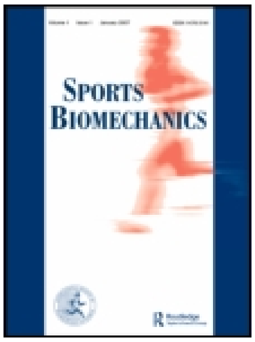

Sports Biomechanics

ISSN: 1476-3141 (Print) 1752-6116 (Online) Journal homepage: https://www.tandfonline.com/loi/rspb20

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To cite this article: Gordon R. Chalmers & Brandi S. Row (2011) Common errors in textbook descriptions of muscle fiber size in nontrained humans, Sports Biomechanics, 10:3, 254-268, DOI: 10.1080/14763141.2011.592211

To link to this article: https://doi.org/10.1080/14763141.2011.592211

Published online: 09 Aug 2011.

Sports Biomechanics
September 2011; 10(3): 254–268

Routledge
Taylor & Francis Group

Common errors in textbook descriptions of muscle fiber size in nontrained humans

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(Received 7 January 2011; accepted 14 April 2011)

Abstract
Exercise science and human anatomy and physiology textbooks commonly report that type IIB muscle fibers have the largest cross-sectional area of the three fiber types. These descriptions of muscle fiber sizes do not match with the research literature examining muscle fibers in young adult nontrained humans. For men, most commonly type IIA fibers were significantly larger than other fiber types (six out of 10 cases across six different muscles). For women, either type I, or both I and IIA muscle fibers were usually significantly the largest (five out of six cases across four different muscles). In none of these reports were type IIB fibers significantly larger than both other fiber types. In 27 studies that did not include statistical comparisons of mean fiber sizes across fiber types, in no cases were type IIB or fast glycolytic fibers larger than both type I and IIA, or slow oxidative and fast oxidative glycolytic fibers. The likely reason for mistakes in textbook descriptions of human muscle fiber sizes is that animal data were presented without being labeled as such, and without any warning that there are interspecies differences in muscle fiber properties. Correct knowledge of muscle fiber sizes may facilitate interpreting training and aging adaptations.

Keywords: *ATPase, classification, morphology, motor unit, skeletal muscle*

Introduction

Human muscle fiber types and sizes have been a target of investigation for decades. Nevertheless, puzzling inconsistencies remain when these data are disseminated. In the research literature, type IIA fibers are most often found to have the largest cross-sectional area when male human muscles are examined, as discussed below. Yet type IIB muscle fibers, recently found to express type IIX myosin, and often interchangeably referred to as fast glycolytic (FG), are commonly described as having the largest mean diameter of the three fiber types in both exercise science (Baechle & Earle, 2008; McArdle et al., 2007; Plowman & Smith, 2008) as well as basic physiology and anatomy texts (Fox, 2009; Marieb et al., 2008; Martini & Nath, 2009; Martini et al., 2009; Tortora & Nielsen, 2009). For example, in their human anatomy textbook Tortora and Nielsen (2009) state 'Fast glycolytic (FG) or type IIB fibers are the largest in diameter and contain the most myofibrils' (p. 299). Some exercise science texts report that type IIA and IIB fibers are the same size (Brown et al., 2006; Foss & Keteyian, 1998), or that all fiber types are the same size (Tipton, 2006). These

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ISSN 1476-3141 print/ISSN 1752-6116 online © 2011 Taylor & Francis
DOI: 10.1080/14763141.2011.592211

discrepancies may interfere with integrating and interpreting muscle physiology literature, as well as understanding training and aging adaptations in muscle fibers.

The purpose of this paper is to review the research data reporting the size of the three primary types of human muscle fibers so as to clarify this apparent inconsistency. Research papers were found by searching Medline, Google scholar and Sport Discus databases, and from the reference lists of papers obtained. Textbooks were obtained by asking exercise science, anatomy and physiology professors at the authors' American university for the titles of the undergraduate texts commonly used in their field. For ease of organization, this review refers to fibers identified as either IIB or IIX in individual papers as IIB fibers, because the vast majority of the papers reviewed utilized myosin ATPase histochemistry to classify fibers, and in this classification scheme the label IIX is not used (Scott et al., 2001). Also, this review only discusses data from type I, IIA, and IIB fibers, although some studies included data from additional hybrid fiber types.

