VIII. Properties of Muscle

Control of Muscle Protein Metabolism During Exercise

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Sponsor: National Institutes of Health
(National Institute of Arthritis, Diabetes, and Digestive and Kidney Diseases)

The broad objectives of this research are to study changes that occur in protein metabolism as a result of exercise and to establish the underlying biochemical mechanisms that bring about these changes. In research already completed, we have clearly established that an acute bout of exercise (either running or swimming) causes a decrease in the rate of muscle protein synthesis and increased rates of protein degradation in muscle and liver. Preliminary evidence from our lab and reports from other investigators suggest that an acute exercise bout also increases the rate of amino acid oxidation.

During the next granting period, we propose to further study the effect of an acute exercise bout on protein synthesis, protein degradation, and amino acid oxidation. To determine mechanisms involved in the decrease in protein synthesis in muscle, we plan to determine the effect of exercise on the various components of protein synthesis: charging of t-RNA, initiation of peptide synthesis, and peptide elongation. An experiment will be conducted to investigate whether an acute bout of exercise increases alanine production by the isolated epitrochlearis muscle. In addition, we plan to continue investigating the biochemical regulation of leucine oxidation in muscle during exercise.

Adaptation of Muscle to High-Resistance Exercise

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The long-term objective of the proposed research is a fundamental understanding of neuromuscular plasticity. We will use as a model neuromuscular adaptation to high-resistance (weightlifting) exercise. Adult cats are operantly conditioned to flex their right wrist against increasing resistance in order to receive a food reward. This procedure has the advantage of inducing significant hypertrophy in the muscles of the right limb, while the muscles of the left limb can be used for comparative studies. Both increases in muscle fiber cross-sectional area (hypertrophy) and number (hyperplasia) have been shown to occur in response to weightlifting exercise.

The proposed study will determine the most effective exercise protocol for inducing muscle fiber hyperplasia and will investigate the importance of hyperplasia in the exercise-induced growth process. In the proposed study, the ultrastructural and histochemical features of exercised muscle fibers that are undergoing necrosis will be characterized. It is anticipated that this project will provide cytological evidence for the initiation of exercise-induced muscle fiber necrosis and help elucidate the significance of fiber turnover in adult muscle. Quantitative ultrastructural measurements of muscle fibers will be made to provide insight into the cytological reorganization that occurs in response to exercise. The physiological, histochemical, and morphological characteristics of motor units will be determined from forelimb muscles of trained cats.

These studies are made important by the observations of exercise-induced muscle fiber necrosis and fiber hyperplasia and will determine if these processes are independent of nervous system (motor) control. Little is known about the long-term effects of weightlifting exercise on muscle structure and function. This information is important in light of the findings of exercise-induced muscle fiber necrosis and hyperplasia and the increasing use of resistance exercise in this country as a component of health maintenance. These studies should should provide for a more informed and effective use of resistance exercise in the rehabilitation of patients suffering neuromuscular dysfunction■

Skeletal Muscle Adaptations Induced by Training

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The greatly elevated energy demands placed on muscle during contractions often lead to a loss of adenine nucleotides (principally ATP) and a loss of contractile function. This phenomenon occurs during less severe contraction conditions in low-oxidative fast-twitch white muscle rather than in high-oxidative fast-twitch red muscle. Further adaptations induced by exercise training make the muscle more resistant to the ATP loss and fatigue. The return of ATP concentration during recovery occurs via the reamination of IMP using the amine donated from aspartate, but originating, in large measure, from the branched-chain amino acids (leucine).

Our proposed work will use the perfused rat hindlimb preparation to evaluate: (i) the contribution of branched-chain amino acid amine to the recovery of adenine nucleotides following intense contractions (specifically, we will determine the impact of leucine concentration in the physiological range), and (ii) during steady-state, long-term, moderately intense activity, where some deamination/reamination cycling may occur without extensive fatigue. The above-mentioned function may account for the increased branched-chain amino acid oxidation observed during and after exercise.

