

Evidence that maximum muscle stress is not a constant: differences in specific tension in elbow flexors and extensors

T.S. Buchanan

Departments of Biomedical Engineering and Physical Medicine & Rehabilitation, Northwestern University Medical School, and Sensory Motor Performance Program, Rehabilitation Institute of Chicago, 345 East Superior St., Chicago, IL 60611, USA

Received 20 June 1994, accepted 7 December 1994

ABSTRACT

The specific tension of muscle (or maximum muscle stress) is the maximum force developed per unit cross-sectional area and is a frequently used parameter by investigators estimating muscle force. Generally, it is assumed to be a constant value for all muscles and, when multiplied by a muscle's cross-sectional area, is used to provide a measure of a muscle's maximum force production. In this study, the specific tension for elbow flexors and for extensors were compared to evaluate the validity of this assumption. Maximum muscle stress was determined using maximum joint moments measured as a function of joint angle and using anatomical parameters reported in the literature. It was observed that the specific tension for elbow flexors was considerably larger than for extensors when measured a variety of ways. The exact reasons for the differences are unknown, but variations in specific tension of individual fibers may play a role. It was concluded that the use of a constant value for specific tension in muscle models is questionable in studies that demand accurate results.

Keywords: Specific tension, muscle stress, physiological cross-sectional area (PCSA), muscle force, muscle moment arm

Med. Eng. Phys., 1995, Vol. 17, 529–536, October

INTRODUCTION

The ratio of the maximum force of a muscle to its cross-sectional area is often assumed to be a constant. This constant, σ , is referred to either as the maximum muscle stress or the muscle's specific tension, and has been reported to be between 35–137 N/cm² for whole muscles (e.g., 35^{1,2}, 39³, 59–98^{4,5}, 62⁶, 90⁷, and 137⁸ N/cm²). Values for specific tension of individual muscle fibers or motor units are generally reported to be lower, varying between 6–38 N/cm²^{9–12}.

The notion that specific tension is constant for all muscles is significant in biomechanics research because this assumption is often used without much question, either as a method for muscle force prediction, as a means for validating predictions made using other methods, or as a constraint equation in muscle models.^{8,13–17}

There has always been a question about the actual value of σ due to the variations in the literature, which, as mentioned, span nearly a four-fold range for whole muscle. Some of this variation is likely due to difficulties in measuring muscle

cross-sectional area. Brand *et al.*¹⁸ developed the concept of 'physiological cross sectional area' (which we will call PCSA or ϕ), which takes into account the fiber length of individual muscles. This was not used in all previous studies that measured σ . Nevertheless, in current studies, once a value for σ is chosen, it is generally used for all muscles in a model.

Although considerable variance in reported values of maximum muscle stress can be found, no investigators have explicitly suggested that such variations might be physiological. However, this does not mean that questions along these lines have not been raised. For example, Maughan *et al.*¹⁹ have noted that maximum muscle force is a poor predictor of cross-sectional area. Differences in σ for muscles or muscle groups might be due to differences in specific tension of different muscle fiber or motor unit populations¹⁰.

In this study we examined the validity of assuming that σ is constant among muscles. We hypothesized that significant variations in σ could be observed in different muscle groups. This was examined for flexors and extensors in the elbow

(chosen for experimental convenience) using measurements of maximum joint moments and anatomical data reported from previous studies. Additionally, we examined whether length-tension characteristics of muscles were sufficient to account for any differences observed.

METHODS

Maximum elbow joint moments were recorded in flexion and extension using a rotary arm device. The device consisted of a rotatable arm to which a torque transducer was attached (*Figure 1*). The arm of the device could be moved to different positions and then locked. While sitting, the subject's right distal forearm was fixed in the device so that the forearm followed the device's arm and so that the elbow was located over the center of rotation of the arm of the device. The subject's arm was attached to the device just proximal to the styloids via an adjustable aluminum post that could slide along the length of the arm of the device. The post was cushioned with rubber to make the task more comfortable. The subject's torso was stabilized using automobile seat belts which passed over the shoulders, crossed at the chest and were secured at the back. This fixed the subject in the heavy, rigid chair in order to minimize shoulder movement during the study.

Maximum flexion and extension moments at an elbow angle of 90° were measured for eleven male subjects age 22–40, all of similar stature. In addition, maximum joint moments were recorded at seven different joint angles for five of these subjects. The angles used were approximately 25°, 50°, 70°, 90°, 110°, 120°, and 130° of elbow flexion. Once the subject had moved to one of these angles, the device was locked and the final (actual) flexion angle was then measured with a goniometer. The joint angles were randomized to eliminate any effects due to order. EMGs were recorded using surface electrodes over the biceps

