

Contents

Preface	ix	Controlling Experimental Variation	61
Chapter 1: Introduction and Historical Perspective	1	Sources of Variation in Behavior	62
Overview	1	Effects of Mutations on Behavioral Phenotypes	64
The Rise of the Modern Field of Behavioral Genetics	1	Environmental Variation	66
The Modern Evolutionary Synthesis	12	Gene–Environment Correlation and Interaction	68
The Rise of Molecular Genetics	14	Summary	69
A Brief History of Neuroscience	16	Study Questions	70
The Emergence of Behavioral Genetics	18	Recommended Reading	70
Summary	20	Chapter 5: Mapping Genotype to Phenotype in Populations	71
Study Questions	20	Overview	71
Recommended Reading	21	Genes in Populations: Random Mating	71
Chapter 2: Mechanisms of Neural Communication	23	Genes in Populations: Inbreeding	72
Overview	23	Quantitative Genetic Model	74
Transmission of Information in the Nervous System	23	Summary	82
The Resting Membrane Potential	24	Study Questions	82
The Mechanism of the Action Potential	25	Recommended Reading	82
Ion Channels, G-protein-coupled Receptors, and Signal Transduction	30	Chapter 6: Partitioning Phenotypic Variance and Heritability	83
Summary	37	Overview	83
Study Questions	37	Components of Variance in Random Mating	
Recommended Reading	37	Populations	83
Chapter 3: Functional Organization of the Nervous System	39	Genotype–Environment Correlation and Interaction	87
Overview	39	Partitioning Phenotypic Variance	88
The Organization of the Mammalian Nervous System	39	Heritability: The Concept	89
Communication between the Brain and the Periphery	41	Controlling and Estimating Environmental Components of Variation	91
Organization of the Nervous System in Insects	45	Summary	93
Neurotransmitters	47	Study Questions	93
Summary	54	Recommended Reading	94
Study Questions	54	Chapter 7: Estimating Heritability	95
Recommended Reading	55	Overview	95
Chapter 4: Measuring Behavior: Sources of Genetic and Environmental Variation	57	Phenotypic Resemblance between Relatives	95
Overview	57	Genetic Causes of Covariance between Relatives	98
Behavioral Assays	57	Environmental Causes of the Relationship between Relatives	99
		Heritability Estimates in Humans	101
		Heritability in Other Populations	104
		Estimates of Heritability for Behavioral Traits	106
		Summary	106
		Study Questions	108
		Recommended Reading	108

Chapter 8: Quantitative Trait Locus Mapping	109	Social Cooperation and Fitness	186
Overview	109	Courtship and Mate Selection	186
Linkage Mapping	110	Affiliative Behavior	193
Interval Mapping	112	Aggression and the Establishment of Social Hierarchies	196
Statistical Analysis	112	Division of Labor: The Genetics of Social Structure	201
Association Mapping	115	Aggregation Behavior	203
Association Mapping	115	Summary	205
Quantitative Trait Locus End Game	121	Summary	205
Summary	125	Study Questions	206
Study Questions	125	Recommended Reading	206
Recommended Reading	125		
Chapter 9: Mutagenesis and Transgenesis	127	Chapter 13: Genetics of Olfaction and Taste	207
Overview	127	Overview	207
The Occurrence or Induction of Mutations	127	The Study of Olfaction	207
Homologous Recombination	131	The Discovery of Odorant Receptors	207
Transposon-mediated Mutagenesis	135	Transgenic Approaches to Determine Odorant Receptor Response Profiles	212
The GAL4-UAS Binary Expression System in <i>Drosophila</i>	141	Transgenic Approaches to Map Projection Patterns of Olfactory Sensory Neurons	215
RNA Interference	143	The Use of Transgenic Reporter Genes to Visualize Odor Coding	216
Summary	144	Taste and Gustatory Receptors	224
Study Questions	145	Summary	229
Recommended Reading	145	Study Questions	229
		Recommended Reading	230
Chapter 10: Genomics Approaches in Behavioral Genetics	147	Chapter 14: Learning and Memory	231
Overview	147	Overview	231
Detecting Large-scale Gene Expression	147	Forming Memories	231
Parallel Sequencing and Transcriptional Analysis	152	Memory Formation: Cellular Mechanisms	233
Plasticity of Transcriptional Profiles	153	Harnessing the Power of Genetics: Learning in <i>Drosophila</i>	236
Analysis of Whole-genome Expression Microarray	154	Identifying Genetic Networks for Learning and Memory	239
Defining Statistical Significance Threshold	155	Learning Disabilities	243
Identifying Genetic Networks	158	Neurodegeneration and Memory Impairment: Alzheimer's Disease	246
Summary	161	Summary	249
Study Questions	164	Study Questions	251
Recommended Reading	164	Recommended Reading	251
Chapter 11: Neurogenetics of Activity and Sleep	165	Chapter 15: Genetics of Addiction	253
Overview	165	Overview	253
Locomotion	165	Hallmarks of Addiction	253
Genetics of Human Locomotion Disorders	168	Alcoholism	255
Circadian Rhythms	171	Linkage and Association Studies	257
Sleep	173	Alcohol Sensitivity in Model Organisms	258
Summary	181	Alcohol-related Phenotypes in Rodent Models	261
Study Questions	182	Smoking	263
Recommended Reading	182	Drug Addiction	266
		Summary	270
Chapter 12: Genetics of Social Interactions	185		
Overview	185		
Social Environment and the Genes-Brain-Behavior Paradigm	185		