Using the same experimental system, we will assess the contribution of branched-chain acid oxidation to the energy demands of working muscle. We will test to see if it is minimal during mild exercise and increases during conditions when the amine donation function, mentioned above, should become more important (e.g., following intense fatiguing contractions). Further, the coupling of branched-chain amino acid oxidation to the purine nucleotide cycle will be evaluated with hadacidin, an inhibitor of adenine nucleotide resynthesis from IMP■

Myoelectric Assessment of Human Lumbar Muscle Function

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The purpose of this project is to develop objective measures of lumbar muscle function for patients with low back pain. Techniques have been developed in this laboratory for measurement and analysis of the frequency spectrum of myoelectric signals obtained during exercise. Based upon information obtained from pilot studies, an isometric trunk exercise device has been constructed for use in collecting data.

Myoelectric data from the erector spinae and rectus abdominis muscles have been collected from a group of 15 young, healthy, normal adults performing isometric extension and flexion exercises on a simple back tester at load levels of 100 percent, 50 percent, and 20 percent of their maximum voluntary contraction (MVC) force. Another group of 10 healthy, young, normal adults (5 males and 5 females), and a group of 20 patients undergoing rehabilitation therapy for low back injuries, have been tested repeatedly on the newly developed back test device using similar protocols.

Mean power frequency slope measures of the myoelectric signal spectrum changes due to fatigue were shown to correlate with the load level. However, other factors for normals have been investigated that suggest that new measures could be developed to reduce this variability and increase the correlation between spectrum changes and load levels for fatigue trials. By normalizing the frequency slope to the initial frequency value, a linear decay measure (expressing slope as a percent decrease per minute) has been shown to improve the correlation. Linear decay measures of the first 20 seconds of a fatigue trial correlate well to measures of the full trial period, indicating that fatigue is measurable soon after load application. This suggests the feasibility of reducing testing time and patient discomfort.

One of the major problems of accurately measuring fatigue is the variability of the MVC due to subject motivation and neurogenic factors. MVC force measures, normalized for body weight, were found to correlate with slope measures obtained at 50 percent MVC, so that subjects who developed a higher force per unit body weight fatigued at a faster rate during the 50 percent trials. We are investigating the possibility of eliminating this variability by expressing the load level as a percentage of body weight, instead of MVC level. Using data obtained from normals, a strong correlation ($r \doteq 0.87$) is evident between the linear decay measure and load levels ranging from 20 to 120 percent of body weight. Pilot data suggest that it is possible to obtain frequency slope measures from patients exercising for short times at maximal effort. The slope measure is then compared to an appropriate normal data curve to find the corresponding load level that would be expected for the patient's age and gender.

Plans for future work involve acquisition of additional normal and patient data to fully test these hypotheses. Publications discussing these activities and findings in detail are in preparation■

Direct Measurement of Muscle Conduction Velocity and Fatigue in Neuromuscular Disease Patients

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The specific objectives of this project are as follows: (i) to measure action potential conduction velocities along skeletal muscles during sustained isometric contraction leading to fatigue, (ii) to measure the power spectrum changes of the electromyogram that occurs during a fatiguing contraction, and (iii) to correlate the conduction velocity measurements with those of the power spectrum. The above measurements will be performed in normal individuals and in subjects afflicted with neuromuscular disease.

As part of this project, a noninvasive procedure will be developed to measure muscle conduction velocity continuous with time. The procedure involves the placement of two sets of wire electrodes over the biceps brachii muscle and recording the electrical activity during a strong contraction. A minicomputer will compute and plot the velocities, as well as the mean frequency of the power spectrum as a function of time, during the course of the contraction. These analyses will be performed for at least two different intensities of contraction in each subject.

