

CHAPTER 1

Overview of Electromyography in Ergonomics

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OVERVIEW OF ELECTROMYOGRAPHY IN ERGONOMICS

William Marras, PhD

INTRODUCTION

Electromyography (EMG) is a tool that can be very valuable in ergonomic studies if it is used correctly and if the associated limitations are appreciated. An understanding of the use of EMG transcends many areas of knowledge including physiology, instrumentation, recording technology, and signal processing and analysis. This chapter provides a general overview of these areas so that an appreciation for how these areas interact and impact on the effective use of EMG. The following chapters will review, in depth, all aspects of EMG use.

GENERAL USES

Electromyography can be a very useful analytical method if applied under proper conditions and interpreted in light of basic physiological, biomechanical, and recording principles. Through proper design of ergonomic studies and by recognition of the limitations of the interpretive process, EMG can be a useful tool in the evaluation of work performance.

The use of EMG is not warranted as a general method for indiscriminately assessing all work situations. The ergonomist should have an idea about which muscles will be affected by the work, before the use of EMG is considered. The ergonomist should also be aware that 1) unless the work place conditions exhibit several key features or 2) certain additional measures of the work positions are taken simultaneously, the amount of information derived from an EMG recording is extremely limited. The key to successful EMG use is to understand the nature of the signal collected, thereby separating the useful information of the signal from the noise and artifact. Thus, procedures require careful calibration, instrumentation, data treatment, and interpretation and use of an experimental design that does not violate the assumptions inherent to the relationships associated with EMG and muscle function.

Electromyography is one of several methods used for analyzing the performance associated with the work place. If the work is heavy, the best techniques often include analysis through physiological measures, such as oxygen consumption, that provide a general measure of whole body work. Electromyography can be used for the same purpose provided that many muscles of the body are assessed during the performance of a task. However, EMG is used more often to evaluate lighter, repetitive

work where the activity of specific muscles is of interest. Ergonomic analyses often include use of this technique when comparing the specific musculoskeletal stress (in given muscles) associated with various work positions, postures, or activities and for validating of ergonomic principles. It also is used as input to biomechanical models that describe the synergistic effects of muscle activities on a joint. The use of EMG, thus, is appropriate when it is suspected that a specified muscle or group of muscles is affected adversely because of the design of the work place.

As the information gained from an EMG signal becomes more quantitative and useful, the complexities involved in muscle testing increase. Applied ergonomic studies usually are involved with an evaluation of worker methods, workplace layout, work pace, or tool design. Most ergonomic studies, therefore, involve investigations that use only a limited number of direct or derived measures. Conditions under which these various measures can be determined and examples of the application and use of these measures in ergonomic investigations will be discussed throughout the following chapters.

RECORDING TECHNIQUE

For purposes of recording EMG in ergonomic studies, two types of electrodes are available. Surface EMG techniques are much more common, unless there is a specific justification for using a fine wire method. In general, surface EMG will represent the activity of individual muscles or muscle groups over which the electrodes are placed. Although muscles that are smaller and of a deep location are more difficult to record from with surface EMG, the major interest probably is in the larger muscles or in muscle groups. In this case, appropriate methods are available for the recording of the EMG. The methods, advantages, and limitations associated with the use of these techniques and the immobilization process necessary are specified in the following chapters. Controls necessary to guarantee a high quality signal also are detailed.

EQUIPMENT AND SIGNAL CONDITIONING

The typical equipment configuration needed to perform an ergonomic study is depicted schematically in

Figure 1-1. Once the signal has been amplified by the preamplifiers, if they exist, it is amplified further by the main amplifiers. After that, the signal is filtered and may be conditioned or processed by a number of means that will be discussed in Chapter 4. For example, processing may consist of rectifying, averaging, integrating, defining a linear envelope, or performing root-mean-square processing of the signal. Only the raw signal may be recorded and interpreted by itself. Most EMG data, however, usually are subjected to some type of processing. Recommended recording devices are FM tape, a strip chart or light pen recorder, or a computer through an analog-to-digital (A-D) converter. If spectral analyses are of interest, these must be performed on a computer. Details of the instrumentation and interpretations are included in subsequent chapters.

SIGNAL INTERPRETATION

To determine the on-off state, force, or fatigue present within a muscle, some form of EMG signal treatment usually is recommended and often is required. The type of EMG signal treatment appropriate for an ergonomic study is a function of 1) the nature of the desired information and 2) the ability of the experimenter to design the process so that the EMG assumptions mentioned earlier are not violated.

The most basic information that can be derived from an EMG signal is knowledge of whether the muscle of interest was in use during an exertion. Little or no signal processing is required to determine this type of information. The experimenter simply needs to make sure the signal is noise and artifact free and does not contain cross talk. If the raw or processed signal exhibited activity, the muscle was in use during the exertion. Usually, it is of interest simply to note whether the muscle was in use or to document the duration of activity during a specified exertion.

If the muscle force is of interest, the EMG signal can be processed by either hardware or software and then treated in several ways, depending on the form of quantification desired. First, the activity level of the muscle may be recorded. It is customary for this factor to be represented in normalized terms. Some researchers, however, describe this quantity in absolute terms (microvolts of muscle activity). This measure simply relates how active the muscle was during the experimental

conditions. The measure is not an indication of muscle force, but simply a function of muscle usage. The signal can be quantified in several ways. Quantification may include peak activity, mean activity, activity as a function of given position or posture, and rate of muscle activity onset.

The processed EMG signal can also be used as an indication of muscle force present during an exertion. As with muscle activity, the signal can be treated in either absolute or relative terms. If muscle force is of interest, the EMG signal must be used in conjunction with other types of calibrations to derive more quantitative information about the muscle. These models and calibration techniques are discussed later in this manual.

Finally, the raw EMG data can be processed so that fatigue information can be derived. This has been done either by observing the processed signal or by observing a change in the frequency content of the raw signal. When the processed signal is used, one attempts to identify an increase in signal amplitude to perform a given task. Most researchers, however, use the frequency information from the EMG signal as an indication of muscle fatigue. The following chapters indicate that there are changes to a lower center frequency after a task that produces muscle fatigue. These measurements will be discussed in some detail in subsequent chapters.

SUMMARY

This chapter provides an overview of the main aspects associated with the use of EMG for those intending to use this technique to study ergonomic problems. Content is designed to assist novices in understanding and using EMG, but more experienced persons also should benefit from the material in subsequent chapters. This manual is limited in that only didactic material can be presented. As direct experience is invaluable, novices are strongly encouraged to work with more experienced persons.

As readers of this manual attempt to gain additional insights into electromyography, they should pay particular attention to the contributors' comments on uses and applications in ergonomics. Given these general but important rules, readers should be able to use EMG effectively in the study of human movement as applied to the work environment.

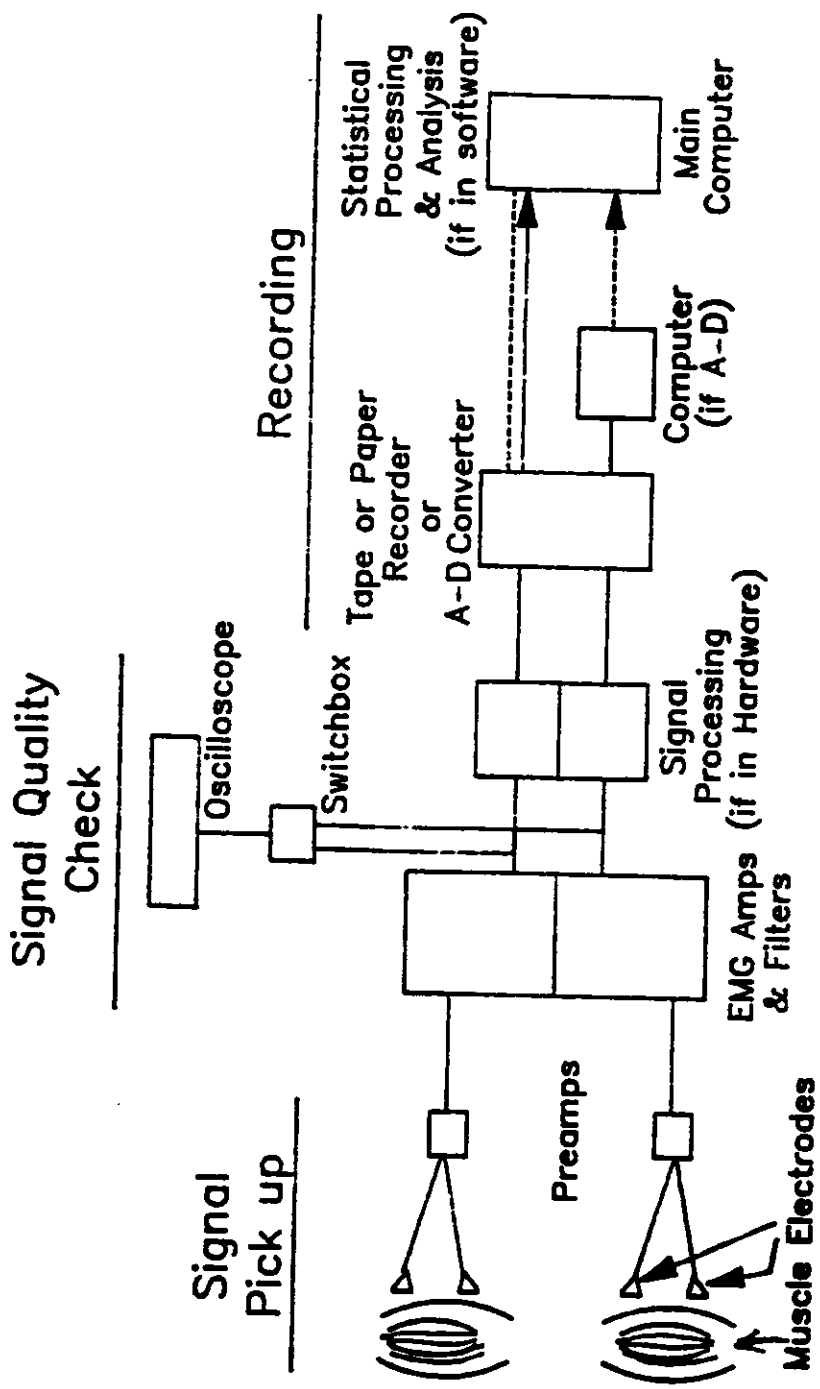


FIGURE 1-1
Equipment Configuration

CHAPTER 2

Anatomic and Physiologic Basis for Surface Electromyography

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Don Hobart, Ph.D., received his B.S. from Western Maryland College and his M.A. and Ph.D. from the University of Maryland at College Park. Presently, he is Associate Professor and Assistant Chairman of the Department of Physical Therapy in the School of Medicine, University of Maryland at Baltimore. He is in his second term as secretary of the International Society of Electrophysiological Kinesiology and was Secretary General of the 9th International Congress of ISEK. He has been an active researcher and author.

