

You might find this additional information useful...

This article cites 45 articles, 21 of which you can access free at:

<http://jap.physiology.org/cgi/content/full/91/3/1341#BIBL>

This article has been cited by 21 other HighWire hosted articles, the first 5 are:

Age-related decline in rate of torque development is accompanied by lower maximal motor unit discharge frequency during fast contractions

M. Klass, S. Baudry and J. Duchateau

J Appl Physiol, March 1, 2008; 104 (3): 739-746.

[\[Abstract\]](#) [\[Full Text\]](#) [\[PDF\]](#)

Gastrocnemius muscle specific force in boys and men

C. I. Morse, K. Tolfrey, J. M. Thom, V. Vassilopoulos, C. N. Maganaris and M. V. Narici

J Appl Physiol, February 1, 2008; 104 (2): 469-474.

[\[Abstract\]](#) [\[Full Text\]](#) [\[PDF\]](#)

Age-related resistance to skeletal muscle fatigue is preserved during ischemia

L. H. Chung, D. M. Callahan and J. A. Kent-Braun

J Appl Physiol, November 1, 2007; 103 (5): 1628-1635.

[\[Abstract\]](#) [\[Full Text\]](#) [\[PDF\]](#)

Peripheral impairments cause a progressive age-related loss of strength and velocity-dependent power in the dorsiflexors

C. J. McNeil, A. A. Vandervoort and C. L. Rice

J Appl Physiol, May 1, 2007; 102 (5): 1962-1968.

[\[Abstract\]](#) [\[Full Text\]](#) [\[PDF\]](#)

Muscle size, neuromuscular activation, and rapid force characteristics in elderly men and women: effects of unilateral long-term disuse due to hip-osteoarthritis

C. Suetta, P. Aagaard, S. P. Magnusson, L. L. Andersen, S. Sipila, A. Rosted, A. K. Jakobsen, B. Duus and M. Kjaer

J Appl Physiol, March 1, 2007; 102 (3): 942-948.

[\[Abstract\]](#) [\[Full Text\]](#) [\[PDF\]](#)

Medline items on this article's topics can be found at <http://highwire.stanford.edu/lists/artbytopic.dtl> on the following topics:

Physiology .. Muscle Activation

Medicine .. Magnetic Resonance Imaging

Medicine .. Aging Society

Updated information and services including high-resolution figures, can be found at:

<http://jap.physiology.org/cgi/content/full/91/3/1341>

Additional material and information about *Journal of Applied Physiology* can be found at:

<http://www.the-aps.org/publications/jappl>

This information is current as of July 11, 2009 .

Normalized force, activation, and coactivation in the arm muscles of young and old men

C. S. KLEIN,^{1,2} C. L. RICE,^{1,2,3} AND G. D. MARSH^{1,2,4}

¹Canadian Centre for Activity and Aging, Lawson Health Research Institute, and
²School of Kinesiology, Faculty of Health Sciences, and ³Departments of Anatomy
and Cell Biology, and ⁴Medical Biophysics, Faculty of Medicine and Dentistry,
The University of Western Ontario, London, Ontario, Canada N6G 2M3

Received 5 March 2001; accepted in final form 18 May 2001

Klein, C. S., C. L. Rice, and G. D. Marsh. Normalized force, activation, and coactivation in the arm muscles of young and old men. *J Appl Physiol* 91: 1341–1349, 2001.—The purpose of this study was to determine whether the loss of muscle strength in the elderly could be explained entirely by a decline in the physiological cross-sectional area (PCSA) of muscle. Isometric force, muscle activation (twitch interpolation), and coactivation (surface electromyograph) were measured during maximal voluntary contractions (MVCs) of the elbow flexors (EFs) and extensors (EEs) in 20 young (23 ± 3 yr) and 13 older (81 ± 6 yr) healthy men. PCSA was determined using magnetic resonance imaging, and normalized force (NF) was calculated as the MVC/PCSA ratio. The PCSA was smaller in the old compared with the young men, more so in the EEs (28%) compared with the EFs (19%) ($P < 0.001$); however, the decline in MVC ($\sim 30\%$) with age was similar in the two muscle groups. Muscle activation was not different between the groups, but coactivation was greater (5%) ($P < 0.001$) in the old men for both muscles. NF was less (11%) in the EFs ($P < 0.01$) and tended to be unchanged in the EEs of the old compared with young subjects. The relative maintenance of NF in the EEs compared with the EFs may be related to age-associated changes in the architecture of the triceps brachii muscle. In conclusion, although the decline in PCSA explained the majority of strength loss in the old men, additional factors such as greater coactivation or reduced specific tension also may have contributed to the age-related loss of isometric strength.

elbow flexors; elbow extensors; specific tension; physiological cross-sectional area; sarcopenia

A COMMON OBSERVATION IN OLDER people is the loss of muscle mass and strength (41). What is controversial, however, is whether the loss of strength (force) is entirely explained by the decrease in muscle size or whether other factors, such as muscle activation, coactivation, and specific tension, are also important (9, 11). The typical approach used to study this problem is to determine the normalized force (NF) in young and old subjects. The NF is the ratio of maximal voluntary force [maximal voluntary contraction (MVC)] to some measure of the size of the muscle(s) producing the force. A number of authors reported no age-related

changes in NF (11, 26, 40), which implies that the decrease in muscle size explains virtually all of the force loss. In contrast, others have found up to a 40% decline in NF with age (8, 27, 32, 48), which indicates that other factors, in addition to a decrease in muscle size, may contribute to the loss of strength.

The explanation for the conflicting findings of NF and aging may relate, in part, to the methods used to measure muscle strength and muscle size. For example, a decline in NF with age seemed to be more prevalent during dynamic rather than isometric contractions, and the decrease may be greater in women compared with men (16, 32, 40). As well, muscle size may have been overestimated in older people because of the inability of indirect techniques to distinguish muscle from noncontractile tissue (8, 32). Moreover, the anatomic cross-sectional area (ACSA), which is the area of muscle measured from a single cross section, commonly measured in NF studies may underestimate the loss of muscle mass with age (2). A more accurate index of muscle size and force-generating capacity, particularly in muscles with a pennate fiber architecture such as the triceps brachii, may be the physiological cross-sectional area (PCSA) (12, 42). The PCSA, which is the total cross-sectional area of all the muscle fibers in a muscle, can be determined in vivo by combining the measurement of muscle volume from magnetic resonance imaging (MRI) with muscle fiber length estimated from cadavers. The PCSA of the upper and lower limb muscles has been measured in young subjects but not in the muscles of the elderly (12, 25).

Neural drive to the agonist and antagonist muscles can influence force-generating capacity. The level of muscle activation, as assessed by the twitch interpolation technique, was reported to be less in the elbow flexors (EFs) in old compared with young people (9, 49). As well, coactivation level of the knee flexors, as measured by surface electromyograph (EMG), was higher with old age during MVCs of the knee extensors (15, 22). A decrease in activation or an increase in coacti-

Address for correspondence: C. L. Rice, Canadian Centre for Activity and Aging, St. Joseph's Health Center Annex, 1490 Richmond St., London, ON, Canada N6G 2M3.