Muscle fiber size in nontrained human muscle

The human muscle most commonly used for studies requiring muscle biopsies is the vastus lateralis. Accordingly, there are an abundance of data describing the size of its muscle fibers, and those data are well represented by Staron and co-workers review (2000) of Staron's numerous previous studies (Table I). In that meta-analysis, data from previous studies were combined, yielding a total of 95 men and 55 women, with fiber types classified by ATPase histochemistry. The young adult subjects were nontrained, as defined as '...had not participated in any regular exercise program for at least 6 months...'. For men, the mean cross-sectional area of the type IIA fibers was significantly larger than the type IIB and type I fibers (data for women reported below) (Staron et al., 2000).

Seventeen additional primary research studies reporting the size of vastus lateralis muscle fibers in nontrained or recreationally active men were located (Table II). The data listed are from control subjects, and use pre-treatment values where measuring of the control group was repeated. While all the studies included statistical analysis, only a minority performed statistical tests to compare differences in the mean sizes of the three fiber types within the untrained control subjects, as this comparison was seldom a research question. Two of the four studies that reported relevant statistical testing demonstrated that type IIA fibers were the largest of the three fiber types (Gregory et al., 2001; Maughan & Nimmo, 1984), one reported that type IIA and IIB fibers were not significantly different in size and both were larger than type I fibers (Gregory et al., 2005), and one reported IIA fibers as significantly larger than IIB fibers but not significantly different in size from type I fibers (Hostler et al., 2001) (Table II). The remaining 13 studies did not include statistical tests comparing the sizes of the control fiber types. Data from these studies are included in Table II for comparison purposes, and will be discussed when summarizing the data.

For nontrained women, type I fibers were most commonly the largest of the three types, in contrast to the observation in men that the type IIA fibers almost always had the greatest mean size. In the meta-analysis performed in Staron's review (2000) (Table I) and in the primary studies that included relevant statistical testing (Table III), type IIB fibers were significantly smaller than both type I and IIA fibers (Hostler et al., 2001; Staron et al., 2000), or type II fibers in general were smaller than type I (Nygaard, 1981). Data from the remaining two studies, which lacked statistical comparison of fiber sizes, are included in Table III.

Studies reporting the cross-sectional size of the three categories of muscle fibers classified by myosin ATPase histochemistry in young adults are available for only a limited number of

Table I. Mean muscle fiber cross-sectional area[a] of three categories of human vastus lateralis muscle fibers, reported in a meta-analysis by Staron et al. (2000).

	Type I	Type IIA	Type IIB	Subject age (years)	Number of subjects	Statistical testing[b]	Statistical results
Men	4844 (1286)[c]	<u>6174</u>[d] (1587)	5160 (1324)	21.5 (2.4)[c]	95	Yes	IIA > I = IIB
Women	<u>4084</u> (895)[c]	3879 (867)	3116 (792)	21.1 (2.2)[c]	55	Yes	I = IIA > IIB

Note: For both sexes, type IIB fibers were not the largest.; [a] Mean cross-sectional area reported as μm^2.; [b] Statistical testing for differences in fiber size, across the three fiber types, within the control group was conducted in the study.; [c] Mean (standard deviation).; [d] The fiber type with the greatest mean value is identified by underline.

Table II. Studies reporting the mean cross-sectional area[a] of muscle fibers classified by myosin ATPase histochemistry in the vastus lateralis muscle of nontrained or recreationally active men.

