465 |
| Concluding Remarks | 466 |
| References | 466 |

CHAPTER 24

| | |
|--|-----|
| Annual Rhythms in Man | 475 |
| <i>Jürgen Aschoff</i> | |
| Preface | 475 |
| Seasons in Physiology | 476 |
| Mortality, Suicides, and Conception Rates | 478 |
| <i>Treatment of Data</i> | 478 |
| <i>Long-Term Trends in Acrophase and Amplitude</i> | 479 |
| <i>Dependence on Latitude</i> | 481 |
| Concluding Remarks | 485 |
| References | 486 |

PART IV RHYTHMS NOT DIRECTLY RELATED TO ENVIRONMENTAL CYCLES

CHAPTER 25

| | |
|--|-----|
| Short-Term Rhythms in Activity | 491 |
| <i>Serge Daan and Jürgen Aschoff</i> | |
| Causal Considerations | 492 |
| Functional Considerations | 495 |
| References | 497 |

CHAPTER 26

| | |
|--|-----|
| Temporal Characteristics of Sleep | 499 |
| <i>Wilse B. Webb and Michael G. Dube</i> | |
| Introduction | 499 |
| A Background of Sleep and Other Biological Rhythms | 499 |
| Sleep as a Biological Rhythm | 501 |
| <i>Dimensions of Sleep</i> | 501 |
| <i>Temporal Characteristics of Human Sleep</i> | 501 |
| <i>Comparative Aspects</i> | 502 |
| <i>Ontogenetic Aspects</i> | 506 |
| <i>Time Schedules of Sleep and Wakefulness</i> | 508 |
| Ultradian Rhythms and Sleep | 510 |
| <i>Ultradian Rhythms within Sleep</i> | 510 |
| <i>Ultradian Sleep Rhythms and Wakefulness</i> | 512 |
| Sleep and Hormonal Rhythms | 513 |
| The Central Nervous System and Sleep Rhythms | 515 |
| References | 517 |

CHAPTER 27

| | |
|--|-----|
| Cyclic Function of the Mammalian Ovary | 523 |
| <i>Constance S. Campbell and Fred W. Turek</i> | |
| Rhythmic Variables Associated with the Ovarian Cycle | 524 |
| <i>The Cycle of the Ovary</i> | 524 |
| <i>The Cycle of Hormones</i> | 526 |
| <i>Behavioral Aspects of the Ovarian Cycle</i> | 528 |
| Factors That Alter Characteristics of the Ovarian Cycle within a Given Species | 530 |
| <i>Light</i> | 530 |
| <i>Temperature</i> | 531 |
| <i>Nutrition</i> | 532 |
| <i>Social Factors</i> | 532 |
| Interspecific Differences in the Temporal Occurrence of Ovarian Cycles | 533 |
| <i>Seasonal versus Nonseasonal Breeders</i> | 533 |
| <i>Continuous Estrous, Polyestrous, and Monestrous Cyclers</i> | 538 |
| The Relationship of Ovarian Cycles to the Circadian System | 538 |
| References | 540 |
| Glossary | 547 |
| Index | 549 |