The Science Journal of the Lander College of Arts and Sciences

Volume 9
Number 1 *Fall 2015*

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1-1-2015

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Abstract
The purpose of this paper is to investigate the adaptations that occur in human skeletal muscle in response to endurance and resistance exercises. The advances made in science over the past several decades increased the number of methods available for the classification of muscle fibers, resulting in many fiber type classes and their corresponding characteristics. This allows for the tracking of changes that occur within the muscle fibers. The heterogeneous collection of fiber types found within a muscle allows for its dynamic nature. Myosin form expression varies according to the muscle's changing functional demands. In response to endurance training, muscle fibers adapt by changing in composition, converting between type IIB and type IIA (i.e. the fast to slow direction). In response to resistance training, muscle fibers undergo both fiber-type shifting and hypertrophy. This muscle plasticity allows for the physiologic changes that take place in athletes and in physical therapy patients. The research available allows for the designing of interventions specific to increasing one's endurance or power.

Introduction: Muscle fiber and motor unit typing
Muscle fiber types can be described using morphological, histochemical, immunohistochemical and biochemical characteristics. Clear morphological differences were seen in birds, with fast muscles appearing white and slow muscles appearing red. The redness of the slow muscle is due to the greater myoglobin and capillary content that permits a greater oxidative capacity of the muscle (Staron, 1997). Research has long shown that there is a clear correlation between myosin ATPase activity and muscle contraction speed. Studies in rats, measuring isolated muscle units, lead to initial classification of muscle fibers based on their isometric twitch contraction speed as fast, intermediate and slow (Pette et. al., 1999). Presently, muscle fibers are classified by means of 3 different techniques: histochemical myosin ATPase staining, immunohistochemical myosin heavy chain isoform identification, and biochemical identification of metabolic enzymes.

Acronyms:	
Myosin ATPase	MATPase
Myosin Heavy Chain	MHC
Sodium Dodecyl Sulfate-Polyacrylamide Gel Electrophoretic	SDS-PAGE
Fast-Twitch Glycolytic	FG
Fast-Twitch Oxidative	FOG
Slow-Twitch Oxidative	SO
Slow-Twitch	S
Fast-Twitch Fatigue-Resistant	FR
Fast-Twitch Fatigue-Intermediate	Fint
Fast-Twitch Fatigable	FF

Histochemical Classification
Myosin ATPase histochemical staining confirmed the diversity of muscle fibers. The stain's intensity differs based on the myofibrillar differences in pH sensitivity. Type I fibers were found to be alkali labile (lighter stain, low ATPase activity) and acid stable (intense stain, high activity), while type II fibers were alkali stable and acid labile (Staron, 1997, Sieck, Prakash, 1997). At first, fibers were identified as slow type I, and fast types IIA and IIB (Pette et. al., 1999). However, advances in the histochemical staining technique has led to the identification of a total of 7 human muscle fiber types (Staron, 1997). The newly identified fibers, types IC, IIC, IIAC, and IIAB, have intermediate myosin ATPase staining characteristics. Type IC, the slowest fiber, stains most similarly to type I fibers, while type IIAB fibers have intermediate staining characteristics between type IIA and IIB fibers. Thus, the 7 human muscle fiber types (from slowest to fastest), as identified by myosin ATPase histochemical staining are: types I, IC, IIC, IIAC, IIA, IIAB, and IIB (Pette et. al., 1999). As seen in the literature, some researchers do not use all 7 fiber types, but rather place all fibers into the original 3 categories (Staron, 1997).

