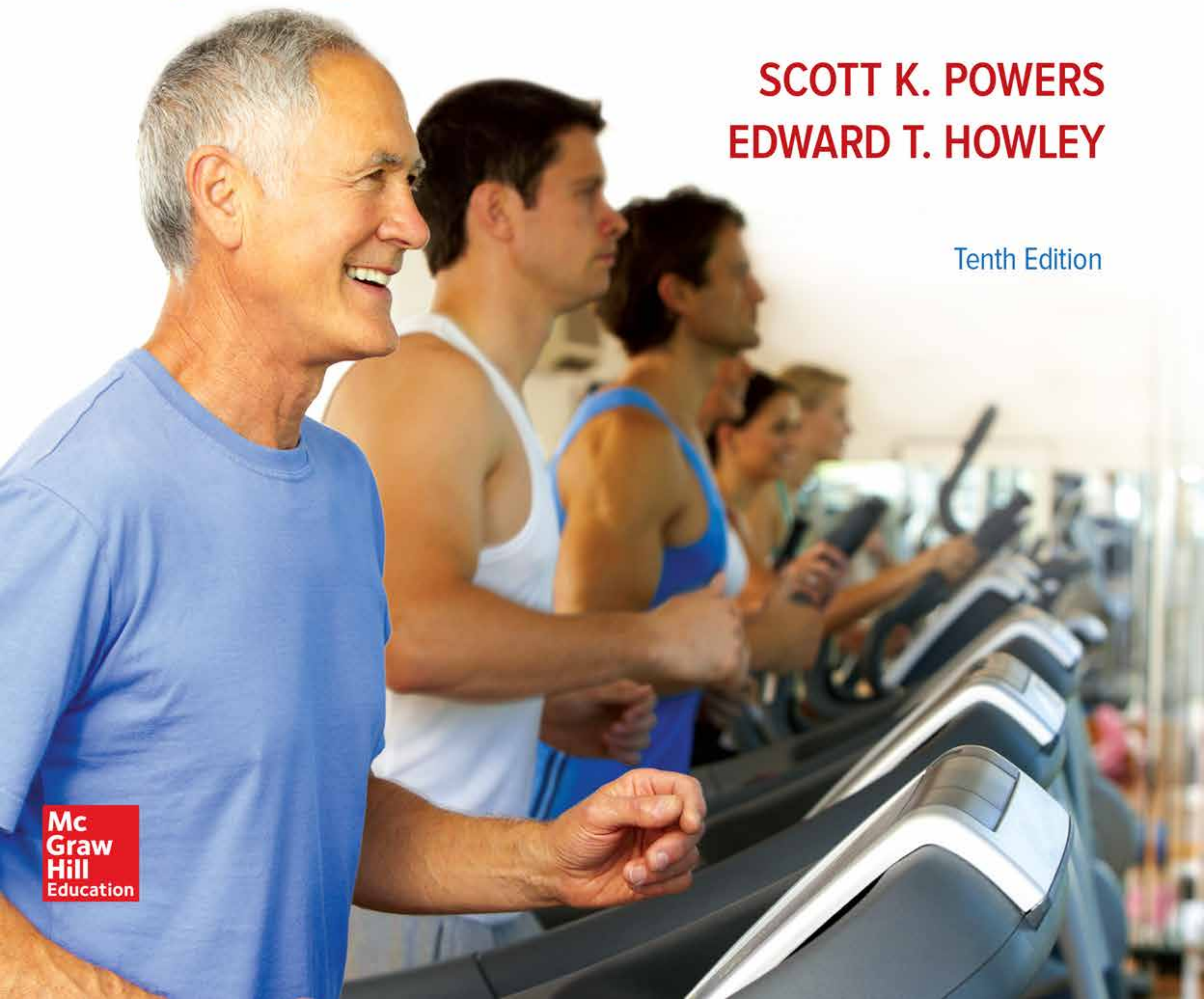



EXERCISE PHYSIOLOGY

Theory and Application to Fitness and Performance

SCOTT K. POWERS
EDWARD T. HOWLEY

Tenth Edition



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Theory and Application to Fitness and Performance

TENTH EDITION

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

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Preface

As with all previous editions, the tenth edition of *Exercise Physiology: Theory and Application to Fitness and Performance* is intended for students interested in exercise physiology, clinical exercise physiology, human performance, kinesiology/exercise science, physical therapy, and physical education. The overall 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 exercise tests to evaluate cardiorespiratory fitness and information on exercise training for improvements in health-related physical fitness and sports performance.