ANATOMIC AND PHYSIOLOGIC BASIS FOR SURFACE ELECTROMYOGRAPHY

Robert Lamb, PhD, PT
Donald Hobart, PhD

INTRODUCTION

The purpose of this chapter is to describe the anatomic and physiologic information fundamental to understanding the recording and subsequent study of the electrical activity of muscle using surface electromyographic (EMG) techniques. For those readers who desire a more in-depth discussion of the issues addressed, references to review articles and textbooks have been included.

ANATOMY OF SKELETAL MUSCLE

The structural unit of skeletal muscle is the muscle fiber, or cell (Figure 2-1). Light and electron microscopes must be used to view the muscle fiber and its parts. A muscle cell is a thin structure ranging from 10 to 100 microns in diameter and from a few millimeters to 40 cm in length. In short muscles, such as the flexor pollicis brevis, a single fiber may extend from the muscle's origin to insertion. In longer muscles, such as the biceps brachii, the fibers do not extend the entire length of the muscle. Instead, the cells are attached to either the origin or insertion tendon at one end and a connective tissue septa at the other end.

Just as in other body organs, muscle is surrounded and supported by a dense connective tissue generally referred to as fascia. Deep fascia, the anatomical term, or epimysium, the histological term, is a thin fibrous membrane that invests the muscle and separates it from adjacent muscles and other structures (Figure 2-2). The resulting architecture resembles a honeycomb. The deep surface of the epimysium gives off septa that penetrate the muscle to provide supporting and connective structure to the various subdivisions of the muscle.

The first subdivision of muscle, fasciculi, are surrounded by perimysium, a sheath formed by extensions of the epimysium into the muscle (Figure 2-2). The deep surface of the perimysium also divides to yield septa, named endomysium, that surround each muscle fiber. Each fasciculus encased by its perimysium may contain from a few to as many as 150 muscle fibers.¹ In muscles such as the lumbricales, only a few fibers are found, whereas in muscles like the gluteus maximus, 150 or more muscle fibers may be contained in each fasciculus. The biceps brachii, a muscle of intermediate coarseness,

has a mean of 100 muscle fibers in each fasciculus.^{2,3} The endomysium, perimysium, and epimysium serve two functions. First, at the ends of the muscles the contractile portion gradually gives way to the connective tissue that blends with and becomes a part of the tendon that ultimately attaches the muscle to bone (Figure 2-3). This attachment allows the muscles to exert tensile forces. Second, the connective tissue serves to bind contractile units and groups of units together to integrate their action. The connective tissue, however, also allows a certain freedom of movement between the contractile units. Even though each fiber and fasciculus is connected and can function as a group, each fiber therefore can move independently of its neighbor. An arrangement that allows independent functioning of the fibers is important because the fibers belonging to a motor unit are spread throughout the muscle. Activation of a motor unit, therefore, results in the contraction of single muscle fibers within many different fasciculi.⁴

The plasma membrane of a muscle cell, or fiber, lies deep to the endomysium and is known as the sarcolemma. Contained within the sarcolemma are many cylindrical myofibrils that make up the muscle fiber (Figure 2-1D). Each myofibril is about 1 micron in diameter and runs the entire length of the muscle fiber. The myofibrils are surrounded by the sarcotubular system that contains transverse tubules and the sarcoplasmic reticulum (Figure 2-4). The transverse tubules form a network of tubes perpendicular to the direction of the myofibrils and connect the sarcolemma with adjacent myofibrils and fibers. The sarcoplasmic reticulum has tubules running longitudinally around the myofibrils. The sarcotubular system controls the contraction and relaxation of myofibrils.

The myofibril is a series of sarcomeres arranged end to end (Figure 2-1D). A single sarcomere, 2.5 microns in length, is composed of thick and thin myofilaments (Figure 2-1E). Because of the precise arrangement of the myofibrils, various landmarks can be identified. Those characterizing skeletal muscle fiber are Z lines (discs) and A, I, and H bands (Figure 2-5). The Z lines are formed by the interconnections of the thin myofilaments from adjacent sarcomeres. Two adjacent Z lines define a sarcomere. The dark A bands of the sarcomere are formed by thick myofilaments, called the myosin filament, and interdigitated thin myofilaments, named actin. The H

SKELETAL MUSCLE

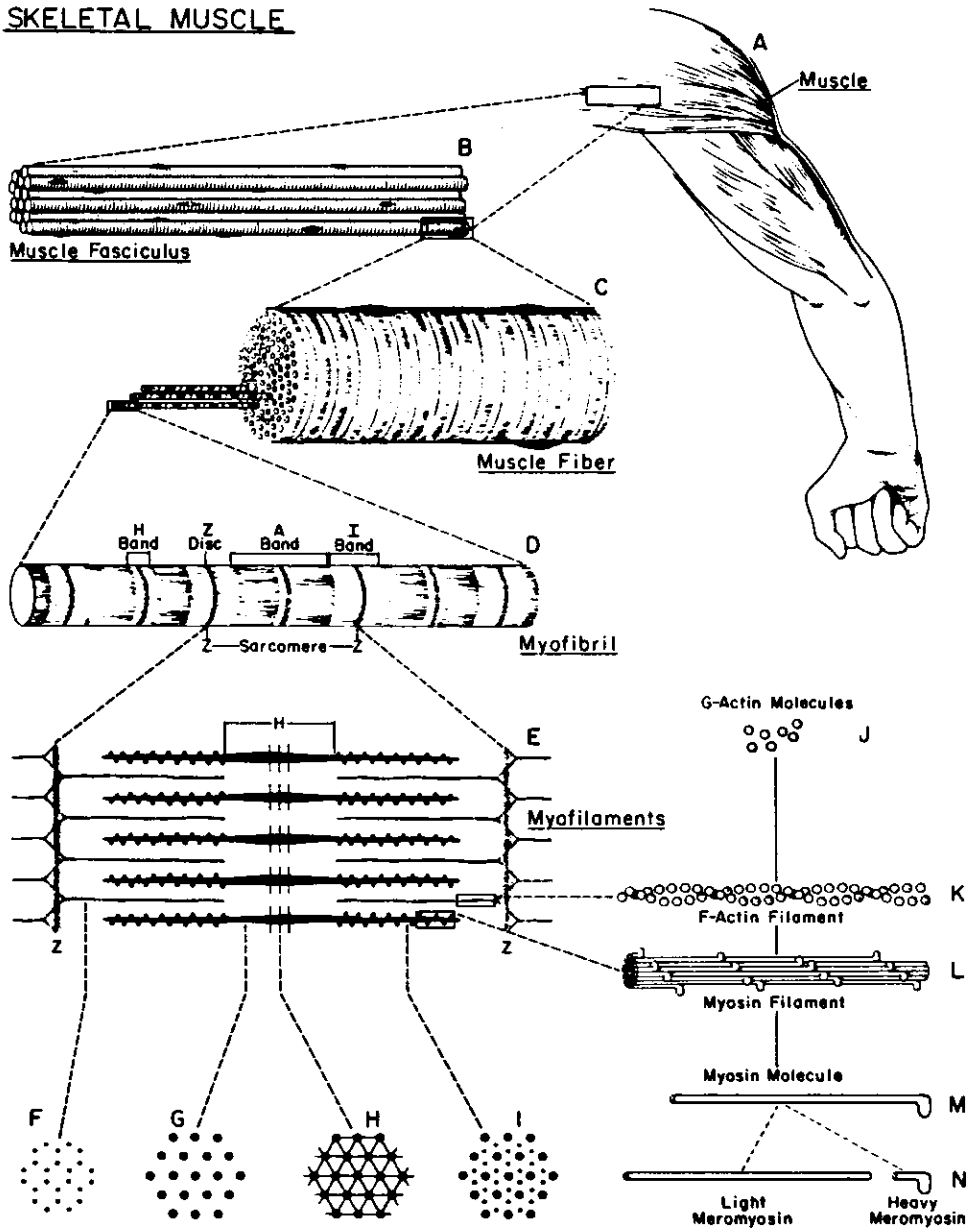


FIGURE 2-1

Diagram of the organization of skeletal muscle from the gross to the molecular level. Cross sections F, G, H, and I are at the levels indicated. Drawing by Sylvia Colard Keene.

Reprinted with permission from Bloom W and Fawcett DW: Textbook of Histology, ed 10. Philadelphia, PA, W B Saunders Co, 1975, Figure 11-19, p 306.

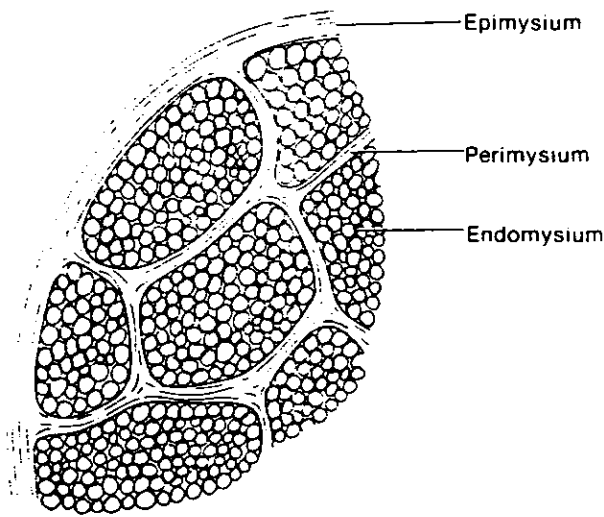


FIGURE 2-2

Cross-section of a small portion of muscle, showing relative size of connective tissue.

Reprinted with permission from Bendall JR: *Muscles, Molecules and Movement*. New York, NY, American Elsevier Publishing Co Inc, 1971, Figure 1-3, p xviii.

