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Journal of Biomechanics 33 (2000) 943–952

JOURNAL OF BIOMECHANICS

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The isometric functional capacity of muscles that cross the elbow

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Accepted 17 February 2000

Abstract

We hypothesized that muscles crossing the elbow have fundamental differences in their capacity for excursion, force generation, and moment generation due to differences in their architecture, moment arm, and the combination of their architecture and moment arm. Muscle fascicle length, sarcomere length, pennation angle, mass, and tendon displacement with elbow flexion were measured for the major elbow muscles in 10 upper extremity specimens. Optimal fascicle length, physiological cross-sectional area (PCSA), moment arm, operating range on the force–length curve, and moment-generating capacity were estimated from these data. Brachioradialis and pronator teres had the longest (17.7 cm) and shortest (5.5 cm) fascicles, respectively. Triceps brachii (combined heads) and brachioradialis had the greatest (14.9 cm^2) and smallest (1.2 cm^2) PCSAs, respectively. Despite a comparable fascicle length, long head of biceps brachii operates over a broader range of the force–length curve (length change = 56% of optimal length, 12.8 cm) than the long head of triceps brachii (length change = 28% of optimal length, 12.7 cm) because of its larger moment arm (4.7 cm vs. 2.3 cm). Although brachioradialis has a small PCSA, it has a relatively large moment-generating capacity (6.8 cm^3) due to its large moment arm (average peak = 7.7 cm). These results emphasize the need to consider the interplay of architecture and moment arm when evaluating the functional capabilities of a muscle. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Elbow; Muscle architecture; Moment arms

1. Introduction

Separately, a muscle's architecture and moment arm provide complementary views of its force- and moment-generating capabilities. For example, physiological cross-sectional area (PCSA, muscle volume/optimal fiber length), a measure of the number of sarcomeres in parallel, determines a muscle's maximum force-generating capacity (Gans, 1982; Sacks and Roy, 1982). Moment arm, the shortest distance between a muscle's line of action and the joint center, transforms muscle force into joint moment. Similarly, optimal fiber length, a measure of the number of sarcomeres in series, determines the maximum length change over which a muscle can actively generate force (i.e., excursion capacity). Moment arm determines musculotendon excursion during joint rotation (An et al., 1984).

Given the influence of both muscle architecture and moment arm, some aspects of a muscle's function cannot be predicted from understanding either its force-generating properties or its moment arm alone. For example, the ratio between moment arm and optimal fascicle length, which expresses length change relative to excursion capacity, indicates how much of the isometric force–length curve the muscle uses during joint rotation (Delp and Zajac, 1992; Hoy et al., 1990; Lieber and Shoemaker, 1992). Assuming constant muscle activation, a muscle's moment arm, PCSA, and its operating range (how much and what portion of the isometric force–length curve the muscle uses during joint rotation) are the key factors that characterize maximum moment-generating capacity as a function of joint position (Gonzalez et al., 1997; Lieber and Boakes, 1988). Thus, a muscle's architecture and its moment arm must be known to estimate its force- and moment-generating capacity over a range of motion.

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PII: S0021-9290(00)00051-8

Previous studies provide quantitative descriptions of architecture and moment arms for the elbow muscles (Amis et al., 1979; An et al., 1981; Brand et al., 1981; Gerbeaux et al., 1996; Lieber et al., 1990, 1992; Murray et al., 1995; Veeger et al., 1991, 1997; Wood et al., 1989). However, no study reports both moment arms and architectural parameters measured in the same specimens. Evaluating function by combining data from different specimens is problematic because there is a high degree of interspecimen variability in the available data.

We hypothesized that the individual elbow muscles have fundamental differences in their isometric functional capacities due to intermuscular differences in muscle architecture, moment arms, and the interplay of each muscle's architecture and moment arm. To test this hypothesis, moment arm and muscle architecture were estimated in the same cadaveric upper extremity specimens and used to calculate fascicle lengths as a function of elbow rotation, the effect of elbow position on muscle force-generating capacity, and the moment-generating capacity of each muscle.

2. Methods

We collected anatomical data from 10 unembalmed upper extremities, taken from nine cadavers. Each extremity was obtained in a frozen state, thawed over 36–48 h, and dissected. Biceps brachii (BIC, long and short heads), brachialis (BRA), brachioradialis (BRD), extensor carpi radialis longus (ECRL), pronator teres (PT) and triceps brachii (TRI, long and lateral heads) were studied in detail. To estimate both architectural parameters and moment arms from the same muscles, a portion of each muscle was first removed and fixed in formalin, tendon displacement measurements were completed, and the remaining muscle segments were fixed in formalin. The cadaveric specimens ranged in size from a 5′0″ female to a 6′4″ male (see Table 1 for anthropometric data). All protocols followed the guidelines and regulations for use of human cadaveric material at Northwestern University (Chicago, IL), the site of data collection.

After fixation, muscles were prepared for further dissection as described by Sacks and Roy (1982). We measured musculotendon length (the length of the entire muscle–tendon unit from origin to insertion), muscle length (the distance from the most proximal fibers at the origin to the most distal fibers at the insertion), pennation angle (the acute angle between the line of action of the tendon and the line of action of the muscle fibers), fascicle length (the length of a small bundle of muscle fibers from the tendon of origin to the tendon of insertion), and sarcomere length in each muscle. Fascicle lengths were measured instead of fiber lengths because it is difficult to isolate individual fibers. Muscle parameters for long head of biceps are not reported in three cadavers (M1, F6, F7) because the tendons were damaged at the shoulder joint and the muscles were pathologically short.

