Muscle Fiber Length and Moment Arm Coordination during Dorsi- and Plantarflexion in the Mouse Hindlimb

Key Words
Fiber length
Sarcomere number
Force velocity
Length tension
Muscle architecture
Muscle mechanics

Abstract
The purpose of this study was to test the hypothesis that muscle fiber length and joint moment arm are combined in such a way that maximum muscle force is produced during locomotion. Plantarflexor (soleus, SOL and medial gastrocnemius, MG) and dorsiflexor (extensor digitorum longus, EDL and tibialis anterior, TA) muscle architecture in the mouse was measured along with their associated moment arms. Fiber length varied significantly between muscles ranging from 5.7±0.2 mm (MG) to 7.6±0.2 mm (TA). Plantarflexor moment arms were over twice as large as dorsiflexor moment arms (1.88±0.06 mm vs. 0.84±0.03 mm) suggesting a greater muscle length change with joint angle for plantarflexors compared to dorsiflexors. Using a simple muscle-joint model, the active sarcomere length range in these muscle groups was calculated and proved to be quite similar between functional groups. The active range for dorsiflexors was 2.2–2.4 μm, while the active range for plantarflexors was 2.2–2.5 μm, indicating that both muscle groups operate primarily near the plateau of their length tension relationship. Finally, when calculating force produced by muscles during locomotion, the combination of moment arm and fiber length measured in all muscle groups yielded muscle-joint systems that produced near maximal forces at the velocities modeled. These data indicate that fiber length and moment arm appear to be coordinated to yield the greatest possible force production during locomotion.

Introduction

Muscles generate the forces that rotate joints and cause animal locomotion. The torque and velocity requirements of a particular muscle-moment arm combination are defined by their role during normal movement, whether it be flying, swimming, hopping, manipulating or grasping. It would be naive to believe that the functional requirements of all muscle-joint systems would be the same under all of these conditions. However, it has been demonstrated that muscle shortening velocities during cat, frog and fish locomotion are in the range of 0.25–0.35 \( V_{\text{mus}} \), which is near the optimal velocity for power production [Walmsley et al., 1978; Altringham et al., 1993; Rome et al., 1993; Lutz and Rome, 1994]. This indicates that, across a variety of species and styles of locomotion, some muscles are used at velocities that result in maximal power production. Walking and trotting of digitigrade animals such as the mouse are characterized by slow ankle plantarflexion during the power stroke (E) followed by rapid dorsiflexion during the swing (F) phase [Goslow et al., 1973]. As such, it may not be surprising that dorsiflexors and plantarflexors show a number
of architectural differences in several species studied, such as the human [Wickiewicz et al., 1983], cat [Sacks and Roy, 1982], rabbit [Lieber and Blevins, 1989], guinea pig [Powell et al., 1984] and mouse [Burkholder et al., 1994]. These descriptions generally characterize the plantarflexors as muscles with relatively short fibers but large cross-sectional areas, an architectural specialization designed for force production, while the dorsiflexors are seen as muscles with relatively long fibers and small cross-sectional areas, an architectural specialization designed for velocity production.

Numerous studies have investigated the relationship between muscle architecture and function [Gans, 1982], but fewer have addressed the relationship between architecture and moment arm [Gans and Gaunt, 1991]. It is known that muscle fiber length and physiological cross-sectional area (PCSA) strongly influence maximum contraction velocity and isometric force, respectively. However, since the moment arm transforms the linear muscle motion into angular joint rotation, the moment arm influences both the muscle length range and shortening velocity required to produce a given joint motion. Thus, the interaction between muscle architectural properties and joint moment arm is critical for producing the correct joint kinematics during locomotion and may provide insights into the functional basis of muscle design. The purpose of this study was to investigate the coordination between muscle fiber length and moment arm in the mouse plantarflexor and dorsiflexor muscles as it relates to their normal function.