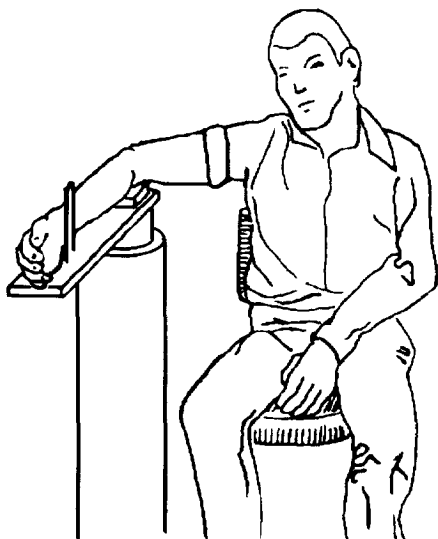


Figure 1 Experimental set-up. Subjects were instructed to maximally flex (shown) or extend against a cushioned block in an apparatus that could be moved to different joint angles. Visual feedback was provided on an oscilloscope (not shown)

brachii and triceps. All subjects were asked to do three repetitions at each different joint angle. To reduce the effects of muscle fatigue, subjects were instructed to pause between each trial for as long as they felt was needed in order to minimize fatigue (between one and five minutes). The subjects were given visual feedback of the torque produced on an oscilloscope and when a maximum torque was reached, 500 ms of data were collected on a Macintosh computer with National Instruments A/D boards (sampling rate: 500 Hz). The subject was then instructed to rest until the next trial. The torque data were analyzed offline by averaging the torque values over the entire collection period. EMG signals were bandpass filtered at 20–200 Hz and then digitally rectified and averaged.

Anatomical data for physiological cross-sectional area (PCSA) and moment arms were taken from studies reported by Amis *et al.*²⁰, An *et al.*²¹, Edgerton *et al.*²², Lieber *et al.*²³, and Murray *et al.*²⁴ (*Table 1*). Two other sources reported in the literature^{25,26} were not included because their data were based on the other studies or because their methods were difficult to ascertain. In addition to these data sets, a weighted average set was composed. Here, the values for PCSA were computed using a weighted average based on the numbers of subjects in each study (Lieber *et al.* used 8, Edgerton *et al.*, 4, An *et al.*, 4, Amis *et al.*, 4). This was done by going back to the reported values of muscle mass and fiber length and finding a weighted average for each. Muscle mass was then divided by muscle density (which, at 1.0597 g/cm³, shows little variation in mammalian muscle²⁷) to get volume, which was then divided by fiber length to get PCSA.

Muscle moment arm data were taken from the studies of Murray *et al.*, An *et al.*, and Amis *et al.* Murray *et al.*'s study computed moment arm based on measuring muscle length with a length transducer at different joint angles and then differentiating to get moment arm ($R_i = \partial l_i / \partial \theta$). The values reported were found at 110° flexion (within the peak plateau region for flexors and extensors) and neutral supination. In An *et al.*'s study, moment arm calculations were based on serial cross-sections. Moment arm data from Amis *et al.* were taken from figures 5–7 of their paper, measured at 110° flexion.

Specific tension values were determined as the ratio of maximum joint moment to the sum of the products of moment arm and cross-sectional area (see below).

RESULTS

Maximum elbow joint moments were recorded in flexion and extension at a variety of joint angles. These values, when taken with moment arm and cross-sectional area values, were used to determine the specific tension (maximum stress) of the elbow flexor and extensor muscle groups.

The absolute maximum values for elbow joint moment were measured for the eleven subjects (*Figure 2*). In all but one subject the peak flexion

Table 1 Anatomical parameters used in this study. Physiological cross-sectional area (PCSA) and muscle moment arms in flexion–extension are from studies by Amis *et al.* (1979), An *et al.* (1981), Edgerton *et al.* (1990), Lieber *et al.* (1993), and Murray *et al.* (1992). A weighted average value for PCSA are also given (see text for details). Moment arm data from Amis *et al.* and Murray *et al.* were taken at 110° flexion and that from An *et al.* is at 100°. All data correspond to a neutral supination position. Muscle abbreviations are as follows: biceps (BIC), long and short heads of biceps (LBIC and SBIC), brachialis (BRA), brachioradialis (BRD), pronator teres (PT), anconeus (ANC), triceps brachii (TRI), and the medial, lateral and long heads of the triceps (MTRI, LTRI, and LnTRI, respectively)

Muscle	Physiological Cross-Sectional Area (cm ²)				Ave'd	Moment Arm (cm)		
	Edgerton	Lieber	Amis	An		Murray	Amis	An
BIC	3.8		5.7	4.6	4.7	3.4	3.8	3.4
LBIC	2.2		3.2	2.5	2.3	3.4	3.8	3.4
SBIC	1.6		2.5	2.1	2.4	3.4	3.8	3.4
BRA	4.7		5.6	7.0	5.0	2.8	3.0	2.1
BRD	1.8	1.3	1.8	1.5	2.0	5.2	5.0	4.2
PT	2.3	4.1	4.6	3.4	5.3	0.5	1.2	1.6
ANC			1.7	2.5	2.2			-1.1
TRI	23.8		41.6	18.8	30.2	-1.7	-2.0	-2.0
MTRI			12.3	6.1		-1.7	-2.0	-2.0
LTRI			17.0	6.0		-1.7	-2.0	-2.0
LnTRI			12.3	6.7		-1.7	-2.0	-2.0

