Predictability of skeletal muscle tension from architectural determinations in guinea pig hindlimbs

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POWELL, PERRY L., ROLAND R. ROY, PAULA KANIM, MAUREEN A. BELLO, AND V. REGGIE EDGERTON. *Predictability of skeletal muscle tension from architectural determinations in guinea pig hindlimbs.* J. Appl. Physiol.: Respirat. Environ. Exercise Physiol 57(6): 1715–1721, 1984.—The maximum tetanic tension (P_o) generated by a skeletal muscle is determined by its functional cross-sectional area (CSA) and its specific tension (tension/CSA). Measurements of average fiber length (normalized to a sarcomere length of 2.2 μm), muscle mass, and approximate angle of pinnation of muscle fibers within a muscle were taken from 26 different guinea pig hindlimb muscles and were used to calculate CSA. The specific tension was assumed to be 22.5 $N \cdot cm^{-2}$ and was used to determine the estimated P_o of each muscle studied. In a second group of guinea pigs the in situ P_o of 11 selected hindlimb muscles and muscle groups were determined. Estimated and measured P_o values were found to have a strong linear relationship ($r = 0.99$) for muscle and muscle groups tested. The specific tension of the soleus, a homogeneously slow-twitch muscle, was shown to be ~15.4 $N \cdot cm^{-2}$ ($P < 0.01$). Therefore, in our hands a specific tension value of 22.5 $N \cdot cm^{-2}$ appears to be a reasonable value for all mixed muscles studied in the guinea pig hindlimb and can be used to estimate their P_o.

skeletal muscle architecture; specific tension; maximum tetanic tension; muscle fiber lengths; cross-sectional area

THE MAXIMUM FORCE GENERATED at the tendon of a skeletal muscle is a function of its cross-sectional area (CSA) and its specific tension producing capability (tension/CSA) (6, 28). Consequently, the maximum tetanic tension (P_o) of any skeletal muscle can be estimated if its specific tension and CSA are known. The CSA of a muscle, in turn, is determined in part, by its architectural design (11, 12, 27).

Since muscle density is assumed to be ~1.0 $g \cdot cm^{-3}$ for mammalian muscles (19, 20) and because the effect of the angle of pinnation is small for the range of angles measured in mammalian hindlimb muscles (27), CSA is primarily dependent upon muscle mass and fiber length. Recently, Sacks and Roy (27) using the same methods have reported wet muscle masses ranging from 1 (pectineus) to 30 g (biceps femoris) and fiber lengths from 8 (tibialis posterior) to 106 mm (sartorius) for the major muscles of the cat hindlimb. The results of this study strongly suggested that for a given muscle mass the relative speed and tension were determined by the number of sarcomeres in series and in parallel, respectively, i.e., by its architectural design.

The values reported for the specific tension of mammalian skeletal muscle from a variety of species generally range from 15.7 to 29.4 $N \cdot cm^{-2}$ (6, 9, 20). However, a commonly reported value for specific tension when the fiber length is normalized to a 2.20-μm sarcomere length is ~22.5 $N \cdot cm^{-2}$ (3, 26, 28, 31). There is also some evidence that the specific tension may be less for slow than for fast muscle fibers (4, 31). The purpose of this study, therefore, was to determine if the P_o of several hindlimb muscles in the guinea pig can be estimated from their CSA assuming a specific tension of 22.5 $N \cdot cm^{-2}$. Also, it was attempted to determine whether the specific tensions of predominately slow and fast muscles are similar. Preliminary results have been presented elsewhere (22).

METHODS

Architectural determinations. Adult female guinea pigs (325–375 g) were killed by cervical fracture or by an overdose of pentobarbital sodium. The muscles of the lower limbs were prepared for architectural determinations using the techniques described by Sacks and Roy (27). The animal was transected at a low lumbar level. After removal of the skin, the muscles on one side were dissected, and each muscle and muscle portion was weighed (wet weight). The contralateral side was fixed to a board with the hip, knee, and ankle joints at ~90° and placed in a 10% buffered formalin solution. The fixation process was facilitated by removing as much deep and intermuscular fascia as possible. After 48–72 h, individual muscles (see Table 1 for listing and abbreviations) were removed carefully and cleared of formalin with a 0.4 M sodium phosphate buffer solution (24 h). The muscles then were placed in a 15–20% sulfuric acid bath to macerate the intramuscular connective tissue and therefore facilitate the dissection of muscle fiber bundles. The amount of time spent in the acid solution ranged from 2 to 7 days. Subsequently, the muscles were rinsed in fresh buffer solution for 24 h and stored in 50% glycerol.

