Eleventh Edition

EXERCISE PHYSIOLOGY

Theory and Application to Fitness and Performance



Scott K. Powers | Edward T. Howley | John Quindry

McGraw Hill

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ELEVENTH EDITION

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EXERCISE PHYSIOLOGY: THEORY AND APPLICATION TO FITNESS AND PERFORMANCE, ELEVENTH EDITION

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Dedicated to Lou, Ann, and Tiffany for their love, patience, and support.

Brief Contents

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Appendices can be found in the Instructor's Resources within Connect

Preface

The eleventh edition of this book has undergone major revisions. Identical to all previous editions, this edition of *Exercise Physiology: Theory and Application to Fitness and Performance* is intended for students interested in exercise physiology, medicine, clinical exercise physiology, exercise science, human performance, physical therapy, and physical education. The objective of this text is to provide the student with an up-to-date understanding of the physiology of exercise. Moreover, the book contains numerous clinical applications including a discussion of the benefits of exercise for multiple sclerosis patients and the latest information on sports-related brain injuries.

This book is intended for a one-semester, upper-level undergraduate or beginning graduate exercise physiology course. Clearly, the text contains more material than can be covered in a single 15-week semester. This is by design. The book was written to be comprehensive and afford instructors the freedom to select the material that they consider to be the most important for their course. Furthermore, if desired, the book could be used in a two-semester sequence of exercise physiology courses (e.g., Exercise Physiology I and II) to cover the entire 25 chapters contained in the text.

NEW TO THIS EDITION

The eleventh edition of this book has undergone *major* revisions to include the latest research in exercise physiology. Importantly, Dr. John Quindry was recruited to join the author team to provide additional expertise in several chapters of the text. To improve the book, every chapter contains new and expanded discussions, new text boxes, new figures, updated references, and contemporary suggested readings.

New Topics and Updated Content

The content of this edition has undergone significant revision to provide up-to-date information across all three sections of the book. Specifically, each chapter has been revised and updated to include new and improved box features, new illustrations, new research findings, and the inclusion of up-to-date references and suggested readings. The following list describes some of the significant changes that have been made to make the eleventh edition more complete and up-to-date:

- **Chapter 0:** This chapter underwent a major revision to provide numerous new elements including a discussion of the research process in exercise physiology, an overview of the scientific method, and a summary of the types of research performed in exercise physiology. A new segment also explains how to read and understand scientific journals articles. Further, a fresh section was added to explain how to search the scientific literature. The chapter closes with an up-to-date discussion on careers in exercise physiology and related fields.
- **Chapter 1:** A new section was added to introduce the major types of ergometers used in exercise physiology laboratories. A new figure was inserted to illustrate the differences in running economy between runners varying in experience and ability.
- **Chapter 2:** The chapter was revised to include an expanded discussion of the gain of a biological control system. A New Research Focus box was provided to introduce the concept of exercise-induced hormesis.

- **Chapter 3:** New material has been included to explain the biological wisdom behind why skeletal muscle stores carbohydrate in the form of glycogen. New Research Focus box added to discuss the formation of free radicals in skeletal muscle fibers. New "Ask the Expert" box with Dr. Wayne Willis introduces a simple hydraulic model to assist students in better understanding oxidative phosphorylation.
- **Chapter 4:** Addition of new "A Closer Look" box to discuss $\dot{V}O_2$ max and its verification. New information provided to discuss the role that excess postexercise oxygen consumption plays in exercise-induced weight loss. New figure added to illustrate the Cori cycle.
- **Chapter 5:** This chapter underwent significant revision to include numerous new and improved figures along with an expanded introduction to the basics of endocrine and neuroendocrine physiology. Moreover, updated information was added on both glucagon and cortisol responses to exercise. New information was provided on skeletal muscle as an endocrine organ.
- **Chapter 6:** Update on the latest research findings about the impact of exercise on the immune system. A new illustration was also provided to facilitate student learning.
- **Chapter 7:** Numerous new figures were added to illustrate key concepts. New discussion on exceptions to the size principle were provided in A Closer Look box. New information provided on the central governor theory of exercise-induced fatigue. Finally, the latest research about exercise and brain health was included.
- **Chapter 8:** Expanded discussion of the steps involved in excitation contraction coupling. New information on the causes of exercise-induced muscle fatigue is presented. Numerous new figures added to improve student learning. New information added to define the four domains of exercise intensity.
- **Chapter 9:** New and improved figures added throughout the chapter. Updated information on exercise-induced cardioprotection was also added. Latest information provided about autonomic control of heart rate and cardiac afterload during exercise. Updated information included to describe exercise-induced changes in blood flow to organs throughout the body. Latest information about the blood pressure responses to high-intensity intermittent exercise was also provided.
- **Chapter 10:** Numerous new figures added to chapter to better illustrate concepts related to respiratory system function during exercise. New information provided to explain the changes in breathing patterns that occur during exercise. Latest research provided about the control of breathing during exercise.
- **Chapter 11:** Several new and improved figures provided to illustrate concepts related to acid-base balance during exercise.
- **Chapter 12:** New box feature added to illustrate the conversion of degrees Fahrenheit to degrees Celsius. Latest information provided on thermoreceptors and their role in temperature regulation during exercise.
- **Chapter 13:** This chapter underwent major revision to focus exclusively on the physiology of aerobic and anaerobic exercise training. Latest research provided about the impact of genetics on $\dot{V}O_2$ max and individual responses to exercise training. New box feature added to discuss microRNA's and the adaptive response to exercise training.
- **Chapter 14:** This is a new chapter in the 11th edition of the book that focuses entirely on the physiological effects of strength training. Specifically, this chapter provides the latest research on resistance training–induced changes to the motor control system and within skeletal muscle fibers. Moreover, the chapter contains a thorough discussion of resistance training–induced changes in muscle biochemistry along with the influence of resistance training on bone and ligament strength. The chapter also discusses detraining following strength training along with the impact that concurrent strength and endurance training has on strength gains.
- **Chapter 15:** This chapter appeared as Chap. 14 in the last edition. The new chapter 15 underwent a major revision to focus on the role of exercise in preventing chronic disease. Major changes include updated information on the risk factors for chronic disease (e.g., hypertension, dyslipidemia, obesity) and a state-of-the-art review of the metabolic syndrome. Further, a new section was added on the impact that regular physical activity has on both diabetes and cancer.