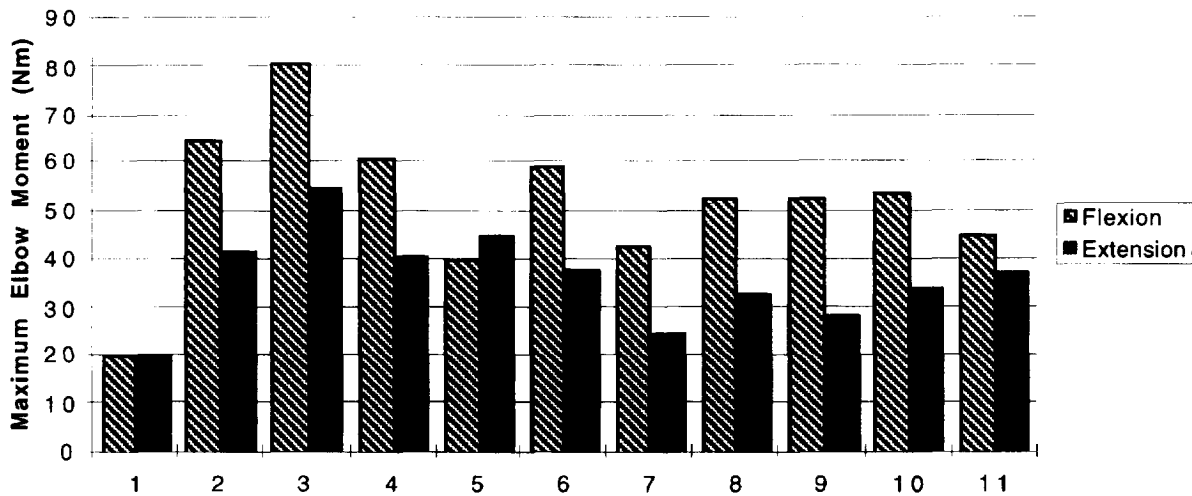


Figure 2 Maximum isometric moments for eleven subjects for elbow flexion and extension at 90°. Each bar represents the maximum of at least three trials. On average, the maximum flexion moment was 1.45 times the maximum extension moment

moment was greater than the peak extension moment. Overall, the average maximum flexion moment was greater than the peak extension moment. Overall, the average maximum flexion moment was found to be significantly greater in flexion than extension ($p < 0.0005$), the ratio of the two being 1.45 with a standard error of 0.18. The EMG data indicated that there was no co-activation of flexors and extensors during these tasks.

Not surprisingly, the maximum moment values were found to be strongly dependent on the joint angle. The moment–angle relationship for a typical subject (*Figure 3*) demonstrates that peak joint moment is produced at elbow angles of 90° and 108° for flexion and extension, respectively, when taken from the peaks of 3rd order polynomial fits. Note that peak flexion occurs at a joint angle of 18° less than that for extension. Note also that at a joint angle of 30° flexion, the maximum joint moment that can be produced is one half of the peak values obtained at the optimum joint angle. This observation holds for both flexion and extension.

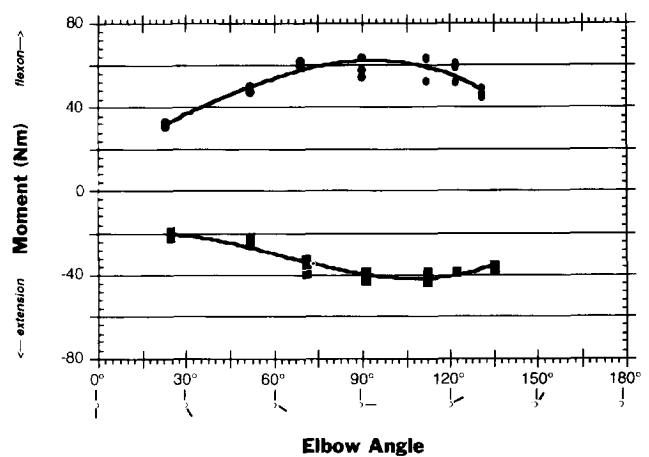


Figure 3 Maximum isometric moment values for one subject for elbow flexion (circles) and extension (squares). Three trials were recorded at each joint angle. A third order polynomial curve was fit to the data ($R^2 = 0.86$ for flexion and 0.91 for extension). Note that for both flexion and extension moments, at joint angles of 30° the maximum moment that can be produced drops to about half of the peak value obtained at optimal joint angles.

The maximum moment-angle relationship was compared across all five subjects for which such data were obtained. Comparisons were made by normalizing the data such that for each subject the maximum extension moment recorded was set to unity. Third order polynomial curves were then fitted through the combined data for all subjects (Figure 4).

