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Effects of electrical stimulation on the recruitment order of motor units in man: Indirect examination by electrically evoked muscle responses

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EFFECTS OF ELECTRICAL STIMULATION ON THE RECRUITMENT ORDER OF MOTOR UNITS IN MAN: INDIRECT EXAMINATION BY ELECTRICALLY EVOKED MUSCLE RESPONSES

by

Mark Herbert Trimble

A Thesis Submitted to the Faculty of the

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This thesis has been approved on the date shown below:

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Roger M. Enoka, Ph.D.
Associate Professor

August 25, 1987
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DEDICATION

To my parents,
my wife, Shelley, and
my daughter, Jessica

ACKNOWLEDGMENTS

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ABSTRACT

Although the neural mechanisms responsible for the orderly recruitment of motor units have been investigated extensively, the flexibility of the underlying neural circuitry remains unclear. For example, the effects of electrical stimulation on the recruitment order of motor units is not well understood.

This project was designed to study the recruitment order of motor units in man during different stimulation protocols. Examination of the compound-twitch characteristics of electrically evoked responses allowed an indirect determination of motor-unit recruitment order.

The results demonstrate that the recruitment order of quadriceps femoris and triceps surae motor units differs according to the stimulation protocols used. Analysis of the compound-twitch characteristics indicated that the recruitment order of motor units during Hoffmann reflexes is similar to volitional muscle contractions but effectively the reverse of that during direct-motor responses. Moreover, the results suggests that cutaneous-afferent stimulation alters the recruitment thresholds of different motor unit types during the Hoffmann reflex.

CHAPTER I

INTRODUCTION

It is widely agreed that the recruitment order of motor units under most physiological conditions occurs in an orderly manner which is relatively fixed and unalterable by will or by changing the velocity of the contraction (Denny-Brown and Pennybacker, 1938; Desmedt and Godaux, 1977a; Henneman, Somjen and Carpenter, 1965a, 1965b; Milner-Brown, Stein and Yemm, 1973b). The general notion is that relatively low-force, slow-twitch (type S) motor units are recruited first during voluntary and reflexly activated contractions; higher force, fast-twitch (types FR and FF) motor units are recruited as the effort or reflex stimulus increases (Burke, Levine, Tsairis and Zajac, 1973; Henneman et al., 1965a, 1965b; Milner-Brown et al, 1973b; for a discussion of motor-unit types see appendix A).

Under certain nonphysiological conditions, however, modifications of the normal recruitment order of motor units has been demonstrated. For example, cutaneous-afferent stimulation (sural nerve stimulation) during contractions induced by tonic-vibration reflexes has been shown to reverse the motor-unit recruitment order in

decerebrate cats (Burke, Jankowska and Bruggencate, 1970; Kanda, Burke and Walmsley, 1977). Similarly, a reversal in recruitment order of single motor units by cutaneous stimulation has also been demonstrated in man during voluntary contractions and reflex responses (Garnett and Stephens, 1980, 1981; Stephens, Garnett and Buller, 1978).

Cutaneous-afferent stimulation is thought to facilitate higher threshold motoneurons innervating fast-twitch muscle fibers and inhibit lower threshold motoneurons innervating slow-twitch muscle fibers (Burke et al., 1970; Garnett and Stephens, 1980, 1981; Kanda et al., 1977). Although cutaneous afferent input provides both excitation and inhibition to a motoneuron pool, the synaptic efficacy of this system is thought to occur on a differential continuum. The highest threshold motoneurons receive largely excitatory input, whereas, input to the lowest threshold motoneurons is mainly inhibitory; the motoneurons intermediate to the two extremes receive varying combinations of excitation and inhibition (Garnett and Stephens, 1980; Kanda et al., 1977).

Another example of nonphysiological activation of muscle modifying the motor-unit recruitment order is that of direct-efferent stimulation. Graded electrical stimulation of the efferent axons to a muscle has been shown to recruit motor units in a reverse order to that

which occurs under normal physiological conditions (Clamann, Gilles, Skinner, and Henneman, 1974; Mortimer, 1984). This phenomenon has been shown directly in animal studies. For example, in several hindlimb and forelimb muscles of reduced cat preparations, the high-propagation-velocity motor axons with the lowest electrical thresholds have been found to innervate fast-twitch motor units, whereas, motor units with slower contraction times were found to have higher electrical thresholds (Eccles, Eccles and Lundberg, 1958). In a heterogeneous muscle (i.e., a muscle consisting of multiple motor-unit types), the compound-twitch contraction time increases with increasing stimulus intensity as higher threshold axons innervating slow-twitch motor units are recruited (Clamann et al., 1974; Eccles et al, 1958). In contrast, when the muscle is activated reflexively by muscle-afferent stimulation, the compound-twitch contraction time shortens as high-threshold motoneurons innervating fast-twitch motor units are recruited (Clamann et al., 1974).

More recently, Mortimer (1984) demonstrated this same phenomenon indirectly in rat tibialis anterior muscle by examining the glycogen-depletion patterns of different muscle-fiber types. Mortimer (1984) found that following electrical stimulation of motor-axon branches the glycogen depletion was greatest in the type FG fibers and least in

the type SO fibers (see Appendix A for a discussion on muscle-fiber types).

Buchthal and Schmalbruch (1970b, 1976) have demonstrated in human muscle that slow-twitch motor units are recruited preferentially during reflex responses while fast-twitch motor units are recruited preferentially during direct motor-axon stimulation. These studies utilized compound-twitch contraction times of electrically evoked reflexes and direct-motor responses, as opposed to single motor-unit twitches. A slight decrease in the compound-twitch contraction time was observed with increasing force of the reflex twitch and a slight increase in the compound-twitch contraction time was associated with increasing twitch force during the efferent stimulation in humans (Buchthal and Schmalbruch, 1970b, 1976; Van Boxtel, 1986). The effect of increasing stimulus amplitude on these two experimental paradigms, however, has not been addressed in humans. Nevertheless, the recruitment order of motor units due to efferent stimulation is undoubtedly a function of the electrical threshold of peripheral nerve axons and the distance between the axon and the active electrode (McComas, 1977; Mortimer, 1984).

Differences in motor-unit recruitment order due to electrical stimulation may explain some of the variant-training responses produced by electrically induced

strength training (Boutelle, Smith and Malone, 1985; Eriksson and Haggmark, 1979; Godfrey, Jayawardena and Welsh, 1979; Laughman, Youdas, Garrett, and Chao, 1983; Williams, Morrissey and Brewster, 1986). It is generally accepted that muscle hypertrophy occurs to the greatest extent in the fibers subjected to the greatest usage (Burke and Edgerton, 1975; Gollnick, Piehl, Saubert, Armstrong, and Saltin, 1972; McDonagh and Davies, 1984). Therefore, if high-threshold, type FF motor units are recruited preferentially by electrically induced contractions, the muscle fibers of these units would receive the greatest training effect. This reasoning has recently been suggested by Parker, Berhold, Brown, Hunter, Smith, and Runhling (1986) to explain the lower contraction intensities necessary to produce a training effect with electrically induced strength training as compared to voluntary exercise (Boutelle et al., 1985; Laughman et al., 1983).

Most clinicians, as well as researchers, who have examined the effects of electrically induced strength training do not realize the artificial effect of the stimulus on motor-unit recruitment order. The comparison of muscle contraction intensity induced electrically and that achieved voluntarily is often used to equate exercise groups and to predict training responses (Boutelle et al.,

1985; Currier and Mann, 1984; Selkowitz, 1985; Romero, Sanford, Scroeder, and Fahey, 1982), although such comparisons may not be justified since different populations of muscle fibers would be activated and thus trained.

The purpose of the study was to provide further evidence that percutaneous electrical stimulation, of the type and method commonly utilized in rehabilitation settings, activates motor units of skeletal muscle in an order which is effectively the reverse of that which occurs under most physiological conditions. The two physiological mechanisms believed responsible for this differential activation, the effects of cutaneous-afferent stimulation and the effects of direct motor-efferent stimulation, were examined.

The experimental methods commonly used to evaluate the recruitment order of motor units has relied primarily on the recording of single motor-unit potentials in both cats and humans (Burke et al., 1970; Desmedt, 1981; Garnett and Stephens, 1981; Kanda et al., 1977; Stephens et al., 1978). Although this method can be used to directly examine changing thresholds of recorded motor units, it is generally limited to low-force, isometric conditions and to the comparison of only a few motor units at a time. The present investigation used an indirect method, similar to

that used by Buchthal and Schmalbruch (1970b, 1976), to examine the motor-unit recruitment order in human quadriceps femoris and triceps surae muscle groups during different electrical-stimulation protocols. The technique involves the measurement of compound twitches that are elicited by graded electrical stimulation of peripheral nerves. In addition, the study examined the differential effects of cutaneous-afferent stimulation on the electrically evoked reflex contractions.

Although this is an indirect way of examining the motor-unit recruitment order of a muscle, the whole population of motor units can be sampled at one time. Larger, more heterogeneous muscles (i.e., consisting of a greater variation of motor-unit types) may respond with greater variation in the compound twitch contraction time.

In summary, the recruitment order of motor units in electrically induced muscle contractions is thought to be opposite that which occurs under normal physiological conditions. The preferential facilitation of high-threshold motoneurons by cutaneous-afferent stimulation and the preferential excitation of high-threshold motor units by direct-efferent stimulation are the two phenomena responsible for this variant response. Although this is a general belief in the neurophysiology literature, it is not commonly recognized in the rehabilitation literature or by

clinicians utilizing electrical stimulation for strength training. This proposal concerns the implications of electrically induced reversals of motor-unit recruitment order for rehabilitation programs.

Statement of the Problem

The purpose of this study was twofold: 1) to compare motor-unit recruitment order during the H-reflex to the order achieved with direct stimulation of the motor efferents; 2) to determine if percutaneous electrical stimulation of cutaneous afferents can alter the motor-unit recruitment order during the H-reflex. Motor-unit recruitment order was evaluated indirectly by examining the compound-twitch contraction times of the H-reflex or the M-response in the quadriceps femoris and triceps surae muscle groups during four experimental protocols. The first protocol involved the generation of H-reflex recruitment curves. This entailed eliciting H-reflexes with a graded stimulation protocol, from threshold to maximum. The second and third protocols involved the generation of M-response recruitment curves. A similar graded stimulation protocol was used for these recruitment curves. The fourth protocol involved the comparison of a test H-reflex before, during and following conditioning

with percutaneous, high-frequency electrical stimulation (below the motor threshold) over the bellies of the test muscles.

Statement of the Hypotheses

The following hypotheses were formulated:

1) The compound-twitch contraction time of the H-reflex will decrease and force will increase with increasing stimulus amplitude due to the progressive recruitment of fast-twitch motor units.
2) The compound-twitch contraction time and force of the M-response will increase with increasing stimulus amplitude due to the progressive recruitment of slow-twitch motor units.
3) A conditioning protocol of percutaneous electrical stimulation over the bellies of the test muscles will shorten the contraction time of H-reflexes generated at a constant stimulus amplitude.

Scope of the Study

There were 22 subjects involved in this study, males and females in the age range of 19 to 53 years, with no history of neuromuscular disease. All subjects were volunteers recruited from among the University of Arizona

college community.

Prior to testing, each subject was introduced to the laboratory and received an explanation of the equipment and procedures to be used.

Limitations of the Study

An attempt was made to control as many variables as possible, but the study was limited in two ways: 1) it was not possible to deliver the same electrical-stimulus amplitudes to all subjects due to variations in the individual response, skin-tissue impedance, and subject tolerance; 2) during the generation of H-reflex recruitment curves it was not possible to eliminate completely the contribution of the M-response to the compound twitch.

Probable Value of the Study

Much of the research comparing electrically induced strength training to voluntary strength training has attempted to equate the muscle-contraction intensities of the two kinds of exercise. The assumption is that the total muscular force is the critical factor necessary to induce strength improvements, which is commonly assumed when comparing voluntary exercise programs. This may not be the case, however, with electrically induced strength

training due to the differences in the way muscle is activated. This study will address the differences in the activation of skeletal muscle by percutaneous electrical stimulation compared to reflexly activated muscle contractions. In addition, this study will provide the necessary data to design futher experiments to examine the physiological mechanisms responsible for the strength gains associated with electrically induced exercise.

This study may have significance for the rehabilitation of orthopaedic injuries. If a differential training effect is possible with electrical stimulation, more appropriate training programs could be designed. In situations when intense muscle contractions are detrimental, such as following joint injuries, this may prove particularly beneficial. By preferentially activating high-threshold motor units with electrically induced exercise, the muscle fibers of these units could be trained at lower contraction intensities minimizing the forces acting across the injured joint.

CHAPTER II

REVIEW OF RELATED LITERATURE

This study concerns the orderly recruitment phenomenon and its dependence upon the mode of activation. To accommodate this focus, this review of literature has been divided into three basic areas of concentration: 1) mechanisms underlying the orderly recruitment of motor units; 2) electrically evoked responses and the associated neural pathways; and 3) electrical stimulation of human muscle to induce tetanic muscle contractions and to enhance voluntary strength.

The first section will discuss the physiological mechanisms responsible for the observed orderly recruitment of motor units. Conditions in which the normal motor-unit recruitment order is altered and the physiological mechanisms involved will also be discussed. The second section, electrically evoked responses and the associated neural pathways, deals with the differences between monosynaptic-reflex responses and direct-motor responses. This section will include a discussion of the mechanisms contributing to these differences and the mechanical responses associated with reflex and direct-motor responses. The third section

describes some of the physiological responses that occur with the strength-training technique of electrical stimulation. The emphasis of this latter section will be on the differences between the physiological responses to electrically induced exercise as compared to voluntary exercise. Finally, a summary section will reiterate the relevance of this literature to the proposed research.

Mechanisms Underlying the Orderly Recruitment of Motor Units

The graded control of movement by the central nervous system is accomplished by the activation of individual motor units. A motor unit, which is the basic functional unit of the neuromuscular system, is defined as a motoneuron with its dendrites and motor axon, and the group of muscle fibers it innervates. The regulation of muscle force occurs by the concurrent variation in the number of active motor units and their rate of activation. Although motor-unit recruitment and frequency control are both important, the mechanisms responsible for the recruitment order of motor units will be the emphasis of this text.

The Normal Physiological Motor-Unit Recruitment Order

It is widely accepted that the recruitment order of motor units under most physiological conditions occurs in an

orderly manner which is relatively fixed and unalterable by will or by changing the velocity of the contraction (Denny-Brown and Pennybacker, 1938; Desmedt and Godaux, 1977a; Henneman et al., 1965a, 1965b). This has been demonstrated in a number of different ways: 1) in man, by recording from a small number of motor units while the subject is performing a graded or rapid voluntary contraction, or by muscle vibration (Desmedt and Godaux, 1977a, 1978; Milner-Brown et al., 1973b); 2) in cat, by recording individual motor-unit potentials or from the ventral roots directly during a reflexly activated contraction (Burke et al., 1973; Henneman et al, 1965b), 3) in rat, by studying the glycogen-depletion patterns following exercise of different intensities (Armstrong, Saubert, Sembrowich, Shepherd, and Gollnick, 1974). The mechanisms responsible for this phenomenon, known as "orderly recruitment", have evolved at the spinal level; the elaborate neural circuitry that would be required for direct control by supraspinal centers would exceed the capabilities of the central nervous system (Enoka and Stuart, 1984).

Alpha motoneurons, located in the anterior horn of the spinal cord, exhibit different functional thresholds which are relatively stable, a fact that is also generally agreed upon (Burke, 1981). However, the factors responsible for these variations in functional threshold are not as clear.

Henneman and associates (Henneman et al, 1965a,b; Henneman, Clamann, Gilles, and Skinner, 1974) have demonstrated a direct relationship between the functional threshold of a motoneuron and its size, suggesting that motoneuron size is the critical factor underlying the orderly recruitment of motor units. Henneman claims that the cell input resistance, which is inversely related to the size of motoneuron soma and the absolute-threshold voltage, is responsible for the differential functional thresholds of motoneurons. Assuming that the synaptic input to a motoneuron pool from all synaptic systems is equally distributed, differences in the size of excitatory postsynaptic potentials would be related to cell input resistance (Mendell and Henneman, 1971; Nelson and Mendell, 1976).

An alternative hypothesis, proposed by Burke and associates (Burke, 1968; Burke et al., 1970; Burke et al., 1976) is that the greater susceptibility of small cells to monosynaptic-reflex discharge is due to preferential distribution of Ia afferent input to small cells. Support for this argument comes from the finding of afferent and supraspinal systems providing synaptic input to the motoneuron pool in a qualitatively different pattern. For example, cutaneous afferents, which provide polysynaptic postsynaptic potentials composed of mixtures of inhibitory and excitatory components to a motoneuron pool, show

predominantly inhibitory components in slow-twitch motor units and a predominance of excitation in fast-twitch motor units (Burke et al., 1970; Kanda et al, 1977). Similarly, rubrospinal synaptic input, which also consists of inhibitory and excitatory components, provides predominantly inhibitory postsynaptic potentials to slow-twitch motor units and mixed or predominantly excitatory postsynaptic potentials to fast-twitch units (Burke et al., 1970). Therefore, both intrinsic (e.g., cell size and membrane input resistance), and extrinsic (e.g., organization and quality of synaptic input) motoneuronal properties appear to be involved in determining the functional thresholds of a motoneuron pool and thus the recruitment order of motor units (Burke, 1981, 1987; Clamann, 1981; Enoka and Stuart, 1985).

The motor-unit recruitment order commonly observed is from type S to type FR to type FF motor units with some overlap between the different types (Burke, 1981; Burke and Edgerton, 1975; see Appendix A for a discussion of motor unit types). Low-threshold motor units, type S and some type FR, are recruited during low-intensity aerobic activities. With more intense activities, higher threshold type FR motor units are recruited and during high-intensity anaerobic exercise type FF motor units are recruited (Burke and Edgerton, 1975). The dynamic usage of motor units is probably directly correlated with the oxidative capacity of their muscle fibers

(Burke and Edgerton, 1975; Edgerton, Saltin, Essen, and Simpson 1975a; Gollnick, Piehl, Saubert, Armstrong, and Saltin, 1972b). Moreover, this recruitment order of motor units makes sense in terms of kinesiologic and metabolic efficiency under most conditions (Burke, 1981).

Since the properties of units differ, it also makes functional sense that motor units are recruited in the order most appropriate for the work intended. For example, Smith, Betts, Edgerton, and Zernicke, (1980) have demonstrated that activation of the fast extensors (lateral gastrocnemius) prior to activation of the slow extensors (soleus) of the ankle of the cat occurs during rapid, alternate flexion-extension movements elicited by placing the hind paw in water or sticking tape on the plantar pads. They suggested that the paw-shaking activity under the described conditions is a natural, automatic movement triggered primarily by cutaneous afferents innervating the central plantar pads.

Alterations in the Normal Physiological Recruitment Order and the Mechanisms Involved

Under other experimental conditions, restructuring of the motoneuron functional thresholds has been demonstrated Burke et al., 1970; Garnett and Stephens, 1980; Kanda et al., 1977; Stephens, Garnett and Buller, 1978). Although it has been argued that these findings are due to artificial laboratory conditions and are unlikely to be encountered in

normal activities, they may in fact represent a certain degree of flexibility of recruitment order depending on input conditions. Several studies have demonstrated that during and following cutaneous-afferent stimulation, the usual functional thresholds of recorded motor units may be reversed (Burke et al., 1970; Garnett and Stephens, 1981; Kanda et al., 1977; Stephens et al., 1978). This phenomenon has been shown in cat triceps surae muscles during tonic-vibration reflex contractions (Burke et al., 1970; Kanda et al., 1977), and in man, during voluntary and reflex contractions (Garnett and Stephens, 1981; Stephens et al., 1980).

Cutaneous afferents provide polysynaptic postsynaptic potentials, consisting of inhibitory and excitatory components, to a motoneuron pool. Inhibitory postsynaptic potentials predominate in slow-twitch motor units, whereas, excitatory postsynaptic potentials predominate in fast-twitch motor units; intermediate, type FR, motor units receive varying combinations of inhibitory and excitatory input along a continuum (Burke et al., 1970; Garnett and Stephens, 1981; Kanda et al, 1977). This has the tendency to not only lower the functional thresholds of type FF motor units, but also to raise the functional thresholds of type S motor units.

Summary

In summary, both intrinsic and extrinsic motoneuronal

properties appear to be involved in determining the functional thresholds of a motoneuron pool. A certain degree of flexibility of motor-unit recruitment order appears to occur depending on input conditions to the motoneuron pool. The afferent system that has provided the majority of evidence for this flexibility has been the cutaneous-afferent system. However, other afferent systems and perhaps some supraspinal pathways may also alter the normal orderly recruitment of motor units.

Electrically Evoked Responses and the Underlying Neural Pathways

Electrical evocation of neural-based responses is a common research technique that has been used to investigate neuromuscular mechanisms. The techniques of interest here involve muscle responses evoked by electrical-current pulses to a peripheral nerve.

