SEVENTH EDITION

Learning and Behavior

PAUL CHANCE

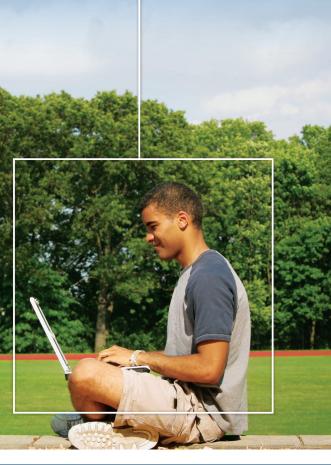
Buy the way you want and save

Get the best grade in the shortest time possible!

CENGAGE brain

Choice (pick your format)Value (get free stuff*)Savings (eBooks up to 65% off print)

Visit **CengageBrain.com** to find... Print • Rentals • eBooks • eChapters Best Buy Packages • Study Tools



www.cengagebrain.com

Your First Study Break



TRANSFORMING LEARNING TRANSFORMING LIVES

Learning and Behavior

PAUL CHANCE



Australia • Brazil • Japan • Korea • Mexico • Singapore • Spain • United Kingdom • United States



Learning and Behavior, Seventh Edition Paul Chance

Publisher: Jon-David Hague

Developmental Editor: Ken King

Assistant Editor: Jessica Alderman

Editorial Assistant: Amelia Blevins

Managing Media Editor: Mary Noel

Senior Brand Manager: Elisabeth Rhoden

Market Development Manager: Christine Sosa

Art and Cover Direction, Production Management, and Composition: PreMediaGlobal

Manufacturing Planner: Karen Hunt Senior Rights Acquisitions Specialist: Dean Dauphinais

Cover Image: Tatyana Vychegzhanina

© 2014, 2009 Wadsworth, Cengage Learning

ALL RIGHTS RESERVED. No part of this work covered by the copyright herein may be reproduced, transmitted, stored, or used in any form or by any means graphic, electronic, or mechanical, including but not limited to photocopying, recording, scanning, digitizing, taping, Web distribution, information networks, or information storage and retrieval systems, except as permitted under Section 107 or 108 of the 1976 United States Copyright Act, without the prior written permission of the publisher.

For product information and technology assistance, contact us at Cengage Learning Customer & Sales Support, 1-800-354-9706.

For permission to use material from this text or product, submit all requests online at **www.cengage.com/permissions**. Further permissions questions can be e-mailed to **permissionrequest@cengage.com.**

Library of Congress Control Number: 2012953850 Student Edition: ISBN-13: 978-1-111-83277-3 ISBN-10: 1-111-83277-3 Loose-leaf Edition: ISBN-13: 978-1-111-83496-8 ISBN-10: 1-111-83496-2

Wadsworth

20 Davis Drive Belmont, CA 94002-3098 USA

Cengage Learning is a leading provider of customized learning solutions with office locations around the globe, including Singapore, the United Kingdom, Australia, Mexico, Brazil, and Japan. Locate your local office at **www.cengage.com/global.**

Cengage Learning products are represented in Canada by Nelson Education, Ltd.

To learn more about Wadsworth, visit www.cengage.com/wadsworth

Purchase any of our products at your local college store or at our preferred online store **www.cengagebrain.com.**

Brief Contents

Preface xiv

Note to the Student: How to Get the Most from this Book xviii

- CHAPTER I Introduction: Learning to Change I
- **CHAPTER 2** The Study of Learning and Behavior 34
- **CHAPTER 3** Pavlovian Conditioning 56
- **CHAPTER 4** Pavlovian Applications 95
- CHAPTER 5 Operant Learning: Reinforcement 126
- **CHAPTER 6** Reinforcement: Beyond Habit 168
- **CHAPTER 7** Schedules of Reinforcement 193
- CHAPTER 8 Operant Learning: Punishment 230
- **CHAPTER 9** Operant Applications 254
- **CHAPTER IO** Observational Learning 279
- CHAPTER II Generalization, Discrimination, and Stimulus Control 313
- CHAPTER 12 Forgetting 345
- **CHAPTER 13** The Limits of Learning 376

Glossary 393 References 400 Author Index 434 Subject Index 442

Contents

Preface xiv

Note to the Student: How to Get the Most from this Book xviii

CHAPTER I Introduction: Learning to Change

Preview I The Constancy of Change 2 Natural Selection 4 Evolved Behavior Reflexes || Modal Action Patterns 13 General Behavior Traits 16 Limits of Natural Selection 19 Learning: Evolved Modifiability 21 Learning Means Change 21 What Changes Is Behavior 22 What Changes Behavior Is Experience 24 Habituation: An Example of Learning 26 Nature vs. Nurture 27 A Final Word 30 Recommended Reading 31 Review Questions 32 Practice Quiz 32 Query Answers 33

34

The Study of Learning and Behavior

Preview 34 The Natural Science Approach 35 Measures of Learning 36 Sources of Data 42 Anecdotes 42 Case Studies 43 Descriptive Studies 44 Experimental Studies 44 Limitations of Experiments 48 Animal Research and Human Learning 49 A Final Word 53 Recommended Reading 53 Review Questions 54 Practice Quiz 54 Query Answers 55