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 the composition of their class. 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 tenth edition of our book has undergone *major* revisions and highlights the latest research in exercise physiology. Indeed, 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 new edition has been markedly updated. Specifically, each chapter has been revised and updated to include new and amended 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 made the tenth edition more complete and up-to-date:

- **Chapter 0:** Two new "A Look Back" features were added to highlight the careers of Elsworth Buskirk and Frances Hellebrandt.
- **Chapter 1:** New suggested readings and updated references were added.
- **Chapter 2:** Updated discussion on the role that heat shock proteins play in the cellular adaptation to stress.
- **Chapter 3:** New illustration and box feature added to highlight the structure and function of the two subpopulations of mitochondria found in skeletal muscle.
- **Chapter 4:** Several figures were upgraded along with the addition of a new section on measurement of $\dot{V}O_2$ max.
- **Chapter 5:** Numerous new and improved figures were added along with a new table highlighting hormonal changes during exercise. New information added on the impact of both growth hormone and anabolic steroids on skeletal muscle size and function.
- **Chapter 6:** Update on the latest research findings on the impact of exercise on the immune system added.
- **Chapter 7:** Expanded discussion on muscle sense organs (i.e., Golgi tendon organ and muscle spindles). New information added about the exceptions to the size principle. Further, a new section was added discussing how central pattern generators control movement during exercise. Additionally, Clinical Applications 7.2 was expanded

to discuss the risk of chronic traumatic encephalopathy (CTE) in contact sports.

- **Chapter 8:** Updated information on the role that satellite cells play in exercise-induced skeletal muscle hypertrophy was added. Further, new information on how exercise training alters the structure and function of the neuromuscular junction was included in this chapter. Lastly, new research on the cause of exercise-related skeletal muscle cramps was added along with a new box feature discussing new pharmacological approaches to prevent muscle cramps.
- **Chapter 9:** Updated information on the prediction of maximal heart rates in older individuals. Expanded discussion highlighting new research on the regulation of muscle blood flow during exercise. Added a new A Closer Look 9.3 to discuss the impact of body position on stroke volume during exercise.
- **Chapter 10:** Updated with the newest research findings on control of breathing during exercise. Also, new research on sex differences in breathing during exercise was also added.
- **Chapter 11:** Several new and improved illustrations were added along with an expanded discussion on intracellular acid-base buffer systems. New section added about how buffering capacity differs between muscle fiber types and how exercise training impacts muscle buffer systems. Further, the chapter was improved by the addition of the latest information on nutritional supplements used to improve acid-base balance during exercise.
- **Chapter 12:** Several new illustrations were added along with a discussion on the impact of a hot environment on exercise performance. Further, a box feature was added to discuss the influence of precooling on exercise performance. Lastly, the discussion of exercise in a cold environment was expanded to discuss the latest research findings.
- **Chapter 13:** Numerous new illustrations were included in this greatly revised chapter along with the addition of two new box features that discuss (1) the impact of genetics on $\dot{V}O_2$ max and (2) the influence of endurance exercise training on skeletal muscle mitochondrial volume and turnover. Moreover, a new section was also added to discuss muscle adaptations to anaerobic exercise. Finally, new and expanded information on the signaling events that lead to resistance training-induced muscle growth was included.
- **Chapter 14:** Major revision to this chapter provides more focus on the importance of physical activity in the prevention of chronic diseases. Section on metabolic syndrome was extensively revised to include an expanded discussion of how physical activity and diet impacts the inflammation that is linked to chronic disease.
- **Chapter 15:** Wide revision of the screening process for individuals entering a physical activity program along with new figures. Latest information regarding the new national standards for $\dot{V}O_2$ max.
- **Chapter 16:** Updated references and suggested readings.
- **Chapter 17:** New information on ACSM's physical activity recommendations for all special populations. New figure added on effect of age on $\dot{V}O_2$ max along with a new Clinical Application box discussing physical activity and risk of cancer.
- **Chapter 18:** Extensive revision to include new information on vitamins and minerals along with the new dietary guidelines for Americans. Widespread revision of the discussion on how to determine body composition along with a focused analysis of the causes and treatment for obesity.
- **Chapter 19:** New "A Look Back" on Brenda Bigland-Ritchie along with an expanded discussion on the linkages between central and peripheral fatigue. Update on the role that free radicals play in exercise-induced muscle fatigue and new information on why Kenyan runners are often successful in long distance races.
- **Chapter 20:** Chapter updated with latest research findings plus the addition of new suggested readings.
- **Chapter 21:** Three new box features added to address the following: (1) What are the physiological limits to the enhancement of endurance performance?; (2) Do compression garments benefit athletes during competition and recovery from training?; and (3) Treatment of delayed onset muscle soreness.
- **Chapter 22:** New illustration was added along with the latest research findings on the female athlete triad coupled with a discussion of the recent proposal to replace the term *female athlete triad* with new terminology.
- **Chapter 23:** Updated information from the 2016 ACSM position stand on nutrition and performance along with an expanded

discussion of the benefits and problems associated for athletes training with low levels of muscle glycogen. Expanded discussion of protein requirements for athletes along with a new discussion of the importance of consuming carbohydrates during long distance endurance events.