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

vation, or both, could reduce NF in aged people. However, in many studies of NF, the level of activation was not measured (27, 32, 48), so it is uncertain whether the young and old recruited all motor units maximally during the MVC. In addition, no studies have reported coactivation measures in relation to old age in the EFs and elbow extensors (EEs) during maximal contractions.

In this study we measured PCSA, MVC, NF, activation, and coactivation in the EFs and EEs of young and old men. The main purpose was to determine whether the NF of the arm muscles changes with age and, if so, whether the EFs and EEs are affected similarly.

METHODS

Subjects. Twenty young men, aged 20–29 yr (mean age 22.6 ± 2.7 yr), and thirteen old men, aged 76–95 yr (mean age 81 ± 6.5 yr), volunteered for the study. The young subjects were university students, and the old subjects were living independently in the community. A written questionnaire and interview determined their medical history and the extent of their participation in physical activity. Exclusion criteria for participation in this study included orthopedic or neurological pathologies of the upper or lower limbs, diabetes, previous myocardial infarction, uncontrolled hypertension, alcoholism, medications that affect muscle performance, and extreme physical activity. Most of the subjects were sedentary and had not participated in weight training or other formal exercise program. The purpose, methodology, and possible risks involved in the experiments were explained, and informed written consent was obtained from each subject. The ethics review committee of the University of Western Ontario approved all procedures.

MRI acquisition. Within 3 wk of recording the MVC, serial T1-weighted images in the axial plane were acquired with MRI using a 20-cm-diameter extremity coil in a 1.5-T whole body magnet and 64-MHz scanner (Siemens Vision System, Siemens Medical, Erlangen, Germany). Subjects were supine with the left elbow extended and adjacent to the trunk and the forearm in a neutral position. Foam padding was placed under the elbow and forearm, so the arm was parallel to the gantry, and the triceps brachii was not compressed. Rather than encircling the arm, the extremity coil was positioned over the dorsal, lateral, and ventral aspect of the arm or forearm and held in place with Velcro straps that crossed the trunk. By not encircling the arm, the origins of the biceps brachii and triceps brachii could be imaged. Reference markers were placed on the medial epicondyle and mid point of the arm.

The arm was imaged in four segments from the top of the humerus to the wrist by moving the extremity coil three times. Using the software, a grid of 20–24 (depending on arm length) slices was centered on a coronal scout image so the slices were perpendicular to the arm (or forearm). Images were acquired using the following parameters: repetition time, 1,000 ms; echo time, 14 ms; number of acquisitions, 1; matrix, 256×256 ; field of view, 200 mm (2 proximal segments, i.e., arm) and 160 mm (2 distal segments i.e., forearm); slice thickness, 7 mm; and interslice gap, 0 mm (imaging time, 4 min/segment). These parameters were selected to delineate muscle borders and differentiate muscle, fat, and connective tissue. To ensure that the four segments were contiguous, the distance between the marker and the most distal slice of a segment was measured (mm) on the scout image using the software. An ink mark, corresponding to this

distance, was placed on the arm so that the extremity coil could be moved the appropriate distance.

Muscles analyzed. The biceps brachii, brachialis, and brachioradialis muscles were traced in each image and together made up the EFs. The triceps brachii and anconeus were traced and together made up the EEs. The pronator teres and the extensor carpi radialis longus muscles, which together generate 15% of EF torque (38), were not included in the EF volume because they were not clearly visible in the images over their entire length. The brachioradialis, extensor carpi radialis longus, and brevis muscles were traced as a group. The brachioradialis volume was then estimated to be 39% of the combined volume of these three muscles (4). The length of the brachioradialis, however, could be determined because the origin and insertion regions were clearly evident in all images. The coracobrachialis muscle was traced as part of the biceps brachii because these two muscles could not be separated convincingly throughout their entire length. In both young and old cadavers, the coracobrachialis is 23% of the weight of the biceps brachii plus the coracobrachialis (47). To exclude the coracobrachialis from the EF volume, the biceps brachii volume was reduced by 23% in all subjects.

Morphological measures. The same investigator analyzed the images with a software program (Analyze 7.5, Mayo Clinic) and was not blinded to subject identity because it was obvious that images with the smaller muscle size and larger amount of fat were of older subjects. However, the data corresponding to images of subjects previously analyzed were not referred to during subsequent analysis and data were not compiled into the young and old groups until all images were analyzed. The cross-sectional area of muscle, bone, and noncontractile tissue were determined in each image for the entire arm. The regions were either manually traced and/or autotraced. During an autotrace, which is based on different ranges of pixel intensity for different tissues, the operator pointed to the region and then moved a bar to progressively highlight the tissue to its border. The cross-sectional area of noncontractile tissue was always determined with the autotrace feature. The different muscles, bone, and noncontractile tissue that were traced were automatically filled with color-coded maps that could be edited and saved (Fig. 1).

Muscle volume was calculated as the summation of cross-sectional area times slice thickness (7 mm) for all slices along the length of the muscle. Muscle length was the distance between the most proximal and the most distal images in which the muscle was visible. The PCSA was calculated by dividing muscle volume by the estimated fiber (fascicle) length. Muscle fiber length was estimated by multiplying muscle length (from MRI) by the fiber length-to-muscle length ratio determined in cadavers (38). The ratios used were 0.60, 0.49, 0.68, and 0.33 for the biceps brachii, brachialis, brachioradialis, and triceps brachii, respectively (38). It was assumed that the fiber length-to-muscle length ratio was the same in the young and old men because no studies have determined whether fiber length changes with age. No data are available for the fiber length-to-muscle length ratio in the anconeus, so it was assumed to be the same as the biceps brachii because the fibers run parallel in both muscles (3). The PCSA of the triceps brachii was multiplied by the cosine of the fiber pennation angle, assumed to be 15° for both groups, whereas the EFs were assumed to have no pennation (24, 38). The largest ACSA of the biceps brachii + brachialis and triceps brachii is also reported for comparison to previous work. The noncontractile tissue, which was subtracted from the muscle cross-sectional area, consisted of visible pockets of intramuscular fat, connective tissue, and tendon within the muscle's border. Noncontractile tissue for each