### Materials and Methods

Architectural properties of the extensor digitorum longus (EDL), medial gastrocnemius (MG), soleus (SOL), and tibialis anterior (TA) muscles of female Swiss-Webster mice (n=6) were measured as described previously [Burkholder et al., 1994]. Briefly, hindlimbs were fixed in 10% buffered formalin with the knee and ankle held at 90°. Muscles were dissected, with special care to collect entire origins and insertions. Muscle mass, muscle length, and pennation angle were measured. Small fiber bundles were then teased from the muscle and mounted on microscope slides. The length of individual fibers was recorded under 60× magnification (Wild Model M3, Wild, Inc. Heerbrugg, Switzerland) to guarantee fiber removal from origin to insertion. Individual muscles were blotted dry, and muscle mass (M) determined using an analytical balance. Muscle length (L_m), defined as the distance from the origin of the most proximal muscle fibers to the insertion of the most distal muscle fibers, was determined using a calibrated digital fiber eyepiece (Lasco Model 112983, Los Angeles, Calif., USA) and sarcomere lengths were measured by laser diffraction [Lieber et al., 1984]. Fiber length (L_f) was determined from individual fibers of each bundle using the fiber eyepiece.

All muscle lengths and fiber lengths were then normalized to a sarcomere length of 2.5 μm to correct for variability induced by differences in the angle of joint fixation. Physiological cross-sectional area (PCSA) was calculated as described by Sacks and Roy [1982] using the equation:

\[
PCSA (\text{mm}^2) = \frac{M (\text{g}) \cdot \cos \theta}{\rho (\text{g/mm}) \cdot L_m (\text{mm})}.
\]

For moment arm determination, with the limbs freed of musculature, 7–0 polypropylene sutures were secured to the distal tendon stumps of dorsif- and plantarflexors. Then, the free end of the suture was led to the muscle origin, over a pulley and tied to a 3.5 gram mass. This mass was sufficient to maintain tension in the tendons, causing them to track along the normal muscle path during joint rotation, but was not so massive as to deform the joint and thus disrupt moment arm measurement. The ankle joint was then rotated through its range of motion, 50–150° (150° being full plantarflexion), while tendon motion was measured using the fiber eyepiece. A line was fit to this excursion-joint angle record, and the slope taken as the average muscle moment arm about the ankle [An et al., 1983].

Architectural and moment arm data were then used to estimate isometric and dynamic joint torques mathematically. The geometric model used was similar to that developed by Zuurbier and Huijing [1992]. Muscle projection areas (A) was calculated as:

\[
A = 2 \cdot L_n \cdot L_s \sin \beta,
\]

where β is the included angle between the aponeurosis and the line of muscle action and L_n is aponeurosis length. Assuming the aponeurosis to be inextensible and the projection area to be constant, the aponeurosis angle can be calculated for any given muscle length from the projection area of the muscle in its reference state. The reference state for each muscle was calculated at sarcomere length 2.5 μm based on the measured architectural properties. The law of sines then yields the relationship between fiber length, muscle length and aponeurosis length as:

\[
\frac{L_n}{\sin[180° - (\alpha + \beta)]} = \frac{L_f}{\sin \beta} = \frac{L_m}{\sin \alpha},
\]

where α is the angle between the fibers and the muscle line of action. Equation 3 yields β and L_n, from L_m, L_s, and α. The fiber velocity function was taken directly from Zuurbier and Huijing [1992]:

\[
V_f = \frac{\cos (\alpha + \beta)}{\cos (\beta)} V_m,
\]

where V_m is muscle velocity.

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Fiber Length-Moment Arm Interaction

**Table 1. Muscle and joint properties for dorsi- and plantarflexors**

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Fiber length mm</th>
<th>PCSA mm²</th>
<th>Moment arm mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>EDL</td>
<td>6.8±0.3</td>
<td>1.2±0.1</td>
<td>0.76±0.03</td>
</tr>
<tr>
<td>TA</td>
<td>7.6±0.2</td>
<td>5.4±0.2</td>
<td>0.89±0.04</td>
</tr>
<tr>
<td>MG</td>
<td>5.7±0.2</td>
<td>22.0±1.0</td>
<td>1.87±0.06</td>
</tr>
<tr>
<td>Soleus</td>
<td>6.4±0.4</td>
<td>1.2±0.06</td>
<td>1.90±0.06</td>
</tr>
</tbody>
</table>

Data obtained from n=4 (moment arm) or n=6 (muscle parameters) specimens. Values shown represent mean ± SEM.

EDL = Extensor digitorum longus; TA = Tibialis anterior; MG = Medial gastrocnemius.
### Table 2. Calculated sarcomere velocity and force reduction

<table>
<thead>
<tr>
<th>Functional group</th>
<th>Muscle</th>
<th>Sarcomere velocity (µm/s)</th>
<th>Force reduction (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dorsiflexor</td>
<td>EDL</td>
<td>6.5</td>
<td>74</td>
</tr>
<tr>
<td>Dorsiflexor</td>
<td>TA</td>
<td>6.0</td>
<td>72</td>
</tr>
<tr>
<td>Plantarflexor</td>
<td>MG</td>
<td>1.3</td>
<td>29</td>
</tr>
<tr>
<td>Plantarflexor</td>
<td>soleus</td>
<td>1.2</td>
<td>37</td>
</tr>
</tbody>
</table>

* Force reduction resulting from shortening at the calculated sarcomere velocity.