Optimal fascicle lengths (ℓ_o^M) were calculated by normalizing measured fascicle lengths (ℓ^F) to a sarcomere length (ℓ^S) of 2.8 μm, the optimal sarcomere length in human muscle (Walker and Schrodt, 1974). That is,

$$\ell_o^M = \ell^F \frac{2.8}{\ell^S}. \tag{1}$$

Table 1
Anthropometric data[a]

Specimen label[b]	Humerus length[c]	Radius length[c]	Ulna length[c]	Trans-epicondylar width[c]	Upper arm circumference[c]	Carrying angle (deg)
M10	34.0	26.6	28.9	7.3	47.8	0
M5	32.9	25.1	26.6	6.6	31.3	9
M3	33.5	24.4	26.4	6.8	17.2	9
F7	32.1	24.1	26.2	6.2	31.9	16
M2	33.1	24.0	25.9	6.7	19.0	12
M1	29.4	23.6	25.0	6.6	17.1	13
F4	31.6	23.5	25.1	6.0	21.0	22
F8	31.7	23.2	24.6	5.8	35.5	14
F6	31.1	22.6	24.2	5.6	23.3	15
F9	30.6	22.1	24.0	5.5	14.3	29

[a] Upper arm circumference and carrying angle were measured before dissection, bone lengths and trans-epicondylar width were measured after dissection. Upper arm circumference was measured at the point where the circumference was the largest. Carrying angle was defined as the acute angle between the long axis of the upper arm and the long axis of the forearm while the arm was in full extension. The carrying angles of specimens that could not be fully extended before dissection (F4, F6, and F8) were measured after dissection was completed. Bone lengths were measured from the most superior point to the most inferior point on each bone. The distance between the epicondyles of the humerus was measured using calipers.

[b] M indicates male specimen, F indicates female specimen.

[c] Values in cm.

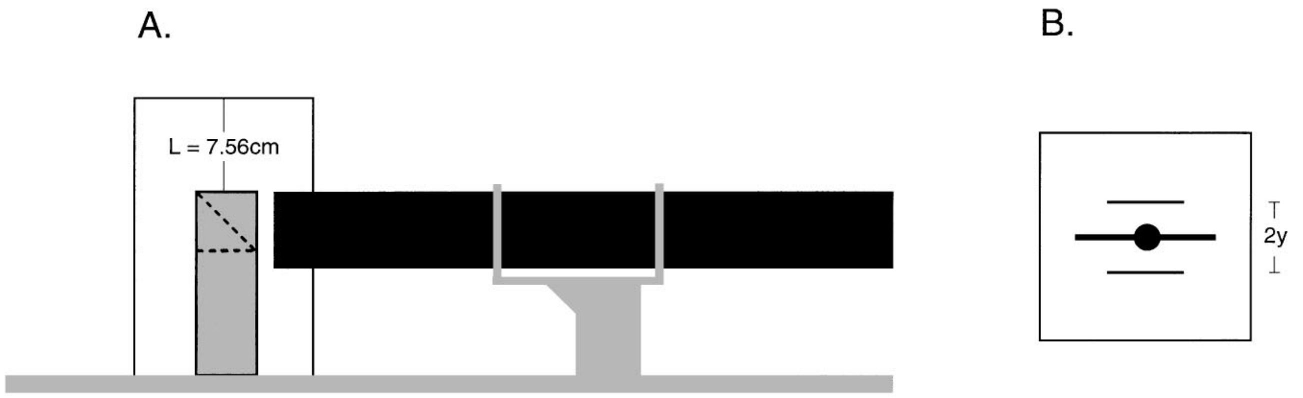

Fig. 1. (A) Side view of laser apparatus used for sarcomere length measurements. A 5 mW He–Ne laser (black rectangle) is shone through a prism (dashed lines) which re-directs the laser beam. The prism is housed in a stand (gray rectangle) directly in front of the laser. Small pieces of muscle fascicles are mounted on a microscope slide, which is placed on the stand and aligned so the laser beam diffracts through a muscle segment. The resulting diffraction pattern is viewed on a frosted glass surface located 7.56 cm from the slide. (B) Top view of the frosted glass surface and a schematic diffraction pattern. A piece of felt (dark circle) shields the undiffracted laser beam. The distance between the first-order diffraction bands ($2y$) is measured and used to calculate sarcomere length.

Reported optimal lengths are the average of 10 normalized fascicle lengths per muscle. Sarcomere lengths were determined using the laser diffraction method (Baskin et al., 1981; Yeh et al., 1980). A 5 mW He–Ne laser was shone through small pieces of each fascicle mounted on a microscope slide. The width of the first-order diffraction pattern ($2y$ in Fig. 1) was measured using calipers (resolution = 0.0025 cm) and used to calculate sarcomere length:

$$\ell^{S} = \frac{\lambda}{\sin\theta}, \tag{2}$$

$$\tan\theta = \frac{y}{L}, \tag{3}$$

where λ is the wavelength of the laser (0.6327 μm), y is the distance between the undiffracted laser beam and the first-order band, and L is the distance from the microscope slide to the frosted glass surface (7.56 cm). Caliper measurements were repeatable to ± 0.038 cm, equivalent to ± 0.05 μm for sarcomere lengths. Twelve measurements were made in each fascicle: three from the origin, six from the middle, and three from the insertion.