- **Chapter 16:** This chapter was Chap. 15 in the previous edition. The chapter was revised to provide new information linking $\dot{V}O_2$ max to health outcomes, updated research about the health impact of different exercise intensities (e.g., vigorous vs. moderate-intensity exercise) on achieving health-related outcomes. Moreover, new information on the latest physical activity recommendations is provided along with a new appendix for determining the energy cost of common exercises.
- **Chapter 17:** This chapter was updated to provide new information about exercise prescriptions in diabetic, asthmatic, hypertension, cardiac rehabilitation, chronic obstructive pulmonary disease, aged, and pregnant populations. A new section detailing exercise prescription recommendations and special considerations for cancer patients was also added. Finally, a new Ask the Expert box featuring Dr. Kathryn Schmitz was added to discuss exercise rehabilitation for cancer patients.
- **Chapter 18:** This chapter underwent extensive revision to provide a state-of-the-art introduction to the science of nutrition. This includes an up-to-date discussion of both macronutrients and micronutrients in the diet along with the current nutritional guidelines and requirements. The discussion on body composition underwent extensive revision to provide a contemporary introduction to the major methods used to determine body composition. The chapter closes with a detailed discussion about body energy balance, popular diet plans, and research related to weight loss and management. Further the impact of exercise combined with diet on weight loss is discussed in detail.
- **Chapter 19:** Updated information was included on radical production and muscular fatigue during exercise. Numerous new figures along with new information about the factors affecting short-term performance and the possible sites of central and peripheral fatigue were added.
- **Chapter 20:** (Chap. 21 in 10th edition) Note that key information from Chap. 20 (10th edition) was updated and included in this revised chapter. For example, new information and figures on laboratory tests to determine endurance exercise potential were provided. Also, fresh information on the measurement of peak running velocity as a predictor of performance was included. Further, several new figures added to illustrate overtraining, individual responses to training, and exercise metabolism during competition. Information was updated about the impact of high-intensity interval training on physiological adaptation.
- **Chapter 21:** (Chap. 22 in 10th edition) New figures added along with a new section discussing the impact of the menstrual cycle influence on performance and training. Latest information on eating disorders in female athletes.
- **Chapter 22:** (Chap. 23 in 10th edition) A new discussion was added to debate the role that antioxidant vitamin supplementation plays in blunting the training adaptation in skeletal muscles.
- **Chapter 23:** (Chapter 24 in 10th edition) A new figure was included along with new information about exercise at altitude, erythropoietin, and red blood cell production.
- **Chapter 24:** (Chap. 25 in 10th edition) Updated information added throughout the chapter. New section provided to discuss the athlete biological passport as a technique to monitor performance enhancing drug use in competitive athletics.

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The eleventh edition of *Exercise Physiology: Theory and Application to Fitness and Performance* is now available online with Connect, McGraw-Hill Education's integrated assignment and assessment platform. Connect also offers SmartBook® 2.0 for the new edition, which is the first adaptive reading experience proven to improve grades and help students study more effectively. All of the title's website and ancillary content is also available through Connect, including:

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- Instructors manual includes lecture outlines, suggested laboratory experiences, group problem solving activities for use the classroom, and homework assignments for students. Selection of homework assignments (linked to textbook chapters) for instructor use. Homework assignments are designed to increase student understanding of exercise physiology and promote problem-solving skills.

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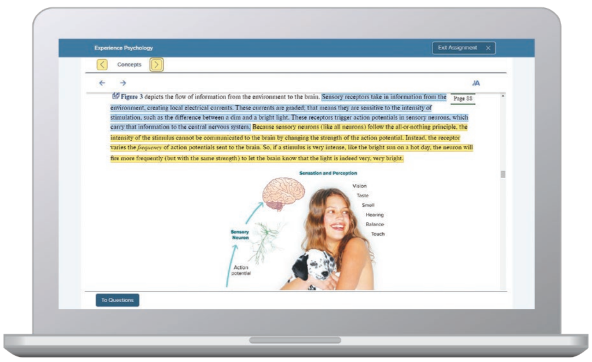