Pavlovian Conditioning CHAPTER 3

Preview 56 Beginnings 57 ■ Ivan Pavlov: An Experimenter from Head to Foot 58 Basic Procedures 59 ■ What's What in Pavlovian Conditioning? 62 Higher-Order Conditioning 63 Measuring Pavlovian Learning 65 Variables Affecting Pavlovian Conditioning 66 How the CS and US Are Paired 66 CS–US Contingency 69 CS–US Contiguity 69 Pavlovian Flowchart 70 Stimulus Features 72 Prior Experience with CS and US 73 Number of CS–US Pairings 75

56

CHAPTER 2

Intertrial Interval 76 Other Variables 76 Extinction of Conditional Responses 78 Theories of Conditioning 81 Stimulus Substitution Theory 81 Preparatory Response Theory 84 Compensatory Response Theory 85 Conditional Awareness 86 Rescorla-Wagner Model 87 Other CS Theories 90 A Final Word 91 **Recommended Reading** 92 Review Questions 92 Practice Quiz 93 Query Answers 94

CHAPTER 4 Pavlovian Applications

Preview 95 Fear 96 ■ Fear of Public Speaking 98 Prejudice 102 The Paraphilias 104 ■ The Boy Next Door 105 ■ Who Are the Victims? 108 Taste Aversion 108 Advertising 111 ■ Nature's Weed Whackers 112 Drug Addiction 115 Health Care 120 A Final Word 122 **Recommended Reading** 123 Review Questions 123 Practice Quiz 124 Query Answers 125

126

CHAPTER 5 Operant Learning: Reinforcement

Preview 126 Beginnings 127 ■ E. L. Thorndike: What the Occasion Demanded 129 Types of Operant Learning 131 ■ B. F. Skinner: The Darwin of Behavior Science 136 Kinds of Reinforcers 138 Primary and Secondary 138 Natural and Contrived 140 ■ Operant and Pavlovian Learning Compared 141 Variables Affecting Operant Learning 142 Contingency 142 Contiguity 144 Reinforcer Characteristics 146 Behavior Characteristics 147 Motivating Operations 148 Other Variables 150 Neuromechanics of Reinforcement 1.50 Theories of Positive Reinforcement 153 Hull's Drive-Reduction Theory 154 Relative Value Theory and the Premack Principle 155 Response-Deprivation Theory 157 Theories of Avoidance 1.59 Two-Process Theory 159 One-Process Theory 163 A Final Word 163 Recommended Reading 164 Review Questions 165 Practice Quiz 166 Query Answers 166

CHAPTER 6 Reinforcement: Beyond Habit

Preview 168 Shaping New Behavior 169 ■ The Shaping of Shaping 170 ■ Tips for Shapers 172 Chaining 173 Insightful Problem Solving 176 Creativity 180 Superstition 184 Quick! Get Some Mud! 187 Helplessness 187 A Final Word 189 Recommended Reading 190 Review Questions 190 Practice Quiz 191 Query Answers 192

CHAPTER 7 Schedules of Reinforcement

Preview 193 Beginnings 194 Simple Schedules 195 Continuous Reinforcement 195 Fixed Ratio 195 Variable Ratio 198 ■ Life Is a Gamble 199 ■ VR Harassment 200 Fixed Interval 200 Variable Interval 203 Extinction 204 Other Simple Schedules 208 Stretching the Ratio 210 Compound Schedules 212

230

The Partial Reinforcement Effect 214 Discrimination Hypothesis 216 Frustration Hypothesis 217 Sequential Hypothesis 217 Response Unit Hypothesis 218 Choice and the Matching Law 220 ■ Ghetto Choice 225 A Final Word 225 Recommended Reading 226 Review Questions 227 Practice Quiz 228 Query Answers 228

CHAPTER 8 Operant Learning: Punishment

Preview 230 Beginnings 231 Types of Punishment 231 Aversive Confusion: Positive Punishment and Negative Reinforcement 233 Variables Affecting Punishment 234 Contingency 234 Contiguity 235 ■ Texting While Driving—Punishable by Death 236 Punisher Intensity 238 Introductory Level of Punisher 239 Reinforcement of the Punished Behavior 240 Alternative Sources of Reinforcement 240 Motivating Operations 241 Other Variables 242 Theories of Punishment 243 Two-Process Theory 243 One-Process Theory 244 Problems with Punishment 245 Alternatives to Punishment 248 A Final Word 250

Recommended Reading 251 Review Questions 251 Practice Quiz 252 Query Answers 253

CHAPTER 9

Operant Applications

Preview 254 Home 255 School 257 Clinic 263 Self-Injurious Behavior 263 Delusions 266 Paralysis 269 Operant Medical Assessment 270 Work 271 Zoo 273 A Final Word 275 ■ Reinforcement Goes to the Dogs 276 Recommended Reading 276 Review Questions 277 Practice Quiz 278 Query Answers 278

