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MYOSIN HEAVY CHAIN ISOFORM EXPRESSION: INFLUENCE ON ISOINERTIAL AND ISOMETRIC PERFORMANCE

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Thirty-six healthy men with varying degrees of physical training background performed maximal-effort isometric and isoinertial knee extensor actions, with relative loads equal to 40% and 70% of one-repetition maximum. Force, velocity, and power were derived from force and linear position transducers at 500 Hz. Biopsies were taken from the vastus lateralis and analyzed by SDS-PAGE for relative myosin heavy chain (MHC) content. Relative MHC IIx content was included in a regression model, and explained variance noted. Relative MHC I content was subsequently added to the regression model to determine what, if any, additional variance was explained beyond that of MHC IIx. Results indicated that no relationship (r = 0.0 to 0.1) exists between the relative expression of MHC isoforms from the vastus lateralis and isometric/isoinertial performance in a population with diverse training backgrounds. Lack of nervous system adaptations in the untrained subjects in the study possibly

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attenuates the significant relationship between MHC and in-vivo muscle performance previously established in trained populations.

Keywords: myosin heavy chain, correlation, muscle performance

INTRODUCTION

Isoforms of myosin heavy chain, a contractile protein in skeletal muscle (205 kDa), have been shown to be highly related to in-vitro (Bottinelli, Pellegrino, Canepari, et al., 1999) as well as in-vivo (Fry, Schilling, Staron, et al., 2003; Fry Webber, Weiss, et al., 2003; Schilling, Fry, Chiu, et al. 2005) muscle performance. Adult human skeletal muscle commonly contains three isoforms of MHC represented as MHC I, MHC IIa, and MHC IIx. Fibers can be classified by their MHC isoforms that are isolated via SDS-PAGE. Fiber types also can be derived by adenosine triphosphatase (mATPase) histochemical staining. The relative expression of MHC from mixed-fiber samples correlates well ($r > 0.90$) with mATPase histochemical stained relative fiber type area determinations, indicating these are quasi-redundant measures of fiber characteristics (Fry, Allemeier, and Staron 1994; Klitgaard, Mantoni, Schaiffino, et al. 1990). The relationships noted in-vitro have prompted scientists to examine the MHC or mATPase profile of a sample containing multiple fibers from various muscle groups. These data have been helpful in providing descriptive data on various athletic and diseased populations, and attempts have been made to correlate the fiber morphology of mixed-fiber samples to strength tasks that utilize the sampled muscle group. The aim of this investigation was to use block-entry regression (Schilling, Fry, Chiu, et al., 2005) to demonstrate the amount of variance in maximal voluntary isoinertial and isometric knee extensor performances that can be explained by relative MHC isoform expression.

Muscle protein morphology is somewhat plastic, and training status has a considerable influence on relative expression of MHC IIx (Harber, Fry, Rubin, et al. 2004; Liu, Schlumberger, Wirth, et al. 2003). Significant decreases in MHC IIx have been shown in as little as 2–6 weeks with resistance training (Liu, Schlumberger, Wirth, et al. 2003; Staron, Karapondo, Kraemer, et al. 1994). Although some studies show significant decreases in MHC I in less than 10 weeks (Kadi and Thornell 1999; Liu, Schlumberger, Wirth, et al. 2003), most studies show no change in <16 weeks (Adams, Hather, Baldwin, et al. 1993; Jurimae, Abernethy, Blake, et al. 1996; Staron, Karapondo, Kraemer, et al. 1994). Some studies (Green, Thomson, Daub, et al. 1979; Thorstensson, Larsson, Tesch, et al. 1977) have noted selective hypertrophy of type IIA fibers; hence the relative area occupied by IIA fibers may be considerably

Table 1. Theoretical Training Time Influences on Relative MHC Expression (Adapted From Schilling, Fry, Chiu, et al., 2005)

	MHC I	MHC IIx
Short-term strength training	Little change	Decrease toward zero
Long-term strength training	Decrease	Little change (may have reached zero)

greater than the relative area of other fiber types, even with a comparatively smaller number of type IIA fibers present. Schilling, Fry, Chiu, and colleagues (2005) proposed a relationship between training time and relative expression of MHC IIx and MHC I (Table 1) that suggests, since training can improve strength, that expression of these proteins may covary with strength performance in trained populations.