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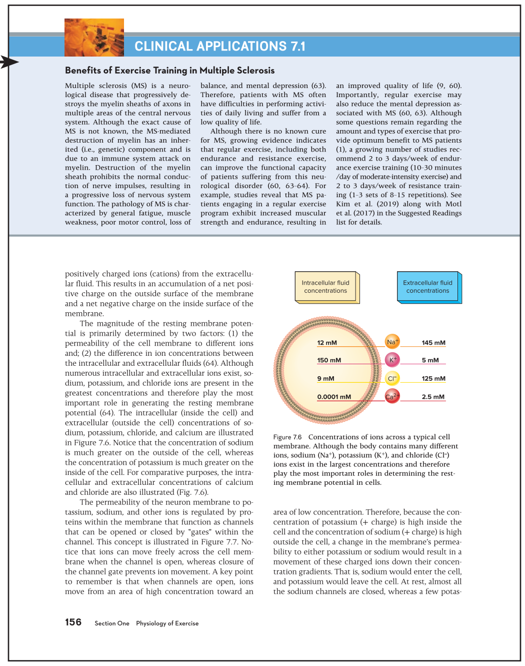
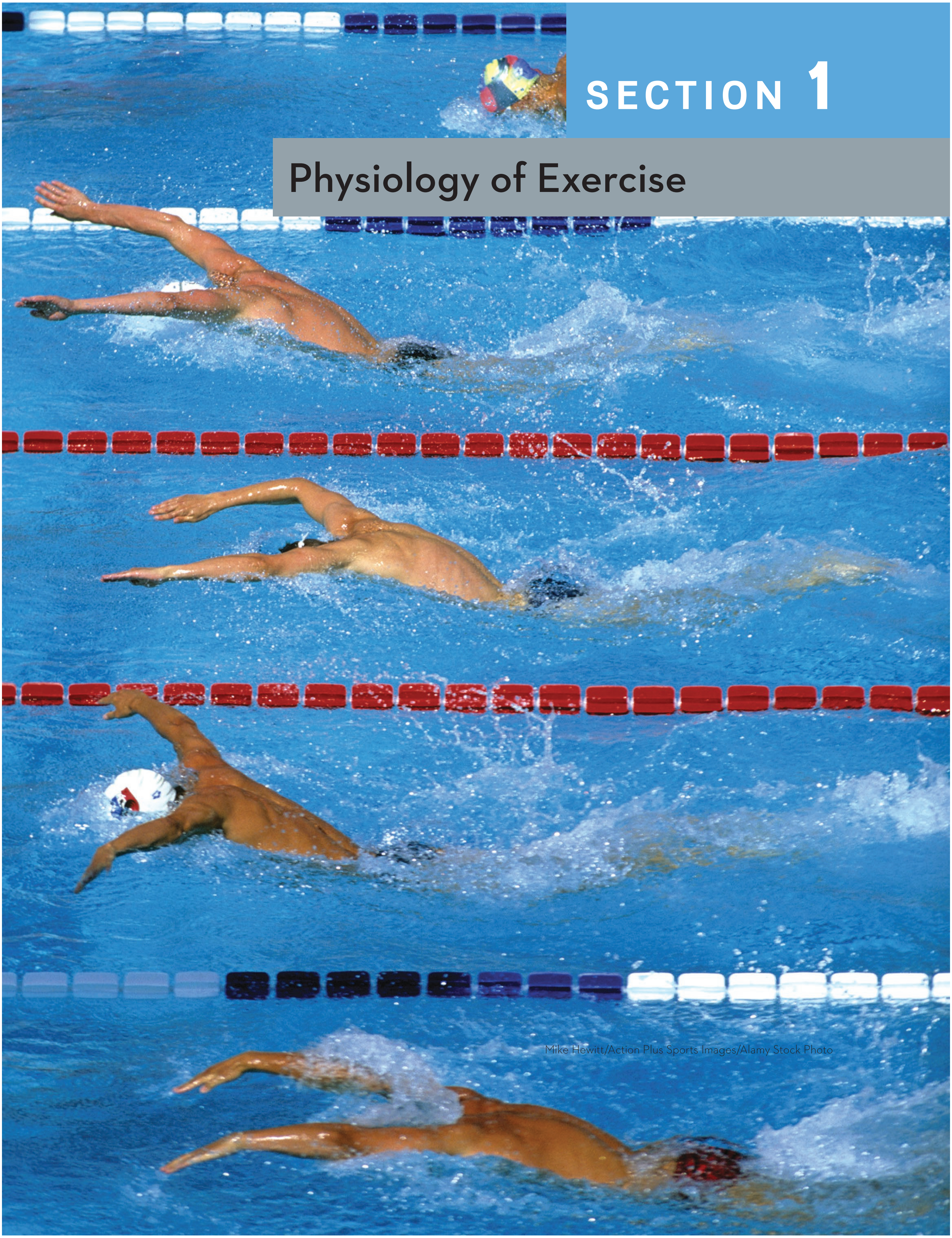


The Winning Edge

How do athletes find the "extra edge" that can make the difference between victory and defeat? These features explain the science behind a winning performance.

SECTION 1

Physiology of Exercise



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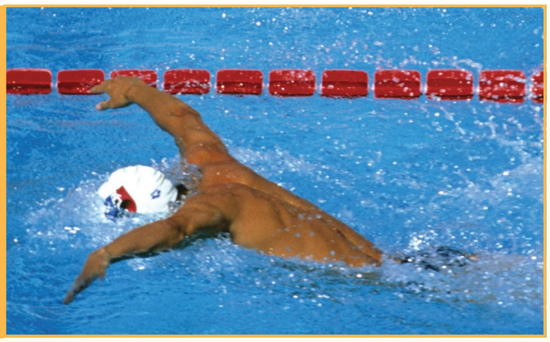

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Introduction to Exercise Physiology

Objectives

By studying this chapter, you should be able to do the following:

1. Define physiology and exercise physiology.
2. Identify the key milestones in the evolution of exercise physiology from 1900 to the present.
3. List the steps involved in the scientific method.
4. Describe the two major categories of research designs.
5. Identify the two primary venues where research in exercise physiology is performed.
6. Define basic and applied research.
7. Explain evidence-based practice in medicine and exercise science.
8. Outline the process of using a search engine to explore the literature and retrieve peer-reviewed research studies on topics related to exercise physiology.
9. Identify and discuss the purpose of the individual sections that comprise a scientific research report.
10. Describe five key steps that can be used to evaluate the quality of a research study.
11. Identify six important professional organizations linked to exercise physiology and sports science.
12. Explain the benefits associated with achieving fitness/clinical certifications offered by professional organizations.
13. List five career opportunities for students with a bachelor's degree in exercise physiology and kinesiology.