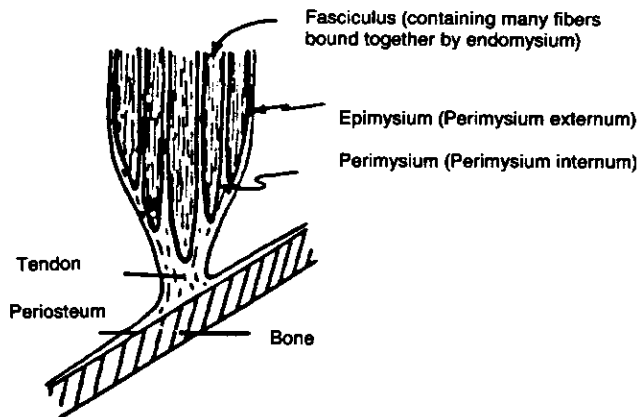


FIGURE 2-3

Cross structure of a skeletal muscle.

Reprinted with permission from Poland JL, Hobart DJ, Payton OD: *The Musculoskeletal System*, ed 2. Garden City, NY, Medical Examination Publishing Co Inc, 1981 (Figure 2.1, p 11).

band is the lighter appearing part of the A band that contains only myosin filaments (Figure 2-1L,M,N). Adjacent to the A band is the lighter I band that is that part of the sarcomere containing only actin filaments (Figure 2-1J,K).

The sarcomere is the smallest contractile unit of muscle. During contraction, the actin filament slides over the myosin filament, resulting in a decrease in the width of the H and I bands and the distance between the Z lines (Figure 2-5). The contraction of all sarcomeres within a muscle fiber results in a total fiber shortening.

ORIGIN OF THE ELECTROMYOGRAPHIC SIGNAL

Resting Membrane Potential

A muscle fiber is surrounded by the sarcolemma. The sarcolemma is a thin semipermeable membrane composed of a lipid bilayer that has channels by which certain ions can move between the intracellular and the extracellular fluid.^{5,7} The composition of the extracellular fluid and intracellular fluid are different (Table 2-1). The intracellular fluid has a high concentration of potassium (K^+) ions and an organic anion (A^-). The K^+ ions are small enough to pass through the channels in the membrane. The organic anions are much too large to flow through the membrane. The interstitial fluid has a high concentration of sodium (Na^+) and chloride (Cl^-) ions. The Cl^- ions are small enough to pass through the membrane channels, but the slightly larger Na^+ ions have difficulty in penetrating the membrane.

To understand the resting membrane potential, consider for a moment that there is no difference in potential between the intracellular and extracellular (interstitial) fluid (Figure 2-6). Because of the higher concentration inside the cell compared with the outside, K^+ diffuses through the cell membrane into the extracellular fluid. The A^- ions are too large to diffuse outward through the membrane. The Na^+ ions cannot move inward through the membrane in sufficient numbers to replace the K^+ ions. A potential difference therefore develops across the membrane. The positive charge that develops on the outside of the membrane slows the diffusion of K^+ ions between the inside and outside of the cell. The Cl^- ions act in a similar manner and remain in equilibrium because

TABLE 2-1

Intracellular and Extracellular Ion Concentrations for Mammalian Muscle (mEq/L)

Ion	Intracellular Fluid	Interstitial Fluid
K^+	140	4
Na^+	14	142
Cl^-	4	125
HCO_3^-	8	28
A^-	150	

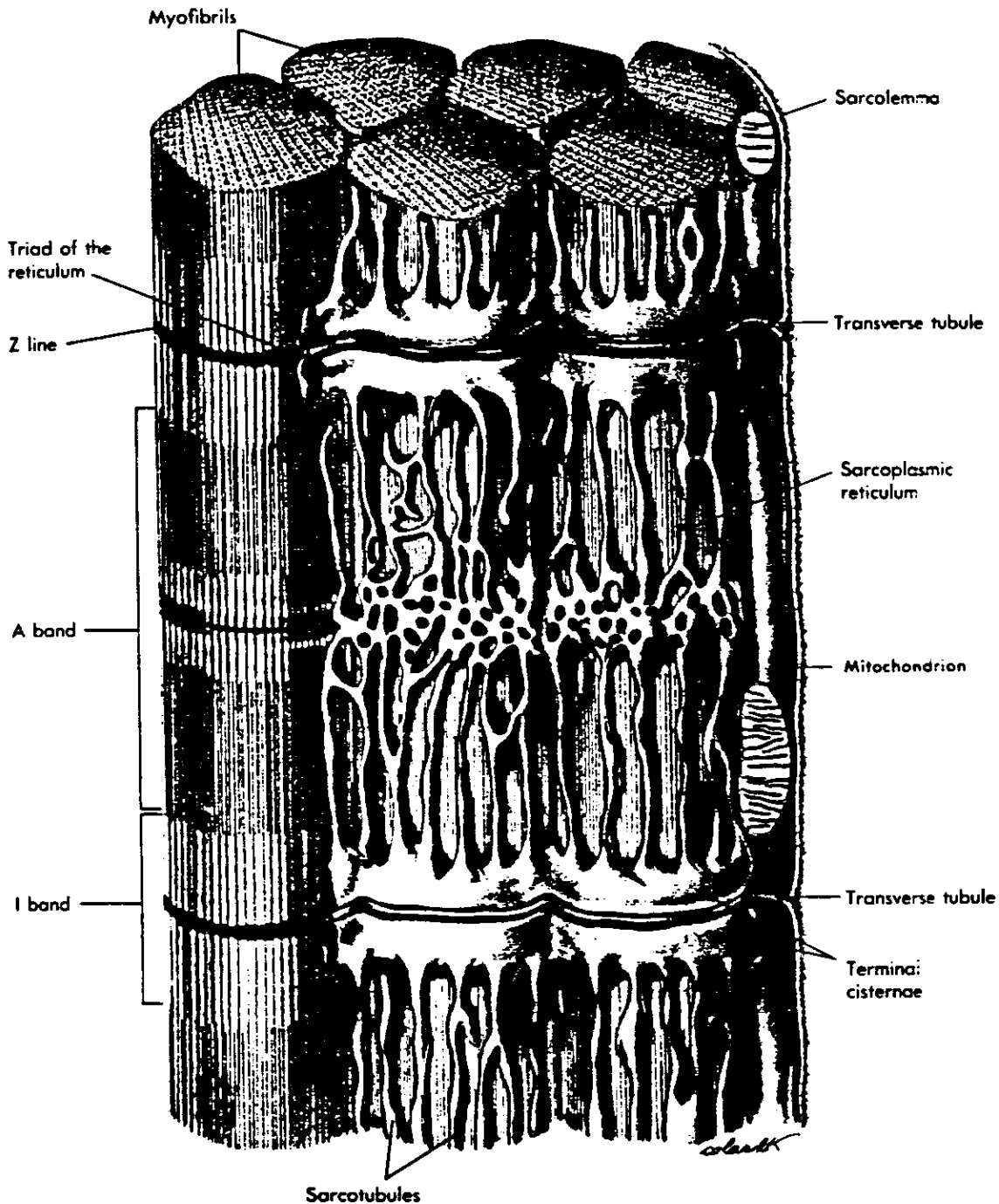


FIGURE 2-4

Schematic representation of the distribution of the sarcoplasmic reticulum around the myofibrils of amphibian skeletal muscle. The longitudinal sarcotubules are confluent with transverse elements called the terminal cisternae. A slender transverse tubule (T tubule) extending inward from the sarcolemma is flanked by two terminal cisternae to form the so-called triads of the reticulum. The location of these with respect to the cross-banded pattern of the myofibrils varies from species to species. In frog muscle, depicted here, the triads are at the Z line. In mammalian muscle, there are two to each sarcomere, located at the A-I junctions. (Modified after L. Peachey: *J. Cell Biol.* 25:209, 1965, from Fawcett DW, McNutt S: Drawn by Sylvia Colard Keene.)

Reprinted with permission from Bloom W, Fawcett DW: Textbook of Histology, ed 10. Philadelphia, PA, W B Saunders Co, 1975, Figures 11-18, p 305.

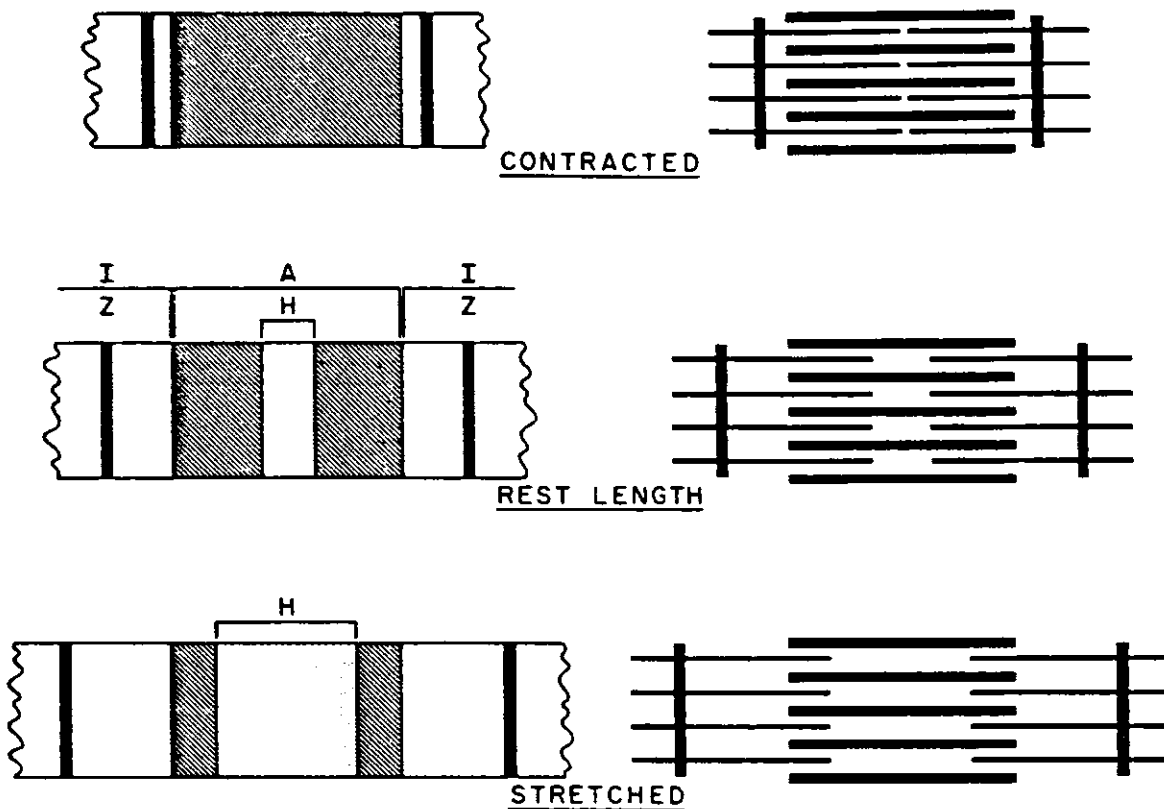


FIGURE 2-5

Schematic representation of the current interpretation of the changing appearance of the cross striations (left) in different phases of contraction, depending on the degree of interdigitation of the sliding filaments (right). The A band is of constant length, but the width of the H band is determined by the depth of penetration of the thin I filaments into the A band. In the contracted state, the thin filaments slide more deeply into the A band, obliterating the H band. In stretched muscle, the thin filaments are drawn out of the A band and the H band is widened.