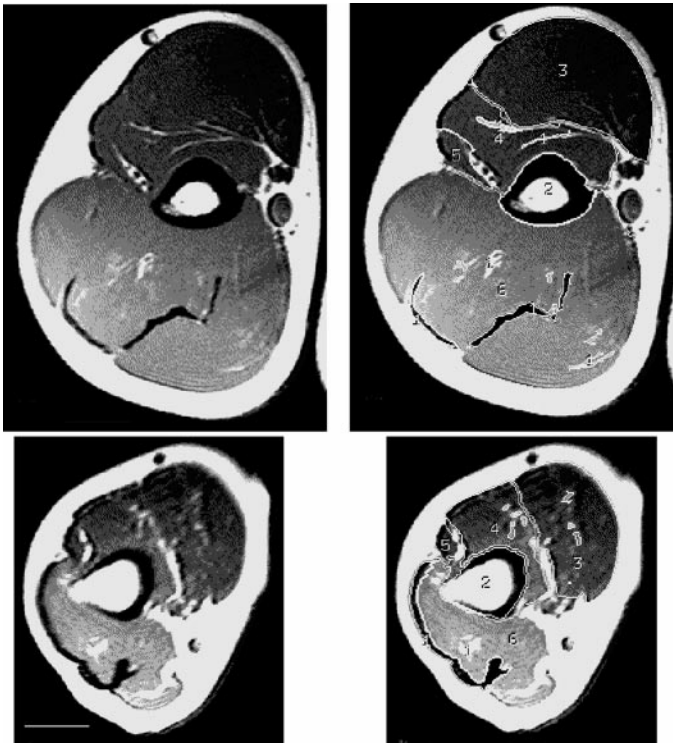


Fig. 1. Axial magnetic resonance images of the arm from a 22-yr-old (top) and a 95-yr-old subject (bottom) showing the range of muscle size in the study. Image at left is the untraced version, and image at right is the traced (analyzed) version. The cross-sectional area of the traced region was determined for noncontractile tissue (1), humerus (2), biceps brachii (3), brachialis (4), brachioradialis (5), and triceps brachii (6). The images are 2 cm distal to the origin of the brachioradialis and are to the same scale. The horizontal bar corresponds to 2 cm.

muscle was calculated as a percentage of the muscle's total volume as follows: noncontractile tissue (%) = [noncontractile tissue volume / (contractile tissue volume + noncontractile tissue volume)] × 100.

Validity and reliability of image analysis. Axial images of a cylindrically shaped acrylic phantom (260-ml volume) filled with saline were acquired on each day to determine the validity of estimating tissue volume. A volumetric flask was used to determine the true volume of the phantom. Over the course of the study the volume of the phantom, as measured by the analysis software, was $252 \pm 3 \text{ cm}^3$ and did not vary significantly. Two investigators (CSK, CLR) analyzed the same four images (10th, 20th, 30th, and 40th) of the arm in each of four subjects (2 old subjects) to determine the intraobserver and interobserver reliability of the CSA measurements. The coefficient of variation (CV) for CSA of muscle and noncontractile tissue was 4 and 22% (intraobserver) and 6 and 25% (interobserver), respectively. The higher variability for noncontractile tissue, which is expected given its small area, has a negligible effect on the percentage of noncontractile tissue we obtained.

Experimental setup for force measurements. Great care was taken to standardize the position of the subjects for recording the MVC. The subjects were supine on a padded table and the left arm (nondominant in all cases) was placed in a custom-designed force dynamometer (Fig. 2). Compared with a seated position, it was assumed that the supine position minimized the effect of body weight and extraneous movements on MVC production. The legs were supported on

a wooden box, with the knee and hip joints flexed to 90° , and the shoulders were secured by straps firmly against a padded metal brace. The box and brace prevented the torso from sliding during the MVCs. Two additional straps were used to stabilize the upper limb during an MVC of the EEs. One was positioned across the arm $\sim 2 \text{ cm}$ proximal to the elbow crease, and the other was placed across the forearm $\sim 5 \text{ cm}$ distal to the elbow crease. Once the subject was secured, the position of the box and the length of all straps were recorded for positioning on subsequent visits.

The elbow joint was flexed 100° ($180^\circ = \text{full extension}$), and the forearm was fully supinated to record optimum MVCs of the EFs and EEs (44). The fingers and wrist were prevented from flexing during an EF MVC by a plastic splint that was strapped to the back of the wrist and hand. The splint was not necessary during an EE MVC because the subjects kept the fingers extended and in line with the forearm. The ventral (or dorsal, for EEs) aspect of the wrist was secured with a strap to a padded curved bar ($11 \times 5.2 \text{ cm}$), that had a strain gauge attached (model SST-700-100A, ASTechnology, Haliburton, ON, Canada). The output from the strain gauge was amplified (Neurolog, models NL 107 and NL 126, Digitimer, Welwyn Garden City, Hertfordshire, UK), and converted to digital format by a 12-bit converter (CED model 1401 Plus, Cambridge Electronic Design, Cambridge, UK) at a sampling rate of 500 Hz. Data were stored concurrently on videotape and computer disk and displayed in front of the subject on an oscilloscope. The strain gauge was calibrated periodically by hanging known weights from the brace. The calculated linear relationship ($r = 0.99$) between the known weights and voltage outputs did not vary throughout the study.

MVC and NF. The subjects did not participate in any activity that required vigorous use of their arms for 48 h before the measurements. The MVCs were determined during each of three visits to the laboratory over 2–4 wk. Three to four MVCs, each held for 4 s with a 3-min rest, were recorded for each of the EFs and EEs during all visits. Strong encouragement was provided during the contractions and visual feedback was provided. The order in which MVCs of the EFs and EEs were recorded was balanced across the three visits and across groups. The force and EMG signals were analyzed off-line using a customized software package (Spike 2, Cambridge Electronic Design). The highest MVC of the three visits was used to calculate muscle activation,

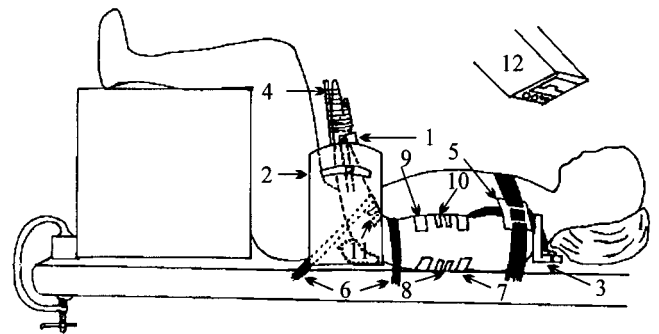


Fig. 2. Experimental setup for force measurements of the elbow flexors (EF) and extensors (EE). 1, Strain gauge; 2, support frame; 3, shoulder brace; 4, wrist splint; 5, shoulder harness; 6, straps for elbow extensor maximal voluntary contraction (MVC); 7, triceps brachii stimulation electrode; 8, triceps brachii electromyograph (EMG) electrode; 9, biceps brachii stimulation electrode; 10, biceps brachii EMG electrode; 11, brachioradialis EMG electrode; 12, oscilloscope.

coactivation, and NF. The NF of the EFs or EEs was calculated as the MVC divided by the PCSA of the respective muscle groups.

Activation level. A modified twitch interpolation technique was used to assess the level of muscle activation during the MVC (1). The stimulating electrodes were made of aluminum foil, measured 3×4 cm to 7×4 cm, and were wrapped in gauze and soaked in saline and conducting gel. The cathode was placed over the motor point of the biceps brachii or triceps brachii and the anode over the distal third of the muscle. Using a constant-current stimulator (model DS7H, Digitimer), two doublets (2 pulses at 100 Hz, 50- μ s pulse duration) were applied both during and after the MVC. The doublets were triggered manually at the peak of the MVC. The stimulus current intensity for the doublets was 50–60% of the level used to obtain the maximal twitch force. Pilot studies and previous reports (6) found that in the arm muscles, submaximal stimulation resulted in larger interpolated twitches than maximal stimulation. Activation level was calculated as: percent activation = $[1 - (T_s/T_r)] \times 100\%$, where T_s is the force of the interpolated response of the doublet at peak force, and T_r is the mean force of the two post-MVC doublets.