Each muscle was oriented on a glass plate that was illuminated from beneath to provide a clear view of the course of the fibers. The base of a protractor was placed along the line of pull of the muscle, and the angle of

pinnation (θ) in one dimension was measured in the proximal, middle, and distal portions of the muscle. Approximately 10 measurements were taken within a muscle, and the variability in θ was less than 20%. Thus an average θ was recorded for each muscle. The length of the muscle was measured, using vernier calipers, as the distance between the termination of the muscle fibers at the origin and at the insertion. The muscles were visually divided into proximal, distal, and deep portions. Using fine-tipped surgical forceps, three to five bundles consisting of 75–100 fibers were teased from each area and placed on a glass plate. Each bundle was further subdivided under a dissection microscope. The lengths of 20–40 small fiber bundles (10–15 fibers) from each muscle area were measured with vernier calipers and were compared for consistency. These small fiber bundle lengths were considered to be the fiber lengths (FL). Generally, the muscle bundle lengths were consistent throughout a given muscle, i.e., the FL ranged between means ± 10% except where noted in RESULTS. Single muscle fibers were isolated from each portion of the muscle and mounted on glass slides in glycerine jelly. Using a microscope (×400) with a calibrated eyepiece micrometer, the number of sarcomeres arranged in series over a 50-μm distance at several sites along the length of the fiber was counted to determine the average length of a sarcomere. The FL then were normalized (corrected FL) to a sarcomere length of 2.2 μm (13) to allow for intermuscular comparisons (see DISCUSSION).

The CSA was calculated from the architectural data using the following formula

$$\text{CSA} = (\text{muscle mass})\ (\cos\theta)/(\text{FL})\ (\text{muscle density})$$

where individual muscle masses were taken from the contralateral limb (g), θ was the average measured angle of deviation from the line of pull of the muscle fibers (degrees), FL was the mean FL for a given muscle (cm), and the muscle density used was 1.056 $g \cdot cm^{-3}$ (19, 20).

The P_o of each muscle was estimated as follows

$$P_o\text{est} = (\text{CSA})\ (\text{specific tension})$$

where the specific tension was assumed to be 22.5 $N \cdot cm^{-2}$ (26, 28).

Physiological determinations. Adult female guinea pigs (300–500 g) were anesthetized with pentobarbital sodium (35 mg/kg ip). The hindlimbs were prepared for the determinations of in situ isometric contractile properties as described by Roy et al. (26) and Spector et al. (28). The muscles to be tested (listed in Fig. 2) were isolated from the surrounding musculature and connective tissue with the normal blood supply left intact. The nerves innervating the muscles were isolated and severed for stimulation of the distal stump. The distal tendons were separated from their attachments and tied with 2-0 nylon ligature. The animal was placed in a frame with the lower extremities stabilized by clamps with a fixed knee position of ~90°. The surrounding skin was used to form a mineral oil bath, which was maintained at 36 ± 1°C using a radiant heat lamp and a thermistor-controlled heating element. Core temperature was maintained at near normal by a water-circulating heating pad and a heat lamp.

The muscle tendons (via the nylon ligature) were attached to an isometric transducer (Statham UC3:ULA-20). All events were recorded simultaneously on a polygraph recorder and an FM tape recorder at 3.75 in./s (Vetter Instruments model D) and monitored on a storage oscilloscope. Contractions were elicited by stimulation through the severed nerve trunk with bipolar silver electrodes. The stimulus was a square-wave pulse of 0.2-ms duration. Initially the muscle length at which the maximum twitch tension could be elicited was determined. Stimulus strength then was set at approximately twice the minimum required to produce the maximum twitch tension at this muscle length. A frequency of 200 Hz with a 330-ms duration was used to determine P_o in all muscles. This frequency was chosen because preliminary results in guinea pigs (unpublished observations) and previous results in rats (26) indicated that there was <5% difference between the tension produced at 100 and 200 Hz even in predominately slow muscles. Muscle length was first decreased and then increased in 1-mm increments until a decrease in tension was recorded at either end of the length-tension curve. Two minutes of recovery, during which the muscle was stimulated at 0.05 Hz, were allowed between each maximum contraction. The maximum force production of each muscle was determined using a minicomputer (Hewlett-Packard MX21). Analog-to-digital sampling rate for each contraction was 1,000 Hz. At the end of the experiment the guinea pigs were given an overdose of pentobarbital sodium. The muscles of interest were removed, carefully trimmed of connective tissue and fat, and weighed (wet weight).