Type I	Type IIA	Type IIB	Subject age (years)	Number of subjects	Statistical testing[b]	Statistical results	Source
4026 (699)[c]	4655[d] (879)	3865 (723)	28 (6)[c]	15	Yes	IIA > I = IIB	Maughan & Nimmo (1984)
5317 (1071)[c]	6594 (1377)	5146 (1126)	20.3 (1.1)[c]	10	Yes	I = IIA > IIB	Hostler et al. (2001)
5003 <311>[e]	6986 <299>	6777 <355>	33 <3>[e]	8	Yes	I < IIA = IIB	Gregory et al. (2005)
5127 <366>[e]	7873 < 645>	6176 <516>	28.5 (8)[c]	8	Yes	I < IIB < IIA[f]	Gregory et al. (2001)
4518 (1336)[c]	4718 (1143)	3901 (1299)	26.1 (3.5)[c]	37	No		Simoneau et al. (1985)
4137	4813	4210	18 [16–20][g]	8	No		Lüthi et al. (1986)
70 (13)[c] [h]	84 (12)	82 (17)	21.9 (1.3)[c]	25	No		Melichna et al. (1990)
medium [i]	large	small	college aged	12	No		Ratzin Jackson et al. (1990)
4113 <275>[e]	5796 <404>	4183 <418>	33 <1>[e]	8	No		Hather et al. (1991)
4840 <145>[e]	6455 <196>	5577 <194>	19.2 <0.5>[e]	6	No		Green et al. (1999)
5208 (1494)[c]	6070 (1944)	4648 (1043)	31.6 (9.8)[c]	6	No		Campos et al. (2002)
5022 (1060)[c]	5577 (1659)	4836 (1389)	38 (5)[c]	16	No		Häkkinen et al. (2003)
4320 <337>[e]	6267 <127>	5163 <412>	20.5 <1.0>[e]	12	No		Harber et al. (2004)
large [i]	medium	small	29.9 <2.01>[e]	5	No		D'Antona et al. (2006)
3611 <288>[e]	3734 <368>	3142 <337>	25 <1>[e]	13	No		Martel et al. (2006)
4647 (1775)[c]	5496 (1408)	4323 (1113)	20.6 (1.5)[c]	7	No		Kesidis et al. (2008)
medium [i]	large	small	25.1 (3.9)[c]	4	No		Vissing et al. (2008)

Note: In all the studies the mean cross-sectional area of the type IIA fibers was larger than type IIB fibers, although only four of these studies included tests of statistical significance when reporting the mean fiber sizes.; [a] Mean cross-sectional area reported as μm^2, except where individually noted.; [b] Statistical testing for differences in fiber size, across the three fiber types, within the control group was conducted in the study.; [c] Mean (standard deviation).; [d] The fiber type with the greatest mean value is identified by underline.; [e] Mean <standard error>.; [f] data presented here are only for the vastus lateralis muscle, while the statistical result is for data from vastus lateralis, soleus, tibialis anterior and lateral gastrocnemius (see Table IV) muscles combined.; [g] Mean [range].; [h] Mean fiber diameter (μm) reported.; [i] Mean fiber cross-sectional area data graphed, but specific values not reported.

Table III. Studies reporting the mean fiber cross-sectional area[a] of muscle fibers classified by myosin ATPase histochemistry, in the vastus lateralis muscle of nontrained women.

Type I	Type IIA	Type IIB	Subject age (years)	Number of subjects	Statistical testing[b]	Statistical results	Source
large[c f]	medium	small	26 [22–40] [d]	42	Yes	I > II	Nygaard (1981)
3948 (541)[e]	4389 (771)	3490 (763)	20.2 (1.2)[e]	16	Yes	I = IIA > IIB	Hostler et al. (2001)
4114 (920)[e]	3585 (1127)	2773 (1162)	24.6 (3.7)[e]	38	No		Simoneau et al. (1985)
2819 <264>[g]	2583 <271>	1988 <466>	26 <0.4>[g]	9	No		Martel et al. (2006)

Note: In most cases type I fibers were the largest, although statistical testing for the mean differences observed was conducted in only two of the studies.; [a] Mean cross-sectional area reported as μm^2, except where individually noted.; [b] Statistical testing for differences in fiber size, across the three fiber types, within the control group was conducted in the study.; [c] Mean fiber cross-sectional area data graphed, but specific values not reported.; [d] Mean [range].; [e] Mean (standard deviation).; [f] The fiber type with the greatest mean value is identified by underline.; [g] Mean <standard error> .

muscles other than the vastus lateralis. For men (Table IV), one study showed no significant difference in the mean size of the three fiber types in two different regions of the erector spinae muscle (Mannion et al., 1997), while in another study, type IIA fibers were found to be significantly larger than the other fiber types in three lower leg muscles (Gregory et al., 2001). Fiber size data from the four muscles examined without statistical comparisons are also included in Table IV.