Coactivation level. Coactivation during the MVC was determined by recording the EMG activity over the antagonist muscle(s). After the skin was abraded with sandpaper and cleansed with ethyl alcohol, bipolar silver-silver chloride strip electrodes (1×3 cm, Marquette Electronics, Milwaukee, WI) were positioned 15 mm apart over the midbiceps brachii, midtriceps brachii, and proximal third of the brachioradialis. The raw EMG signals were amplified ($\times 500$) and filtered (between 10 Hz and 10 kHz) using a Neurolog NL284 (Digitimer) preamplifier, amplifier, and filter and sampled at 2.5 kHz. A 0.5-s period of the EMG was analyzed corresponding to the point of peak force, which usually occurred within the first 2 s of the MVC. The EMG signals were full-wave rectified and integrated (IEMG) over a 500-ms time constant. Coactivation level was expressed as a percentage of the muscle's maximal IEMG recorded during the MVC.

The extent of possible cross talk between the biceps brachii and triceps brachii was determined by examining whether M waves were recorded concurrently over both muscles during supramaximal stimulation of the musculocutaneous or radial nerve. A custom-designed bar electrode was used for stimulation and placed over the musculocutaneous nerve just medial to the anterior deltoid at the axilla. For stimulation of the radial nerve, the electrode was placed over medial head of the triceps brachii at the posterior axilla. Because the nerves were not easily accessible in the supine position, the M waves were recorded with the subject seated and the elbow joint flexed 100° . Bipolar electrodes for recording the voluntary EMG were used but were placed on the distal third of the biceps brachii and triceps brachii to record M waves that were uncontaminated by stimulus artifact.

Statistical analysis. A two-by-two-factor of ANOVA was used to assess the influence of age (young and old) and muscle (EFs, EEs) on PCSA, ACSA, MVC, and NF. A two-by-three-factor ANOVA determined the effect of age and muscle (biceps brachii, brachioradialis, and triceps brachii) on coactivation level, and post hoc comparisons of the three muscles was done with the Tukey's test. Muscle activation level was assessed using the Mann-Whitney test because the data were not normally distributed. Pearson's product-moment correlation coefficients were applied to determine the relationships between MVC and PCSA and between NF, activation, and coactivation. The CV was calculated to determine the reliability of measurements. Analyses were per-

formed using SPSS software (version 10 for Windows). Differences were considered significant when $P < 0.05$, and all data are presented as means \pm SD.

RESULTS

Anthropometric and morphological measures. The subjects' weight, height, and length of the humerus were not different ($P > 0.05$) between the young and old men (Table 1). Muscle volume, excluding noncontractile tissue, was less in the old compared with the young men in the EFs (297 ± 56 vs. 375 ± 54 cm³) and EEs (323 ± 62 vs. 444 ± 61 cm³) ($P < 0.001$). The results for morphological measures, MVC, NF, and activation are presented in Table 2. The PCSA was 19 and 28% smaller with age in the EFs and EEs respectively ($P < 0.001$), and the decrease was significantly greater in the EEs (age \times muscle interaction, $P = 0.001$). The percent decrease in PCSA was the same among muscles that constitute the EFs and EEs. Because age had no effect on muscle length in the EFs or EEs, the lower PCSA in the old men was due to a smaller CSA over the length of the muscle. The ACSA of the biceps brachii + brachialis and triceps brachii were also lower in the old compared with the young men, and the decrease was less (2%) than the decline in PCSA. The relatively larger age-related decrease in PCSA compared with ACSA was significant in the triceps brachii (age \times measurement interaction, $P = 0.01$) but not in the biceps brachii + brachialis ($P = 0.43$). The percentage of muscle volume that was noncontractile tissue was greater ($P < 0.001$) with age (Table 2). The PCSA and noncontractile tissue were smaller ($P < 0.001$) in the EFs compared with the EEs in the young and old. In both the young and old groups, the brachialis, biceps brachii, and brachioradialis were 52, 36, and 12%, respectively, of EF PCSA, and the anconeus was 5% of EE PCSA.

MVC. The highest MVC on each of the three visits was highly reproducible; the CV was 3 ± 2 and $6 \pm 4\%$ in the young and 3 ± 1 and $5 \pm 3\%$ in the old men for the EFs and EEs, respectively. The MVC was less ($P < 0.001$) in the EFs (-27%) and EEs (-33%) in the old compared with the young, but the magnitude of the decrease was not different between the muscles (age \times muscle interaction, $P = 0.84$) (Table 2). The MVC of the EFs were significantly ($P < 0.001$) greater than the

Table 1. Subject characteristics

	Young ($n = 20$)	Old ($n = 13$)
Age, yr	23 ± 3 (21–29)	81 ± 6 (76–95)
Weight, kg	76 ± 9 (62–99)	80 ± 8 (68–97)
Height, cm	177 ± 7 (166–190)	176 ± 6 (163–185)
Humerus length, cm	32.7 ± 1.6 (30.1–35.7)	33.5 ± 2.1 (30.8–37.1)

Values are means \pm SD, with the range of each value in parentheses; n , is no. of subjects. Except for age, there were no significant group differences in any measurements. Length of the humerus was determined using magnetic resonance imaging.

Table 2. Contractile and morphological measures in the elbow flexors and extensors

	Elbow Flexors		Elbow Extensors	
	Young	Old	Young	Old
MVC, N	331 ± 40	241 ± 50‡	292 ± 49	197 ± 48‡§
PCSA, cm ²	28.2 ± 3.5	22.9 ± 4.4‡	53.0 ± 7.3	38.1 ± 6.0‡§
ACSA, cm ²	20.2 ± 3.0	16.9 ± 3.2‡	28.3 ± 3.5	20.9 ± 3.5‡§
NCT, %	1.0 ± 0.6	4.6 ± 2.4‡	4.6 ± 0.9	8.9 ± 1.7‡§
MVC/PCSA, N/cm ²	11.8 ± 1.0	10.5 ± 1.1†	5.5 ± 0.6	5.1 ± 0.9§
MVC/ACSA, N/cm ²	16.5 ± 1.3	14.3 ± 1.6†	10.3 ± 1.3	9.5 ± 2.2§
Activation, %	98.4 ± 1.8	96.9 ± 2.5	98.2 ± 2.0	97.1 ± 2.0

Values are means ± SD for 20 young and 13 old men. The MVC is the highest force produced during a maximal voluntary isometric contraction. Physiological cross-sectional area (PCSA) of the elbow flexors is the biceps brachii + brachialis + brachioradialis. The PCSA of the elbow extensors is the triceps brachii + anconeus. Anatomic cross-sectional area (ACSA) is the largest cross-sectional area of the biceps brachii + brachialis or triceps brachii. Noncontractile tissue (NCT) is expressed as a percentage of the elbow flexor or elbow extensor muscle volume. Normalized force (NF) was calculated as the MVC/PCSA ratio. Muscle activation (activation %) was determined using the twitch interpolation technique. The age-related reduction in PCSA and ACSA was greater in the elbow extensors than the elbow flexors (significant age × muscle interaction, $P = 0.001$). The NF was significantly lower in the elbow flexors with age. The NF of the elbow extensors tended to be less affected by age (age × muscle interaction, $P = 0.06$). † $P < 0.01$, ‡ $P < 0.001$ compared with the young group. § $P < 0.001$ compared with the elbow flexors in both the young and old.