- **Chapter 24:** Updated discussion on the "Live High Train Low" training strategy. New recommendations for prevention and treatment of heat illnesses coupled with new information on how the WBGT Index fits into planning workouts in hot/humid environments.
- **Chapter 25:** Latest data on the prevalence and use of ergogenic aids. New information of dietary supplements for improving endurance performance along with additional information on the impact of stretching on performance.

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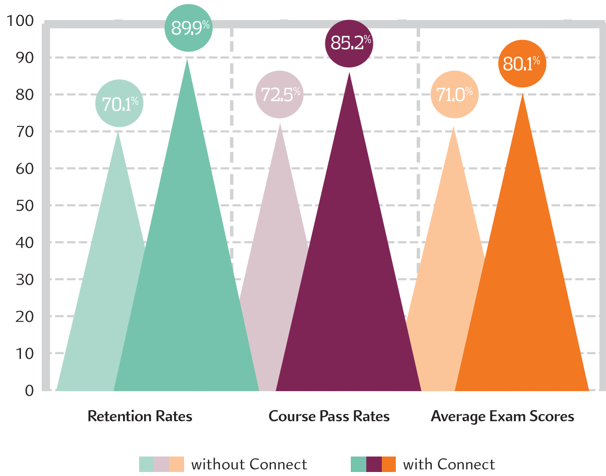

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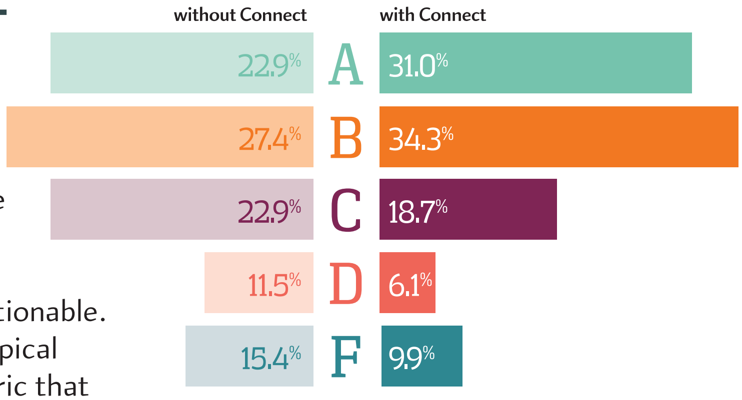

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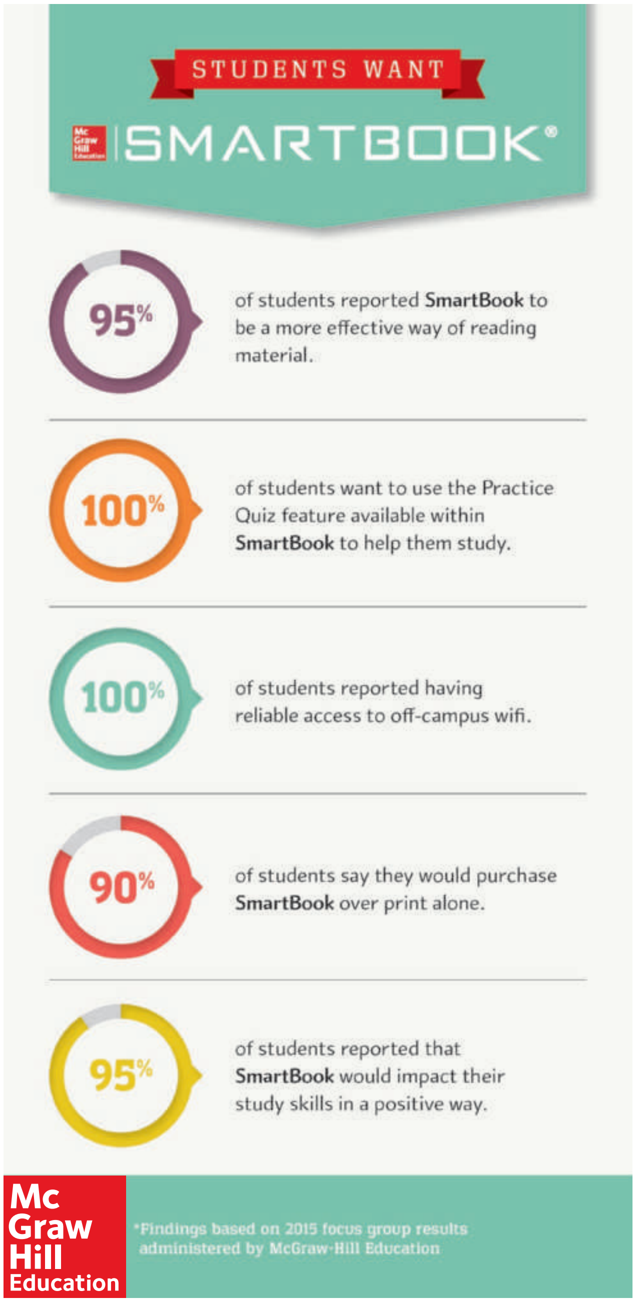