PCSA was calculated as muscle volume divided by optimal fascicle length. Muscle volume was calculated from muscle mass, measured after the tendon was removed, and muscle density, 1.06 g/cm^3 (Mendez and Keys, 1960). The PCSA of lateral head of triceps includes the combined masses of the medial and lateral heads. Tendon length (ℓ^{T}) was estimated by subtracting average fascicle length (ℓ^{F}) from musculotendon length (ℓ^{MT}), taking pennation angle (α) into account:

$$\ell^{T} = \ell^{MT} - \ell^{F}\cos\alpha. \tag{4}$$

Pennation angle was measured using a handheld goniometer.

Architectural parameters are not reported for eight of the 80 muscles because diffraction patterns could not be obtained in these muscles. Thus, measured fascicle lengths could not be normalized to a common sarcomere length, which is critical because large differences in sarcomere lengths were observed (e.g., Fig. 2A). One source of variation in sarcomere lengths was elbow posture. While frozen, five of the specimens were in an extended position and five were flexed approximately 90°. Upon thawing and before dissection, the five extended specimens had a limited range of elbow flexion and three of the flexed specimens could not be extended. The average sarcomere length of the major elbow flexors (BIC long, BIC short, BRA, BRD, and ECRL) from the five extended specimens was significantly longer ($p < 0.05$) than the average sarcomere length from the three flexed specimens (Fig. 2B). Also, the average sarcomere length of the flexors was significantly longer ($p < 0.05$) than the sarcomere length of the extensors (TRI long and lateral) in the five extended specimens, but not in the three flexed specimens.

Moment arms were estimated using the tendon displacement method (An et al., 1984) and a protocol similar to that described previously (Murray et al., 1995). Each muscle was connected to a position transducer (Celesco Transducer Products, Canoga Park, CA) with a wire. Elbow flexion angle was measured with an electrogoniometer (Penny and Giles Biometrics, United Kingdom). The outputs of the position transducer and the electrogoniometer were sampled at 15 Hz while the forearm was slowly moved through its range of motion. The forearm was maintained in 0° pronation–supination during data collection.

Moment arms were estimated between 20° and 120° flexion for the elbow flexors and between 30° and 120° flexion for triceps. Five trials of tendon displacement

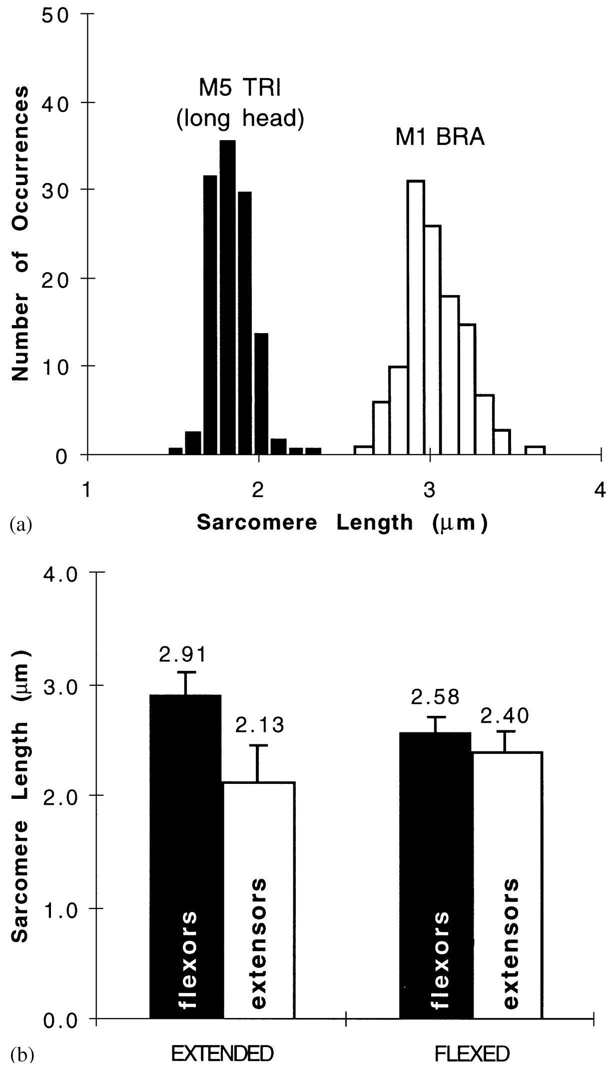

Fig. 2. (A) Distributions of sarcomere lengths measured in the long head of TRI (filled bars) in specimen M5 ($n = 120$) and BRA (white bars) in specimen M1 ($n = 118$). Both specimens M5 and M1 were extended specimens. As illustrated here, large differences in average sarcomere lengths were often observed across muscles. (B) Average sarcomere lengths of the major elbow flexors (BIC long, BIC short, BRA, BRD, and ECRL, filled bars) and the extensors (TRI long and TRI lateral, white bars) for the extended and flexed specimens. Elbow posture was a source of variation in sarcomere lengths across muscles.

vs. elbow flexion angle were collected per muscle. The numerical derivative of each trial was digitally filtered using a second-order Butterworth filter with a cutoff frequency of 1 radian^{-1}. The five filtered derivatives were averaged to estimate moment arm as a function of elbow position, and the peak and average of this curve are reported. Moment arms for brachialis in one specimen (M2) and ECRL in a second specimen (M5) are not reported due to difficulties in dissection and data collection, respectively.