These data suggest three things. First, there is a decrease in maximum moment for joint angles away from the optimal angle. Again, a decrease of 50% is observed at flexion angles of 30°. Similar decreases begin to occur sharply at angles greater than the peak or optimal angle, but limits on the range of motion preclude such dramatic declines. Second, the peak moments for flexors were found at a joint angle of 97° from the polynomial curve fit. Peak moments for extensors were found at 120°, at joint angles of about 23° greater than those for flexion. Third, for these subjects the value for maximum joint moment in flexion is on average 40% greater than that in extension. This corresponds with the results from the first study (i.e., Figure 2).

Specific tension was computed by using the following relationship (reducing the system to one degree-of-freedom and assuming that vector cross-product terms are taken into account in the moment arm values):

$$T = \sum_{i=1}^M (R_i F_i) \tag{1}$$

or

$$T = \sigma \sum_{i=1}^M (R_i \phi_i) \tag{2}$$

where T is maximum joint moment, R_i is the moment arm for muscle i , and F_i is the maximum force in muscle i , which can also be expressed as ϕ times σ , the maximum muscle stress or specific

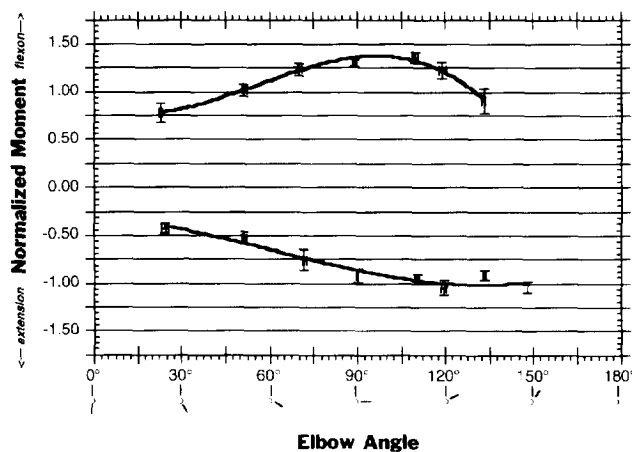


Figure 4 Normalized maximum isometric moments for five subjects for elbow flexion and extension. The error bars indicate confidence intervals ($p < 0.05$). The moment values are normalized such that average maximum extension moment was set to unity. Third order polynomial curves were fit to the data. Correlation coefficients for the curves were $R^2 = 0.97$ and 0.94 for flexion and extension moment, respectively. Note that maximum flexion moment is 40% greater than maximum extension moment

tension. In the above equation it is assumed that σ is the same for all muscles. Hence, by knowing the maximum joint moment, moment arms, and cross-sectional area, the values for σ can readily be obtained by solving equation (2).

Values for specific tension were computed this way for flexors and extensors using five different sets of anatomical data (Figure 5). Data from An *et al.* from Table 1 were used for the first comparison. Since some wrist and finger muscles attach on the humerus and thus could be influencing the results, in the second comparison, PCSA and moment arm values from additional finger and wrist muscles²⁰ were also included. Third, data from Amis *et al.*'s moment arms and PCSA were used. A fourth comparison used Edgerton *et al.*'s PCSA values and Murray *et al.*'s moment arms. Finally, the weighted average PCSA values and the Murray *et al.*'s moment arms were used. The specific tension values ranges from 99 to 148 N/cm² for flexors and from 43 to 91 N/cm² for extensors. In all cases, the specific tension for flexors was greater than for extensors. Unfortunately, because the published moment arm data are each based on at most two subjects, statistical significance cannot be ascertained. However, it is clear that the same trend is observed for all published data.

The length-tension relation and its influence on the muscle stress was evaluated by computing an average force-angle curve for the flexor and extensor groups (Figure 6). Taking the maximum joint moment curves (Figure 4) and dividing by average muscle moment arm curves gives a maximum lumped-muscle force versus joint angle relation. The average moment arm for the flexors was computed by averaging moment arm curves for the primary flexors (biceps, brachialis, brachioradialis, and pronator teres) using Murray *et al.*'s model with the wrist in a neutral position. (These muscles all had similar relationships for moment arm as a function of joint angle at a neutral wrist position.) Curves for the extensors were computed from the same model using an average triceps moment arm relation. Once these lumped muscle force curves were created, they were divided by the total PCSA for the flexors and exten-

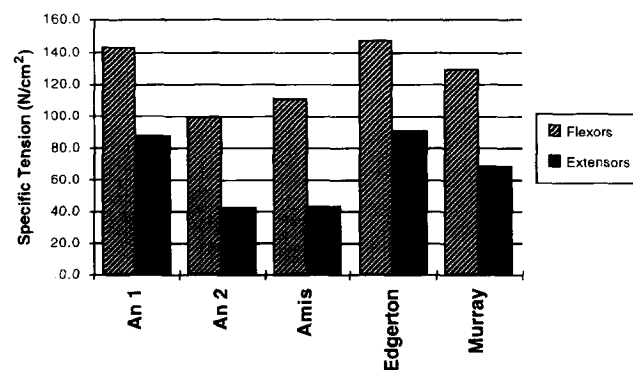


Figure 5 Specific tension computed from the maximum moment values of Figure 4 and different anatomical data sets. The data from An *et al.* were computed two ways, first using just the primary elbow muscles, and, second, using all muscles that cross the wrist (i.e., including all relevant wrist and finger muscles). Note that for all cases the calculated specific tension was greater for flexors