Outline

Key Terms

applied research
basic research
case study
dependent variable
evidence-based practice
experimental research
independent variable
nonexperimental research
placebo
translational research

Physiology is the study of living organisms. Physiologists study questions related to how cells, tissues, and organ systems function in humans and other animals. Exercise physiology is a branch of physiology that investigates how a single bout of exercise (acute exercise) and repeated bouts of exercise (i.e., training programs) impact cells, tissues, and organ systems of the body. Moreover, exercise physiology explores the responses to acute exercise and exercise training at environmental extremes (e.g., high altitudes or high ambient temperatures) to determine the impact of these influences on our ability to perform and adapt to exercise training. Exercise physiology studies are also performed on young and old individuals, both healthy and those with disease. This important research helps to understand the role that regular exercise plays in the prevention of disease or rehabilitation from chronic illnesses. Finally, exercise physiology also explores many sports performance-related questions such as "Does an individual require a genetic gift to become an outstanding distance runner, or can anyone become an exceptional endurance athlete with sufficient training?" "What adaptations occur in your skeletal muscles when you engage in regular resistance training?" "What changes occur in your cardiovascular system and skeletal muscles as a result of an endurance-training program?" The answers to these and many other questions related to human performance, nutrition, and the health-related benefits of exercise are provided throughout this book.

Our knowledge about exercise physiology has expanded over the years because of the quantity and quality of research in this field. This chapter provides an introduction into exercise physiology research, professional organizations, and careers available to individuals with training in exercise physiology and kinesiology. More specifically, we begin with a brief history of research advances in exercise physiology and then describe the research process. We will also discuss how to read and understand research studies published in scientific journals. This chapter ends with an overview of exercise physiology professional organizations, exercise/fitness certifications, and careers in exercise physiology and related fields.

MILESTONES IN THE EVOLUTION OF EXERCISE PHYSIOLOGY

A brief overview of some of the milestones in the growth of exercise physiology will help you understand where the field of exercise physiology has been and where its future lies. Note that throughout the text, a variety of eminent exercise physiology scientists are highlighted in various chapters as physiology subject matter is presented. We hope that by linking a particular scientist to a major accomplishment in exercise physiology, the history of exercise physiology will come alive and will stimulate you to learn more about this exciting field.

This section provides a brief history of the evolution of exercise physiology research. Because a detailed history of exercise physiology is beyond the scope of this chapter, we will limit our discussion to highlights of the field during the past 120 years. Further, although numerous organizations and hundreds of scientists have contributed to the advancement of exercise physiology, space limitations will permit the discussion of only a few milestone events during the evolution of this field.

Milestones in Exercise Physiology—the Early Years (1900–1950)

Figure 0.1 provides a graphical timeline for selected milestones in exercise physiology research during the first half of the twentieth century. During this early period of exercise physiology, almost all of the research was descriptive. That is, most published reports during this time period merely described the physiological responses (i.e., heart rate, blood pressure, etc.) to a bout of acute exercise. Nonetheless, work performed by the Danish scientists August Krogh and Johannes Linhard was an exception to this practice. These investigators often collaborated on research that explored how the body regulates major organ systems during exercise. For example, one of their important studies investigated the control of both the respiratory and circulatory system during exercise (11).

The Nobel Prize in Physiology or Medicine is awarded yearly for outstanding discoveries in the fields of life sciences or medicine that benefit mankind. This prize is one of the five Nobel Prizes established in 1895 by the Swedish chemist Alfred Nobel, the inventor of dynamite. In the long history of the Nobel Prize in Physiology or Medicine, only three researchers have been honored with this award for research focused on skeletal muscles or exercise physiology. The first of these Nobel winners was August Krogh. Krogh was awarded the Nobel Prize in Physiology or Medicine in 1920 for his work on the mechanisms responsible for the regulation of capillary blood flow to skeletal muscles. Further, the British scientist A.V. Hill and the German scientist Otto Meyerhof shared the 1922 Nobel Prize in Physiology or Medicine for their research in two separate areas of exercise physiology. Hill was recognized for his discovery that skeletal muscle produces heat during exercise whereas Meyerhof's recognition originated from his contributions to our understanding of the