CHAPTER IO Observational Learning

Preview 279 Beginnings 280 Types of Observational Learning 281 Social Observational Learning 281 Asocial Observational Learning 286 *Vicarious Pavlovian Conditioning*? 286 Imitation 289 Variables Affecting Observational Learning 292 Difficulty of the Task 292 Skilled vs. Unskilled Model 293 Characteristics of the Model 294 Characteristics of the Observer 296 Consequences of Observed Acts 297 Consequences of the Observer's Behavior 298 Observational Learning and Human Nature 298 Cross-Species Observational Learning 299 Theories of Observational Learning 299 Bandura's Social Cognitive Theory 299 Operant Learning Model 301 Applications of Observational Learning 303 Education 303 Social Change 305 ■ The Down Side of Observational Learning 309 A Final Word 310 Recommended Reading 310 Review Questions 311 Practice Quiz 311 Query Answers 312

CHAPTER II Generalization, Discrimination, and Stimulus Control

Preview 313
Beginnings 314
Generalization 314 *Generalized Therapy 320*Discrimination 320
Stimulus Control 328
Generalization, Discrimination, and Stimulus
Control in the Analysis of Behavior 329
Mental Rotation as Generalization 329
Concept Formation as Discrimination Learning 331
Smoking Relapse as Stimulus Control 334

xii CONTENTS

Theories of Generalization and Discrimination 336
Pavlov's Theory 336
Spence's Theory 337
The Lashley-Wade Theory 338
A Final Word 341
Recommended Reading 342
Review Questions 342
Practice Quiz 343
Query Answers 344

CHAPTER 12 Forgetting

Preview 345 Beginnings 346 Defining Forgetting 346 ■ Learning for the Future 347 ■ A Taxonomy of Knowledge 349 Measuring Forgetting 350 Sources of Forgetting 353 Degree of Learning 354 Prior Learning 356 ■ The Man Who Couldn't Forget 356 Subsequent Learning 359 Changes in Context 361 ■ The State of Learning 364 Applications 365 Eyewitness Testimony 365 Learning to Remember 366 ■ Say All Fast Minute Each Day Shuffle 371 A Final Word 372 Recommended Reading 373 Review Questions 374 Practice Quiz 375 Query Answers 375

CHAPTER 13 The Limits of Learning

Preview 376 Physical Characteristics 377 Nonheritability of Learned Behavior 378 Heredity and Learning Ability 379 ■ Recipe for Genius 381 Neurological Damage and Learning 382 Critical Periods 383 Preparedness and Learning 385 ■ Learning and Humanity 389 The Last Final Word 390 Recommended Reading 390 Review Questions 391 Practice Quiz 391 Query Answers 392 Glossary 393 References 400 Author Index 434

Subject Index 442

376

Preface

A textbook is like a city: It is never finished. Go into any city and you see old buildings being torn down and new ones being built, trees being planted in vacant lots, jackhammers tearing up streets to install phone lines underground. The same is true of textbooks: Some topics are dropped, new ones added, chapters or sections moved from here to there. Here are some of the changes you'll see in *Learning and Behavior*, 7th edition:

- Updated content. The reference list includes over 100 items dated 2011 or later.
- New topics, including evaluative conditioning, asocial observational learning, computer-based VRET, progressive schedules, and constraint-induced movement therapy, among others.
- More studies are cited to document findings, especially those that are counterintuitive or controversial, such as that learning sometimes occurs without awareness of the contingencies involved.
- New applications, including the use of Pavlovian and operant procedures for diagnosis, assessment, and treatment of medical disorders.
- The Miller–Dollard theory of observational learning has been replaced with a generic operant learning model.
- Increased emphasis on the role of context in forgetting, and the idea that forgetting may be largely a matter of stimulus control, a view taken by increasing numbers of psychologists.
- Footnotes are replaced by brief marginal notes that students are more likely to read.
- An increased emphasis in the recommended reading lists on items students are likely to read, such as Hal Markowitz's *Enriching Animal Lives*, Susan Schneider's *The Science of Consequences*, and articles in *The New Yorker* and other popular periodicals.
- An increase in the number and variety of illustrations, including photographs and sketches.
- Increased coverage of research by evolutionary biologists, primatologists, ethologists, rehabilitation psychologists, developmental psychologists, and cognitive psychologists.

- An increase in coverage of research done outside the United States.
- Researcher affiliations are sometimes provided, mostly involving recent studies, to convey to students that not all noteworthy learning research comes out of Ivy League schools.
- A brief section near the end of each chapter called "A Final Word." My hope is that these will prompt the students to think about and discuss the implications of their reading.
- To make room for new material, I have deleted the workbook (students will find a study guide online); reduced chapter review questions from 20 to 10; shortened the discussion of memory; removed Edwin Twitmyer, the discussion of semantic conditioning, self-control, self-awareness, and mnemonic systems. Some of this material will be available on the book's website.

