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ORIGINAL COMMUNICATION

Fiber Type Composition and Maximum Shortening Velocity of Muscles Crossing the Human Shoulder

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A study of the fiber type composition of fourteen muscles spanning the human glenohumeral joint was carried out with the purpose of determining the contribution of fiber types to overall muscle cross-sectional area (CSA) and to estimate the maximum shortening velocity (V_{max}) of those muscles. Muscle biopsies were procured from 4 male cadavers (mean age 50) within 24 hr of death, snap frozen, mounted, and transversely sectioned (10 μm). Slides were stained for myofibrillar ATPase after alkaline preincubation. Photoimages were taken of defined areas (100 fibers) using the Bioquant system, and fiber type and CSA were measured from these images. Staining for mATPase produced three different fiber types: slow-oxidative (SO), fast-oxidative-glycolytic (FOG), and fast-glycolytic (FG). On average, the muscle fiber type composition ranged from 22 to 40% of FG, from 17 to 51% of FOG, and from 23 to 56% of SO. Twelve out of the 14 muscles had average SO proportions ranging from 35 to 50%. V_{max} was calculated from the fiber type contribution relative to CSA and shortening velocity values taken from the literature. The maximum velocities of shortening presented here provide a physiological basis for the development of human shoulder musculoskeletal models suitable for predicting muscle forces for functionally relevant tasks encompassing conditions of muscle shortening and lengthening. Clin. Anat. 20:144–149, 2007.

Key words: shoulder; elbow; muscle architecture; fiber type

INTRODUCTION

Maximum velocity of muscle shortening is an important parameter in musculoskeletal models (McGill and Norman, 1986; Kaufman et al., 1991; Thelen, 2003). In formulations accounting for force generation during eccentric or concentric muscle contractions, a muscle's shortening velocity at a point in time is normalized against its maximum shortening velocity to determine muscle force (Hatze, 1978, 1981; Zajac, 1989). It has been shown that muscles are able to effectively generate muscle force under shortening or lengthening contractions in proportion to the fiber type composition (Bárány, 1967; Thorstensson et al., 1976). Fiber type composition can be determined by histochemical staining used to identify the mATPase activity according to three groups: type I, type IIa, and type IIb (Burke, 1981). More recently immunohistochemical assays have been used to correctly identify previously considered type IIb fibers as type IIx (Smerdu et al., 1994; Bamman et al., 1998; Scott et al., 2001). In their review article detailing fiber type staining methodologies, Scott et al. (2001) stated that the I, IIa, and IIx fiber types can be identified by their relative speed and oxidative/glycolytic capabilities as slow-oxidative (SO),

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TABLE 1. Sampling of Fibers for Analysis in Shoulder Muscles

Muscle	Abbrev.	*N* (specimens)	*N* (areas)	*N* (fibers)
Anterior deltoid	AD	4	22	1,603
Middle deltoid	MD	4	31	2,124
Posterior deltoid	PD	4	35	2,036
Coracobrachialis	Cb	1	9	898
Infraspinatus	Inf	3	13	768
Subscapularis	SbS	4	29	2,033
Supraspinatus	SSP	3	20	1,119
Teres minor	Tmi	2	7	495
Teres major	Tma	4	30	1,579
Latissimus dorsi	LD	3	45	1,896
Long head biceps	LHB	3	22	1,832
Short head biceps	SHB	3	24	1,599
Long head triceps	Tri	4	41	3,013
Pectoralis	Pec	3	31	1,580

fast-oxidative-glycolytic (FOG) and fast-glycolytic (FG), respectively. Consequently, the force generating potential of muscle under shortening or lengthening conditions is dependent on the relative contributions of muscle fibers containing the various myosin isoforms, slow-oxidative (SO), fast-oxidative-glycolytic (FOG), and fast-glycolytic (FG) fibers, to the muscle as a whole. As their names suggest, each fiber type is known to possess different maximum shortening velocities, which are described in some range (Thorstensson et al., 1976; Larsson and Moss, 1993; Larsson et al., 1997; Cheng et al., 2000) for each muscle fiber type.

Previous studies have examined the fiber type composition for a subset of upper extremity muscles (Jennekens et al., 1971; Johnson et al., 1973) or for individual upper extremity muscle (Jozsa et al., 1978; Fitts et al., 1989; Klitgaard et al., 1990; Jürimäe et al., 1996; Trappe et al., 2000); in addition, fiber type cross-sectional areas (CSA) have been measured in supraspinatus and deltoid muscles (Gansen and Irlenbusch, 2002). However, a complete set of fiber typing and CSA analysis data for all of the 14 muscles that cross the human glenohumeral joint is unavailable.