Maximum force is related to muscle cross-sectional area (CSA) and the force expressed per unit CSA is known as specific tension (Ryushi, Hakkinen, Kauhanen, et al. 1988; Schantz, Randall-Fox, Hutchison, et al. 1983). Correlations between fiber characteristics and maximum force measures may be masked by CSA variance or they may covary (Schantz, Randall-Fox, Hutchison, et al. 1983). The relationship between these measures is not perfect, as training can increase strength without changes in CSA, but some consideration of the amount of muscle involved is needed to determine fiber type influence on strength. One method of partially controlling for CSA is to adjust strength values for a measure of lean mass of the entire body (Fry, Webber, Weiss, et al. 2003; Suter, Herzog, Sokolosky, et al. 1993) or localized lean mass (Schilling, Fry, Chiu, et al. 2005), and those studies have shown correlations between muscle proteins and adjusted peak force measures.

Relative area of the fiber types is likely a better estimation of the possible functional influence of a fiber type than simply its relative number, yet some investigations neglect this fact (Clarkson, Kroll, and McBride 1980; Ivy, Withers, Brose, et al. 1981; Suter, Herzog, Sokolosky, et al. 1993). This may be one inherent advantage of MHC analyses, as it gives relative amounts without the potential errors in mATPase histochemistry due to fibers coexpressing multiple MHC, and without the need to calculate relative area, as MHC and percent fiber area are highly correlated (Fry, Allemier, and Staron 1994; Klitgaard, Mantoni, Schiaffino, et al. 1990). In addition to relative fiber area, MHC is a more user-friendly method to determine the subtypes of type II fibers (IIa and IIx), although they also can be derived from mATPase staining. Many studies do not use type II subtypes in their analyses (Borges and Essen-Gustavsson 1989; Gregor, Edgerton, Perrine, et al. 1979; Houston, Norman, and Froese 1988; Ivy, Withers, Brose, et al. 1981; Sleivert, Backus, and Wenger

1995; Suter, Herzog, Sokolosky, et al. 1993; Taylor, Humphries, Smith, et al. 1997; Tesch and Karlsson 1978; Tihanyi, Apor, and Fekete 1982), which may reduce the ability to correlate fiber type to performance. In-vivo research has shown negative relationships between MHC IIx (IIX fiber area) and performance (Fry, Schilling, Staron, et al. 2003; Fry, Webber, Weiss, et al. 2003; Jurimae, Abernethy, Quigley, et al. 1997; Schilling, Fry, Chiu, et al. 2005), which is somewhat contradictory to single fiber in-vitro findings (Bottinelli, Pellegrino, Canepari, et al. 1999) and is due to training-induced changes in MHC IIx.

The intent of this investigation was to determine the amount of explained variance in voluntary isometric quadriceps force/time and power parameters that is due to the MHC composition of a biopsy sample from the vastus lateralis, in an attempt to expand findings on the relationship between MHC and performance from earlier investigations (Maughan and Nimmo, 1984; Schilling, Fry, Chiu, et al. 2005; Taylor, Humphries, Smith, et al. 1997). Our goal is to apply these methods to a more diverse subject group and to a wider range of knee-extensor performance measures.

MATERIALS AND METHODS

Subjects

Thirty-six healthy men with varying degrees of physical training background were selected for this investigation. In order to obtain a large continuum in both performance and muscle parameters, the sample included highly trained weightlifters (n = 4), endurance trained (n = 9), recreationally active (n = 15), and sedentary (n = 8) individuals between the ages of 18 and 33. Subjects self-reported that they were free from orthopedic, cardiovascular, musculoskeletal, and psychological injuries or illnesses that might have limited their performance. Height and body mass data were collected, as well as body composition. Three-site skinfolds were measured with Lange calipers and body composition estimated by the method of Jackson and Pollock (1978).

Research Design

A cross-sectional design was used for subjects with varying degrees of training background. Block-entry regression according to the method of Schilling, Fry, Chiu, and Weiss (2005) was used to examine MHC isoform-explained variance in performance. MHC IIx was entered into the regression to account for both genetic influence and short-term training status, and MHC I subsequently was added to show additional explained

variance above that of MHC IIx. MHC I is less plastic but may give important performance information (Schilling, Fry, Chiu, et al. 2005).