Although cities are constantly being "revised," some things remain the same for decades. The same is true of texts. The following key features of *Learning and Behavior* remain essentially unchanged:

- A readable style and a cordial tone that help make reading the text a welcome activity rather than a tedious chore, so that students get more out of their class sessions.
- Certain themes continue to run through the text: that learning is a biological mechanism (I call it evolved modifiability) by which individuals cope with change; that changes in behavior are the products of biological and environmental events; and that the natural science approach is the best way to study behavior.
- An abundance of examples and applications to help students "get" the principles, not merely memorize them.
- Though many of the experiments involve animal subjects, the emphasis is on what that research tells us about *human* behavior.
- Chapter 2 reviews the basic research methods used to study learning, including the single-subject designs that are unfamiliar to many students.
- Queries appear at irregular intervals to help keep students alert and help them monitor their progress.
- A practice quiz and review questions appear at the end of each chapter *without* answers. I believe the absence of answers prompts students to think about and discuss the questions and may result in interesting class discussions.
- Data graphs that represent findings in an easy-to-grasp form.

I hope you will find that this is the best edition yet of *Learning and Behavior*, but I'm already making notes for the next edition. As I said, textbooks, like cities, are never really finished.

Acknowledgments

As always, many people contributed to the "renovation" of this book. Several instructors reviewed the 6th edition and suggested changes that were, as always, a great help. My thanks to:

Kim Andersen, Brigham Young University—Idaho Shawn R. Charlton, University of Central Arkansas W. Matthew Collins, Nova Southeastern University Joanne Hash Converse, Rutgers, the State University of New Jersey Runae Edwards-Wilson, Kean University Yoshito Kawahara, San Diego Mesa College Dennis K. Miller, University of Missouri H. D. Schlinger, California State University—Los Angeles David Widman, Juniata College

Other instructors and researchers who offered helpful comments or provided articles, images, or raw data include Willem-Paul Brinkman, Delft University of Technology; Adam Doughty, College of Charleston; Robert Epstein, American Institute for Behavioral Research and Technology; Susan Friedman, Utah State University; Chad Galuska, College of Charleston; Bryan Gibson, Central Michigan University; Reese Halter, Global Forest Science Institute; David Harrison, Bay Cove Human Services in Boston; William Heward, Ohio State University; Lydia Hopper, Georgia State University; Todd Huspeni, University of Wisconsin at Stevens Point; Marianne Jackson, California State University in Fresno; Kent Johnson, Morningside Academy, Seattle; Munsoo Kim, Chonnam National University, South Korea; Nobuo Masataka, Kyoto University, Japan; Koichi Ono, Komazawa University, Japan; David Palmer, Smith College; Thomas Parish, formerly of Kansas State University; James Pfister, Poisonous Plant Research Lab, Utah; Alan Poling, Western Michigan University; Albert Rizzo, University of Southern California; Erica Bree Rosenblum, now at the University of California at Berkeley; Barbara Rothbaum, Emory University; Carolyn Rovee-Collier, Rutgers University; Kurt Salzinger, Hofstra University; Stephen Scherer, San Diego Community College; Susan Schneider, Pacific University, Stockton; Satoru Shimamune, Hosei University, Japan; Edwin Taub, University of Alabama; and Andrew Whiten, University of St. Andrews, Scotland. I owe a special thanks to H. D. ("Hank") Schlinger, long a fan of Learning and Behavior, who sent me two dozen journal articles (most of them *not* by him), and with whom I exchanged numerous emails about this book.

I am also grateful to my editor, Ken King, who provided moral support and editing comments as I drafted the revision. I also want to thank Vernon Boes of Cengage Learning and Brenda Carmichael of PremediaGlobal and others who had a hand in producing what must be one of the best cover designs ever seen on a learning text. I also thank Gunjan Chandola and others at PreMedia-Global for turning out the most aesthetically pleasing edition yet of *Learning and Behavior*. Finally, I want to thank the students who emailed me with comments, mostly positive but always helpful, about the 6th edition. I cannot list them all, but Michael Allison, a student at San Diego Community College, and Kim Katsaros, a student at the University of Massachusetts in Lowell, seem representative. Michael thanked me for the occasional humor in the book and added, "I'm glad I don't have to read a stuffy and boring learning text." Kim also praised the book but criticized a passage she found offensive (and which, as a result, I deleted). When I hear from students, I often reply, "You made my day!" That is no exaggeration. Thank you, Michael and Kim, and thanks to all the students who took the time to share their thoughts, positive or negative, about *Learning and Behavior*.

As you can see, I am indebted to a lot of people, and I'm sure there are still more who deserve to be on my list. My apologies to you if you are among them. All of you, named and unnamed, have contributed in one way or another to *Learning and Behavior*, 7th edition. Any flaws in the text are my responsibility. Write to me about them at pc@paulchance.net.