Matched pairs Student's *t* tests were performed to evaluate intermuscular differences in optimal fascicle lengths, PCSAs, peak moment arms, and average moment arms. Because multiple comparisons were performed for each parameter (e.g., BRD vs. BIC, BRD vs. BRA,…), a higher level of significance for individual comparisons is required if all of the comparisons are to reach the desired level ($p < 0.05$). The levels of significance for intermuscular comparisons for PCSA, peak moment arm, average moment arm ($p < 0.0033$) and optimal fascicle length ($p < 0.00179$) were calculated using the Bonferroni method (McClave and Dietrich, 1991). Linear regressions were performed to evaluate relationships between optimal fascicle length, PCSA, and moment arm and relationships between specimen size and architectural parameters. Results were considered significant for $p < 0.05$.

To evaluate how the interplay of muscle architecture and moment arm influences function, the operating ranges and moment-generating potentials of the elbow muscles were estimated. Assuming inelastic tendon and aponeurosis, fascicle excursions during elbow flexion were estimated from the tendon displacement measurements. Estimated excursions were normalized by optimal fascicle lengths and superimposed on a normalized isometric force–length curve based on the average sarcomere lengths of the five extended specimens. For the elbow flexors, we assumed sarcomere lengths of 2.9 μm at 10° elbow flexion (see Fig. 2B) and constant moment arms between 10° and 20° elbow flexion. For the long and lateral heads of triceps we assumed sarcomere lengths of 2.1 μm at 10° flexion and constant moment arms between 10° and 30° elbow flexion. Moment-generating potential was estimated as the product of PCSA, average moment arm, and the cosine of pennation angle.

3. Results

The elbow muscles posses a broad range of excursion capacities and force-generating potentials, and undergo a wide range of length changes during elbow flexion as indicated by substantial differences in optimal fascicle lengths, PCSAs, and moment arms (Table 2). The intermuscular differences in architectural parameters and moment arms are evident despite large variations observed between specimens (see Figs. 3 and 4). For example, the optimal fascicle length of brachioradialis varied by 9.7 cm (54% of the average length) across specimens, yet brachioradialis had the longest fascicles in each specimen. The optimal fascicle length of pronator teres varied by 4.3 cm (78% of the average length), but had the shortest fascicles in each specimen. On average, the PCSA of the combined heads of triceps brachii (14.9 cm^2, range = 6.8–28.1 cm^2) was approximately 10 times greater than brachioradialis (1.2 cm^2, range = 0.5–2.3 cm^2; $p < 0.0005$) or ECRL (1.5 cm^2, range = 0.8–2.1 cm^2; $p < 0.0008$). The peak moment arm of

Table 2
Summary of muscle moment arms and architectural parameters

	N		Peak moment arm (cm)	Average moment arm ^{a} (cm)	Tendon length (cm)	Optimal muscle length^b (cm)	Optimal fascicle length (cm)	PCSA (cm^2)	Pennation angle (deg)
	Moment arm	Muscle archi							
Brachioradialis	10	10	7.7 (0.7)^c	5.4 (0.6)	16.9 (1.7)	26.0 (4.7)	17.7 (3.0)	1.2 (0.6)	0
Biceps	10		4.7 (0.4)	3.7 (0.3)					
(1) Long		6			22.9 (1.6)	21.6 (4.5)	12.8 (3.2)	2.5 (1.1)	0
(2) Short		8			18.3 (2.5)	23.4 (4.2)	14.5 (3.2)	2.1 (0.6)	0
Combined							13.6 (3.7)^d	5.1 (1.6)^e	
ECRL	9	10	3.2 (0.5)	2.1 (0.4)	24.8 (1.0)	13.9 (2.1)	9.2 (1.8)	1.5 (0.5)	1 (2)
Brachialis	9	9	2.6 (0.3)	2.1 (0.3)	11.6 (1.3)	21.2 (2.9)	9.9 (1.6)	5.4 (1.3)	0
Pronator teres	10	9	1.7 (0.3)	1.2 (0.2)	12.0 (1.6)	17.6 (2.9)	5.5 (1.2)	2.8 (0.9)	13 (6)
Triceps	10		2.3 (0.3)^f	2.0 (0.2)^f					
(1) Long		9			21.7 (2.9)	35.6 (7.6)	12.7 (2.1)	4.3 (1.8)	10 (3)
(2) Lateral		8			18.7 (1.8)	29.1 (5.2)	9.3 (2.8)	10.5 (5.2)^g	8 (2)
Combined							10.3 (2.5)^d	14.9 (6.7)^e	

[a] Average of moment arm values between 20 and 120° elbow flexion for flexors and between 30 and 120° elbow flexion for triceps.

[b] Measured muscle length normalized to sarcomere length of 2.8 μm.

[c] Standard deviations in parenthesis.

[d] Combined $\ell_o^M = \dfrac{\mathrm{PCSA}_{(1)}\,\ell^M_{o(1)} + \mathrm{PCSA}_{(2)}\,\ell^M_{o(2)}}{\mathrm{PCSA}_{(1)} + \mathrm{PCSA}_{(2)}}$.

[e] Combined PCSA $= \mathrm{PCSA}_{(1)} + \mathrm{PCSA}_{(2)}$.

[f] Magnitude of triceps extension moment arm. By convention, if flexion moment arms are positive, extension moment arms are negative.

[g] $\mathrm{PCSA}_{(2)} = \dfrac{\mathrm{mass}_{(2)} + \mathrm{mass}_{(\mathrm{medial})}}{1.06\ell^M_{o(2)}}$.