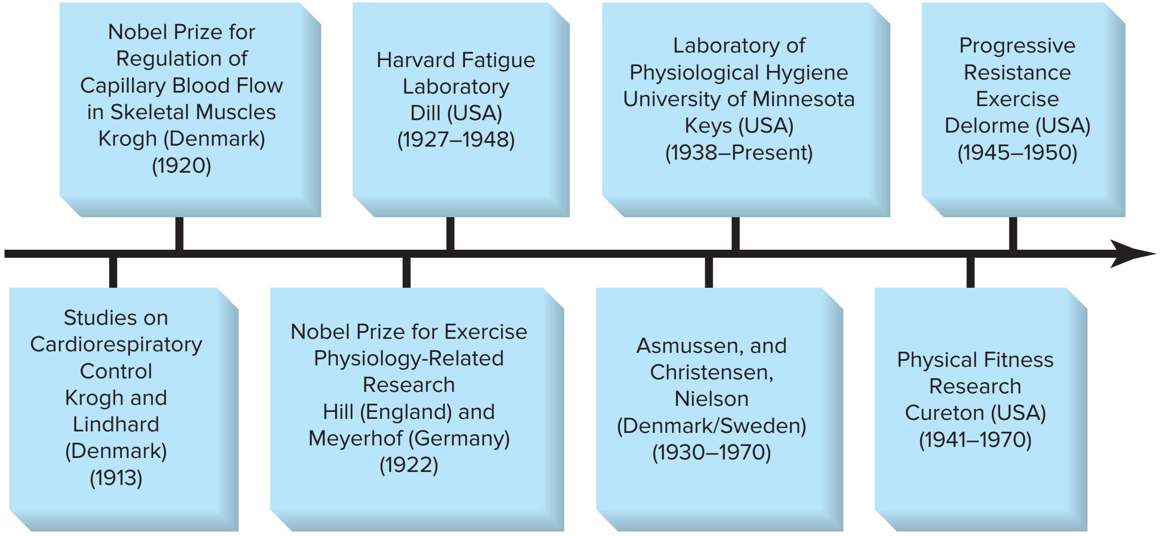

Figure 0.1 **Selected historical milestones in exercise physiology that occurred during 1900–1950. See text for details.**

relationship between exercise intensity, oxygen consumption, and lactate metabolism.

The establishment of the Harvard Fatigue Laboratory in 1927 was an important event in exercise physiology research in the United States. Interestingly, this exercise physiology research laboratory was established by the Harvard Business School. While a business school seems like an unlikely home for human physiology research, this lab was created during a time in history when human fatigue in industrial factories was of major interest. The Harvard Fatigue Laboratory was founded by Lawrence Henderson and directed by David Bruce Dill. Without question, the Harvard Fatigue Lab played a major role in stimulating research in exercise physiology worldwide. Indeed, this laboratory was the research home for not only outstanding American physiologists, but also was regularly visited by renowned exercise physiologists from around the world. During the lab's existence (1927–1948), researchers in the Harvard Fatigue Laboratory published over 350 research studies on a variety of exercise physiology topics along with many investigations on the influence of the environment on exercise tolerance. The Harvard Fatigue Laboratory also played a key role in training young exercise physiologists. For instance, after earning their PhD's from Harvard University, both Sid Robinson and Steven Horvath became internationally renowned exercise and environmental physiologists. Sid Robinson performed research throughout his career at Indiana University whereas Steven Horvath directed the Institute for Environmental Stress at the University of California, Santa Barbara. More details about the Institute of Environmental Stress will be provided later.

Founded by Ansel Keys in 1937, the Laboratory of Physiological Hygiene at the University of Minnesota was an important research center for exercise physiology, environmental, and nutrition research. During his long and productive research career (1930–1975), Keys completed many important studies focusing on nutrition. One of Keys' most novel investigations determined the physiological effects of starvation on the body. This important study established nutritional guidelines for treating individuals following starvation and these guidelines have been used many times in developing countries experiencing economic hardship and famine. Keys was also involved in research that developed nutritional strategies for the U.S. military. During World War II, American soldiers were provided food called K-rations. These K-rations (K for Keys) were small portions of high caloric food developed by Keys to provide sufficient energy for solders during combat. Key's research also played an important role in establishing that high blood cholesterol is a risk factor for heart disease. Finally, Keys and his wife Margaret published the first book on the health benefits of a low-fat, Mediterranean diet.

Henry Longstreet Taylor was also an important researcher at the Laboratory of Physiological Hygiene from 1941 until his death in 1983. Taylor's undergraduate education was at Harvard where he worked in the Harvard Fatigue Laboratory. After completing his PhD from the University of Minnesota, he joined forces with Ansel Keys to perform many important research studies including his influential work that helped to establish maximal oxygen uptake (VO_2 max) as the standard measure of cardiorespiratory work capacity. Notably, Taylor was also responsible for training several graduate students in exercise physiology including Ellsworth Buskirk who advanced to an outstanding career in exercise and environmental research at Penn State University.

Outside of the United States, three Danish scientists (Erling Asmussen, Eril Hohwu-Christensen, and Marius Nielson) became important contributors to exercise physiology research during the 1930 to 1940s. These Scandinavian scientists were friends as graduate students, and following graduation they often collaborated on research. Because of their long-time friendship and scientific collaboration, the three were nicknamed the "three musketeers" by August Krogh (17). Together, their studies added significantly to the foundation of our understanding of exercise physiology.

Another key event in the evolution of exercise physiology research in the United States occurred when Thomas Cureton founded the exercise physiology laboratory at the University of Illinois in 1941. During his long career, Dr. Cureton trained numerous exercise physiology graduate students who later achieved distinguished research careers by themselves. Work by Cureton and his students provided some of the early evidence supporting the physiological rationale that regular exercise promotes a healthy body.

Another important exercise physiology milestone during the first half of the twentieth century was the research performed by Dr. Thomas Delorme investigating the therapeutic benefits of resistance training. Delorme was a physician assigned to a U.S. military hospital that treated soldiers injured during World War II. Because of his personal interest in resistance training, Delorme reasoned that resistance exercise training can play an important role in rehabilitative therapy for injured soldiers. To test his prediction, Delorme completed several experiments revealing that progressive resistance exercise accelerated strength gains and recovery in patients suffering from bone and soft tissue injures. Much of Delorme's work was published between1948 and 1950 and this early work provided the scientific basis for the resistance training protocols used in physical therapy today (3–5, 7).