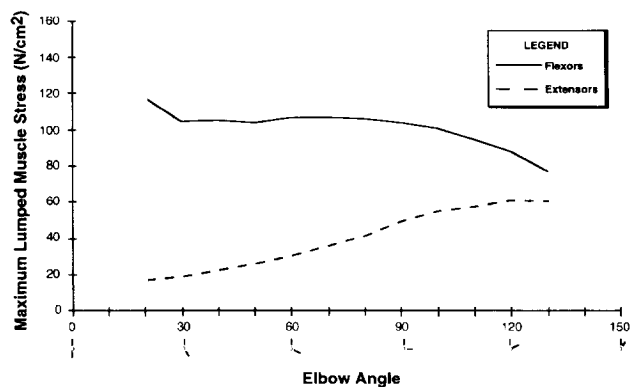


Figure 6 Maximum lumped muscle stress versus elbow angle. These are computed by first taking the maximum joint moment curve (from Figure 4) and dividing by average muscle moment arm curves (using the model by Murray, 1992) to give an average force-angle relation. Finally, these curves are divided by the total cross-sectional area (from Table 1, column 5). The shape of these curves should reflect an average length-tension relation for the flexor and extensor groups. Note that the peak stress for the extensors is considerably less than the peak for the flexors

sors in order to get an average muscle stress relation. Because a constant value was used for the PCSA, the shapes of the calculated force-length relation is still preserved in Figure 6. These curves demonstrate that the extensor muscle force peaks towards flexion (where these muscles are most fully stretched) whereas the flexor muscle force peaks towards full extension (where the flexors are near maximum length).

The stress curves also show that there is a large difference in maximum muscle stress, σ , between flexors and extensors. This is the same conclusion that was reached from our comparison of previously reported anatomical data and our maximum moment values (Figure 5). Furthermore, it demonstrates that these differences are not due to length-tension effects.

DISCUSSION

It was observed that maximum elbow flexion moment averaged to be 1.45 times greater than maximum extension moment with the elbow in a neutral supination position. This finding is in general agreement with previous studies. Askew *et al.*²⁸ found that maximum flexion moment at the elbow was 1.64 times that of maximum extension moment. In another study, Provins and Salter²⁹ found that maximum flexion moment was 33% greater than maximum extension moment. Our values are between those of these two studies. It is likely that higher values would have been obtained if the supination angle had been varied. The biceps brachii's length-tension relation would be significantly altered with changes in supination angle, thus presumably higher and lower values for maximum flexion moment could have been obtained. Notwithstanding, the data from this and other studies indicate that maximum elbow flexion moment is greater than that for maximum extension moment by a factor from 1.33 to 1.64.

Maximum muscle force is joint angle dependent

To determine if the calculated differences in specific tension could be explained by differences in the moment-angle or length-tension relationships in the flexors vs. extensors, maximum joint moment was calculated as a function of joint angle. It was observed that maximum joint moment was strongly dependent on joint angle, as has been demonstrated for the elbow flexors³⁰. This is not surprising because muscle fibers are known to have non-linear length-tension relationships³¹ and because muscle moment arms are also joint angle dependent³². Individual muscle length-tension relationships demonstrate that for any muscle there is an optimal length (or joint angle) at which it will produce the most force. This is generally found at joint angles where the muscle is nearly at (or even beyond) the point of being fully stretched. (The peak of the length-tension curve has been observed in detached muscles under laboratory conditions and for a specific muscle, this part of the curve may never be reached during physiological range of motion.) Any increase or decrease from the optimal muscle length (or joint angle) will result in a decrease in possible maximal muscle force production. The moment arms for the elbow flexors reach a peak at roughly the same joint angle as does maximum flexion moment^{20,24}. On the other hand, length-tension relationships for flexors would most likely peak at lower joint angles (much closer to full extension), as this is where the muscles would be at maximum length. The same studies also show that the moment arms of the elbow extensors peak at much lower joint angles (closer to full extension), although because these muscles wrap around the ulna, their moment arms do not vary as much from flexion to extension. The length-tension relation of the muscles must therefore be the driving force in the moment-angle curve for the extensors, as it would be expected to peak where the muscles were most fully stretched—at high flexion angles.

Arguments against a single value for σ

From the anatomical data and assuming a constant value of σ , one would predict that the maximum joint moment for elbow flexion and extension would be the same. This fact, although not intuitively obvious, can be easily seen from the anatomical data. For example, let us take the data reported by An *et al.*¹⁹ for the case when the elbow is in a neutral position at 100° flexion. At maximum activity (maximum muscle force), the contribution to joint moment made by a single muscle is:

$$T_i = \sigma \phi_i R_i \quad (3)$$

Comparing flexors (biceps, brachialis, brachioradialis, and pronator teres) and extensors (triceps and anconueus):

$$\sum_{\text{extensors}} T = \sigma (-42.0 \text{ m}\cdot\text{cm}^2) \quad (4)$$

$$\sum_{\text{flexors}} T = \sigma (41.1 \text{ m}\cdot\text{cm}^2). \quad (5)$$

Note that the major difference between the magnitude of the maximum joint moment contribution between flexors and extensors lies in the σ term. If the values for σ were the same for flexors and extensors, we would predict that the maximum joint moment in flexion (with flexors at maximum activation and extensors relatively quiet) would be equal to the similar maximum value at extension. This is not the case, as has been shown (Figure 4). On the contrary, calculated values of σ (Figure 5) show that it is considerably different for flexors and extensors.