RESULTS

The architectural characteristics of the muscles studied are listed in Table 1. Several muscles require special consideration. The semitendinosus (ST) had a distinct connective tissue band that separated the muscle into proximal (STp) and distal (STd) compartments, an arrangement that is similar to that found in the cat (2) and in humans (23, 29, 30). The STp in the guinea pig had two portions: a dorsal head (STpd), which originated from fascia covering the first three caudal vertebrae, and a ventral head (STpv), which attached to the ischial tuberosity. The semimembranosus (SM) had two muscle bellies, a rostral head (SMr) and a caudal head (SMc), originating along the ischial tuberosity to the pubic symphysis. The SMc inserted on the medial condyle of the tibia and along the upper medial surface of the tibia. The SMr attached along the distal medial surface of the femur. The biceps femoris (BF) also had two separate portions: a dorsal head (BFd), which originated from the S_1 and S_2 sacral vertebrae, and a ventral head (BFv), which originated from the ischial tuberosity deep to the STpv origin. BFv inserted as a narrow tendon in fascia covering the lateral patella and the BFd as a broad tendon over the cranial margin of the tibia that appeared to be continuous distally to the calcaneus. The gracilis (GR) had two separate parallel portions, the rostral (GRr) and caudal (GRc) heads. The rostral portion originated at the posterior pubic symphysis and inserted into

TABLE 1. *Architectural features of guinea pig hindlimb muscles*

	Muscle Mass, g	Muscle Length, mm	Fiber Length, mm	Corrected Fiber Length, mm	Fiber Angle (θ),°	CSA, cm^2	$P_o$est, N
Rectus femoris (RF)	0.95 ± 0.02	30.6 ± 0.6	11.8 ± 0.5	11.0 ± 0.5	8	0.82	18.3
Vastus intermedius (VI)	0.19 ± 0.01	32.2 ± 1.9	9.6 ± 0.5	9.6 ± 0.5	17	0.18	4.1
Vastus medialis (VM)	0.21 ± 0.01	30.9 ± 1.6	13.5 ± 0.6	12.9 ± 0.6	17	0.15	3.4
Vastus lateralis (VL)	0.81 ± 0.07	33.0 ± 1.4	15.2 ± 0.6	15.8 ± 0.6	18	0.46	10.4
Semitendinosus (ST)	1.12 ± 0.04	44.4 ± 1.1					
Proximal compartment (STp)							
Ventral head (STpv)	0.06 ± 0.01		5.9 ± 0.1	5.5 ± 0.1	0	0.10	2.3
Dorsal head (STpd)	0.26 ± 0.01		10.5 ± 0.8	9.8 ± 0.7	0	0.23	5.2
Distal compartment (STd)	0.80 ± 0.04		29.0 ± 0.6	27.0 ± 0.6	0	0.26	5.9
Semimembranosis (SM)							
Caudal head (SMc)	0.46 ± 0.04	42.5 ± 1.0	39.1 ± 0.7	36.1 ± 0.6	0	0.12	2.7
Rostral head (SMr)	0.21 ± 0.02	37.0 ± 1.1	32.3 ± 0.8	31.4 ± 0.8	0	0.06	1.4
Semimembranosis accessorius (SMA)	0.12 ± 0.01	28.9 ± 1.4	25.2 ± 2.1	22.2 ± 1.8	0	0.05	1.1
Biceps femoris (BF)	2.20 ± 0.02						
Dorsal head (BFd)	1.32 ± 0.03	38.7 ± 0.8	32.3 ± 3.1	33.4 ± 3.2	0	0.37	8.3
Ventral head (BFv)	0.88 ± 0.01	40.8 ± 0.7	33.1 ± 0.5	34.2 ± 0.5	0	0.24	5.4
Adductor longus (AL)	0.14 ± 0.01	25.0 ± 1.0	17.7 ± 0.5	15.0 ± 0.5	0	0.09	2.0
Adductor magnus (AM)	0.42 ± 0.04	29.8 ± 0.1	22.5 ± 0.4	19.0 ± 0.3	0	0.21	4.7
Adductor brevis (AB)	0.09 ± 0.01	22.9 ± 3.3	17.1 ± 2.7	13.9 ± 2.2	0	0.06	1.4
Pectineus (PC)	0.06 ± 0.02	18.5 ± 1.2	8.7 ± 0.9	6.6 ± 0.7	0	0.09	2.0
Adductor crureus caudalis (ACC)	0.17 ± 0.01	33.8 ± 0.9	30.4 ± 1.0	30.1 ± 1.0	0	0.05	1.1
Gracilis (GR)							
Rostral head (GRr)	0.48 ± 0.03	40.7 ± 1.3	28.8 ± 0.8	23.5 ± 0.7	0	0.19	4.3
Caudal head (GRc)	0.24 ± 0.01	43.8 ± 0.8	41.4 ± 0.7	35.7 ± 0.6	0	0.07	1.6
Sartorius (SR)	0.27 ± 0.03	36.3 ± 0.8	27.6 ± 3.1	27.4 ± 3.1	0	0.09	2.0
Gastrocnemius (G)							
Medial head (MG)	0.45 ± 0.03	30.2 ± 0.8	10.1 ± 0.4	9.8 ± 0.4	14	0.42	9.5
Lateral head (LG)	0.26 ± 0.03	26.7 ± 0.4	9.4 ± 0.6	9.2 ± 0.5	14	0.26	5.9
Soleus (SOL)	0.11 ± 0.01	30.0 ± 0.8	11.2 ± 0.2	10.4 ± 0.2	7	0.10	2.3
Plantaris (PLT)	0.27 ± 0.01	31.9 ± 1.1	10.5 ± 0.5	9.9 ± 0.5	13	0.25	5.6
Tibialis posterior (TP)	0.06 ± 0.01	17.1 ± 0.1	3.6 ± 0.1	3.4 ± 0.1	16	0.16	3.6
Flexor hallicus longus (FHL)	0.28 ± 0.25	29.9 ± 2.6	9.7 ± 0.4	8.9 ± 0.4	11	0.29	6.5
Tibialis anterior (TA)	0.11 ± 0.02	24.5 ± 0.7	14.7 ± 0.5	14.0 ± 0.5	6	0.07	1.6
Tibialis anterior accessorius (TAA)	0.04 ± 0.01	14.8 ± 0.5	5.2 ± 0.2	5.0 ± 0.2	14	0.07	1.6
Extensor digitorum longus (EDL)	0.11 ± 0.01	24.7 ± 1.2	7.5 ± 0.9	6.3 ± 0.7	11	0.16	3.6
Peroneus longus (PL)	0.05 ± 0.01	19.3 ± 0.6	5.7 ± 0.6	5.0 ± 0.5	8	0.09	2.0
Peroneus brevis (PB)	0.03 ± 0.01	23.6 ± 1.3	5.6 ± 0.8	4.7 ± 0.6	13	0.06	1.4
Peroneus tertius (PT)	0.07 ± 0.01	24.3 ± 0.1	7.8 ± 0.2	6.4 ± 0.2	9	0.10	2.3

