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# Magnetic resonance imaging and electromyography as indexes of muscle function

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ADAMS, GREGORY R., MARC R. DUVOISIN, AND GARY A. DUDLEY. *Magnetic resonance imaging and electromyography as indexes of muscle function*. *J. Appl. Physiol.* 73(4): 1578–1583, 1992.—Electromyography (EMG) is commonly used to determine the electrical activity of skeletal muscle during contraction. To date, independent verification of the relationship between muscle use and EMG has not been provided. It has recently been shown that relaxation- (e.g.,  $T_2$ ) weighted magnetic resonance images (MRI) of skeletal muscle demonstrate exercise-induced contrast enhancement that is graded with exercise intensity. This study was conducted to test the hypothesis that exercise-induced magnetic resonance (MR) contrast shifts would relate to EMG amplitude if both measures reflect muscle use during exercise. Both MRI and EMG data were collected for separate eccentric (ECC) and concentric (CON) exercise of increasing intensity to take advantage of the fact that the rate of increase and amplitude of EMG activity are markedly greater for CON muscle actions. Seven subjects  $30 \pm 2$  (SE) yr old performed five sets of 10 CON or ECC arm curls with each of four resistances representing 40, 60, 80, and 100% of their 10 repetition maximum for CON curls. There was 1.5 min between sets and 30 min between bouts (5 sets of 10 actions at each relative resistance). Multiple echo, transaxial  $T_2$ -weighted MR images (1.5 T, TR/TE 2,000/30) were collected from a 7-cm region in the middle of the arm before exercise and immediately after each bout. Surface EMG signals were collected from both heads of the biceps brachii and the long head of the triceps brachii muscles. CON and ECC actions resulted in increased integrated EMG (IEMG) and  $T_2$  values that were strongly related ( $r = 0.99$ ,  $P < 0.05$ ) with relative resistance. The rate of increase and absolute value of both  $T_2$  and IEMG were greater for CON than for ECC actions. IEMG and  $T_2$  for both CON and ECC actions were correlated ( $r = 0.99$ ,  $P < 0.05$ ). The results suggest that 1) surface IEMG accurately reflects the contractile behavior of muscle and 2) exercise-induced increases in MRI  $T_2$  values reflect some processes that scale with muscle use.

muscle function

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MAGNETIC RESONANCE SPECTROSCOPY (MRS) has become an accepted tool for in vivo biochemical studies of muscle tissue. Magnetic resonance (MR) imaging (MRI) is a variant of this methodology that is rapidly becoming the standard for many clinical diagnostic applications because it provides unparalleled visualization of anatomic detail of soft tissues such as muscle, tendon, cartilage, and various organs. MRI has also begun to be used in basic muscle research. For example, MR images of skeletal muscle show exercise-induced contrast enhance-

ment, which appears to be graded with exercise intensity (7). This has been used to infer which muscles were used during the activity and the extent of their contribution.

Electromyography (EMG) has long been the noninvasive method of choice for analyses of muscle activation during exercise (2). It entails sampling electrical activity from a muscle region of interest with needle or surface electrodes. There is good relation between EMG amplitude and force development for a variety of types of voluntary muscle actions, suggesting that increases in force necessitate greater muscle use. This suggestion, however, has not been independently verified.

It has long been known that EMG responses differ markedly between concentric and eccentric exercise. Although EMG activity is strongly related to work rate for both eccentric and concentric actions, EMG amplitude is much less for eccentric actions (1, 3, 18, 21). This study exploited these well-established observations to test the following hypotheses: 1) contrast shifts in MR images will be linearly related to exercise intensity if the changes relate to the extent of muscle use, 2) the magnitude of these shifts will be greater for concentric than for eccentric actions over a range of exercise intensities, because less muscle is used during eccentric actions, and 3) contrast shifts in MR images will correspond to EMG amplitude if both measures reflect muscle use during exercise. The results support all three hypotheses, suggesting that shifts in MRI contrast after exercise are an excellent measure of muscle use.

## METHODS

*Subjects.* Seven subjects (6 males and 1 female) participated in the study. Their age, height, and weight averaged  $30 \pm 2$  yr,  $178 \pm 4$  cm, and  $81 \pm 6$  (SE) kg, respectively. All were familiar with upper body resistance exercise. The procedures, purpose, and risks associated with the study were explained, and written consent was provided. The study was approved by the Human Research Review Board at the Kennedy Space Center, FL.