The Hoffmann Reflex

First described by Hoffmann in the early 1920's (cited in Magladery and McDougal, 1950), a short-latency reflex response thought to be part of the myotatic-reflex arc is referred to as the Hoffmann reflex (H-reflex). The H-reflex can be obtained in certain muscles by passing a single, submaximal electrical impulse through a mixed peripheral

nerve. At appropriate stimulus strengths, such current pulses will selectively activate the group Ia afferents from muscle spindles (Hugon, 1973; Magladery and McDougal, 1950). Synchronous volleys of impulses from these afferents monosynaptically excite the alpha motoneuron pool producing a compound motor response (Magladery and McDougal, 1950). The largest group Ia afferents, with the lowest electrical thresholds, are recruited first (Hugon, 1973; Jack, 1978; Magladery and McDougal, 1950; Van Boxtel, 1986). The amplitude and waveform of the compound muscle twitch elicited in this way is dependent upon the number, type and temporal association of motor units recruited (Gydikov et al. 1976).

The EMG representation of the H-reflex, the H-wave, is commonly used as a relative indicator of motoneuron excitability (Magladery and McDougal, 1950; Mongia, 1970; Hugon, 1973; Spencer et al., 1984). However, the mechanical muscle twitch it elicits can also be examined as an indicator of the motor-unit types recruited in this reflex (Buchthal and Schmalbruch, 1970a, 1976).

Muscle activated in this way demonstrates a motor-unit recruitment order which is qualitatively similar to natural conditions since the H-reflex utilizes the same neural pathways as the myotatic reflex (Magladery and McDougal, 1950). That is, this electrically evoked reflex recruits the lowest-threshold motoneurons first because they have the

greatest convergence of Ia input (Burke, 1968; Burke et al., 1976). Slow-twitch motor units are therefore recruited first when eliciting an H-reflex, and with increasing stimulus intensities fast-twitch motor units are recruited.

At successively higher stimulus intensities the H-reflex is extinguished. This is associated with the onset of a direct-motor response (M-response). The diminution of the H-reflex may, inpart, be due to antidromic impulses in the efferent axons, either by collisions with orthodromic impulses originating from afferent excitation of the alpha motoneurons or by simple refactoriness of the alpha motoneuron if the antidromic action potential were to reach the axon hillock before the arrival of the reflex action potential (Gottlieb and Agarwal, 1976). It may also reflect other mechanisms since a plateau in the H-reflex recruitment curve at its maximum amplitude is commonly found before the direct-motor response (M-response) has begun to increase (Hugon, 1973); these other possible mechanisms include Renshaw cell inhibition (Hugon, 1973; Gottlieb and Agarwal, 1976) and the fact that the highest threshold, type FF, motor units under normal conditions are not as responsive to Ia excitation (Burke et al., 1976).

The Direct-Motor Response

The M-response is due to excitation of the efferent

axons which have electrical thresholds only slightly higher than Ia fibers (Magladery and McDougal, 1951). The EMG representation of the M-response is called the M-wave (Hugon, 1973; Magladery and McDougal, 1951). Since electrical thresholds of mammalian peripheral nerves are an inverse function of axonal cross-sectional area and propagation velocity (Erlanger and Gasser, 1937; Wiederholt, 1970), the motor units with the largest-diameter axons will be recruited first with direct, graded stimulation of the motor efferents (Mendell and Henneman, 1971; Mortimer, 1984). Therefore, type FF motor units with the fastest axonal propagation velocities (Burke et al., 1973), will be the units recruited first in the M-response; with increasing stimulus amplitudes type FR motor units will be recruited and only at the maximal stimulus amplitudes will type S units be recruited.

Mechanical Twitches Associated with these Electrically Evoked Responses

Because of these differences in the way motor units are recruited by afferent and efferent stimulation, the compound twitch produced by the M-response has been found to have a shorter contraction time than that of the H-reflex (Buchthal and Schmalbruch, 1976; Homma and Kona, 1962). These two types of twitch contractions may not be qualitatively comparable, however, since the desynchronization of the impulse volley is theoretically greater for the H-reflex due

to differences in propagation velocity among the afferents and to differences in synaptic transmission. This would have the tendency to increase the temporal dispersion of the resulting efferent impulses and therefore the muscle-fiber activation, increasing the compound-twitch contraction time of the H-reflex disproportionately (Gerilovsky et al, 1985). However, Hugon (1973) has suggested that the synchronization of the H-reflex and the M-response are comparable based upon the examination of monopolarly recorded field potentials. Therefore, any desynchronization of the motor-unit potentials during these compound-twitch responses is principally due to the intrinsic pattern of motor-axon innervation (i.e., inequalities in the motor-axon branches), and consequently the H-reflex and M-response from the same muscle or muscle group would be similar.

The compound-twitch contraction times of H-reflexes tend to be inversely related to the twitch force (i.e., compound-twitches with shorter contraction times usually produce greater force; Buchthal and Schmalbruch, 1970b, 1976; Van Boxtel, 1986). This is presumably due to the successive recruitment of fast-twitch motor units with this type of reflex activation. In contrast, the compound-twitch contraction time of the M-response is directly related to the twitch force (i.e., compound-twitches with longer contraction times tend to produce greater force; Buchthal and

Schmalbruch, 1970b), suggesting that slow-twitch motor units are recruited with greater stimulus amplitudes.

Summary

In summary, electrically evoked muscle responses can be a useful research technique to examine indirectly the recruitment order of motor units. By examining the contraction times of either reflex or direct-motor responses while the stimulus amplitude is varied, one should be able to evaluate the motor-unit recruitment order of the tested muscle. H-reflex responses, elicited by electrically stimulating Ia (muscle spindle) afferents, under normal conditions should recruit motor units in an order resembling natural physiological conditions. In contrast, direct-motor responses, elicited by electrically stimulating muscle-efferent axons directly, should recruit motor units in a reverse order. Moreover, by examining the compound-twitch contraction times of reflex responses under different motoneuron input conditions, one should be able to examine the motor-unit recruitment order under the altered conditions.

Electrical Stimulation to Induce Tetanic Muscle Contractions and to Enhance Voluntary Strength

Although traditional strength-improvement techniques

have centered around resisted voluntary exercise, electrical stimulation is often used as an adjunct, particularly when limb muscles are in a weakened state. The efficacy of electrically induced strength training has been based on the concept of muscle reeducation (Godfrey et al., 1979; Kramer and Mendryk, 1982) and on the belief that electrically induced exercise is a way of bypassing the limitations imposed by the central nervous system (Currier et al., 1979; Moritani and DeVries, 1979; Cummings, 1980; Romero et al., 1982).

The concept of muscle reeducation depends on the normal processes of learning, starting at a reflex level (Knapp, 1978). It was thought that by stimulating proprioceptive pathways through passive manipulation of the limb (Basmajian, 1978) or via electrical muscle stimulation (Benton et al., 1980; Cummings, 1980; Curwin et al., 1980; Kramer and Mendryk, 1982), previous motor patterns could be strengthened and normal function restored. The physiological rationale for this concept was not clear but possibly represented alterations in the afferent feedback to motor control centers. If the individual could view a strong electrically induced muscle contraction, further influence on the reeducation process was thought possible (Benton et al., 1980). Once the individual could exert an adequate voluntary muscle contraction, voluntary exercise was then of greater

benefit in restoring the volitional control and muscular strength (Currier et al., 1979; Curwin et al., 1980; Kramer and Mendryk, 1982). This was the philosophy adhered to in the rehabilitation programs of North America until about 1975.

In 1977 Yakov Kots, a Soviet scientist lecturing in Canada, reported on work suggesting that electrical stimulation of skeletal muscle may be more effective than voluntary exercise in enhancing the strength of normal, healthy muscle as well as atrophied muscle (as cited in Kramer and Mendryk, 1982). Kots claimed to have designed an electrical stimulator that could induce contraction intensities 10-30% greater than the maximal voluntary contraction in highly trained athletes. Furthermore, strength training programs based on this electrical-stimulation technique were reported to produce strength improvements of 30-40% (as cited in Kramer and Mendrk, 1982). The success of this technique was based upon a complex stimulation protocol. The Soviet stimulator utilized a sinusoidal, medium frequency of 1600-2500 Hz which was modulated to produce trains of impulses at a frequency of 50 Hz (as cited in Kramer and Mendryk, 1982). This format reportedly blocked cutaneous perception while preferentially stimulating muscle efferents. A tetanic contraction with complete motor-unit recruitment was supposedly possible since

the electrical stimulus was not limited by pain (as cited in Kramer and Mendryk, 1982).

Although the description and documentation of the Soviet technique has been incomplete, many investigators in Canada and the United States have attempted to replicate Kots' work (Laughman et al., 1983; Owens and Malone, 1983; Currier and Mann, 1984; Boutelle et al., 1985; Selkowitz, 1985). These attempts have not been wholly successful, but the renewed interest in electrical stimulation as a strength-training technique has led the way for significant improvements in the technique.

Studies Comparing the Effectiveness of Electrically Induced and Voluntary Exercise

Improvement in voluntary strength as a result of electrically induced training has been reported in both normal muscle (Boutelle et al., 1985; Currier et al., 1979; Currier and Mann, 1983; Laughman et al., 1983; Romero et al., 1982; Selkowitz, 1985) and hypotrophic muscle (Eriksson and Haggmark, 1979; Godfrey et al., 1979; Johnson et al., 1977; Williams et al., 1986). In most cases, the studies that have used normal, healthy subjects are more recent and have been better controlled than the studies involving detrained individuals. Most of the more recent studies have defined muscular strength as the maximal voluntary torque exerted isometrically on a dynanometer as

opposed to determining strength by the weight lifted. Although improvements in maximal voluntary torque capabilities have been reported in normal individuals following electrical stimulation, the comparisons with voluntary exercise have indicated either equivalence between the two modes of training (Currier and Mann, 1983; Laughman et al., 1983) or superiority of voluntary exercise (Mohr et al., 1985). Even when electrical stimulation was superimposed over a maximal voluntary contraction (MVC), the combination was no more effective in increasing strength than maximal voluntary exercise (Currier et al., 1979; Currier and Mann, 1983).

Failure to replicate the Soviet work is most often attributed to an inability to produce a strong enough muscle contraction with electrical stimulation. None of the previously cited studies have reported electrically induced contraction intensities greater than a MVC; this includes electrical stimulation superimposed over a MVC. The contrasting results may also reflect differences in the state of training of the subjects, that is, the Soviets used elite athletes.

Studies that have investigated the effects of electrical stimulation on hypotrophied muscle have reported findings contrasting those found in the studies involving healthy individuals. A study by Godfrey et al. (1979) compared

strength training by electrical stimulation with voluntary exercise in subjects who had recently suffered a knee injury or undergone knee surgery. They reported superiority of the electrical-stimulation group in improving the ability to exert knee-extensor torque (Godfrey et al., 1979). In a more recent study involving postmeniscectomy patients, Williams et al. (1986) compared electrical stimulation superimposed over a voluntary exercise program with the results achieved by a voluntary exercise program alone. Maximal voluntary exercise with superimposed electrical stimulation was found to be more effective in improving maximal voluntary torque capability than voluntary exercise alone. The discrepancy in these results reflects a possible differential training effect produced by electrical stimulation, as well as, emphasizes the importance of considering the prior state of training or physical condition of the subjects when comparing training programs.

Physiological Differences Between Electrically Induced and Voluntary Exercise

A differential effect of electrically induced strength training on hypotrophic muscle may reflect a difference in the physiological response to this type of training. Physiological differences between electrically induced and voluntary muscle contractions may be associated with a differential training response due to: 1) differences

in the recruitment order of motor units; and 2) the effect of cutaneous afferent feedback.

The motor-unit recruitment order that occurs with electrically induced muscle contractions is different than that which occurs during normal physiological conditions. As discussed in detail in the first section of this chapter, the motor-unit recruitment order under most physiological conditions is rather fixed and occurs in a predictable manner (Denny-Brown and Pennybaker, 1938; Desmedt and Godaux, 1977a; Milner-Brown et al., 1973b). In general, type S motor units are recruited first during voluntary and reflexly activated contractions followed by the recruitment of type FR units as the effort or reflex stimuli increases and, finally, type FF motor units are recruited with intense muscle contractions (Burke et al., 1973; Henneman et al., 1965a, 1965b; Milner-Brown et al., 1973).

In contrast, motor-unit recruitment during electrically induced muscle contractions is thought to occur in a reverse order to that which occurs under most physiological conditions (i.e., from type FF to type S motor units). In considering this concept, one must first realize that when electrically stimulating a muscle with an intact peripheral nervous system, the resulting muscle contraction is induced via excitation of the motor nerves (or branches thereof) to the muscle (Mortimer, 1984; Hultman et al., 1983). This

occurs since the electrical excitability of skeletal muscle is much lower than that of its motor nerve.

Therefore, instead of a dependence on the properties of the alpha motoneurons in the anterior horn of the spinal cord to determine the recruitment order of motor units, recruitment by electrical stimulation is a function of: 1) the diameter of the motor axons, 2) the distance between the axon and the active electrode (cathode) (Gorman and Mortimer, 1983; McComas et al., 1971; Mortimer, 1984), and 3) the effect of cutaneous-afferent input to the alpha motoneuron pool (Kanda et al., 1977; Garnett and Stephens, 1981). Although the threshold of electrical excitability for different motor axons is dependent on both axonal diameter and the distance separating the axon from the stimulating electrode, McComas et al. (1971) claims that the axon-electrode geometry is the critical factor.

Although a reversal of the normal motor-unit recruitment order during electrically induced muscle contractions is wellfounded, based on classical electrophysiological concepts, contrasting results have been reported. Brown, Kadrie, and Milner-Brown (1981) have reportedly found motor-unit recruitment elicited by graded electrical stimulation of a peripheral nerve that was similar to that found physiologically. These findings, on the contrary, may reflect: 1) an alternation of motor units due to overlapping

thresholds, or 2) anatomical differences, such as innervation ratios, the relative position of axons in the motor nerve or a species effect.

With electrical stimulation over the muscle belly, as opposed to over the peripheral nerve to the muscle, a reversal in the recruitment order would be more likely for two reasons. First, muscles containing predominantly type FR and FF motor units appear to be anatomically superficial to muscles containing predominantly type S motor units, in humans as well as a variety of mammals (Ariano et al., 1973, Edgerton et al., 1975; Mortimer, 1984). Therefore, the motor-nerve branches of the larger type FR and FF motor units are closer to the stimulating electrodes and are more likely to be excited first with graded electrical stimulation. Secondly, with electrical stimulation superimposed over a voluntary contraction, a reversal of the normal physiological motor-unit recruitment order may, inpart, result from a differential effect on alpha motoneurons by stimulation of cutaneous afferents. Several investigators (Burke et al., 1970; Garnett and Stephens, 1981; Kanda et al., 1977; Stephens et al., 1980) have demonstrated an excitatory effect on large motoneurons as well as an inhibitory effect on smaller motoneurons by cutaneous-afferent feedback.

Evidence For Neural Adaptation with Electrically Induced Strength Training

Improvements in strength by electrically induced exercise may be due, particularly during the early phases of training, to neural adaptive changes resulting from the stimulation of various afferent systems. Since alteration of motoneuron activity by cutaneous (Garnett and Stephens, 1981; Kanda et al., 1977) and muscle afferent stimulation (Magladery et al., 1951; Upton et al., 1971) has been demonstrated, any chronic alteration of afferent feedback due to electrical stimulation would affect the muscular force capability.

It has been assumed by many researchers (Currier et al., 1979; Romero et al., 1982; Moritani and DeVries, 1979) and clinicians that improvements in voluntary strength induced by training with electrical stimulation is largely due to an increase in the myofibrillar content of muscle. Moritani and DeVries (1979) have suggested that since the motor pathways are minimally involved with electrically induced exercise the training stimulus probably resides in the muscle tissue itself. This however might not be the case. Neural adaptations with electrically induced strength training is probable in studies demonstrating an increase in strength without appreciable increases in the cross-sectional area of the muscle (Eriksson et al., 1981; Laughman et al., 1983).

Eriksson et al. (1981) investigated the effect of electrical stimulation on normal, healthy individuals and reported significant improvements in voluntary strength after a 4 week training program in the absence of muscular changes. These changes were assessed with muscle biopsies that were taken before and after the training program and analyzed histochemically for muscle fiber-type composition and area. In addition, other studies that have reported significant strength gains as a result of training with electrical stimulation have utilized training periods of less than 5 weeks (Boutelle et al., 1985; Currier and Mann, 1983; Godfrey et al., 1979; Laughman et al., 1983; Romero et al., 1982; Selkowitz, 1985), although training periods of such a brief duration are thought to predominantly affect the neural components of strength during voluntary-exercise regimens (Hakkinen and Komi, 1983; Moritani and DeVries, 1979).

There have been other indications of electrical stimulation affecting the neural component of strength. For example, electrically induced strength training appears to improve strength at lower contraction intensities than is usually considered necessary with voluntary exercise (Boutelle et al., 1985; Laughman et al., 1983; Parker et al. 1986).

Strength training by voluntary exercise has long been known to be dictated by the Overload Principle. The basis of

this principle is that the stimulus for inducing strength gains is dependent on and proportional to the intensity of the muscle contraction (Delorme, 1945). The minimum intensity generally thought necessary to stimulate muscle hypertrophy is 60% of one maximal voluntary contraction (McDonagh and Davies, 1984). Considering this, it is interesting that Boutelle et al. (1985) and Laughman et al. (1983) have demonstrated significant gains in strength as a result of electrical stimulation alone even though the muscle contraction intensities during the training period were well below this minimum. For example, Laughman et al. (1983) compared training with electrical stimulation alone with a voluntary, isometric exercise program. Although the duration of the contractions and the number of treatments and repetitions were the same, the contraction intensities were quite different. The average training intensity for the voluntary-exercise group was 78% of the maximal voluntary contraction intensity as measured by isometric torque, whereas the training intensity for the electrical-stimulation group was only 33% of the maximal voluntary contraction. The exercise group increased maximal voluntary-torque capability by 18% compared to a 22% improvement for the electrical-stimulation group (Laughman et al., 1983). The between-groups difference, however, was not significant. This finding of an enhanced training effect at lower training

intensities is possibly the result of a preferential recruitment and facilitation of large motor units by percutaneous electrical stimulation (Garnett and Stephens, 1981; Kanda et al., 1977; Parker et al., 1986), but may also reflect limitations in evaluating the training (contraction) intensity of this type of exercise.

Another finding suggesting neural adaptation is an observed cross-training effect, an increase in maximal torque capability in the contralateral untrained extremity, with electrically induced strength training alone (Laughman et al., 1983). This finding suggests that some of the neural adaptations that are responsible for the cross-training effect occur at the spinal level. Perhaps contralateral afferent feedback provides excitatory synaptic input to the ipsilateral motoneuron pool. Direct support for this supposition is the finding of increased motoneuron excitability with contralateral cutaneous nerve stimulation (Delwaide et al., 1981). In addition, indirect evidence has recently been observed by Howard (1987; Howard and Enoka, 1987); acute, maximal, voluntary-force capability was enhanced during contralateral percutaneous electrical stimulation in strength-trained athletes.

A neural phenomenon possibly unique to electrically induced muscle contractions was described by Alon (1985), while investigating the effect of electrode size on the

responses of muscle to stimulation. He noted an average increase of 13.3% in the maximal torque exerted following one session of electrical stimulation. Alon suggested that this was due to posttetanic potentiation. This is unlikely in that posttetanic potentiation of muscle is a submaximal (eg., twitch) phenomenon (Schiff, 1858 as cited in Hughes, 1958; Standaert, 1964; Desmedt and Hainaut, 1968; Olson and Swett, 1971; Krarup, 1977). The potentiated twitch force is thought to more closely approximate the tetanic force since the maximum tetanic-force has been found to be unchanged during this same time interval (Sandow, 1964; Desmedt and Hainaut, 1968). The observation of Alon (1985) raises the question as to whether the increase in force was an acute facilitatory effect or the beginning of neural adaptive changes. This observation is possibly related to the early strength gains attributed to muscle reeducation following injury.

Summary

In summary, it is difficult to compare data across studies investigating electrically induced strength training for two main reasons: 1) variation in the prior state of training of the subjects, 2) the physiological responses underlying electrical stimulation are not fully understood. Previous studies have related the electrically elicited muscle-contraction intensity to the maximal voluntary

contraction. The assumption is that, like voluntary-strength training, muscular force is the critical factor necessary to induce muscle-strength improvements. This may not be the case, however, with electrically induced strength training. Even if the muscle force is identified as a critical factor, the net muscular torque induced by electrical stimulation may not be an accurate indicator of the contraction intensity. The electrical stimulus could overflow into the antagonist muscle group producing a cocontraction which would invalidate the estimation of contraction intensity as based upon the exerted torque. Also, the electrical-stimulus parameters, and hence the neural effects, are not comparable even if the intensity of the muscle contractions induced are similar.

Summary

Although the normal orderly recruitment of motor units is fixed under most physiological conditions, alterations have been demonstrated by changing the afferent input to the motoneuron pool. Cutaneous afferents have provided the majority of evidence for this flexibility in motor-unit recruitment order (Burke et al., 1970; Garnett and Stephens, 1981; Kanda et al., 1977; Stephens et al., 1978).