Values are means ± SE. Muscle mass (wet weight) was determined for the contralateral limbs. Average muscle length was determined after formalin fixation. Average length of small fiber bundles was taken throughout muscle. Average fiber lengths were normalized to a sarcomere length of 2.2 μm (13). θ, one dimensional measurement of apparent deviation of muscle fibers from long axis of muscle; CSA, physiological cross-sectional area; $P_o$est, estimated maximum tetanic tension.

the medial border of the tibia and tibial crest. The caudal portion originated from the pubic ramus and inserted into the medial tibial tuberosity. The medial and lateral heads of the gastrocnemius were treated as separate muscles. In addition, the guinea pig had a tibialis anterior complex which was composed of two distinct muscles: the tibialis anterior (TA), a relatively long muscle that had long paralleled fibers, and the tibialis anterior accessorius (TAA, our terminology), a small fusiform muscle that was embedded deep into the posterior surface of the TA and had short pinnated fibers. The muscles originated from the proximal anterior surface of the tibia and interosseus membrane (TA only) and inserted on the medial and plantar surfaces of the navicular. However, the TAA had extremely long thin tendons extending to both the origin and the insertion, whereas the TA had a broad fleshy origin and a broad tendon of insertion.

Of the muscles studied, wet weights ranged from 30 mg for the peroneus brevis to 2.2 g for the biceps femoris. Muscle lengths ranged from 14.8 to 49.2 mm, while the uncorrected fiber lengths ranged from 3.6 to 41.4 mm (Table 1). FL were generally consistent throughout a given muscle or muscle head. The one exception was the vastus lateralis (VL). The VL appeared to have a thin