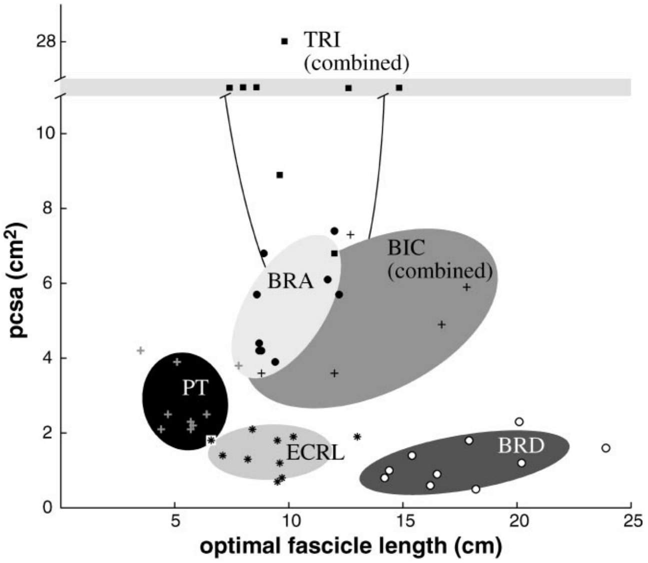

Fig. 3. Physiological cross-sectional area (PCSA) and optimal fascicle lengths estimated for the elbow muscles. Ellipses show the 68% confidence regions and are centered at the average optimal fascicle length and PCSA for each muscle. The upper boundary of the confidence region for TRI extends beyond PCSA values of 11 cm^2 and is not pictured. TRI data points that have PCSAs greater than 11 cm^2 but less than 28 cm^2 are aligned at the appropriate fascicle lengths in the horizontal shaded region of the plot. These architectural parameters indicate that the elbow muscles possess a broad range of excursion capacities and force-generating potentials. These differences are evident despite substantial interspecimen variability.

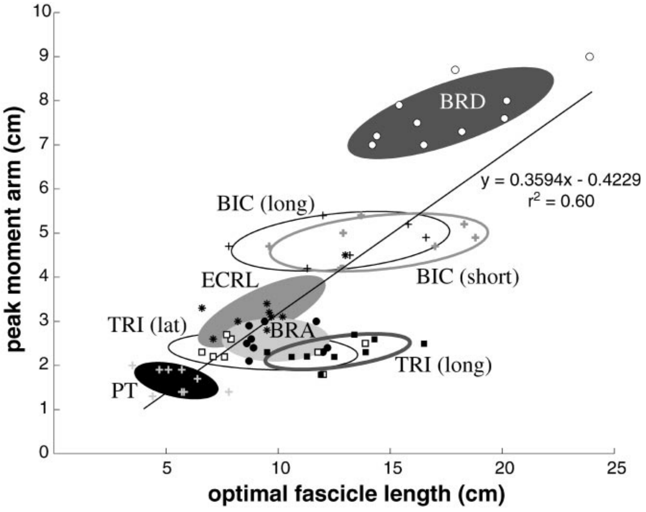

Fig. 4. Peak moment arms and optimal fascicle lengths estimated for the elbow muscles. Ellipses show the 68% confidence regions and are centered at the average optimal fascicle length and moment arm for each muscle. Optimal fascicle length was significantly correlated to peak moment arm across the elbow muscles. The regression line and regression equation for optimal fascicle length and peak moment arm across all muscles in this study are shown.