Performance Testing

Immediately before testing, each subject was instructed on the procedure and allowed to practice the isometric and isoinertial tests. Performance tests were conducted on a modified Body-Solid® (Forest Park, IL) knee extension machine, adjusted so that the knee was at 90° flexion at the beginning of the movement (Figure 1). All trials were performed with the dominant leg. Subjects were instructed to keep the arms folded across the chest with eyes closed and to contract as hard and fast as possible on a command signal. Subjects were secured to the testing apparatus with straps to prevent motion of the body. A rest period of 120 s was given between each maximal-effort attempt. For the isoinertial tests the subject performed single repetitions at incremental load increases up to a unilateral one repetition maximum (1-RM). Subsequent to 1-RM identification, the selector pin was set in the weight stack at a supramaximal load, and the isometric action was performed. The isometric action was held for approximately 4 s, and subjects were instructed to stop contracting

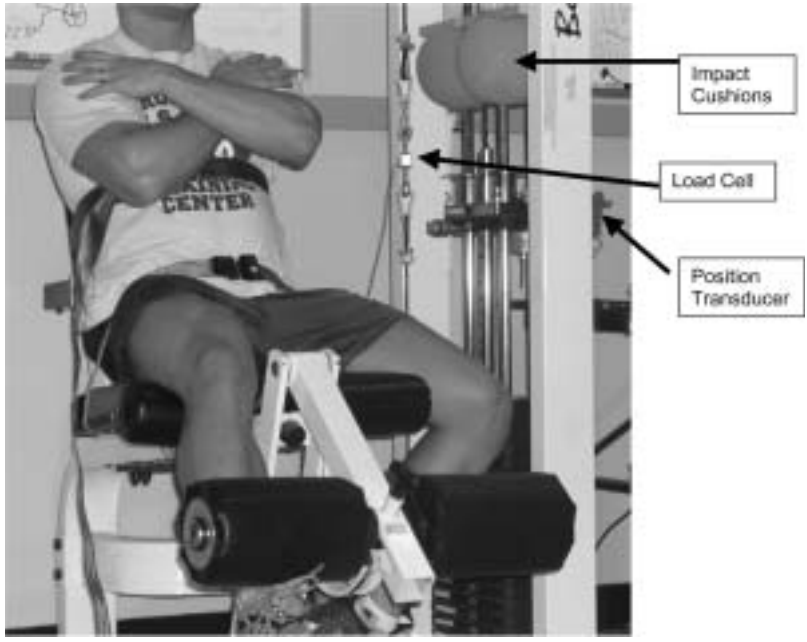

Figure 1. Subject performing knee extension in research apparatus.

immediately upon a verbal command. Subjects then performed maximal-effort isoinertial attempts at loads of 70% and 40% 1-RM. Load increments were to the nearest 0.5 kg. Foam cushions were placed at the end of the range of motion (ROM) to reduce the impact of the weight stack plates and allow subjects to maximally extend the knee joint through the entire ROM.

In the center of the leg extension machine cable, a tension/compression load cell (MLP-500; Transducer Techniques, Temecula, CA) was attached. The load cell was channeled through a signal conditioner (TMO-2; Transducer Techniques) that supplied power to the load cell and amplified the electrical output. The balance and gain for the signal conditioner was calibrated prior to each trial according to manufacturer's instructions. From the signal conditioner, a 0–5VDC electrical output was channeled through a 12-bit analog-to-digital (A/D) conversion board (Ariel Dynamics, San Diego, CA) interfaced with a personal computer (PC). Position was sampled simultaneously with a linear position transducer (P510–80-NJC-004-TS; Unimeasure, Corvalis, OR). The linear position transducer had a resolution of 4.920 $mV \bullet mm^{-1}$ with a repeatability of 0.015% of the full-scale voltage measure (Chiu, Schilling, Fry, et al. 2004). Data were sampled at 500 Hz using the Analog module of the Ariel Performance Analysis System® (APAS version 9.50; Ariel Dynamics, San Diego, CA). Data were analyzed with BioProc2 v2.03 for Windows® (D.G.E. Robertson [author/provider], Ottawa, ON). Force and position signals underwent low-pass filtering with a fourth-order recursive Butterworth filter with cut-off frequencies of 20 Hz and 10 Hz, respectively. Cut-off frequencies were determined by Fourier analyses of the respective power spectrums. Velocity was calculated from the first derivative of position, and power was calculated as the product of force and velocity. Instantaneous rate of force development (RFD; 20 ms peak) was calculated from the first derivative of force. Average rate of force development was calculated with the method of Chiu, Fry, Schilling, and Weiss (2002):

$$\text{Average RFD} = [F(\text{peak}) - F(\text{initial})]/\{t_{F(\text{peak})} - t_{F(\text{initial})}\} \quad (1)$$