*Exercise protocol.* The maximum amount of resistance with which each subject could perform 10 unilateral concentric “dumbbell curls,” flexion of the forearm about the elbow joint, in the standing position was determined ~1 wk before data collection. On the test day, subjects performed five sets of 10 concentric or eccentric unilateral actions at four different resistances of increasing magnitude: 40, 60, 80, and 100% of the 10 repetition max-

TABLE 1. Exercise protocol for standing unilateral dumbbell curls

Regimen	Arm	
	Left	Right
Muscle action	Eccentric	Concentric
Relative resistance	40% Con 10 RM	40% Con 10 RM
Rest	30 min	30 min
Relative resistance	60% Con 10 RM	60% Con 10 RM
Rest	30 min	30 min
Relative resistance	80% Con 10 RM	80% Con 10 RM
Rest	30 min	30 min
Relative resistance	100% Con 10 RM	100% Con 10 RM

Five sets of 10 actions were performed at each relative resistance, with 1.5 min of rest between sets. Exercise session started with eccentric actions performed with left or right arm. In this example, the left arm was used for eccentric muscle actions, the right for concentric (Con) actions. RM, repetition maximum.

imum (RM) for concentric curls (Table 1). Each subject started the exercise session by performing five sets of 10 eccentric actions with the left or right forearm flexors at the lightest resistance. After MR images of the "exercised" arm (see below), concentric curls with the same resistance were performed with the opposite arm. These were repeated until the four different resistances had been used. There was 1.5 min of rest between sets and 30 min between eccentric or concentric actions with a given resistance. Exercise conditioning that emphasized use of the forearm flexors was precluded for the 3 days immediately before data collection to ensure optimal performance. The prescribed exercise bouts were completed by all but two subjects, who performed 5 to 7, instead of 10, concentric actions for each of the last two sets at the heaviest relative resistance, 100% of the concentric 10 RM.

Eccentric actions were performed by lowering a dumbbell from the fully flexed to fully extended position of the forearm. An investigator raised the resistance for the subject between actions. Subjects raised the dumbbell from the fully extended to the fully flexed position for each concentric action, while an investigator lowered it between actions. Subjects were encouraged to hold proper form and to maintain the same cadence for all actions. Exercise was stopped if this was not the case.

**MRI.** Subjects were imaged before exercise and immediately ( $2.3 \pm 0.1$  min) after performance of five sets of 10 eccentric or concentric actions at each relative resistance. Transaxial MR images were acquired at a field strength of 1.5 T using a Signa (General Electric, Milwaukee, WI) imaging system.  $T_2$ -weighted images (TR/TE 2000/30, 60, 90, 120) were collected using a 25-cm-diam extremity coil. A  $256 \times 128$  matrix was acquired with one excitation and a 20-cm field of view; total collection time was 5 min 12 s. Five 10-mm slices were collected at 5-mm intervals, with the third cross section in the middle of the forearm flexors. This resulted in a sampling region that spanned 7 cm along the length of the arm. Ink marks on the arm and forearm along with the cross hairs of the imager were used to ensure a similar elbow joint angle and position of the arm in the magnet bore over repeated MR images. Successive MR collec-

tions were spaced  $\geq 30$  min apart to allow recovery of  $T_2$  in previously exercised muscle (7).

$T_2$  calculations were performed using the software routines on the Signa system.  $T_2$  values were determined for ten 1-cm<sup>2</sup> regions of the biceps brachii muscle, five in the triceps brachii muscle, and one in the bone marrow on each slice. MR image files were ported to a personal computer for calculation of muscle cross-sectional area (CSA) by use of a modified version of the Image software package (Research Services Branch, National Institutes of Mental Health).

**EMG.** EMG electrodes were placed over the midbelly of the long head and short head of the biceps brachii muscle and the long head of the triceps brachii muscle. Electrode sites were prepared using a razor, sandpaper, and alcohol. The EMG equipment and techniques used have been described previously (6).

A potentiometric goniometer was attached to the lateral aspects of the arm and forearm, and the axis of rotation was "aligned" with that of the elbow. The signal from the potentiometer was calibrated with the elbow joint at 90° to provide a measure of range of motion during exercise. The elbow joint angle with relaxed full extension was  $\sim 30^\circ$ , whereas full flexion with minimal effort gave an angle of  $\sim 160^\circ$ .

Signals from the three EMG sensor units and the potentiometer were digitized in real time at a rate of 1,000 samples/s with a personal computer. The signal from the potentiometer was used to trigger 1 s of data acquisition. The trigger point was set 10° from relaxed full extension for concentric actions and 10° from full flexion for eccentric actions. The integrated root mean squared EMG (IEMG) was determined by taking the 1-s integral of the EMG and multiplying by the square root of 2. Data were obtained for the first and last set of eccentric or concentric actions at each relative resistance. Data for the two sets were averaged to provide a cumulative index of EMG activity.