Paul Chance

Note to the Student: How to Get the Most from this Book

As always, I've done what I can to make this book interesting and easy to understand, but you've still got your work cut out for you: There's a lot to learn about learning. Here are some suggestions on how to get the most from this book:

- First, turn to Chapter 12 and study the section called "Learning to Remember." This information will help you learn any course content.
- Second, be sure to read the "Preview" and "In This Chapter . . ." sections at the start of each chapter. This material will help you see where the chapter is headed.
- Third, as you are reading through the text, answer the queries that appear. Write your answer on a slip of paper or say it aloud, then check your answer by reviewing the text above the query or by flipping to the query answers at the end of the chapter.
- Fourth, after you've read a chapter, read the review questions and consider how you would answer them if you were asked those questions in class or on an exam. This is a great thing to do in a study group, since many of these questions can be answered in various ways.
- Fifth, take the practice quiz provided at the end of the chapter. Be sure to *write* your answers as you would if you were taking a quiz in class, or say them to a study partner. These quizzes will help you learn the content *and* give you a rough idea of how well you have mastered it.
- Sixth, take a look at the book's Cengage website. The study guide there should help you master chapter content.

If you really want to get the most from a text or a course, you have to be an active learner. If you want to get the most out of a class, you can't just sit back and listen to the instructor. You have to be actively involved—ask questions, make comments, take notes. The same thing is true when learning from a text: Ask questions, answer queries, make notes, think about the implications and applications of what you read, discuss what you read with other students, and review, review. If you are an active learner, you will not only have a far better chance of acing the exams, you will be able to put more of what you learn to practical use for years to come.

If you have read the Preface, you know that I am eager to get feedback about the book from students as well as instructors. If you have thoughts about the book you'd like to share, email me at pc@paulchance.net.

CHAPTER

Introduction: Learning to Change

IN THIS CHAPTER ...

Preview

The Constancy of Change Natural Selection **Evolved Behavior** Reflexes Modal Action Patterns General Behavior Traits Limits of Natural Selection Learning: Evolved Modifiability Learning Means Change What Changes Is Behavior What Changes Behavior Is Experience Habituation: An Example of Learning Nature vs. Nurture A Final Word **Recommended Reading Review Questions** Practice Quiz Query Answers

Change is the only constant.

—Lucretius

PREVIEW

This chapter raises basic questions about the adaptation of humans and other living things to a changing environment. It looks at the adaptation of both species and individuals. The chapter devotes a good deal of space to topics usually covered in biology texts. The reason is that learning is a biological mechanism. Learning did not evolve so that you could learn to solve algebra word problems or program a computer. It is first and foremost a survival mechanism, a means of meeting the challenges that threaten our survival. One question I hope you will consider as your read this book is whether human learning ability is up to the challenges that threaten our survival today.

THE CONSTANCY OF CHANGE

Keiko, a woman in her sixties, was walking in the underground boarding area in Shinjuku train station, one of the largest train stations in Tokyo, on a spring afternoon. Suddenly she felt very dizzy, so much so that she leaned on a nearby wall to keep from falling. When she looked around, she saw that other people were doing the same thing. It was not dizziness, then, but what was it? There were a few seconds of silence, then a woman nearby shouted, "Jishin da!" (Earthquake!). With that a couple of teenage girls standing nearby screamed.

Earthquakes are a common occurrence in Japan, so after a moment during which there were no signs the building was about to collapse, people continued on their way. Keiko boarded her train, but it did not move; instead there was an announcement: "All train traffic in Tokyo has been suspended."

No trains meant no subways. Keiko's apartment was miles away; how was she to get home? As she emerged from the station, another earthquake struck and someone shouted, "Mite!" ("Look!") and pointed toward the top of a skyscraper. Keiko looked up at Cocoon Tower, a building with a structure that fits its name, and saw it swaying back and forth, like the inverted pendulum of an old-fashioned clock. She wondered how it could sway so far without the upper part breaking off.

The area outside the station was packed with people, so Keiko knew there was little chance of getting a cab. Perhaps a bus? She got into a long line at a bus stop and waited. When a bus came, those at the front of the line boarded, but the bus went nowhere. Finally someone announced that bus transportation



Cocoon Tower in Tokyo, Japan. The tower swayed back and forth during the March 11, 2011, earthquake, though it was 150 miles from the quake's epicenter. was suspended. The only way for Keiko to get home was to walk, but it was a long way from Shinjuku station and she had no map. She knew the way to her sister's home and it was closer, but there was no way to know what she might encounter along the way. Another quake might bring down buildings along her route. Her options were limited, however, so she set off on foot. It took her three hours, but she made it safely. Keiko had been lucky.

Many of the people who lived 150 miles to the northeast, nearer the earthquake's epicenter, were not so lucky. The Great East Japan Earthquake of March 11, 2011, at magnitude 9.0, was the strongest earthquake ever known to have hit Japan and one of the five most powerful earthquakes worldwide since 1900. The earthquake moved the northern part of Honshu, Japan's largest island, about *eight feet* to the east. A tsunami followed the quake, and a wall of water, in some places well over 100 feet high, crashed into the coast, washing away cars and trucks like leaves in a stream, destroying over 300,000 homes, schools, and factories, and killing over 15,000 people. The tsunami also inflicted severe damage on nuclear power plants, resulting in the release of radioactive material that poisoned dairy products, crops, and farmland within a 50-mile radius of the plants, and adding the threat of disease throughout much of Japan for weeks afterward.

