

Journal of Biomechanics 35 (2002) 893–902

JOURNAL OF BIOMECHANICS

www.elsevier.com/locate/jbiomech www.JBiomech.com

Estimation of cat medial gastrocnemius fascicle lengths during dynamic contractions

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Abstract

In typical muscle models, it is often assumed that the contractile element (fascicle) length depends exclusively on the instantaneous muscle-tendon length and the instantaneous muscle force. In order to test whether the instantaneous fascicle length during dynamic contractions can be predicted from muscle-tendon length and force, fascicle lengths, muscle-tendon lengths, and muscle forces were directly measured in cat medial gastrocnemii during isometric and dynamic contractions. Two theoretical muscle models were developed: model A was based on force-time data obtained during the activation phase and model D on force-time data obtained during the deactivation phase of *isometric* contractions. To test the models, instantaneous fascicle lengths were predicted from muscle-tendon lengths and forces during dynamic contractions that simulated cat locomotion for speeds ranging from 0.4 to 1.6 m/s. The theoretically predicted fascicle lengths were compared with the experimentally measured fascicle lengths. It was found that fascicle lengths were not uniquely associated with muscle-tendon lengths and forces; that is, for a given muscle-tendon length and force, fascicle lengths varied depending on the contractile history. Consequently, models A and D differed in fascicle length predictions; model D (maximum average error = 8.5%) was considerably better than model A (maximum average error = 22.3%). We conclude from this study that it is not possible to predict the exact fascicle lengths from muscle-tendon lengths and forces alone, however, adequate predictions seem possible based on such a model. The relationship between fascicle length and muscle force and muscle-tendon length is complex and highly non-linear, thus, it appears unlikely that accurate fascicle length predictions can be made without some reference contractions in which fascicle length, muscle-tendon length, and force are measured simultaneously. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Fascicle length prediction; Muscle-tendon length; Muscle force; Muscle model; Cat locomotion; Cat gastrocnemius; In vivo muscle properties

1. Introduction

There are many muscle models that have been developed in an attempt to understand neuromuscular control (e.g., Hatze and Buys, 1977; Pandy et al., 1990; He, 1998), loads acting on the musculoskeletal system (e.g., Crowninshield and Brand, 1981; Hase and Yamazaki, 1997), or the mechanism of muscular contraction (e.g., Huxley, 1957; Zahalak, 1981). The primary goal of many muscle models is to estimate the forces exerted by individual muscles. For a given level of activation, muscle forces depend on the instantaneous contractile conditions and the history of contraction.

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Specifically, it is well documented and accepted that muscle forces depend on the instantaneous contractile element (CE) (fascicle) length (e.g., Gordon et al., 1966), the instantaneous rate of change in CE length (e.g., Hill, 1938), and the time history of these two variables (e.g., Abbott and Aubert, 1952; Maréchal and Plaghki, 1979). Therefore, it is essential that instantaneous CE length can be calculated from other variables in a muscle model.

Typically, it has been assumed that CE length depends exclusively on the instantaneous muscle-tendon length and force in Hill-type models (Winters and Stark, 1987; Pandy et al., 1990; Schultz et al., 1991; Soest et al., 1993; Gerritsen et al., 1995; Hase and Yamazaki, 1997). Total muscle-tendon complex length may be estimated from joint angles, and the initial CE length may be known or given. The length of tendon and aponeurosis

(i.e., the series elastic element (SE) part of the muscle tendon complex) is then determined by subtracting the CE length from the muscle-tendon length while accounting for the angle of pennation. Then, muscle force is given by the SE force-length relationship. In order to estimate the CE length at the next time step, the CE length and muscle force are substituted into the CE force-length/velocity relationship, and the time derivative of the CE length is calculated. This time derivative is integrated to predict the CE length at the next time step.

Many Hill-type models have been developed for specific muscles. Brown et al. (1996) measured muscletendon length, muscle force, and fascicle length of cat soleus (virtually parallel fibred) and developed a Hilltype model. Their model accurately predicted the CE force-velocity/length relationship, the SE force-length relationship, and the parallel elastic element (PE) forcelength relationship. However, they only developed their model for steady-state contractions. Sandercock and Heckman (1997) developed a Hill-type model, based on measured muscle-tendon length and muscle force, for the cat soleus, and investigated the reliability of muscle force predictions for dynamic contractions by comparing predicted muscle forces with experimentally observed muscle forces. They found that the greatest errors in muscle force predictions occurred during the relaxation phase of contraction.