Dependent Variables of Interest

- **IF_{max}-maximum isometric force per kg lean mass of the body.**
- **IRFD-isometric rate of force development (Average and 20 ms peak).**
- **$W_{max40\%}$-maximum power of the quadriceps at 40% 1-RM.**
- **$W_{max70\%}$-maximum power of the quadriceps at 70% 1-RM.**
- **$V_{max40\%}$-maximum velocity at 40% 1-RM.**
- **$V_{max70\%}$-maximum velocity at 70% 1-RM.**

Biopsy Procedure and Sample Preparation

Biopsies (80–160 mg) were taken from the vastus lateralis muscle with the percutaneous needle biopsy methods of Bergström (1962). The muscle sample was taken one-half the distance from the greater trochanter of the femur to the apex of the patella. The sample site was cleaned and shaved, and a local anesthetic was cutaneously injected (2% Xylocaine). A small (~1 cm) incision was made through the skin and deep fascia with a #11 scalpel. A UCH needle was used (Popper and Sons, New Hyde Park, NY) with the double chop method (Staron, Malicky, Leonardi, et al. 1990; Staron 1991) and suction (Evans, Pinney, and Young, 1982). The incisions were closed with steri-strips and a pressure bandage placed over the incision site. Incisions were examined 24–48 hours postprocedure.

Biopsy samples were oriented in tragacanth gum so that all fibers were parallel and on end, then frozen in isopentane cooled to −160 °C with liquid nitrogen, and stored at −80 °C. Twelve to 15 serial sections, each 12 μm thick, were taken from the sample in a cryostat with the temperature set at −20 °C. Sections were lysed by placing them in 0.5 ml of a buffer containing 10% (w/v) glycerol, 5% (v/v) 2-mercaptoethanol, and 2.3% (w/v) SDS in 62.5 $mmol^{-1}$ TRIS/HCL buffer (pH 6.8) and heating them in a dry bath at 60 °C for 10 minutes.

Myosin Heavy Chain Analyses

Determination of relative MHC isoform expression was performed using sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) based on the methods of Carraro and Cantani (1983) and Perrie and Bumford 1986, with modifications used for single fiber analysis (Staron and Hikida, 1992). Three to 25 μL of lysed sample were loaded into a 4%–8% gradient SDS polyacrylamide gels (30% glycerol) with a 4% stacking gel, and run overnight for ~20 hours at a constant voltage (120 V). Gels were removed and stained with Coomassie blue, with MHC isoforms identified by migration patterns compared with marker proteins and migration patterns of single fibers (Staron and Hikida 1992; Staron and Johnson 1993).

All gels were scanned and plotted using Scion image for Windows v4.0.2, and plots were converted to points and analyzed with PeakFit 4.11 for Windows. Autofit Peaks I Residuals were used to find local maxima, and peaks for each isoform were converted to areas. Relative expression was determined by calculating the percent area for each peak, determined by dividing individual areas by total area under all peaks.

Statistical Analyses

Analyses were conducted with SPSS 11.0. A priori alpha level was set at 0.05. Linear regression for in-vivo performance variables was carried out by entering percent type IIx MHC and percent type I MHC variables one at a time and evaluating R-square change to determine the portion of variance explained and significance of the change (Schilling, Fry, Chiu, et al., 2005). MHC IIx was chosen to be first in the model based on its high relative plasticity that appears to represent short-term training status (Liu, Schlumberger, Wirth, et al. 2003; Staron, Karapondo, Kraemer, et al. 1994). MHC I is less plastic (Kadi and Thornell 1999; Liu, Schlumberger, Wirth, et al. 2003), but relative expression of this isoform may give insight into long-term training status (Schilling, Fry, Chiu, et al. 2005; Table 1). Tests for multicollinearity, homoscedasticity, normality, and influential data points were used to determine that the assumptions of regression were met.

RESULTS

Subject descriptive data are shown in Table 2. MHC expression (mean ± SD) for MHC IIx, IIa, and I were 16.63 ± 8.5%, 44.61 ± 11.5%, 38.76 ± 10.8%, respectively. Peak isometric force was significantly correlated with estimated lean body mass (LBM; $r = 0.482$, $p = 0.003$). Thus LBM was used to correct for peak force of the quadriceps in subsequent analysis. Performance data are shown in Table 3. Regression analyses indicated that relative MHC expression does not explain performance variance in isometric or isokinetic knee extensor performance for this group of subjects (Table 4).