Immunohistochemical Classification
A second fiber type classification is based on the identification of different myosin heavy chain (MHC) isoforms (Pette et. al., 1999). Immunohistochemical analysis of human muscle began after scientists discovered antigenic differences between the myosin types of different human muscle (Staron, 1997). Isoforms were identified using antimyosin antibodies or by sodium dodecyl sulfate-polyacrylamide gel electrophoretic (SDS-PAGE) separation (Pette et. al., 1999). A general correlation was discovered between the histochemically classified fiber types and the MHC isoforms they express (Sieck, Prakash, 1997, Fry et. al., 1994). The original 3 myosin isoforms identified were MHCI, MHCIIa, and MHCIIb, corresponding to those identified by myosin ATPase staining as pure types I, IIA, and IIB, respectively. However, each muscle fiber can contain more than one myosin heavy chain isoform, forming hybrid fibers. This phenomenon explains the existence of more muscle fiber types than the amount of pure isoforms. These mixed fibers almost always contain "neighboring" myosin heavy chain isoforms (i.e., MHCI and MHCIIa or MHCIIa and MHCIIb) (Pette et. al., 1999). Type IIAB fibers that have a predominance of the MHCIIa isoform stains more like type IIA fibers, but fibers that have a predominance of the MHCIIb isoform stains more like type IIB fibers

(Staron, 1997). Consequently, the histochemical myosin ATPase types express their isoform genes to varying degrees, according to the variable ratio of isoforms present in the fiber. Due to its quantitative nature, the SDS-PAGE technique is perhaps the best method for muscle fiber typing, as electrophoretic separation permits the recognition of the relative concentrations of different myosin heavy chain isoforms in mixed muscle fibers (Pette et. al., 1999, Fry et. al., 1994).

A fourth myosin heavy chain isoform, MHCIIx or MHCIId, and its corresponding fiber type IIX, is present in small mammals. Evidence shows that MHCIIb in humans in homologous to MHCIIx/d of small mammals (Pette et. al., 1999, Hilber et. al., 1999). In actuality, MHCIIb in humans is really MHCIIx/d, as humans do not express MHCIIb, the fastest myosin heavy chain isoform (Pette et. al., 1999). In fact, recent data shows that fibers that were histochemically identified as type IIB in humans contain low amounts of MHCIIa, and therefore, in reality, are hybrid type IIAB fibers (Staron, 1997). Therefore, the 3 myosin heavy chain isoforms present in human limb muscles are (from slowest to fastest): MHCI, MHCIIa, and MHCIIx/d (previously incorrectly known as MHCIIb).

Biochemical Classification

A third classification technique reflects the energy metabolism of the muscle fibers. Histochemical myosin ATPase fiber typing of type I or type II corresponds to slow and fast muscle fibers, respectively, and the enzymes involved reflect the metabolic pathways that are either aerobic/oxidative or anaerobic/glycolytic (Pette et. al., 1999). This classification scheme leads to 3 fiber types: fast-twitch glycolytic (FG), fast-twitch oxidative (FOG), and slow-twitch oxidative (SO) (Pette, Staron, 1997). Type I and IIA fibers have a greater mitochondrial density and oxidative capacity than type IIB and IIX fibers (Sieck, Prakash, 1997). Accordingly, there is a good correlation between type I and SO fibers, but correlations between type IIA and FOG and type IIB and IIX and FG fibers are more diverse (Hamalainen, Pette, 1995). This can be explained by the fact that changes in oxidative capacity can take place without changes in MHC isoforms (Staron, 1997). Generally, type I fibers rely primarily on aerobic/oxidative energy metabolism and type II fibers rely primarily on anaerobic/glycolytic metabolism, but as it cannot be assumed, the terms type IIB and FG or type IIA and FOG cannot be used interchangeably (Pette et. al., 1999).

Myosin Light Chains

The myosin light chains also exist in different isoforms, slow and fast, and affect the contractile speed of the fiber (Talmadge, Pette, 1995). A homogeneous/pure myosin heavy chain isoform can be heterogeneous in regard to its myosin light chain isoform. Usually, however, fast heavy chain isoforms fuse with fast light chain isoforms, and slow heavy chain isoforms fuse with slow light chain isoforms (Pette et. al., 1999, Jostarndt-Fogen et. al., 1998).