In Hill-type models, it is implicitly assumed that CE length is a unique function of muscle-tendon length and force. However, this assumption has not been tested rigorously. Recent evidence suggests that, in pennate muscles, the angle of pennation may change substantially during force production (Kawakami et al., 1995; Fukunaga et al., 1997; Carvalho, 2000), and that fascicle length has history-dependent properties (Carvalho, 2000). However, pennation angles are typically assumed to be constant, or negligibly small, and history-dependent effects are typically ignored in Hill-type muscle models (e.g., Zajac 1989; Brown et al., 1996). However, these factors may influence the relationship between fascicle length, muscle-tendon length and force.

The purpose of this study was to test whether the instantaneous fascicle lengths during dynamic contractions can be predicted from muscle-tendon lengths and muscle forces exclusively. If so, previous theoretical research in this area would largely be vindicated. In order to achieve this purpose, muscle-tendon lengths, muscle forces, and fascicle lengths were directly measured in the unipennate cat medial gastrocnemius (MG) during isometric and dynamic contractions. From the isometric results, a theoretical model of the muscle was developed, and fascicle length predictions during dynamic contractions were made from muscle-tendon length and force.

2. Methods

2.1. Experimental preparation

Three medial gastrocnemii (MG) from adult, outbred cats (3.0-4.5 kg) were used to perform the experimental contractions. Animals were sedated with a subcutaneous injection of Atravet[®] (Ayerst Laboratory, Toronto, ON, Canada), deeply anaesthetized with a 4–5% halothane/ 0.71/min O₂/0.61/min N₂O mixture administered through an anesthetic mask, intubated and maintained throughout the experiment with a 0.5–1.0% halothane oxygen/nitrous oxide mixture. Muscle temperature was monitored, and maintained at 34–35°C using a heat lamp, warming pad, and saline (0.9%) bath that completely submerged the MG. The study was approved by the University of Calgary Animal Ethics Committee.

Cats were fixed in a stereotaxic frame. The experimental hind limb was firmly attached to the frame with sharp, bilateral bone pins at the pelvis, femoral condyles, and the malleoli. The MG tendon was cut from its insertion leaving a remnant piece of bone for attachment to a muscle puller (MTS model 242-02 hydraulic actuator) via sutures. The muscle puller (natural frequency $> 1 \, \text{kHz}$) was equipped with a 100 N load cell (100 N/10 V) to measure the muscle force and was set for a functional length range of 20 mm (20 mm/10 V) to control the muscle-tendon length. Maximal muscle contractions were performed via tibial nerve stimulation using an implanted nerve cuff electrode and a stimulator (Model S8800, Grass Instrument Division, Astro-Med, Inc., West Warwick, RI, USA). Muscle forces and fascicle lengths were measured throughout the isometric contractions at different muscle-tendon lengths.

2.2. Muscle deformation measurement

Seven piezoelectric crystals were implanted on the MG to determine three fascicle lengths (proximal, central, and distal), the three corresponding angles of pennation, muscle height, two aponeurosis segment lengths on the medial and lateral aponeuroses, and the tendon lengths (Fig. 1). Measurements of the distance between piezoelectric crystals were made with a sono-micrometer (TRX8, Sonometric Corporation, London, ON, Canada) using the ultrasound transmit time technique (Griffiths, 1987). A set of all measurements from a single isometric contraction is shown in Fig. 2. The central fascicle length (distance between crystals 3 and 4 in Fig. 1) was used in the theoretical model.

2.3. Isometric contractions

The experimental protocol consisted of isometric contractions at nine muscle-tendon lengths. The refer-



Fig. 1. A schematic representation of the location of piezoelectric crystals on the cat MG. The length of the medial and lateral aponeurotic sheaths are defined by crystals (2–4, 4–6) and (1–3, 3–5), respectively. The three fascicle lengths are defined by crystals (1–2, 3–4, 5–6), and the tendon length is defined by crystals (1–7). The three angles of pennation (α , β , γ) were defined as the angle between crystals (1–2) and (1–3), crystals (3–4) and (3–5), and crystals (5–6) and (3–5), respectively. Crystal 1 was placed at the myotendinous junction, and crystal 7 was placed at the most distal portion of the tendon. The central fascicle length indicated by the thick line between crystals 3 and 4 was used for the derivation of the model. The muscle force, F_m , and the muscle–tendon length, L_m , were measured by the muscle puller.