DISCUSSION

In a previous study (Schilling, Fry, Chui, et al., 2005) using resistance trained subjects, MHC isoforms explained a significant amount of the variance in several isometric knee extensor performance variables including

Table 2. Subject Descriptive Data

	Mean	SD
MHC IIx (%)	16.6	8.5
MHC IIa (%)	44.6	11.5
MHC I (%)	38.8	10.8
Age (y)	24	4.2
Body mass (kg)	89.7	19.4
Percent body fat (%)	22.8	11.1
Lean body mass (kg)	69.2	10.0

Table 3. Subject Performance Data

	Mean	St. Dev.
Isometric force/kg lean body mass (N/kg)	11.50	2.0
Average rate of isometric force development (N/s)	2016.47	612.7
Peak (20 ms) rate of isometric force development (N/s)	4780.38	1623.2
Peak force at 70% 1RM (N)	490.49	90.6
Peak power at 70% 1RM (W)	512.9	120.5
Peak velocity at 70% 1RM (m/s)	1.34	0.1
Peak force at 40% 1RM (N)	322.28	70.9
Peak power at 40% 1RM (W)	522.92	117.65
Peak velocity at 40% 1RM (m/s)	2.08	0.2

Table 4. R-square Change Values for Block Entry Regression of MHC IIx and MHC I Based on the Methods of Schilling, Fry, Chiu, et al., 2005.

	MHC IIx	MHC I
Isometric force/kg lean body mass (N/kg)	.002	.004
Average rate of isometric force development (N/s)	.003	.000
Peak (20 ms) rate of isometric force development (N/s)	.008	.042
Peak force at 70% 1RM (N)	.044	.006
Peak power at 70% 1RM (W)	.006	.034
Peak Velocity at 70% 1RM (m/s)	.047	.049
Peak force at 40% 1RM (N)	.103	.004
Peak power at 40% 1RM (W)	.066	.002
Peak velocity at 40% 1RM (m/s)	.052	.065

RFD and peak force; therefore, the present findings were unexpected. In studies controlling for the amount of muscle mass involved, only Clarkson, Kroll, and Melchionda (1981); Sleivert, Backus, and Wenger (1995); Schilling, Fry, Chiu, and Weiss (2005); and Tesch and Karlsson (1978) determined relationships between muscle fiber makeup and peak isometric force performance. Clarkson, Kroll, and Melchionda (1981) found positive relationships of the fast-twitch/slow-twitch fiber area ratio and body weight adjusted isometric force, while Sleivert, Backus, and Wenger (1995), and Tesch and Karlsson (1978) reported positive relationships of percent fast-twitch fiber area with isometric force (r = 0.43 and 0.49, respectively). Without close examination of the fast-twitch subtypes in these studies, a clear conclusion is elusive. Schilling, Fry, Chiu, and Weiss (2005) reported that MHC IIx is negatively correlated with peak force measures, but no additional variance was explained by adding percent MHC I and strength performance, suggesting no difference in specific tension between fast- and slow-twitch fibers.

Only four studies examined specific tension while controlling for muscle size, using percent area as a measure of muscle protein makeup, and accounted for subtypes of type II fibers for correlational analysis (Clarkson, Kroll, and Melchionda 1981; Klitgaard, Mantoni, Schiaffino, et al., 1990; Maughan and Nimmo 1984; Schilling, Fry, Chiu, et al. 2005), and thus far only Schilling, Fry, Chiu, and Weiss (2005) have shown this negative relationship between MHC IIx and voluntary isometric strength. Information on training status of subjects was not always presented (Clarkson, Kroll, and Melchionda, 1981; Klitgaard, Mantoni, Schiaffino, et al. 1990; Maughan and Nimmo 1984), and from this it can be assumed that only Schilling, Fry, Chiu, and Weiss (2005) had no sedentary subjects and also included some highly trained subjects.

