PHYSIOLOGICAL BASIS OF EXERCISE

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Summary

Skeletal muscle consists of slow-oxidative fibers, fast-oxidative glycolytic fibers, and fast-glycolytic fibers. Slow-oxidative fibers are recruited during low-intensity endurance events, such as marathon running. Fast-oxidative-glycolytic fibers, generating more force but fatiguing easily, are used mainly during shorter, higher-intensity endurance events, such as in a 1 mile run. Fast-glycolytic fibers are predominantly used in highly explosive events, such as the 100 m dash. Endurance training increases the number of mitochondria in the slow-oxidative and fast-oxidative glycolytic fibers and also the capillaries around them. On the other hand, short-duration, high-intensity exercise, such as weight lifting, affects primarily the fast-glycolytic fibers, resulting in muscle hypertrophy. Energy for short-duration and high-intensity exercise is provided by the immediate energy system, including ATP and creatine phosphate, and anaerobic glycolysis, while it is mainly provided by oxidative phosphorylation for endurance-type exercise.

Both heart rate and stroke volume increase proportionally to exercise intensity, the latter leveling off earlier. The increase in stroke volume results from increased contractility of the ventricle and venous return. Most of the increase in cardiac output goes to the exercising muscles, heart, and skin during exercise. Endurance training increases capillary density in muscles and stroke volume but decreases heart rate with no change in cardiac output at rest. Systolic blood pressure increases during exercise with either no change or a slight decrease in diastolic pressure. Plasma volume decreases owing to increased capillary filtration and more oxygen is extracted from the blood by the active muscles during exercise. The respiratory system provides adequate aeration of the blood, even in heavy exercise. Therefore, respiration is mainly controlled by neurogenic mechanisms during exercise. The exercise capacity is usually limited by the ability of the heart to pump blood to the muscles. The respiratory muscles can, however, be weak. Regular aerobic exercise can provide a prolonged, healthy life span by decreasing heart attacks, brain strokes, and excess weight by its beneficial effects on metabolism, circulation, and blood lipid profile.

1. Introduction

During exercise, many adjustments occur in our body functions. They require a series of interactions involving practically all of the body's systems, for example:

- skeletal muscles contract and relax moving the body or body parts,
- cardiovascular and respiratory systems work together to provide oxygen to the cells and also to remove CO_2,
- skin helps to maintain body temperature by dissipating heat,
- the nervous system coordinates activities, and
- digestive functions are slowed down.

The functions of many of these systems can be observed during exercise. For example, electrical activity of the heart can easily be recorded by heart rate meters, which are already used by many athletes to follow their individual endurance programs. Electrical

activity of the individual muscles can also be recorded during training for later analysis to evaluate the efficacy of the program (see Figure 1).

Figure 1. Measurement of the electrical activity of quadriceps femoris muscles of an athlete with a portable electromyograph.The coach is attaching the surface electrodes before the running test. Surface electrodes cause no pain and do not hamper the performance. The device stores the signals for later computer analysis.

Once the muscle fiber is stimulated by an impulse from the nervous system, contraction processes become activated. They involve specific protein molecules—actin and myosin—and energy systems to provide the fuel necessary for contraction. As can be seen, physical activity—exercise—is a complicated process.

Basically, athletic activities can be classified as power, speed, and endurance events. Examples of these are the shot put, the 400 m sprint, and the marathon run, respectively. Skeletal muscle has three energy systems, each of which is used in these three types of activities:

- the immediate energy system, including ATP and creatine phosphate (CP)—these two together are also known as the phosphagen system—in cytosol;
- anaerobic glycolysis in cytosol; and
- oxidative phosphorylation in mitochondria.

In this article, the functions of skeletal muscle; muscle fiber types and their importance in exercise; muscle fitness, adaptation to activity and energy systems of the skeletal muscle; alterations in cardiovascular functions, such as heart rate, stroke volume, distribution of cardiac output, muscle blood flow, blood pressure, and blood itself during exercise, respiratory adjustments occurring in exercise; and finally fatigue are briefly reviewed.

If physical activity is decreased, skeletal muscles become progressively smaller in diameter. The amount of contractile proteins decreases (called atrophy) owing to the lack of contractions, which may result from denervation, such as in stroke and paralysis or long-term immobilization of the muscle (e.g., because of bone, cartilage, or tendon trauma).