Twenty normal adult individuals, male and female, and approximately 20 patients with signs of myopathic disease will be tested■

Origin of Limb Position and Movement Signals in Humans

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Sponsor: National Institutes of Health
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This project will study how the senses of static limb position and limb movement originate from sensory receptors in skin, joint, and muscle in humans. The tests use matching one limb or digit to another, and detecting movements or misalignments. To distinguish movement sense from position sense, we measure how rate of movement alters subjects' ability to sense displacements. Using healthy adult volunteers, we first establish baseline performance levels, then selectively eliminate sensory inputs from skin, muscle, or joint and measure the resulting deficit, if any. Some tests will use patients having a complete rupture of the Achilles tendon to check the validity of our nerve block experiments.

Our goal remains to test the hypothesis that muscle spindles provide the necessary and sufficient sensory input for position sense, with the hand providing a possible exception. We now have clear evidence for both propositions and plan to elaborate and document our findings over this next year.

Finally, we will test the importance of gamma control of muscle spindle activity for position sense with: (i) relaxed muscles, (ii) partial (gamma) block of motor nerves, and (iii) nerve recordings from spindle afferents in humans noting changes (that reflect gamma activity) during position discriminations.

Knowing the sources of the limb-position and movement detectors, and more about coding and fusimotor control, we can then do meaningful experiments with animals■

Surface Electrode for Detecting Myoelectric Signals

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Sponsor: Liberty Mutual Insurance Company

Many aspects of muscle activity during contraction may be observed by analyzing the myoelectric signal originating from the muscle fibers. The myoelectric signal can be detected by placing metallic electrode contacts on the surface of the skin directly above the muscle. This is a noninvasive recording technique and therefore well suited for a variety of laboratory and clinical observations of muscle status. For accurate signal analysis, detection of myoelectric activity must be reliable and consistent.

Designing an electrode to record this activity is not an easy task. The amplitude of the myoelectric signal at the skin's surface is extremely small, typically less than one millivolt. External interference from power lines and fluorescent lights can easily mask or distort the desired signal. The problems can be further compounded by poor electrical contact with the detection surface due to dry or oily skin. It is common, therefore, to place electrically conducting pastes and gels between the skin and electrode.

To minimize these effects and maintain consistent results, we have developed a standard surface recording electrode which does not require the use of conducting pastes and gels. Two configurations of this pasteless electrode have been designed. One configuration consists of two signal detection surfaces formed from 3 mm diameter metallic disks spaced 1.0 cm apart, surrounded by a metallic ring which serves as an electrical ground. This version is especially suited for probing areas of myoelectric activity from large or small muscle groups. In the other configuration, the detection surfaces are formed by two parallel 1.0 cm long metallic bars spaced 1.0 cm apart. This version is useful for measuring signals related to localized muscular fatigue.

Both configurations are mounted directly on small epoxy packages containing high-impedance, low-noise differential preamplifiers. The high-impedance feature minimizes the effect of dry or oily skin. The differential preamplifier reduces the effect of unwanted electrical interference. The preamplifier also amplifies the signal and filters frequency components outside the range of interest. This process improves the signal-to-noise ratio of the system.

We have found that these surface electrodes have the mechanical and electrical stability necessary for reliable and consistent low-noise myoelectric recordings, and we now use these electrodes in all the surface myoelectric recordings in our laboratory. We hope that this standard will be adopted by other researchers■

The Myoelectric Signal Decomposition Technique

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During the past several years, we have developed a system of studying the behavior of muscle units known as motor units, which consist of individual functionally distinct groups of muscle fibers within the muscle. With this system we can extract from the muscle information which helps us to understand the nature of the control schemes that the central nervous system uses to govern muscle contractions. Our system works in three phases: (i) the data signal acquisition phase, (ii) the data preprocessing and decomposition phase, and (iii) the analysis phase. Improvements have been made this year in all these phases.

The data signal acquisition phase is managed by a computer-controlled data collection system. We have modified this system to allow monitoring and tracking of two-dimensional force trajectories. A newly constructed restraint device can measure two force vectors in a plane. The outputs of the force transducers are connected directly to an analog-to-digital converter on the minicomputer that controls the data collection. The recorded forces themselves may be displayed on a screen, or the computer may generate force trajectories and display them simultaneously with the recorded forces.