MHC IIx is highly plastic and can be reduced with training, which happens at least partially in concert with nervous system adaptations leading to greater strength (Sale, 1992). The inclusion of trained subjects in the investigative sample likely increases the variability of MHC IIx, thereby increasing the likelihood of a correlation between it and adjusted peak force. In this case, however, it seems that the influence of the untrained subjects reduces the relationship noted previously (Schilling, Fry, Chiu, et al. 2005). The subjects in Schilling, Fry, Chiu, and Weiss' study (2005) had a lower mean relative content of MHC IIx (mean ± SD; 12.94 ± 5.20%) than the subjects in the current study (16.63 ± 8.5%). A t test for independent samples suggests that the difference was significant at $p < 0.1$ ($p = 0.054$; unpublished data). Because MHC IIx decreases with training, this suggests that the subjects in the current investigation were less trained and also suggests a wider range in training status. This difference in variance was significant in Levene's test for equality of variances ($p < 0.047$; unpublished data). Because there is natural variation in MHC IIx regardless of training status, future investigations will benefit from a detailed training history and additional physiological measures to get precise information on training status.

Average rate of force development during isometric performance also was measured in the current investigation, and again no relationships were noted. Using stimulated force, Taylor, Humphries, Smith, and Brooks (1997) found no significant relationship for 5 ms peak isometric RFD and combined type II MHC expression ($r = 0.58$, $p > 0.1$), whereas Schilling, Fry, Chiu, and Weiss (2005) showed significant variance in average RFD that is accounted for by type I MHC ($r^2 = 37.7$) after variance accounted for by MHC IIx was considered. The lack of statistical power in Taylor, Humphries, Smith, and Brooks' study (1997) may be responsible for the lack of significance, but their relatively large r value supports the relationship between RFD and MHC expression. Only Sleivert, Backus, and Wenger (1995) had a similar wide range in training status as

the current investigation, and contrary to the present investigation, those authors found a correlation between type II fiber area and 3.5 ms rate of tension development (r = 0.46). Harridge, Bottinelli, Canepari, and Colleagues (1996) were able to show a very strong relationship (r = 0.99) between time-to-peak tension and percent MHC II in trained men. This investigation used stimulated contractions, which is likely a quite different method from the volitional performance in the current investigation. This study also used several muscle groups for the analysis, and they did not examine the correlation with fast MHC subtypes.

Isoinertial performance was also not correlated with performance in this investigation, and this type of performance is not commonly researched in knee-extensor actions. Houston, Norman, and Froese (1988) found percent fast-twitch area to be correlated with peak acceleration during the acceleration region of maximal isokinetic knee extensions, but, again, this study did not examine subtypes of MHC II. The only other investigation to use isoinertial knee extension was by Tihanyi, Apor, and Fekete (1982), who showed that subjects with greater percent area type II developed more power and angular velocity at loads of 5% and 15% of peak isometric torque (r = 0.73 and r = 0.69). Since these loads were not relative to the maximum force, nor were they adjusted for body mass, the precise interpretation of these results is not possible in the context of the current investigation.

The unilateral knee extension task was selected to minimize the amount of muscle mass used in the exercise in relation to the biopsy sample. There are no data to suggest that there is a large degree of within-subject variability in the muscle fiber composition quadriceps muscle group (Johnson, Polgar, Weightman, et al., 1973; Polgar, Johnson, Weightman, et al., 1973). The common assumption in studies that attempt to correlate vastus lateralis biopsy to performance is that the relative fiber or MHC composition of the four quadriceps muscles is not markedly different within subjects. The addition of the leg ankle extensors, however, is not likely to increase the relationship, and therefore knee extension is commonly selected over leg extension as in this investigation.

Future application of the block-entry regression model developed herein should utilize electromyographic data as an indicator of nervous system influence on these performance variables. The time course of nervous and MHC adaptations could then be compared in training studies to determine the degree of covariance between MHC and nervous system adaptations to training. In addition, utilizing stimulated contractions could serve as a tool for eliminating the effect of volition, as well as providing an indication of nervous system adaptation. By using interpolated twitch methods, the number of motor units not recruited can be measured (Oskouei, van Mazijk, Schuiling, et al. 2003). In the case of stimulated contraction,

motor units expressing primarily MHC IIx are likely to have a higher recruitment rate than involuntary actions. If those motor units are recruited in the stimulated condition, this is likely to reverse (or greatly reduce) the volitional relationship between MHC IIx and performance as they then will contribute to force/time characteristics.

The findings herein suggest that correlations between performance and relative MHC isoform expression are not present across groups with a large range in training status. It is possible that nervous system adaptation (Sale 1992) that is not present in untrained individuals is an intervening factor that reduces the relationship between muscle protein morphology and performance.

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