Study Questions	271	The Evolutionary Genetics of Burrowing and Nest Building	288
Recommended Reading	271	The Astounding Diversity of Cichlids and Sticklebacks	289
Chapter 16: Evolution of Behavior	273	Understanding the Evolution of Behavior: How Much Do We Really Know?	293
Overview	273	Summary	296
Population Genetics and Evolution	273	Study Questions	297
Models of Evolution	276	Recommended Reading	297
Selection Models	277	Glossary	299
Assessing Deviations from Neutrality	279	Index	323
Behavior as a Vehicle for Evolution	280		
Insect-Host Plant Interactions: An Example of Evolutionary Adaptation	281		
Co-evolution of Sexual Communication Systems	284		

experience. Truly, our behavior reflects our humanity. In each intraspecific context it is clear that, at the animal level, behavior is essential for survival and reproduction. The behavior provides the stage on which natural selection acts and, therefore, which by evolution it leaves its stamp on the developmental history of the individual, its genetic constitution, the connectivity of its nervous system, its physiology, its morphology and its anatomy, and, at the molecular level, ultimately the carefully orchestrated display of a host of biochemical reactions. Indeed, we might fairly say that behavior provides a window through which we can view much of biology.

During most of the twentieth century, studies of behavior were almost entirely descriptive. Understanding the complexity of behavior from an individual to organismal integration was considerable challenge, typically insurmountable challenge. This changed with David Huber's pioneering studies during the last quarter of the century and the subsequent genetic revolution, which provided a means and unprecedented opportunities to study the "gene-brain-behavior" axis, which is the underlying genetic principle that enables the nervous system to express behaviors. Neurogenetics has, in the way in this enterprise and a variety of analytical methods on behavioral consequences have become available. Comprehensive syntheses of the genetics of behavior, however, are far and few between, although the pioneering text of 1974 by McClearn and the first dedicated textbook, which is the 2000 edition of *Behavioral Genetics* by Plomin et al., which focuses especially on human cognition.

Here, we have attempted to define the field of behavioral genetics as a comprehensive discipline that encompasses both studies on model organisms and people, with emphasis on unifying principles whenever possible. Whereas this book treats the study of behavior deliberately from a genetic viewpoint, we recognized that phenotypological and ecological aspects could not be ignored, and had to be integrated with the more fundamental behavioral genetics concepts. We showed various touching on evolutionary genetics and gene flow in populations.

Behaviors are complex traits that result from the coordinated action of multiple segregating genes that are sensitive

In the first half of the book, we present an introductory chapter that describes the history of the field, the role of behavioral genetics, followed by chapters that describe the evolution of the behavior and the role of the nervous system, and chapters that describe the role of the brain and the role of the environment in the development of behavior. The second half of the book focuses on a range of commonly studied behaviors, including social behavior, stress response, learning and memory, aggression, decision-making, and sleep and attention. Each chapter has an overview, the description of the behavior, its development and a summary that summarizes the major principles. Each chapter ends with a list of recommended reading, a list of commonly studied behaviors, and a list of recommended reading of classical and contemporary papers. A glossary of terminology is included for the reader's convenience.

Each chapter of this book has been used to teach a course on Principles of Behavioral Genetics at North Carolina State University in the fall of 2004. We received valuable feedback, both from students and nonclassical students, which was greatly appreciated. We would like to thank especially Peter Smith and Susan Harrison for valuable and perceptive comments on Chapter 14 and Chapter 11, respectively. Our colleagues at North Carolina State University, John Colborn, Robert Gelfand, Christian Griesinger, and Anne Lachner, also provided valuable input on several of the chapters. Special thanks are due to Mark Winters from Cornell University for comments and detailed review of many of the chapters, and to Peter Heston from the University of Texas at Austin for critical reading of Chapter 16. Numerous old friends have provided us with valuable comments on manuscript in the preparation of this book. They are John Carlson (Yale University), Joshua Dubman (Clark Spring Harbor Lab), Robert Howard (Indiana University School of Medicine), Hope Hockema (Harvard