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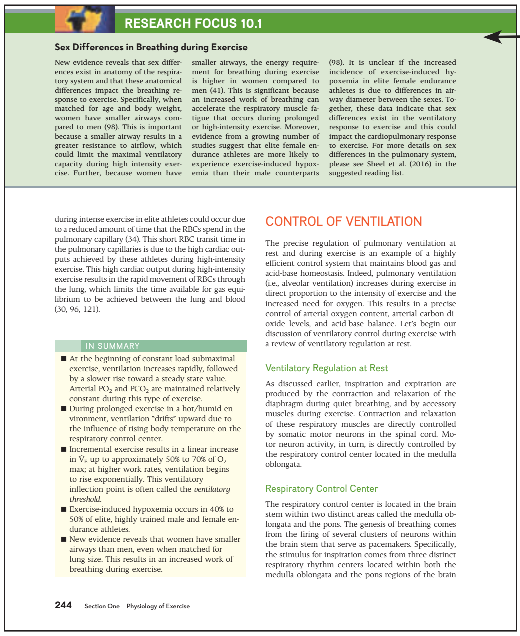

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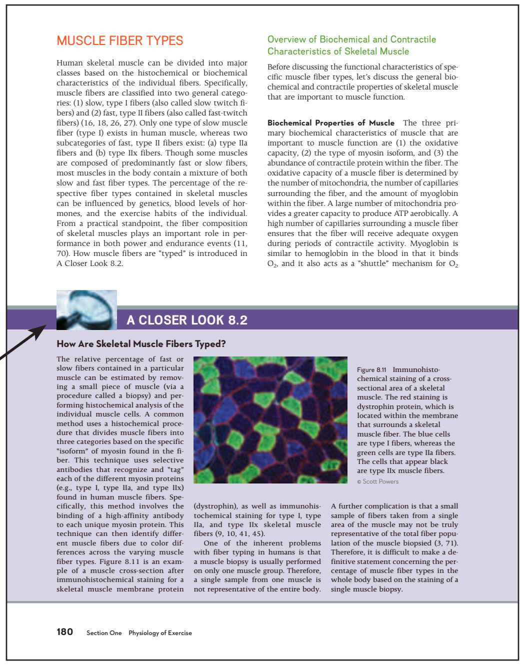

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Clinical Applications

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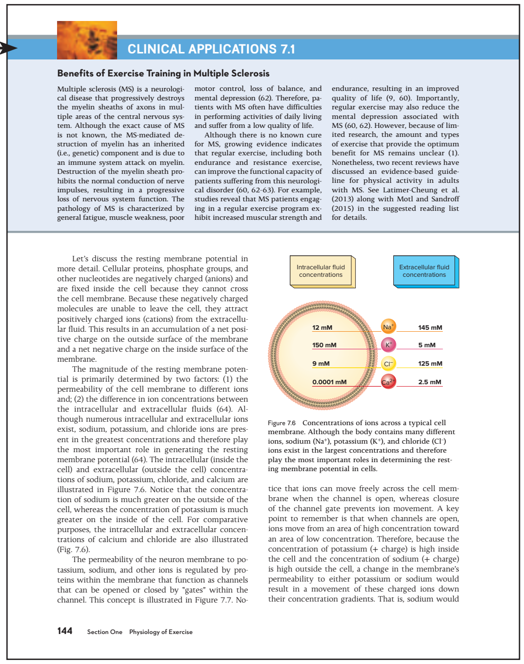