We are not the first to suggest problems with the idea of an invariant maximum muscle stress. Maughan *et al.*⁹ examined the use of maximum muscle force (or strength) to predict muscle cross-sectional area and concluded that "a wide variation in the ratio of strength to muscle cross-sectional area was observed. . ." and ". . . is such that strength is not a useful predictive index of muscle cross-sectional area." It is not clear whether Maughan *et al.* were questioning the validity of invariant maximum muscle stress, or just its usefulness as an anthropometric tool.

Along these same lines, there are anatomical and physiological differences in muscle fibers that could be important in determining the ψ 's. For example, it is unclear whether or not the values for ϕ_i adequately take into consideration the different types of muscles (e.g., pennate, bipennate, fusiform, etc.), although Brand *et al.*¹⁸ do claim that their parallelepipedon method (as first reported by Sterno in 1667) of measuring physiological cross-sectional area accounts for this. Also, there are different motor unit types that have been labeled according to their fatiguing properties: types FF, FR, and S³³. However, besides fatiguing at different rates, these units may also have different specific tensions. Burke and Tsairis¹⁰ showed that the specific tension for type S units in the cat gastrocnemius is considerably smaller (about 6 N/cm²) than either type FF units (about 15 to 20 N/cm²) or type FR units (26–29 N/cm²). Close⁹ reported that specific tension in female rat extensor digitorum longus is 30 N/cm², but is 20 N/cm² for soleus. McDonagh *et al.*³⁴ have shown that the same types of units (e.g., type S or FF) may have different specific tensions in different muscles. Furthermore, Kanda and Hashizume¹² recently reported statistically significant differences between specific tension in S units (16.7 ± 2.9 N/cm²) and FF units (25.1 ± 2.9 N/cm²) of rat medial gastrocnemius.

These studies indicate that differences in specific tension of muscle fibers may have a role in influencing σ . However, Close³⁵ argues that specific tension differences that he has observed are not due to fiber type differences, but rather are due to "extrinsic factors that influence activation." Additionally, a study by Lucas *et al.*³⁶ stands in

opposition to the above studies. They found rather little difference between the specific tension of type I units (i.e., slow or S units) and type II units (i.e., fast units) of the cat medial gastrocnemius. Obviously, the role of motor unit type on values for specific tension is still a matter of debate, with a wide variation of specific tension values being reported.

It has been shown in humans that different muscles have different mixtures of fiber types which implies that different muscles could have significantly different properties which, in turn, could effect the value of σ . Fiber types for some of the muscles examined in this study have been reported³⁷. The percentage of fibers that were type I (i.e., type S units) ranged from, within 95% confidence limits, 34–51% for biceps brachii surface fibers, 40–60% for deep fibers of the biceps, 30–53% for brachioradialis fibers, and 16–49% for surface fibers of the triceps brachii. Unfortunately, there is not a consistent pattern here and composition of 40–49% type S units would fall within the 95% confidence limits for all of these muscles. Additionally, it should be noted that Maughan and Nimmo³⁸ reject the hypothesis that fiber type can account for the variations observed in maximum muscle stress.

Alternate explanations & sources of error

Besides the hypothesis stated (i.e., of different values of specific tension for different muscles or muscle groups), there are other factors that could play a role in the phenomenon discussed. At the experimental level, there could be errors in the data due to anatomical variability among subjects and effects of fatigue. Also, muscle moment arms are difficult to estimate. However, the fact that our data are supported by many previous studies makes these possibilities remote.

It has been demonstrated for some muscles that different parts of the muscle are activated for different tasks^{39–42}, which implies that the effective muscle moment arm, pulling direction, and cross-sectional area are a function of neuronal activation. This could be significant, but at the maximum activation levels examined, it is unlikely it this could influence the results.

Also, the values of ϕ_i (physiological cross-sectional area) are very difficult to estimate and there is disagreement on how to define ϕ_i . Brand *et al.*¹³ have shown that muscle force predictions are quite sensitive to changes in ϕ_i . It is possible that the ϕ_i should not be taken as constants, but rather as functions of joint angle. It could also be a function of moment direction if the muscles are compartmentalized such that different segments of a muscle are used for different tasks. Furthermore, the magnitude of the error introduced by the complicated changes in ϕ_i is difficult to ascertain because few studies on this have been done.