**Statistics.**  $T_2$ , CSA, and EMG data were each compared over the four different exercise intensities with use of a two-way analysis of variance (muscle action type by resistance) with repeated measures over subjects. Simple regression analysis was used to examine relationships among variables. Correlations between variables ( $T_2$  vs. CSA,  $T_2$  vs. EMG) were assessed by determining Pearson's product  $r$  values. The level of significance was set at  $P < 0.05$ .

## RESULTS

The range of motion about the elbow joint for EMG data collection was  $52 \pm 2^\circ$  to  $141 \pm 2^\circ$  for concentric actions and  $153 \pm 4^\circ$  to  $61 \pm 3^\circ$  for eccentric actions. The average angular velocities over these movement arcs were  $89^\circ/\text{s}$  and  $92^\circ/\text{s}$ , respectively. IEMG activity of the two heads of the biceps brachii muscle was similar during exercise (data not shown); thus the values were averaged for subsequent analyses.

IEMG activity of the biceps brachii muscle was markedly less ( $P < 0.05$ ) for eccentric than for concentric actions at any given exercise intensity (Fig. 1). It increased ( $P < 0.05$ ) as a function of relative resistance for both

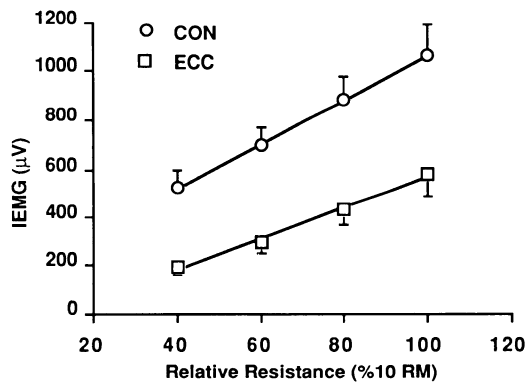


FIG. 1. Average integrated root mean squared electromyogram (IEMG) activity of the long and short heads of biceps brachii muscle for 5 sets of 10 unilateral concentric (CON) or eccentric (ECC) actions of forearm flexors. Values are means  $\pm$  SE, recorded for 1st and last sets, when 6 subjects performed against a relative resistance of 40, 60, 80, and 100% of 10 repetition maximum (10 RM) for concentric curls. IEMG data were lost for 7th subject because of technical problems. IEMG was related to relative resistance for concentric ( $IEMG = 9.07 \times \%10 RM + 159, r = 0.99, P < 0.05$ ) and eccentric ( $IEMG = 6.42 \times \%10 RM - 73.4, r = 0.99, P < 0.05$ ) actions.

types of actions, with the rate somewhat greater ( $P < 0.05$ ) for concentric actions. The triceps brachii muscle showed minimal, if any, increases in IEMG activity with exercise (data not shown).

The relationship between relative resistance and  $T_2$  of the biceps brachii muscle was similar for each transaxial MR image (Fig. 2).  $T_2$  changes were also uniform across the 10 regions sampled in each image of the biceps brachii muscle (data not shown). Values for the 10 regions within each slice, and subsequently the individual slices, were therefore averaged for analyses of  $T_2$  responses to exercise.

Concentric actions resulted in an increase ( $P < 0.05$ ) in the biceps brachii  $T_2$  that was strongly related to and graded with relative resistance (Fig. 3). Eccentric actions induced a smaller ( $P < 0.05$ ) but significant increase in

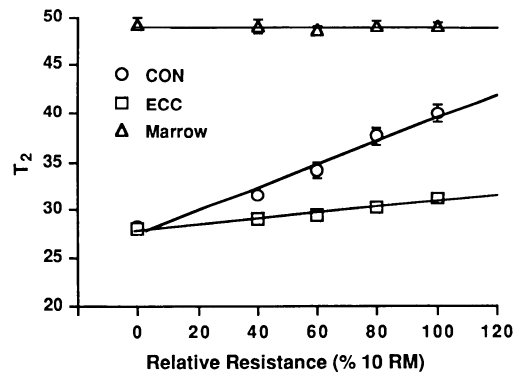


FIG. 3. Average  $T_2$  (means  $\pm$  SE;  $n = 7$ ) of bone marrow of humerus and biceps brachii at rest and immediately after CON or ECC actions performed with forearm flexors.  $T_2$  of bone did not change ( $P > 0.05$ ) over repeat measures.  $T_2$  of biceps brachii was related to relative resistance for CON ( $T_2 = 0.12 \times \%10 RM + 27.5, r = 0.99, P < 0.05$ ) or ECC ( $T_2 = 0.03 \times \%10 RM + 27.8, r = 0.99, P < 0.05$ ) actions. See Fig. 1 and METHODS for more detail.

the biceps brachii  $T_2$  that was also related to relative exercise intensity. Over the course of the experiment,  $T_2$  of bone (Fig. 3) and triceps brachii did not change ( $P > 0.05$ ). The triceps brachii data have been omitted for clarity.