CLINICAL APPLICATIONS 7.1

Benefits of Exercise Training in Multiple Sclerosis

Multiple sclerosis (MS) is a neurological disease that progressively destroys the myelin sheaths of axons in multiple areas of the central nervous system. Although the exact cause of MS is not known, the MS-mediated destruction of myelin has an inherited (i.e., genetic) component and is due to an immune system attack on myelin. Destruction of the myelin sheath prohibits the normal conduction of nerve impulses, resulting in a progressive loss of nervous system function. The pathology of MS is characterized by general fatigue, muscle weakness, poor motor control, loss of balance, and mental depression (62). Therefore, patients with MS often have difficulties in performing activities of daily living and suffer from a low quality of life.

Although there is no known cure for MS, growing evidence indicates that regular exercise, including both endurance and resistance exercise, can improve the functional capacity of patients suffering from this neurological disorder (60, 62-63). For example, studies reveal that MS patients engaging in a regular exercise program exhibit increased muscular strength and endurance, resulting in an improved quality of life (9, 60). Importantly, regular exercise may also reduce the mental depression associated with MS (60, 62). However, because of limited research, the amount and types of exercise that provide the optimum benefit for MS remains unclear (1). Nonetheless, two recent reviews have discussed an evidence-based guideline for physical activity in adults with MS. See Latimer-Cheung et al. (2013) along with Motl and Sandroff (2015) in the suggested reading list for details.

Let's discuss the resting membrane potential in more detail. Cellular proteins, phosphate groups, and other nucleotides are negatively charged (anions) and are fixed inside the cell because they cannot cross the cell membrane. Because these negatively charged molecules are unable to leave the cell, they attract positively charged ions (cations) from the extracellular fluid. This results in an accumulation of a net positive charge on the outside surface of the membrane and a net negative charge on the inside surface of the membrane.

The magnitude of the resting membrane potential is primarily determined by two factors: (1) the permeability of the cell membrane to different ions and; (2) the difference in ion concentrations between the intracellular and extracellular fluids (64). Although numerous intracellular and extracellular ions exist, sodium, potassium, and chloride ions are present in the greatest concentrations and therefore play the most important role in generating the resting membrane potential (64). The intracellular (inside the cell) and extracellular (outside the cell) concentrations of sodium, potassium, chloride, and calcium are illustrated in Figure 7.6. Notice that the concentration of sodium is much greater on the outside of the cell, whereas the concentration of potassium is much greater on the inside of the cell. For comparative purposes, the intracellular and extracellular concentrations of calcium and chloride are also illustrated (Fig. 7.6).

The permeability of the neuron membrane to potassium, sodium, and other ions is regulated by proteins within the membrane that function as channels that can be opened or closed by "gates" within the channel. This concept is illustrated in Figure 7.7. Notice that ions can move freely across the cell membrane when the channel is open, whereas closure of the channel gate prevents ion movement. A key point to remember is that when channels are open, ions move from an area of high concentration toward an area of low concentration. Therefore, because the concentration of potassium (+ charge) is high inside the cell and the concentration of sodium (+ charge) is high outside the cell, a change in the membrane's permeability to either potassium or sodium would result in a movement of these charged ions down their concentration gradients. That is, sodium would

Figure 7.6 Concentrations of ions across a typical cell membrane. Although the body contains many different ions, sodium (Na^+), potassium (K^+), and chloride (Cl^-) ions exist in the largest concentrations and therefore play the most important roles in determining the resting membrane potential in cells.

144 Section One Physiology of Exercise

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.

THE WINNING EDGE 11.1

Exercise Physiology Applied to Sports

Nutritional Supplements to Buffer Exercise-Induced Acid-Base Disturbances and Improve Performance

Because intramuscular acidosis is associated with muscle fatigue, numerous studies have explored nutritional supplements to increase buffering capacity in hopes of improving athletic performance during high-intensity exercise. Indeed, it appears that supplements including sodium bicarbonate, sodium citrate, and beta-alanine have the potential to improve buffering capacity and enhance exercise performance during, high-intensity exercise. Let's discuss these supplement strategies to improve muscle buffering capacity in more detail.