ence length corresponded to the muscle-tendon length, that produced approximately 1 N of passive tension. This length corresponded to an ankle and knee joint angle of 80° and 140° , respectively, and an average muscle length of 120 mm. From a previous study (Herzog et al., 1992), the physiological range of the cat MG was found to be on the ascending limb and plateau of the force-length relationship (i.e., just when passive force comes into play in cat MG). Therefore, the muscle length used here corresponded approximately to the range of muscle lengths obtained during cat locomotion. Whole muscle-tendon length was changed in 2 mm increments, for a total range of 16mm (i.e., 9 lengths from -10 to +6 mm relative to the reference length). At each muscle-tendon length, measurements were performed twice for a total of 18 sets of isometric contractions from each muscle. During the isometric contractions, MG was maximally stimulated at three times the α motoneuron threshold (3 T) via an implanted tibial nerve cuff electrode. The stimulation parameters were: frequency = 60 Hz, pulse duration = 0.1 ms,



Fig. 2. Raw data of a typical isometric contraction: fascicle length, aponeurosis length, tendon length, muscle-tendon length, and muscle force from a single contraction are shown. The numbers on the length traces indicate the location of the crystals shown in Fig. 1.

stimulation duration = 2 s. A 2-min rest was given between contractions. Data were sampled at a rate of 200 Hz, and muscle–tendon lengths, fascicle lengths, and muscle forces were stored on line to a personal computer.

2.4. Dynamic contractions

For the dynamic contractions, muscle-tendon length and muscle stimulation were controlled in a way to approximate the timing of stimulation and the pattern of muscle-tendon length change during cat walking/ trotting at four different speeds: 0.4, 0.8, 1.2, and 1.6 m/ s. Stimulation of MG was applied to coincide with experimentally observed EMG patterns during cat locomotion on the treadmill at speeds of 0.4, 0.8, 1.2, and 1.6 m/s (Herzog et al., 1993). The stimulation parameters were the same as those used during isometric contractions. Muscle-tendon length change patterns for these four speeds (e.g., 0.8 m/s in Fig. 3) were approximated based on data from Prilutsky et al. (1994). Dynamic simulations of step cycles were produced for two to ten consecutive steps. Muscle stimulations and muscle-tendon length changes were controlled by computer.



Fig. 3. Example of a single approximated cat step cycle for a nominal speed of locomotion of 0. 8 m/s.

2.5. Theoretical models

Two theoretical models were developed. Model A was based on the force-time data obtained during the activation phase of the isometric contractions. Model D was based on the force-time data during the deactivation phase (Fig. 4). The terminal point of the deactivation phase was determined by the threshold force level defined as the average force of the last 20 data points of each contraction. This threshold level was typically 1-2% of the maximum isometric force at each isometric contraction. Based on a sensitivity analysis, this force threshold level produced the least amount of average error in fascicle length predictions.

2.6. Parameter estimates from the isometric contractions

Model parameters were estimated by using muscle– tendon length, muscle force, and fascicle length data from all isometric contractions for each muscle (i.e., 18 isometric tests from each muscle). In order to develop a generic model, the relationship between fascicle length



Fig. 4. Definition of "activation" and "deactivation" phase during isometric contractions. In each isometric trial, maximum and minimum activation/deactivation fascicle length, $L_{\rm fa}^{\rm max}$, $L_{\rm fa}^{\rm min}$, $L_{\rm fa}^{\rm max}$, $L_{\rm fa}^{\rm min}$, $L_{\rm fd}^{\rm max}$, $L_{\rm fd}^{\rm min}$, constraint of the central fascicle fiber is shown.