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of this interaction between its concentration gradient and the electrical charge.

The net effect of the movement of K^+ and Cl^- ions is the creation of a positive charge on the outside of the membrane and a negative charge on the inside of the membrane. Because like charges repel each other, the positive charge on the outside of the membrane in combination with the large concentration gradient of Na^+ drives Na^+ into the cell. If Na^+ movement into the cell persists, the inside of the cell would become positively charged with respect to the outside. The membrane potential, however, is maintained by an active ion transport system called the sodium-potassium pump.^{5,7} This

pump system uses metabolic energy to transport Na^+ ions actively from inside the cell to outside and, to a lesser extent, to pump K^+ ions back inside the cell.

The effect of the concentration gradients, the difference in potential across the membrane, and the active transport system, results in the maintenance of a potential difference across the membrane when the muscle fiber is in a resting state. This voltage difference is the resting membrane potential and measures about -80 mV inside the muscle fiber with respect to the outside (Figure 2-7). In a healthy neuromuscular system, this polarized muscle fiber remains in equilibrium until upset by an external or internal stimulus.

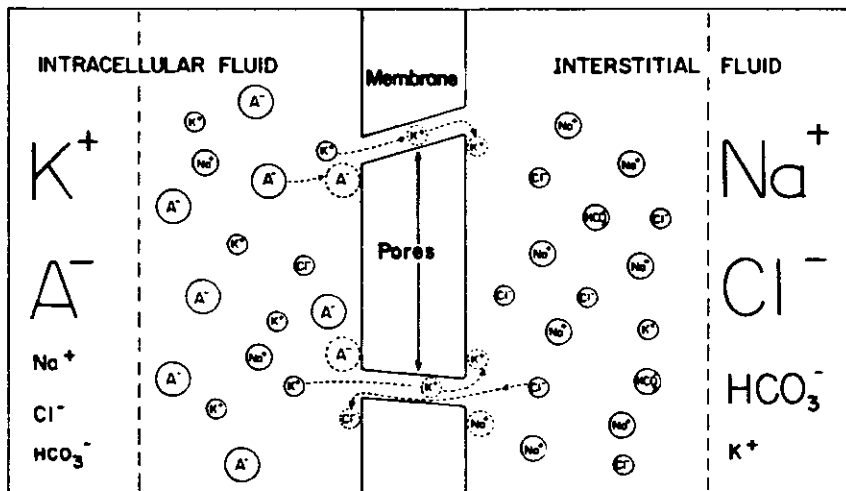


FIGURE 2-6

Development of transmembrane voltage by an ion concentration gradient. Diagram of an intracellular fluid-membrane-interstitial fluid system. Membrane shown has some, but not all properties of a real cell membrane. Hypothetical membrane is pierced by pores of such size that K^+ and Cl^- can move through them easily, Na^+ with difficulty, and A^- not at all. Sizes of symbols in left- and right-hand columns indicate relative concentrations of ions in fluids bathing the membrane. Dashed arrows and circles show paths taken by K^+ , A^- , Na^+ and Cl^- as a K^+ or Cl^- travels through a pore. Penetration of the pore by a K^+ or Cl^- follows a collision between the K^+ or Cl^- and water molecules (not shown), giving the K^+ or Cl^- the necessary kinetic energy and proper direction. An A^- or Na^+ unable to cross the membrane is left behind when a K^+ or Cl^- , respectively, diffuses through a pore. Because K^+ is more concentrated on left than on right, more K^+ diffuses from left to right than from right to left, and conversely for Cl^- . Therefore, right-hand border of membrane becomes positively charged (K^+ , Na^+) and left-hand negatively charged (Cl^- , A^-). Fluids away from the membrane are electrically neutral because of attraction between + and - charges. Charges separated by membrane stay near it because of their attraction.

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Muscle Fiber Action Potential

Several events must occur before a muscle fiber contracts. Central nervous system activity initiates a depolarization in the motoneuron. The depolarization is conducted along the motoneuron to the muscle fiber's motor endplate. At the endplate, a chemical substance, acetylcholine, is released that diffuses across the synaptic cleft causing a rapid depolarization of the muscle fiber under the motor endplate. This rapid depolarization, and the subsequent repolarization of the muscle fiber, is an action potential.

Specific detail of the genesis of the action potential can be found in most basic physiology textbooks.^{6,7} Briefly, stimulation of the muscle fiber causes an increase in the muscle fiber membrane's permeability to Na^+ . The increased permeability to Na^+ , and the ion's concentration gradient, cause a sudden influx of Na^+ into the muscle fiber (Figure 2-8). A rapid depolarization of

the muscle fiber occurs and continues until the fiber reverses its polarity and reaches about +20 mV positive inside with respect to the outside. Near the peak of the reverse polarity, the decreased influx of Na^+ and increased efflux of K^+ causes a rapid repolarization of the muscle fiber.

When depolarization of the membrane under the motor endplate occurs, a potential difference is established between the active region and the adjacent inactive regions of the muscle fiber (Figure 2-9). Ion current therefore flows between the active and the inactive regions. This current flow decreases the membrane potential of the inactive region to a point where the membrane permeability to Na^+ rapidly increases in the inactive region and an action potential is generated. In this manner, the action potential propagates away from the initial active region in both directions along the muscle fiber. The propagated action potential along the muscle

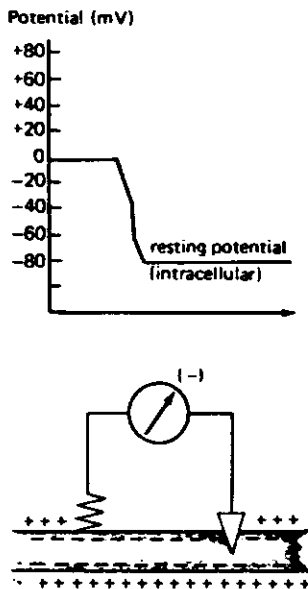


FIGURE 2-7

The intracellular resting potential can be measured by inserting a recording electrode inside the cell and connecting it by a voltage meter to a reference electrode on the surface of the cell. The cell is immersed in a suitable salt solution. The potential difference between the inside and outside of the cell is -80 mV.

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fiber is a muscle fiber action potential. In vivo, a muscle fiber action potential can be recorded using microelectrode techniques,⁸ but cannot be seen in isolation using surface electromyographic techniques.

The propagated action potential spreads along the sarcolemma and into the muscle fiber through the transverse tubules (Figure 2-4). In response to the action potential, the sarcoplasmic reticulum releases stored calcium. The calcium binds with troponin, altering the location of tropomyosin. This frees the active site on the actin, allowing a muscle contraction to take place.⁹

Extracellular Recording of Action Potentials

The basis of surface electromyography is the relationship between the action potentials of muscle fibers and the extracellular recording of those action potentials at the skin surface. Electrodes external to the muscle fiber can be used to detect action potentials.

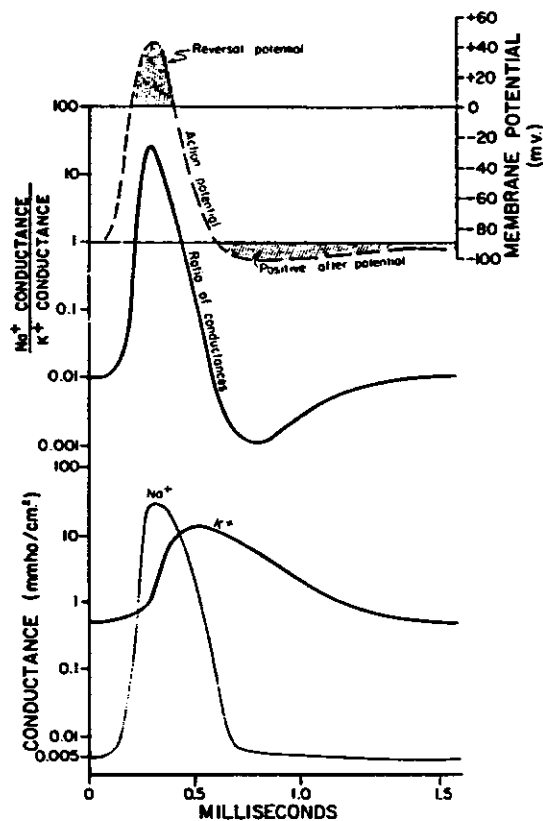


FIGURE 2-8

Changes in sodium and potassium conductances during the course of the action potential. Note that sodium conductance increases several thousandfold during the early stages of the action potential, while potassium conductance increases only about thirtyfold during the latter stages of the action potential and for a short period thereafter. (Curves constructed from data in Hodgkin and Huxley papers but transposed from squid axon to apply to the membrane potentials of large mammalian nerve fibers.)

Reprinted with permission from Guyton AC: Textbook of Medical Physiology, ed 6. Philadelphia, PA, WB Saunders Co, 1981, Figure 10-3, p 110.

A simple model can be used to aid in understanding the recording of action potentials with extracellular electrodes. Two electrodes are placed a considerable distance apart, directly on the surface of a muscle fiber (Figure 2-10). The electrodes are attached to an oscilloscope that measures voltage changes. To further simplify the model, depolarization, reverse polarization, and repolarization are the only phases of the action potential considered.

In a resting state, the muscle fiber is in equilibrium and, electrically, is positive on the outside and negative

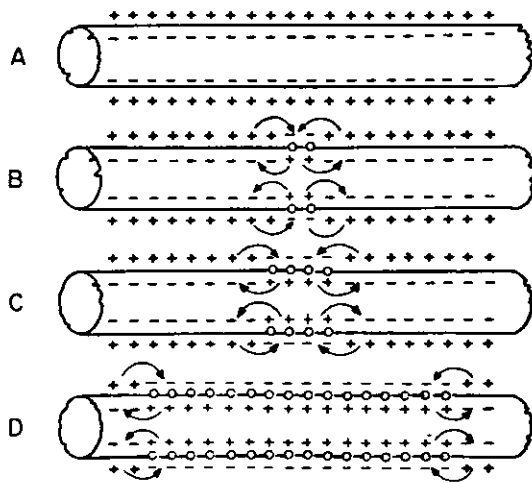


FIGURE 2-9

Propagation of action potentials in both directions along a conductive fiber.