We have improved the second phase, preprocessing and decomposition, by capitalizing on the greater computing power of the VAX computer over the PDP-11/34. New features have been added to the decomposition program to make it easier to use. We now have the capability of decomposing from up to 19 simultaneously active motor units. Finally, we have added an option that handles time synchronization between records generated simultaneously from different muscles.

For the analysis phase, we have added a set of programs to allow rapid cross-correlation between motor-unit firing rates and computer storage of the cross-correlation results. A program has also been developed to analyze any instantaneous interaction between the muscle fiber activity.

Overall our improvements in the system have expanded the range of motor-control aspects that we can examine with the decomposition technique; at the same time they have increased the ease of our experiments and decreased the time for data processing.

The Common Drive Concept

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The central nervous system modulates muscle force either by varying or recruiting the number of motor units which contract, or by varying the firing rate at which they are activated to contract. Thus, when we begin to understand the strategy or strategies which the nervous system uses to control motor units and to generate and modulate the force of a muscle, two central questions arise.

1. Is there a strategy or rules which govern the process of motor unit recruitment?
2. Is there a strategy or rules which govern the behavior of firing rates of active motor units?

The first question has received considerable attention. The second question has received very limited attention since experimental procedures are so technically complex. Our decomposition technique has removed some of the technical barriers.

Our investigations into the firing rates of motor units have consistently demonstrated a universal property of firing rates: the firing rates of all concurrently active motor units are modulated in unison when viewed as a function of time or force. We have termed this property the common drive. Its existence indicates that the nervous system does not control the firing rates of motor units individually, but instead it acts uniformly on a group of motor units.

We are convinced that our observations reflect a basic physiological control scheme of the nervous system. We have seen common drive in hundreds of muscular contractions of various kinds, in over a dozen muscles in the upper and lower limbs. We have seen it in every one of two dozen subjects, including sedentary normal individuals, Olympic-caliber athletes, and accomplished pianists. Common drive appears to be a truly universal property.

Common drive is important because it demonstrates, by example, that the central nervous system (the brain and spinal cord) is not involved in supervising the details that govern the behavior of individual motor units during a contraction. By implication, the central nervous system is concerned with more gen-

eral control schemes. Several other observations made in our laboratory support this conclusion. Common drive also gives us an avenue for studying the communality of different muscles involved in a task■

The Control of Individual Muscles: Relationship Between Firing Rate and Recruitment

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Firing rate and recruitment, the two modes of motor unit control, are used differentially between contractions requiring slow versus fast rates of force production, and specific muscles employ different degrees of one or the other of the two modes. Our past experiments have documented an interplay between motor-unit recruitment and firing rates; recruitment of a new motor unit may reduce the firing rates of previously activated motor units.

We have now identified the likely pathway of action in this effect. At least partially, the pathway may involve some specific sensors within the muscle which are responsible for the stretch reflex (muscle spindle and Golgi tendon organs) and possibly some specific nerve cells in the spinal cord (Renshaw cells). The logic of this possibility is that, when a new motor unit is recruited, it cannot contribute less to the total muscle-force output than its characteristic quantal value. Thus, when the motor unit is recruited, a step increase would occur in the total output force unless simultaneously the contributions of the already active motor units are reduced, via a decrease in their firing rates.

The significance of this in terms of motor-control strategy is that a smoother output force may be achieved via peripheral nervous system circuitry, lessening the amount of detailed supervision that the central nervous system has to perform. (An article is being prepared for publication.)■

Synchronization of Motor Unit Discharges

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Synchronization is the tendency for two muscle fibers, each connected to separate nerves, to contract at the same time, or at almost the same time, more often than we would expect if the two fibers were actually contracting independently. During the past 50 years, numerous controversies have surrounded the very existence and usefulness of synchronization. Factual investigations of voluntary contractions have been limited due to limitations in detection and analysis techniques. Our decomposition technique removed some of these limitations. Having complemented this technique with an analytic technique called the conditional intensity, we can now objectively observe and measure synchronization.