EEs in both the young and old. There was a significant correlation between PCSA and MVC ($r \geq 0.74$) in the EFs and EEs in the young and old men (Figs. 3 and 4). When data of both groups were combined the correlation coefficients between PCSA and MVC were $r = 0.86$ for the EFs and $r = 0.87$ for the EEs ($P < 0.01$). These correlations were larger than the correlations between ACSA and MVC in both the EFs ($r = 0.83$) and EEs ($r = 0.80$) for the groups combined.

Activation and coactivation level. The level of activation during the MVCs was incomplete (<100%) in the biceps brachii (range 92–100%) and triceps brachii (94–100%) in both groups. The deficit in activation was

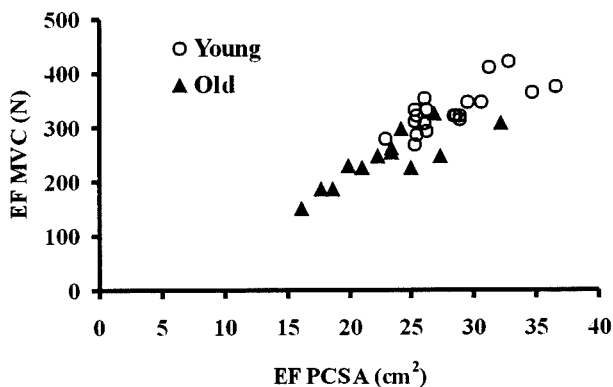


Fig. 3. Relationship between physiological cross-sectional area (PCSA) and MVC in the EF of young and old men. There was a significant correlation between PCSA and MVC in the young ($r = 0.75$) and old ($r = 0.83$).

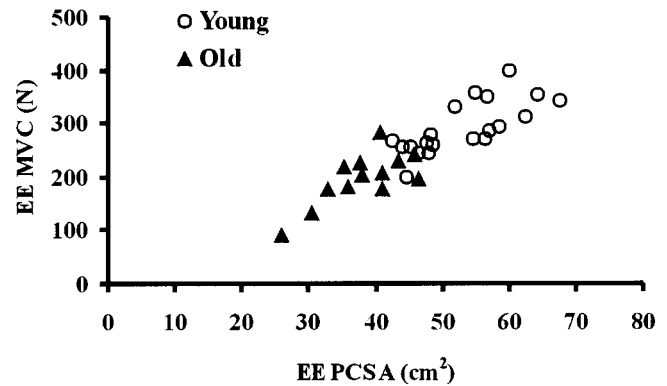


Fig. 4. Relationship between PCSA and MVC in the EE of young and old men. There was a significant correlation between PCSA and MVC in the young ($r = 0.73$) and old ($r = 0.74$).

similar in both groups for the triceps brachii ($P = 0.13$) but tended to be greater ($P = 0.07$) in the biceps brachii of the old compared with the young (Table 2). The level of coactivation in the antagonist muscles during MVCs of the EFs and EEs was ~5% greater ($P < 0.001$) with age (Fig. 5). There was no evidence of cross talk because M waves were not evident in the biceps brachii or triceps brachii during supramaximal stimulation of the radial and musculocutaneous nerves, respectively.

NF. The NF was less in the old compared with the young group (main effect for age, $P = 0.001$). The decrease in NF with age was more prevalent in the EFs (11%) compared with the EEs (7%), and the difference between the muscles approached significance (age × muscle interaction, $P = 0.06$) (Table 2, Figs. 3 and 4). The MVC/ACSA also was reduced more in the EFs compared with EEs with age. There were no significant ($P > 0.05$) correlations between activation or coactivation and NF in either group or when the data from both groups were combined. The NF of the EFs were greater

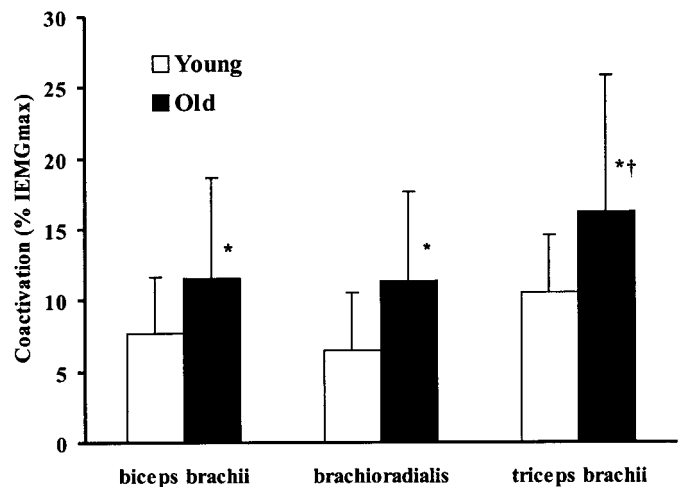


Fig. 5. Coactivation levels in the biceps brachii and brachioradialis during an MVC of the EE and coactivation levels in the triceps brachii during an MVC of the EF in 20 young and 13 old men. Values are means ± SD. IEMG, integrated EMG. * $P < 0.001$ compared with the young group. † $P < 0.05$ compared with the biceps brachii and brachioradialis in both the young and old.

($P < 0.001$) than the EEs in both the young and old (Table 2).

DISCUSSION

In this study, we determined the age-related differences in PCSA, NF, and muscle activation and coactivation in the arm muscles of young and old men. The NF was significantly less in the EFs (-11%), but not the EEs, of the old men compared with the young men. In addition, coactivation was $\sim 5\%$ higher with old age in both muscles. These findings suggest that additional factors, besides the decrease in PCSA, contribute to the loss of strength in the EFs, whereas the decline in muscle size seems to explain much of the strength loss in the EEs of the old men.

Morphological measures. The PCSA was lower in the old compared with the young group, more so in the EEs (-28%) compared with the EFs (-19%). Age-related changes in PCSA have not been reported previously, but the reduction in ACSA found in this study was consistent with others (26, 27, 40, 43, 48). The greater percent decrease in the PCSA of the EEs compared with the EFs may have been due to differences in activity level between the muscles (i.e., amount and/or intensity of contractions). In addition, the EEs may atrophy at a greater rate than the EF because the triceps brachii, at least in young men, seems to have a higher percentage ($\sim 10\%$) of type II fibers than the biceps brachii (33, 34, 35). Type II fiber area is less, whereas type I fiber area is minimally affected in the biceps brachii with age (14). The effect of age on the triceps brachii fiber area or the daily activity patterns of the EFs and EEs, however, has not been determined. On the basis of our findings, it is apparent that the extent of muscle loss with age differs even among the muscles in the same limb.