Although several techniques have been used to evaluate

motor-unit recruitment order in animal preparations, the choices with human subjects are more limited. An indirect method utilizing the mechanical twitch of electrically evoked responses has been described by Buchthal and Schmalbruch (1970a, 1970b, 1976). The longer the compound-twitch contraction time of a particular electrically evoked response, the greater the contribution of slow-twitch motor units to the composite twitch, and conversely, the shorter the contraction time, the greater the contribution of fast-twitch motor units. This technique has the advantage of evaluating many motor units at one time; however, it is limited to isometric conditions. The present study will use this technique to examine the effect of cutaneous-afferent stimulation on the order of motor-unit recruitment during reflex responses.

By demonstrating that a reversal in motor-unit recruitment order is possible with electrical stimulation, preferential training of different populations of motor units and their muscle fibers appears possible. This may in fact explain some of the differential training responses observed with electrically induced exercise (Godfrey et al, 1979; Laughman et al., 1983; Williams et al., 1986).

Knowledge of the differential response of electrically induced muscle contractions and training may prove beneficial when designing training programs. This would be

particularly pertinent to rehabilitation situations when strong muscle contractions may be detrimental, such as following injury to joint structures. That is, if it is possible to selectively train different motor-unit populations, joint-compressive forces may be minimized while still training the greatest part of the muscle crossing the joint.

CHAPTER III

DESIGN AND PROCEDURES

This chapter is divided into four sections. The first section describes the characteristics and source of the subjects to be recruited. The second section details the methods, materials and equipment to be used while the third specifies the protocols to be employed. The final section describes the proposed treatment and analysis of the data.

Subjects

There were 22 subjects involved in this study, 15 male and 7 female. Their ages ranged from 19 to 53 years. All subjects were without prior history of neuromuscular disease or serious injury to the leg to be tested. They were volunteers recruited from among the University of Arizona college community.

Methods, Materials and Equipment

The study was based upon measurements of force and EMG that were associated with electrically evoked compound-twitch responses. Data was obtained from the quadriceps femoris muscle groups of 15 subjects and from

the triceps surae muscle groups of 20 subjects (see Table I). These two large muscle groups of the leg were chosen for two reasons. First, previous studies investigating the effects of cutaneous-afferent stimulation have only used muscles of the upper extremity. Secondly, the quadriceps femoris group is commonly treated in rehabilitation settings with an electrical stimulation protocol similar to that used in this study.

The subjects were positioned on a specially designed bench in one of two ways depending on the muscle group to be examined. Force was measured isometrically by a load-cell attached by an inelastic nylon belt to either the subject's shin or the plantar surface of the foot. Therefore, the mechanical twitch response, obtained from either the quadriceps femoris or triceps surae muscle groups of one leg, was recorded during an experiment.

Experiments in which the quadriceps femoris muscle group was tested required the subject to be in a supine position with the hip of the leg to be tested in a fully extended position (Fig. 1). The lower leg was supported with the knee in approximately 20-30 degrees of flexion by a support extending from the bench. The subject's shin was secured to a load-cell by an inelastic nylon belt, compressing the subjects lower leg between the support apparatus and the nylon belt. The load-cell measured the

Table I. The Distribution of Subject Participation.

The values of Table I represent the number of subjects. The table has been organized to indicate the total number of subjects tested and the number from whom data was obtained. There were some subjects who participated in more than one protocol and others who generated data with both their quadriceps femoris and triceps surae muscle groups. Therefore, the number of subjects tested does not represent a sum of subjects in each protocol or each muscle group.

Table I. The Distribution of Subject Participation.

	Total	Quadriceps Femoris Muscles	Triceps Surae Muscles
Subjects Tested			
Total	22	15	20
Males	15		
Females	7	3	7
Data Obtained			
Protocol I			
Total	7	4	3
Male	6	4	2
Female	1	0	1
Protocol II			
Total	3	0	3
Male	2	0	2
Female	1	0	1
Protocol III			
Total	14	11	14
Male	10	8	10
Female	4	3	4
Protocol IV			
Total	7	5	2
Male	6	5	1
Female	1	0	1

Fig. 1 Photographs of the Experimental Arrangement for the Quadriceps Femoris Muscle Group

The top photograph depicts the force measuring apparatus. The bottom photograph depicts the EMG electrode placements for the vastus lateralis muscle, the large stimulating electrodes placed over the muscle bellies, and the constant current unit (on chair in lower left corner).

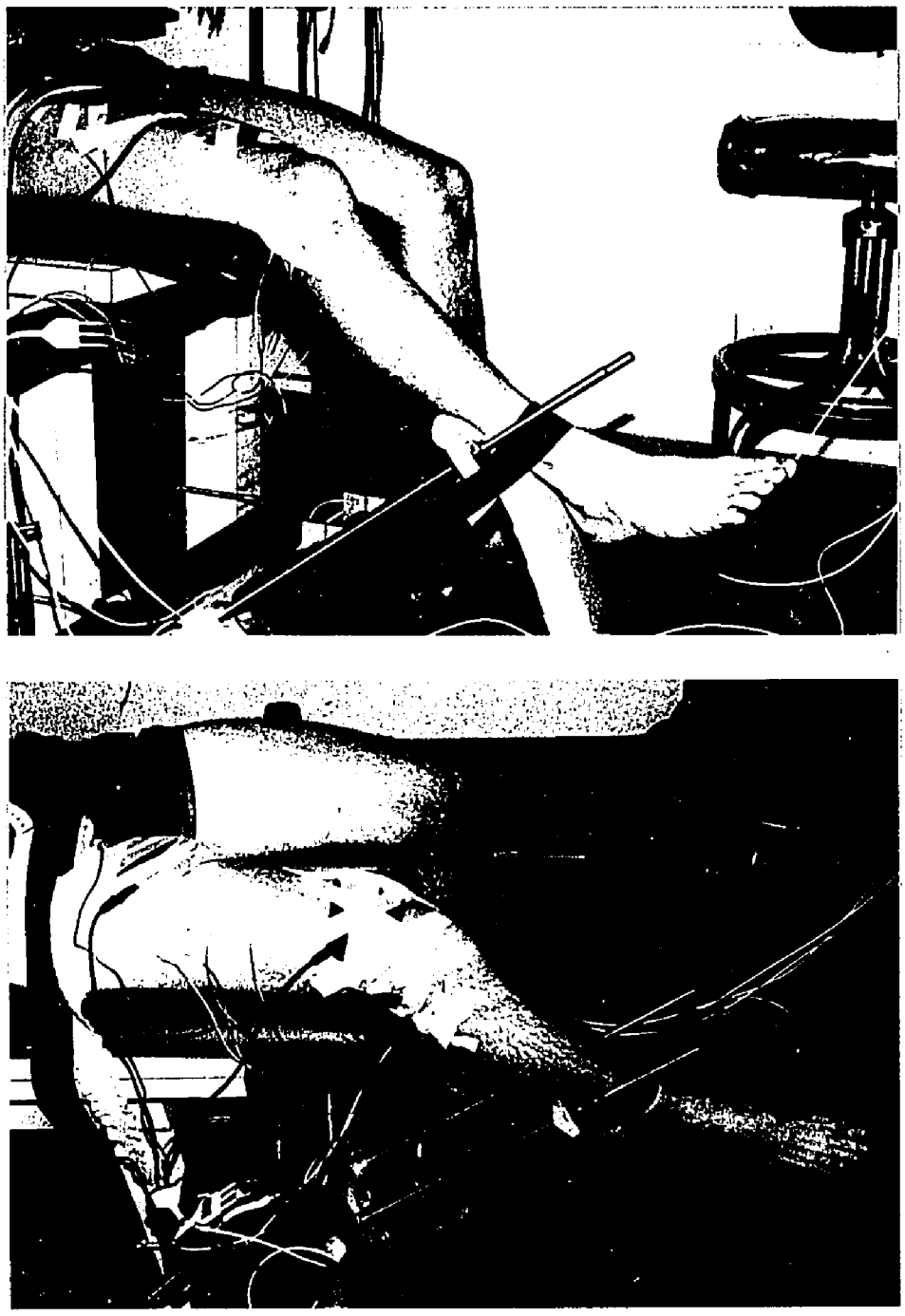


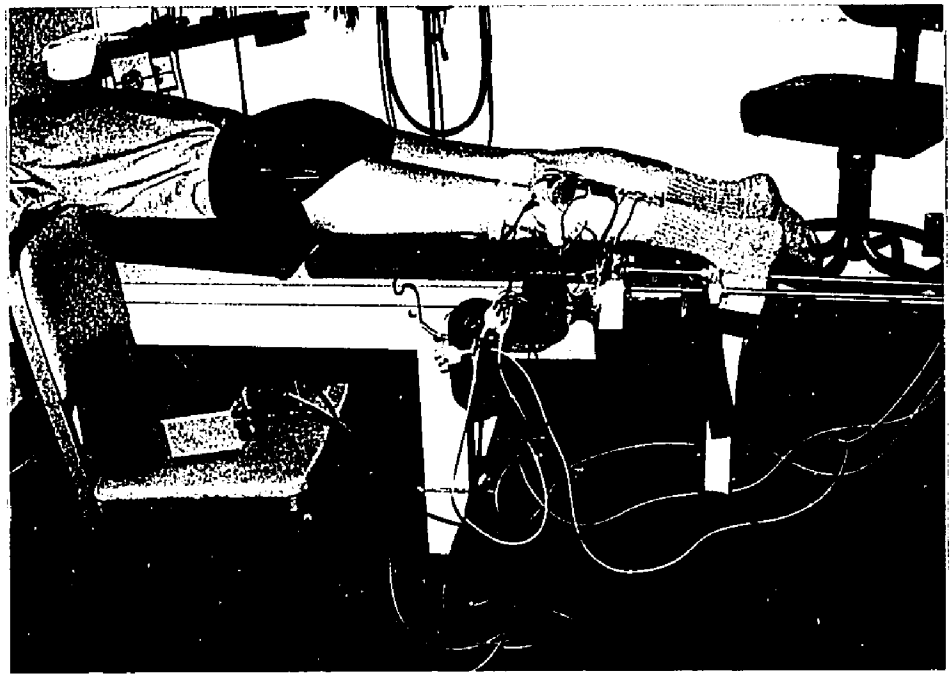
Fig. 1 Photographs of the Experimental Arrangement for the Quadriceps Femoris Muscle Group

isometric force exerted by the lower leg during the electrically evoked twitch responses. Although the knee angle of the tested leg was the same for every trial of a particular subject, there was a small (less than 10 degrees) between-subject variance due to the inability of the load-cell attachment to completely accommodate legs of different size.

When examining electrically evoked responses in the triceps surae muscles, the subjects were in a prone position on the bench with the hip and knee of the test leg in a fully extended position (Fig. 2). Both feet hung over the end of the bench with the ankles at approximately a 90 degree angle. A nylon belt secured the test foot to a load-cell with slight to moderate tension on the triceps surae muscles. This tension was found to be fairly critical in that too much tension depressed the excitability of the H-reflex and too little reduced the sensitivity of the force-measuring apparatus. That is, if the compliance of the soft tissues of the foot was not reduced, excessive dampening of the mechanical twitch response occured. Therefore, a padded support extending from the load-cell mounting bracket was placed to prevent the dorsum of the foot from being forced into dorsiflexion while the nylon belt was tightened. In other words, the foot was compressed between the nylon belt and the padded

Fig. 2 Photographs of the Experimental Arrangement for the Triceps Surae Muscle Group.

The top photograph depicts the force measuring apparatus. The bottom photograph depicts the EMG and large stimulating electrodes, the patient position, and the constant current unit (on chair in lower left corner).



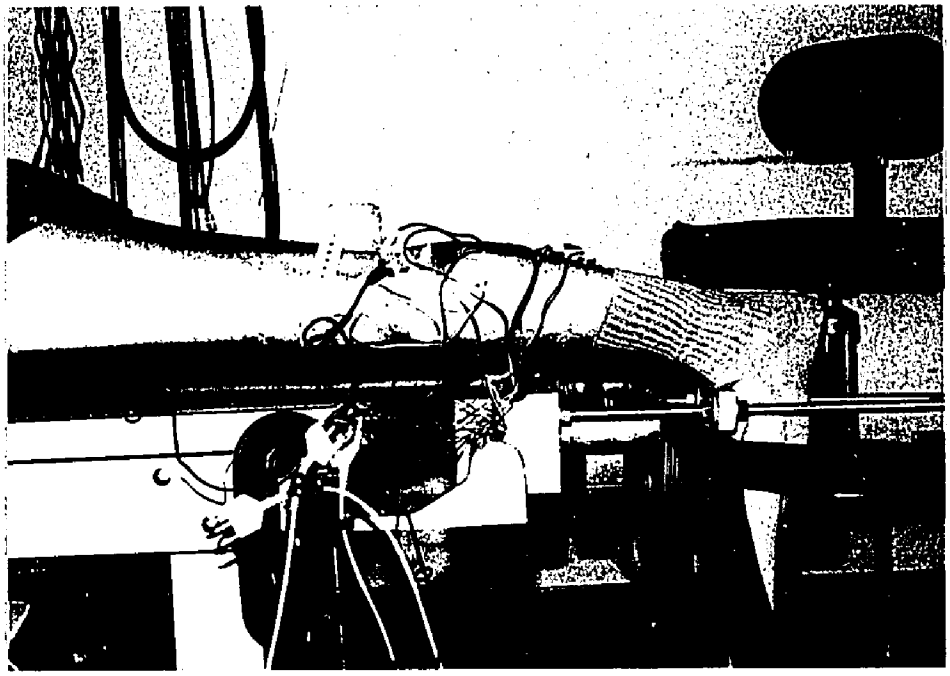


Fig. 2 Photographs of the Experimental Arrangement for the Triceps Surae Muscle Group.

support, effectively reducing the compliance of the interposed soft tissues without depressing the H-reflex.

The subjects were instructed to relax and refrain from all movement during data collection. In addition, they were asked to maintain their heads in a forward-facing direction. This was done to avoid H-reflex variability caused by the tonic-neck reflexes (Hayes and Sullivan, 1976). To maintain a relatively constant state of mental alertness, the subjects in which the triceps surae muscle group was tested were asked to engage in light reading (Ishikawa, Ott, Porter, and Stuart, 1966). The subjects in which the quadriceps femoris muscle group was tested were unable to do this because of their position.

The EMG and mechanical-twitch parameters were simultaneously recorded on an FM tape recorder (Honeywell 7600) and displayed on an oscilloscope (Tektronix 5111A) during all data collection sessions. However, only data from the mechanical-twitch waveform were analyzed quantitatively in this study. The EMG data were used to identify the contributions of the H-reflex and the M-response to the mechanical twitch response.

Surface EMG measurements were obtained from either the vastus lateralis and vastus medialis muscles of the quadriceps group, or from the soleus and lateral gastrocnemius muscles of the triceps surae group in all the

experiments of Protocols I, II, and IV. In later experiments, recordings from the rectus femoris and medial gastocnemius muscles were included. Bipolar electrodes were placed approximately 3 cm apart over the belly of the muscle. The recording electrodes were positioned as follows: 1) for the vastus medialis, one-fifth of the distance from the medial margin of the knee to the anterior superior iliac spine (Zipp, 1982); 2) for the vastus lateralis, one-third of the distance from the superior pole of the patella to the greater trochanter (Zipp, 1982); 3) for the rectus femoris, two-thirds of the distance from the anterior superior iliac spine to the superior pole of the patella; 4) for the soleus, approximately 4 cm above the point where the two heads of the gastrocnemius join the Achilles tendon (Hugon, 1973); and 5) for the lateral gastrocnemius, one-third of the distance from the head of the fibula to the calcaneus (Zipp, 1982); 6) for the medial gastrocnemius, one-third of the distance from the medial margin of the knee to the calcaneus. Prior to the placement of the recording and the stimulating electrodes, the skin was cleaned with isopropyl alcohol. The EMG electrodes were prepared with conductive gel (Coulbourn) and adhesive-tape jackets. In addition, the subjects with hairy thighs were requested to shave the areas of skin where the electrodes were to be placed, but this was not be

required.

The EMG leads were connected to isolated bioamplifiers (Coulbourn S75-05) with a preamplifier coupling of 10 Hz. The signal was then passed through a low-pass filter with a high cutoff of 5 kHz before being recorded on FM tape. These band-pass frequencies were optimal for reducing the stimulus artifact without attenuating the EMG signal to any significant degree. Prior to beginning data collection, the preamplifier gains were adjusted as necessary to achieve approximately a 3 V peak-to-peak signal on the oscilloscope from a maximal H-wave or M-wave (whichever was higher). This optimized the signal-to-noise ratio of the recorded EMG signal.

The percutaneous electrical stimulation imposed on the subjects was of two types: 1) single or double square-wave, monophasic pulses to the posterior tibial nerve, or single square-wave, monophasic pulses to either the femoral nerve or over the muscle bellies of either the triceps surae or quadriceps femoris groups; 2) a sinusoidal, biphasic, high-frequency (33 kHz) current that was modulated to give bursts of stimulus pulses at a frequency of 60 Hz, delivered over the muscle bellies of either the triceps surae or quadriceps femoris groups.

The square-wave stimulator (Grass S88) was utilized to elicit H-reflexes and M-responses in the respective

muscles. It was connected in series with a stimulus-isolation unit (Grass SIU5) and a constant-current unit (Grass CCU1a) before interfacing with the subject. This stimulator system was used in four ways. The first two procedures utilized custom-made silver-chloride-plated silver electrodes to stimulate the peripheral nerve (either the femoral or the posterior tibial) to the respective muscle group. Stimulation of the femoral nerve involved placement of the cathode (1.5 cm X 1.5 cm) in the femoral triangle and the anode (4.0 cm X 5.5 cm) along the gluteal fold opposite the cathode. Stimulation of the posterior tibial nerve was accomplished with the cathode in the popliteal fossa and the anode over the superior aspect of the patella. The exact electrode placements were determined by carefully moving an electrode (usually the cathode) while observing the oscilloscope for a maximal H-wave or M-wave at a constant stimulus intensity. During an experiment, stimulus intensity was adjusted at the constant-current unit; however, due to unknown skin-electrode resistance, the actual current injected could not be measured. The stimulus-gain control was therefore relative to and constant for a particular experimental setup (i.e., subject, electrode placements, leg position). The use of a constant-current source provided a stable stimulus pulse that was relatively independent of tissue

and electrode impedances (see Appendix D for current stability). The stimulus-current adjustment on the constant-current unit comprised a 10 step scale. Since there was only limited control of the gain sensitivity, once the appropriate response was obtained stimulus intensity was increased in one-quarter gain steps on the constant current unit. This effectively produced a scale of 40 steps on the constant-current unit.

The last two procedures in which the square-wave stimulator system was utilized involved large electrodes (12.5 cm X 8.0 cm or 6.0 cm X 6.0 cm) placed over the bellies of the test muscle group, either the quadriceps femoris or triceps surae. With this method of stimulation, employment of the standard 10 step scale was possible because the gain sensitivity was controlled by adjusting the stimulus duration. Stimulus duration was varied between 1-10 ms until an adequate twitch was obtained, but then was held constant during the data collection.

All stimulating electrodes were prepared with conductive gel in the same way as the recording electrodes. Skin preparation for the nerve-stimulation electrodes, however, included shaving the hair from the area and light sanding of the skin to reduce the electrical resistance at the electrode-skin interface. These electrodes were held in place by a nylon belt and a rolled elastic bandage. The elastic bandage was placed over the cathode to maintain

constant pressure during stimulation.

The high-frequency electrical stimulation imposed on the subjects was produced by an Electrostim 180-2i variable-frequency stimulator. Stimulation of the quadriceps muscles involved two large (12.5 cm by 8.0 cm) rectangular electrodes positioned over the distal aspect of the anterior thigh. Stimulation of the triceps surae muscles involved one large (12.5 cm by 8.0 cm) rectangular electrode and one small (6.0 cm by 6.0 cm) square-shaped electrode positioned over the proximal aspect of the calf. In cat preparations, stimulation of the distal anterior thigh and proximal calf have been shown to provide the optimal cutaneous-afferent excitatory input to the extensor motoneurons of the quadriceps femoris and triceps surae muscle groups, respectively (Hagbarth, 1952). Stimulus intensity was adjusted to elicit the maximal sensation below the motor threshold. When the high-frequency stimulator was being used, the EMG leads were disconnected. It was not possible to record EMG with this type of stimulation, because the resulting stimulus artifact would overdrive the bioamplifiers and mask the EMG.

Experimental Protocols

There were four experimental protocols involving

either the quadriceps femoris or the triceps surae muscle groups. Protocols I, II, and IV utilized the EMG recordings to determine the contribution of the H-reflex and M-response to the compound-twitch responses. Protocol I involved the generation of an H-reflex recruitment curve. This entailed eliciting H-reflexes with a spectrum of stimulus intensities, from threshold to maximum, in the absence of an M-response or with a minimal unchanging M-response. Protocol II basically was the reverse of Protocol I, that is, it involved the generation of an M-response recruitment curve. This entailed eliciting M-responses with a spectrum of stimulus intensities, from threshold to maximum, in the absence of H-reflexes or with minimal H-reflexes. Protocol III was an extension of Protocol II in that M-response recruitment curves were obtained. However, in Protocol III the M-responses were generated by stimulating the muscles via large electrodes placed over the muscle bellies. Protocol IV involved obtaining a stable H-reflex of maximum amplitude in the absence of an M-response (a small M-response was tolerated) before, during and following cutaneous-afferent stimulation via the high-frequency stimulator. The actual testing protocols were the same for both muscle groups, although subject positioning and setup differed.