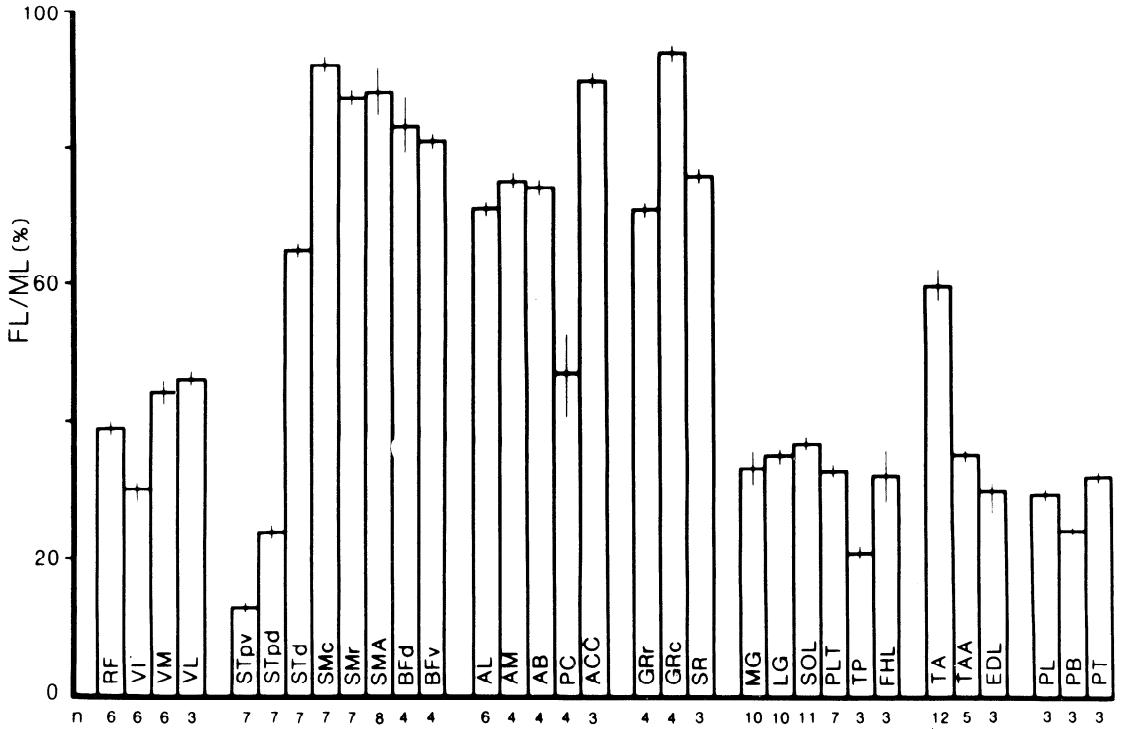

FIG. 1. Histogram showing average relative fiber length-to-muscle length ratios (FL/ML) of the guinea pig hindlimb muscles. *Bars* represent SE. Muscles are shown in functional muscle groups, i.e., from *left* to *right*, the knee extensors, knee flexors, hip adductors, gracilis and sartorius, ankle plantarflexors, ankle dorsiflexors, and ankle everters. *n* is listed below each muscle. See Table 1 or text for abbreviations.

pale-colored portion of fibers in the superficial region of the muscle that were ~30% longer than the fibers in the deeper portions of the muscle. This variability in FL is not reflected in the SE shown in Table 1 because this portion of the muscle was a small percentage of the total muscle mass. The fiber length-to-muscle length ratios (FL/ML) were consistent for any muscle and were similar for muscles having similar functions (Fig. 1). The angles of pinnation varied between 0 and 18° and were relatively consistent for individual muscles. The VL had the highest θ, while several muscles, including the ST, SM, semimembranosis accessorius (SMA), BF, all adductors, pectineus (PC), GR, and sartorius (SR), had virtually no θ. Sarcomere lengths ranged from 2.12 to 2.9 μm at the lengths that the muscles were fixed. The hip adductors and the PC appeared to have been stretched due to the abducted position of the limbs during fixation, and the sarcomere lengths ranged from 2.6 μm for the adductor longus (AL) and adductor magnus (AM) to a high of 2.9 μm for PC. The peroneus longus (PL), peroneus tertius (PT), peroneus brevis (PB), and extensor digitorum longus (EDL) also were stretched with sarcomere lengths of 2.5, 2.6, 2.7, and 2.6 μm, respectively. The EDL appeared to have been stretched due to a flexing of the digits during fixation. All other muscles ranged from 2.12 to 2.40 μm. All fiber lengths were normalized to a sarcomere length of 2.20 μm (13) to allow for intermuscular comparisons (see METHODS). CSA ranged from a maximum of 0.81 cm^2 for the rectus femoris (RF) to 0.05 cm^2 for the adductor crureus caudalis (ACC) and SMA. The $P_o$est ranged from 18.3 N for the RF to 1.1 N for the ACC and SMA.

The measured P_o values ranged from 21.3 N for the gastrocnemius medial and lateral heads and plantaris (MG-LG-PLT) complex to 1.67 N for the soleus (SOL). The relationship between the $P_o$est for various muscles and muscle groups and the corresponding maximum tensions measured in situ ($P_o$meas) is shown in Fig. 2. There was a strong linear relationship ($r = 0.99$) between these values for all muscles and muscle groups tested. The specific tension of the SOL (a 100% slow-twitch muscle) was 32% less than that for the mixed fast muscles (Fig. 3).

DISCUSSION

The absolute P_o of a muscle can be determined rather easily and reliably using standard in situ preparations (5, 6, 9, 16, 17, 20, 24, 26, 28, 31). However, there are difficulties in determining its specific tension (tension/CSA) because of the inconsistencies and inherent problems in calculating the CSA of a muscle (6). These problems are made obvious when one considers the wide range of specific tension values reported for mammalian muscle (3, 5, 10, 16, 17, 20, 25, 28, 31). In this study the CSA was calculated from measurements of muscle mass (wet weight), θ in one dimension, average FL (normalized to a sarcomere length of 2.2 μm), and an assumed muscle density of 1.056 $g \cdot cm^{-3}$ (19, 20).