Motor Unit Classification

The proper functional unit of the neuromuscular system, the motor unit, reflects the characteristics of its individual fibers. Motor units are categorized based on their contractile speeds and fatigue characteristics. Contractile speed classifies motor units into slow-twitch (S), usually comprised of type I fibers, or fast-twitch (F), usually comprised of type II (Burke, 1999). The

Table 1: Summary of fiber types and their corresponding characteristics

	Type I fibers (I, IC)	Type IIA fibers (IIC, IIAC, IIA, IIAB)	Type IIX fibers	Type IIB fibers (not present in humans)
MHC isoforms	MHCI	MHCIIa	MHCIIx/d	MHCIIb
Contraction time	Slow	Moderately Fast	Fast	Very Fast
Oxidative Capacity	High	High	Intermediate	Low
Glycolytic Capacity	Low	High	High	High
Biochemical Fiber Type (generally)	SO (slow oxidative)	FOG (fast-twitch oxidative)	FG (fast-twitch glycolytic)	FG (fast-twitch glycolytic)
Resistance to Fatigue	High	Fairly High	Intermediate	Low
Motor Unit Class (generally)	S (slow twitch)	FR (fast-twitch fatigue-resistant)	Fint (fast-twitch fatigue-intermediate)	FF (fast-twitch fatigable)
Activity used for	Aerobic	Long-term anaerobic	Short-term anaerobic	Short-term anaerobic
Mitochondrial Density	High	High	Intermediate	Low
Capillary Density	High	Intermediate	Low	Low

F motor units are additionally classified by their type II fiber subdivisions. Fast-twitch fatigue-resistant (FR) are comprised of type IIA fibers, fast-twitch fatigue-intermediate (Fint) are comprised of type IIX, and fast-twitch fatigable (FF) are comprised of type IIB (Burke, 1993). The fatigue resistance of the muscle unit is explained by the mitochondrial density and oxidative capacity of the muscle fibers. The motor unit typically reflects the function of the muscle. The diaphragm muscle employs its fatigue-resistant S and FR units to produce normal breathing, but must recruit its Fint and FF units for actions that require greater force, such as gagging or sneezing. Contrariwise, the extensor digitorum longus muscle of the limb, which is used for motor activities demanding short periods of greater force production, is composed mostly of FF type IIB fibers. Consequently, type I and IIA fibers are intended to sustain longer periods of activation, while type IIX and IIB fibers are intended to produce shorter bursts of activation (Sieck, Prakash, 1997).

Therefore, the overall properties of a muscle reflects the properties of its heterogeneous collection of fiber types and their overall proportions. It is this range of fiber types that allows for the wide range of muscle function a single muscle can display. Muscle fibers adapt to their motor unit's changing stimuli not only by changing their size, but by converting their fiber type composition to suit the functional demands. This muscle plasticity serves as the physiologic basis for the adaptions of skeletal muscle to resistance and endurance exercises.

Methods

EBSCO multi-search, ProQuest Medical Library, Wiley Library, Journal of Applied Physiology, MEDLINE, and PubMed databases were used to find material for this paper. Access was gained to these databases through the Touro College Online Library and Einstein Online Library websites. Key words, such as "muscle fiber types" and "effects of exercise on muscle" were used to search for scientific articles. After reading through these articles, other key words were identified, such as "fiber-type shifting", and "resistance vs endurance". Additionally, sources listed as references for review articles on the APTA website (American Physical Therapy Association) were searched for to find the original papers.

Discussion

The plasticity of the heterogeneous composition of muscle fibers allows for adaptations in the contractile and metabolic properties of skeletal muscle. Various phenotypes are therefore possible in response to different workloads. This plasticity has practical implications, both for athletes and rehabilitation patients alike.