Muscle fiber length may also play a role. Amis *et al.*²⁰ have reported that triceps fiber lengths average 67 mm while biceps, brachialis and brachioradialis fiber lengths average 153, 142, and 123 mm, respectively. These differences should

make triceps force production much more sensitive to changes in overall muscle length (i.e., joint angle) than that of the elbow flexors and indeed, this is seen in the length–tension relation (Figure 6). However, fiber length is taken into account in determining the value of ϕ_n , and, from our analysis (Figure 6), it does not appear to be able to account for the differences in specific tension.

The differences in fiber length between flexors and extensors imply that tendon slack lengths may be different. Although no data are available, it is likely that tendon slack length is longer for flexors. (Upon dissection, the brachioradialis and biceps brachii have long, visible tendons whereas the triceps brachii does not.) If this is the case, it could shift the peaks of the length–tension curves in the angular domain and, to some measure, move the curves upwards or downwards as well⁴⁴. This could account for some of the differences observed in Figure 6, where tendon length was not considered. Accounting for tendon slack length would tend to lower the curves which may have a larger effect on flexors than extensors. However, it is unlikely that it would be of such magnitude to completely explain the differences observed. Also, it should be noted that whereas the brachioradialis muscle may have very long tendons, the brachialis muscle (which contributes the most force and hence dominates the elbow flexor moment–angle relationship), most likely does not have long tendons relative to the extensors.

Conclusions and implications

The foregoing analysis indicates that maximum muscle stress is not the same for elbow flexors and extensors. This may explain some of the vast differences in what has been reported by previous studies. The exact reasons underlying these differences are unclear. Considerable variation in specific tension of individual motor units have been reported and are the most likely candidates to play a role, although physiological data to support this are inconclusive.

Our goal here, however, was not to make specific conclusions about the elbow, but rather to examine the validity of the assumption of a uniform value for specific tension that could be used for all muscles. These results indicate that biomechanical models using this assumption could be introducing errors of up to 50%. This technique is often used to estimate muscle forces and this work clearly shows that its application should be reconsidered in situations where accurate solutions are required.

Acknowledgements

This work was supported, in part, by NIH grant R29-AR40408. The author wishes to thank S.L. Delp, D.G. Lloyd, D.A. Shreeve, W.Z. Rymer, and J.L. Lewis for their comments and helpful suggestions for this work at its various stages.

References

1. Arkin AM Absolute muscle power. The internal kinesiology of muscle. *Research Seminar Notes. Dept. Ortho. Surg., State Univ. of Iowa* 1938; **12D**: 123
2. Reclhinghausen N. *Gliedermechanik und Lahmungsprothesen*. Berlin: Springer, 1920.
3. Hertinger T. In: M.H. Thurlwell (ed) *Physiology of Strength*. Springfield, IL, Thomas, 1964.
4. Fick H. *Handbuch der Anatomie und Mechanik der Gelenke*. Jena, G. Fischer, 1904.
5. Johnson JV *Ergebnisse der Physiologie*. 1903; **2(2)**: 623.
6. Ikai M, Fukunaga T. Calculation of muscle strength per unit cross-sectional area of human muscles by means of ultrasonic measurements. *Int. Z. Angew. Physiol.* 1962; **26**: 26–32.
7. Morris CB The measurement of the strength of muscle relative to the cross-section. *Res. Q. Am. Assoc. Hlth. Phys. Edu.* 1948; **19**: 295–303.
8. Prium GT, de Jongh HJ, ten Bosch JJ Forces acting on the mandible during bilateral static bite at different bite force levels. *J. Biomech.* 1980; **13**: 755–63.
9. Close RI. Dynamic properties of fast and slow skeletal muscles of the rat after nerve cross-union. *J. Physiol. (London)* 1969; **204**: 331–46.
10. Burke RE, Tsairis P. Anatomy and innervation ratios in the motor units in cat gastrocnemius. *J. Physiol.* 1973; **234**: 769–5.
11. Lännergren J, Westerblad H. The temperature dependence of isometric contraction of single, intact fibres dissected from a mouse foot muscle. *J. Physiol* 1987; **390**: 285–93.
12. Kanda K, Hashizume K. Factors causing difference in force output among motor units in the rat medial gastrocnemius muscle. *J. Physiol* 1992; **448**: 677–95.
13. DeLuca CJ, Forrest WJ. Force analysis of individual muscles acting simultaneously in the shoulder joint during isometric abduction. *J. Biomech.* 1973; **6**: 385–93.
14. Takashima ST, Singh SP, Haderspeak KA, Schultz AB. A model for semi-quantitative studies of muscle actions. *J. Biomech.* 1979; **12**: 929–39.
15. Alexander RMcN. Mechanics of skeleton and tendons. In: *Handbook of Physiology: The Nervous System*. Section 1, Vol. 2 (Part 1). American Physiological Society, Bethesda, MD, 1981; pp 17–42.
16. Schultz AB, Andersson GBJ, Haderspeck K, Örtengren R, Nordin M, Björk R. Analysis and measurement of lumbar trunk loads in tasks involving bends and twists. *J. Biomech.* 1982; **15**: 669–75.
17. An KN, Kwak BM, Chao EY, Morrey BF. Determination of muscle and joint forces: A new technique to solve the indeterminate problem. *J. Biomech. Engng.* 1984; **106**: 364–7.
18. Brand PW, Beach RB, Thompson DE. Relative tension and potential excursion of muscles in the forearm and hand. *J. Hand Surg.* 1980; **6**: 209–19.
19. Maughan RJ, Watson JS, Weir J. Strength and cross-sectional area of human skeletal muscle. *J. Physiol. London* 1983; **338**: 37–49.
20. Amis AA, Dowson D, Wright V. Muscle strengths and musculo-skeletal geometry of the upper limb. *Engng. Med* 1979; **8**: 41–8.
21. An KN, Hui FC, Morrey BF, Linchield RL, Chao EY. Muscles across the elbow joint: a biomechanical analysis. *J. Biomech.* 1981; **14**: 659–69.
22. Edgerton VR, Apor P, Roy RR. Specific tension of human elbow flexor muscles. *Acta Physiol. Hung* 1990; **75**: 205–16.
23. Lieber RL, Jacobson MD, Fazeli BM, Abrams RA, Botte MJ. Architecture of selected muscles of the arm and forearm: anatomy and implications for tendon transfer. *J. Hand Surg* 1992; **17**: 787–98.
24. Murray W, Delp SL, Buchanan TS. Variation of muscle