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on the inside (Figure 2-10). Because the two electrodes are on the outside of the muscle fiber, there is no potential difference between them. The electrical difference and the oscilloscope, thus, remain at baseline. If the fiber is excited to the left of Electrode A, an action potential is initiated and propagated along the fiber toward Electrode A. When the action potential reaches the region under Electrode A, it becomes negative with respect to Electrode B, and the oscilloscope deflects upward. As the action potential continues toward Electrode B, the region under Electrode A repolarizes, and the oscilloscope returns to baseline. When the action potential is between the two electrodes, the region under Electrode A has recovered and the region under Electrode B has not yet depolarized. The difference in potential between the electrodes, therefore, is again zero. The oscilloscope remains at baseline until the region under Electrode B is depolarized. As the action potential moves under the Electrode B, the region becomes negative with respect to the region under Electrode A, and the oscilloscope deflects downward. As repolarization occurs under Electrode B, the difference in potential returns to zero.

The output of this model is two monophasic waves separated by a brief period of time when no potential difference is measured (Figure 2-10). The time between the two waves depends on the conduction velocity of the muscle fiber and the distance between the two electrodes. If

the electrodes are placed very close together, for example, the two waves temporally summate forming a biphasic wave with a smaller peak to peak amplitude than the monophasic waves. This biphasic wave is similar in appearance to a muscle fiber action potential.

Motor Unit Action Potential

Living tissue acts as a volume conductor; therefore, the measurement and recording of the action potential is not limited to the surface of the membrane. In a volume conductor, a potential source, such as the muscle fiber action potential, is conducted away from its origin, through ion movement. Living tissue also acts as a filter. In reality, electrodes within the muscle or on the surface of the skin thus can record, from a distance, an attenuated version of the muscle fiber action potential.

If one applies the principles of the previously discussed model to the schematic representation presented in Figure 2-11, the variables that effect the amplitude and shape of the recording of a motor unit action potential, the smallest functional unit of the neuromuscular system, can be understood. In healthy tissue, the action potential propagates along a motoneuron to the motor end plate of the muscle fibers. Asynchronous activation of muscle fibers belonging to the same motor unit differ because the axon branches differ in diameter and length; thus, their conduction times differ. All the muscle fibers of the motor unit, therefore, are not activated at the same time. The muscle fiber action potentials spatially and temporally summate to form a motor unit action potential.

The exact amplitude and shape of a motor unit action potential cannot be predicted. The majority of motor unit action potentials, however, are biphasic or triphasic in shape.¹⁰ Amplitude and shape depend on the characteristics of the muscle fibers, the spatial orientation of the muscle fibers to the recording electrodes, the filter characteristics of the electrodes and the tissues surrounding the active muscle fibers, and the specifications of the electronic instrumentation used (Figure 2-11).¹¹

Individual motor units can be recorded and measured using needle and fine wire electrodes (Figure 2-12). The duration of electrical potentials of motor units vary from a few milliseconds to 14 ms; their amplitude vary from a few microvolts to 5 mV.¹¹ Under certain circumstances, single motor-unit action potentials can be observed by using surface electrodes. Usually, when using surface electromyographic techniques, the measurement and recording of the myoelectric activity of skeletal muscle as a whole is more appropriate. The myoelectric signal is the temporal and spatial summation of all active motor units within the recording area of the electrodes (Figure 2-13). The amplitude range for the myoelectric signal is from 0.01 to 5 mV.

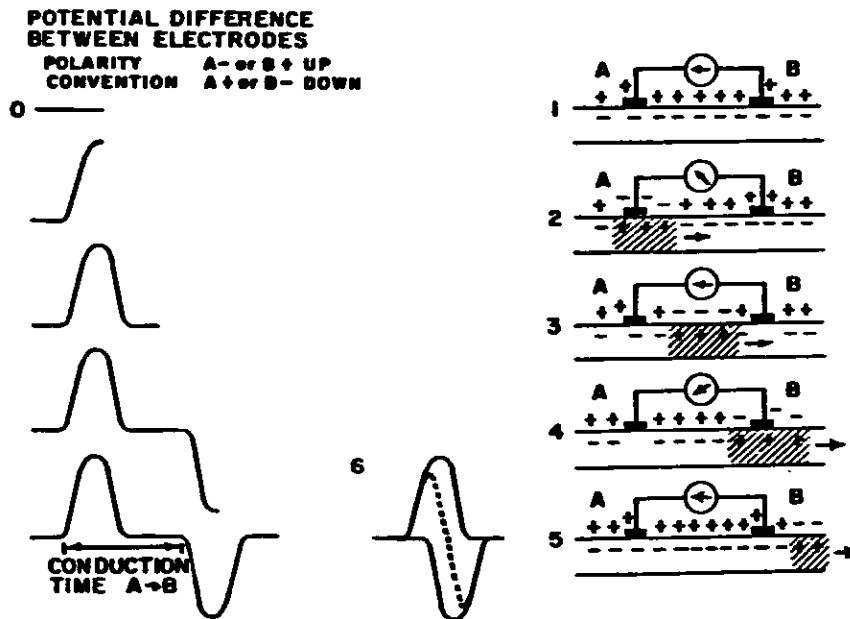


FIGURE 2-10

The measurement of action potentials, with electrodes placed on the surface of isolated irritable tissue.

Reprinted with permission from Geddes LA: Electrodes and the Measurement of Bioelectric Events. New York, NY, Wiley-Interscience, John Wiley & Sons Inc, 1972, Figure 6-1, p 252.

FUNCTIONAL CONSIDERATIONS OF MOTOR UNITS

The smallest functional unit of the neuromuscular system is the motor unit. A motor unit is defined as an anterior horn cell, its axon, and all of the muscle fibers innervated by the axon.¹² A typical motor unit includes the cell body of an alpha motoneuron in the ventral horn of the spinal cord. The axon of this neuron exits the spinal cord and travels to the muscle as part of a peripheral nerve. As it enters the muscle, the axon branches several hundred or more times. Each branch of the axon terminates on a single muscle fiber.

The muscle fibers of a single motor unit are scattered throughout a large portion of the cross-sectional area of a skeletal muscle. A few fibers of one motor unit may be surrounded by fibers of many other motor units.¹³

Several investigators have attempted to determine the number of muscle fibers innervated by one axon.¹⁴⁻¹⁶ This information has been calculated by counting the number of muscle fibers in the muscle and dividing that number by the number of alpha motor neurons supplying the muscle. The innervation ratios differ from muscle to muscle, and these differences have been interpreted

as being functionally significant. Apparently, small muscles that produce precise movements tend to have a low innervation ratio and larger muscles that produce gross movements used for weight bearing activities have high innervation ratios.

Fiber Types

Innervation ratios may not be an appropriate means of understanding the function of motor units during human movement. A better approach may be to think about the characteristics of muscle fibers. Motor units and muscle fibers can be classified on the basis of their mechanical, metabolic, and histochemical properties. Most studies describing these characteristics use animal models, and the results must be applied cautiously to humans. There are several methods of classifying muscle fibers. One method identifies three major fiber types: types I, IIA, and IIB.¹⁷ Another system classifies the three types as SO (slow twitch oxidative), FOG (fast twitch oxidative), and FG (fast twitch glycolytic)¹⁸ (Figure 2-14).

The type I, or SO, fibers are characterized as red fibers having a high resistance to fatigue. These fibers,

with a high concentration of mitochondria and an excellent blood supply, use aerobic metabolism almost exclusively. These slow twitch fibers are well suited for sustained muscle contractions.

The intermediate type IIA, or FOG, fibers are pale, fast twitch fibers having considerable capacity for aerobic metabolism. They have a reasonable concentration of mitochondria and capillaries making them suitable for sustained phasic activity.

The type IIB, or FG, fibers are white or fast twitch fibers with a high capacity for anaerobic glycolysis and a low capacity for aerobic metabolism. They have a low concentration of mitochondria and a poor capillary bed giving them a low resistance to fatigue. These fibers probably are best suited for short term phasic activity.

Type IIA (FOG) and IIB (FG) muscle fibers are innervated by alpha motor neurons with fast conduction velocities. Type I (SO) fibers are innervated by slower conducting alpha motor neurons. The same type of muscle fibers congregate to form homogeneous motor units.^{4,19} We, therefore, can speak of and functionally describe fast twitch motor units and slow twitch motor units.¹⁹

Burke classified motor units as S (slow twitch) containing type I (SO) muscle fibers, FR (fast twitch, fatigue resistant) motor units containing type IIA (FOG) muscle fibers, and FF (fast twitch, fatigable) units containing type IIB (FG) muscle fibers. Motor unit classification is more functional and useful in ergonomics than muscle fiber classifications.

The slow twitch motor units (S) have distinctive characteristics that differentiate them from the other two types of motor units. The S motor unit has low conduction velocity, long twitch contraction times, and low contraction velocity. Twitch contraction times of 90 to 160 msec and contraction velocities of 2 fiber lengths/sec have been reported.¹⁹⁻²¹ Slow twitch motor units have a low contraction threshold of below 30% of twitch tension. They can fire continuously for long periods at relatively low frequencies. This ability makes the S motor unit particularly well suited and economical for both low-level isometric, concentric, and eccentric contractions that occur repetitively at low frequencies.^{21,22}

The fast twitch, fatigue resistant (FR) motor units have a high conduction velocity and short twitch contraction time. The FR motor units have a low contraction threshold and, for the most part, are recruited with the slow twitch motor units. The FR units exhibit a greater resistance to fatigue and produce less tetanic force than FF motor units.^{19,20,23}

The fast twitch, fatigable (FF) motor units have high conduction velocities, short twitch contraction times and

high contraction velocities. Twitch contraction times of 40 to 84 msec and contraction velocities of 6 fiber lengths/sec have been reported.^{19,21,23} The FF motor units have a contraction threshold of above 30% twitch tension. They fire intermittently at high rates for short intervals and are well suited for short-duration powerful isometric, concentric, or eccentric contractions. There is a positive relationship between power output and percentage of fast twitch glycolytic fibers.²⁴ The peak power output of FOG fibers, in fact, has been reported as fourfold that of SO fibers, as a result of shortening velocity.²⁵

Recruitment and Rate Coding

Humans are capable of performing motor tasks that require muscles to generate a wide variety of force levels. These forces range from those required for the precise and delicate movements of a watchmaker to those involved in heavy lifting activities. A muscle is capable of adjusting its tension output to meet the demands of various types of tasks by the interaction of two physiologic mechanisms: recruitment and rate coding. Recruitment is when inactive motor units are activated initially as demand is increased for more tension output from the muscle. Rate coding is defined as an increase in the frequency of discharge of active motor units when increased effort is required. Although minimum and maximum discharge rates of motor units probably differ among muscles, 5 to 50 discharges per second have been reported in the literature.^{26,27}

Numerous questions exist about the role recruitment and rate coding play in adjusting the tension output of a muscle. Some investigators emphasize rate coding as the predominate mechanism.²⁸⁻³⁰ Other investigators consider recruitment to be the predominate mechanism. The data on which arguments are based have been obtained by observing motor unit discharges during slowly varying muscle contractions. Many questions about the role of these physiologic mechanisms are unanswered. Additionally, extrapolating what is known to faster movements must be done cautiously. A reasonable hypothesis, however, can be formulated that may help in understanding EMG.