This range of myosin form expression in response to exercise regimes is evident in the vastus lateralis. In untrained, physically active subjects, the vastus lateralis is made up of roughly 50% of slow type I fibers and 50% type II fibers (40% type IIA and 10% IIX). Power athletes, such as sprinters, power weight lifters and throwers, are constituted chiefly of IIA and IIX fibers, with a percentage of type I as little as 20%. Ultra-endurance athletes, such as long-distance runners, have a 95% constitution of type I fibers. The variability of the composition of the vastus lateralis muscle is due to fiber type shifting. Long-term endurance training induces a substantial transformation from fast muscle fibers to slow muscle fibers. Slow muscle fibers rely mainly on aerobic metabolism and, for that reason, are vital for endurance activities such as swimming, cycling and marathon running. The shift in MHC isoform type depends on changes at the molecular level. New slow MHC polypeptides, which are still categorized as type IIA fibers, are produced, marking the start of their transition towards the slow type I fibers (Zawadowska et. al., 2004).

In response to training, the most common fiber conversions are between type IIB and type IIA. Slow to fast/ type I to type II conversions are possible in response to the loss of function related to deconditioning, as shown in studies on humans with spinal cord injury and microgravity exposure during their time in space. Detraining in humans (i.e., decreased use of skeletal muscle following a formerly high activity level) leads to shifts MHCIIa to MHCIIx/d and possibly MHCI to MHCIIa. Additionally, there is a related decrease in aerobic-oxidative metabolic enzymes (Pette, Staron, 1997). In short, immobilization of skeletal muscle may cause conversions in the slow to fast direction. Scientists assumed that power training may also cause the transformation in slow to fast direction. This was a logical assumption, since fast muscle fibers depend mainly on anaerobic metabolism and are consequently essential for power training, such as sprinting and weight lifting. Additionally, IIX fibers produce a greater maximal power output than IIA fibers and are therefore essential for such activities. However, studies have proven that all methods of training (both endurance and power/resistance) cause a conversion toward the slow direction (Zawadowska et. al., 2004).

Endurance

Many studies have proven that endurance exercises (low-resistance, repeated contractions that require the muscle to produce a high aerobic metabolic rate) lead to several adaptations within the muscle to augment aerobic metabolism and resistance to fatigue (Staron et. al., 1990). Firstly, the oxidative capacity of all fiber types will increase by increasing the amount of mitochondria, oxidative/aerobic enzymes and capillaries in the muscles being trained (Holloszy, Booth, 1976, Fitts, Widrick 1996). Based on metabolic classification scheme, there is a transition from the FG fiber type to the FOG fiber type without, necessarily causing a change in the myosin heavy chain composition (Pette, Staron, 1997).

Secondly, there are alterations in myosin heavy chain isoform. It has been suggested that there is an increase in the percentage of type I fibers following aerobic training, and a subsequent decrease following detraining in elite endurance athletes. Additionally, within type II fibers, MHCIIx/d (IIB) are converted to MHCIIa (IIA). In other words, there is a decrease in the population of pure type IIB fibers and an associated increase in the population of pure type IIA fibers. It also seems that there is an increase in the hybrid population of type I and type II fibers, known as type IIC (Staron et. al., 1990). Evidence as to the conversion of type II to type I fibers, as stated previously, is lacking (Ricoy et. al., 1998). The transformation of type IIB fibers to type IIA in response to endurance training is fairly logical. Although there are variations on the oxidative capacities within a muscle type, as a class, type IIA fibers generally have a greater oxidative capacity than type IIB fibers. Therefore, an increase in the population of type IIA fibers makes the muscle more oxidative. In fact, there is a negative correlation between the percentage of type IIB fibers and maximum oxygen intake. Therefore, as stated previously, detraining and immobilization cause a conversion in the slow to fast direction, from type IIA to type IIB (Staron et. al., 1990).

Thirdly, there can be a transformation in myosin light chain isoforms. Type I fibers show an increase in contractile speed in response to endurance exercises, but show a decrease following deconditioning in humans. Logically, this change cannot be explained by a conversion of fiber type, but rather, by a conversion in the myosin light chain isoforms from slow to fast and from fast to slow, respectively (Larsson et. al., 1996, Widrick et. al., 1996). The conversion from slow to fast allows the fibers to maintain their properties of efficient energy usage while increasing their contractile speed to keep up with the demands of the exercise (Fitts, Widrick, 1996). Such a conversion would not be detected by the histochemical technique, as there is no change in the myosin ATPase (Pette, Staron, 1997). To summarize, muscle fiber adaptations to endurance exercise varies based on fiber type. In all types, the oxidative capacity of the fibers increases. Type II fibers shift in the type I direction, leading to slower, oxidative types. Type I fibers convert their myosin light chains to increase their contractile speeds.