The PCSA is the total cross-sectional area of all the muscle fibers in a muscle, whereas the ACSA includes only those fibers in a particular cross section. Thus PCSA is considered to be a better index of force-generating capacity than the ACSA (12, 42), especially in muscles in which the fibers extend through a small proportion of the total muscle length (i.e., triceps brachii). When the data from both groups were combined, the correlation was higher between MVC and PCSA than between MVC and ACSA for both muscles. As well, the PCSA was reduced more than the ACSA with age, although this difference was small (2%) and was significant only in the EEs. Alway and colleagues (2) also reported a larger decrease (12%) in muscle volume compared with the ACSA in the triceps surae with age. They suggested that the loss of muscle mass with age may be nonuniform over the length of a muscle. Thus it may be that the ACSA underestimates the age-related decline in PCSA and the extent of this difference may depend on the size and architecture of the muscle examined. Although there may be subtle differences in the relative decrease of ACSA compared with PCSA, the age-related change in NF was the same

whether ACSA or PCSA was employed in the calculation of NF.

In this study, the PCSA was calculated as muscle volume/fiber length \times cosine of the fiber pennation angle. An accurate comparison of the relative change in PCSA between the groups depends on the validity of measuring muscle volume using MRI and estimating muscle fiber length and pennation angle from cadaveric data (38). Previous reports have demonstrated clearly the utility of MRI for the determination of muscle volume (37). Because the fiber length-to-muscle length ratio was assumed to be the same in the two groups and muscle length was unchanged, the estimated fiber length was not different with age. We are unaware of any studies that have examined whether fiber length or pennation angle is altered with age in humans. A decrease in fiber length in old compared with young rats, however, was reported and attributed to a decline in the number of sarcomeres in-series (18). As well, the pennation angle is smaller after disuse atrophy (39) and larger in hypertrophied muscles of young subjects (24). Thus, if fiber length and pennation angle are less with age in humans, the PCSA would be underestimated and NF overestimated in our old compared with young men.

MVC, activation, and coactivation. The MVC was less ($\sim 30\%$) in the EFs and EEs in the old compared with the young men. Others have reported similar (9, 10) or smaller (-20%) (36) losses of EF strength with age, but no previous data on the isometric strength of the EEs are available. A primary question of the present study was whether there is an age-related change in the neural drive to the agonist and antagonist muscles and, if so, what effect this would have on NF. Neural drive to the agonists was estimated by measuring the activation level of the biceps brachii and triceps brachii using the twitch interpolation technique. Similar to previous work (9, 49), our results indicate that activation was incomplete ($<100\%$) and tended to be less in the EFs with age, although this age difference was not significant. A deficit in activation in the old men could imply that the neural drive (i.e., motor unit recruitment and/or firing rate) is less during strong contractions and this could contribute to the lower NF of the EFs. However, there was no correlation between activation (range of 94–100%) and NF in either the young or old men. Although the age-related difference in activation was small and not significant, larger differences may occur during dynamic compared with isometric contractions. For example, the IEMG of the vastus lateralis tended to be reduced more with age during the standing long jump than during isometric maneuvers (15). Although Herbert and Gandevia (17) have questioned whether twitch interpolation is a sensitive measure of motoneuron excitation, a larger impairment in activation with age may become apparent if stimulation is applied during dynamic movements.

Neural drive to the antagonist muscles during the MVC was estimated by measuring the level of coactivation in the biceps brachii, brachioradialis, or triceps brachii. Coactivation was higher ($\sim 5\%$) in all muscles

of the old compared with the young men. Age-related increases in coactivation were previously reported in the biceps femoris during downward stepping (19) and during maximal dynamic and isometric contractions (15, 22), although coactivation was not different with age during submaximal contractions of the EFs (13). Because the MVC represents the net force about the joint (i.e., agonist minus antagonist forces), the greater coactivation in the old could contribute to the lower NF in the EFs. There was, however, no correlation between coactivation and NF in either group. For example, NF of the EFs was not lower than the group average in the two old subjects with the highest coactivation in the triceps brachii (32 and 35%). Thomas and colleagues (45) also reported no significant relationship between EE MVC and biceps brachii coactivation levels of 15–50% in controls and subjects with spinal cord injuries. It may be difficult, however, to derive a significant correlation between coactivation and NF because these measures are affected by many factors. Although greater coactivation may reduce NF, it may also prove beneficial for the elderly by increasing joint stiffness and postural stability during movement (19).

NF. The NF was 11% lower in the EFs and tended to be less affected in the EEs with ageing. As mentioned previously, the lower NF in the EFs could stem from an increase in coactivation. Other factors, however, such as a decline in specific tension of the muscle fibers could also contribute to a decrease of NF (11). It is unclear why NF in the EEs is less affected than the EFs with old age. One possible explanation is a reduction in fiber pennation angle in the triceps brachii, secondary to muscle atrophy, compensates for any age-related changes in coactivation and specific tension, by transmitting relatively more tension to the tendon during a contraction (31, 39). In young athletic subjects, the pennation angle of the triceps brachii is positively correlated with muscle size (24) and negatively correlated with NF of the EEs (21). It is interesting that Frontera and co-workers (11) reported a decrease (30%) in specific tension of single fibers but no change in NF in the quadriceps with age. This paradoxical finding may be a reflection of age-related changes in muscle architecture and connective tissue (43) that sustains NF by enhancing force transmission *in vivo* (20).

In previous studies, investigators found either no change in NF with age (11, 26, 40) or a decrease of up to 40% (8, 23, 27, 32, 46, 48). Similar to our findings, Klittgaard et al. (27) reported a 14% decrease in isometric NF (MVC/ACSA) in the EFs of old (68 yr) compared with young men when computed tomography was used to measure ACSA. As well, in these same subjects, the age-related decrease (27%) in NF of the knee extensor muscles was larger than in the EFs (27). Young and co-workers (48) also reported a 27% decline in isometric NF of the knee extensors with age using ultrasound imaging. However, other investigators reported no change in isometric NF with age in the knee extensors using computed tomography (11, 40) or in

the ankle dorsiflexors using MRI (26). An age-related decline in NF during dynamic (isokinetic) contractions also has been reported (23, 32, 40). For example, Overend et al. (40) found that isokinetic NF, but not isometric NF, of the knee extensors and flexors was 10–20% lower in men aged 70 yr compared with 20-yr-old men. Jubrias and co-workers (23) used MRI and reported a 21% decrease in NF of the knee extensors at contraction speeds of 120°/s and greater, but not at 60°/s, in 42 men and women between the ages of 65 and 80 yr. In a large sample of men aged 19–91 yr, Lynch and co-workers (32) reported a decrease in isokinetic (30–45°/s) NF of 28 and 40% in the arm (EFs plus EEs) and thigh (knee flexors plus knee extensors) muscles, respectively, using dual-energy X-ray absorptiometry (DXA). The prevalence of a decline in isokinetic NF with age evident in previous studies, particularly at faster contraction speeds, may be due to a number of factors, including a decrease in fast-twitch fiber area (30), a decline in muscle activation, and increased coactivation (15, 22).