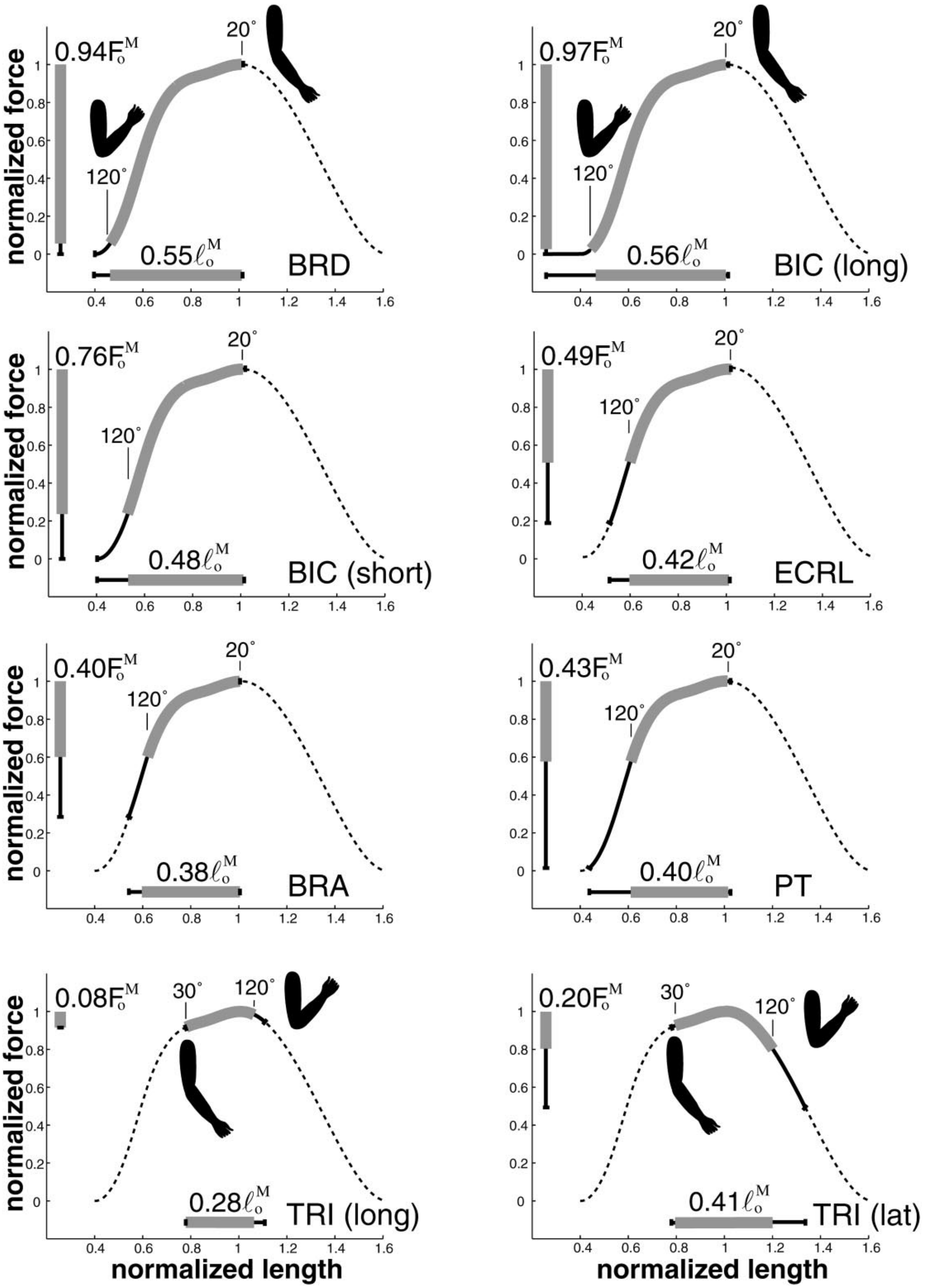

Fig. 5. Estimated operating ranges of the elbow flexors over 100° of elbow flexion and of the extensors over 90° flexion. Estimated fascicle excursions were normalized by optimal fascicle length (ℓ_o^M) and superimposed on a normalized force–length curve based on the sarcomere lengths measured from the five extended specimens. The variation in force-generating capacity during elbow flexion is expressed as a proportion of peak isometric force (F_o^M). Results shown are averages ($\pm$ one standard deviation) of the 10 extremities in this study. Both muscle moment arm and optimal fascicle length determine how much of the isometric force–length curve each muscle uses.

brachioradialis (7.7 cm^2, range = 7.0–9.0 cm^2) was more than four times greater than the peak moment arm of pronator teres (1.7 cm^2, range = 1.3–2.0 cm; $p < 0.0001$).

Across the elbow muscles, muscles with larger moment arms generally have longer fascicles. Given all the muscles in this study ($n = 68$), optimal fascicle length was significantly correlated to peak moment arm ($r = 0.775$; $p < 0.0001$; Fig. 4). Across specimens, moment arm and optimal fascicle length were significantly correlated in brachioradialis ($r = 0.712$; $p < 0.02$) and ECRL ($r = 0.752$; $p < 0.01$). Optimal fascicle length was significantly correlated to humerus ($r = 0.656$; $p < 0.04$), radius ($r = 0.671$;$p < 0.03$), and ulna lengths ($r = 0.720$; $p < 0.02$) in brachioradialis, and radius ($r = 0.753$; $p < 0.01$) and ulna lengths ($r = 0.780$; $p < 0.01$) in ECRL. PCSA was not correlated to peak moment arm, optimal fascicle length, or bone lengths for any muscle in this study.

Brachioradialis and long and short heads of biceps brachii have broad operating ranges on the isometric force–length curve during elbow flexion; long head of triceps brachii has a narrow operating range. Brachioradialis and the two heads of biceps brachii have significantly different peak and average moment arms ($p < 0.0001$); biceps brachii experiences a smaller *absolute* length change than brachioradialis during elbow flexion. However, the two heads of biceps also have shorter fascicles than brachioradialis ($p < 0.001$), indicating a smaller excursion capacity. Thus, as a result of substantial differences in *both* moment arms and optimal fascicle lengths, the length change experienced *relative* to excursion capacity is comparable in brachioradialis (55%), long head (56%), and short head (48%) over 100° of elbow flexion (Fig. 5). Long head of triceps has fascicles of comparable length to long head of biceps, but uses only 28% of its isometric force–length curve over 90° of elbow flexion because of its smaller moment arm ($p < 0.0001$). Given the sarcomere lengths measured in this study (Fig. 2B), this difference in the ratio between moment arm and optimal fascicle length has important functional consequences. The force-generating potentials of brachioradialis and biceps brachii are compromised in flexed elbow postures, while long head of the triceps has a relatively constant force-generating capacity over a broad range of elbow postures (Fig. 5). For the remaining muscles (ECRL, BRA, PT, and TRI, lateral head), operating ranges and force-generating capacities during elbow flexion are intermediate to the described extremes.

Triceps brachii (combined heads) had the greatest moment-generating potential in every specimen (Fig. 6), a result of its substantial PCSA. Biceps brachii (combined heads) had the largest moment-generating potential of the flexors in each specimen. The moment-generating capacity of biceps originates from a smaller PCSA and a larger moment arm than triceps. The isometric moment-generating potentials of ECRL and pronator teres at the elbow are comparable to each other and are the smallest of the muscles studied. This would not be predicted from muscle architectural parameters alone because brachioradialis had the smallest PCSA in eight of ten extremities. The PCSA of pronator teres was 2.3 times greater than brachioradialis ($p < 0.0008$). Because force-generating capacity and elbow muscle moment arms vary as a function of elbow flexion angle, the relative strengths of the individual elbow muscles may also vary as a function of elbow position.