There were three objectives of this study: (1) to measure the relative fiber type composition of 14 muscles spanning the glenohumeral joint in muscle biopsies from recently deceased human bone and soft tissue donors; (2) to determine the contribution of each fiber type to the overall muscle CSA; and (3) to estimate the maximum shortening velocity of each of these muscles.

MATERIALS AND METHODS

Up to 14 muscles crossing the glenohumeral joint were dissected from four adult human males within 24 hr of death. All muscle biopsies were obtained from anatomical donors intended for bone and soft tissue recovery for transplant; that is, the dissections and muscle biopsies performed for this study were secondary to bone recovery for transplant. The tissue recovery process, specifically the removal of the humerus, led to the disruption of the muscles requested for this study. As a result, complete sets of all 14 muscles were not obtained from each donor. Additionally, volumes of muscle were not consistently obtainable from specific different depths of the same muscle. Thus, volumes obtained were classified only by muscle region (anterior deltoid vs. middle deltoid, etc.). The donors ranged in age from 17 to 75 years-old (mean 50); each donor was screened by the tissue procurement agency for research suitability and had no history of shoulder surgery, musculoskeletal injury, or musculoskeletal disease.

Muscle samples were removed from the right side of the body, snap frozen at -196°C in liquid nitrogen, and stored at -80°C. The muscle samples were later divided into blocks approximating 1 cm^3 and mounted in Optimal Cutting Temperature embedding medium (Sakura Finetek, Torrance, CA). After warming the blocks to -25°C, transverse sections (10 μm) were cut using a cryostat. Sections (6–10 per block) were mounted on gelatin coated slides and air dried for between 15 min and 1 hr prior to staining. Following alkaline preincubation at a pH of 10.4, the sections were stained for myofibrillar ATPase at a pH of 9.4, according to the procedure described by Guth and Samaha (1970) with the same modifications made by Singh et al. (2002).

A pilot study was conducted to assess the inter-rater reliability of fiber typing and CSA determination, as described by Portney and Watkins (1993). Two people independently graded the type and the CSAs of 100 fibers.

The average fiber type proportion was determined across the four donors. As described by Singh et al. (2002), areas (each of ~50–100 fibers) were selected from a muscle section for analysis. Areas were chosen based on the following exclusion criteria: two toned fibers, lack of distinct fiber outline, and incomplete muscle fibers. The specific number of areas and muscle of origin are listed in Table 1. Photoimages of each of the areas were taken using the Bioquant system with a camera (BIOQUANT Image Analysis Corporation, Nashville, TN) connected to a light microscope. The fiber type classification was carried out in Photoshop 7.0 (Adobe Systems, San Jose, CA) by the two individuals who took part in the inter-rater reliability pilot study. According to the criteria outlined by McIntosh et al. (1985) and Richmond et al. (1999) lightly staining fibers were classified as type I or slow-oxidative (SO), intermediate staining fibers were classified as type IIa or fast-oxidative-glycolytic (FOG), and dark staining fibers were classified as type IIx or fast-glycolytic (FG). The muscle of origin and the corresponding number of specimens, areas, and fibers are listed in Table 1. Average fiber type proportions were calculated for each muscle and recorded in Table 2.

Fiber CSA was also measured for each of the three fiber types using Photoshop 7.0. According to the procedure described by Singh et al. (2002), 20 fibers of each type

TABLE 2. Relative Proportions of Fiber Types, Contributions of Each Fiber Type to Whole Muscle CSA, and the V_{max} Values for Shoulder Muscles

	Mean % (SD)			CSA %			V_{max}
	FG	FOG	SO	FG	FOG	SO	(Lo/s)
AD	27 (11)	25 (10)	47 (9)	21	23	55	1.2
MD	30 (10)	23 (9)	47 (12)	33	21	46	1.6
PD	27 (13)	17 (6)	56 (14)	28	14	57	1.4
Cb	26	51	23	17	54	29	1.3
Inf	29 (10)	23 (11)	48 (14)	23	24	54	1.3
SbS	38 (9)	25 (7)	37 (10)	34	24	42	1.6
SSP	29 (14)	21 (5)	50 (15)	28	21	51	1.4
Tmi	22 (7)	29 (8)	49 (11)	18	29	53	1.2
Tma	23 (10)	29 (11)	48 (14)	20	32	48	1.2
LD	35 (9)	17 (10)	48 (12)	33	20	47	1.6
LHB	36 (15)	25 (10)	39 (10)	37	31	32	1.8
SHB	40 (13)	23 (13)	37 (8)	35	26	38	1.7
Tri	30 (11)	27 (14)	44 (14)	29	28	43	1.5
Pec	40 (14)	25 (14)	35 (7)	38	26	36	1.8

were selected and analyzed from three representative areas in up to fourteen muscles from each of the four donors. Average CSA ratios were calculated for the slow-oxidative and/or fast-oxidative-glycolytic fibers for each individual muscle. These ratios were used to calculate the relative contribution to total muscle CSA by each fiber type (Table 2).