2. Skeletal Muscle

2.1. Sliding Filaments

Skeletal muscle usually refers to a number of muscle bundles bound together by connective tissue, and usually linked to bones by bundles of collagen fibers—tendons—located at each end of the muscle. In addition to the elastic components in series like the tendons, the muscles also contain significant amounts of elastic components in parallel with the contractile elements (i.e., muscle fibers). One of the such components is titin. These elastic components store energy, for instance in running, when the leg hits the ground. Their role increases with speed and may mean an increase of 60–70% in efficiency. Each muscle bundle is composed of thousands of individual muscle cells or fibers. Each fiber has a diameter of between 10 and 100 μm and a length that may extend up to 20 cm. Most of the fiber cytoplasm is filled with myofibrils, which extend from one end to the other. The number of myofibrils varies from several hundred to thousands per fiber depending on the fiber diameter.

Each myofibril is divided along its length into sarcomeres, which are the functional units of the contractile system. Each sarcomere contains two types of filaments: thick and thin. The thick filaments are composed almost entirely of the contractile protein myosin, while the thin filaments contain the contractile protein actin, as well as two other proteins: troponin and tropomyosin, which play important roles in regulating contraction.

In order for the cross bridges to bind to actin, the tropomyosin molecules must be removed from their actin-blocking positions. This occurs when calcium binds to specific binding sites on troponin. Cytosolic calcium-ion concentration determines the number of cross bridges, which can bind to actin and exert force on the thin filaments. Changes in cytosolic calcium concentration are controlled by electrical events occurring in the plasma membrane.

During muscle contraction, cross bridges extending from the surface of the thick filaments make contact with the thin filaments and exert force on them. The actin filaments slide past the myosin filaments by cross-bridge attachments between the two filaments, so that the length of the sarcomere becomes shorter owing to the inward movement of the actin.

The globular end of myosin has an active enzymatic site that catalyzes the breakdown of adenosine triphosphate (ATP), thus releasing the chemical energy stored in ATP needed for the cross-bridge movement. ATP is also needed to pump Ca^{+2}-ions back into the sarcoplasmic reticulum and thus to break the link of myosin and actin at the end of a contraction (see *Excitation–Contraction Coupling in Skeletal Muscle*).

2.2. Skeletal Muscle Fiber Types

In human beings, all skeletal muscle fibers do not have the same mechanical and metabolic characteristics. Different types of muscle fibers can be identified on the basis of their maximal velocities of shortening (fast and slow) and the major pathway they use to form ATP (oxidative and glycolytic) (see *Muscle Energy Metabolism*). Muscle fibers are generally classified as slow-oxidative (SO) and fast-glycolytic fibers. Fast-glycolytic fibers are further classified as fast-oxidative-glycolytic (FOG) and fast-glycolytic (FG) fibers.

Fast and slow fibers contain myosin isozymes that differ in the maximal rates at which they split ATP to release energy for contraction or to allow relaxation. Fibers containing myosin with high ATPase activity are classified as fast fibers, and those containing myosin with a lower ATPase activity are slow fibers.

Slow oxidative fibers contain numerous mitochondria and have a high capacity for oxidative phosphorylation. These fibers may contain significant amounts of lipid but less glycogen. Most ATP produced by such fibers is dependent upon blood oxygen supply and fuel molecules. Numerous capillaries surround these fibers. They also contain large amounts of oxygen-binding myoglobin, which increases the oxygen extraction and provides a small intracellular store of oxygen. Myoglobin gives a dark red color, and thus oxidative fibers are often referred to as red muscle fibers.

In contrast, fast fibers, also called glycolytic fibers, have few mitochondria, but they possess a high concentration of glycolytic enzymes and a large store of glycogen. Corresponding to their limited use of oxygen, relatively few capillaries surround them, and they contain little myoglobin. They are called white muscle fibers owing to their lighter color compared with the red oxidative fibers.

The glycolytic fibers generally have much larger diameters than oxidative fibers. The larger the diameter, the greater the maximal tension it can develop (i.e., the greater its strength).

A motor unit is a single motor neuron and the muscle fibers it innervates. When a single SO motor neuron stimulates its fibers, far fewer muscle fibers contract than when a single FG motor neuron stimulates its fibers. Consequently, FG motor fibers reach peak tension faster and collectively generate more force than SO fibers do.

Skeletal muscle fibers also differ in their capacity to resist fatigue. FG fibers fatigue rapidly, whereas SO fibers are very resistant to fatigue. The fast-oxidative fibers have an intermediate capacity to resist fatigue. The characteristics of skeletal muscle fiber types are summarized in Table 1.