Resistance/Power

High-intensity resistance strength training involves short, maximal contractions that require the muscle to produce a large amount of anaerobic energy (Staron et. al., 1990). Resistance training, such as high-load–low-repetition exercises, leads both to the fiber type shifting seen with endurance training and to muscle hypertrophy, which plays a significant role in increasing force production (Kraemer et. al., 1996). Initial strength gains made with high-intensity resistance training are caused by neural factors, rather than hypertrophy of the actual muscle fibers. However, adaptations may also be occurring in the contractile proteins of skeletal muscle within a short duration of training, even two weeks, with sufficient intensity (McArdle et. al., 1994). Visible hypertrophy is not evident until later in the training period (>8 weeks) (Kraemer et. al., 1996), around the same time researchers found a shift in muscle fiber type composition from MHCIIx/d to MHCIIa (Staron et. al., 1994, Kraemer et. al., 1995, Staron et. al., 1990).

To explore this plasticity, twenty four male subjects were categorized into three groups according to their sports/physical activity. Group A was made up of untrained students, group B of national and sub-national level endurance athletes (7.8+/-2.9 years of specialized training) and group C of sprint-power athletes (12.8+/-8.7 years of specialized training). Biopsies of the vastus lateralis muscle were obtained and immunohistochemically analyzed for fast/slow MHC composition. This muscle is easily accessible and easily trained. Most importantly, it expresses all three myosin isoform types at specific amounts, and so its phenotype visibly mirrors any adaptive modifications that occur after different forms of exercises. Unpredictably, group C sprint-power athletes (such as ice hockey, volleyball, karate, soccer players and modern dancers), who were expected to display the highest percentage of MHCIIX, were no different in this aspect from group B endurance athletes (such as marathon runners, cyclists and cross country skiers). The muscle phenotypes of both groups were similar, containing a small proportion of the MHCIIX isoform and a predominance of slow MHCI isoform. Clearly, the muscle phenotype was adapted for long lasting, sustainable activities (similar to what happens in endurance athletes), rather than activities that require a maximum power output in minimal time. Moreover, the fastest isoform, MHCIIX, was relatively lower in group C athletes than in group A students. This myosin profile in group C athletes is unfavorable to their sport. Muscles that contain a higher percentage of type IIX fibers have a greater maximum shortening velocity, which is the most important factor in maximum power output and therefore vital for their sports regime. This is a possible explanation for why, despite years of training, these athletes could not reach international level (Zawadowska et. al., 2004).

A study performed on women proved similar to the results shown by men. To examine the adaptations that take place following a high-intensity resistance strength training program (i.e. hypertrophy and fiber type shift), twenty-four women participated in a 20- week program for the lower extremity. Biopsies were obtained both before and after the training program from the superficial part of the vastus lateralis. Once again, this muscle was chosen due to its easy accessibility, broad fiber type composition, and potential for training (Staron et. al., 1990).

Based on staining intensities using MATPase histochemistry, six fiber types (I, IC, IIC, IIA, IIAB, and IIB) were distinguished, and three groups were determined based on fiber type (I, IIA and IIA+IIB) . Dramatic hypertrophy of all three groups (I= 15%, IIA= 45%, and IIAB +IIB= 57%) following a high- intensity strength training regime showed that fast twitch fibers are not the only fibers affected. There appears to be an increase in contractile elements within the muscle fibers, leading to an increase in both muscle strength and size, similar to the adaptations found in men following strength exercises (Staron et. al., 1990).