Although skeletal muscles are composed of a variable amount of contractile and noncontractile protein, water, vascular components, etc., it appears that the calculation of CSA using wet muscle weight is a reasonable, consistent, and widely accepted procedure (6). The θ measured

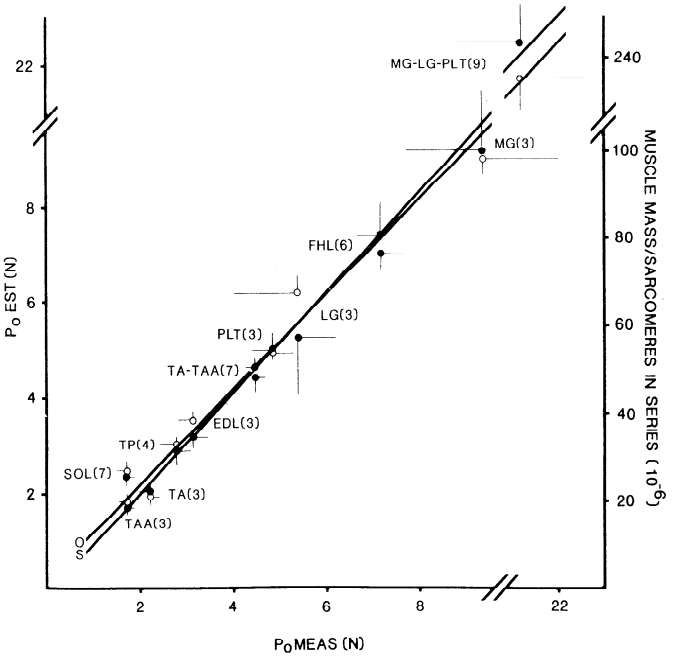

FIG. 2. A plot demonstrating relationship between *1*) measured maximum tetanic tension ($P_o$meas) and the estimated P_o ($P_o$est) of selected muscles and muscle groups in guinea pig hindlimb (○) and *2*) $P_o$meas and a ratio of muscle mass-to-number of sarcomeres in series (●). Linear regressions are plotted for each comparison. For $P_o$meas:$P_o$est (*line S*), slope = 1.05, *Y*-intercept = −0.18, r = 0.99; for $P_o$meas:muscle mass/number of sarcomeres in series (*line O*), slope = 10.9, *Y*-intercept = 2.07, r = 0.98. Number of muscles tested is in parentheses. *Bars* represent SE. Apparent large SE for muscles such as gastrocnemius medial and lateral heads (MG and LG) are related to sample size and to large range in body weights (~300–500 g) of animals used to determine $P_o$meas. $P_o$est values in Table 1 are different from those found here because body weights of animals used for architectural data have a smaller range of body weights (325–375 g) than those used for physiological measurements. Muscle mass/number of sarcomeres in series ratios were calculated using muscle masses from animals used for physiological determinations. See Table 1 or text for abbreviations.

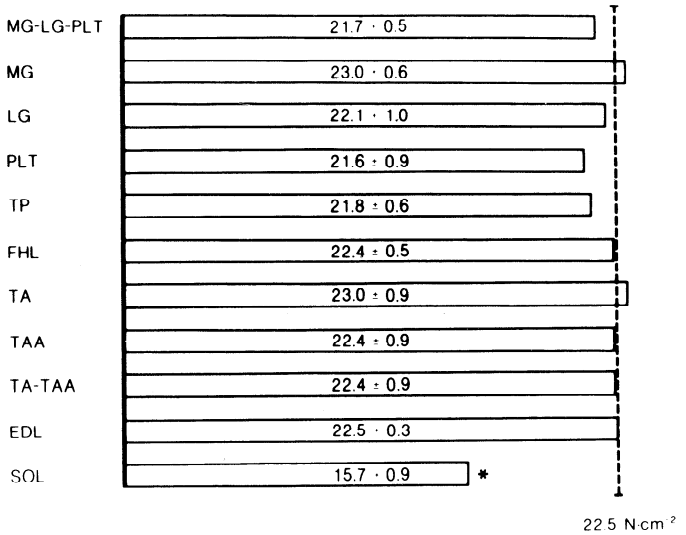

FIG. 3. Histogram showing specific tension values of muscles tested physiologically. Number of muscles tested is same as in Fig. 2. All muscles or muscle groups had specific tension values similar to 22.5 N·cm^{-2} except for soleus which was 32% less (*$P < 0.01$, Student's t test). See Table 1 or text for abbreviations.

in this study was a static measure in one dimension and minimally affected the CSA value (see below). On the other hand, FL were dramatically affected by the limb position during fixation, since the sarcomere lengths varied considerably across muscles. Our solution was to normalize FL to a sarcomere length of 2.2 μm and thus at the least allow for relative comparisons across muscles. The critical measure would be to determine the sarcomere length of the fiber of a muscle under maximum isometric conditions and to use this FL in the CSA calculations. Although a sarcomere length of 2.2 μm appears to be a valid measure for frog muscle fibers (3, 13, 14), the little data that is available for mammalian muscle is inconsistent. Sarcomere lengths ranging from 2.85 μm for the mouse gracilis (10) to values approaching 2.3 μm in the rabbit psoas muscle (14) have been reported. To address this problem we have plotted our $P_o$meas relative to *1*) the $P_o$est (assuming a sarcomere length of 2.2 μm) and *2*) a value of muscle mass relative to only the number (and not the length) of sarcomeres in series (Fig. 2), which we believe is representative of the number of sarcomeres in parallel or the CSA. Based on the similarity and the strength (r = 0.99 and 0.98, respectively) of these relationships, it appears that normalization of sarcomere length to 2.2 μm is a reasonable procedure for guinea pig hindlimb muscles. However, this question is far from being resolved.