- moment arms with elbow and forearm position. *J Biomech.* 1995; **28**: 513–525.
25. Klewano DG, Winters JM. Sensitivity of upper-limb strength curves to 3-D geometry: model results. *Proc. ASME Winter Mtg.* 1988; pp 53–6.
 26. Pauwels F. *Biomechanics of the Locomotor Apparatus*. Berlin: Springer-Verlag, 1980.
 27. Mendez RA, Keys A. Density and composition of mammalian muscle. *Metabol. Clin. Exp.* 1960; **9**: 184–8.
 28. Askew IJ, An KN, Morrey BF, Chao EYS. Isometric elbow strength in normal individuals. *Clin. Orthop. Rel. Res.* 1987; **222**: 261–6.
 29. Provins KA, Salter N. Maximum torque about the elbow joint. *J. Appl. Physiol.* 1955; **7**: 393–8.
 30. Winters JM, Klewano DG. Effect of initial upper-limb alignment on muscle contributions to isometric strength curves. *J. Biomech.* 1993; **26**: 143–53.
 31. Gordon AM, Huxley AF, Julian FJ. The variation in isometric tension with sarcomere length in vertebrate muscle fibres. *J. Physiol* 1966; **184**: 170–92.
 32. Hoy MG, Zajac FE, Gordon ME. A musculoskeletal model of the human lower extremity: the effect of muscle, tendon, and moment arm on the moment-angle relationship of musculotendon actuators at the hip, knee, and ankle. *J. Biomech.* 1990; **23**: 157–69.
 33. Burke RE, Levine DN, Tsairis P, Zajac FE. Physiological types and histochemical profiles in motor units of the cat gastrocnemius. *J. Physiol.* 1973; **234**: 723–48.
 34. McDonagh JC, Binder MD, Reinking RM, Stuart DG. A commentary on muscle unit properties in cat hindlimb muscles. *J. Morph.* 1980; **166**: 217–30.
 35. Close RI. Dynamic properties of mammalian skeletal muscles. *Physiol. Rev* 1972; **52**: 129–97.
 36. Lucas SM, Ruff RL, Binder MD. Specific tension measurements in single soleus and medial gastrocnemius muscle fibers of the cat. *Exp. Neurol.* 1987; **95**: 142–54.
 37. Johnson A, Polgar J, Weightman D, Appleton D. Data on the distribution of fibre types in thirty-six human muscles: An autopsy study. *J. Neuro. Sci.* 1973; **18**: 111–29.
 38. Maughan RJ, Nimmo MA. The influence of variations in muscle fibre composition on muscle strength and cross-sectional area in untrained males. *J. Physiol. London* 1984; **351**: 299–311.
 39. Paré EB, Stern JT, Schwartz JM. Functional differentiation within the tensor fasciae latae. *J. Bone and Joint Surg.* 1981; **63A**: 1457–71.
 40. Ter Harr Romeny BM, Denier van der Gon JJ, Gielen CCAM. Relation between location of a motor unit in the human biceps brachii and its critical firing levels for different tasks. *Exp. Neurology* 1984; **85**: 631–50.
 41. English AW, Weeks OI. Compartmentalization of single muscle units in cat lateral gastrocnemius. *Exp. Brain Res.* 1984; **56**: 361–8.
 42. Weeks OI, English AW. Compartmentalization of the cat lateral gastrocnemius motor nucleus. *J. Comp. Neurol.* 1985; **235**: 255–64.
 43. Brand RA, Friederich JA. The sensitivity of muscle force predictions to changes in physiologic cross-sectional area. *J. Biomech.* 1986; **19**: 589–966.
 44. Zajac FE. Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. *CRC Reviews in Biomed. Engng.* 1989; **17(4)**: 359–411.