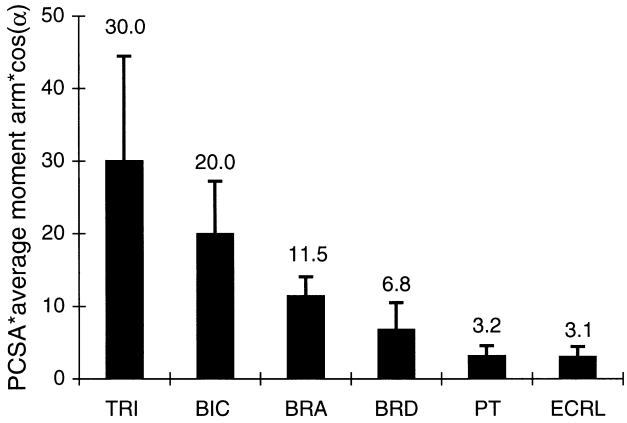

Fig. 6. Isometric moment-generating capacity, estimated as the product of PCSA, average moment arm, and the cosine of pennation angle. Results shown are averages (± one standard deviation), units are cm^3. Triceps brachii (combined heads) had the greatest moment-generating capacity in each specimen. Biceps brachii (combined heads) had the greatest moment-generating potential of the elbow flexors.

4. Discussion

This work evaluated the isometric functional capabilities of muscles that cross the elbow based on architectural parameters and moment arms estimated in differently sized upper extremity specimens. We hypothesized that the individual elbow muscles have fundamental differences in their isometric functional capacities due to intermuscular differences in muscle architecture, moment arms, and the interplay of each muscle's architecture and moment arm. The anatomical data indicate that the excursion capacities of the elbow muscles vary by as much as threefold, the force-generating capacities vary by as much as tenfold, and the length changes experienced during elbow flexion vary by as much as fourfold. Long head of biceps and long head of triceps use substantially different amounts of the isometric force–length curve during elbow flexion despite having comparable excursion capacities. Despite having the smallest force-generating potential, brachioradialis has the potential to contribute significantly to elbow flexion moment because of its large flexion moment arm. This study emphasizes that understanding how a muscle

Table 3
Summary of published muscle architectural parameters

	Optimal fascicle length (cm)	PCSA (cm^2)	Pennation angle (deg)
BRD[a]	14.2–23.9	0.5–2.3	0
Amis ($N = 1$)	14.2	3.2	0
An ($N = 4$)	16.4	1.5	—
Brand ($N = 5$)	16.1	3.4	—
Lieber and Shoemaker (1992) ($N = 8$)	15.4	1.0	2
Veeger et al. (1997) ($N = 1$)	—	2.9	< 15
Wood ($N = 1$)	—	1.3	—
BIC (long)	7.8–16.6	1.4–4.3	0
Amis ($N = 1$)	15.0	4.1	0
An ($N = 4$)	13.6	2.5	—
Veeger et al. (1997) ($N = 1$)	—	2.8	< 15
Veeger et al. (1991) ($N = 14$)	—	3.2	—
Wood ($N = 1$)	—	1.9	—
BIC (short)	9.6–18.8	1.6–3.2	0
Amis ($N = 1$)	15.7	3.9	5
An ($N = 4$)	15.0	2.1	—
Veeger et al. (1997) ($N = 1$)	—	2.6	< 15
Veeger et al. (1991) ($N = 14$)	—	3.1	—
Wood ($N = 1$)	—	1.3	—
ECRL	6.6–13.0	0.7–2.1	0
Amis ($N = 1$)	10.8	3.3	4–6
An ($N = 4$)	7.8	2.4	—
Brand ($N = 5$)	9.3	4.9	—
Lieber et al. (1990) ($N = 5$)	9.7	1.1	2.5
BRA	8.6–12.2	3.9–7.4	0
Amis ($N = 1$)	12.3	9.4	0
An ($N = 4$)	9.0	6.6	—
Veeger (1997) ($N = 1$)	—	5.6	< 15
Wood ($N = 1$)	—	9.0	—
PT	3.5–7.8	2.1–4.2	6–27.5
Amis ($N = 1$)	6.7	4.4	5–9
An ($N = 4$)	5.6	3.4	—
Brand ($N = 5$)	5.1	7.8	—
Lieber and Shoemaker (1992) ($N = 8$)	4.6	3.3	10
Veeger et al. (1997) ($N = 1$)	—	1.7	< 15
TRI (long)	9.5–16.5	2.8–8.2	6.5–15
Amis ($N = 1$)	7.4	21.0	16
An ($N = 4$)	10.2	6.7	—
Veeger et al. (1997) ($N = 1$)	—	4.7	30
Veeger et al. (1991) ($N = 14$)	—	6.8	—
Wood ($N = 1$)	—	3.9	—
TRI (lat)	6.6–13.9	4.0–19.9[b]	6–10
Amis ($N = 1$)	6.8	28.3[b]	8–12
An ($N = 4$)	8.4	10.2[b]	—
Veeger et al. (1997) ($N = 1$)	—	8.1[b]	30
Wood ($N = 1$)	—	6.9[b]	—

[a] For each muscle, the first line summarizes the data reported in this study. With the exception of the data from Leiber et al., lengths from other studies are not normalized to a common sarcomere length. Fiber length data reported by Leiber et al. were scaled by a factor of 2.8/2.2 to reflect lengths at 2.8 μm. For equivalent comparison with this study, PCSA values were calculated from other studies as follows:

Amis: muscle weight/fiber length × 1.06
An: reported PCSA (muscle volume/fiber length)
Brand: 141 cm^2 × tension fraction
Lieber (1990, 1992): muscle weight/(fiber length at 2.8 μm × 1.06)
Veeger (1997): reported PCSA (muscle volume/muscle length)
Veeger (1991): reported PCSA (PCSA was digitized)
Wood: reported PCSA (muscle volume/muscle length)

[b] For an equivalent comparison with the data from this study, PCSA data for TRI (lat) was calculated using the combined masses (or volumes) of the medial and lateral heads and the length of the lateral head.

functions within the musculoskeletal system requires an understanding of the unique combination of its moment arm and architectural parameters, especially optimal fascicle length and PCSA.

The effects of several assumptions and limitations of this study should be considered. We assumed the tendons and aponeuroses of the elbow muscles are inelastic. We evaluated this assumption using a musculoskeletal model of the elbow joint (Murray et al., 1995) to simulate fascicle excursions given an inelastic tendon (0.1% tendon strain at peak muscle force) and a compliant tendon (5% tendon strain at peak force). The length changes differed by less than 10% in the two simulations. Given that 5% tendon strain is well above the reported tendon strain of ECRL at peak isometric force (1.78%, Loren and Lieber, 1995), we believe this study provides reasonable approximations of fascicle length changes with elbow flexion.

The conclusions about the effect of elbow position on force-generating capacity are sensitive to our assumptions about the relationship between sarcomere length and elbow position. Sarcomere shortening is associated with rigor mortis. Freezing, thawing, and fixation of muscle could influence sarcomere lengths (Cutts, 1988; Friederich and Brand, 1990). The effect of elbow flexion on force-generating capacity should be further investigated in human subjects, using intramuscular stimulation (Leedham and Dowling, 1995) or intraoperative measurements (Freehafer et al., 1979; Lieber et al., 1994). In this study, measured fascicle lengths were normalized to a common sarcomere length to minimize the effects of the anatomical preparation on optimal fascicle lengths, PCSAs, and fascicle excursions during joint rotation.

The form of the normalized force–length curve is based on several assumptions: fascicle lengths are identical to fiber lengths, sarcomere lengths and fascicle lengths are homogeneous within a muscle, and muscle shortening or lengthening involves uniform length changes. There is evidence that, in some muscles, fascicles are composed of shorter, interdigitated fibers (Chanaud et al., 1991). Also, distributions of sarcomere and fiber lengths within a muscle influence the form of the isometric force–length relationship (Allinger et al., 1996; Ettema and Huijing, 1994). Experimental studies have shown that fibers within a muscle reach optimum length at different muscle lengths, broadening the range of lengths over which a muscle can actively generate force (Heslinga and Huijing, 1993; Willems and Huijing, 1994; Zuurbier and Huijing, 1993). The relationship between muscle length and isometric force development is influenced by complexities that could not be evaluated by this study. However, we believe that the basic relationships presented here provide the underlying characteristics upon which the effects of these complexities are superimposed.

The significant relationship between peak moment arm and optimal fascicle length across the elbow muscles implies a degree of biomechanical specialization. In these muscles, we found that the greater the length change a muscle experiences during joint rotation, the greater its overall excursion capacity. Across specimens, a significant relationship between moment arm and fascicle length was identified in only two muscles (BRD and ECRL). Multiple factors influence muscle fascicle lengths (Herzog et al., 1991; McClearn, 1985; Williams and Goldspink, 1978), so it is reasonable that moment arms do not fully explain interspecimen variability in optimal fascicle lengths. Importantly, the data indicate that moment arm and optimal fascicle length are correlated across the elbow muscles, even when brachioradialis and ECRL are excluded from the analysis ($n = 49, r = 0.635, p < 0.0001$). However, the data also illustrate an exception; long head of biceps and long head of triceps have comparable fascicle lengths but significantly different moment arms. The functional consequence of the difference is that long head of triceps has the potential to generate nearly maximal forces over a broad range of elbow positions, whereas long head of biceps does not.

This study improves upon previous anatomical investigations of the elbow muscles; a larger number and a broader size range of specimens were studied, architecture and moment arm data were obtained in the same specimens, and sarcomere lengths were quantified. Previously published architectural parameters for muscles that cross the elbow (Amis et al., 1979; An et al., 1981; Brand et al., 1981; Lieber et al., 1990, 1992; Veeger et al., 1991, 1997; Wood et al., 1989) generally fall within the range of values reported here (Table 3). The PCSA values reported by Amis et al. (1979) and Brand et al. (1981) are larger than the data from this and other studies. With the exception of the data collected by Lieber et al. (1990, 1992) previous studies did not measure sarcomere lengths. The differences in sarcomere lengths measured in this study illustrate that it is critical to account for variations in sarcomere lengths when reporting architectural parameters. Peak moment arms reported in earlier studies are also comparable to the data from this study (see Murray et al., 1995, for review).

Acknowledgements

We would like to thank Allison Arnold, Mahidhar Durbhakula, and David Wyles for assistance with data collection and analysis, Dr. Randolph Perkins for his assistance in the anatomy lab, and the Orthopaedics Department of Northwestern University for the use of the anatomy lab. We would like to acknowledge the contribution of Andrew Krylow (1960–1998) for designing the laser system. This work supported by NSF BES-9257229, NIH, and an NIDRR Training Grant.

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