The extent of the age-related decline in NF demonstrated in previous work may be related to the method used to measure muscle size as well as the general health, motivation, and physical activity level of the subjects. In the present study the subjects were equally motivated to give their best effort during the MVCs. This conclusion is based on the small day-to-day variability of the MVC and activation level. As well, the subjects were healthy and not highly trained and the nondominant arm was measured in all cases. Thus the group differences in PCSA, strength, and NF are more likely related to the effects of aging *per se* rather than to differences in physical activity level, although we have no direct measures of activity level. More importantly, the large age-related deficits (27–40%) in NF reported in some studies (8, 32, 46) could be exaggerated because the techniques that were used may not have adequately distinguished muscle and noncontractile tissue. Because the noncontractile tissue is increased in the elderly (43), ultrasound (46), DXA (29, 32), and less direct techniques (8) may overestimate muscle size and thereby underestimate NF. For example, Lynch et al. (32) reported a 20% decrease in arm and thigh muscle mass between young and old (>80 yr) men with DXA. In the present study, we found a 20–28% decrease in EF and EE PCSA and Lexell et al. (30) reported a 45% decrease in the ACSA of the vastus lateralis muscle in cadavers across the same age range. A 45% decrease in ACSA would be enough to account for all of the strength loss commonly reported in the knee extensors (41). The age-related deficit (15–25%) in specific tension of whole animal muscle may also be exaggerated because noncontractile tissue was not accounted for in the ACSA measurements (7, 28). Ansved and Larsson (5), however, measured specific tension with (ACSA minus total fiber area) and without (muscle wet weight) correction for noncontractile tissue in young and old rats. Specific tension was reduced by 20% in the old rats when wet weight was used but was unaffected when noncontractile tissue was accounted

for. Thus it may be that NF and whole muscle specific tension during isometric contractions are not greatly impaired when adequate techniques are used to measure muscle size.

The EEs were ~10–20% weaker than the EFs in both groups despite having almost twice the PCSA. This resulted in a lower NF in the EEs compared with the EFs by almost 50%. Part of the difference in NF between the muscle groups is because the pronator teres and the extensor carpi radialis longus muscles, which can function as elbow flexors, were not included in the EF volume. Consequently, NF of the EFs was likely overestimated by ~15% in the present study (38). A more important factor contributing to the lower NF in the EEs compared with the EFs is the smaller moment arm length of the triceps brachii compared with the EFs (38). We have since confirmed using MRI that the moment arm length of the triceps brachii is approximately one-half that of the EFs in young and old men and that the specific tension of the two muscle groups is similar (25).

In conclusion, isometric strength and PCSA of the EFs and EEs were reduced in old compared with young men. The percent loss in strength and PCSA with old age was similar in the EEs resulting in an unchanged NF for this muscle group. In contrast, since strength was reduced more than PCSA, the NF of the EFs was reduced in the old men compared with the young men. Possible mechanisms that may contribute to the lower NF of the EFs include an increase in coactivation, or a decline in specific tension of the muscle fibers.

We acknowledge the assistance of Jean Theberge in the acquisition of the magnetic resonance images. We also thank Brian Allman and Dr. Jennifer Jakobi for assistance during pilot testing and reading an earlier draft of the manuscript. Finally, we are grateful to all the subjects who participated in this study.

This work was supported by the National Sciences and Engineering Research Council of Canada, St. Joseph's Health Centre, and the Academic Development Fund of the University of Western Ontario. C. S. Klein was a recipient of an Ontario Graduate Scholarship in Science and Technology during the course of this study.

REFERENCES

- Allen GM, McKenzie DK, Gandevia SC. Twitch interpolation of the elbow flexor muscles at high forces. *Muscle Nerve* 21: 318–328, 1998.
- Alway SE, Coggan AR, Sproul MS, Abduljalil AM, and Robitaille PM. Muscle torque in young and older untrained and endurance-trained men. *J Gerontol A Biol Sci Med Sci* 51: 195–201, 1996.
- Amis AA, Dowson D, and Wright V. Muscle strengths and musculo-skeletal geometry of the upper limb. *Eng Med* 8: 41–48, 1979.
- An KN, Hui FC, Morrey BF, Linscheid RL, and Chao EY. Muscles across the elbow joint: a biomechanical analysis. *J Biomech* 14: 659–669, 1981.
- Ansved T and Larsson L. Effects of ageing on enzyme-histochemical, morphometrical and contractile properties of the soleus muscle in the rat. *J Neurol Sci* 93: 105–124, 1989.
- Awiszus F, Wahl B, and Meinecke I. Influence of stimulus cross talk on results of the twitch-interpolation technique at the biceps brachii muscle. *Muscle Nerve* 20: 1187–1190, 1997.
- Brooks SV and Faulkner JA. Contractile properties of skeletal muscles from young, adult and aged mice. *J Physiol (Lond)* 404: 71–82, 1988.
- Bruce SA, Newton D, and Wolejda RC. Effect of age on voluntary force and cross-sectional area of human adductor pollicis muscle. *Q J Exp Physiol* 74: 359–362, 1989.
- De Serres SJ and Enoka RM. Older adults can maximally activate the biceps brachii muscle by voluntary command. *J Appl Physiol* 84: 284–291, 1998.
- Doherty TJ, Vandervoort AA, Taylor AW, and Brown WF. Effects of motor unit losses on strength in older men and women. *J Appl Physiol* 74: 868–874, 1993.
- Frontera WR, Suh D, Krivickas LS, Hughes VA, Goldstein R, and Roubenoff R. Skeletal muscle fiber quality in older men and women. *Am J Physiol Cell Physiol* 279: C611–C618, 2000.
- Fukunaga T, Roy RR, Shellock FG, Hodgson JA, and Edgerton VR. Specific tension of human plantar flexors and dorsiflexors. *J Appl Physiol* 80: 158–165, 1996.
- Graves AE, Kornatz KW, and Enoka RM. Older adults use a unique strategy to lift inertial loads with the elbow flexor muscles. *J Neurophysiol* 83: 2030–2039, 2000.
- Grimby G, Danneskiold-Samsøe B, Hvid K, and Saltin B. Morphology and enzymatic capacity in arm and leg muscles in 78–81 year old men and women. *Acta Physiol Scand* 115: 125–134, 1984.
- Hakkinen K, Alen M, Kallinen M, Izquierdo M, Jokelainen K, Lassila H, Malkia E, Kraemer WJ, and Newton RU. Muscle CSA, force production, and activation of leg extensors during isometric and dynamic actions in middle-aged and elderly men and women. *J Aging Phys Act* 6: 232–247, 1998.
- Hakkinen K, Kraemer WJ, Kallinen M, Linnamo V, Pastinen UM, and Newton RU. Bilateral and unilateral neuromuscular function and muscle cross-sectional area in middle-aged and elderly men and women. *J Gerontol A Biol Sci Med Sci* 51: B21–B29, 1996.
- Herbert RD and Gandevia SC. Twitch interpolation in human muscles: mechanisms and implications for measurement of voluntary activation. *J Neurophysiol* 82: 2271–2283, 1999.
- Hooper AC. Length, diameter and number of ageing skeletal muscle fibres. *Gerontology* 27: 121–126, 1981.
- Hortobagyi T and DeVita P. Muscle pre- and coactivity during downward stepping are associated with leg stiffness in aging. *J Electromyogr Kinesiol* 10: 117–126, 2000.
- Huijing PA. Muscle as a collagen fiber reinforced composite: a review of force transmission in muscle and whole limb. *J Biomech* 32: 329–345, 1999.
- Ichinose Y, Kanehisa H, Ito M, Kawakami Y, and Fukunaga T. Relationship between muscle fiber pennation and force generation capability in Olympic athletes. *Int J Sports Med* 19: 541–546, 1998.
- Izquierdo M, Ibanez J, Gorostiaga E, Garrues M, Zuniga A, Anton A, Larrion JL, and Hakkinen K. Maximal strength and power characteristics in isometric and dynamic actions of the upper and lower extremities in middle-aged and older men. *Acta Physiol Scand* 167: 57–68, 1999.
- Jubrias SA, Odderson IR, Esselman PC, and Conley KE. Decline in isokinetic force with age: muscle cross-sectional area and specific force. *Pflügers Arch* 434: 246–253, 1997.
- Kawakami Y, Abe T, and Fukunaga T. Muscle-fiber pennation angles are greater in hypertrophied than in normal muscles. *J Appl Physiol* 74: 2740–2744, 1993.
- Kawakami Y, Nakazawa K, Fujimoto T, Nozaki D, Miyashita M, and Fukunaga T. Specific tension of elbow flexor and extensor muscles based on magnetic resonance imaging. *Eur J Appl Physiol* 68: 139–147, 1994.
- Kent-Braun JA and Ng AV. Specific strength and voluntary muscle activation in young and elderly women and men. *J Appl Physiol* 87: 22–29, 1999.
- Klitgaard H, Mantoni M, Schiaffino S, Ausoni S, Gorza L, Laurent-Winter C, Schnohr P, and Saltin B. Function, morphology and protein expression of ageing skeletal muscle: a cross-sectional study of elderly men with different training backgrounds. *Acta Physiol Scand* 140: 41–54, 1990.
- Klitgaard H, Marc R, Brunet A, Vandewalle H, and Monod H. Contractile properties of old rat muscles: effect of increased use. *J Appl Physiol* 67: 1401–1408, 1989.