We have observed synchronization between fibers within a muscle both during rapid-force, varying contractions, and during constant-force, non-fatiguing contractions. The degree of synchronization is greater during the rapid-force, varying contractions. We have not observed synchronization of fiber contractions between antagonist muscles such as flexion-extension pairs.

Several possible sources and causes of synchronization have been identified. We are now attempting to demonstrate a causal relationship between the sources and the observed phenomenon. We expect that our systematic and accurate approach will provide some explanations that have eluded us in the past■

The Control of Antagonist Muscles During Contraction

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We are working to clarify the control mechanism of antagonist muscles during initiation and continued production of force during voluntary contractions.

Using the decomposition techniques, we acquired and processed the myoelectric signal from two forearm antagonist muscles, the long flexor and the long

extensor muscles of the thumb. Our experimental procedure aimed to relate the firing-rate behavior of motor units in the two antagonist muscles under various conditions.

The experiments showed that during pure joint stiffening the two cocontracting antagonist muscles are controlled by the nervous system as if they constituted an individual muscle; this we inferred from observing that the motor units of antagonist muscles display in-phase firing-rate fluctuations. Conversely, during alternating flexion and extension contractions, the two antagonist muscles are reciprocally activated; when the firing rates of motor units in one muscle decrease, they increase in the antagonist muscle.

These results are consistent with the concept that the central nervous system has two separate control schemes of coactivation and reciprocal inhibition, and that the two schemes may be used in different ways to control the torque or stiffness of a joint. These results further support the notion that the central nervous system does not control motor units individually during a muscle contraction and imply that muscles acting on a joint may not be controlled individually. (An article is being prepared for publication.)■

The Control of Synergist Muscles During Contraction

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Synergist muscles act in concert and have an additive force contribution during a specific function. Since the body's musculature is composed of both groups, antagonist muscles and synergist muscles, it is important for us to complement our work on antagonist muscles with studies of synergist muscle control.

The muscles under study are two forearm muscles which control the extension of the wrist, the ulnar extensor muscle of the wrist, and the long radial extensor muscle of the wrist. We first had to construct a new apparatus to stabilize the forearm during contractions and to couple the hand to force transducers. We also designed methods for measuring force and for video communications with subjects. To detect, record, and analyze the muscles' signals, we used the quadripolar needle electrode described in our 1982 Activities Report and our computer-controlled system for myoelectric data acquisition, decomposition, and analysis. Initial results with three subjects show some interesting relationships to our results from experiments on antagonist muscles■

Muscle Fatigue and the Myoelectric Signal

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The frequency spectrum of the myoelectric signal detected with surface electrodes shifts toward the low-frequency end during sustained muscle contractions. High-frequency components decrease while the low-frequency components increase in amplitude. Various studies during the past two decades have searched for the cause of this frequency shift, whether it originates from the physical properties of muscle fibers such as their conduction velocity or from control properties such as firing statistics.

We investigated this question by deriving mathematical expressions for the power-density spectrum of the myoelectric signal. Separate functions expressed the individual effects of the firing statistics and of the shape of the motor-unit action potentials. Experiments and detailed data analysis were performed on sustained muscle contractions.

Our results strongly suggest that the effect of firing on the power-density spectrum of the myoelectric signal is significant, but that firing statistics alone cannot account for all of the frequency shift during sustained contractions. Therefore, both the control properties and the physical properties of muscle fibers are implicated.