Earthquakes, tsunamis, and other natural disasters are a part of life, but we tend to regard them as an aberration, a brief disruption in a normally constant world. When a great volcano erupts, as Mt. St. Helens in Washington State did in 1980, knocking over thousands of trees and covering the ground for miles around with a blanket of volcanic ash; when a gigantic tsunami hits land, as happened in the Indian Ocean in December 2004, killing over 200,000 people and destroying thousands of homes; when a heat wave kills over 50,000 people, as in Europe in the summer of 2003; when a drought rages across a continent, destroying crops and wiping out herds of sheep and cattle, as in Australia from 2006 until 2011, we think how strange it is that nature should misbehave so. It is, we tell ourselves, a momentary lapse, a kind of geological tantrum; soon our old planet will regain its composure, its constancy. But the truth is, as the Roman philosopher Lucretius said 2,000 years ago, "Change is the only constant." We live in a world that is ever-changing, like the varicolored patterns of a steadily rotating kaleidoscope.

Change is not the exception to the rule, it *is* the rule. Throughout nature, the struggle to survive is an effort to cope with change: The climate changes, prey animals become harder to see, predators become faster, diseases strike without warning, population increases put added stresses on the availability of food, water, habitable space, and other resources. Some changes, such as the movement of continents, take place over eons; others, such as the advance or retreat of glaciers, normally take hundreds or thousands of years; some, such as the changes in climate we are now seeing due to human use of fossil fuels, take decades; still others, such as the rise and fall of the sun or the abrupt lane change of an aggressive driver, occur on a daily basis. The one constant in our lives is change. Any individual or species must be able to cope with change if it is to survive. But how? By what mechanisms can we and other animals deal with such a fickle world? Charles Darwin offers one answer.

To see a video of skyscrapers swaying during the Japan earthquake of 2011, go to youtube.com and search "Japan earthquake." If you think earthquakes are uncommon events, Google, "U. S. Geological Survey earthquake maps."

The earth's crust is constantly moving. To see a brief video on how whole continents have moved over millions of years, go to youtube.com and search "650 million years in under 2 minutes." CAPSULE **REVIEW**

The world in which we live is not a stagnant place. It is constantly changing. Mountains rise and fall, forests become deserts, new diseases appear, countries rise and fall, famine is followed by abundance and visa versa. The history of humanity, and your own personal history, is about coping with change. One way species cope with change is through natural selection.

NATURAL SELECTION

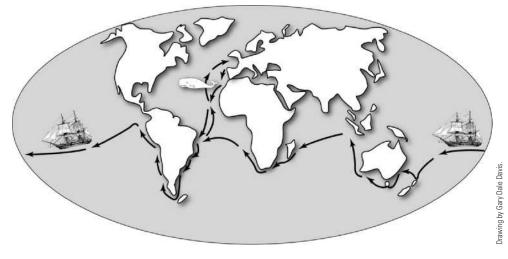
Charles Darwin was born in England in 1809. The son of a physician, he went to the University of Edinburgh in 1825 to study medicine. His heart was not in it, however, and when the blood and screams of a patient undergoing surgery without anesthesia sent him scurrying to the exit, he decided to pursue a degree in theology at Cambridge University. His heart wasn't in that field, either, and he spent much of his time pursuing his true love, natural history.

Shortly after graduating, Darwin accepted an offer to join an expedition on the British naval vessel HMS *Beagle* as the ship's naturalist. The *Beagle* was under the leadership of Captain Robert FitzRoy, a 23-year-old aristocrat who wanted a naturalist who would also serve as a suitable dinner companion. The chief purpose of the voyage was to map the shorelines of land areas around the world. It was a great success in this endeavor, but it is now remembered only because it gave Darwin the opportunity to gather hundreds of specimens of plants and animals in his effort to understand "that mystery of mysteries," the origin of species.

Darwin took a copy of Charles Lyell's *Principles of Geology* with him on the *Beagle*. Lyell, considered by many the father of geology, got many things wrong (he rejected the idea of ice ages, for example), but his view that the earth



Portrait of Charles Darwin in the late 1830s when he was about 30 years old.



The course of HMS Beagle. The Beagle left Plymouth, England, on December 27, 1831, and returned on October 2, 1836.

Work on selective breeding in foxes over a period of 40 years shows that behavioral characteristics can be selectively bred so that the descendants behave more like a different species than like their own ancestors. See Kukekova and Trut (2007);Trut (1999); also see Goldman (2010) for a nontechnical summary. changes gradually over eons gave Darwin a new perspective on where species came from. If the earth had been around for millions of years and changed slowly, as Lyell argued, there was no reason to think that the vast variety of life forms had appeared overnight in their current form.

