Several difficulties arise when investigating the human lateralis biopsies (6, 13, 15, 20-22, 27, 28). First, accurate determination of the percentage of fast twitch (%FT) muscle fibers or the area of FT fibers in the muscle [as estimated from vastus lateralis needle biopsy, not only due to fiber type differences between muscles (3) but also due to such differences within a muscle (7, 9)]. Third, it is not clear to what extent the motor unit population is activated during a maximal voluntary contraction.

Thus the complexity of the human neuromuscular system precludes detailed elucidation of the factors that contribute to maximum isometric torque. The purpose of this study, therefore, was to investigate these factors in one system in which muscle and joint properties can be precisely measured, the frog hindlimb. A portion of this work has been previously presented (11).

METHODS

The dorsal head of the semitendinosus muscle from the grassfrog (Rana pipiens) was chosen because of its well-established sarcomere length-tension relationship (6) and longitudinal fiber architecture. The semitendinosus is a biarticular muscle, functioning primarily in the frontal plane as both a hip extensor and a knee flexor. Frogs [mass = 25.9 ± 4.5 (± SD) g (n = 9)] were killed by double pithing.

In nine animals, immediately after death, the thighs were exposed bilaterally and all of the thigh musculature and skin were removed except the dorsal head of the semitendinosus muscle. The muscle-bone complex, consisting of the pelvis, femora, tibiae, and semitendinosus muscles, was secured to the horizontal arm of a specially designed jig using 3-0 stainless steel suture for measurement of joint torque as described in the previous paper (12). The force generated at the distal tibia, muscle moment arm, and resulting torque were determined at 10° increments over the range of 0° to 180° of knee flexion as previously described (12).

Measurement of maximum tetanic tension. After torque measurements, the semitendinosus origin and insertion tendons were cut free from the pelvis and tibia, respectively, and secured with 4-0 silk suture. One suture was attached to a force transducer (Entran model ELF-T500-2, Entran Devices, Fairfield, NJ) driven by a strain-gauge conditioner (Daytronic model 3270, Daytronic, Miamisburg, OH), and the other tendon was secured to

Determination of the factors that limit performance is of interest in sports and medicine. A common method used to investigate these factors is to measure the extension torque of the quadriceps musculature (5, 18, 21, 22). Studies that implement isometric and isokinetic testing of the quadriceps muscles have also documented the nature of muscle adaptation to exercise training (5, 18, 27) and have elucidated the relationship between muscle structure and human performance (1, 4, 13-15, 21-25, 27-29). Generally, investigators agree that maximum extension torque is correlated with quadriceps cross-sectional area (CSA) as measured by ultrasound (8) or computed tomography (13-15), although these correlations are relatively low, ranging from 0.4 to 0.6 (8, 13-15). In addition, differences exist as to whether isometric or isokinetic extension torque is correlated with the percentage of fast twitch (%FT) muscle fibers or the area of FT fibers in the muscle [as estimated from vastus lateralis biopsies (6, 13, 15, 20, 22, 27, 28)].

In spite of the information gained from these studies, several difficulties arise when investigating the human quadriceps musculature. First, accurate determination of muscle fiber CSA is difficult through use of current technology, especially in light of the complex fiber arrangement that exists in the quadriceps (26). Second, it is difficult to precisely determine the fiber type distribution of the quadriceps muscles based on a single vastus lateralis needle biopsy, not only due to fiber type differences between muscles (3) but also due to such differences within a muscle (7, 9). Third, it is not clear to what extent the motor unit population is activated during a maximal voluntary contraction.

LIEBER, RICHARD L., AND JENNETTE L. BOAKES. Muscle force and moment arm contributions to torque production in frog hindlimb. Am. J. Physiol. 254 (Cell Physiol. 23): C769-C772, 1988.—The relative contribution of maximum muscle tetanic tension (P tet) and muscle moment arm to maximum knee flexion torque was investigated in the frog hindlimb. Isometric torque was measured in frog semitendinosus muscle-bone complexes throughout the range of 0° to 160° of flexion. Optimal joint angle (the angle at which isometric torque was maximum) was observed at 140° of flexion. After torque measurements, the muscle was excised and the muscle length-tension relationship measured for determination of P tet and optimal muscle length. In addition, the kinematics of the knee joint and therefore, the muscle moment arm was measured as a function of joint angle using principles of rigid body kinematics. Stepwise linear regression indicated that maximum torque was most highly correlated with P tet (r = +0.77, P < 0.01) and accounted for > 75% of the measured torque. In addition, there was no significant correlation between maximum torque and maximum muscle moment arm (r = +0.11, P > 0.7) suggesting that muscle force, not musculoskeletal anatomy, represents the major determinant of maximum torque production in the frog hindlimb.