For women (Table V), in two regions of the erector spinae muscle type I muscle fibers were significantly larger than the other fiber types (Mannion et al., 1997), while in the deltoid muscle there was no significant difference in the size of the three fiber types (Nygaard, 1981). Four additional studies provided data on fiber sizes in additional muscles examined in women, although without statistical comparisons (Table V).

A study by Häggmark et al. (1979) is reported separately here (Table VI) because its data from four abdominal muscles were combined from nine women and four men. Statistical examination revealed that all three fiber types were the same size in two muscles, type IIA and IIB fibers were the same size and larger than type I in one muscle, and type I fibers were the largest in the remaining muscle examined.

Only two human studies were found that reported the size of nontrained muscle fibers identified using the slow oxidative (SO), fast oxidative glycolytic (FOG) and fast glycolytic (FG) classification system. Some studies use the metabolic SO, FOG, FG nomenclature, although they do not classify fibers based on their myosin ATPase and metabolic properties as the classification system intended, and instead use other methods such as z-band width or only myosin ATPase data. Only studies using myosin ATPase and metabolic properties to classified fibers as SO, FOG, and FG are considered here. Prince et al. (1976, 1977) examined the vastus lateralis muscle of five men and five women who were nontrained or recreationally physically active. The women were of college age. The age of the men was not reported, but they were probably young adults as these controls were being compared with trained athletes. Notably, the authors commented that the human muscles differed from muscles in lower mammals in that the FOG fibers rather than the FG fibers were the largest (Prince et al., 1976). Saltin et al. (1977) also described human vastus lateralis muscle fiber properties in a review paper, using the slow twitch (ST), fast twitch subgroup a (FTa) and fast twitch subgroup b (FTb) nomenclature. They provided data reporting the myosin ATPase activity, fiber size, and glycolytic and oxidative enzymatic activity of the fibers examined. The fibers they listed as ST match others' (Peter et al., 1972) definition of SO, their FTa fibers match FOG fiber characteristics, and their FTb fibers match FG fibers. Although statistical tests of the differences in mean fiber sizes were not performed in these studies (Prince et al., 1976, 1977; Saltin et al., 1977), the data are included in Table VII for comparison with the size data in the previous tables for fibers classified by myosin ATPase histochemistry.

Summary of data on muscle fiber size in nontrained human muscle

In studies which included a statistical comparison of mean fiber sizes, in men type IIA fibers were most commonly the largest (six out of 10 cases); in two cases there was no difference in the size of the three fiber types; and in the remaining two cases type IIA fibers were the largest together with either type IIB or type I fibers. In women, type I fibers were most commonly the largest (three out of six cases); in two cases type I fibers were the largest together with type IIA fibers; and in one case there was no significant difference in the size of the three fiber types. In the one study which combined abdominal muscle data from men and women, in two muscles there was no significant difference in muscle fiber sizes across the three types, in one muscle

Table IV. Studies reporting the mean cross-sectional area[a] of muscle fibers classified by myosin ATPase histochemistry in muscles other than the vastus lateralis of nontrained or recreationally active men.

Muscle	Type I	Type IIA	Type IIB	Subject age (years)	Number of subjects	Statistical testing[b]	Statistical results	Source
Thoracic erector spinae	6314 (1245)[c]	6707[d] (2531)	6032 (2574)	23.0 (4.3)[c]	17	Yes	I = IIA = IIB	Mannion et al. (1997)
Lumbar erector spinae	5058 (1349)[c]	4941 (1371)	4703 (1703)	23.0 (4.3)[c]	17	Yes	I = IIA = IIB	Mannion et al. (1997)
Soleus	5235 <333>[h]	7505 <465>	6053 <526>	28.5 (8)[c]	8	Yes	I < IIB < IIA[i]	Gregory et al. (2001)
Tibialis anterior	4381 <340>[h]	7926 <232>	6956 <367>	28.5 (8)[c]	8	Yes	I < IIB < IIA[i]	Gregory et al. (2001)
Lateral gastrocnemius	5209 <513>[h]	6723 <692>	6138 <461>	28.5 (8)[c]	8	Yes	I < IIB < IIA[i]	Gregory et al. (2001)
Lumbar longissimus	70 (7)[c e]	74 (8)	71 (9)	[20–30][f]	9	No		Thorstensson & Carlson (1987)
Lumbar multifidus	67 (7)[c e]	75 (13)	70 (14)	[20–30][f]	9	No		Thorstensson & Carlson (1987)
Vastus medialis longus	60.1 (12.5)[c e]	59.2 (12.2)	56.5 (12.3)	29.3 [18–44][g]	9	No		Travnik et al. (1995)
Vastus medialis obliquus	63.8 (13.5)[c e]	63.9 (14.4)	56.7 (14.2)	29.3 [18–44][g]	9	No		Travnik et al. (1995)