IN SUMMARY

- Numerous Scandinavian scientists contributed to the growth of exercise physiology studies during the first half of the twentieth century.
- August Krogh, A.V. Hill, and Otto Meyerhof won the Nobel Prize for research related to skeletal muscle and exercise physiology.
- The Harvard Fatigue Laboratory played a central role in exercise physiology research in the United States from 1927 to 1948.
- Ansel Keys founded the Laboratory for Physiological Hygiene at the University of Minnesota in 1937; this important research center completed many important exercise and nutritional studies from the 1930s to 1970s.
- Thomas Cureton performed numerous fitness studies and mentored many exercise physiology graduate students at the University of Illinois from 1941 to 1970.
- Thomas DeLorme was a pioneer in research investigating the benefits of progressive resistance exercise on recovery from injury

Milestones in Exercise Physiology—Second Half of the Twentieth Century (1951–2000)

The second half of the twentieth century represented a period of significant achievements in exercise physiology research (Fig. 0.2). A key event that stimulated growth in exercise physiology research and education was the founding of the American College of Sports Medicine (ACSM). This professional organization was created to promote scientific research, education, and the practical applications of exercise science and sports medicine. Since ACSM's formation in 1954, this prominent professional organization has grown

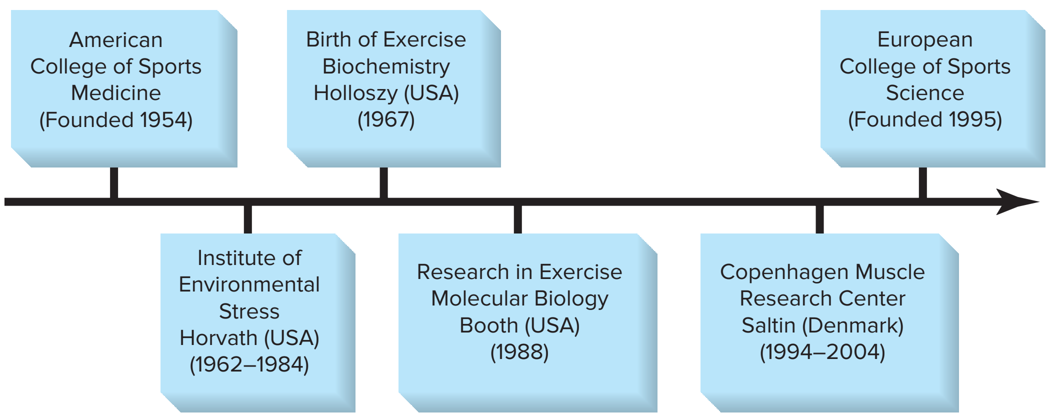

Figure 0.2 Selected historical milestones in exercise physiology that occurred during 1951–2000. See text for details.

to more than 50,000 members and ACSM has become the world's largest professional organization associated with exercise physiology and sports science. Importantly, ACSM has advanced the field of exercise physiology in several important ways. First, in the 1970s, ACSM established certification programs and continuing education for fitness professionals as well as clinicians; these ACSM certifications continue today and are widely accepted around the world as the gold standard for health and fitness qualifications. Further, the ACSM annual meeting has become an important venue for exercise physiology and sports medicine research. Finally, ACSM contributes to educational growth in exercise physiology by publishing two highly regarded peer-reviewed research journals (i.e., (1) *Medicine and Science in Sports and Exercise*; and (2) *Exercise and Sport Sciences Reviews*).

The closing of the Harvard Fatigue Laboratory in 1948 created a void in both exercise physiology research and venues for postdoctoral training. Fortunately, this void was filled in 1962 when Steven Horvath founded the Institute of Environmental Stress at the University of California-Santa Barbara (Fig. 0.3). Similar to the Harvard Fatigue Laboratory, this institute conducted exercise physiology/environmental physiology research studies and was a postdoctoral training ground for many exercise/environmental physiologists. Indeed, during its 22-year existence, the Institute of Environmental Stress produced hundreds of important research studies and provided exceptional training for many exercise physiologists who later achieved national and international acclaim for their research.

In addition to the outstanding exercise research performed at the Institute of Environment Stress, Dr. John Holloszy also established a robust research program in exercise physiology at Washington University (Saint Louis, Missouri) in the late 1960s. Indeed, many consider John Holloszy to be the "father of exercise biochemistry research" following his 1967 landmark study demonstrating that endurance exercise training increases mitochondrial volume in the trained skeletal muscles. During his 50+ year career, Dr. Holloszy published more than 380 research reports and served as the mentor for approximately 100 postdoctoral research fellows.

Although the first molecular biology study on the effects of exercise on muscle was published by Sandy Williams and colleagues (18), it is widely agreed that the advocacy and research of Dr. Frank Booth launched the field of exercise molecular biology in 1988 (17) (Fig. 0.4). Dr. Booth inspired exercise physiology researchers by his own research and his writings that challenged exercise physiologists to pursue mechanistic questions by using the tools of molecular biology. A review of the exercise physiology literature today reveals that Dr. Booth has achieved his vision as the research literature is now filled with studies using the

Figure 0.3 Dr. Steven Horvath standing in front of an environmental chamber designed to simulate high-altitude conditions. Dr. Horvath was the founder and director of the Institute of Environmental Stress at the University of California-Santa Barbara from 1962 to 1984.
Dr. Peter Horvath

Figure 0.4 Dr. Frank Booth played a major role in the evolution of research in exercise molecular biology.
Dr. Frank Booth

tools of molecular biology to address important questions related to exercise-induced changes in tissues.

Dr. Bengt Saltin provided major contributions to exercise physiology research from the 1960s till his death in 2018. Dr. Saltin was trained in both medicine and physiology at the Karolinska Institute in Sweden where he worked under the tutorage of the esteemed physiologist Per-Olof Astrand. In 1994, Dr. Saltin organized the Copenhagen Muscle Research Center at the University of Cophenhagen, Denmark. Saltin was joined in this venture by other outstanding Scandinavian exercise physiologists including Henrik Galbo, Erik Richer, Bente Kiens, Carsten Juel, Niels Secher, and Bente Pedersen (8). The research focus of this center was on the regulation of muscle metabolism and its coupling to blood flow; these investigations generated numerous significant research reports (8).