The biceps brachii  $T_2$  and IEMG were correlated for both concentric and eccentric actions when the same relative resistance was used by different subjects during exercise (Fig. 4).

DISCUSSION

MRS has added significantly to our understanding of muscle metabolism. In recent years this technology has been used to conduct in vivo studies on exercising human muscle. Technical considerations (e.g., presence of a magnetic field, magnet bore size) have limited the types of exercise used. Early studies used bulb squeezing to increase metabolic demand because the forearm would fit in the magnet bore (15). It was assumed that different subjects performed the exercise consistently (i.e., similar patterns of muscle recruitment) for the muscle groups sampled. This assumption may not have been valid, thereby confounding interpretation of the metabolic data (15, 31).

EMG data collection requires assumptions similar to

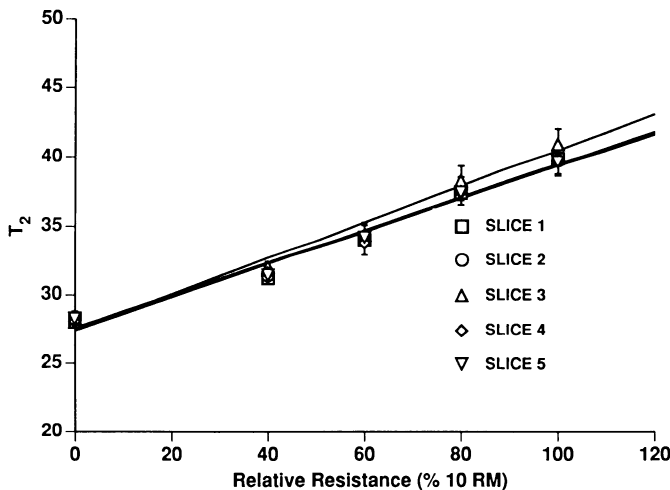


FIG. 2.  $T_2$  values (means  $\pm$  SE,  $n = 7$ ) of biceps brachii muscle in 5 different transaxial magnetic resonance (MR) images obtained through midbelly of arm. Values were obtained at rest and immediately after concentric curls.  $T_2$  was not different among slices ( $P > 0.05$ ). Overall, it was related to relative resistance ( $T_2 = 0.12 \times \%10 RM + 27.4, r = 0.99, P < 0.05$ ). See METHODS and Fig. 1 for more detail on MR images and exercise protocol.

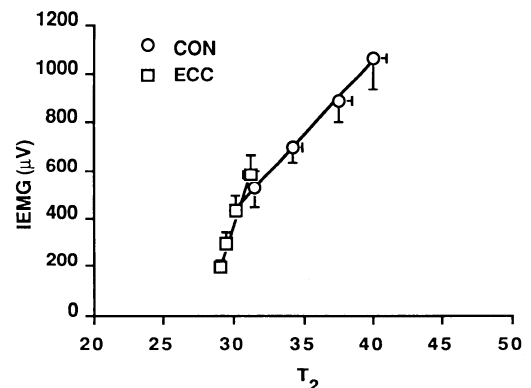


FIG. 4. IEMG during CON or ECC actions of forearm flexors plotted against  $T_2$  of biceps brachii obtained immediately after exercise (means  $\pm$  SE;  $n = 6, r = 0.99, P < 0.05$ ). See METHODS and Fig. 1 for more detail.