Additionally, the data shows that strength training causes muscle fiber-type conversions. In the pre-training biopsy sample, group 1 (type I) had the largest cross-sectional area (4253±949 μm2), group 2 (type IIA) had intermediate (3370±1048 μm2), and group 3 (type IIAB+IIB) had the smallest (2697±931 μm2). Despite a hypertrophy of all three groups, the "hierarchy of fiber sizes" was changed following training. The areas of group 1 and 2 were not significantly different from each other (type I = 4893±770 μm2, type IIA = 4888±967 μm2), and the area of

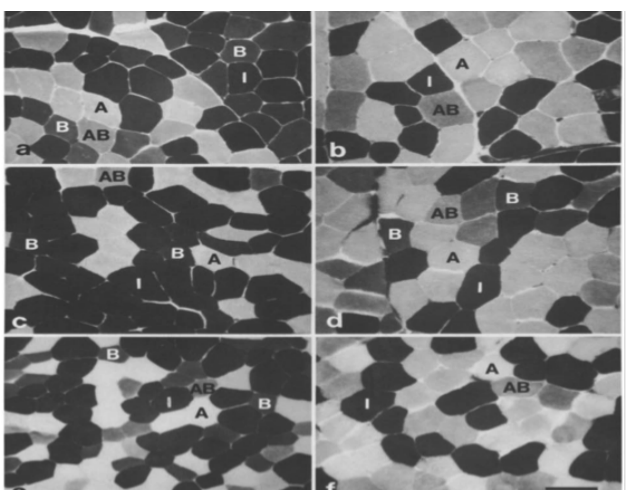

Figure 1: Cross sections of pre (left) and post (right) biopsies examined for MATPase activity from three different women. The dark staining type IIB fibers have visibly disappeared in the post-biopsy biopsy (Staron et. al., 1990).

group 3 was still significantly smaller (4233±1433 μm2) than the areas of both group 1 and 2. Therefore, despite the fact that the total area of type IIB fibers increased, the percentage of IIB fibers (MHCIIx/d) significantly decreased, with a concomitant increase in the percentage of IIA (MHCIIa) fibers (Staron et. al., 1990, Figure 1).

It is assumed that the recruitment of the infrequently activated IIB fibers caused their transformation to type IIA fibers. This increases the oxidative capacity of strength-trained muscle, as supported by the findings of significantly greater volumes of mitochondria in weightlifters' muscles compared to untrained subjects. This also explains the observation of an increase in short-term endurance following an intense-resistance training routine (Staron et. al., 1990). As a result of this shifting, reductions in myosin heavy chain "coexpression" has been reported both after endurance and resistance training, with a corresponding increase in pure fibers (Williamson et. al., 2000).

Conclusion

The study of muscle fiber types has constantly been evolving over the past several decades. New systems of classification that categorize the fibers into more specific groups enables researchers to accurately track the changes that occur within a muscle's fibers. Endurance training is known to increase the muscle's endurance by increasing the oxidative capacity of its fibers, as supported by the increase in type I fibers. Resistance/power training is known to increase the volume of the contractile proteins in the muscle fibers, promoting hypertrophy of the muscles. However, research shows that rather than increasing the percentage of fast muscle fibers, as expected, resistance exercises leads to fiber type shifting in the slow direction, increasing the oxidative capacity of the muscle.

While research has proven that resistance exercises leads to hypertrophy and muscle type shifting in both men and women, such studies are fairly new. Research conducted on the effects of endurance exercises far exceeds the research conducted on the effects of resistance exercises. As such, studies pertaining to resistance exercises do not always agree, and the pool of available research is not large enough to evaluate which studies are most accurate. For example, some papers claim that fiber type shifting causes type IIB to convert to type I fibers, while other papers say that type IIA is the farthest it can go. Therefore, additional research must be conducted to shed light on this topic and determine which theory is correct. However, it is clear that just like endurance exercises, resistance exercises lead to conversions in the fast to slow direction, and not in the slow to fast direction (as was originally assumed).

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