Finally, another important milestone in exercise physiology that transpired during the second half of the twentieth century was the formation of the European College of Sport Science in 1995. Similar to ACSM, this important professional organization is dedicated to the promotion of both education and research in exercise science. Moreover, the European College of Sport Science annual meeting has become an important venue for distribution of the latest research in both exercise physiology and biomechanics.

IN SUMMARY

- The American College of Sports Medicine was founded in 1954 and has played an important role in promoting exercise physiology research during the past 60+ years.
- The Institute of Environmental Stress was founded by Steven Horvath in 1962. This important laboratory was an epicenter for exercise and environmental research in the United States from 1962 to 1984.
- John Holloszy's research at Washington University played a major role in launching the era of exercise biochemistry research.
- Frank Booth was instrumental in promoting research in exercise molecular biology.
- The Copenhagen Muscle Research Center was founded by Bengt Saltin in 1994 and this research laboratory made significant contributions to exercise physiology research.
- The European College of Sport Science was formed in 1995; this important professional organization promotes research in both exercise physiology and biomechanics.

Milestones in Exercise Physiology Research—2001 to Present

Figure 0.5 highlights both the emergence of several important research tools and discoveries in exercise physiology that occurred during the first 20 years of the twenty-first century. Moreover, note the large increase in the number of published research papers during the past 19 years (Fig. 0.6). Indeed, the number of exercise-related research studies published each year increased from 13,968 in 2000 to 52,551 papers published in 2019.

In the previous sections describing important milestones in the history of exercise physiology, we emphasized both individuals and professional organizations that made significant contributions to the advancement of this field. In this final section describing the historical evolution of exercise physiology, we highlight advancements in research tools and describe several important experimental discoveries in exercise physiology that have ensued during the past two decades. We begin with a discussion of advances in research tools.

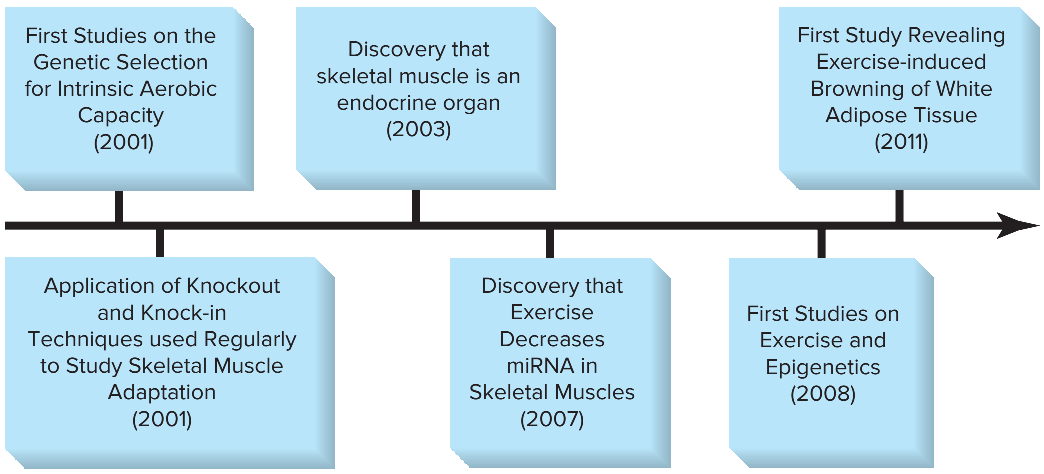

Figure 0.5 Selected historical milestones in exercise physiology that occurred from 2001 to the present time. See text for details.

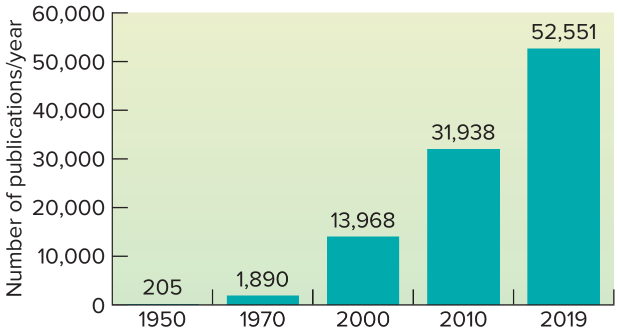

Figure 0.6 Illustration of the growth of scientific publications in exercise physiology from 1950 to 2019.

Advances in Research Tools in Exercise Physiology In recent years, our knowledge in exercise physiology has grown significantly, in part, because of advancements in research technology. For example, the technique to manipulate genes within cardiac or skeletal muscle fibers is a powerful experimental tool to study muscle physiology. Although the technology to add or remove genes from cells of laboratory animals evolved during the 1980 to 1990s, these tools were not widely used in exercise physiology research until early in the twenty-first century. Indeed, because of these powerful tools, research progress has been remarkable during the past two decades. A brief overview of how these tools have advanced our understanding of exercise physiology follows.

The development of genetic tools have markedly improved our grasp of cardiac and skeletal muscle function. Indeed, these tools have provided techniques used to study the influence of a single protein on muscle fiber function. As you may recall from a previous course, a gene is a segment of DNA located in the nucleus of cells; each gene directs the synthesis of a specific protein (see Chap. 2 for details). The term "gene knockout" refers to a technique to inactivate a specific gene (i.e., gene is knocked out of the cell). The end result of a gene knockout procedure is that following the "knockout" the affected cells cannot manufacture the specific protein generated by this gene. Therefore, the ability to knockout specific genes in a tissue (e.g., skeletal muscle) has provided researchers with a powerful tool to determine what happens to the function of a skeletal muscle fiber when a specific protein is removed; these types of experimental approaches reveal important information about the function of individual muscle proteins.