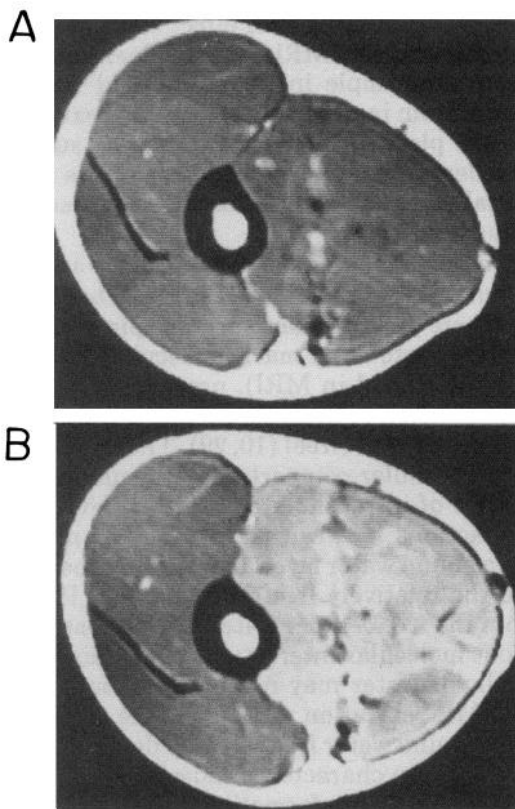


FIG. 5. Representative  $T_2$ -weighted images of arm, demonstrating contrast in forearm flexors before (Control, A) and after (100%, B) 5 sets of 10 concentric curls with resistance equal to 100% of CON 10 RM.

those made in early *in vivo* MRS studies. Surface EMG collections sample a relatively small region of a few muscles, and it is virtually impossible to sense all the muscles of interest and/or limit cross talk. Thus uniform activation of muscle outside the range of the electrodes or of unsensored muscle is often assumed.

Recent observations suggest that exercise induces an enhancement of MRI contrast between inactive and previously active muscles (Fig. 5) (7, 9). This effect has been used to guide MRS coil placement for studies of muscle metabolism (8, 14, 30, 31). In the present study, we sought to compare MRI measures of activated muscle with values obtained using EMG. Although EMG values have been used to assess the extent of muscle activation, no previous studies have independently validated this assumption.

The results of the present study show that IEMG activity of the biceps brachii increases as a function of the relative resistance used during concentric or eccentric actions of the forearm flexors (Fig. 1). The rate of increase, as well as the absolute IEMG, was found to be greater for concentric than eccentric actions. Similar results during submaximal cycle ergometry (1, 3), leg press exercise on a sledge (18), and forearm curls (21) have been reported. The increase in IEMG with exercise intensity has been suggested to reflect increased motor unit recruitment, because increasing firing frequency of already active units has minimal effect on IEMG (2). The suggestion that less skeletal muscle recruitment is needed for eccentric than for concentric actions to coun-

teract the same resistance is believed to reflect the inherent ability of skeletal muscle to develop greater force during eccentric actions (16). The ratio of the IEMG to relative force for concentric vs. eccentric actions of the forearm flexors in the present study was  $\sim 1.5$  (Fig. 1). This suggests that the *in vivo* force-generating ability of the forearm flexors is  $\sim 50\%$  greater for eccentric than for concentric actions performed at an angular velocity of  $\sim 90^\circ/\text{s}$ . This seems reasonable if the forearm flexors present an *in vivo* speed-torque relationship similar to that of the knee extensors. Force output by the knee extensors is  $\sim 50\%$  greater for eccentric than for concentric actions at  $90^\circ/\text{s}$  (4).

The shifts in  $T_2$ -weighted MR images on the biceps brachii after exercise in the present study showed remarkable correspondence to the IEMG data obtained from the same muscle.  $T_2$  increased as a function of relative resistance when either concentric or eccentric actions were performed (Fig. 3). The range of motion, speed of movement, resistance, and therefore work rate were the same for both types of actions. The rate of  $T_2$  increase, however, was markedly greater for concentric actions. Therefore, the concept that the magnitude of increase in  $T_2$  after exercise is dependent on work rate per se is not supported by our results (7). A similar notion has recently been put forth by Shellock et al. (26), who found greater increases in  $T_2$  of the forearm flexors after subjects performed a bout of concentric actions to failure than when the same exercise was performed using eccentric actions.