A detailed review of the literature and our work suggested that the frequency shift could be monitored by tracking the median or the mean frequency. Mathematical analyses and available empirical results yield the logical explanation that a series of biochemical events, muscle architecture, physiological properties, and signal propagation properties can explain the frequency shift during sustained contractions. This explanation also supports the idea that the frequency shift can be used as an objective measure of localized muscle fatigue■

Muscle Fatigue Differences Due to Handedness and Gender

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Hand dominance offers a model, within the same subject, of lifelong endurance training in some muscles (of the dominant side) and comparatively less training in others (of the nondominant side). We exploited this model by testing the median frequency of the myoelectric signal of the muscle that controls the index finger. We tested the signal in both of the hands of 18 right- and 17 left-handed normal young subjects, 16 men and 19 women. The median frequency of the myoelectric signal, which is directly related to the intramuscular conduction velocity, was measured during constant force contractions at different maximal voluntary contraction levels.

Previous results had shown that the higher the contraction level, the faster would be the decreases in the median frequency of the myoelectric signal and in intramuscular conduction velocity. In this study, our right-handed subjects showed a significantly greater decrease in the median frequency of the nondominant-side muscle than in the dominant-side muscle. In the left-handed subjects, however, no measurable difference appeared between the median frequency of the dominant and nondominant sides.

These results suggest that the dominant-side muscle is less fatigable than the nondominant-side muscle in right-handed but not in left-handed subjects, adding support to the notion that left-handed subjects are more ambidextrous. These results also imply a possible difference in the muscle fiber composition or blood-vessel arrangement (vascularization) between comparable muscles on the two sides of right-handed subjects. (No measurable differences were found between male and female counterparts.)

One practical implication of the difference we found in right-handed subjects is that isomorphic assumptions about a right-handed individual's right or left side may lead to erroneous conclusions when one-sided injuries are being evaluated. (A manuscript is being prepared for publication.)■

The Muscle Fatigue Monitor

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Sponsor: Liberty Mutual Insurance Company

For several years we have been developing the Muscle Fatigue Monitor (MFM), a device that estimates automatically and on-line the median frequency of the myoelectric signal. The MFM will help us to obtain objective measures of localized muscle fatigue. This year we have implemented an entirely new version.

The MFM now contains two independent plug-in data channels for processing the median frequency information in fatigue measurements. The two-channel arrangement enables us to evaluate simultaneously a two-muscle system's fatigue process. To make the new data acquisition system compatible with other devices, we installed an RS-232 serial interface. This hardware allows us to write or store programs or data using the center's VAX computer system.

The new device is highly flexible. Each user may tailor the system to a particular experiment by selecting various stored programs. Preliminary software programs have been written to control the system, to sample data, and to plot results from the median-frequency channels.

We plan to generate and store more specific and detailed software in a program library on the VAX. Plans are in progress to expand the scope of the MFM data acquisition system to include plug-in hardware modules for measuring the conduction velocity of a muscle and the range of motion of a subject's limb. With these new modules, the system will be able to monitor and record data from more complex muscle fatigue experiments. (A detailed description appears in our paper, "Muscle Fatigue Monitor (MFM): Second Generation," which has been submitted for publication.)■

The Estimation of Muscle Fiber Conduction Velocity

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Average conduction velocity has been conventionally measured by cross-correlating two surface waveforms obtained from different locations along the muscle. This conventional technique uses a configuration of these spatially distinct electrode sites on the muscle surface which in turn yield two differential sources.

In our experiments, however, we ascertained that this configuration still gave erroneous conduction velocity values from some muscles. Some of the cross-correlated signals exibited almost a zero time delay, probably due to the fact that muscles are electrically nonhomogenous and signals do not exhibit the same time delay on different axes. To overcome this problem, we added a fourth electrode and inserted another layer of differential amplifiers in the recording arrangement. The new technique correctly estimated the average conduction velocity in all subjects tested.

We are now constructing a device to implement our innovative method. Prototype circuitry has been fabricated, using the 4-electrode configuration. The device will compare the two output signals using cross-correlation and will then compute the conduction velocity of the muscle fibers. Once refined, the circuitry will be incorporated into a new channel in the new MFM data acquisition system. With the existing median-frequency measurement channels and the new muscle fiber conduction velocity channel, we will be able to compare directly each method of fatigue measurement. We expect that these two noninvasive methods will improve the objective assessment of localized muscular fatigue■