The effect of the θ of muscle fibers on P_o is a function of the cosθ (12, 21, 27). In other words, at 0° of pinnation, there is no decrease in the tension produced at the tendon by a given muscle fiber compared with the intrinsic tension of that fiber. However, as the θ increases, the net force developed at the tendon decreases as a function of cosθ. It appears that few muscles in the guinea pig hindlimb lose a significant amount of tension due to the θ. The maximum decrement in the tension of a fiber due to the θ was 4.9% (θ = 18°) for the VL (Table 1). It should be recognized, however, that the θ is subject to considerable error. For example, the measurement itself is only an estimate from the fibers on the surface of the muscle and is only in one dimension. More critical, however, is the fact that these angles probably change when the muscle is activated even when the contraction is isometric. Therefore, an accurate assessment of the effect of the θ on the force and the velocity potentials of a contracting muscle remains unknown.

The effect of the length of the individual muscle fibers on P_o is exemplified by a comparison of two closely associated synergists, the TA and the TAA (Table 1). One point to be emphasized is that a muscle with approximately one-third the mass of another muscle can have the same potential to produce tension because of its architectural design. The TAA has short fibers (5.0 mm) arranged in a pinnate manner (θ = 14°) thus increasing its effective CSA. This design, however, decreases its potential speed of contraction, since the number of sarcomeres in series (i.e., the fiber length) dictates the maximum velocity at which a muscle can shorten assuming similar biochemical properties (2, 8). The TA has relatively long fibers (14.0 mm) arranged almost in parallel (θ = 6°) which minimizes its CSA and maximizes its velocity and displacement potential.