$T_2$  and IEMG of the biceps brachii were correlated in the present study for both concentric and eccentric actions (Fig. 4). Two independent measures of muscle use therefore support the validity of one another. These results indicate that  $T_2$  shifts after exercise reflect some aspect of muscle activation. Bigland-Ritchie and Woods (3) showed that the ratio of the EMG to torque for concentric vs. eccentric submaximal cycle exercise at 50 rpm was  $\sim 2$ . The ratio relating energy cost of exercise to torque for concentric vs. eccentric cycling was  $\sim 6$ . The finding that energy cost increased at a greater rate than EMG activity as a function of concentric vs. eccentric cycling intensity was interpreted to indicate not only less motor unit activation during eccentric cycling but also less energy demand per unit force development for eccentric exercise (3, 5, 18). If a similar analogy can be made from the  $T_2$  and EMG data in the present study, the results suggest that  $T_2$  changes are somewhat but not completely related to the metabolic response to exercise. The ratio of the IEMG to torque for concentric vs. eccentric actions found in the present study was  $\sim 1.5$ , whereas the rate of increase in  $T_2$  as a function of resistance was about four times as great for concentric actions. The latter ratio would have been much greater if the metabolic response to exercise had been responsible for the  $T_2$  changes, because it was recently shown that seven times more energy is required to raise than to lower a given load during resistance exercise performed in a fashion similar to that in the present study (5).

The molecular mechanisms resulting in exercise-induced MRI contrast enhancement have yet to be established. MR signals are generated by placing samples in a

powerful static magnetic field and then pulsing them with radio-frequency energy. Susceptible nuclei will be boosted to a higher energy state, producing a detectable signal. The signal declines over time via two concurrent processes described as "relaxation."  $T_1$  relaxation involves the loss of energy to surrounding nuclei with similar resonant frequencies.  $T_2$  relaxation results from interactions between the excited nuclei and any perturbing magnetic fields with no transfer of energy. The nondiscriminatory nature of  $T_2$  relaxation mechanisms greatly increases the probability of such interactions; thus  $T_2$  tends to be much shorter than  $T_1$  in heterogeneous solutions.

Contrast in MR images depends primarily on nuclear density (i.e., the number of rotational free protons) of the tissue imaged. Bone, fat, muscle, connective tissue, blood, and various organs have different proton nuclear density. However, alterations in relaxation processes, and thereby  $T_1$  and  $T_2$ , can have a significant impact on the final image produced. As seen in this and other studies, images of skeletal muscle collected after bouts of exercise demonstrate an enhancement of contrast between the active and nonactive muscle groups that appears to be graded with exercise intensity (7). This change in proton signal intensity causes exercised muscles to appear to "light up" in  $T_2$ -weighted images (Fig. 5). Chronic exercise conditioning may also alter MR image contrast.  $T_2$  has been shown to vary between trained and untrained subjects (19, 22) and to correlate with fiber type in resting human and rabbit muscle (20, 23).

These changes in  $T_2$  result from the dependence of relaxation on the local molecular environment of the nuclei under study (10, 17). The signals used to produce the MR images in this study arise from the protons of either water or lipid. As evidenced by the bone marrow  $T_2$ , no gross changes in lipid signals were evident. Assuming that these acute bouts of exercise did not cause substantial changes in intramuscular fat, it is reasonable to conclude that the signal changes must arise from one or more of the water compartments in muscle. Polak et al. (23) demonstrated that differences between resting  $T_2$  values for rabbit soleus and gastrocnemius muscles are related to the size of their extracellular fluid spaces. Increased perfusion would therefore seem to be an obvious agent causing exercise-induced MR changes. The volume of exercising muscle is known to increase as a result of a redistribution of body water. In the present study, average CSA of the forearm flexors increased 18% ( $P < 0.05$ ) after five sets of 10 concentric curls were performed with the heaviest resistance. This redistribution can be attributed to increased perfusion and the production and translocation of ionic species, which would alter the osmotic behavior of muscle cells (24, 25). Low-intensity exercise is believed to be associated with an increase in extracellular water, whereas high-intensity exercise is primarily associated with a change in intracellular water (27, 28). Changes in either intra- or extracellular water would be expected to alter the relaxation characteristics of the excited nuclei in a muscle sample (10). However, Fisher et al. (7) found that muscle volume changes similar in magnitude to those seen with exercise, but elicited

by venous occlusion, had little effect on  $T_2$ . Hence exercise-induced enhanced MRI contrast does not appear to result from the simple increases in fluid volume that would result from increased perfusion and extravascular movement of plasma water. These findings suggest that more complex, probably intracellular, events may be at least partially responsible for exercise-induced contrast enhancement.