Joint torque; joint kinematics; muscle contraction; knee joint; semitendinosus muscle; Rana pipiens
a micromanipulator. The muscle was stimulated in 0.5-
mm increments in length through use of the above pa-
rameters. This provided a muscle length-tension curve
from which maximum tetanic tension ($P_0$) and optimal
muscle length ($L_o$) were obtained. The muscles were then
dissected free of the bones, muscle mass was determined,
and the tibiae and femura were stored with the joint
capsule intact at $-10^\circ C$ for future measurement of joint
kinematics.

Muscle CSA was calculated using

$$CSA (cm^2) = \frac{mass (g)}{density (g/cm^3) \cdot fiber\ length\ (cm)}$$

where muscle density is $1.056\ g/cm^3$ (17).

**Determination of muscle architecture.** Muscle architec-
ture was determined according to a modification of the
methods of Sacks and Roy (2). Briefly, muscles were
fixed in 10% buffered Formalin (formaldehyde solution)
for 24–72 h, rinsed in 0.4 M phosphate buffer at pH of
7.2, and placed in 15% $H_2SO_4$ for 24 h. Muscle length
was measured with dial calipers as the distance from the
origin of the most proximal muscle fibers to the insertion
of the most distal fibers. Bundles consisting of 10–15
muscle fibers were then dissected from the muscle for
bundle length measurement. Bundle lengths were nor-
malized to a sarcomere length of 2.2 $\mu m$ (6) to correct
for variability caused by differences in muscle fixation
lengths. Sarcomere length was measured along the length
of the fiber bundles using laser diffraction (10). Pina-
tion angle, as measured using a dissecting microscope
and goniometer, was not measurably different from 0°.

**Statistical analysis.** Variables measured for each ani-
mal included $P_0$ (g), muscle moment arm (cm), maximum
torque (g/cm), frog mass (g), muscle mass (mg), $L_o$ (cm),
and CSA (cm$^2$). To determine the relative contribution
of each variable to maximum torque, stepwise linear
regression was implemented (BMDP program P2R; 2).
In the preliminary analysis, F-to-enter and F-to-remove
were set to 3.000 and 2.996, respectively. Next, each
variable was forced to enter the regression equation to
quantify the proportion of maximum torque, which was
accounted for by each variable. The relationship between
$P_0$ and maximum joint torque and maximum muscle
moment arm and maximum joint torque were analyzed by
linear regression (BMDP program P1R; 2). All results
were considered significant for $P < 0.05$.

**RESULTS**

**Experimental torque measurements.** For each muscle
studied, the force measured at the distal tibia during
semitendinosus contraction and the measured moment
arms were combined to yield the relationship between
torque and joint angle (compare Figs. 4 and 5 of Ref. 12).
Isometric torque demonstrated a linear increase from 0
to 140° and a sharp drop in torque from 140 to 100°.
Architectural analysis yielded a bundle length-to-muscle
length ratio of 0.70 that was used to calculate the bundle
length (from muscle length), which was then used for
CSA calculations. The average calculated CSA for the
muscles was $0.23 \pm 0.18\ (\pm SE)\ cm^2\ (n = 9)$.

Of the seven variables investigated, only two were
significantly correlated with maximum torque (Table 1). These were $P_0$ ($r = +0.77, P < 0.01$) and frog mass ($r = +0.67, P < 0.05$). Muscle mass was nearly significantly
related to maximum torque ($r = +0.59, P = 0.09$).
Stepwise linear regression revealed that the variables
most highly correlated with maximum joint torque were
in the following order ($F$ value from step 1 ANOVA): $P_0$
(10.35); frog mass (5.69); muscle mass (3.77); CSA (2.25);
and $L_o$ (1.35). Thus, in the first step of the stepwise
regression, $P_0$ was entered in the equation. In the second
step, based on the high covariance between $P_0$ and the
other variables, $F$ values dropped significantly with the
highest correlations seen in the following order: $L_o$ (1.17);
frog mass (0.58), muscle mass (0.25); moment arm (0.10),
and CSA (0.02). Thus the remainder of the variables
contained no significantly unique information relative to
that contained by $P_0$.