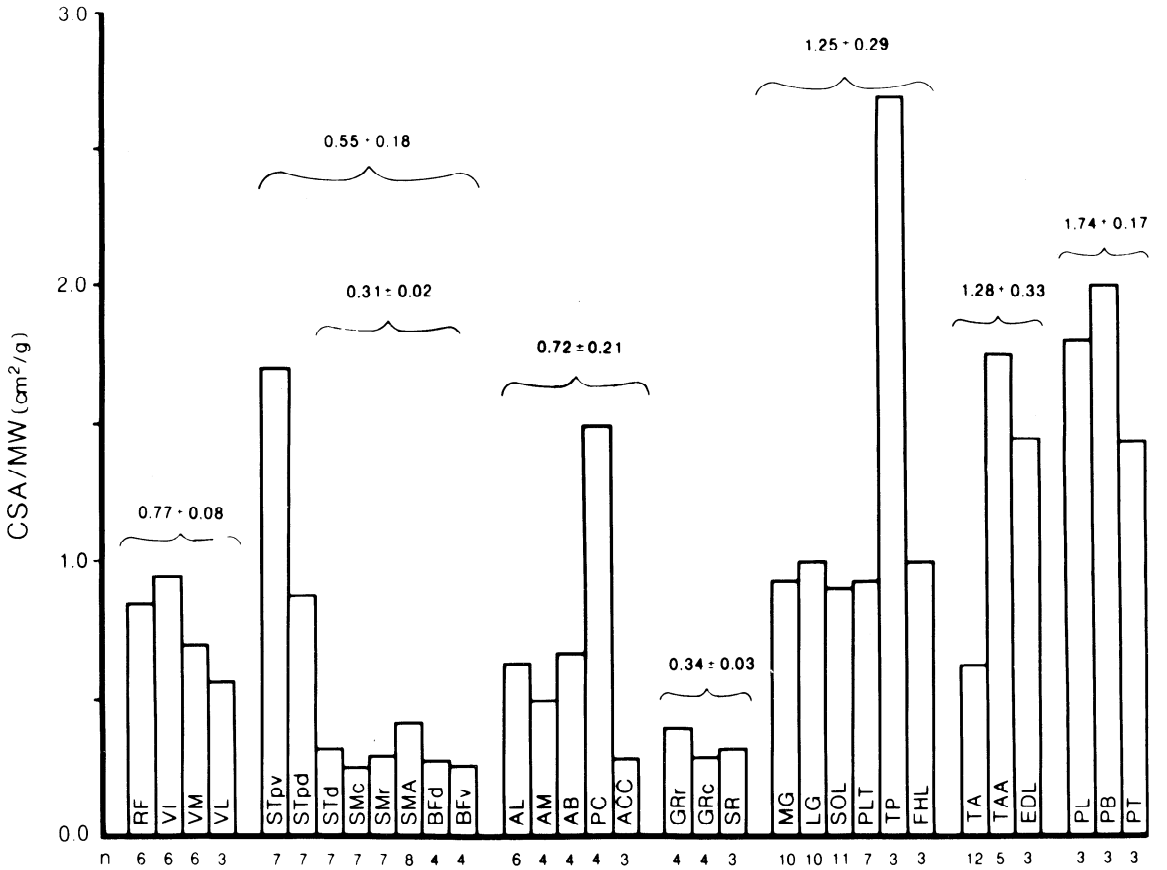

FIG. 4. Histogram showing average cross-sectional area (CSA) relative to muscle weight (MW) for guinea pig hindlimb muscles. Muscles and groupings are same as in Fig. 1. Means ± SE are shown for each muscle group. The larger the ratio the greater relative CSA and thus relative tension-producing capability. Individual muscle and muscle group comparisons are made in text. See Table 1 or text for abbreviations.

Figure 4 shows CSA:muscle weight (MW) ratios for the muscles and muscle groups studied. The higher the ratio the more specifically designed the muscle or muscle group is for tension production. It appears that the extensors of the knee are designed with relatively more emphasis for tension production than are the flexors, i.e., the quadriceps have a CSA:MW ratio more than twice that of the hamstrings if you exclude the STpv and STpd, which only account for 8% of the total hamstring muscle mass. In contrast, the ankle plantarflexors and dorsiflexors have almost identical ratios. The PC, tibialis posterior (TP), TAA, EDL, and the peroneal muscles also are designed to maximize tension production, while the GR, SR, and the knee flexor-hip extensor muscles are designed to maximize displacement and velocity (Fig. 4). These comparisons, however, must be considered in light of the multiple functions of different combinations of muscles (e.g., inversion, eversion, flexion, and extension about the ankle).

As mentioned previously, the SOL was found to have a 32% lower specific tension than all the other muscles tested (15.7 vs. 22.5 $N \cdot cm^{-2}$) (Fig. 3). These values are similar to the specific tension values reported recently by Witzmann et al. (31) for the rat SOL (15.2 $N \cdot cm^{-2}$) and EDL (23.5 $N \cdot cm^{-2}$) muscles. Rowe and Goldspink (25) have reported a similar specific tension in the SOL of male mice. Other investigators using female rats (5, 6) have found the specific tension to range from 18.6 to 20.6 $N \cdot cm^{-2}$ for the SOL and 28.4 to 29.4 $N \cdot cm^{-2}$ for the EDL. Although these absolute values are different from those reported in the present study, the relative difference between the predominately fast and predominately slow muscles are identical (32%). One important factor may be the fiber type composition of the muscles. The guinea pig SOL is a 100% slow-twitch muscle, while the other muscles tested were mixed (~80% fast twitch, 20% slow twitch) (1). However, other factors may be as important as fiber type since Spector et al. (28) have shown that the tension/CSA is the same (22.5 $N \cdot cm^{-2}$) for both the homogeneously slow-twitch SOL and the predominately fast-twitch MG of the same cat. Using different techniques for determining the architectural properties of the muscle, other investigators have reported specific tensions of ~28 $N \cdot cm^{-2}$ for both slow (20) and fast (9) cat muscle. In addition the data of Kushmerick and Krasner (15) strongly suggests that the relative myosin adenosinetriphosphatase (ATPase) and isometric tension levels in skinned fiber preparations are closely related when determined as a function of calcium concentration. Whether these relationships differ between fast and slow muscles in different species remains to be determined.

Similar disparities are evident when considering the specific tension of single motor units. Existing data suggest that there is a wide variation in the tension/CSA of motor unit types in the same muscle as well as the

same motor unit type in different muscles in the cat (see Ref. 4 for a recent review). For example, the specific tension for the fast-fatigable, fast-fatigue resistant and slow motor units of the cat (flexor digitorum longus) (FDL) are 34.5, 28.6, and 5.9 $N \cdot cm^{-2}$, respectively (7). Further, the specific tension of the slow units of the MG (4) and FDL (7) are ~5.9 $N \cdot cm^{-2}$, while that of the SOL (7) and the TP (18) are ~15.5 $N \cdot cm^{-2}$. It is obvious that more data are needed before any definitive conclusions related to specific tension of motor units or whole muscle can be made.

In summary, our results indicate that, in our hands, 22.5 $N \cdot cm^{-2}$ is an appropriate estimate of the specific tension for the mixed predominately fast-twitch muscles of the guinea pig hindlimb. However, it appears that the slow-twitch SOL muscle has a much lower tension/CSA. Further, our results demonstrate that the maximum tension-producing capability of a mixed fast-twitch muscle of the guinea pig hindlimb can be estimated within 5% of the measured value based on its wet weight, average FL (normalized to 2.20 μm sarcomere length), approximate θ, and assuming a specific tension of 22.5 $N \cdot cm^{-2}$.

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