Sodium bicarbonate. Bicarbonate is a buffer that plays an important role in maintaining both extracellular and intracellular pH, despite its inability to freely cross the muscle membrane (i.e., sarcolemma). Although controversy exists (2), many studies conclude that performance during high-intensity exercise is improved when athletes ingest sodium bicarbonate prior to exercise (6, 7, 26, 30-32, 34, 37, 40). Specifically, results from numerous studies reveal that boosting the blood-buffering capacity by ingestion of sodium bicarbonate increases time to exhaustion during high-intensity exercise (e.g., 80% to 120% $\dot{V}O_2$ max). For example, a recent survey of the scientific literature reveals that sodium bicarbonate is effective in improving a 60-second "all out" exercise bout by approximately 2% (5). Further, laboratory studies employing repeated bouts of high-intensity exercise (i.e., >100% $\dot{V}O_2$ max) have reported that ingestion of sodium bicarbonate prior to exercise can enhance performance by more than 8% (18). In addition to these laboratory studies, evidence exists that sodium bicarbonate is also beneficial to sport performance in activities where the metabolic demands are primarily anaerobic, such as judo, swimming, and water polo (18).

It appears that sodium bicarbonate improves physical performance by increasing the extracellular buffering capacity, which, in turn, increases the transport of hydrogen ions out of the muscle fibers (38). This would reduce the interference of hydrogen ions on muscle ATP production and/or the contractile process itself.

In deciding whether to use sodium bicarbonate prior to a sporting event, an athlete should understand the risks associated with this decision. Ingestion of sodium bicarbonate in the doses required to improve blood-buffering capacity can cause gastrointestinal problems, including diarrhea and vomiting (7, 37).

Sodium Citrate. Similar to sodium bicarbonate, sodium citrate is another agent capable of increasing extracellular buffering capacity (18). The question of whether ingestion of sodium citrate can improve exercise performance during high-intensity exercise remains controversial because experimental results are often inconsistent. Nonetheless, a review of the research literature suggests that although low doses of sodium citrate does not improve performance, ingestion of high doses of sodium citrate (i.e., >0.5 grams/kilogram body weight) improves performance during high-intensity cycling exercise lasting 120 to 240 seconds (18).

Unfortunately, similar to sodium bicarbonate, ingestion of high doses of sodium citrate can produce undesired side effects such as nausea, gastrointestinal discomfort, and headaches. Therefore, before deciding whether to use sodium citrate prior to competition, athletes should consider the negative side effects associated with the use of sodium citrate.

Beta-alanine. Recent evidence suggests that supplementation with beta-alanine can play a beneficial role in protecting against exercise-induced acidosis and improve performance during short, high-intensity exercise (39). Beta-alanine is a non-essential amino acid produced in the liver, gut, and kidney. However, fasting blood levels of beta-alanine are low indicating that endogenous synthesis of this amino is limited.

The link between beta-alanine and protection against acidosis is linked to the fact that beta-alanine is an important precursor for the synthesis of carnosine in skeletal muscle. As discussed in the text, carnosine is a small molecule (dipeptide) found in the cytoplasm of excitable cells (i.e., neurons, skeletal and cardiac muscle fibers) (18). Carnosine has several important physiological functions including the ability to buffer hydrogen ions and protect against exercise-induced decreases in cellular pH (18).

The availability of beta-alanine is the rate limiting factor for carnosine synthesis in muscle fibers. However, supplementation (2 to 3 grams/day) with beta-alanine for >2 weeks results in a 60% to 80% increase in muscle carnosine levels. Importantly, this increase in muscle carnosine levels is associated with a 3% to 5% increase in muscle buffering capacity (18). Theoretically, this increase in intracellular buffering capacity could translate into improvements in performance during high-intensity exercise. In this regard, growing evidence suggests that beta-alanine supplementation improves high-intensity exercise performance in both running and cycling events lasting 1 to 4 minutes (18). Interestingly, some of these studies have recorded performance improvements of 12% to 14% (18).

The only known side effect of beta-alanine supplementation is paraesthesia (tingling of the skin); this sensation begins within 20 minutes after ingestion and lasts up to 60 minutes (18). Although harmless, paraesthesia is unpleasant and, several investigations have reported that paraesthesia can be avoided by staggering dosing throughout the day (18).

Final words of caution on use of "supplement buffers" to improve exercise performance. Regardless of the type of buffer ingested, extremely large doses of any buffer can result in severe alkalosis and pose negative health consequences. Another important consideration in the use of any ergogenic aid is the legality of the drug. In regard to the use of acid-base buffers, some sports regulatory agencies have banned the use of sodium buffers during competition. See Sahlin (2014) and Junior et al. (2015) in Suggested Readings for detailed information about the possible ergogenic effects of sodium bicarbonate, sodium citrate, and beta-alanine.