Note: In most muscles, type IIA fibers were the largest, although statistical comparison of mean sizes were performed in only the first five cases listed.; [a] Mean cross–sectional area reported as μm^2, except where individually noted.; [b] Statistical testing for differences in fiber size, across the three fiber types, within the control group was conducted in the study.; [c] Mean (standard deviation).; [d] The fiber type with the greatest mean value is identified by underline.; [e] Mean fiber diameter (μm) reported.; [f] [Range].; [g] Mean [range].; [h] Mean <standard error> .; [i] Statistical result for data from vastus lateralis (see Table II), soleus, tibialis anterior and lateral gastrocnemius muscles combined.

Table V. Studies reporting the mean cross-sectional area[a] of muscle fibers classified by myosin ATPase histochemistry in muscles other than the vastus lateralis of nontrained women.

Muscle	Type I	Type IIA	Type IIB	Subject age (years)	Number of subjects	Statistical testing[b]	Statistical results	Source
Deltoid	Medium[c]	Largest[d]	smallest	26 [22–40][e]	25	Yes	I = IIA = IIB	Nygaard (1981)
Thoracic erector spinae	4846 (1149)[f]	3343 (1081)	2981 (930)	29.4 (10.6)[f]	14	Yes	I > IIA = IIB	Mannion et al. (1997)
Lumbar erector spinae	3809 (664)[f]	2560 (676)	2374 (723)	29.4 (10.6)[f]	14	Yes	I > IIA = IIB	Mannion et al. (1997)
Lumbar longissimus	62 (5)[f g]	50 (12)	48 (8)	[20–30] [h]	7	No		Thorstensson & Carlson, (1987)
Lumbar multifidus	63 (7)[f g]	49 (10)	43 (8)	[20–30] [h]	7	No		Thorstensson & Carlson, (1987)
Iliocostalis and longissimus	Largest[c i]	Largest[i]	Smallest	23.4 (5.8)[f]	9	No		Mannion et al. (1998)
Trapezius	4127 [2756–5876][e]	3669 [2194–5381]	3791 [2462–6370]	48 (6)[f]	19	No		Larsson et al. (2001)

Note: In most cases type I fibers were the largest, however, statistical tests for differences in mean sizes were included in only three of the muscles examined.; [a] Mean cross-sectional area reported as μm^2, except where individually noted.; [b] Statistical testing for differences in fiber size, across the three fiber types, within the control group was conducted in the study.; [c] Mean fiber cross-sectional area data graphed, but specific values not reported.; [d] The fiber type with the greatest mean value is identified by underline.; [e] Mean [range].; [f] Mean (standard deviation).; [g] Mean fiber diameter (μm) reported.; [h] [Range].; [i] Type I and IIA same size.

Table VI. Study data reporting the mean fiber diameter[a] of muscle fibers classified by myosin ATPase histochemistry in nontrained abdominal muscles in nine women and four men.

Muscle	Type I	Type IIA	Type IIB	Subject age (years)	Number of subjects	Statistical testing[b]	Statistical results	Source
Rectus abdominis	50 (10)[c]	52[d] (14)	52 (15)	44 [24–55][e]	13	Yes	I = IIA = IIB	Häggmark & Thorstensson (1979)
Obliquus externus	50 (8)[c]	52 (14)	54 (12)	44 [24–55][e]	13	Yes	I = IIA = IIB	Häggmark & Thorstensson (1979)
Obliquus internus	50 (14)[c]	51 (15)	52 (15)	44 [24–55][e]	13	Yes	I < IIA = IIB	Häggmark & Thorstensson (1979)
Transverse abdominis	49 (10)[c]	47 (9)	43 (8)	44 [24–55][e]	13	Yes	I > II & IIA > IIB	Häggmark & Thorstensson (1979)

[a] Mean fiber diameter reported as μm.; [b] Statistical testing for differences in fiber size, across the three fiber types, within the control group was conducted in the study.; [c] Mean (standard deviation).; [d] The fiber type with the greatest mean value is identified by underline.; [e] Median [range].