An experimental session began with a brief explanation

of the equipment and procedures. This was followed by measurement of the EMG electrode placements, skin preparation and attaching the electrodes over the appropriate muscles. Next, the subject was positioned on the specially designed bench and the load-cell apparatus secured. Following connection of the EMG electrodes and leads to the preamplifier, the recording equipment were tested by performing tendon taps with a reflex hammer. At this point, the square-wave stimulator system was turned on and the exact electrode placements for the H-reflex and M-response were determined.

Once a satisfactory EMG H-wave and/or M-wave and a twitch response were observed, a recruitment curve for these two responses was performed. The selective appearance of the H-wave and/or M-wave is known to be variable between subjects (Desmedt and Godaux, 1978; Hugon, 1973; Ishikawa et al. 1966; Magladery and McDougal, 1950, Mongia, 1972). A small M-wave and twitch (M-) response is often observed before the H-wave appears. With increasing stimulus amplitude, an H-wave appears and increases in amplitude while the small M-wave remains relatively unchanged. If the stimulus amplitude is increased further, the H-wave begins to plateau; at this point or shortly following, the M-wave starts increasing in amplitude. At still higher stimulus amplitudes the H-wave begins

decreasing in amplitude while the M-wave increases. This continues until the M-response is maximal and the H-reflex is extinguished. However, the M-wave may not occur until after the H-wave appears and increases in amplitude, or the M-wave may become quite large before the H-wave appears. Part of this variability can be controlled by altering the positions of the stimulating electrodes or the leg. Nevertheless, because of these subject variances, H-reflex recruitment curves that are relatively uncontaminated by M-responses can be obtained in some subjects, whereas, M-response recruitment curves are more easily obtained in other subjects. It is for this reason that the first two protocols were usually not performed on the same subject.

Protocol I, the H-reflex recruitment curve, began with a threshold H-wave in one of the EMGs; the stimulus intensity was then increased in one-step increments (one-quarter gain step increments on the constant-current unit) until an M-wave appeared or started increasing in amplitude in one of the EMGs. At each current step, 5 stimulus pulses were given at 8 s intervals.

Protocol II, the M-response recruitment curve generated by nerve stimulation, began with a threshold M-wave in one of the EMGs and the stimulus increased in one-step increments (one-half gain step increments on the constant-current unit) until the M-waves and corresponding

M-response no longer increased in amplitude. If a substantial H-wave remained after adjusting the stimulating electrodes and leg for an optimal M-wave, techniques to depress the H-reflex were attempted. We initially tried to depress the H-wave to varying degrees with two different techniques. The first technique employed the concept of low-frequency depression; the second utilized the inhibitory effects of the tonic vibration reflex.

Low frequency depression of monosynaptic reflexes appears during stimulation frequencies ranging from 0.1 Hz to 10 Hz (Cook, 1968; Ishikawa et al., 1966). This depression appears to be presynaptic in origin, although the exact mechanism is unclear (Cook, 1968; Ishikawa et al., 1966). There is considerable between-subject variance with this phenomenon (Cook, 1968). High-frequency depression, in contrast, occurs with stimulation frequencies of 10 Hz or greater and is supposedly postsynaptic in origin (Ishikawa et al., 1966). Although the depression in H-reflex amplitude is inversely related to the stimulation frequency, we were limited to frequencies less than 2.2 Hz; stimulation frequencies greater than 2.5 Hz caused summation of the twitch responses. Stimulation at 2 Hz depresses submaximal H-reflexes by approximately one half (Ishikawa et al., 1966). Instead of stimulating at a constant 2 Hz, however, we

utilized a twin-pulse stimulus pattern, with an interpulse period of 450-650 ms, delivered once every 8 s. The first stimulus pulse evoked a control response with which to compare the H-wave of the second response. Only the second twitch response, which we assume represents predominantly an M-response, was used in data analysis. However, this technique was not particularly effective since often times the maximal H-waves were not depressed to the same extent that submaximal ones were. Only one satisfactory trial was obtained in this way although several were attempted.

The second technique which can be used to depress the H-reflex utilizes the inhibitory effects of the tonic-vibration reflex. Vibration of a muscle tendon induces presynaptic inhibition of the Ia spindle afferents and depresses the H-reflex (Delwaide, 1973; Desmedt and Godaux, 1978; Lance, Burke and Andrews, 1973). This inhibitory effect is a function of vibration frequency, amplitude and duration (Desmedt and Godaux, 1978; Heckman, Condon, Hutton, and Enoka, 1984). Depression of the H-reflex increases with increasing vibration amplitude (0.4 -2.0 mm) and decreases with increasing vibration frequency (40 - 200 Hz; Desmedt and Godaux, 1978). The H-reflex depression increases with the duration of the vibratory stimulus (Jack, 1978). Furthermore, the duration of the inhibitory effect can last up to 35 min in some subjects following 20

min of tendon vibration (Heckman et al., 1984). Interestingly, with some vibration protocols, this inhibition can be overcome with higher electrical-stimulus intensities, i.e., H-waves approximating control values can be elicited at relatively high stimulus amplitudes (Heckman et al., 1984). Thus, tendon vibration is thought to effectively raise the threshold of Ia electrical excitability (Heckman et al., 1984; Jack, 1978).

The use of the tendon vibration to depress the H-reflex in the present study was also not very effective. Most likely this was due to the vibrator (Bicor Massager) used. No data was acquired using this technique.

Protocol III was an extension of Protocol II in that M-response recruitment curves was obtained. However, this protocol utilized large electrodes over the muscle bellies of the respective muscle group to elicit M-responses. In addition, EMG was not monitored during these experiments.

Protocol IV involved high-frequency, cutaneous-afferent stimulation in addition to the peripheral-nerve stimulation. H-reflexes of maximal amplitude, without an M-response or with a minimal M-response, were obtained before, during and following a period of high-frequency, cutaneous stimulation over the bellies of the muscle group to be tested. The intensity of the high-frequency stimulator was set just under the motor threshold such that

there were no visible signs of a muscle contraction. In short, 14-24 H-reflexes during each phase (pre-, post-and during cutaneous stimulation) of Protocol IV were recorded for subsequent averaging.

Data Analysis

The data statistically analyzed in all four protocols were the mechanical-twitch waveforms of the electrically evoked responses. Part of the statistical analyses was performed on the VAX (supercomputer) with the SPSS-X software package.

Analysis of Protocols I, II and III, the H-reflex and the M-response recruitment curves, involved averaging the contraction times and amplitudes of the five twitch responses at each stimulus strength. The mean values, ranges and standard deviations were calculated followed by the performing of analyses of variance (ANOVA) and trend analyses. The ANOVAs compared the stimulus-intensity levels on a within-subject basis only. A significance level of $p < 0.05$ was used to test these hypotheses. Compound-twitch contraction time and twitch force were plotted against the stimulus-current step and displayed graphically (see Chapter IV).

A multiple ANOVA was performed on the data of Protocol

IV to compare the differences in compound-twitch contraction time of the pre-, post- and during cutaneous stimulation responses. This again included only a within-subject comparison. At least 10 responses in each phase was required for analysis. The results of this analysis is displayed in tabular form (see Chapter IV). A significance level of $p < 0.05$ was also used to test this hypothesis.

CHAPTER IV

RESULTS

This chapter has been divided into four sections, a section for each of the four experimental protocols.

Protocol I - Effect of Stimulus Intensity on H-Reflex Muscle Twitches

The two compound-twitch characteristics considered in this study were contraction time and force. The twitch-contraction times of the two muscle groups (quadriceps femoris and triceps surae) for the H-reflex were similar, whereas, the twitch forces were not. The contraction times of the quadriceps femoris muscle group ranged from 65-100 ms and those of the triceps surae muscle group ranged from 56-102 ms. The twitch force ranged from 19-195 N for the quadriceps femoris group and from 17-83 N for the triceps surae muscle group.

The results of Protocol I address the first hypothesis: Compound-twitch contraction time of the H-reflex will decrease and force will increase as the stimulus intensity is increased. Fig. 3 represents an H-reflex recruitment curve in the quadriceps femoris muscle group as indicated by monitoring the EMG waveforms of the vastus medialis and vastus lateralis muscles. Although it

Fig. 3 A Series of 5 EMG Traces Representing an H-reflex Recruitment Curve in the Quadriceps Femoris Muscle Group.

The top trace of A-E represents the vastus medialis EMG and the bottom trace, the vastus lateralis EMG. The stimulus artifact can be observed in the left part of each trace. A represents responses acquired at the threshold stimulus intensity. H-waves can be observed in the vastus medialis trace (top), with a latency of approximately 17 ms, and in the vastus lateralis trace (bottom), with a latency of approximately 14 ms. In addition, a longer latency wave can be seen in the vastus lateralis trace of A (latency of approximately 22 ms). B through H were acquired by graded stimulation and arranged in order of increasing stimulus intensity. The H-waves that appeared in A increase in amplitude in B. Also in B, a wave with a latency of approximately 5 ms appears in the vastus lateralis trace. With increasing stimulus intensity, this short-latency wave (M-wave) increases in amplitude (C and D). In C, a wave (M-wave) with a latency of approximately 7 ms appears in the vastus medialis trace. As the stimulus intensity (D and E) is increased, this M-wave and the M-wave of the vastus lateralis trace increase in amplitude while the H-waves start to decrease in amplitude.

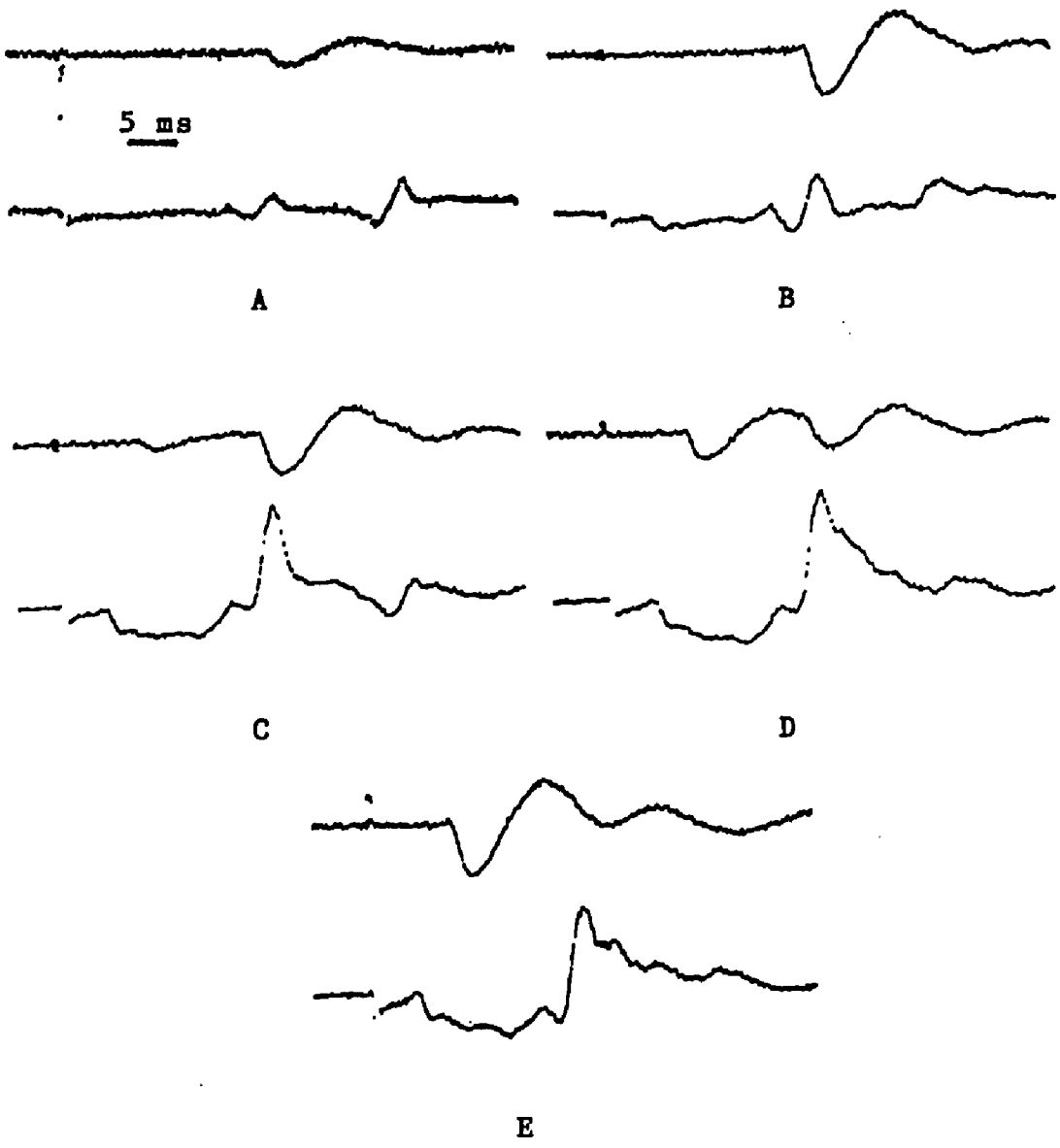


Fig. 3 A Series of 5 EMG Traces Representing an H-reflex Recruitment Curve in the Quadriceps Femoris Muscle Group.

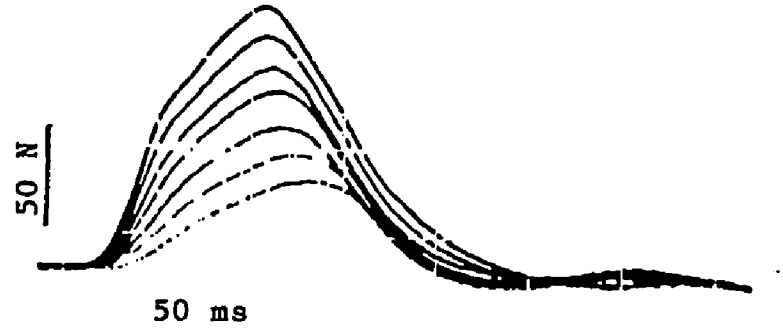
is difficult to clearly distinguish the onset of the H-wave from the M-wave at times in these muscles, because of the short latencies and long durations of the two waveforms, it can be shown that two distinct responses are represented in these sequences of EMG traces (Fig. 3). Threshold H-waves can be observed in both traces of A. The H-wave in the vastus medialis (top) EMG has a latency of approximately 17 ms, whereas, the H-wave in the vastus lateralis (bottom) EMG has a latency of approximately 14 ms. These H-reflex latencies are consistent with those reported by Mongia (1972) and Spencer et al. (1984). The H-waves of both muscles increase in amplitude in B (second stimulus gain step) and C (third stimulus gain step). An M-wave appears in the vastus lateralis trace of B with a latency of approximately 4 ms and then in the vastus medialis trace of C with a latency of approximately 7 ms. These latencies are also consistent with those reported by Spencer et al. (1984). Increases in amplitude of these short-latency M-waves are apparent in D (fourth stimulus gain step) and E (fifth stimulus gain step) and are accompanied by a diminution in the H-wave amplitudes. The EMG patterns observed in these sequences of traces, which are associated with graded stimulation of the femoral nerve, indicate that two distinct responses are being evoked from the vastus medialis and vastus lateralis muscles.

The effect of stimulus intensity on the force and timecourse of the mechanical twitch responses for the H-reflex is shown in Fig. 4. The superimposed twitch responses from the triceps surae and quadriceps femoris muscle groups were generated by graded stimulation while monitoring the H-wave amplitude; therefore, a set of responses obtained under constant, experimental conditions from one subject represents an H-reflex recruitment curve. The total sample size consisted of ten recruitment curves, six from quadriceps femoris and four from triceps surae. In Fig. 4 it can be seen that the smaller amplitude (force) twitches, of both the triceps surae and quadriceps femoris traces, have longer twitch-contraction times than the larger amplitude twitches. The effects of stimulus intensity on H-reflex twitch-contraction time and force are also represented in Figs. 5 and 6. The mean compound-twitch contraction time and force values of five responses at each stimulus intensity are plotted against the gain-step setting of the constant-current unit (see Appendix C for the reliability of the stimulus current injection).

Stimulus intensities just above threshold for an H-reflex elicited small-force twitches with relatively long twitch-contraction times; leftmost values of each line in both Figs. 5 and 6. As anticipated in the first hypothesis, the compound-twitch contraction time decreased

Fig. 4 Superimposed Reflex-Activated (H-reflex) Twitches.

These twitch reponses are from the triceps surae (top) and quadriceps femoris (bottom) muscle groups and were generated by graded stimulation over the posterior tibial and femoral nerves, respectively. Twitch-contraction time was measured as the time from baseline at onset of the twitch to the peak of the twitch. In A, the quadriceps femoris traces, the maximal twitch force of 164.3 N is associated with a twitch-contraction time of 77.5 ms and the minimal twitch force of 45.3 N is associated with a twitch-contraction time of 96.9 ms. In B, the triceps surae traces, the maximal twitch force of 27.4 N is associated with a twitch-contraction time of 82.7 ms and the minimal twitch force of 18.8 N is associated with a twitch-contraction time of 94.9 ms.



A

B

Fig. 4 Superimposed Reflex-Activated (H-reflex) Twitches.

with increasing stimulus intensity (Fig. 5). Conversely, the twitch force increased as the stimulus intensity increased (Fig. 6). Although the curves differ in shape and length, partly due to variable starting and ending points of the H-reflex recruitment curve for different subjects and even for different sessions of the same subject, the trends are similar for all curves.

The analyses of variance performed on the triceps surae and quadriceps femoris data of Protocol I indicated these relationships with the stimulus-intensity level were significant ($p < 0.05$; see Table III). The trend analyses indicated a significant ($p < 0.05$) linear component was present for the relationship between stimulus intensity and twitch-contraction time in both muscle groups (see Table IV).

An H-reflex recruitment curve was terminated either by the onset of an M-wave or when a small M-wave started increasing in amplitude. Some trials were quite short (e.g., 3 gain steps), whereas others were relatively long (e.g., 10 gain steps). Some difficulty was encountered in determining the termination point for the H-reflex recruitment curves in the trials involving the quadriceps femoris muscle group. M-waves in these muscles were often

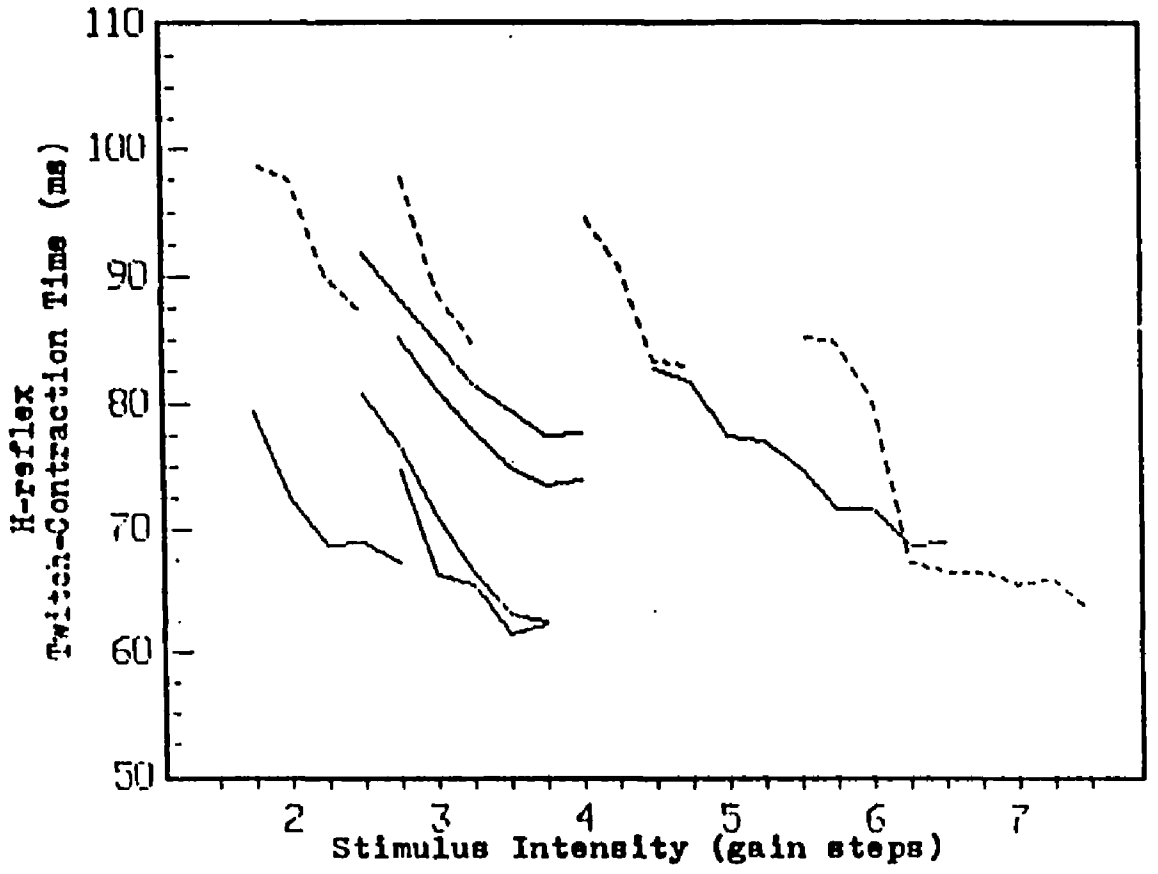


Fig. 5 Relationship Between Stimulus Intensity and Contraction Time with the Reflex-Activated (H-reflex), Compound-Twitch Responses.