When forcing the variables into the regression equa-
tion in a stepwise fashion, it was observed that the serial
correlation coefficient increased slightly as variables
were added (Table 2). The variables and the associated
correlation coefficients were $P_0$ (0.772), $P_0$ + moment
arm (0.776), $P_0$ + moment arm + frog mass (0.808), $P_0$
+ moment arm + frog mass + muscle mass (0.809), $P_0$
+ moment arm + frog mass + muscle mass + CSA (0.855).
These correlation coefficients (Table 2) indicate that $P_0$
accounted for the greatest proportion of maximum torque
(77%, Fig. 1), whereas moment arm accounted for a much
lower proportion (0.4%, Fig. 1).

Linear regression demonstrated that there was a sig-
ificant relationship between $P_0$ and maximum torque
(Fig. 2A, $r = +0.77, P < 0.01$) but no significant relation-
ship between maximum torque and maximum muscle

table 1. Correlation matrix for measured variables

<table>
<thead>
<tr>
<th>Variable</th>
<th>$P_0$</th>
<th>Moment Arm</th>
<th>Maximum Torque</th>
<th>Frog Mass</th>
<th>Muscle Mass</th>
<th>$L_o$</th>
<th>CSA</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_0$</td>
<td>1.00</td>
<td>0.24</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moment arm</td>
<td>0.24</td>
<td>1.00</td>
<td>0.11</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum torque</td>
<td>0.77*</td>
<td>0.11</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frog mass</td>
<td>0.69*</td>
<td>0.38</td>
<td>0.67*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Muscle mass</td>
<td>0.64*</td>
<td>0.10</td>
<td>0.59</td>
<td>0.79*</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$L_o$</td>
<td>0.19</td>
<td>0.04</td>
<td>0.40</td>
<td>0.24</td>
<td>0.23</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>CSA</td>
<td>0.60</td>
<td>0.07</td>
<td>0.49</td>
<td>0.74*</td>
<td>0.97*</td>
<td>1.00</td>
<td></td>
</tr>
</tbody>
</table>

$P_0$, maximum muscle tetanic tension; $L_o$, optimal length; CSA, cross-
sectional area. *Significant correlation between variables ($P < 0.05$).

**Table 2. Correlation between maximum torque and
determinants forced into multiple regression equation**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Serial Correlation Coefficient</th>
<th>% Maximum Torque Explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum tetanic tension</td>
<td>0.772</td>
<td>77.2</td>
</tr>
<tr>
<td>Moment arm</td>
<td>0.776</td>
<td>0.4</td>
</tr>
<tr>
<td>Frog mass</td>
<td>0.808</td>
<td>3.2</td>
</tr>
<tr>
<td>Muscle mass</td>
<td>0.800</td>
<td>0.1</td>
</tr>
<tr>
<td>CSA</td>
<td>0.855</td>
<td>4.6</td>
</tr>
</tbody>
</table>

CSA, cross-sectional area.
The main result of this study was that maximum isometric torque was most significantly correlated with the maximum tetanic tension of the muscle involved. Frog mass was also significantly correlated but covaried with $P_e$ and thus was not entered into the regression equation without forcing.

The result is in agreement with the numerous human studies that demonstrate statistically significant correlations between maximum isometric torque and muscle cross-sectional area (8, 13, 15, 21, 22) and body mass and maximum isometric torque (21, 22). It was interesting that moment arm and maximum tetanic torque were not significantly correlated. Several investigations of knee mechanics have alluded to the importance of the knee moment arm acting at the patellar tendon in determining maximum torque (15, 21). However, the data from the present study indicate that, for the frog semitendinosus, moment arm is not a major determinant of torque magnitude. It thus appears that moment arm is more closely correlated with muscle fiber length than muscle cross-sectional area (16) and that moment arm variations are not used in the frog system as a mechanism for increasing joint torque. Moment arm magnitude might be more closely linked to muscle fiber length (number of sarcomeres in series) to match sarcomere shortening to joint rotation. Whether such a hypothesis applies only to the semitendinosus-knee system, or whether it is a general strategy applied to other joints and muscles, requires further investigation.

The correlation coefficient between $P_e$ and maximum torque was 0.77. In human studies, lower correlations have been reported and thought to be caused by variability associated with muscle cross-sectional area measurement techniques, uncertainties associated with estimating pinnation angle, and motivational differences of human subjects. Such limitations were not part of the present study. In the present study, $>85\%$ of the variability in maximum torque was accounted for by all of the measured parameters (multiple correlation coefficient $>0.85$, Fig. 1, Table 2).

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