Table VII. Mean muscle fiber cross-sectional area[a] of three categories of human vastus lateralis muscle fibers, reported by studies using metabolic classification systems.

	SO or ST	FOG or FTa	FG or FTb	Subject age (years)	Number of subjects	Statistical testing[b]	Source
Men	3303[c]	4105[d]	3418	Not reported	5	No	Prince et al. (1976, 1977)
Men	5310 (1210)[e]	6110 (1200)	5600 (1450)	[20–30][f]	10	No	Saltin et al. (1977)
Women	2784[c]	3392	2425	College aged	5	No	Prince et al. (1976, 1977)
Women	3948 (740)[e]	3637 (820)	2235 (605)	[20–30][f]	25	No	Saltin et al. (1977)

Note: In most cases, type FOG, interchangeably called FTa, fibers exhibited the largest mean size, although statistical testing of size differences was not conducted.; [a] Mean cross-sectional area reported as μm^2.; [b] Statistical testing for differences in fiber size, across the three fiber types, within the control group was conducted in the study.; [c] Variability measures of group means were not reported.; [d] The fiber type with the greatest mean value is identified by underline.; [e] Mean (standard deviation).; [f] [Range].

type IIA and IIB fibers were not significantly different and were larger than type I, and in the fourth muscle type I fibers were the largest. Notably, none of these studies reported that type IIB fibers were significantly larger than both of the other fiber types, and in only seven out of 20 cases were IIB fibers the largest in size with one or two of the other fiber types.

Studies that did not include a statistical comparison of mean fiber sizes cannot be used to demonstrate differences or similarities in the size of the different fiber types. The pattern of mean fiber sizes is, however, important as the IIB, or FG, fiber type has never been reported to have a larger mean size than the other two types.

Why do fiber size descriptions in textbooks commonly not match the research data?

The initial work documenting motor unit and muscle fiber properties was conducted using cat hind limb muscles, and found that muscle fibers within the greatest force producing fast fatigable (FF) motor units have the largest cross-sectional area, compared with muscle fibers within type slow (S) or type fast and resistant to fatigue (FR) motor units (Pierotti et al., 1991; Unguez et al., 1993). Muscle fibers in FF motor units were subsequently identified as type FG muscle fibers (Clamann, 1993), and in the cat hindlimb type FG muscle fibers have the largest mean cross-sectional area of the three fiber types (SO, FOG, FG) (Martin et al., 1988; Roy et al., 1992). These animal data have been reported in physiology textbooks (Burke, 1981) and in an early review paper on motor unit and muscle fiber properties by Burke and Edgerton in the journal *Exercise and Sport Sciences Reviews* (1975). It is essential to note that in Burke and Edgerton's review in a journal devoted to exercise and sport sciences, virtually all of the data presented, and all of the muscle fiber size data, were animal (typically feline) rather than human. This is an important consideration given that large interspecies differences in muscle fiber and motor unit properties are known to exist (Clamann, 1993; Prince et al., 1976, 1981; Saltin et al., 1977; Simoneau, 1990).