The  $T_2$  of muscle cytoplasm is reduced  $\sim 40$ -fold from that of similar electrolyte solutions (13). It has been theorized that there are three basic proton spin groups within cells: organic protons on macromolecules (which would not contribute signal in MRI), protons of water within the hydration shell of macromolecules (bound), and the protons of bulk water (free) (10, 29). These fractions also exist in extracellular compartment of muscle (10). The MR behavior of intracellular water is believed to result from interactions between the surface of macromolecules and a bound water layer and exchange between this layer and the relatively free cellular water. Proton motion within the free cellular water is itself fast enough to average out molecular interactions; thus this large fraction of cellular water may not be contributing proportionally to MR relaxation processes. The smaller slowly exchanging bound water fraction may determine much of the MR relaxation character of muscle cells. Muscle cell contraction involves conformational changes in the large contractile proteins as well as mechanical alterations in intracellular surfaces (11). Such surface alterations may affect the bound water layer, which in turn may determine MR relaxation (10). In addition to alterations in the size, shape, and charge of surfaces in muscle cells, contraction involves the production and/or translocation of ions and metabolites. These processes would have osmotic effects that alter the concentration of water as well as direct effects on the MR relaxation of water; e.g.,  $T_2$  was shown to increase as pH was lowered (12).

In all probability, exercise-induced changes in MR images result from some complex combination of all the above processes. Whatever the mechanism, the results of this study indicate a correspondence between IEMG activity and contrast shifts in proton-weighted MR images for assessing work-related muscle activity. The validity of both techniques is thus supported. Each modality possesses attributes and capabilities that ensure their continued contribution to our understanding of muscle contraction. In addition to providing a value that appears to scale with exercise intensity ( $T_2$ ), MRI can provide anatomic information such as muscle CSA. EMG is useful for acute observations of motor unit activation in both small and large muscle groups in real time.