Normalized muscle force-length and force-velocity properties were obtained from reasonable approximations in the literature. The force-length property was based on the relationship presented by Gordon et al. [1966] corrected for optimal force production at a sarcomere length of 2.5 µm, the force-velocity relationship was that presented by Katz [1939] with values for a and b obtained from the literature for mammalian muscle [Close, 1972]. The shortening force-velocity relation was described by:

\[
F = \frac{V_{\text{max}} - V}{V_{\text{max}} + 4V}
\]

\( V_{\text{max}} \) was taken to be 17.6 µm/s for fast fibers, and 9.0 µm/s for slow fibers. Fast and slow fibers were considered to have the same specific tension of 250 kPa.

Measured moment arms were then used to relate muscle lengths to joint angles. Joint kinematics during normal locomotion were taken from James et al. [1995]. Since the knee remains close to 90° during plantar- and dorsiflexion, it was held fixed throughout the model motions. Dynamic modeling was performed only during the time each muscle was activated, extrapolated using the EMG data of Nicolopoulos-Stournaras and Iles [1984]. Plantarflexion velocity was estimated as 220°/s, while dorsiflexion velocity was approximated as 1,300°/s [James et al., 1995], which represent the average angular velocities of shortening during a slow trot.

### Results

Complete architectural results are presented elsewhere [Burkholder et al., 1994]; fiber lengths and PCSAs for the muscles discussed here are included in table 1 along with the appropriate values for moments arms. All linear regression fits to the excursion-joint angle were well approximated by the linear function as \( r^2 \) values always exceed 0.98.

Calculations based on measurement of sarcomere number and moment arm alone suggested that the dorsiflexor range of motion consisted primarily of the plateau region and ascending limb of the length-tension relation, where force is relatively constant, varying by 5–10% (fig. 1). The plantarflexor range of motion included a much larger portion of the ascending limb, indicating a decrease in force potential with shortening which could vary by over 200% (fig. 2). Sarcomere lengths were calculated across the full anatomical range of motion, and were closely conserved within each functional group. MG and soleus had sarcomere lengths ranging from approximately 1.4–2.7 µm, while EDL and TA had shorter sarcomere length ranges, from 2.3 to 2.9 µm.

In contrast to the anatomically possible sarcomere length ranges, the active range of sarcomere lengths in
these muscle groups was quite similar between functional groups (shaded bars, fig. 1). The active range for dorsiflexors was approximately 2.2–2.4 μm (EDL: 2.30–2.48; TA: 2.15–2.33), while the active range for plantarflexors was 2.2–2.5 μm (MG: 2.25–2.56; SOL: 2.2–2.47). These data indicate that both muscle groups operate primarily near the plateau of their length tension relation.

Sarcomere velocity was also calculated to be similar within each of the two functional groups, though quite different between groups (table 2). The higher velocity of the dorsiflexor muscles reflected the higher angular velocity of dorsiflexion compared to plantarflexion, although the ratio of dorsiflexor sarcomere velocity to plantarflexor sarcomere velocity (5.5:1) was significantly less than their angular velocity ratio (10:1). This was a simple geometrical consequence of the greater fiber length:moment arm ratio of the dorsiflexors compared to the plantarflexors. The mouse ankle thus represents a muscle-joint system where differences in muscle architecture are partially offset by differences in joint kinematics.

**Discussion**

The most significant result of this study is that, within a functional group, moment arms and fiber lengths are matched to yield nearly identical sarcomere velocities. For the dorsiflexors, despite differences between TA and EDL muscle, fiber and moment arm lengths (table 1), active sarcomere shortening velocity in both muscles was roughly 0.35 V_{mus} (table 2), very close to that predicted for optimal power generation. The conservation of sarcomere length range and shortening velocity in spite of architectural differences suggests a functional necessity of such a design.

The plantarflexors, in conjunction with the digital flexors, are the primary muscles of digitigrade locomotion. They must be capable of the constant, low level activity associated with foraging, as well as the short bursts required for fleeing from predators. The former requires efficient production of low torques while the latter requires short bursts of great power. The dorsiflexors, on the other hand, act primarily in a nearly unloaded state to ‘cock’ the foot and toes during swing phase in preparation for the next step. As such, they must be capable of short bursts of rapid contractions against very low loads.