29. **Levine JA, Abboud L, Barry M, Reed JE, Sheedy PF, and Jensen MD.** Measuring leg muscle and fat mass in humans: comparison of CT and dual-energy X-ray absorptiometry. *J Appl Physiol* 88: 452–456, 2000.
30. **Lexell J, Taylor CC, and Sjøstrom M.** What is the cause of the ageing atrophy? Total number, size and proportion of different fiber types studied in whole vastus lateralis muscle from 15- to 83-year-old men. *J Neurol Sci* 84: 275–294, 1988.
31. **Lieber RL and Friden J.** Functional and clinical significance of skeletal muscle architecture. *Muscle Nerve* 23: 1647–1666, 2000.
32. **Lynch NA, Metter EJ, Lindle RS, Fozard JL, Tobin JD, Roy TA, Fleg JL, and Hurley BF.** Muscle quality. I. Age-associated differences between arm and leg muscle groups. *J Appl Physiol* 86: 188–194, 1999.
33. **MacDougall JD, Elder GC, Sale DG, Moroz JR, and Sutton JR.** Effects of strength training and immobilization on human muscle fibres. *Eur J Appl Physiol* 43: 25–34, 1980.
34. **MacDougall JD, Sale DG, Alway SE, and Sutton JR.** Muscle fiber number in biceps brachii in bodybuilders and control subjects. *J Appl Physiol* 57: 1399–1403, 1984.
35. **McCall GE, Byrnes WC, Dickinson A, Pattany PM, and Fleck SJ.** Muscle fiber hypertrophy, hyperplasia, and capillary density in college men after resistance training. *J Appl Physiol* 81: 2004–2012, 1996.
36. **McDonagh MJ, White MJ, and Davies CT.** Different effects of ageing on the mechanical properties of human arm and leg muscles. *Gerontology* 30: 49–54, 1984.
37. **Mitsiopoulos N, Baumgartner RN, Heymsfield SB, Lyons W, Gallagher D, and Ross R.** Cadaver validation of skeletal muscle measurement by magnetic resonance imaging and computerized tomography. *J Appl Physiol* 85: 115–122, 1998.
38. **Murray WM, Buchanan TS, and Delp SL.** The isometric functional capacity of muscles that cross the elbow. *J Biomech* 33: 943–952, 2000.
39. **Narici MV, Capodaglio P, Minetti AE, Ferrari-Bardile A, Maini M, and Cerretelli P.** Changes in human skeletal muscle architecture induced by disuse-atrophy (Abstract). *J Physiol (Lond)* 506P: 59P, 1998.
40. **Overend TJ, Cunningham DA, Kramer JF, Lefcoe MS, and Paterson DH.** Knee extensor and knee flexor strength: cross-sectional area ratios in young and elderly men. *J Gerontol A Biol Sci Med Sci* 47: M204–M210, 1992.
41. **Porter MM, Vandervoort AA, and Lexell J.** Aging of human muscle: structure, function and adaptability. *Scand J Med Sci Sports* 5: 129–142, 1995.
42. **Powell PL, Roy RR, Kanim P, Bello MA, and Edgerton VR.** Predictability of skeletal muscle tension from architectural determinations in guinea pig hindlimbs. *J Appl Physiol* 57: 1715–1721, 1984.
43. **Rice CL, Cunningham DA, Paterson DH, and Lefcoe MS.** Arm and leg composition determined by computed tomography in young and elderly men. *Clin Physiol* 9: 207–220, 1989.
44. **Singh M and Kapovich PV.** Isotonic and isometric forces of the forearm flexors and extensors. *J Appl Physiol* 21: 1435–1437, 1966.
45. **Thomas CK, Tucker ME, and Bigland-Ritchie B.** Voluntary muscle weakness and co-activation after chronic cervical spinal cord injury. *J Neurotrauma* 15: 149–161, 1998.
46. **Vandervoort AA and McComas AJ.** Contractile changes in opposing muscles of the human ankle joint. *J Appl Physiol* 61: 361–367, 1986.
47. **Veeger HE, Van der Helm FC, Van der Woude LH, Pronk GM, and Rozendal RH.** Inertia and muscle contraction parameters for musculoskeletal modelling of the shoulder mechanism. *J Biomech* 24: 615–29, 1991.
48. **Young A, Stokes M, and Crowe M.** The size and strength of the quadriceps muscles of old and young men. *Clin Physiol* 5: 145–154, 1985.
49. **Yue GH, Ranganathan VK, Siemionow V, Liu JZ, and Sahgal V.** Older adults exhibit a reduced ability to fully activate their biceps brachii muscle. *J Gerontol A Biol Sci Med Sci* 54: M249–M253, 1999.