Chapter Eleven Acid-Base Balance during Exercise 263

EXERCISE PHYSIOLOGY

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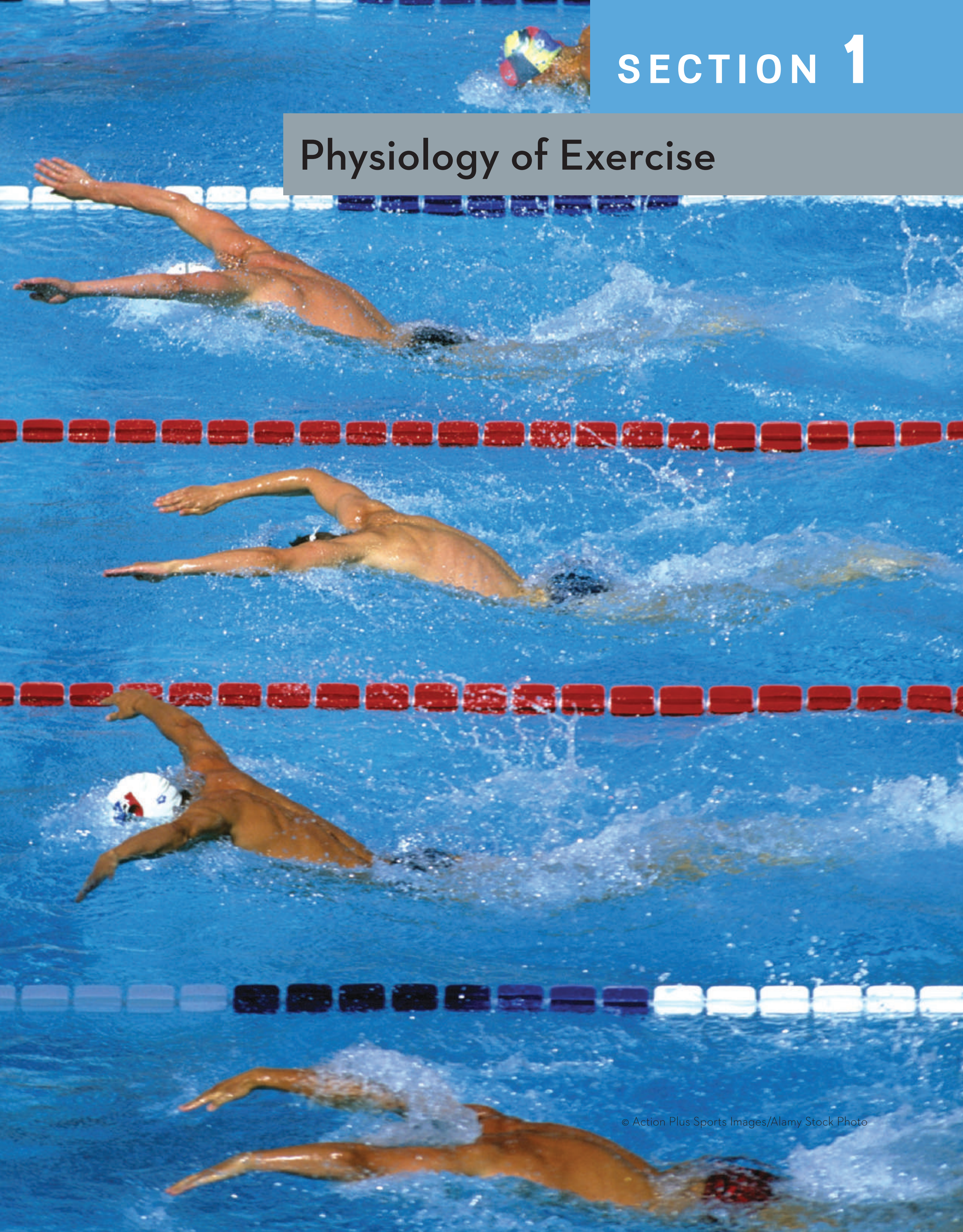
SECTION 1

Physiology of Exercise



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Introduction to Exercise Physiology

Objectives

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

1. Describe the scope of exercise physiology as a branch of physiology.
2. Describe the influence of European scientists on the development of exercise physiology.
3. Name the three Nobel Prize winners whose research work involved muscle or muscular exercise.
4. Describe the role of the Harvard Fatigue Laboratory in the history of exercise physiology in the United States.
5. Describe factors influencing physical fitness in the United States over the past century.
6. List career options for students majoring in exercise science or kinesiology.