Maximum velocities of shortening were calculated by weighting the velocities of shortening for each fiber type by the relative contribution to total muscle CSA. Velocities of shortening for slow-oxidative (0.35 L_0/sec), fast-oxidative-glycolytic (1.07), and fast-glycolytic (3.68) fibers were taken from the literature of Larsson and Moss, (1993). Two-sample *t*-tests were used to test for differences in mean fiber types between agonists and antagonists for shoulder rotation, ab/adduction, flexion/extension, and elbow flexion/extension.

RESULTS

The results of the pilot study determined intraclass correlation coefficients of 0.99 for both determination of fiber type, and determination of fiber CSA. Our method for determining these measures was therefore determined to be reliable. For each muscle the number of specimens and areas sampled, as well as the total number of fibers analyzed, were recorded (Table 1). Across the four donors over 22,000 muscle fibers were analyzed. The mean and range of fiber type proportions for the muscles varied considerably (Table 2). On average, the muscle fiber type composition ranged from 22 to 40% of FG, from 17 to 51% of FOG, and from 23 to 56% of SO. For all muscles except coracobrachialis, pectoralis, subscapularis, and biceps (short head), SO type fibers were generally more highly present (37 to 56%) than the other types.

The relationship between the different fiber types was observed by plotting the percentages of FG or FOG fiber types against the slow fiber types (SO) for each of the muscles measured (Fig. 1). The percentages of FOG and SO fibers were inversely correlated with each other ($r^2 = 0.42$, $P < 0.05$), and the proportions of FOG and FG ($r^2 = 0.10$) and FG and SO ($r^2 = 0.22$) were not correlated with one another ($P > 0.05$).

Most of the studied muscles (12/14) had average SO proportions of 35–50%. Two muscles did not fall in this range. The posterior deltoid had a particularly high average SO proportion of 56%, whereas the coracobrachialis had a low average SO proportion of 23%. Coracobrachialis was the only muscle with FOG fibers, making the largest contribution (51%). However, these findings may not be typical as samples of coracobrachialis were obtained from only one specimen.

We tested for differences in the relative proportions of the different fiber types between elbow flexors and extensors and found no significant differences. We grouped muscles according to their function at the shoulder (flexors vs. extensors, abductors vs. adductors, internal vs. external rotators), and found no statistically significant differ-

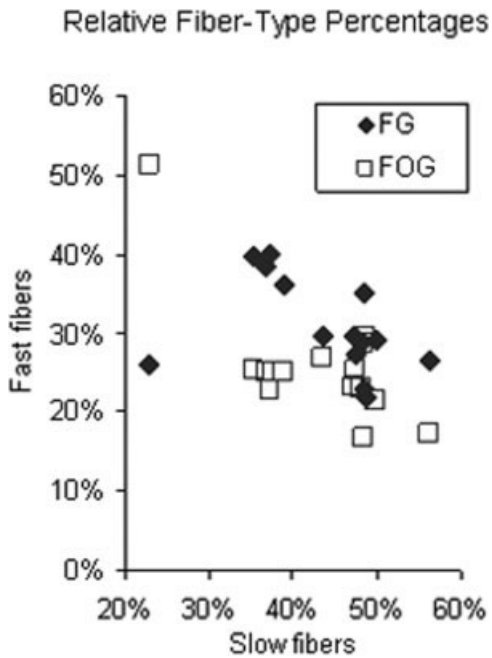

Fig. 1. Proportions of FG (dark diamonds) and FOG (open squares) versus SO fibers.

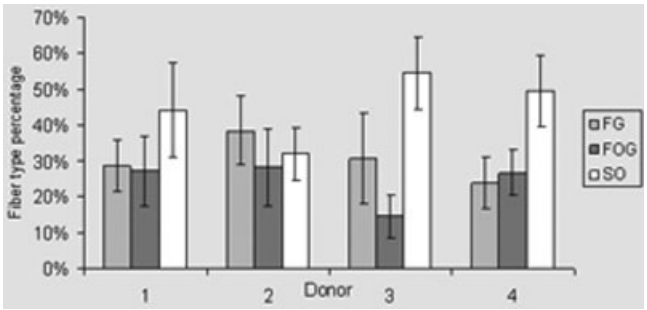

Fig. 2. Mean fiber type composition by donor. The respective ages for the donors 1–4 were as follows: 57, 51, 75, and 17.

ence in fiber type proportions, except for the proportions of FOG fibers between abductors and adductors ($P = 0.026$).