There is evidence under certain circumstances that motor units are recruited and derecruited in order.^{31,32} The small, slow, fatigue resistant motor units (S) are recruited first. These units appear to be best suited for postural functions and finely graded movements. The larger, faster, fatigable motor units (FF) are recruited last and appear best suited for movements that are rapid and powerful. Each time a muscle contraction is repeated, a motor unit is recruited at a similar force threshold for each contraction.

MOTOR UNIT ACTION POTENTIAL

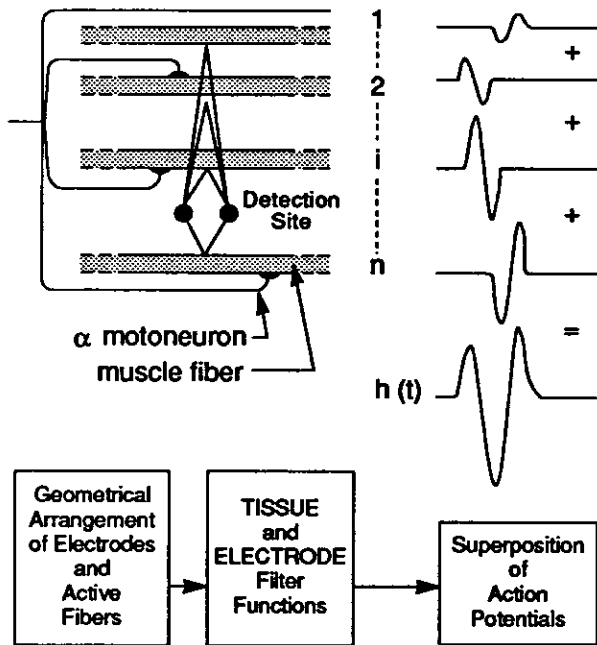


FIGURE 2-11

Schematic representation of the generation of the motor unit action potential.

Reprinted with permission from Basmajian JV, DeLuca CJ: *Muscles Alive, Their Functions Revealed by Electromyography*, ed 5. Baltimore, MD, Williams & Wilkins, 1985, Figure 3-2, p 68.

The minimum amount of tension that can be exerted on a tendon is the result of a twitch contraction from the muscle fibers of a motor unit. As the muscle's force requirement increases above the unit's force level, its firing frequency increases. As the demand for force further increases, additional motor units are recruited. Each of these units, however, may be producing a twitch contraction because the asynchronous firing of all the units their twitches summate to produce a smooth pull on the muscle's tendon.

At the lower force levels there is a strong interaction between rate coding and recruitment. At very high force levels, all the motor units are recruited before 100% of maximum contraction is reached.^{29,30} The additional force required above the force threshold of the last motor unit recruited, therefore, is a result of increased frequencies of firing of already activated motor units.

MUSCLE MECHANICS

The mechanics of muscle is concerned with the tension created in a contraction and the factors that affect the level of tension. This section briefly describes some of the most important factors affecting muscle tension. Only the mechanics and their physiologic basis are discussed. The relationship between these factors and the EMG signal is considered in greater detail in Chapter 6.

Architecture of Muscle

The arrangement of the fibers within the muscle help determine that muscle's function. To understand the relationship between architecture and function, two hypotheses must be accepted. First, a muscle fiber can shorten to about 60% of its resting length. Second, the force a muscle is capable of generating is related directly to its physiological cross sectional area.

Muscle fibers and fasciculi of a muscle can be arranged either parallel or at an angle to the long axis of a muscle. Where the fasciculi are arranged parallel to the muscle's long axis, the muscle takes full advantage of the shortening capability of the sarcomeres. Because a muscle's maximum displacement is proportional to fiber length or the number of sarcomeres in series, muscles with this type of architecture are found across joints with great ranges of motion. Examples of this type of muscle are the fusiform and strap muscle (Figure 2-15A,B). A strap muscle, such as the sartorius, almost has no tendon and yields the greatest range, because its entire length is composed of contractile tissue. A fusiform muscle, such as the brachioradialis, has tapered ends terminating in tendons. This type of muscle does not produce the same range of motion in accord with its overall muscle length because the tendon reduces the contractile portion of the muscle.

When two or three fusiform shaped muscle bellies attach to the same tendon, the muscle is called bicipital or tricipital (Figure 2-15C,D). Examples of muscles of this type are the biceps brachii and triceps brachii. The characteristics of bicipital muscles are the same as for the fusiform muscles. The triangular muscles (eg, gluteus medius) have fasciculi that are arranged at a slight angle to the long axis of the muscles because of a wide origin and a narrow tendon insertion. Their characteristics are also similar to fusiform.

Muscles with their fasciculi arranged obliquely to the direction of pull or long axis of the muscle resemble a feather. They, therefore, are called penniform muscles. Their fiber arrangement corresponds to the barbs of the feather; their tendons correspond to the feather's quill. A unipennate muscle resembles one half of a feather (Figure 2-15E). Examples of this type of muscle are the



FIGURE 2-12

Individual motor units recorded by fine wire electrodes. Scales as shown in the figure per division on oscilloscope.

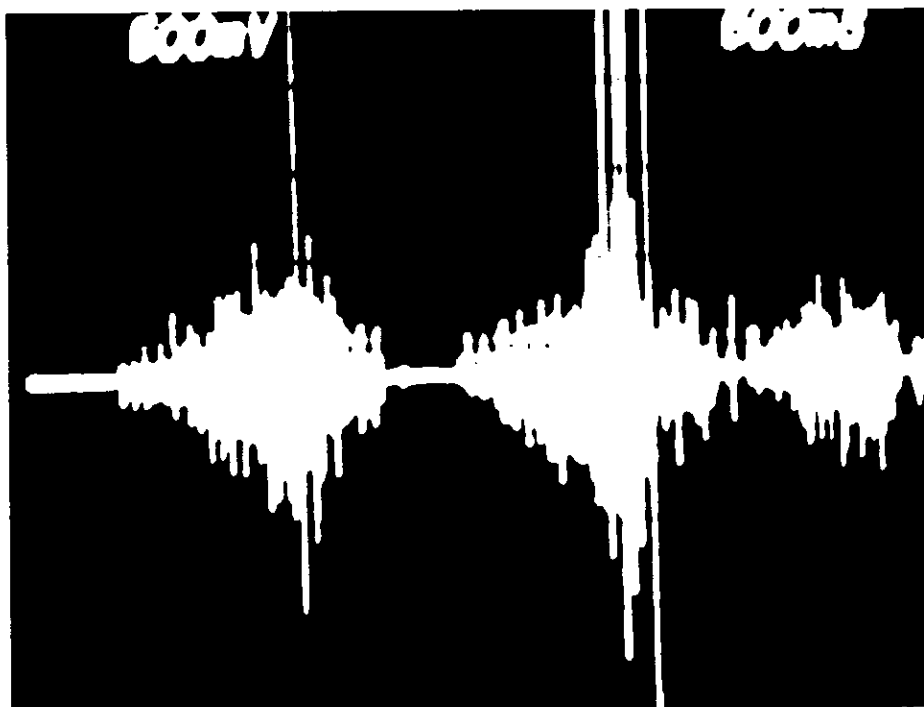


FIGURE 2-13

Sample surface EMG recordings. Scales as shown per division as on the oscilloscope screen.

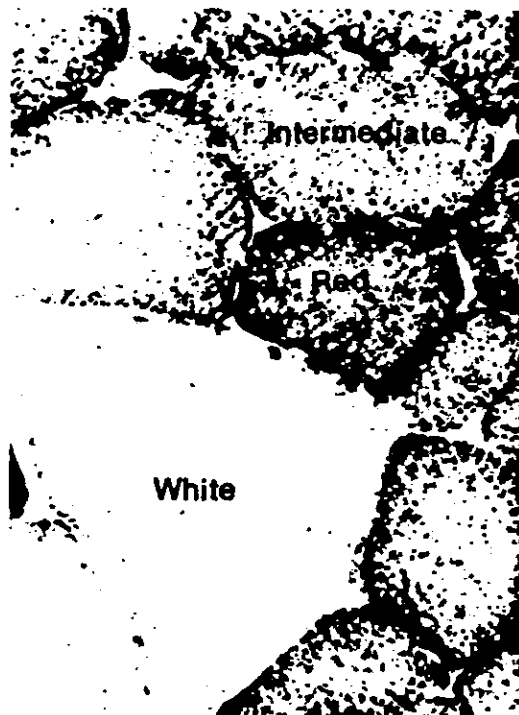


FIGURE 2-14

Photomicrograph of a transverse section of skeletal muscle stained for the enzyme succinic dehydrogenase, which resides in mitochondria. Three categories of fibres are recognizable: small red fibers rich in mitochondria, especially around the periphery; large white fibers with relatively few mitochondria; and fibers with intermediate characteristics. (Photomicrograph courtesy of G. Gautier.)

Reprinted with permission from Bloom W, Fawcett DW: Textbook of Histology, ed 10. Philadelphia, PA, WB Saunders Co, 1975, Figures 11-14, p 302.

flexor pollicis longus and semimembranosus. The bipennate muscle resembles a complete feather (Figure 2-15F). The rectus femoris and dorsal interossei muscles exemplify a bipennate fiber arrangement. A multipennate muscle such as the deltoid is one that has many groups of bipennate fasciculi attached to many intermuscular tendons (Figure 2-15G).