Accordingly, a likely explanation of the mistakes seen in some human physiology, anatomy and exercise science textbook descriptions of muscle fiber sizes is that animal data may have been presented without being labeled as such, and without the caveat of interspecies differences in muscle fiber properties. For example, the exercise physiology text by Plowman and Smith (2008), when stating that type FG fibers are the largest of the three fiber types, does not mention species (pp. 515–6, Table 19.2, Figure 19.15) and cites a previous exercise physiology text by Edington and Edgerton (1976). Plowman and Smith's Figure 19.15 illustrating that type FG muscle fibers are the largest of the three fiber types is adapted from Edington and Edgerton's Figure 4–2, which also does not mention species. These figures, however, are the same as presented in Figure 1 in the review article by Burke and Edgerton (1975), in which the data are labeled as being from motor units in the cat medial gastrocnemius muscle. Clearly, the identification of the species under examination was lost as the data moved from source to source. Similarly, in McArdle et al.'s exercise physiology text (2007), type IIB muscle fibers are listed as the largest, with the table reporting this information citing an article in *Exercise and Sport Sciences Reviews* by Kraus et al. (1994). The data presented and relevant sources cited by Kraus et al. showing type IIB fibers as the largest type, however, are animal data. This review by Chalmers and Row found one human exercise physiology text that did state that its muscle fiber data were from animals as well as humans (Tipton, 2006). Unfortunately, however, the text did not specify which muscle fiber properties were from which species (Tipton, 2006). Notably, in Enoka's text *Neuromechanics of Human Movement* the table reporting that type IIB fibers are the largest of the three fiber types clearly states that the data are from cat muscle (Enoka, 2008), although the reader is not cautioned that these muscle characteristics may not apply to human muscle.

Human muscle fiber size data and the size principle

Researchers examining human muscle have described type IIB muscle fibers as '. . . rarely recruited and activated . . . ' (Staron et al., 1989) and '. . . used to meet the demands of unaccustomed physical activity' (Adams et al., 1993), which indicates that type IIB fibers are found late in the recruitment order. The fact that type IIB muscle fibers are not the largest in humans does not violate the size principle because the size principle is based on motor neuron size (Henneman et al., 1965), not muscle fiber size. It has been reported for humans that the magnitude of motor unit tension increases through the recruitment order (Dideriksen et al., 2010; Milner-Brown et al., 1973). If type IIB muscle fibers are not the largest fiber type, how can they produce greater motor unit forces than previously recruited motor units, some of which may consist of similarly sized or larger muscle fibers? This would be possible if the number of muscle fibers innervated by the larger, later recruited, motor neurons in humans is greater than the number of muscle fibers innervated by smaller motor neurons. Innervation ratio is difficult to quantify definitively, even in animals, because it requires the counting of all the muscle fibers innervated by a single motor neuron (Lieber, 2010). In humans, indirect evidence suggests that motor neurons with larger twitch forces, later in the recruitment order, innervate a greater number of muscle fibers (Buchthal et al., 1959; Hamilton-Wright & Stashuk, 2005), which could allow a greater motor unit force production even if the muscle fibers were a similar size or smaller than previously recruited muscle fibers.

Implications

To understand the contribution of different types of muscle fibers to force generation, and the adaptive changes in muscle fiber size following chronic changes in activity or with aging, it is essential to start with correct information about the size of type identified fibers in nontrained muscle of young adults, including gender specific differences. Unfortunately, it is the authors' experience that students typically enter advanced exercise science classes with the wrong belief that type IIB fibers are the largest fiber type in humans, learned from the textbooks used in anatomy and introductory exercise science classes. This creates confusion when the students are exposed to research literature that accurately reports fiber sizes as discussed in this review, and when students interpret reported changes in muscle fiber sizes. For example, it has been reported that resistance training may result in a reduction in the proportion of type IIB fibers in a muscle, as a greater proportion of fibers express type IIA myosin heavy chain (Campos et al., 2002; Hather et al., 1991; Staron et al., 1989). It can, perhaps, contribute to understanding why this could be advantageous when it is realized that the shift is occurring in a direction towards type IIA muscle fibers that are most commonly innately larger (13 out of 20 cases examined with statistical analysis), or may be equal in size (seven out of 20 cases) compared with IIB fibers, and not that the largest fiber type in the nontrained muscle is being lost. Similarly, the observation that detraining or spinal cord injury produces an increased proportion of type IIB fibers in afflicted muscles (Biering-Sørensen et al., 2009; Staron et al., 1991) may be better understood by recognizing that in these reduced activity situations, type IIA muscle fibers are not converting to a fiber type that is innately larger. Course instructors and textbook authors, in human focused programs such as exercise science, could best prepare students with regard to muscle physiology if they made it clear when they were describing human versus animal data, and if when presenting animal data they included a caution regarding possible interspecies differences.

Acknowledgements

The authors thank Dr. Jeff Ives and Dr. Dave Suprak for comments made during the preparation of this manuscript.

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