Each line represents a recruitment curve. The ten recruitment curves were obtained from seven subjects; four triceps surae curves were obtained from three subjects and six quadriceps femoris curves from four subjects. That is, two quadriceps femoris curves each were obtained from two subjects under different experimental conditions (i.e., different electrode placements, different stimulus duration and/or a different leg position). The triceps surae curves are designated by ------- and the quadriceps curves are designated by ———. The data were accumulated in one-quarter, gain-step increments (abscissa) and are shown as the average of five responses at each stimulus intensity. The standard deviations of these mean values are given in Table II.

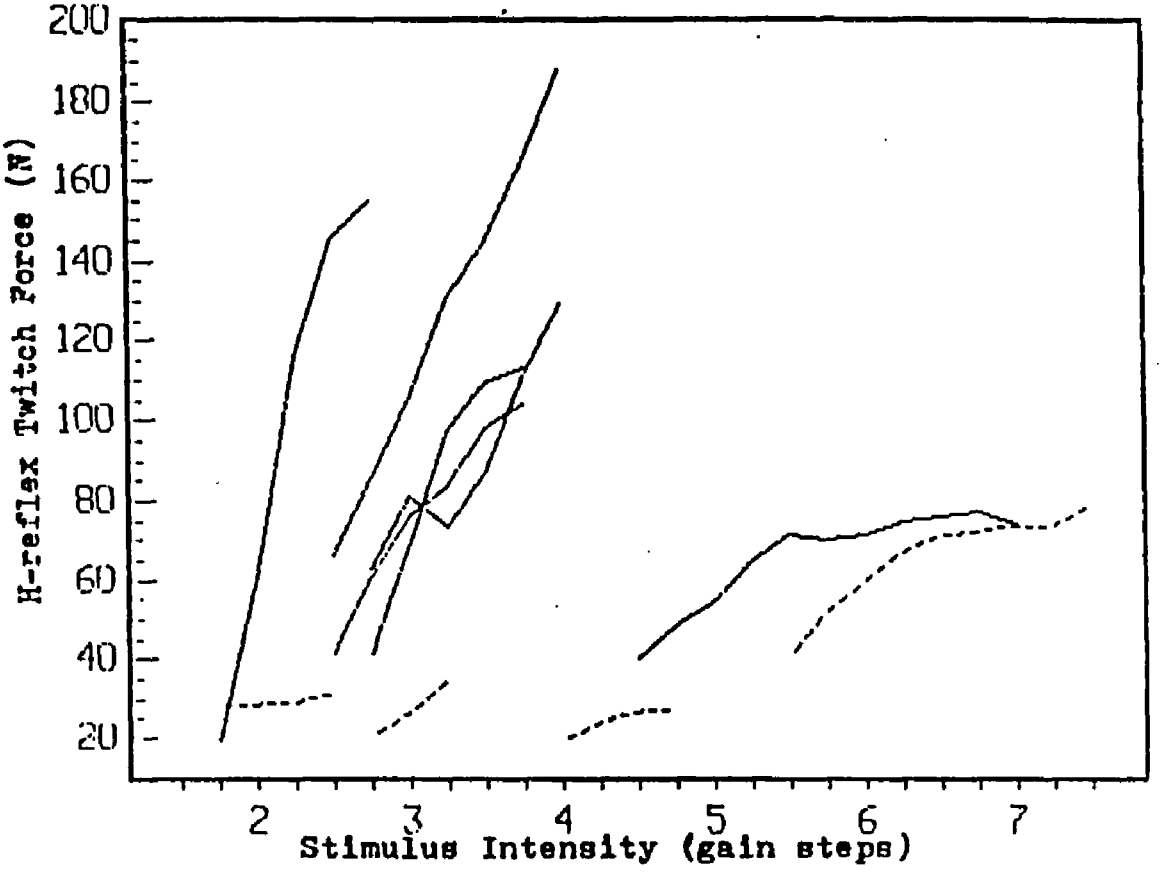


Fig. 6 Relationship Between Stimulus Intensity and Force with the Reflex-Activated (H-reflex), Compound-Twitch Responses.

Each line represents a recruitment curve. The ten recruitment curves were obtained from seven subjects; four triceps surae curves were obtained from three subjects and six quadriceps femoris curves from four subjects. That is, two quadriceps femoris curves each were obtained from two subjects under different experimental conditions (i.e., different electrode placements, different stimulus duration and/or a different leg position). The triceps surae curves are designated by ------- and the quadriceps femoris curves are designated by ———. The data were accumulated in one-quarter, gain-step increments (abscissa) and are shown as the average of five responses at each stimulus intensity. The standard deviations of these mean values are given in Table II.

TABLE II. The Characteristics and Reliability of the H-reflex and M-response Twitch Responses.

The data obtained in Protocols I, II and III are arranged into five groups. The first two groups display the values obtained from the quadriceps femoris muscle group, whereas, the last three groups represent triceps surae values. The data indicated the following: [a] range of individual values, [b] group mean + SE, [c] standard deviation of the mean value (5 responses) at each gain step, [d] M-responses elicited by stimulation with large electrodes over the muscle bellies, [e] M-responses elicited by stimulation of the posterior tibial nerve. Sample size is indicated by the letter n and is located below each group heading.

TABLE II. The Characteristics and Reliability of the H-reflex and M-response Twitch Responses

	Twitch-Contraction Time (ms)	Twitch Force (N)
Quadriceps Femoris Muscle Group		
H-reflex	65-100[a]	19-195[a]
(n = 40)	74.2[b] ± 7.4 ± 5%[c]	88.9[b] ± 36.8 ± 7%[c]
M-response[d]	48-87	7-169
(n = 63)	73.5 ± 9.8 ± 6%	53.8 ± 33.1 ± 7%
Triceps Surae Muscle Group		
H-reflex	56-102	17-83
(n = 17)	80.6 ± 12.3 ± 5%	47.2 ± 21.9 ± 10%
M-response[e]	53-87	17-162
(n = 28)	80.3 ± 15.5 ± 6%	73.7 ± 45.1 ± 6%
M-response[d]	61-147	10-131
(n = 85)	103.5 ± 17.5 ± 6%	70.0 ± 35.4 ± 6%

Table III. Summary of the Analyses of Variance of the H-reflex and M-response Recruitment Curves.

	Analyses of Variance	
	F-ratios	Significance of F
H-reflex (Protocol-I)		
Contraction Time		
Both	41.2	0.000[a]
Quadriceps Femoris	18.5	0.000[a]
Triceps Surae	26.9	0.001[a]
Force		
Both	9.5	0.002[a]
Quadriceps Femoris	28.4	0.000[a]
Triceps Surae	8.4	0.018[a]
M-response (Protocol-II)		
Contraction Time		
Triceps Surae	4.6	0.033[a]
Force		
Triceps Surae	4.1	0.043[a]

Table III. Continued.

	Analyses of Variance	
	F-ratios	Significance of F
M-response (Protocol-III)		
Contraction Time		
Quadriceps Femoris	182.8	0.000[a]
Triceps Surae	32.9	0.000[a]
Force		
Quadriceps Femoris	53.2	0.000[a]
Triceps Surae	103.5	0.000[a]

[a] $p < 0.05$

b - not tested

Table IV. Summary of the Trend Analyses of the H-reflex and M-response Recruitment Curves.

	Trend Analyses		
	Linear	Quadratic	Cubic
H-reflex (Protocol-I)			
Contraction Time			
Both	60.6[a,b]	4.5[b]	c
	0.000	0.064	
Quadriceps Femoris	19.9[b]	5.3	c
	0.007	0.070	
Triceps Surae	48.0[b]	0.9	c
	0.006	0.398	
Force			
Both	9.8[b]	1.6	c
	0.012	0.238	
Quadriceps Femoris	29.1[b]	2.8	c
	0.003	0.155	
Triceps Surae	8.7	0.03	c
	0.060	0.882	

Table IV. Continued.

	Trend Analyses		
	Linear	Quadratic	Cubic
M-response. (Protocol-II)			
Contraction Time			
Triceps Surae	4.7 0.118	5.1 0.109	1.4 0.327
Force			
Triceps Surae	4.4 0.127	0.4 0.552	2.1 0.247
M-response. (Protocol-III)			
Contraction Time			
Quadriceps Femoris	182.8[b] 0.000	53.2[b] 0.000	0.7 0.604
Triceps Surae	67.1[b] 0.000	23.9[b] 0.000	0.1 0.760
Force			
Quadriceps Femoris	59.0[b] 0.000	0.01 0.928	10.3[b] 0.013
Triceps Surae	129.9[b] 0.000	2.1 0.172	0.2 0.645

[a] F-ratio
F significance

[b] $p < 0.05$

c - not tested

joined to H-waves due to small differences in latency between the two responses. This often caused difficulty in discriminating waveform variances (duration and amplitude) due to changing stimulus intensity. For this reason, some quadriceps femoris H-reflex recruitment curves may have been contaminated by an increasing M-response.

The variability of the responses evoked at a given gain step can be seen in Table I. There was generally less than a 6% variability (SD < 6%) in the twitch-contraction time and force of the five responses.

Protocol II - Effect of Stimulus Intensity on M-response Muscle Twitches Evoked by Stimulation of the Posterior Tibial Nerve

The effect of stimulus intensity on the direct-motor twitch contractions of the triceps surae muscles, evoked by stimulation of the posterior tibial nerve, is represented in Figs. 7 and 8. As in Protocol I, the mean compound-twitch contraction time and force values of five responses at each stimulus intensity are plotted against the gain-step setting of the constant-current unit. Stimulus intensities just above threshold for an M-response elicited small-force twitches with relatively short twitch-

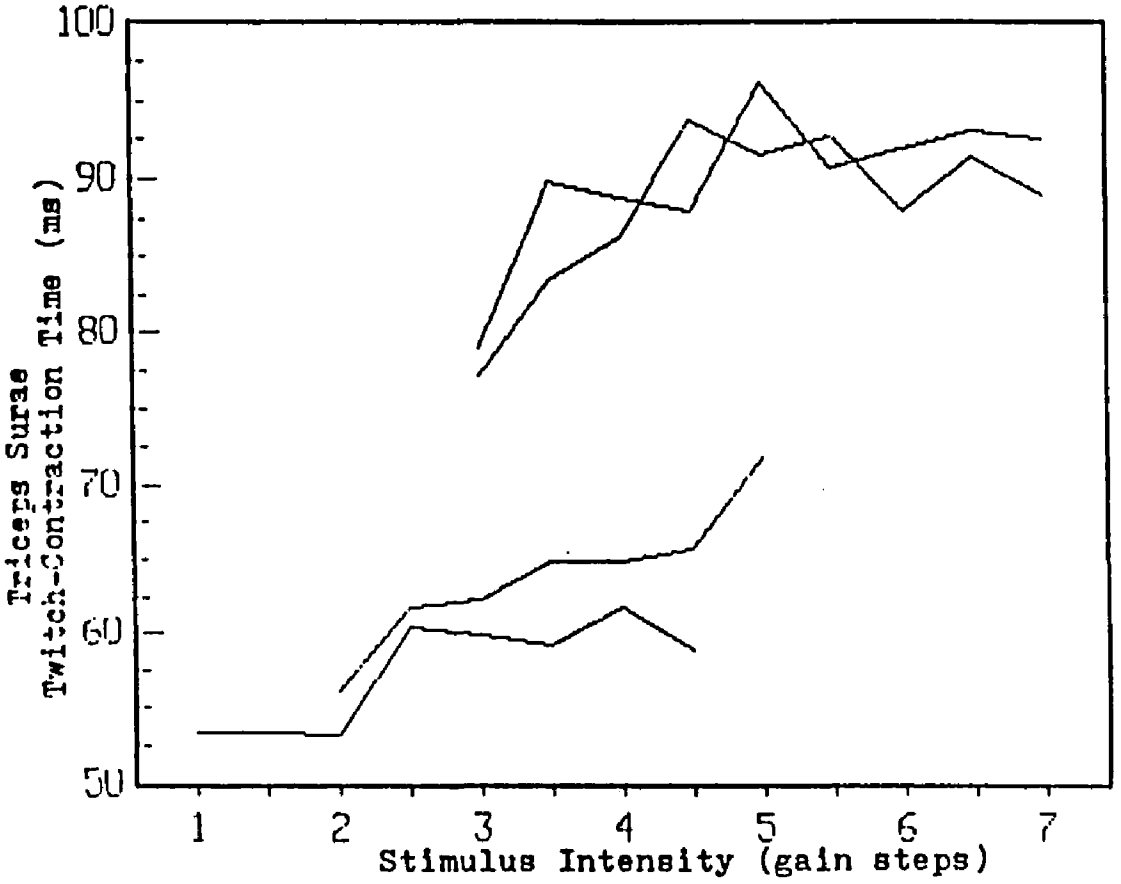


Fig. 7 Relationship Between Stimulus Intensity and Contraction Time of Triceps Surae M-responses Generated by Posterior Tibial Nerve Stimulation.

These compound-twitch responses were generated by direct motor-efferent stimulation over the posterior tibial nerve. Each line represents a recruitment curve. The four recruitment curves were obtained from three subjects; two curves were obtained from the same subject under different experimental conditions (i.e., different electrode placements, different stimulus duration and/or a different leg position). The data were accumulated in one-half gain-step increments (abscissa) and are shown as the average of five responses at each stimulus intensity. The standard deviations of these mean values are given in Table II.

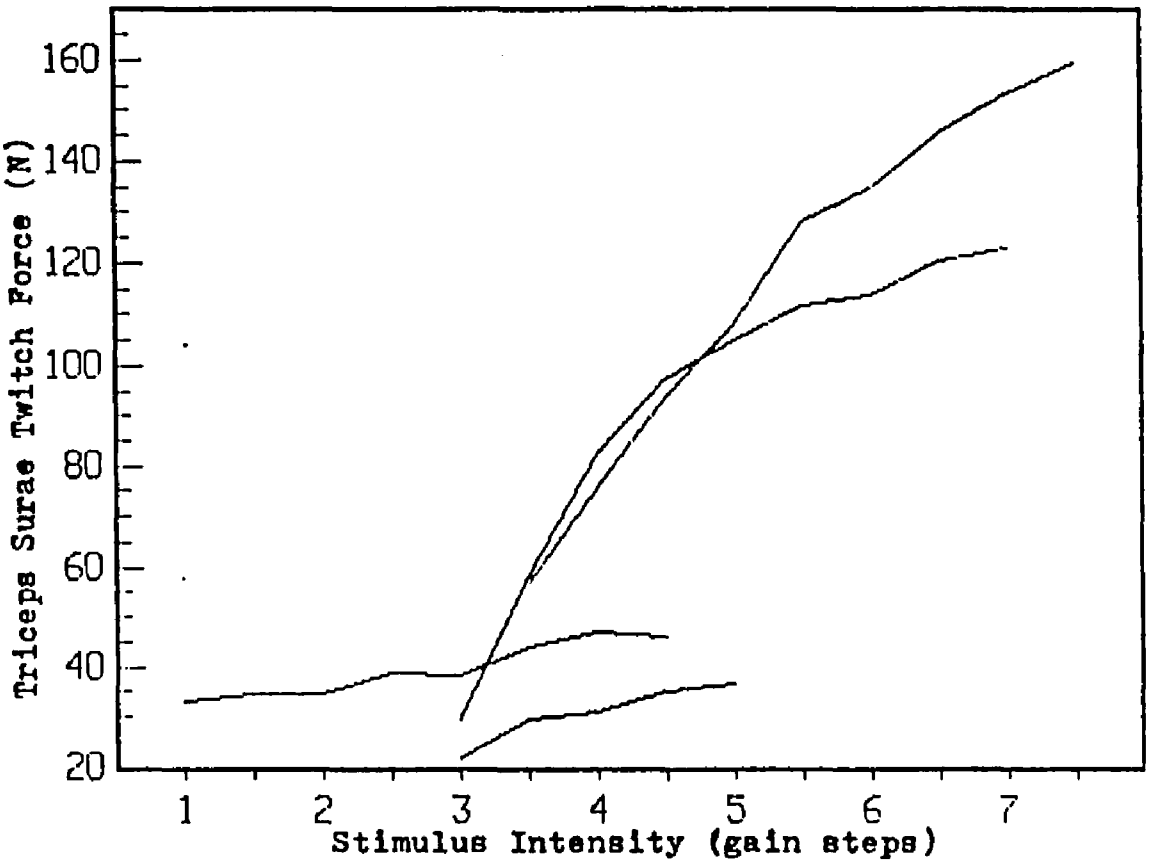


Fig. 8 Relationship Between Stimulus Intensity and Force of Triceps Surae M-responses Generated by Posterior Tibial Nerve Stimulation.

These compound-twitch responses were generated by direct motor-efferent stimulation over the posterior tibial nerve. Each line represents a recruitment curve. The four recruitment curves were obtained from three subjects; two curves were obtained from the same subject under different experimental conditions (i.e., different electrode placements, different stimulus duration and/or a different leg position). The data were accumulated in one-half, gain-step increments (abscissa) and are shown as the average of five responses at each stimulus intensity. The standard deviations of these mean values are given in Table II.

contraction times. An increase in the stimulus intensity was associated with an increase in the compound-twitch contraction time during the M-response recruitment curve. This is in contrast with the effect of increasing stimulus intensity on the twitch-contraction time of H-reflexes (Fig. 5). However, the force-stimulus intensity relationship was similar in the H-reflex and M-response recruitment curves; with increasing stimulus intensity there was an increase in the compound-twitch force.

The analyses of variance performed on this data indicated the relationships between stimulus intensity and twitch-contraction time and between stimulus intensity and twitch force were significant ($p < 0.05$; see Table III). However, the trend analyses did not show these relationships to have either a linear, quadratic or cubic component (see Table IV).

Only four trials (from three subjects) could be unambiguously extracted from the data on twelve subjects tested (Figs. 7 and 8). The use of the tendon vibration and twin-pulse stimulation techniques did not prove sufficient in depressing the H-wave at higher stimulus intensities. In fact, at times the twin-pulse stimulus pattern facilitated the H-wave, particularly in the quadriceps femoris muscle group. Nevertheless, one of the trials analyzed was obtained in this way.

In most cases, discrimination of an increasing M-wave independent of an H-wave was not possible. In several subjects, a small M-wave that did not change in amplitude for 3-4 gain steps could be elicited prior to the onset of an H-wave; this was not considered sufficient and therefore the data were not used. For one triceps surae recruitment curve, a varying M-wave was isolated in both the soleus and lateral gastrocnemius muscles. However, on examination of the twitch response it was apparent that considerable twitch force occurred prior to the onset of any EMG wave. This was considered to be due to a response from the medial gastrocnemius, a muscle in which EMG was not recorded. Most likely this was an H-reflex because on examination of this data the twitch-contraction time did not change with increasing stimulus intensity, as it did in the other trials. In subsequent experiments, EMG recordings from the medial gastrocnemius and the three superficial muscles of the quadriceps femoris group were also monitored.

Confident discrimination of a graded, isolated M-response in the quadriceps femoris muscles was not possible because the EMG waveforms commonly overlapped. For this reason, M-response curves from the quadriceps femoris muscles, generated by femoral nerve stimulation, were not obtained.

The range of triceps surae twitch-contraction times,

which were associated with M-responses generated by posterior tibial nerve stimulation (53-87 ms), were slightly shorter than those associated with triceps surae H-reflexes (56-102 ms); however, the group mean values were similar (see Table I). Generally, the present values are in agreement with those reported by Buchthal and Schmalbruch (1970). However, Buchthal and Schmalbruch (1970) observed a difference in the group mean values; that is, the mean, M-response twitch-contraction time was shorter than that of the H-reflex.

Protocol III - Effect of Stimulus Intensity on M-response Muscle Twitches Evoked by Stimulation Over the Muscle Bellies

An experiment, similar to Protocols I and II, was performed which involved 1-10 ms square-wave shocks via large electrodes over the muscle bellies of either the triceps surae or quadriceps femoris muscle groups. However, in this case EMG was not monitored. This method of stimulation was originally performed to provide an estimate of the sensitivity of the force-measuring apparatus. The results from two subjects proved interesting enough to include this as a separate protocol in this study. The results of Protocol III address the second hypothesis: Compound-twitch contraction time of the M-response and force will increase as the stimulus

intensity is increased.