Because the length of the muscle fibers and direction of pull determine the range of motion of a muscle, the fusiform-type muscle yields a much greater range than a pennate muscle. The length of the fiber has little effect on maximum tension. The force a muscle can generate, however, is directly proportional to its physiologic cross-sectional area.³³ The penniform type muscles have more fibers per unit area than the fusiform; therefore, they

generate more force than the fusiform muscles. Fusiform muscles thus provide greater range of motion at the expense of force production, whereas pennate muscles produce greater forces through less range of motion.

Length-Tension Relationship

Two basic components of the muscle are responsible for producing the relationship between tension and length. The active component is the muscle tension produced by the contractile process; the passive component is the tension produced by the connective tissue surrounding the muscle fibers. The sum of the active and passive tensions equals the total tension generated by a muscle contraction.

The length of muscle has an effect on both active and passive tension. Figure 2-16 graphically demonstrates the relative effect of length changes. The resting length of a muscle is defined as 100% of muscle length. The passive tension produced (Curve 1) monotonically increases from resting length. The active tension (Curve 2) is maximal at the resting length and decreases with either lengthening or shortening. Curve 3 is the sum of these two components.

The maximum muscle tension attainable in a physiologic range of motion is found at about 125% of resting length. This length coincides with the length of the muscle when the joint is in a relaxed position.¹³ These length-tension relationships have been reported in isolated muscle fibers³⁴ and in whole muscle preparations.³⁵⁻³⁷

Until 1966, investigators were unable to relate active tension to specifics of the contractile process. Gordon *et al* postulated, from data obtained by evaluating the sarcomeres of single muscle fibers of the frog, that length changes involve the interaction of actin and myosin.³⁴ In shortened muscle, the actin filaments overlap in a manner that decreases the number of sites in which myosin can combine with actin. The fewer actin binding sites available, the less tension developed. In a lengthened muscle, there also are fewer sites at which myosin can combine with actin; therefore, less tension is produced. (See Huxley³⁸ for a discussion of the sliding filament theory).

Velocity-Tension Relationship

The contraction velocity of a muscle also has an effect on the tension produced.³⁹ The general shape of the relationship between tension and the velocity of shortening is presented in Figure 2-17. Note that the muscle responds differently for lengthening (eccentric) and shortening (concentric) contractions. In concentric muscle contractions, as the speed of shortening increases, the maximum tension that a muscle can produce decreases. At P_0 in the figure, there is zero velocity; thus, an

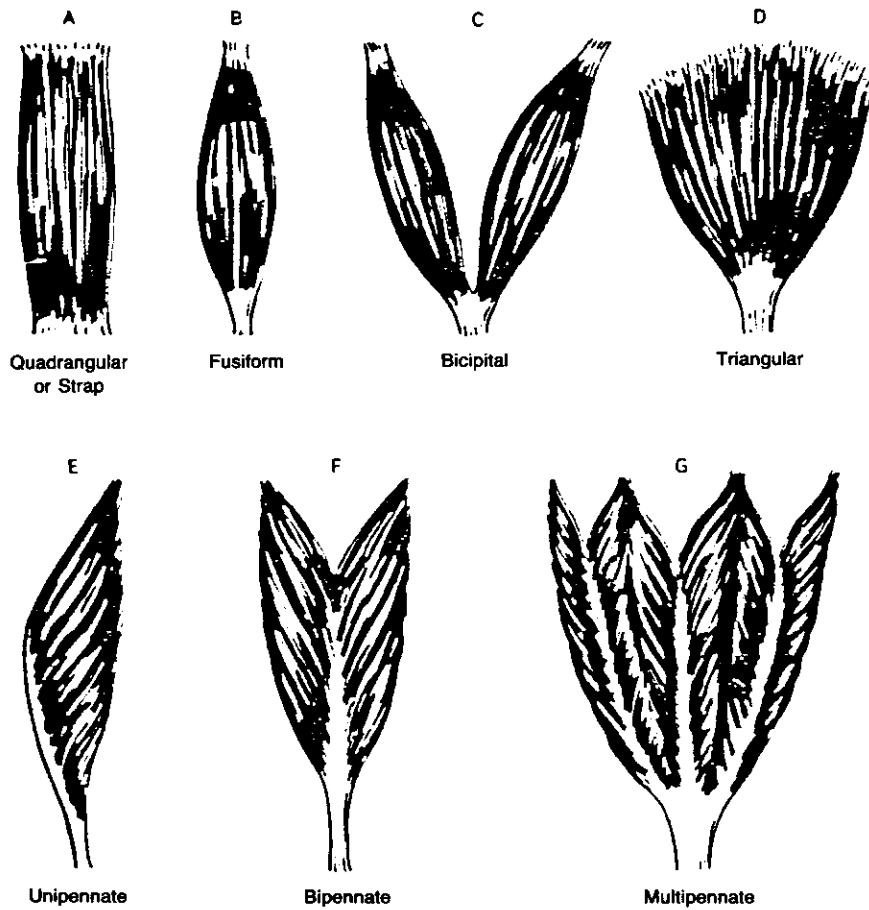


FIGURE 2-15

Illustration of the variety of shapes and fiber arrangements of muscles.

Reprinted with permission from Hall-Craggs ECB: Anatomy As a Basis for Clinical Medicine. Baltimore, MD, Urban and Schwartzberg Publ Co, 1985, Figures 1-21, p 19.

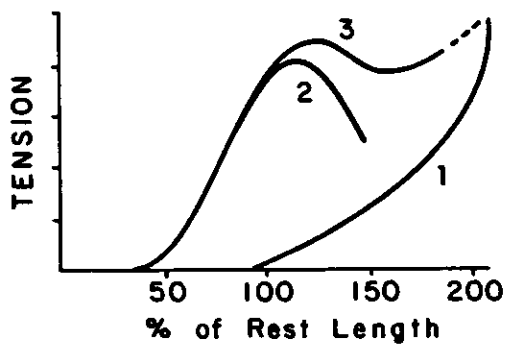


FIGURE 2-16

The length-tension relationship of muscle. Curve 1 is the passive force. Curve 2 is the active muscle force. Curve 3 is the total muscle force (Curve 1 plus Curve 2).

Reprinted with permission from Basmajian JV, DeLuca CJ: Muscles Alive, Their Functions Revealed by Electromyography, ed 5. Baltimore, MD, Williams & Wilkins, 1985.

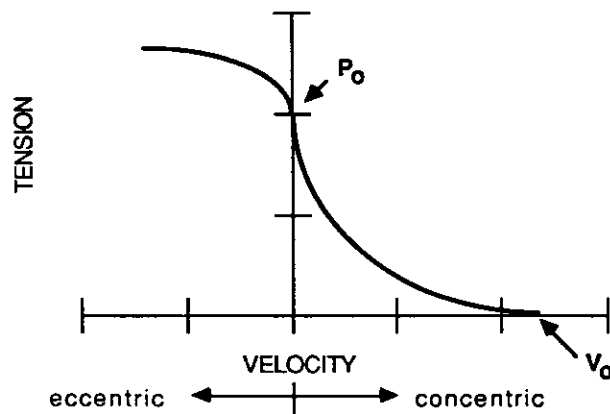


FIGURE 2-17

Velocity-active tension relationship for muscle.

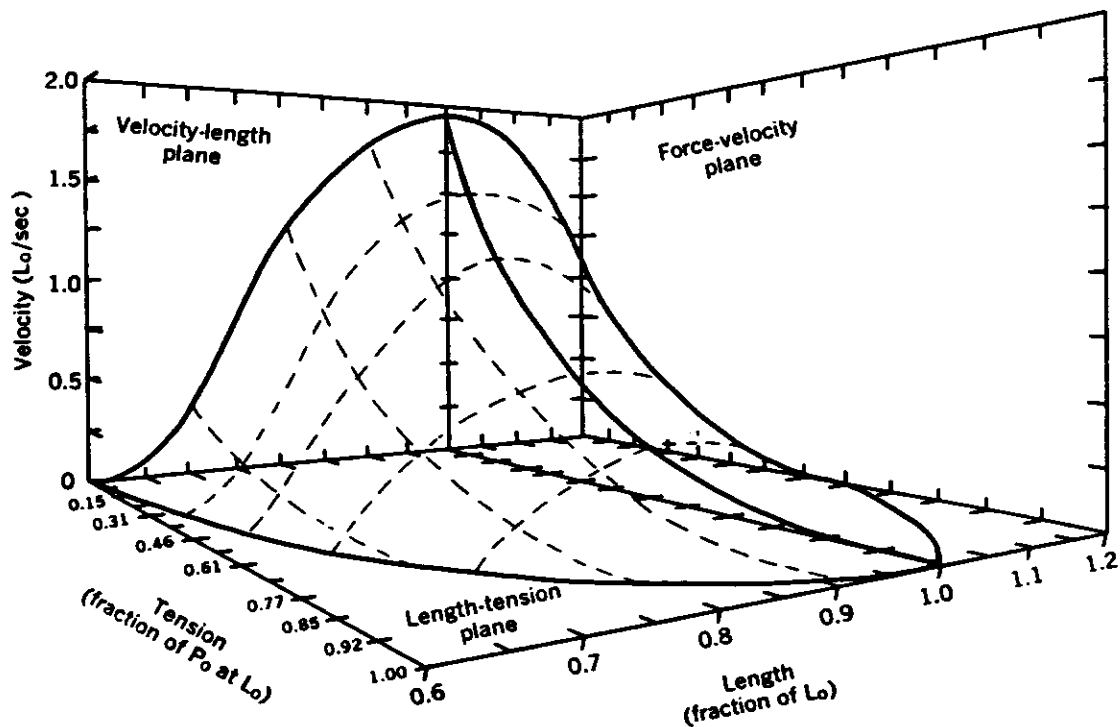


FIGURE 2-18

Semischematic three-dimensional representation of interrelationship between length, tension, and velocity. Based on data from gracilis muscle of rat at approximately 16° C. Isometric length-tension diagram forms the base of the figure in the length-tension plane. Force-velocity curve at initial length L_0 is given as a heavy continuous line with its own velocity-length axes. The foot on velocity-length curve at short lengths and small loads is extrapolated beyond experimental data in order to meet isometric length-tension diagram. Other force-velocity and velocity-length relations are shown by broken lines to suggest curvature of surface. There is a family of such three-dimensional figures, depending on available chemical energy for contraction.

Reprinted with permission from Zierler KL: Mechanism of muscle contraction and its energetics. In: Mountcastle VB (ed): Medical Physiology, ed 12. St. Louis, MO, C V Mosby Co, 1968, vol 2, p 1141.

isometric contraction occurs. In eccentric contractions, as the speed of lengthening increases, the maximum tension a muscle produces increases.