Once back in England, Darwin focused attention on animal breeding as a source of insights into the variations in living things. He was himself a breeder of doves, and knew that breeders had long changed the characteristics of cows, horses, pigs, sheep, chickens, dogs, cats, and other domestic animals by selectively cross-breeding individuals with desirable characteristics. Such breeding seemed to provide a model for changes in species in the wild, but breeding was the result of deliberate, thoughtful intervention by the breeder. Who was nature's breeder?

The answer occurred to Darwin when he read a book by a fellow Englishman, Thomas Malthus (1798), called *An Essay on the Principle of Population*. Malthus was a clergyman who did not accept the then-popular idea that human population growth was the path to utopia. On the contrary, Malthus argued that it was the road to ruin. Resources are limited, and eventually an expanding population spells disaster. There are limits to all resources, and as populations increase, these resources prove inadequate to supply all individuals. "The power of population," he wrote, "is indefinitely greater than the power in the earth to produce subsistence for man."

Malthus focused on the effects of human population growth, but Darwin realized that all species of animals and plants produce far more offspring than the environment can possibly support, which inevitably leads to competition for resources. Some survive, but most do not. What determines which individuals and species will win out? Clearly the winners must have features that give them an advantage. Those of their offspring that share their parents' advantage will also tend to survive and reproduce. Over generations, these advantages, some of them very subtle, may accumulate and result in very different species. Darwin saw that the mechanism for change was analogous to the breeder's practice of selectively mating animals with desirable characteristics. The difference is that in the wild, *nature is the breeder:*

Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, . . . will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving. . . . I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection, in order to mark its relation to man's power of selection.

In writing "its relation to man's power of selection," Darwin is drawing attention to the analogy of **natural selection** to the *artificial* selection of breeders. "There is no obvious reason," he wrote, "why the principles which have acted so efficiently under domestication should not have acted under nature."

In Darwin's day, little was known about how characteristics were transmitted from one generation to the next. As Darwin noted, "The laws governing inheritance are quite unknown...." The Austrian friar and founder of genetics, Gregor Mendel, did not publish his work on inheritance in peas until 1866, and it did not become widely known among scientists until the early 1900s. Nevertheless, it was clear that characteristics were somehow passed from one generation to another, and these characteristics were beneficial, detrimental, or of no significance in a particular environment.

It is important to note that natural selection depends on variations among the members of a species. If all members of a species were genetically identical, natural selection would be impossible. As Darwin wrote, "unless profitable variations do occur, natural selection can do nothing."

Darwin's critics have often said that even with variation, natural selection cannot possibly account for the sudden appearance of complex organs such as the human eye. You may be surprised to learn that Darwin agreed. But Darwin went on to say that complex organs do not normally appear suddenly. Far from it.

Evidence suggests that the human eye, for example, had its origin millions of years ago with the appearance of a few light-sensitive cells on the skin of some primitive animals. These light-sensitive cells would have proved helpful since anything that cast a shadow on them could, for example, warn of an approaching predator. Through additional variations and natural selection, more light cells appeared, and the light-detecting organ became more and more complicated until it gradually reached the sophisticated light-sensitive organ found in higher animals, including humans (Lamb, 2011; Schwab, 2011).

This may seem to be pure speculation, since we have no videotape of the evolution of the eye, but it is based on evidence suggesting increasing sophistication of organs, including the eye, as we go through the animal kingdom from the simplest to the more complex species. Consider, for example, the trematode *cercaria*, a parasitic flatworm that invades fish brains (Lafferty & Morris, 1996). Cercaria has two spots that, though they may look a bit like eyes, are nothing at all like any mammal's eye (see Figure 1-1). There is no

Very few biologists question natural selection today, and it is widely accepted throughout Europe and Asia, but a Gallup poll found that four in ten Americans still believe that God created all forms of life in their present form about 10,000 years ago (Newport, 2010).

To see how the increasing complexity of the eye improves vision, go to youtube. com and search "Dawkins eye."

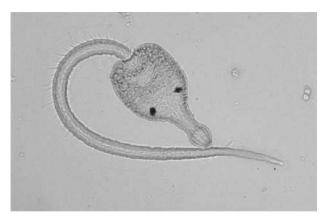


Figure 1-1 The flatworm cercaria with two light-sensitive eye spots. (Image courtesy of Todd C.Huspeni, Curator of Parasites, Department of Biology and Museum of Natural History, University of Wisconsin—Stevens Point.)

iris, no retina, no vitreous humor, nothing, really, except light-sensitive cells. (Light-sensitive cells form the retina of your more sophisticated eyes.) The cercaria's eyespots help it to find its way to a higher water level where it is more likely to encounter the killifish on which it depends. Go up the evolutionary scale and you see increasingly complex visual equipment. The eye of a reindeer, for example, not only sees more or less what you see, it also responds to ultraviolet light, which helps it to identify both predators and food in snow-covered areas (Hogg et al., 2011).

The human brain is another complex organ that did not appear overnight. The jellyfish has a simple network of neurons, but this primitive nervous system, which serves to coordinate its swimming movements, has no brain at all. The first true brains appear in worms. The brain of the earthworm is about the size of a mustard seed, but it is an advance over the jellyfish. Generally, the further up the evolutionary scale you go, the more complicated the brain and the greater its capacity for dealing with environmental changes.