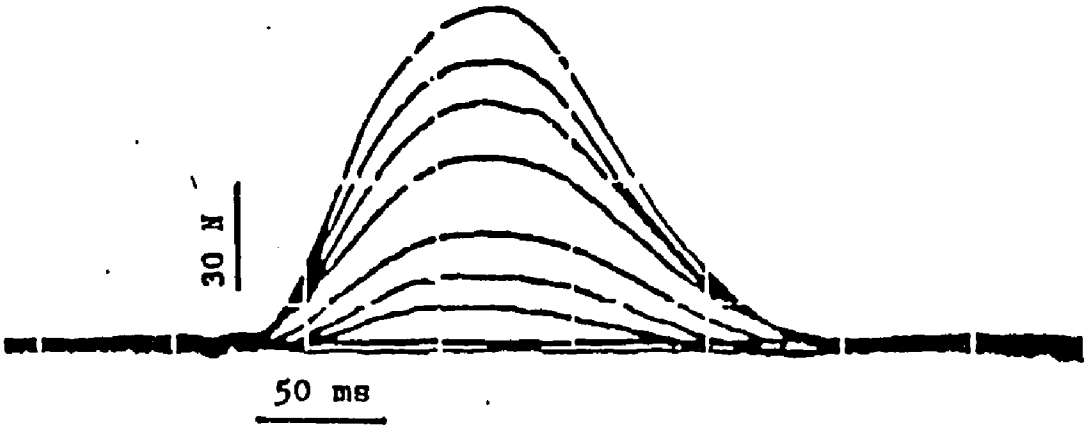
Protocol III utilized 14 subjects, 4 of whom were also in either Protocol I or II. From these 14 subjects, 14 triceps surae and 11 quadriceps femoris recruitment curves were obtained.

When compound-twitch responses were generated in this way, twitch force, twitch-contraction time and stimulus intensity were directly related. Fig. 9 illustrates superimposed twitch responses, generated by graded stimulation over the muscle bellies of the triceps surae (top traces) and quadriceps femoris (bottom traces). With this method of stimulation, the twitches with the smallest forces had the shortest contraction times. With increasing stimulus intensity, the compound-twitch contraction time (Figs. 10 and 11) and force (Figs. 12 and 13) increased. This is similar to the twitch characteristics of the M-responses generated through stimulation of the posterior tibial nerve. Therefore, the lengthening of the twitch-contraction time found in these data was interpreted as the result of successive activation of smaller efferent-axon branches. This finding also supported the second hypothesis.

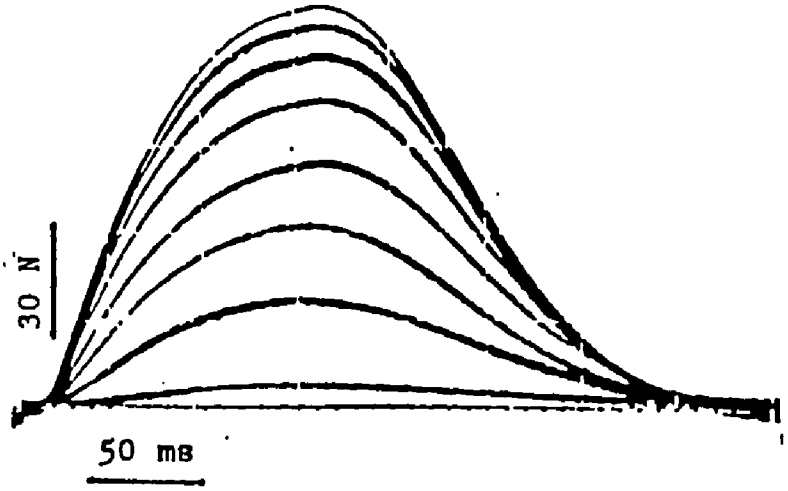
The analyses of variance performed on the triceps surae and quadriceps femoris data of Protocol III indicated twitch-contraction time and force at the separate stimulus-

Fig. 9 Superimposed M-responses Generated by Graded Stimulation Via Large Electrodes Over the Muscle Bellies.

These compound-twitch responses from the triceps surae (top) and quadriceps femoris (bottom) muscle groups were generated by graded stimulation via large electrodes over the muscle bellies. Twitch-contraction time was measured as the time from baseline at onset of the twitch to the peak of the twitch. In A, the quadriceps femoris traces, the maximal twitch force of 93.6 N is associated with a twitch-contraction time of 85.2 ms and the minimal twitch force of 12 N is associated with a twitch-contraction time of 63.8 ms. In B, the triceps surae traces, the maximal twitch force of 124.3 N is associated with a twitch-contraction time of 118.2 ms and the minimal twitch force (second twitch from the bottom) of 25.9 N is associated with a twitch-contraction time of 83.4 ms.



A



B

Fig. 9 Superimposed M-responses Generated by Graded Stimulation Via Large Electrodes Over the Muscle Bellies.

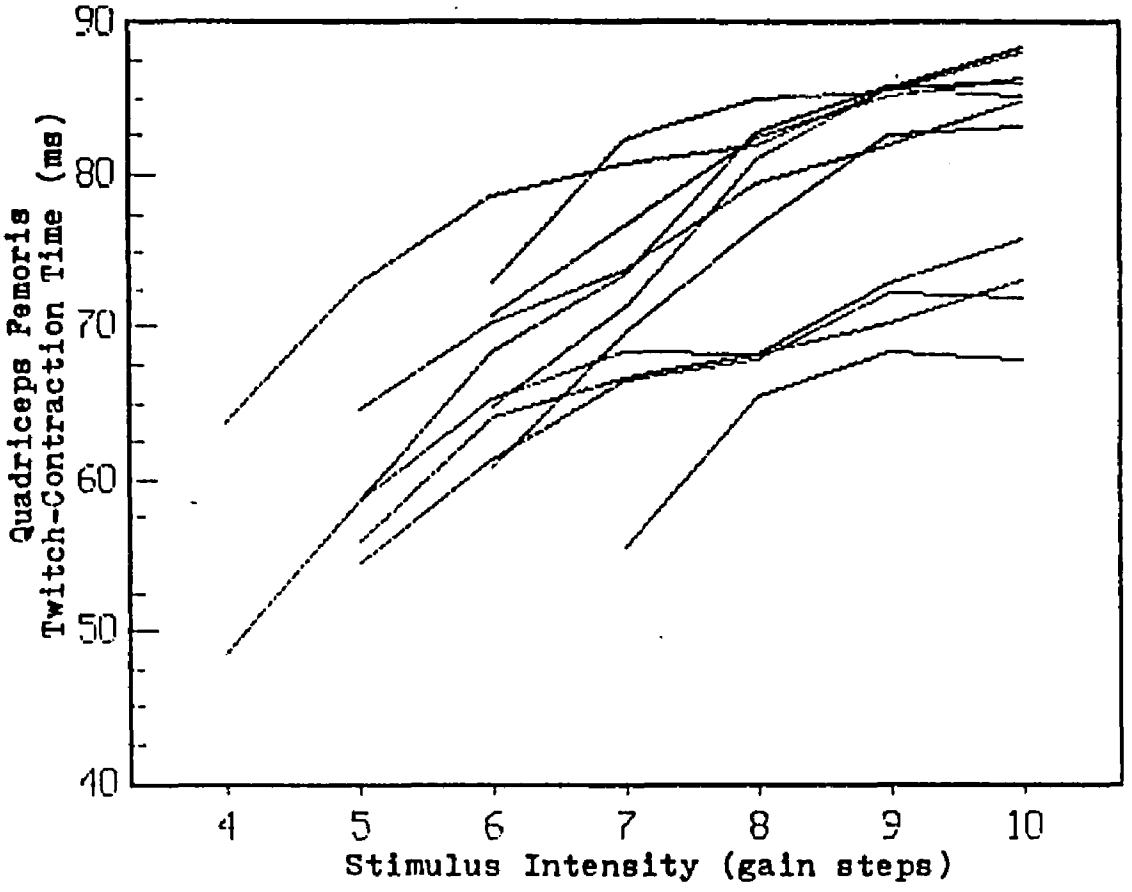


Fig. 10 Relationship Between Stimulus Intensity and Twitch-Contraction Time of Quadriceps Femoris M-Responses Elicited by Stimulation Over the Muscle Bellies.

Each line represents a recruitment curve for a separate subject. The data were accumulated in full gain-step increments (i.e., 4,5,6,...10) on the constant current unit and are shown as the average of five responses at each stimulus intensity. The standard deviations of these mean values are given in Table II.

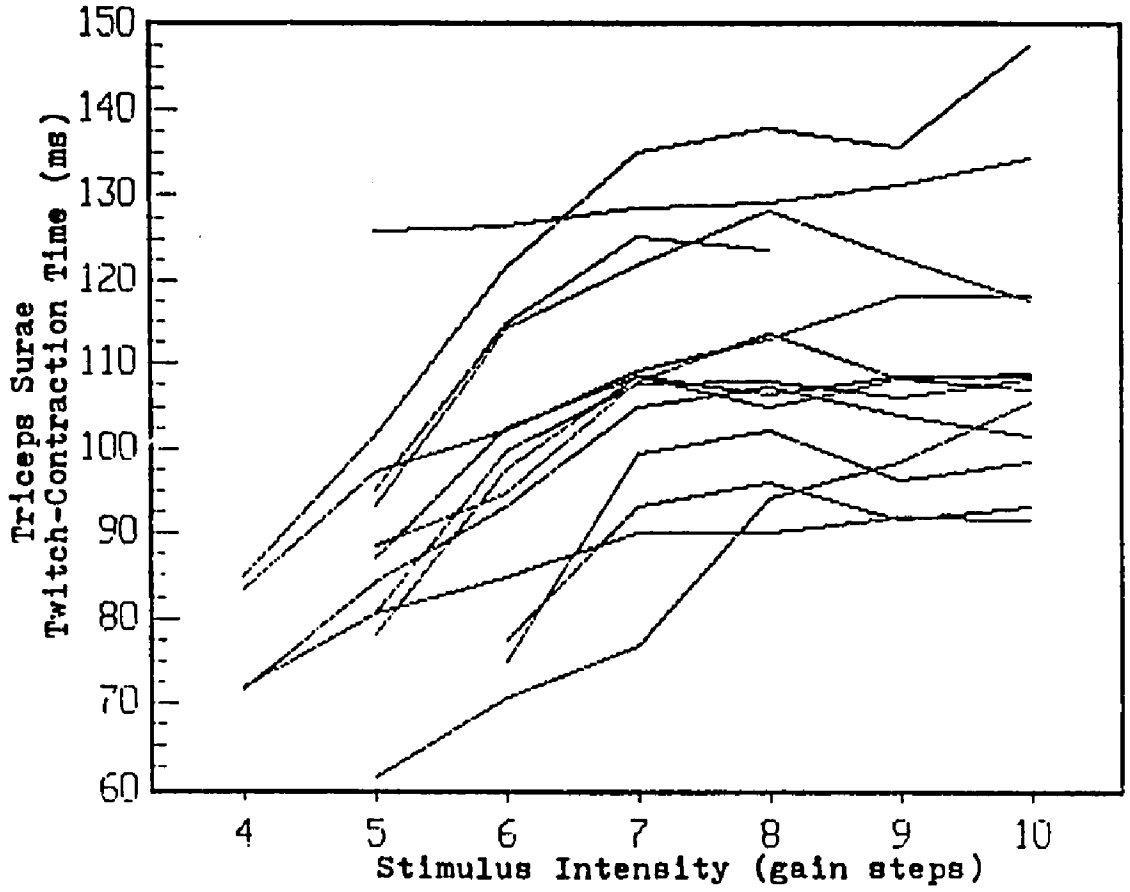


Fig. 11 Relationship Between Stimulus Intensity and Twitch-Contraction Time of Triceps Surae M-Responses Elicited by Stimulation Over the Muscle Bellies.

Each line represents a recruitment curve for a separate subject. The data were accumulated in full gain-step increments (i.e., 4,5,6,...10) on the constant current unit and are shown as the average of five responses at each stimulus intensity. The standard deviations of these mean values are given in Table II.

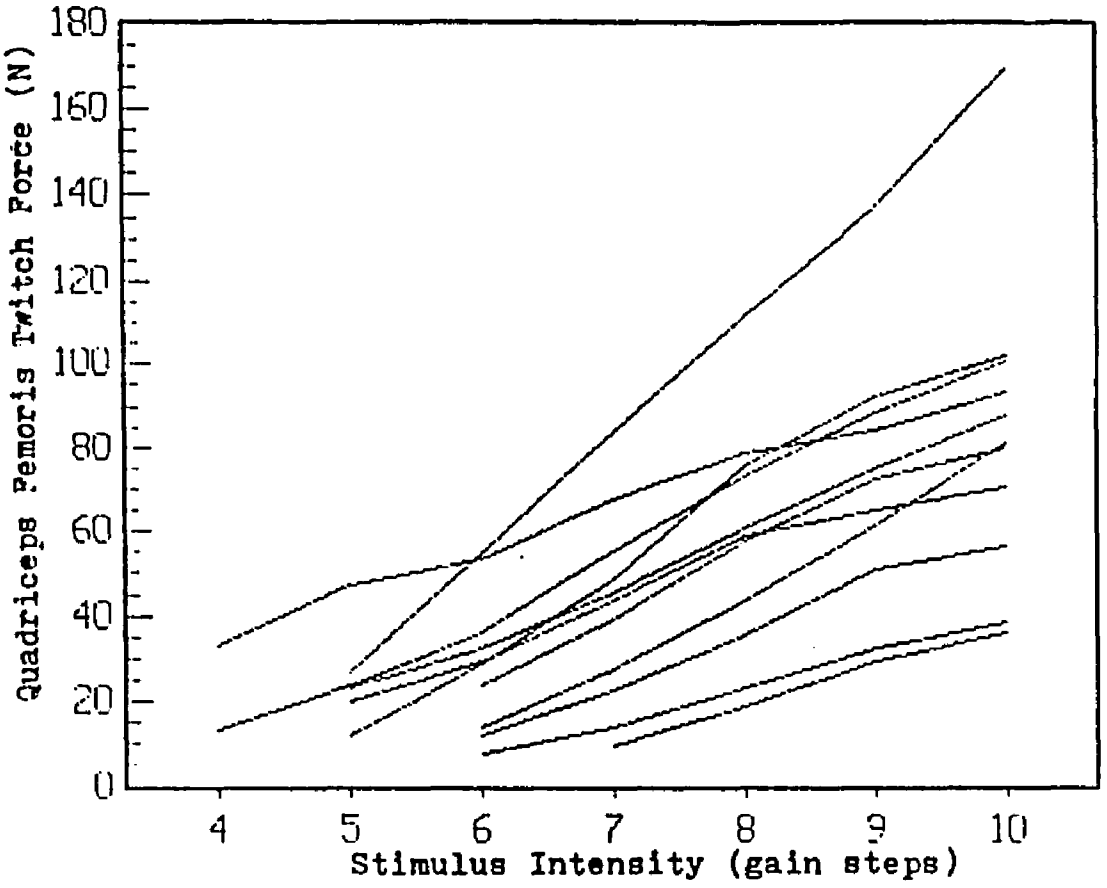


Fig. 12 Relationship Between Stimulus Intensity and Twitch Force of Quadriceps Femoris M-Responses Elicited by Stimulation Over the Muscle Bellies.

Each line represents a recruitment curve for a separate subject. The data were accumulated in full gain-step increments (i.e., 4,5,6, ...10) on the constant current unit and are shown as the average of five responses at each stimulus intensity. The standard deviations of these mean values are given in Table II.

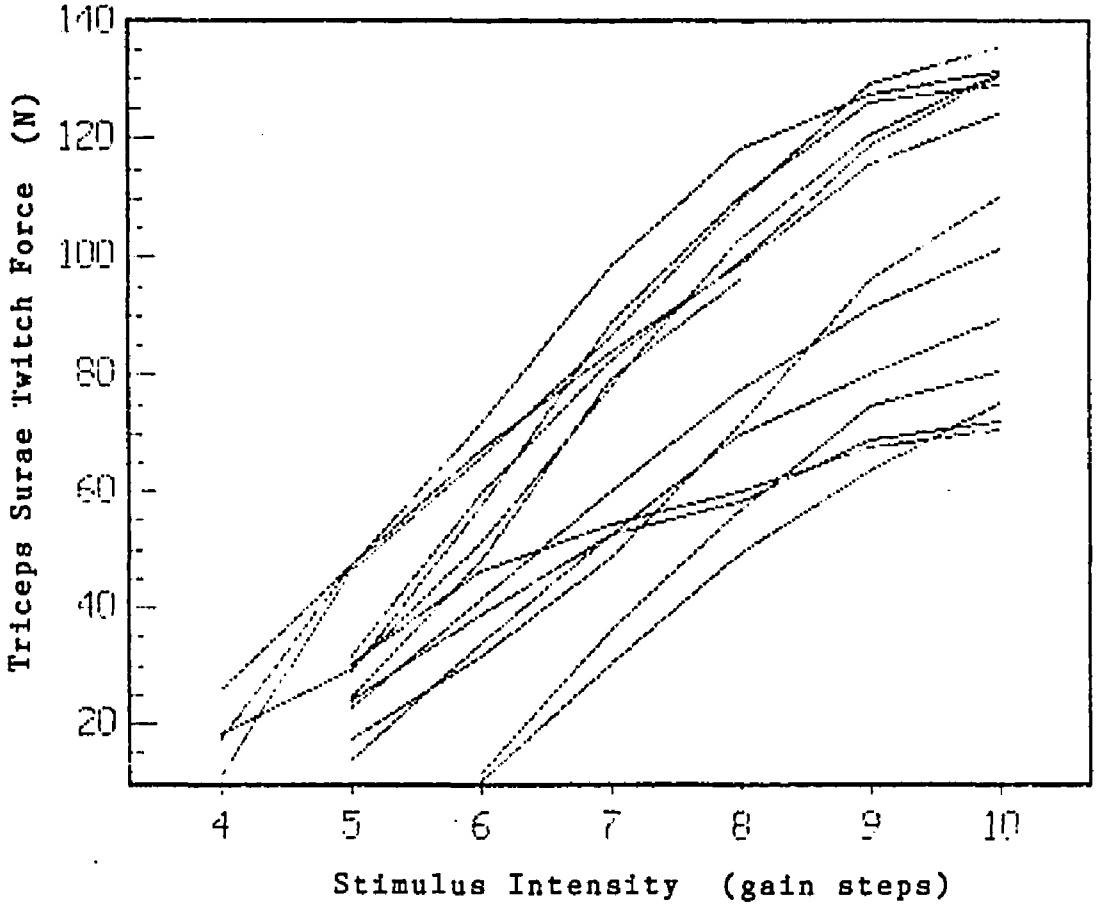


Fig. 13 Relationship Between Stimulus Intensity and Twitch Force of Triceps Surae M-Responses Elicited by Stimulation Over the Muscle Bellies.

Each line represents a recruitment curve for a separate subject. The data were accumulated in full gain-step increments (i.e., 4,5,6, ...10) on the constant current unit and are shown as the average of five responses at each stimulus intensity. The standard deviations of these mean values are given in Table II.

intensity levels were significantly ($p < 0.05$) different (see Table III). The trend analyses indicated a significant ($p < 0.05$) linear component was present for the relationships between stimulus intensity and twitch-contraction time and between stimulus intensity and twitch force in both muscle groups (see Table IV). In addition, a quadratic component was found to be significant ($p < 0.05$) in the relationship between twitch-contraction time and stimulus intensity.

Protocol IV - Effect of Cutaneous-Afferent Stimulation on Reflex Muscle Twitches

The results of Protocol IV support the third hypothesis. A three minute conditioning period of cutaneous-afferent stimulation over the bellies of the test muscles shortened the contraction time of H-reflexes generated at a constant stimulus intensity. Mean values and standard deviations for the responses prior to, during and following the cutaneous-afferent stimulation are given in Tables V and VI.

An analysis of variance indicated that the twitch-contraction time values during the cutaneous-afferent stimulation were significantly different ($p < 0.05$) from both the pre- and poststimulation values (see Tables VII and VIII). However, the pre- and poststimulation values

were not significantly different from each other. The twitch-force values of all three groups (pre-, during, and poststimulation) were also not significantly different.

Stability of the H-reflex performed before and after the cutaneous-afferent stimulation is shown in Figs. 14 and 15. There was little variability in the pre- and poststimulation H-reflexes. Fig. 14 shows 40 superimposed EMG traces, 20 prestimulation and 20 poststimulation; the top portion of the figure represents the soleus H-wave and the bottom portion that for the lateral gastrocnemius. Fig. 15 represents 40 superimposed EMG traces, 20 prestimulation and 20 poststimulation, in the vastus medialis (top portion) and the vastus lateralis (bottom portion) muscles. The sweep on the oscilliscope was triggered by the stimulus, as a result, the stimulus artifact is only partly visible. For this reason, the latencies of the H-waves can be measured from the beginning of each trace.

TABLE V. The Effect of Cutaneous Afferent Stimulation on the Compound-Twitch Parameters of Quadriceps Femoris H-Reflexes: Mean Values and Standard Deviations.

		Pre-Stimulation	During Stimulation	Post-Stimulation
Twitch-Contraction Time (ms)				
Subject				
1		73.6[a] ± 1.7	64.9[a] ± 2.5	73.2[a] ± 2.2
2		71.8 ± 1.5	64.4 ± 1.7	74.2 ± 1.6
3		72.9 ± 1.9	62.7 ± 2.8	71.1 ± 1.8
4	trial A	80.6 ± 3.6	64.9 ± 3.6	72.9 ± 2.2
	trial B	80.3 ± 1.6	72.2 ± 4.6	81.2 ± 3.6
5	trial A	87.0 ± 1.6	74.6 ± 1.6	81.4 ± 1.4
	trial B	87.0 ± 1.9	77.8 ± 1.5	82.1 ± 1.7
Twitch Force (N)				
Subject				
1		96.9[b] ± 2.3	93.8[b] ± 2.8	93.9[b] ± 2.6
2		81.3 ± 3.7	79.9 ± 4.2	79.9 ± 3.5

TABLE V Continued.