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#### REFERENCES

1. ABBOTT, B. C., B. BIGLAND, AND J. M. RITCHIE. The physiological cost of negative work. *J. Physiol. Lond.* 117: 380-390, 1952.
2. BASMAJIAN, J. V., AND C. J. DELUCA. *Muscles Alive*. Baltimore, MD: Williams & Wilkins, 1985.
3. BIGLAND-RICHIE, B., AND J. J. WOODS. Integrated electromyogram and oxygen uptake during positive and negative work. *J. Physiol. Lond.* 260: 267-277, 1976.
4. DUDLEY, G. A., R. T. HARRIS, M. R. DUVOISIN, B. M. HATHER, AND P. BUCHANAN. Effect of voluntary vs. artificial activation on the relation of muscle torque to speed. *J. Appl. Physiol.* 69: 2115-2221, 1990.
5. DUDLEY, G. A., P. A. TESCH, R. T. HARRIS, C. L. GOLDEN, AND P. BUCHANAN. Influence of eccentric actions on the metabolic cost of resistance exercise. *Aviat. Space Environ. Med.* 62: 678-682, 1991.
6. DUVOISIN, M. R. Development of an ambulatory electromyography (EMG) monitoring system. *Proc. IEEE Trans. Biomed. Eng.* 12: 64-68, 1990.
7. FISHER, M. J., R. A. MEYER, G. R. ADAMS, J. M. FOLEY, AND E. J. POTCHEN. Direct relationship between proton T<sub>2</sub> and exercise intensity in skeletal muscle MR images. *Invest. Radiol.* 25: 480-485, 1990.
8. FLECKENSTEIN, J. L., L. A. BERTOCCI, R. L. NUNNALLY, R. W. PARKEY, AND R. PESHOCK. Exercise-enhanced MR imaging of variations in forearm muscle anatomy and use: importance in MR spectroscopy. *Am. J. Radiol.* 153: 693-698, 1989.
9. FLECKENSTEIN, J. L., R. C. CANBY, R. W. PARKEY, AND R. M. PESHOCK. Acute effects of exercise on MR imaging of skeletal muscle in normal volunteer. *Am. J. Radiol.* 151: 231-237, 1988.
10. FULLERTON, G. D., J. L. POTTER, AND N. C. DORNBLUTH. NMR relaxation of protons in tissues and other macromolecular water solutions. *Magn. Reson. Imaging* 1: 209-228, 1982.
11. FUNG, B. M. Carbon-13 and proton magnetic resonance of mouse muscle. *Biophys. J.* 19: 315-319, 1977.
12. FUNG, B. M., AND P. S. PUON. Nuclear magnetic resonance transverse relaxation in muscle water. *Biophys. J.* 33: 27-38, 1981.
13. HAZLEWOOD, C. F., D. C. CHANG, B. L. NICHOLS, AND D. E. WOESSNER. Nuclear magnetic resonance transverse relaxation times of water protons in skeletal muscle. *Biophys. J.* 14: 583-606, 1974.
14. JENESON, J., M. W. WESSELING, R. W. BOER, AND H. G. AMELINK. Peak-splitting of inorganic phosphate during exercise: anatomy or physiology? A MRI-guided <sup>31</sup>P-MRS study of human forearm muscle. Works in progress (Abstract). *Soc. Magn. Reson. Med.* 1: 1030, 1989.
15. JENESON, J. A. L., J. S. TAYLOR, D. B. VIGNERON, T. S. WILLARD, W. L. CARVAJAL, S. J. NELSON, J. MURPHY-BOESCH, AND T. R. BROWN. <sup>1</sup>H MR imaging of anatomical compartments within the finger flexor muscles of the human forearm. *Magn. Reson. Med.* 15: 491-496, 1990.
16. KATZ, B. The relation between force and speed in muscular contraction. *J. Physiol. Lond.* 96: 45-64, 1939.
17. KOENIG, S. H., AND R. D. BROWN. The importance of the motion of water for magnetic resonance imaging. *Invest. Radiol.* 20: 297-305, 1985.
18. KOMI, P. V., M. KANEKO, AND O. AURA. EMG activity of the leg extensor muscles with special reference to mechanical efficiency in concentric and eccentric exercise. *Int. J. Sports Med.* 8: 22-29, 1987.
19. KUNO, S., S. KATSUTA, M. AKISADA, I. ANNO, AND K. MATSUMOTO. Effect of strength training on the relationship between magnetic resonance relaxation time and muscle fiber composition. *Eur. J. Appl. Physiol. Occup. Physiol.* 61: 33-36, 1990.
20. KUNO, S., S. KATSUTA, T. INOUE, I. ANNO, K. MATSUMOTO, AND M. AKISADA. Relationship between MR relaxation time and muscle fiber composition. *Radiology* 169: 576-588, 1988.
21. MORITANI, T., S. MURAMATSU, AND M. MURO. Activity of motor units during concentric and eccentric contractions. *Am. J. Phys. Med.* 66: 338-350, 1988.
22. NEDERVEEN, D., J. A. L. JENESON, C. J. G. BAKKER, AND W. B. M. ERICH. MR imaging of skeletal muscle of the forearm after hand-grip exercise: a method to differentiate between trained and untrained muscles (Abstract). *Soc. Magn. Reson. Med.* 2: 710, 1989.
23. POLAK, J. F., F. A. JOLESZ, AND D. F. ADAMS. NMR of skeletal muscle differences in relaxation parameters related to extracellular/intracellular fluid spaces. *Invest. Radiol.* 23: 107-112, 1988.
24. ROWELL, L. B. Muscle blood flow in humans: how high can it go? *Med. Sci. Sports Exercise* 20: S97-S103, 1988.
25. SALTIN, B., G. SJØGAARD, F. A. GAFFNEY, AND L. B. ROWELL. Potassium, lactate, and water fluxes in human quadriceps muscle during static contractions. *Circ. Res.* 48, Suppl. 1: I18-I24, 1981.
26. SHELOCK, F. G., T. FUKUNAGA, J. H. MINK, AND V. R. EDGERTON. Acute effects of exercise on MR imaging of skeletal muscle. *Am. J. Roentgenol. Radium Ther. Nucl. Med.* 156: 765-768, 1991.
27. SJØGAARD, G., R. P. ADAMS, AND B. SALTIN. Water and ion shifts in skeletal muscle of humans with intense dynamic knee extension. *Am. J. Physiol.* 248 (Regulatory Integrative Comp. Physiol. 17): R190-R196, 1985.
28. SJØGAARD, G., AND B. SALTIN. Extra- and intracellular water spaces in muscles of man at rest and with dynamic exercise. *Am. J. Physiol.* 243 (Regulatory Integrative Comp. Physiol. 12): R271-R280, 1982.
29. SOBOL, W. T., I. G. CAMERON, W. R. INCH, AND M. M. PINTAR. Modeling of proton spin relaxation in muscle tissue using nuclear magnetic resonance spin grouping and exchange analysis. *Biophys. J.* 50: 181-191, 1986.
30. VOCK, P., H. HOPPELER, W. HARTL, AND P. FRITSCHY. Combined use of magnetic resonance imaging (MRI) and spectroscopy (MRS) by whole body magnets in studying skeletal muscle morphology and metabolism. *Invest. Radiol.* 20: 486-491, 1985.
31. WEIDMAN, E. R., H. C. CHARLES, R. NEGRO-VILAR, M. J. SULLIVAN, AND J. R. MACFALL. Muscle activity localization with <sup>31</sup>P spectroscopy and calculated T<sub>2</sub>-weighted <sup>1</sup>H images. *Invest. Radiol.* 26: 309-316, 1991.