Measurements of fiber type CSA demonstrated considerable variability among different muscles (Table 2). Additionally, there was considerable variability for the fiber type composition and CSA ratios by specimen. SO fibers were the most predominant fiber type for donors 1, 3, and 4 (respective ages of 57, 75, and 17 years-old). For donor 2, age 51, FG fibers contributed most to the fiber type composition. FOG fibers made the smallest contribution for donors 1, 2, and 3. For donor 4, FG fibers contributed the least to the fiber type composition (Fig. 2). For donors 1 and 2, with respective ages of 57 and 51 years-old, the average CSA contribution for the FG fibers was less than that made by both the SO and FOG. For donor 3, age 75 years-old, the average FG fiber CSA was greater than the average FOG CSA and the average SO CSA. However, for donor 4, age 17 years-old, the average FG CSA was greater than the average SO CSA and less than the average FOG CSA (Fig. 3).

The maximum shortening velocities determined for each of the fourteen muscles ranged from 1.2 to 1.8 L_0/sec (Table 2). Arranged from slowest to fastest, the order of muscles is as follows: anterior deltoid, teres minor, and teres major (1.2 L_0/sec), coracobrachialis and infraspinatus (1.3 L_0/sec), posterior deltoid and supraspinatus (1.4 L_0/sec), triceps (1.5 L_0/sec), middle deltoid, latissimus dorsi, and subscapularis (1.6 L_0/sec), short head of biceps (1.7 L_0/sec), long head of biceps, and pectoralis (1.8 L_0/sec).

DISCUSSION

Fiber type data has been collected for muscles crossing the glenohumeral joint and has been used to estimate the maximum velocity of shortening of each muscle (V_{max}); this is a crucial parameter when incorporating the force-velocity relationship into a musculoskeletal model. The data presented here increases our understanding of the performance of shoulder muscles under nonisometric conditions, and allows for models to be constructed for predicting muscle forces under conditions of muscle shortening or lengthening.

Little attention is given to values for V_{max} in upper extremity musculoskeletal models, despite the fact that maximum velocities of shortening for each muscle fiber type are relatively well established. The models are used to make muscle force predictions for isometric, isokinetic, and isotonic conditions. Prediction of muscle forces for the isometric case is relatively simple. But in cases where the models are used to predict forces for conditions of muscle lengthening or shortening, predicted forces are dependent on the maximum velocity of shortening. The development of an upper extremity model for isokinetic conditions at increasing joint velocities, as has been done for other extremities, necessitates an accurate and complete dataset of muscle fiber type composition as well as maximum shortening velocities. This requirement is increasingly important when considering the current paradigm of measuring joint kinematics and calculating muscle kinematics (i.e., velocity of shortening at a point in time) for concentric and eccentric muscle conditions.

Models of the lower extremity have been used to make predictions of how various factors alter the V_{max} and commensurate force generation in aged human subjects (Thelen et al., 2003). For the shoulder, such an examination would be interesting, but without a complete dataset, the exercise would be little more than a sensitivity analysis. The data presented here serves as a baseline set of values.

Of note, Johnson et al. (1973) measured muscle fiber types in six upper extremities for deltoid, triceps, supraspinatus, pectoralis major, latisimus dorsi, and biceps brachii but did not differentiate between FG and FOG fibers. When we examine the data from this study, combining FOG and FG fibers as fast fibers, we see relatively favorable comparison with that presented by Johnson et al. (1973) (Fig. 4).

Models of the shoulder and upper extremity have used a wide range of maximum shortening velocities. There appears to be no consensus of appropriate values. Zajac (1989) suggests that 10 L_0/sec is appropriate, and this value was used in an early upper extremity version of SIMM (Delp and Loan, 1995). Other models have used 5 L_0/sec (Happee and Van der Helm, 1995), and 10 L_0/sec (Soechting and Flanders, 1997). The data presented here suggests that the maximum velocities of shortening of upper extremity muscles are less than the range of values used in these models. Consequently, the forces predicted from models using the values presented here would be greater than the values previously reported.