In dynamic movements, the effects of length and velocity combine to have dramatic effects on the active tension output of muscle. A summary of these relationships is well described by Figure 2-18, taken from Zierler.⁴⁰ The plot shows the interaction of length, velocity, and tension for shortening contractions.

SUMMARY

In this chapter, anatomical, physiologic, and mechanical concepts basic to understanding surface electromyography are presented. Specific topics discussed are anatomy of skeletal muscle, origin of the electromyographic signal, functional considerations of motor

units, and mechanics of muscle.

The contractile unit of muscle is the sarcomere. Many sarcomeres placed end to end form a myofibril. Many myofibrils wrapped in the sarcolemma make up a muscle fiber. The three major types of muscle fibers are Type I (SO) slow twitch oxidative, Type IIA (FOG) fast twitch oxidative, and Type IIB (FG) fast twitch glycolytic. The muscle fibers are bundled together by connective tissue to form fasciculi; groups of fasciculi make up a muscle. Connective tissue provides a means for the muscle fibers to be attached to each other and to bone.

The inside of a muscle fiber has a resting membrane potential of approximately -80 mV with respect to the outside. The polarized muscle fiber remains in equilibrium until upset by a stimulus. The stimulus causes

a rapid depolarization followed by a repolarization that can be measured; it is called the action potential. The spatial and temporal summation of the action potentials from the homogenous muscle fibers of a motor unit form the typical biphasic or triphasic wave shapes of a single motor unit action potential. When surface electrode techniques are used, the myoelectric activity recorded represents the spatial and temporal summation of many motor unit action potentials.

A group of homogenous muscle fiber types innervated by a single axon is called a motor unit. Three types of motor unit are recognized. Slow twitch motor units (S) can fire continuously for long periods at low frequencies. Fast twitch fatigue resistant (FR) motor units produce more force than slow twitch motor units but cannot fire continuously for long periods of time. The fast twitch fatigable motor units (FF) produce the greatest force but for very short periods.

The actual force and velocity of movement is controlled by motor unit recruitment and rate coding. Slow twitch motor units are recruited first and the fast twitch fatigable units are recruited only when rapid powerful movements are required. Each time a contraction is repeated, a particular motor unit is recruited at the same force level. At high force levels after all motor units have been recruited, additional force is created by increasing the firing frequencies of the motor units.

The tension created by a muscle contraction also depends on the geometric arrangement of muscle fibers, the length of the muscle, and the velocity of contraction. Muscles with their fibers parallel to their tendon tend to produce greater range of movement, whereas muscles with their fibers placed at an angle to their tendon tend to produce greater force per unit area. A muscle produces the maximum amount of tension when it is lengthened slightly beyond resting length. In concentric muscle contractions, the tension a muscle can produce decreases as shortening velocity increases. In eccentric muscle contractions, the maximum tension a muscle can produce increases as the speed of lengthening increases.

REFERENCES

1. Clark DH: Exercise Physiology. Englewood Cliffs, NJ, Prentice Hall, Inc, 1975
2. Etemadi AA, Hosseini F: Frequency and size of muscle fibers in athletic body building. *Anatomical Record* 162:269, 1968
3. Hollinshead WH: Anatomy for Surgeons: The Back and Limbs, ed 3. Hagerstown, MD, Harper & Row Publishers Inc, 1982, vol 3
4. Burke RE: Motor units: Anatomy, physiology and functional organization. In *Handbook of Physiology: Sec 1. The Nervous System: Motor Control*. Bethesda, MD, American Physiological Society, 1981, vol 2, pp 345-422
5. Mountcastle VB (ed): *Medical Physiology*, ed 14. St. Louis, MO, C V Mosby Co, 1980
6. Strand F: *Physiology: A Regulatory System Approach*. ed 2. New York, NY, Macmillian Publishing Co, 1983
7. Guyton AC: *Textbook of Medical Physiology*, ed 6. Philadelphia, PA, W B Saunders Co, 1981
8. Ekstedt J, Stalberg E: Single fibre electromyography for the study of the microphysiology of the human muscle. In Desmedt JE (ed): *New Developments in Electromyography and Clinical Neurophysiology*. Basel, Switzerland, Karger, 1973, vol 1, pp 113-129
9. Dowben RM: Contractility with special reference to skeletal muscle. In Mountcastle VB (ed): *Medical Physiology* (ed 14). St. Louis, C V Mosby Co, 1980, 104-105
10. Buchthal F, Guld C, Rosenfalck P: Action potential parameters in normal human muscle and their dependence on physical variables. *Acta Physiol Scand* 32:200-218, 1954
11. Basmajian J, DeLuca C: *Muscles Alive: Their Functions Revealed by Electromyography*, ed 5. Baltimore, MD, Williams & Wilkins, 1985, pp 1972
12. Burke RE, Edgerton VR: Motor unit properties and selective involvement in movement. In Wilmore JW, Keogh JF (eds): *Exercise and Sports Sciences Review*. New York, NY, Academic Press, 1975, vol 3
13. Buchthal F, Guld C, Rosenfalck P: Multielectrode study of the territory of a motor unit. *Acta Physiol Scand* 39:83-103, 1957
14. Feinstein B, Lindegard B, Nyman E, Wohlfart G: Morphological studies of motor units in normal human muscles. *Acta Anat* 23:127-142, 1955
15. Wersall R: The tympanic muscles and their reflexes: Physiology and pharmacology with special regard to noise generation by the muscles. *Acta Otolaryngol* 139 (suppl): 1-112, 1958
16. Ruedi L: Some observations on the histology and function of the larynx. *J Laryngol Otol* 73:1-20, 1959
17. Brook MH, Kaiser KK: Muscle fiber types: How many and what kind? *Arch Neurol* 23:369-379, 1970
18. Peter JB, Barnard RJ, Edgerton VR, et al: Metabolic profiles of three fiber types of skeletal muscle in guinea pigs and rabbits. *Biochemistry* 11:2627-2633, 1972
19. Garnett RAF, O'Donovan MJ, Stephens HA, et al: Motor unit organization of human medial gastrocnemius. *J Physiol (London)* 287:33-43, 1978
20. Sica RE, McComas AJ: Fast and slow twitch units in a human muscle. *J Neurol Neurosurg Psychiatry* 34:113-120, 1971
21. Faulkner JA, Chafin DR, McCully KK: Power output of fast and slow fibers from human skeletal muscles. In Jones NL, McCartney N, McComas AJ (eds): *Human Muscle Power*, 1986, pp 81-94
22. Wendt IR, Gibbs CL: Energy production of mammalian fast and slow-twitch muscles during development. *Am J Physiol* 226:642-647, 1974
23. Burke RE, Levine DN, Tsairis P, et al: Physiological types and histochemical profiles in motor units of the cat gastrocnemius. *J Physiol (London)* 234:723-748, 1973

24. Thorstensson A, Grimby G, Karlsson J: Force-velocity relations and fiber composition in human knee extensor muscles. *J Appl Physiol* 40:12-16, 1976
25. Costill DL, Daniels J, Evans W, et al: Skeletal muscle enzymes and fiber composition in male and female track athletes. *J Appl Physiol* 40:149-154, 1976
26. Burke RE, Rudomin P, Zajac FE III: The effect of activation history on tension production by individual muscle units. *Brain Res* 109:515-529, 1976
27. Milner-Brown HS, Stein RB, Yemm R: The orderly recruitment of human motor units during voluntary isometric contractions. *J Physiol (London)* 230:359-370, 1973
28. Adrian ED, Bronk DW: Impulses in motor nerve fibers: I. Impulses in single fibers of the phrenic nerve. *J Physiol (London)* 66:81-101, 1928
29. Milner-Brown HS, Stein RB, Yemm R: Changes in firing rate of human motor units during linearly changing voluntary contraction. *J Physiol (London)* 230:359-370, 1973
30. Milner-Brown HS, Stein RB, Yemm R: Changes in firing rate of human motor units during linearly changing voluntary contractions. *J Physiol (London)* 230:371-390, 1973
31. Henneman E: Recruitment of motoneurons: The size principles. In Desmedt JE (ed): *Motor Unit Types, Recruitment and Plasticity in Health and Disease: Progress Clinical Neurophysiology*. Basel, Switzerland, Karger, 1981, vol 9, pp 26-60
32. DeLuca CJ, LeFever RS, McCue MP, et al: Behavior of human motor units in different muscles during linearly varying contractions. *J Physiol (London)* 329:113-128, 1982
33. Green HJ: Muscle power: Fibre type recruitment, metabolism and fatigue. In Jones NL, McGartney N, McComas AJ (eds): *Human Muscle Power*. 1986, pp 65-79
34. Gordon AM, Huxley AF, Julian FJ: The variation in isometric tension with sarcomere length in vertebrate muscle fibers. *J Physiol (London)* 184:170-192, 1966
35. Fenn WO: The mechanics of muscular contraction in man. *J Appl Physiol* 9:165-177, 1938
36. Buller AJ, Eccles JC, Eccles RM: Differentiation of fast and slow muscle in cat hind limb. *J Physiol (London)* 150:399-416, 1960
37. Ismail HM, Ranatunga KW: Isometric tension development in a human skeletal muscle in relation to its working range of movement: The length-tension relationship of biceps brachii muscle. *Exp Neurol* 62:595-604, 1978
38. Huxley AF: Muscular contraction: A review of lecture. *J Physiol (London)* 243:1-43, 1974
39. Hill AV: The heat of shortening and the dynamic constants of muscle. *Proc R Soc London [Biol]* 126:136-195, 1938
40. Zierler KL: Mechanisms of muscle contraction and its energetics. In Mountcastle VB: *Medical Physiology*, St. Louis, MO, C V Mosby Co, 1974

Suggested Readings

Bigland B, Lippold OCJ: Motor unit activity in voluntary contraction of human muscle. *J Physiol (London)* 125:322-335, 1954

Clamann HP: Activity of single motor units during isometric tension. *Neurology* 20:254-260, 1970

Geddes LA, Baker LE: *Principles of Applied Biomedical Instrumentation*. New York, NY, John Wiley & Sons Inc, 1968, pp 262-324

Geddes LA: *Electrodes and the Measurement of Bioelectric Events*. New York, NY, Wiley-Interscience, John Wiley & Sons Inc, 1972, pp 251-305

Ramsey RW, Street SF: The isometric length-tension diagram of isolated skeletal muscle fibers of the frog. *J Cell Comp Physiol* 15:11-34, 1940

Tanji J, Kato M: Firing rate of individual motor units in voluntary contraction of abductor digiti minimi muscle in man. *Exp Neurology* 40:771-783, 1973