System 1	**Slow-oxidative (SO) fibers**	**Fast-oxidative-glycolytic (FOG) fibers**	**Fast-glycolytic (FG) fibers**
System 2	**Slow-twitch**	**Fast-twitch A**	**Fast-twitch B**
System 3	**Type I**	**Type IIa**	**Type IIb**

Primary source of ATP production	Oxidative phosphorylation	Oxidative phosphorylation	Anaerobic glycolysis
Type of myosin-ATPase activity	Slow	Fast	Fast
Mitochondria	Many	Many	Few
Myoglobin content	High (red muscle)	High (red muscle)	Low (white muscle)
Glycolytic enzyme activity	Low	Intermediate	High
Glycogen content	Low	Intermediate	High
Fiber diameter	Small	Intermediate	Large
Motor unit size	Small	Intermediate	Large
Contraction velocity	Slow	Fast	Fast
Motor unit force	Low	High	High
Capillaries	Many	Many	Few
Rate of fatigue	Slow	Intermediate	Fast

Table 1. Characteristics of muscle fiber types. System 1 is used in the text to classify muscle fibers, but names used in other systems are also shown.

In humans, all muscles have varying percentages of the FG and SO muscle fibers. Depending on the proportions of the fiber types present, muscles can differ considerably in their maximal contraction speed, strength, and fatigability. For instance, the gastrocnemius muscle has a higher preponderance of FG fibers, which gives it the capability of forceful and rapid contraction, used, for example, in jumping. On the other hand, the soleus muscle has more SO muscle fibers and is used for prolonged muscle activity in the legs.

In general, SO muscle fibers have a high level of aerobic endurance. The ability to maintain muscular activity for a prolonged period is known as muscular endurance. Since SO fibers have high aerobic endurance, they are recruited most often during endurance events (e.g., marathon running) and during most daily activities, where the muscle force requirements are low (e.g., walking).

FG muscle fibers, on the other hand, have relatively poor aerobic endurance. The FG fibers are used rather infrequently in normal, low-intensity activity, but they are predominantly used in highly explosive events. They are presumed to become active when the anaerobic threshold is exceeded during exercise; then the lactic acid level starts to increase in blood and in the muscle fibers a bit earlier.

FOG motor units generate considerably more force than SO motor units, but they fatigue easily because of their limited endurance. Thus, FOG fibers appear to be used mainly during shorter, higher-intensity endurance events, such as the 1 mile run or the 400 m swim.

Athletic training has not been shown to change the relative proportions of FG and SO fibers. Instead, this seems to be determined almost entirely by genetic inheritance, and this in turn could determine the basic athletic capabilities of different individuals. In practical terms the motor nerve dictates the type of the muscle fibers in a motor unit. If a nerve innervating a slow motor unit is cut and reunited with another nerve fiber innervating a fast motor unit, this formerly fast motor unit can gradually change and become a slow one.Varying percentages of fiber types in quadriceps muscles of some athletes from different disciplines are shown in Table 2.

	Slow-oxidative fibers (%)	**Fast-glycolytic fibers (%)**
Marathon runners	82	18
Weight lifters	45	55
Sprinters	37	63
Average human	45	55

Table 2. Percentages of SO versus FG fibers in quadriceps muscles of athletes compared to an average human

Horse races interest many people. Horses also participate in the Olympic Games—of course not alone. A Finnish horse (fast fibers composing about 70% of their muscle) can run 12.5 m in a second, while a quarter horse (fast fibers composing about 90% of their muscle) can run 20 m in a second—clear indications of their different properties, which have developed over generations.

Muscles also contain totally different types of muscle fibers in their muscle spindles. These structures sense the tension of the muscle. The sensitivity of the muscle spindles can be adjusted by the contraction of their specialized intrafusal muscle fibers. The spindles are in parallel with the main muscle or extrafusal fibers. The gamma-motoneurons control the tension level of the intrafusal muscle fibers in spindles whereas the alfa-motoneurons regulate the extrafusal muscle fibers, which are responsible for the muscle contraction itself.

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Biographical Sketches

Mustafa Gül is a Doctor of Medicine (MD). He graduated from the Faculty of Medicine, Ege University, Turkey, 1987, and specialized in physiology (the same faculty, 1991). He was in the Department of

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His special interests in research are biotransformation and adaptation to chemical loading, biomonitoring of toxicants, comparative biochemical toxicology; muscle metabolism and function; and ergonomics.

He has contributed 266 papers to refereed journals, 72 to proceedings, written 55 reviews, and 30 books and book chapters. He serves on the editorial board of four international journals and is at present the European Journal Editor of *Pathophysiology*.

Of his postgraduate students (32 in Biotransformation, 27 in Muscle Metabolism and Physiology, and five others) 12 serve as professors in China, Finland, Greece, Sweden, and the United States.