A second research tool that has advanced our understanding of the function of a particular protein is gene transfection. In brief, gene transfection results in overexpression of a single protein. The term "gene overexpression" refers to the "switching on" of genes to produce more of a specific protein. One of the ways to promote gene overexpression in cells is to transfect additional copies of the gene into the cells of interest. Transfection is the process of inserting specific genes into cells; this typically results in the increased manufacture of the protein generated by this gene. The ability to transfect genes into skeletal muscle and overexpress specific proteins has provided researchers in exercise physiology with another powerful tool to understand the functions of specific muscle proteins. For example, exercise training increases the production of several different proteins in the trained muscle fibers. Because training increases the abundance of numerous proteins in the trained muscle fibers, it is impossible to determine the unique role that each of these proteins play in the training-induced improvement in muscle performance. However, using the technique of gene transfection, it becomes possible to investigate the unique role that an individual protein plays in muscle function by transfecting and overexpressing a specific gene that increases the abundance of a single protein.

The relative contribution of genes versus environmental factors to define the observed differences in endurance capacity between individuals is difficult to investigate in humans (2). In an effort to overcome this problem, researchers have used selective breeding to produce rats with intrinsically low- and high-endurance capacities (10). The development of these genetically unique animals eliminates the environmental factors that influence a high-endurance capacity and provides researchers with a powerful tool to study the physiological factors that contribute to a high-endurance capacity (2).

Novel Research Discoveries in Exercise Physiology (2001 to Present) Numerous important research breakthroughs have occurred during the past two decades. In this section, we discuss four innovative findings in exercise physiology: (1) Skeletal muscle is an endocrine organ; (2) Exercise stimulates the production of microRNA in skeletal muscle; (3) Exercise training promotes epigenetic changes in skeletal muscle; and (4) Endurance exercise training results in a "browning" of white fat cells. Let's begin with a brief discussion about the unique finding that skeletal muscle is an endocrine organ.

In 2003, Bente Pedersen and colleagues discovered that skeletal muscle is an endocrine organ (15). This important research revealed that contracting skeletal muscles release peptides (chains of amino acids) into the circulation; these circulating muscle-released "hormones" are called "myokines." After release from the contracting muscle fiber, myokines move into the circulation and travel throughout the body to exert changes in various tissues. The fact that skeletal muscle produces and releases myokines provides a new understanding of how skeletal muscles communicate with other organs such as adipose tissue (i.e., fat cells), bone, liver, pancreas, and the brain (9). Research in myokines is advancing rapidly and this new knowledge will markedly improve our understanding of how muscular exercise promotes good health.

A microRNA (abbreviated miRNA) is a small RNA molecule that regulates gene expression by binding to messenger RNA and preventing the production of a particular protein. Although miRNA was discovered in 1993, these molecules were not recognized as important biological regulators in skeletal muscle until the early 2000s. Notably, in 2007, it was discovered that overload of skeletal muscles (i.e., resistance exercise training) decreases two specific miRNA in skeletal muscle fibers (14). This key finding suggests that changes in miRNA levels may play a key role in skeletal muscle adaptation in response to exercise training (12, 13). Research in the exciting field of exercise-induced changes in miRNAs continues and there is much more to be learned about this important topic.

Epigenetics is a new and rapidly developing field that investigates the changes in gene function that occur without alterations in the DNA sequence of the gene. An example of a mechanism that can produce an epigenetic change is DNA methylation (i.e., adding a methyl group (CH3) to DNA); this modification of DNA can result in a change in gene expression. The discovery that exercise promotes epigenetic changes in tissues occurred in 2008. Since this original finding, many studies have confirmed that regular muscular exercise results in epigenetic changes within numerous tissues and these changes can be passed along to offspring of trained individuals (6). Importantly, several of the exercise-induced epigenetic changes within body tissues likely contribute to the health benefits of exercise. Future studies in this expanding field will provide additional insight into how different modes and doses of exercise (i.e., intensity, frequency, and duration) promote these epigenetic changes in the body.

Another important discovery is the finding that endurance exercise modifies the structure and function of white fat cells to improve overall health. While it has long been known that regular exercise training promotes adaptations to white adipose tissue including a decrease in fat cell size, growing research reveals that exercise-induced changes in white fat cells plays an important role in the health benefits of exercise. A brief summary of this exciting new area of exercise physiology research follows.

The major fat depots in the body are white fat cells located beneath the skin (subcutaneous fat cells) and in the abdominal cavity (visceral fat cells). Recent animal studies reveal that endurance exercise training results in a "browning" of white fat cells.

Figure 0.7 **Dr. Laurie Goodyear is a professor of medicine at Harvard University. Dr. Goodyear is a leader in research investigating the impact of endurance exercise training on fat cells.**

Dr. Laurie Goodyear

Much of this research has been guided by the laboratory of Dr. Laurie Goodyear at Harvard University (Fig. 0.7). Investigations by Dr. Goodyear and colleagues reveals that this exercise-induced "browning effect" of white fat cells results from increases in mitochondrial volume (cellular organelles responsible for aerobic production of ATP) and other proteins involved in energy metabolism. This apparent conversion of white fat cells to brown fat cells is important because an increase in the abundance of brown adipose tissue is associated with increased resting energy expenditure and improvements in blood glucose control. Therefore, this exercise-induced browning of white fat cells might be an important mechanism by which endurance exercise training improves health and reduces the risk of developing type II diabetes (16). Research in this new area of exercise physiology remains at an early stage and future studies are required to determine if the exercise-induced changes in white adipose tissue that occur in animals also happen in humans.