The devices resulting from natural selection are rarely, if ever, as simple and efficient as they could be, but they generally work (Marcus, 2009; Olshansky, 2009). What natural selection demands is not perfection, but devices that are good enough to aid survival. Natural selection is a crude, inefficient mechanism, so it typically takes countless generations to develop sophisticated tools. You might compare it to carving the sculptures of Mt. Rushmore with a hammer and chisel while blindfolded. Nevertheless, it helps species meet the challenges of a changing environment.

All kinds of changes in the environment can affect the characteristics of a species. Climate change is perhaps the most important of these environmental changes, a point made by Darwin (1859). The west coast of Scotland is famous for its cold winters and its warm wool. Until recently the Soay sheep that produced that wool tended to be large, since smaller sheep often succumbed to the cold before reaching reproductive age. Over the past 25 years, however,

the sheep of this area have been getting smaller and lighter (Ozgul et al., 2009; Maloney, Fuller, & Mitchell, 2010). This reduction in size parallels a change in climate due to global warming: Winters in Scotland have gotten shorter and milder in recent decades, so smaller sheep now are more likely to survive and reproduce.

Changes in terrain (due to a change in the course of a river or volcanic eruption, for example) can also induce changes in species through natural selection. Evolutionary biologist Erica Rosenblum and her colleagues at the University of Idaho (Rosenblum et al., 2010), studied three species of lizards in White Sands, New Mexico. All three species have dark skins in other geographic areas, but those that live in White Sands, an area with dunes composed of white gypsum, have developed lighter skins (Figure 1-2). The lizards evolved in areas where their dark skin made them difficult for predators to see, but when they moved into the white dunes, those dark skins made them vulnerable to predators. Those with lighter skins were more likely to survive and reproduce, and this selection process continued over generations until the lizards in the dunes were far lighter than their ancestors.

Pollution provides another example of how changes in the environment affect species characteristics. The classic example is the peppered moth, one

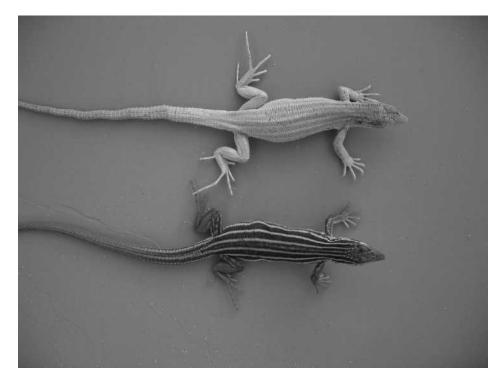


Figure 1-2 The natural selection of skin color. Descendants of lizards that were darkskinned elsewhere (bottom photo) became light in color when living among white sand dunes in New Mexico. (Photo courtesy of Erica Bree Rosenblum, Department of Biological Sciences, University of Idaho at Moscow.)

of many large moths found in the British Isles. The peppered moth feeds at night and rests during the day on the trunks and limbs of trees. Its survival depends in large part on its ability to escape detection by the birds that find it an appetizing food. At one time, nearly all of these moths were a mottled light gray color, closely resembling the lichen-covered trees on which they rested. A rare black variation of the moth, first observed in 1848, stood out against this background like coal against snow, making it highly vulnerable. But when pollutants from burning coal killed the lichen and darkened the bark of trees, the light-colored moths increasingly fell prey to birds, whereas the dark moths tended to survive and reproduce. In forests near industrial centers, where pollution was common, the black moths increased in number, and the lightcolored variety declined. In some areas, 90% of the moths were of the once-rare black variety (Kettlewell, 1959; see Figure 1-3). In recent years, improvement in local air quality has reversed this trend, so that the lighter variety of moth is once again dominant.

Predators are an important part of most animals' surroundings, and changes in predators play an important role in natural selection. Swanne Gordon of the University of California at Riverside and his colleagues (2009) did an experiment with guppies that demonstrates this. The researchers moved wild guppies in Trinidad from a stream that had no predators to a stream with guppy-eating fish. Eight years later Gordon transferred more guppies from the safer stream and compared the survival rate of their young with the young of guppies that had lived among the predators for many generations. The evolved guppies had a survival rate more than 50% higher than that of the newcomers.

Changes in the environment also affect human characteristics. Human skin color is largely due to the amount of melanin, a substance found in the

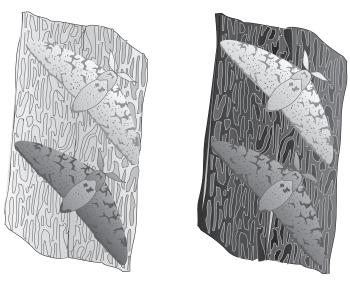


Figure 1-3 The peppered moth and pollution. Prior to 1850, the gray peppered moth was hard to detect against the light trees on which it rested. After soot darkened the trees, the once-rare black variety became dominant. (Drawings by Diane Chance.)