		Pre-Stimulation	During Stimulation	Post-Stimulation
Twitch Force (N)				
Subject				
3		92.0 ± 6.2	90.1 ± 4.3	88.3 ± 4.8
4	trial A	83.9 ± 5.5	75.5 ± 7.0	75.7 ± 7.2
	trial B	79.4 ± 2.5	80.1 ± 4.8	78.6 ± 3.9
5	trial A	137.8 ± 3.6	121.7 ± 2.8	128.4 ± 3.5
	trial B	217.3 ± 22.0	236.6 ± 11.9	247.0 ± 14.7

[a] Mean + SD twitch-contraction time

[b] Mean + SD twitch force

TABLE VI. The Effect of Cutaneous Afferent Stimulation on the Compound-Twitch Parameters of Triceps Surae H-Reflexes: Mean Values and Standard Deviations.

	Pre-Stimulation	During Stimulation	Post-Stimulation
Twitch-Contraction Time (ms)			
Sub. 1	89.0[a] ± 5.5	78.4[a] ± 4.1	88.3[a] ± 4.2
Sub. 2	94.2 ± 2.5	83.0 ± 4.9	95.5 ± 3.2
Twitch Force (N)			
Sub. 1	74.1[b] ± 2.2	72.8[b] ± 1.7	73.3[b] ± 2.2
Sub. 2	32.4 ± 2.2	30.5 ± 2.5	31.9 ± 2.1

[a] Mean + SD twitch-contraction time

[b] Mean + SD twitch force

TABLE VII. The Effect of Cutaneous Afferent Stimulation on the Compound-Twitch Parameters of Quadriceps Femoris H-reflexes: Mean Differences.

Mean Differences[a]		Pre to Stim	Stim to Post	Pre to Post
Twitch-Contraction				
Subject				
1		8.7	8.2	0.4
2		7.4	9.8	2.4
3		10.2	9.4	1.8
4	trial A	15.7	8.0	7.7
	trial B	8.1	9.0	0.9
5	trial A	12.4	6.8	6.6
	trial B	9.2	4.3	4.9
Group Mean		10.2[b]	7.9[b]	3.5
SE		± 2.9	± 1.9	± 2.9
Twitch Force				
Subject				
1		3.8	0.1	3.0
2		1.4	0.0	1.4
3		1.9	1.8	3.7
4	trial A	8.4	0.2	8.2
	trial B	0.6	1.5	0.8
5	trial A	16.1	6.7	9.4
	trial B	19.3	10.4	29.7

TABLE VII. Continued

Mean Differences[a]	Pre to Stim	Stim to Post	Pre to Post
Twitch Force			
Group Mean	7.4	2.9	8.0
SE	± 7.6	± 4.0	± 10.1

[a] Pre = before cutaneous stimulation, Stim = during cutaneous stimulation, Post = after cutaneous stimulation.

[b] $p < 0.05$

TABLE VIII. The Effect of Cutaneous Afferent Stimulation on the Compound-Twitch Parameters of Triceps Surae H-reflexes: Mean Differences.

Mean Differences[a]	Pre to Stim	Stim to Post	Pre to Post
Twitch-Contraction			
Subject 1	10.6	11.2	1.0
2	11.2	12.5	0.7
Group Mean	10.9[b]	11.2[b]	1.0
SE	± 0.4	± 1.8	± 0.4
Twitch Force			
Subject 1	1.3	1.0	0.8
2	1.9	1.4	0.5
Group Mean	1.6	1.2	0.7
SE	± 0.4	± 0.3	± 0.2

[a] Pre = pre-cutaneous stimulation, Stim = during cutaneous stimulation, Post = post-cutaneous stimulation.

[b] $p < 0.05$

Fig. 14 Stability of Quadriceps Femoris H-reflexes Before and After a Period of Cutaneous-Afferent Stimulation.

The top trace is from the vastus medialis muscle and the bottom trace is from the vastus lateralis muscle. Both traces represent 40 superimposed H-waves, 20 before and 20 after a 3 min. period of cutaneous-afferent stimulation.

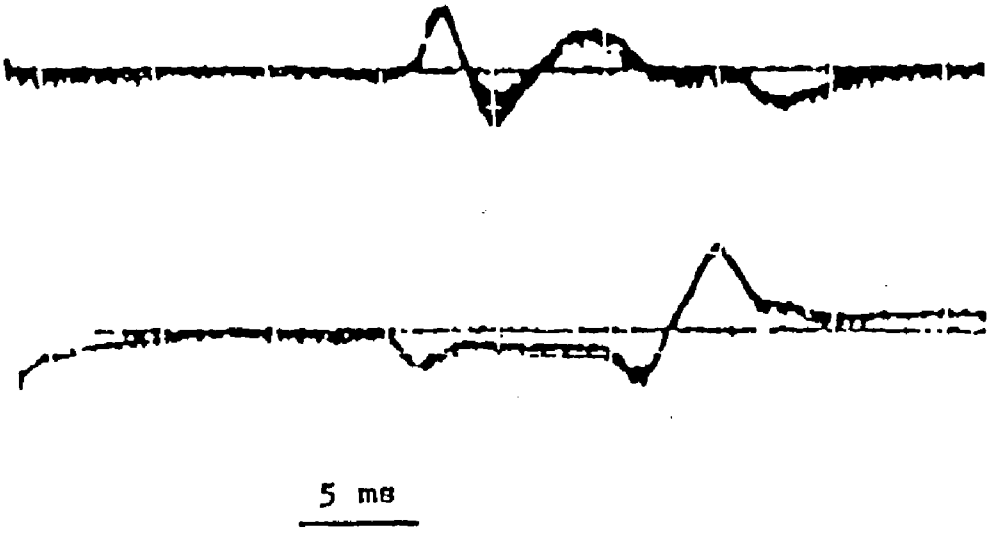


Fig. 14 Stability of Quadriceps Femoris H-reflexes Before and After a Period of Cutaneous-Afferent Stimulation.

The top trace is from the vastus medialis muscle and the bottom trace is from the vastus lateralis muscle. Both traces represent 40 superimposed H-waves, 20 before and 20 after a 3 min period of cutaneous-afferent stimulation.

Fig. 15 Stability of Triceps Surae H-reflexes Before and After a Period of Cutaneous-Afferent Stimulation.

The top trace is from the soleus muscle and the bottom trace is from the lateral gastrocnemius muscle. Both traces represent 40 superimposed H-waves, 20 before and 20 after a 3 min. period of cutaneous-afferent stimulation.

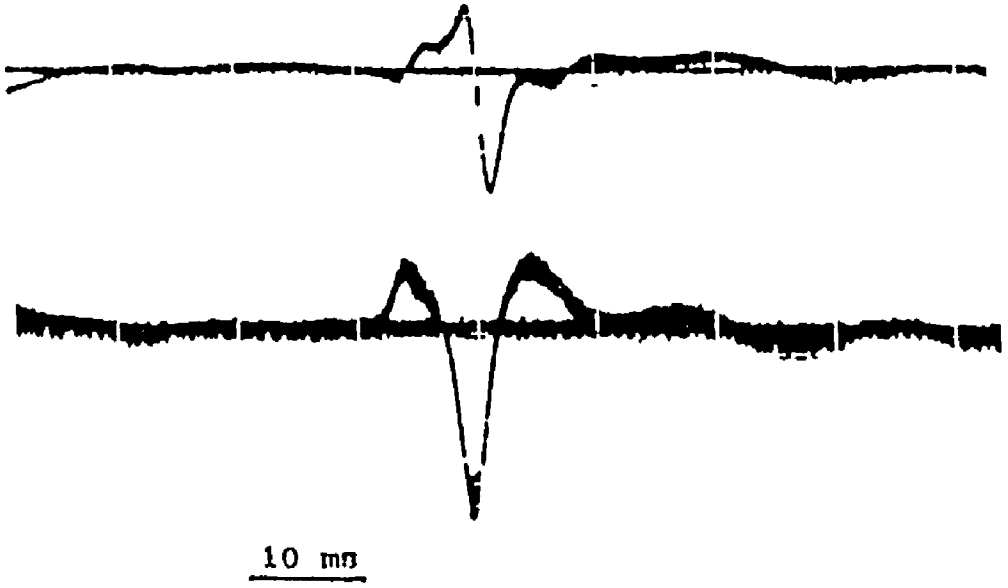


Fig. 15 Stability of Triceps Surae H-reflexes Before and After a Period of Cutaneous-Afferent Stimulation.

The top trace is from the soleus muscle and the bottom trace is from the lateral gastrocnemius muscle. Both traces represent 40 superimposed H-waves, 20 before and 20 after a 3 min period of cutaneous-afferent stimulation.

CHAPTER V

DISCUSSION

The discussion of the experimental observations will focus on the differences in the way skeletal muscle is activated by electrical stimulation as compared to voluntary and reflex activation. In addition, the clinical implications of these effects are considered.

Electrical vs Voluntary and Reflex Activation

Although several animal studies (Burke et al., 1970; Clamann et al., 1974; Eccles et al., 1958; Kanda et al., 1977; Mortimer, 1984) and a few human studies (Garnett and Stephens, 1980, 1981; Stephens et al., 1978) have addressed the issue of a differential activation of skeletal muscle by electrical stimulation, there seems to have been limited acknowledgment of this work by those who investigate and utilize electrically induced exercise. This has led to some misconceptions among clinicians and other investigators. For example, some believe that the activation of muscle electrically is the same as that which occurs by volition (Petrofsky and Phillips, 1983). Others have considered the electrical activation of muscle only as a means of bypassing the central nervous system (Cummings,

1980; Currier et al., 1979; Moritani and DeVries, 1979; Romero et al., 1982). As a result, the clinical use of electrically induced exercise has, at times, been inappropriate and ineffective (Boutelle et al., 1985; Currier et al., 1979; Currier and Mann, 1984; Owens and Malone, 1983; Selkowitz, 1985).

The results of Protocol I demonstrate that the motor-unit recruitment order during the H-reflex occurs in a manner which is similar to voluntary muscle contractions. That is, relatively slow-twitch motor units are recruited first, followed by the progressive recruitment of fast-twitch-motor units. This was indicated by the compound-twitch responses of quadriceps femoris and triceps surae muscle groups. The twitch-contraction time of these responses decreased as stimulus intensity was increased and twitch force increased (see Figs. 4, 5, and 6). These findings supported the first hypothesis of this study.

In contrast, the results of Protocols II and III demonstrate that direct electrical activation of skeletal muscle recruits motor units in an order which is qualitatively the reverse of physiological activation. This supported the second hypothesis put forth in this study. With this type of stimulation, the contraction time and force of these compound-twitch responses increased as

stimulus intensity was increased, indicating that fast-twitch motor units are recruited first and slow-twitch motor units are progressively recruited (see Figs. 7-13).

The results of Protocol IV demonstrate another effect of electrical stimulation on the recruitment order of motor units. The shortening of the twitch-contraction time of the H-reflex, elicited at a constant stimulus intensity, by cutaneous-afferent stimulation suggests that a modification in the recruitment thresholds of a population of motor units can occur with this type of stimulation (see Tables V and VI). Fast-twitch motor units are facilitated and slow-twitch motor units concurrently inhibited causing the composite twitch response to shorten its contraction time while maintaining a similar force output. This was in support of the third hypothesis.

The results of all four protocols of this study support the findings of previous animal studies (Burke et al., 1970; Clamann et al., 1974; Eccles et al., 1958; Kanda et al., 1977; Mortimer, 1984) and demonstrate that at least two mechanisms are responsible for the differential effect of electrically activated muscle contractions. The first mechanism, direct-efferent stimulation, has been shown in animal models to recruit the motor-unit population of a muscle in a reverse order to that which occurs by normal reflex activation (Clamann et al., 1974; Eccles et

al., 1958). However, this has not been adequately demonstrated in humans. In fact, Brown et al. (1981) claim to have demonstrated motor-unit recruitment in humans by graded electrical stimulation similar to that which occurs during normal, physiological muscle contractions. The present results, in contrast, support the findings in animal studies that graded electrical stimulation of muscle-efferent axons recruit fast-twitch motor units prior to slow-twitch motor units.

The second mechanism by which electrical stimulation produces a differential effect on the activation of skeletal muscle is by cutaneous-afferent stimulation. Activation of cutaneous afferents has been shown to alter the recruitment thresholds of motor units participating in voluntary and reflex muscle contractions in both animals (Burke et al., 1970, Kanda et al., 1977) and humans (Garnett and Stephens, 1980, 1981; Stephens et al., 1978). However, the human studies have only demonstrated this in the first dorsal interosseous muscle of the hand. The present results suggest that a modification in the functional recruitment thresholds of motor units during cutaneous-afferent stimulation may also occur in the large muscle groups of humans. Although recruitment thresholds were not directly examined, a shortening of the compound-twitch contraction time of H-reflexes in the absence of

changing twitch force is believed to reflect a differential alteration in the recruitment thresholds of the responding motor-unit population. That is, a lowering of the recruitment thresholds in fast-twitch motor units and an elevation of the recruitment thresholds in slow-twitch motor units would be a plausible explanation.

Given the validity of the interpretation of the change in compound-twitch contraction time, the results of this study suggest that a reversal of recruitment thresholds of slow-twitch and fast-twitch motor units does not require selective stimulation of cutaneous nerves but can result from stimulation directly over the bellies of the test muscles. Such an electrical-stimulation protocol is common among clinical attempts to strengthen hypothrophic muscle.

This method of stimulating the cutaneous afferents also raises the question of whether other afferent systems are affected. Although the activation of other afferent systems is possible, particularly group I muscle afferents, their contribution is unclear. The application of subthreshold stimuli to the group Ia muscle afferents would facilitate the motoneuron pool (Mao, Ashby, Wang, and McCrea, 1984; Pierrot-Deseilligny, Morin, Bergego and Tankov, 1981). However, such input is known to facilitate low-threshold, slow-twitch motor units to a proportionally

greater extent than high-threshold, fast-twitch motor units (Buller, Garnett and Stephens, 1980; Burke et al, 1987; Kanda et al, 1977). As a consequence, compound-twitch force would be expected to increase in association with the shortening of the twitch-contraction time as higher threshold, fast-twitch units were recruited. This effect was not seen in our data. Conversely, the application of subthreshold stimuli to the group Ib muscle afferents would cause an overall inhibition of the motoneuron pool (Pierrot-Deseilligny et al., 1981). This would likely lengthen the compound-twitch contraction time in association with a reduction in twitch force as derecruitment of high-threshold units occurred. This effect was also not seen in our data. Only the cutaneous afferents have been shown to produce a differential effect on the motoneuron pool to which they project (Burke et al., 1970; Kanda et al., 1977).

The compound-twitch response, although an indirect approach to evaluating the order of motor-unit recruitment, allows one to examine an entire muscle group instead of sampling a few, isolated, single motor units. To our knowledge it has not been used for this purpose prior to this study. Buchthal and Schmalbruch (1970b, 1976) utilized this technique to describe the contraction times of whole muscle twitches produced by the H-reflex and by

intramuscular stimulation at the motor end-plate zone.

The compound-twitch responses of triceps surae in the present study, which were elicited by posterior nerve stimulation, were observed to have twitch-contraction times (H-reflex range 56-102 ms; M-response range 53-87 ms; see Table I) similar to those reported by Buchthal and Schmalbruch (1970b, 1976) for the soleus muscle (H-reflex range 84-112 ms; M-response range 52-102 ms). However, the triceps surae M-responses, generated by stimulation over the muscle bellies, had twitch-contraction times which were longer (range 61-147 ms) than either the H-reflex or M-response, elicited by posterior tibial nerve stimulation. This was not expected since the faster and superficial gastrocnemious muscle would have likely received the greater stimulus-charge density and been activated first with graded stimulation.

Longer twitch-contraction times for the triceps surae M-responses may be due in part to the use of different subjects in Protocols II and III. However, the mode of stimulation is probably the major factor. Activating the muscle by stimulation of the efferent-axon branches may produce longer compound-twitch contraction times than the responses generated by nerve stimulation. Since the axon-branches are separated from the stimulating electrodes to a greater and more varying degree than axons in the nerve

trunk, a greater temporal dispersion of the neural activation would likely be expected. This variation, however, was not seen in the data from the quadriceps femoris muscles. In the quadriceps femoris trials, M-responses generated by electrodes over the muscle bellies had shorter twitch-contraction times (range 48-87 ms) than those of the H-reflexes (range 65-100 ms). This differential response would be expected if the fast-twitch motor units are preferentially recruited by stimulation over the muscle bellies as is suggested by the other results. Other explanations for the varying responses with the different modes of activation and between the two muscle groups are anatomical differences between the muscle groups and the electrode placements.

Clinical Implications

In addition to describing the differences in muscle activation by electrical stimulation, a secondary purpose of this study was to propose that the differential response to electrically induced strength training was due to the variant way in which electrical stimulation activates muscle. This is believed to be true for voluntary contractions with superimposed electrical stimulation and electrically induced exercise alone. In addition, the contradictory findings of many studies which have compared

electrically induced and volitional strength training may also be accounted for by this differential response. The effect of the cutaneous-afferent stimulation probably plays a much greater role when electrical stimulation is superimposed over a voluntary contraction. The effect of direct-motor efferent stimulation is probably just as important with or without additional voluntary effort.

A differential training effect with electrically induced exercise has significance for rehabilitation settings. In situations in which strong muscle contractions may be detrimental to an injured extremity, electrically induced exercise in conjunction with or in alternation with voluntary exercise could train the populations of high threshold motor units at lower overall contraction intensities. Generally, these populations of motor units are inaccessible in rehabilitation paradigms.

CHAPTER VI

SUMMARY

It is generally thought that the recruitment order of motor units under most physiological conditions occurs in an orderly manner which is relatively fixed and unalterable (Denny-Brown and Pennybacker, 1938; Desmedt and Godaux, 1977a; Henneman, Somjen and Carpenter, 1965ab; Milner-Brown, Stein and Yemm, 1973b). Modifications of this normal orderly recruitment of motor units has been demonstrated with electrical stimulation. At least two mechanisms are responsible for this effect. The first mechanism is the effect of direct-motor efferent stimulation. The motor-unit recruitment order by electrical stimulation of the motor-efferent axons is a function of: the diameter of the motor axons, and the distance between the axon and the active electrode. The second mechanism concerns the effect of cutaneous-afferent stimulation. Cutaneous-afferent input to a motoneuron pool alters the functional, recruitment thresholds of the constituent motor units. This phenomenon has been shown to occur in voluntary and reflex muscle contractions (Burke et al., 1970, Garnett and Stephens, 1981; Kanda et al., 1977;

Stephens et al., 1978).

This study examined these two mechanisms indirectly by characterizing compound-twitch responses. First, it was demonstrated that with increasing stimulus intensity the compound-twitch contraction time of H-reflexes shortened (Fig. 5). This was believed to reflect the recruitment of fast-twitch motor units as stimulus intensity increased. Moreover, this is considered the usual order in which motor units are recruited during voluntary and most reflex muscle contractions. In contrast, direct-motor efferent stimulation caused the compound-twitch contraction time to increase as slow-twitch motor units were recruited (Figs. 7 and 9).

Secondly, this study demonstrated the effects of cutaneous-afferent stimulation on H-reflexes evoked by a constant stimulus amplitude. With this paradigm the compound-twitch contraction time was found to decrease during a three minute period of electrical stimulation (subthreshold for a motor response) over the bellies of the test muscles without an associated increase in compound-twitch force (see Table V and VI). This shortening of the contraction time may reflect an alteration of the recruitment thresholds of different motor-unit types, fast-twitch motor units contributing more and slow-twitch units contributing less to the compound-twitch response during

the cutaneous stimulation.

These findings have implications on future research and present clinical applications of electrical stimulation. Further use of this technique, the characterization of compound-twitch responses, may elucidate similar mechanisms which alter the functional thresholds of motor units.

APPENDIX A

MOTOR-UNIT AND MUSCLE-FIBER TYPING

Appendix A has been divided into three sections: 1) motor-unit classification, 2) muscle-fiber typing, and 3) relationship between physiological properties and histochemical characteristics.

Motor-Unit Classification

A motor unit is considered the basic functional unit of motor activity in the neuromuscular system. First introduced by Sherrington (Liddell and Sherrington, 1925) over fifty years ago, a motor unit is defined as a motoneuron with its dendrites, motor axon and the group of muscle fibers it innervates. When a motoneuron discharges an action potential, normally all of the muscle fibers of that motor unit are activated more or less simultaneously (Kugelberg, 1981). The classification of motor units therefore considers the muscle fibers and the motoneuron of a particular unit together. The term "muscle unit" is often used to describe the muscle-fiber component of a motor unit. Since a motor unit is a functional entity, motor-unit classification is based upon physiologic

properties, whereas muscle fibers can be classified according to their physiologic, histologic and/or metabolic properties.