The fiber lengths and moment arms of these two muscle groups are combined in such a way so as to be suited for each of these particular tasks. The relatively short plantarflexor fiber lengths, and high pennation angles, particularly in the gastrocnemius, reflect a tendency toward packeting sarcomeres in parallel to generate high force. The larger moment arm of the plantarflexors reflects a sacrifice of velocity for force production. To produce the same angular velocity, the plantarflexors would be required to shorten more than twice as fast as their antagonists. Although plantarflexion velocities may be quite large during the flight response, the normal daily activity of a caged laboratory mouse is better represented by the slower motions modeled here.

The dorsiflexors, with their longer fiber lengths and smaller moment arms reflect the alternate optimization –
the sacrifice of force for speed. Both muscles are composed of long fibers, fairly parallel to the muscle axis, acting through moment arms that magnify angular rotation at the cost of mechanical advantage. The moment arm also permits these muscles to produce a great deal of joint rotation while maintaining near optimal sarcomere lengths. By virtue of the reduced linear velocity required for a given angular velocity, compared to the plantarflexors, the dorsiflexors benefit both in terms of their force-velocity and length-tension properties.

In theory, it is possible to arrange a given quantity of sarcomeres (i.e., a fixed muscle mass) to produce any combination of optimal muscle length and maximum shortening velocity simply by adjusting fiber length. This can be illustrated by changing the fiber length of the model TA from its observed fiber length of 7.6 mm to longer and shorter lengths while maintaining constant muscle length and muscle mass. The constraint of maintaining muscle mass, of course, requires a decrease in PCSA, and thus decreased isometric muscle force, with increasing fiber length (fig. 3a). In contrast, as fiber length increases, sarcomere velocity decreases for a given angular velocity, resulting in increased muscle force (fig. 3b). These two effects oppose one another resulting in a theoretically 'optimal' fiber length, representing the optimal simultaneous satisfaction of both criteria. By calculating the dynamic tension (i.e., tension during muscle shortening) as a function of calculated fiber length variation, the interaction between isometric force production (resulting from PCSA) and dynamic force production (sarcomere number and velocity) are seen (fig. 4). This presence of an optimal fiber length is the result of the fact that, at longer fiber lengths, PCSA continues to decrease hyperbolically, while sarcomere velocity decreases linearly. This diminishing sarcomere velocity increases force asymptotically towards $P_0$, as fiber length increases but the concomitant reduced PCSA results in decreases in $P_0$, with increasing fiber length that outweighs the effect of reduced shortening velocity. At shorter fiber lengths, the increased sarcomere shortening velocity overpowers the increased isometric force potential, again resulting in lower dynamic force production. For the mouse TA, dynamic tension peaked at a fiber length (8.1 mm) that was close to that observed by direct measurement (7.6 mm). The tension produced by the observed 7.6 mm fiber was still 99% of maximum.

This relationship was calculated for each muscle group studied and all muscles are plotted in figure 5 on a normalized fiber length scale for comparison. (The normalization value was the actual measured fiber length for each muscle.) For the EDL as with the TA, the observed fiber length was slightly shorter than that required for peak force production during our modeled motion. The MG, on the other hand, displayed fibers that were about two times longer length than would be optimal for this motion. The longer fiber lengths of the MG may indicate optimization for a faster motion. At faster gaits, the E phase becomes faster.
while the F phase remains relatively constant. As gait speed increases, the fiber length required for peak dynamic force production in the plantarflexors increases. Thus, the MG, which is activated at faster gaits, has fiber lengths that would be considered too long for the slow locomotion modeled here, and thus may reflect its use at higher velocities. The SOL muscle yielded a result intermediate between the ‘optimized’ TA and EDL and the MG. Whether this reflects the uniaxial nature of the SOL or its increased slow twitch fiber type percentage [Burkholder et al., 1994] remains to be determined.

In summary, this simulation suggests that muscle fiber length and moment arms of the mouse EDL, TA, MG, and soleus are well designed to produce the appropriate function during normal gait. Sarcomere lengths during shortening are appropriate for near peak isometric force production. Fiber length and moment arm appear to be coordinated to yield the greatest possible power production subject to the velocity requirements of the observed motion.

Acknowledgments

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References