Practical neuromusculoskeletal models, whether they be based on optimal control (Pandy et al., 1995; Thelen et al.,

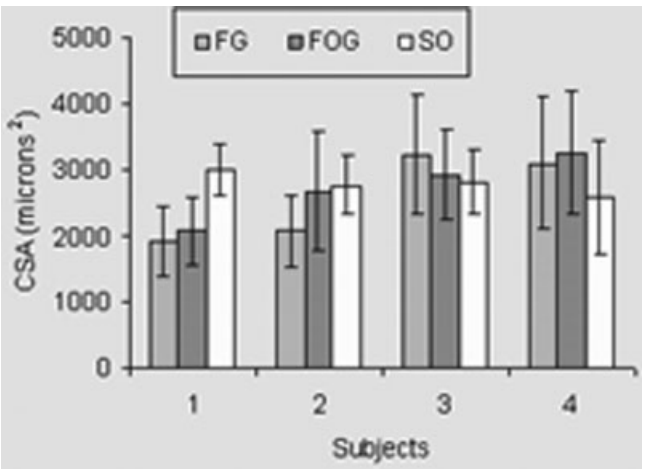

Fig. 3. Mean fiber CSA (μm^2) for each individual donor. The respective ages for the donors 1–4 were as follows: 57, 51, 75, and 17.

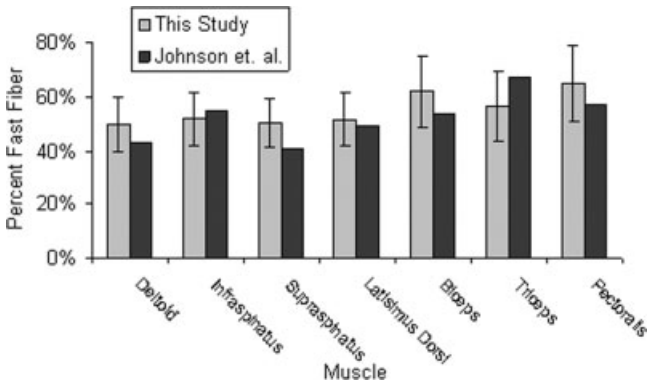

Fig. 4. Mean fast fiber contribution across donors for this study and for the study of Johnson et al. (1973). Johnson et al. (1973) reported deltoid and triceps measured at the surface and deep regions, and pectoralis major was measured for the sternal and clavicular heads. For these muscles, the values presented in this chart are the averages of values reported in Johnson et al. (1973).

2003) or filtered electromyographic signals (Manal et al., 2002; Langenderfer et al., 2005), assume an independence between neural activation and maximum shortening velocity. Some models assume linear scaling (Manal et al., 2002; Langenderfer et al., 2005). The size principle of motorunit recruitment, however, requires small motor units containing SO fibers to be recruited first. That is, there is not a fixed proportion of fiber types recruited across activation level. Therefore, submaximal shortening velocity of a muscle may not scale linearly with activation. The maximum velocity of shortening data reported here should be used in modeling studies with this caveat in mind.

Previous studies have shown that fiber type composition and CSA varies with age (Klitgaard et al., 1990; Larsson et al., 1997). Because of the small number of donors used in this study, it was not possible to draw definitive conclusions regarding differences in fiber type composition and CSA relative to age. However, this data was collected on predominantly aged donors, and is therefore most appropriate for modeling muscle force for people in the fifth through seventh decades of life. Because of the tissue procurement method, a second limitation of this study was the inability to analyze fiber type distribution within different depths of the same muscle.

A third limitation of this study is that fiber type shortening velocities were not measured directly, but were taken from the literature (Larsson and Moss, 1993), and used to estimate muscle shortening velocities based on their proportion of CSA. Larsson and Moss (1993) reported shortening velocities for fibers obtained using two different methods: chemical skinning and freeze-drying. The mean maximum shortening velocities determined with the chemically skinned method were used in this study. While the results for type I fibers were similar using the two methods (0.35 $\pm$ 0.16 vs. 0.31 $\pm$ 0.14 L_0/sec), the velocities for the faster fibers were reduced for the freeze-drying method as compared to the chemically skinned results (1.07 $\pm$ 0.37 vs. 0.77 $\pm$ 0.47 for type IIA fibers, and 3.68 vs. 3.04 $\pm$ 0.86 for type IIB fibers). As a result, the data reported here may slightly overestimate maximum velocities of shortening, particularly for muscles composed of greater proportions of fast muscle fibers.

Despite its limitations, to date, this study is the most comprehensive description of muscle fiber type and maximum shortening velocities for muscles crossing the shoulder joint. The data presented here provide values for maximum velocities of shortening for use in musculoskeletal models, which can be used to predict physiologically based muscle forces for functionally relevant tasks under conditions of muscle shortening and lengthening.

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