Outline

Brief History of Exercise Physiology 3
- European Heritage 3
- Harvard Fatigue Laboratory 4

Physiology, Physical Fitness, and Health 6

Physical Education to Exercise Science and Kinesiology 8

Graduate Study and Research in the Physiology of Exercise 9

Professional and Scientific Societies and Research Journals 11
- Training in Research 11

Careers in Exercise Science and Kinesiology 12

Does one need to have a "genetic gift" of speed to be a world-class runner, or is it all due to training? What happens to your heart rate when you take an exercise test that increases in intensity each minute? What changes occur in your muscles as a result of an endurance-training program that allows you to run at faster speeds over longer distances? What fuel—carbohydrate or fat—is most important when running a marathon? Research in exercise physiology provides answers to these and similar questions.

Physiology is the study of the function of tissues (e.g., muscle, nerve), organs (e.g., heart, lungs), and systems (e.g., cardiovascular). Exercise physiology extends this to evaluate the effect of a single bout of exercise (acute exercise) and repeated bouts of exercise (i.e., training programs) on these tissues, organs, and systems. In addition, the responses to acute exercise and training may be studied at high altitude or in extremes of heat and humidity to determine the impact of these environmental factors on our ability to respond and adapt to exercise. Finally, studies are conducted on young and old individuals, both healthy and those with disease, to understand the role of exercise in the prevention of or rehabilitation from various chronic diseases.

Consistent with this perspective, we go beyond simple statements of fact to show how information about the physiology of exercise is applied to the prevention of and rehabilitation from coronary heart disease, the performances of elite athletes, and the ability of a person to work in adverse environments such as high altitudes. The acceptance of terms such as *sports physiology, sports nutrition,* and *sports medicine* is evidence of the growth of interest in the application of physiology of exercise to real-world problems. Careers in athletic training, personal-fitness training, cardiac rehabilitation, and strength and conditioning, as well as the traditional fields of physical therapy and medicine, are of interest to students studying exercise physiology. We will expand on career opportunities later in the chapter.

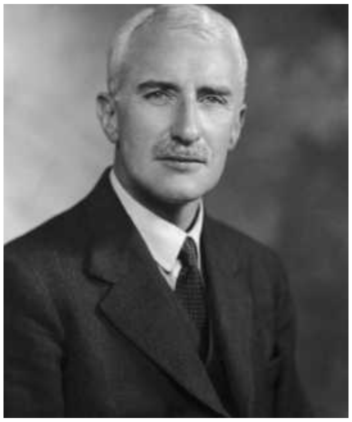
In this chapter, we provide a brief history of exercise physiology to help you understand where we have been and where we are going. In addition, throughout the text a variety of scientists and clinicians are highlighted in a historical context as subject matter is presented (i.e., muscle, cardiovascular responses, altitude). We hope that by linking a person to a major accomplishment within the context of a chapter, history will come alive and be of interest to you.

BRIEF HISTORY OF EXERCISE PHYSIOLOGY

The history of exercise physiology represents a global perspective involving scientists from many different countries. In this section, we begin with the impact European scientists have had on the development of exercise physiology. We then describe the role of the Harvard Fatigue Laboratory in the growth of exercise physiology in this country.

European Heritage

A good starting place to discuss the history of exercise physiology in the United States is in Europe. Three scientists, A. V. Hill of Britain, August Krogh of Denmark, and Otto Meyerhof of Germany, received Nobel Prizes for research on muscle or muscular exercise (13). Hill and Meyerhof shared the Nobel Prize in Physiology or Medicine in 1922. Hill was recognized for his precise measurements of heat production during muscle contraction and recovery, and Meyerhof for his discovery of the relationship between the consumption of oxygen and the measurement of lactic acid in muscle. Hill was trained as a mathematician before becoming interested in physiology. In addition to his work cited for the Nobel Prize, his studies on humans led to the development of a framework around which we understand the physiological factors related to distance-running performance (6) (see Chap. 19).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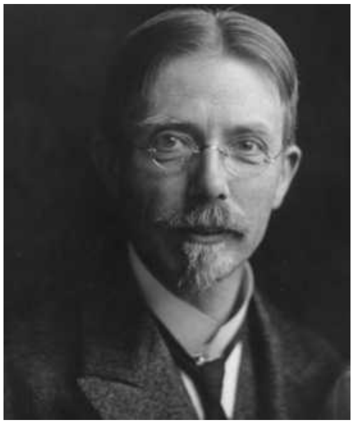
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A. Archibald V. Hill, B. August Krogh, C. Otto F. Meyerhof