Because of technical limitations, most of the data concerning motor-unit characteristics have been derived from anesthetized experimental animals. A popular tripartite scheme of motor-unit classification has been put forth by Burke and associates (Burke et al., 1973, 1974) derived from cat tricep surae muscles. This group identified three major motor-unit types in cat gastrocnemius (Burke et al., 1973) and one type in soleus muscles (Burke et al., 1974) based upon a combination of physiological properties. Letter designations, used to differentiate motor unit classes in this system, indicate the physiological parameters characteristic of the group: 1) 'type S' motor units have a relatively slow twitch contraction, produce the least force of the three types and are resistant to fatigue, 2) 'type FR' units have relatively fast twitch contractions, produce relatively greater force and are also relatively fatigue resistant, and 3) 'type FF' units also have fast twitch contractions, produce the greatest force of the three types but are fast-to-fatigue (Burke et al., 1973). The motor-unit properties of force (twitch and tetanic) and twitch-contraction time are inversely related and occur on a continuum with some

overlapping between types. In contrast, fatigue resistance and the shape of the unfused tetani can clearly distinguish the different motor-unit types. Consequently, motor units can be classified on the basis of these latter parameters (Burke et al., 1973).

More recently, Burke (1981b) has described a fourth class of motor units with properties intermediate between those of the two fast-contracting groups. These motor units, previously labeled 'unclassified' because only a few were observed (Burke et al., 1973), have now been designated 'type F(Int)'. This identification is suggestive of the fast-twitch and intermediate characteristics of these motor units. On the basis of this finding, a quadripartite classification scheme is now being employed by Burke's group.

Development of physiological techniques to study the contractile properties of single motor units in man have allowed limited classification of units in certain muscles. Using spike-triggered averaging and microstimulation techniques, the motor units of the first dorsal interosseous muscle have been classified according to twitch force, twitch-contraction time, fatigue resistance and functional threshold (Milner-Brown, Stein, French, Mannard, and Yemm, 1972; Stephens and Usherwood, 1977; Young and Mayer, 1981). The twitch force of a first dorsal

interosseous motor unit varies almost linearly as a function of the level of voluntary force at which it is recruited (Milner-Brown et al, 1977). Motor-units recruited at higher contraction strengths have shorter contraction times and are more fatigue sensitive than the smaller, low-threshold motor units (Milner-Brown et al, 1977; Stephens and Usherwood, 1977).

Garnett, O'Donovan, Stephens and Taylor (1979), using the microstimulation technique, classified the motor units of human medial gastrocnemius muscle according to Burke's classification scheme. Similarly to the findings in the cat gastrocnemius muscle, they described three distinct types, types S, FR, and FF, based upon twitch-contraction time, force produced and fatigue resistance. Although the human data on motor-unit organization is incomplete, it is sufficient to support the principle of a tripartite (Garnett et al., 1979; see Table I) and possibly a quadripartite classification scheme (Stuart, Binder and Enoka, 1984).

Muscle-Fiber Typing

Histochemistry was first applied to human muscle-fiber typing by Dubowitz (1960) to classify pathological muscle. Dubowitz (1960) utilized the nomenclature of type I and type II to classify individual fibers by enzymatic

TABLE A-I

Human Motor-Unit Characteristics

Motor unit type:	FF	FR	S
Physiological properties			
Twitch-contraction time (ms)	45-85[a] 33-68[b]	55-75[a] 38-69[b]	99-110[a] 70-146[b]
Twitch force (mN)	50-2040[a] 10-260[b]	60-260[a] 5-9[b]	20-230[a] 5-50[b]
Resistance to fatigue	low	high	very high
Histochemical profiles[a]			
Myofibrillar ATPase	high	low	low
Succinic dehydrogenase	low	int. to high	high

[a] Data of medial gastrocnemius muscles cited from Garnett et al. (1979)

[b] Data of first dorsal interosseous muscles of the hand, cited from Stephens and Usherwood (1977) and Young and Mayer (1981)

histochemical properties. Type I fibers were high in oxidative enzymes (diphosphopyridine nucleotide dehydrogenase and succinic dehydrogenase) and low in phosphorylase and myosin adenosine triphosphatase (ATPase), whereas, the reverse was true for type II fibers. Later, it was generally believed that the myosin-ATPase reaction

alone was sufficient to distinguish fiber types of this classification scheme (Engel, 1962; Brooke and Kaiser, 1970).

Brooke and Kaiser (1970) expanded this histological classification of muscle fibers to three major types and one minor type characterized by variations of the histochemical reaction for myosin ATPase. Finer gradations to the myosin ATPase reaction were found possible when the tests were performed at different pH levels. Types I, IIA and IIB are the three constant categories in normal muscle, however, a fourth type, referred to as type IIC, are occasionally observed (Brooke and Kaiser, 1970). In human muscle, type IIa and IIC fibers are not usually differentiated (Brooke and Kaiser, 1970).

Types I and II fibers are distinguished by a calcium-activated reaction for myosin ATPase (Dubowitz, 1960; Brooke and Kaiser, 1970). This test reflects the fast and slow forms of myosin (Kugelburg and Thornell, 1983). Type II fibers are further subdivided on the basis of their susceptibility to preincubation at pH 4.6 (Brooke and Kaiser, 1970). Brooke and Kaiser (1970) observed similar distinguishing features in human, rat and rabbit skeletal muscle using this classification scheme (see Table II).

Brooke and Kaiser (1970) tried to correlate the

TABLE A-II

Muscle-Fiber Characteristics			
Muscle-fiber type	IIB	IIA	I
Myofibrillar ATPase	high	high	low
Myosin-ATPase reaction	inhibited at pH 4.3	inhibited at pH 4.5	

Data cited from Brooke and Kaiser (1970) and Dubowitz (1960) Data from rabbit, rat and human skeletal muscle

myosin-ATPase reactions with oxidative enzyme and phosphorylase reactions. Type I fibers corresponded to fibers staining the darkest for oxidative (diphosphopyridine nucleotide dehydrogenase) enzymes, type IIB fibers stained the least and type IIA fibers stained intermediately in humans. However, in rat and rabbit skeletal muscle this was not the case. In addition, the periodic acid-Schiff test and phosphorylase reaction did not correspond well with the myosin ATPase reaction in human, rat or rabbit muscle.

Relationship Between Physiological Properties and Histochemical Characteristics.

Interrelationships between physiological and histochemical profiles of single motor units have been demonstrated in cat triceps surae muscles (Burke et al., 1973, 1974) and in human gastrocnemius muscle (Garnett et

al., 1979). The term 'histochemical profile' is used to refer to the set of staining characteristics of a particular muscle unit. Each of the physiologically classified motor-unit types in the S-FR-FF classification scheme exhibit a unique histochemical profile common to all the muscle units in a particular class (Burke et al., 1973, 1974). In cat triceps surae muscles, the fibers staining dark for oxidative enzymes (diphosphopyridine nucleotide dehydrogenase and succinic dehydrogenase), and light for periodic acid-Schiff, phosphorylase and myofibrillar ATPase belong to type S motor units. Whereas, the muscle fibers of type FF motor units stain just the opposite. The muscle fibers of type FR motor units demonstrate a histochemical profile intermediate to the other two motor-unit classes (Burke et al., 1973, 1974). A similar relationship has been demonstrated in human gastrocnemius muscle (Garnett et al., 1979; see Table I).

Peter, Barnard, Edgerton, Gillespie, and Stempel (1972) also relating physiological characteristics with histochemical characteristics defined another useful classification system to categorize different muscle fibers. Their system made use of a more descriptive nomenclature to describe three different categories of fibers: 1) fast-twitch, glycolytic (FG), 2) fast-twitch, oxidative-glycolytic (FOG), and 3) slow-twitch, oxidative

(SO) in guinea pig and rabbit muscle.

Muscle fibers with short contraction times (i.e., fast-twitch fibers) are common in the vastus lateralis and gastrocnemius muscles and can be subdivided into two categories, FG and FOG, by histochemical analysis (Peter et al., 1972). Both FG and FOG fibers stain darker for myofibrillar ATPase than do the slow-twitch fibers of these muscles. However, of the two fast-twitch fibers, the FG fibers stain the darkest for myofibrillar ATPase and for glycolytic enzymes (mitochondrial alpha-glycerophosphate dehydrogenase and phosphorylase). In addition, FG fibers stain the lightest for oxidative enzymes (hexokinase and succinate dehydrogenase activity). In contrast, FOG fibers of the vastus lateralis and gastrocnemius muscles stain the darkest for the oxidative enzymes.

The SO fibers of the soleus muscles, which stain negligibly for myofibrillar ATPase and for the glycolytic enzymes, stain intermediately (between the FOG and FG fibers of the vastus lateralis and gastocnemius muscles) for the oxidative enzymes (Peter et al., 1972; see Table III).

Several investigators (Burke et al., 1973; Barany, 1967; Kugelberg, 1973; Peter et al., 1972) have observed a correlation between the staining of myosin ATPase and the twitch-contraction time in a variety of muscles from

different species. This is one of the bases for comparing the physiologic-based (S-FR-FF) and myosin-ATPase-based (I-IIA-IIB) classification schemes. More recently however, Kugelberg and Thornell (1983) found that the myosin-ATPase reaction did not correlate with twitch-contraction time when comparing muscle units of rat soleus and tibialis anterior muscles. Although the twitch-contraction time of soleus and tibialis anterior units correlated with myosin-ATPase staining within the same muscle, soleus type II and tibialis anterior type I fibers had similar contraction times. Twitch-contraction time was found to correspond inversely with the volume density of sarcoplasmic-reticulum terminal cisternae within and between both the soleus and tibialis anterior muscles (Kugelberg and Thornell, 1983). This suggests that the volume density of the terminal cisternae, which is related to the amount and rate of calcium release, is a better indicator of twitch-contraction time than myofibrillar ATPase.

There does not appear to be a close correspondence between the S-FOG-FG and I-IIA-IIB classification systems (Nemeth and Pette, 1981); however, this may depend on the species. In rat muscle, type I and type SO fibers correspond as do type IIA and FOG fibers, yet type IIB and type FG fibers do not. Nemeth and Pette (1981) contended that the myosin ATPase-based classification system could

TABLE A-III

Guinea Pig Skeletal Muscle Characteristics

Muscle fiber type	FG	FOG	SO
Time-to-peak force (ms)	20.1	19.0	82.3
Myofibrillar ATPase (umol/min/mg)	0.59	0.49	0.18
Phosphorylase* (umol/min/mg) [a]	7.13	6.67	1.54
Lactate dehydrogenase (umol/min/mg) [a]	449	218	105
∝-Glycerophosphate dehyg. (umol/min/mg)	1.62	1.67	0.61
Hexokinase** (nmol/min/mg) [b]	297	620	978
Succinate dehydrogenase (umol/min/mg)	0.72	2.49	1.95
Myoglobin (mg/g)	0.31	1.44	1.39
Capillaries/fiber	3.9	4.5	5.3

Data cited from Peter et al. (1972) and Barnard et al. (1971)

[a] key enzymes of the glycolytic pathway

[b] key enzymes of the oxidative pathway

not differentiate the oxidative capacity of type II fibers. Nevertheless, the type I-IIA-IIB classification system will probably continue to be used in classifying muscle fibers in man because of convenience. The use of the myosin-ATPase reactions in combination with oxidative-histochemical reactions to classify muscle fibers, as Dubowitz (1960) originally proposed, may prove more

desirable.

The FG-FOG-SO classification of muscle fibers is considered equivalent to the muscle-unit component of the FF-FR-S classification system (Burke and Edgerton, 1975). However, these classification systems are also relative to the muscles tested. For example, oxidative-enzyme staining in the extremely fatigue-resistant type S units or SO fibers, at times and in certain muscles, appears less than the type FR units or FOG fibers (Burke and Edgerton, 1975). Even the same motor-unit types are not equivalent in different muscles of the same species. An example of this is the type S motor units in the cat; type S motor units in soleus muscle are qualitatively dissimilar to those in the gastrocnemius muscle (Burke et al., 1974).

Summary

Although the characteristics of motor units or muscle units vary more or less on a continuum, classification provides a convenient method of comparing features of the muscles whose units have been studied. There are advantages and pitfalls to all three classification schemes described; however, the evaluation of both physiologic and biochemical-histochemical features, which is possible with glycogen-depletion techniques, provides a more detailed description of the muscle units studied.

Some generalizations can be made within mammalian species even though the characteristics of different populations of motor and muscle units are species specific (Burke and Edgerton, 1975; Edgerton and Cremer, 1981). Most of the data have been obtained from different animal models (Burke et al., 1973, 1974; Peter et al., 1972) and extrapolated to human muscle based on limited samples from more recent human studies (Garnett et al., 1979; Stephens and Usherwood, 1977; Young and Mayer, 1981). Still, much remains to be done to clarify the potentially important differences in human skeletal muscle. With additional technological advances and continued refinement of the present techniques (microstimulation, signal averaging and microchemistry) more descriptive data from human studies appears forthcoming.

APPENDIX B

SUBJECT CONSENT FORM

SUBJECT CONSENT FORM
FOR

THE EFFECTS OF ELECTRICAL STIMULATION ON THE WAY SKELETAL MUSCLE IS ACTIVATED

You are being invited to participate in the above-titled research project. The purpose of this project is to examine the differences in the way muscle is activated by electrical stimulation as compared to voluntary effort. You have been invited because you are an adult that has not been diagnosed as having a neurological impairment or suffered serious injury to both your legs. We hope to enroll 10 to 12 subjects in this study.

If you decide to participate, you will be asked to agree to a 90 min testing session. This will involve the use of two different electrical-stimulator devices, an electromyograph and a device that measures the force your thigh or calf muscles can exert. Several surface electrodes will be applied over your thigh or calf from the electrical stimulators and for the electromyograph. These electrodes will be separated from the skin by a thin layer of conductive gel and are therefore painless. The electrical stimulation will be gradually increased in intensity to familiarize you with the sensation gradually. It will not be painful but will likely be a new sensation to you. One electrical-stimulator device will evoke muscle twitches which will be measured by the electrical signal and mechanical-force response your muscles produce. The other electrical stimulator will produce a tingling sensation over you thigh or calf muscles. There will be no effort required on your part. However, you will be asked to remain very still during different parts of the experiment.

Your participation in this study involves some possible mild side effects and risks. Your thigh may be mildly sore for a few days following the testing session as a result of skin preparation for the stimulation electrodes. In addition, you may perceive the electrical stimulation as uncomfortable. The discomfort from this stimulation is thought to be due to the different type of muscle contraction produced rather than a shock sensation.

Painful stimulation is not necessary and would possibly have a negative effect on the results of the study; therefore pain due to the stimulation will be avoided. Most people are initially anxious about the sensation of the electrical muscle stimulation, for this reason we will precede slowly. You will be able to have the stimulation turned off at any point in the experiment.

Although there are no personal benefits to be derived from this project, the information gained from this project may prove useful in athletic and orthopedic rehabilitation.

Adverse reactions are a possibility in any research program despite the use of high standards of care and could occur without negligence attributable to either the subject or the investigator. Reactions which can be foreseen have been described in this consent form. However, unforeseeable injury may also occur, and may require care. Financial compensation for research-related injury or for wages or time lost is not available. For further information concerning possible adverse reactions you may contact Mark Trimble, PT (phone numbers 621-4702 or 888-7869).

Your involvement in this study will not cost you any money, nor will you be reimbursed for your participation.

The information concerning your performance will be kept confidential and all data will be filed by code. Published data will consist of predominantly group data; however if individual data is displayed, no reference to you by name or code will be used. Only those individuals directly involved in the study (Mark Trimble, PT or Roger Enoka, Ph.D.) will have direct access to the data.

I have read this subject's consent form. The nature, demands, risks, and benefits of the project have been explained to me. I understand that I may ask questions and that I am free to withdraw from the project at any time without incurring ill will or affecting my medical care. I also understand that this consent form will be filed in an area designated by the Human Subjects Committee with access

restricted to the principle investigator or authorized representatives of the particular department. A copy of this consent form will be given to me.

Subject's Signature	Date
_____	_____
Investigator's Signature	Date
_____	_____

APPENDIX C

HUMAN SUBJECTS APPROVAL

The University of Arizona
Human Subjects Committee
1609 N. Warren (Building 220), Room 112
Tucson, Arizona 85724
(602) 626-6721 or 626-7575

11 May 1987

Mark Trimble, B.S.
Department of Exercise and Sport Sciences
McKale Center, Room 8222V
MAIN CAMPUS

Dear Mr. Trimble:

We have received your project, "The Effects of Electrical Stimulation on the Recruitment Order of Motor Units: Examination by Comparing the Compound-Twitch Contraction Times of Electrically Evoked Responses", which was submitted to this Committee for review. The procedures to be followed in this study pose no more than minimal risk to participating subjects and the device to be used is commercially available. Regulations issued by the U.S. Department of Health and Human Services [45 CFR Part 46.110(b)] authorize approval of this type project through the expedited review procedures, with the condition(s) that subjects' anonymity be maintained. Although full Committee review is not required, a brief summary of the project procedures is submitted to the Committee for their endorsement and/or comment, if any, after administrative approval is granted. This project is approved effective 11 May 1987.

Approval is granted with the understanding that no changes or additions will be made either to the procedures followed or to the consent form(s) used (copies of which we have on file) without the knowledge and approval of the Human Subjects Committee and your College or Departmental Review Committee. Any research-related physical or psychological harm to any subject must also be reported to each committee.

A university policy requires that all signed subject consent forms be kept in a permanent file in an area designated for that purpose by the Department Head or comparable authority. This will assure their accessibility in the event that university officials require the information and the principal investigator is unavailable for some reason.

Sincerely yours,

Milan Novak

Milan Novak, M.D., Ph.D.
Chairman
Human Subjects Committee

MN/jm

cc: Departmental/College Review Committee

The University of Arizona
Human Subjects Committee
1609 N. Warren (Building 220), Room 112
Tucson, Arizona 85724
(602) 626-6721 or 626-7575

25 June 1987

Mark Trimble, B.S.
Department of Exercise and Sport Sciences
McKale Center, Room 8222V
MAIN CAMPUS

Dear Mr. Trimble:

We received your letter to Dr. Patricia Fairchild and the accompanying revised consent form for your project, "Effects of Electrical Stimulation on the Recruitment Order of Motor Units: Examination by Comparing the Compound-Twitch Contraction Times of Electrically Evoked Responses". The changes reflected in this revision pose no further risk to participating subjects. Therefore, approval for this revised form is granted effective 25 June 1987.

The changes approved are:

1. The addition of 10-12 subjects.

2. EMG monitoring will be eliminated.

3. Change of site of stimulation and use of larger surface electrodes.

Approval is granted with the understanding that no further changes or additions will be made either to the procedures followed or to the consent form(s) used (copies of which we have on file) without the knowledge and approval of the Human Subjects Committee and your College or Departmental Review Committee. Any research-related physical or psychological harm to any subject must also be reported to each committee.

A university policy requires that all signed subject consent forms be kept in a permanent file in an area designated for that purpose by the Department Head or comparable authority. This will assure their accessibility in the event that university officials require the information and the principal investigator is unavailable for some reason.

Sincerely yours,

Milan Novak

Milan Novak, M.D., Ph.D.
Chairman
Human Subjects Committee

MN/ms

cc: Departmental/College Review Committee

APPENDIX D

THE RELIABILITY OF THE STIMULUS CURRENT INJECTION: CONSTANT CURRENT UNIT CALIBRATION

Table D-I Constant Current Unit Calibration

CCU gain step	Current(mA) at 0.1 kohm	Current(mA) at 1 kohm	Current(mA) at 1.5 kohm	Current(mA) at 2 kohm
0	2.7	2.6	2.7	2.7
1	5.0	5.0	4.9	4.8
1.25	6.5	6.4	6.3	6.2
1.5	7.7	7.8	7.9	7.7
1.75	8.7	9.3	9.3	9.1
2	10.3	10.5	10.5	10.7
2.25	11.8	11.9	12.3	11.9
2.5	13.2	13.3	13.2	13.2
2.75	14.5	14.5	14.5	14.4
3	15.7	15.8	15.9	15.7
3.25	17.1	17.3	17.2	17.1
3.5	18.2	18.7	18.5	18.4
3.75	19.7	19.8	19.8	19.8
4	21.0	21.1	21.0	21.1
4.25	22.2	22.2	22.2	22.2
4.5	23.3	23.4	23.4	23.5
4.75	24.5	24.6	24.6	24.6
5	25.6	25.8	25.9	25.7
5.25	26.8	27.0	27.0	27.0
5.5	28.0	28.2	28.0	28.1
5.75	29.1	29.2	29.2	29.2
6	30.3	30.7	30.7	30.6
6.25	31.5	32.1	31.8	31.7
6.5	32.9	33.3	33.3	33.1
6.75	34.4	34.9	34.8	34.5
7	35.6	36.1	36.3	35.7
7.25	36.8	37.3	37.8	36.8
7.5	37.9	38.7	38.7	37.6
7.75	39.0	39.8	39.8	37.7
8	40.1	40.9	40.9	37.7
8.25	41.5	42.2	41.9	37.7
8.5	42.7	43.3	43.0	37.7
8.75	43.8	44.8	43.5	37.6
9	45.0	45.8	43.5	37.7
9.25	46.1	47.0	43.6	37.7
9.5	47.1	48.0	43.6	37.7
9.75	48.2	48.5	43.7	37.7
10	48.5	48.5	43.7	37.7

See Moreno-Aranda and Seireg (1981a,b) for the range of skin impedance during percutaneous electrical stimulation.

The constant current unit (CCU) was in series with the stimulus isolation unit and the square-wave stimulator. The square-wave stimulator was set at 150 V for a 3 s duration. A decade-resistor box of known resistance was used for calibration.

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