and muscle force was normalized (Fig. 5). For all contractions, the normalized fascicle length-muscle force relation was quantified by fitting the data with the following equations:

$$\bar{L}_{fi} = \frac{1}{a_i} \ln[(1 - e^{a_i}) \,\bar{F}_{mi} + e^{a_i}],\tag{1}$$

$$\bar{L}_{fi} = (L_{fi}(t) - L_{fi}^{\min}) / (L_{fi}^{\max} - L_{fi}^{\min}),$$
(2)

$$\bar{F}_{\mathrm{m}i} = F_{\mathrm{m}i}(t) / F_{\mathrm{m}}^{\mathrm{max}},\tag{3}$$

i = a (activation phase), d (deactivation phase), where \bar{L}_{fi} and \bar{F}_{mi} are the normalized fascicle length and normalized muscle force, respectively, and a_i is a constant. The normalized fascicle length was defined as the instantaneous fiber excursion $(L_{fi}(t) - L_{fi}^{\min})$ divided by the maximum fiber excursion $(L_{fi}^{\max} - L_{fi}^{\min})$; Fig. 4). The normalized muscle force was defined as the instantaneous muscle force $F_{mi}(t)$ divided by the maximum isometric force (F_{max}^{\max}) ; Fig. 4).



Fig. 5. Fit to the normalized fascicle length–muscle force relation of MG #3 during (a) the activation phase and (b) the deactivation phase of all isometric contractions. The arrows indicate the sense of direction of the curves in time.

The maximum isometric force as a function of muscle-tendon length was described by

$$F_{\rm m}^{\rm max} = b_{1i}L_{\rm mi}^4 + b_{2i}L_{\rm mi}^3 + b_{3i}L_{\rm mi}^2 + b_{4i}L_{\rm mi} + b_{5i}, \qquad (4)$$

where $b_{1i} - b_{5i}$ are constants and L_{mi} is the muscle-tendon length.

The maximum fascicle lengths for the activation and deactivation phase were defined as the fascicle length at the beginning of the activation phase and the end of the deactivation phase, respectively ($L_{\rm fa}^{\rm max}$ and $L_{\rm fd}^{\rm max}$; Fig. 4). The maximum fascicle length was also described as a function of muscle–tendon length,

$$L_{\rm fi}^{\rm max} = c_{1i} L_{\rm mi}^3 + c_{2i} L_{\rm mi}^2 + c_{3i} L_{\rm mi} + c_{4i}, \tag{5}$$

where $c_{1i} - c_{4i}$ are constants.

The minimum fascicle length was defined as the fascicle length at which force reached the maximum isometric value. The minimum fascicle length was the same for the activation and deactivation phases $(L_{\text{fa}}^{\min} = L_{\text{fd}}^{\min})$; Fig. 4). It was expressed as a function of muscle–tendon length,

$$L_{mi}^{\min} = d_{1i}L_{mi}^3 + d_{2i}L_{mi}^2 + d_{3i}L_{mi} + d_{4i}, \tag{6}$$

where $d_{1i} - d_{4i}$ are constants.

2.7. Estimates of fascicle lengths during dynamic contractions

The instantaneous fascicle lengths during dynamic contractions were given by

$$L_{fi} = \bar{L}_{fi} (L_{fi}^{\max} - L_{fi}^{\min}) + L_{fi}^{\min},$$
(7)

The normalized fascicle lengths, and the maximum and minimum fascicle lengths during the dynamic contractions were determined using Eqs. (1) and (3)–(6), and using muscle–tendon length, L_{mi} , muscle force, F_{mi} , and the constants in Eqs. (3)–(6) that were determined from the isometric contractions. Then, these variables were substituted into Eq. (7) to estimate the instantaneous fascicle lengths during the dynamic contractions.

2.8. Model validation

Validation of the dynamic fascicle length model was made by comparing the theoretically predicted and experimentally measured fascicle lengths during the dynamic contractions:

$$E = \sum_{i=1}^{N} \left\{ \frac{|L_{fi}^{t} - L_{fi}^{e}|}{L_{fi}^{e}} \right\} / N,$$
(8)

where L_{fi}^t and L_{fi}^e are the theoretically predicted and the experimentally observed fascicle lengths, and N is the number of time instants. The coefficient *E* represents the average error of the theoretically predicted fascicle lengths with respect to the corresponding experimentally observed fascicle lengths.

The correlations between the theoretically predicted and experimentally observed fascicle lengths were used for evaluation of the theoretical model.

3. Results

MG fascicle length as a function of muscle-tendon length and muscle force predicted by model D is shown in Fig. 6. The solid line at the bottom (muscle-tendon length-muscle force plane) is the maximum isometric force-length relation. The meshed area indicates the solution area of model D. The fascicle length-muscletendon length-muscle force points estimated using model D are present on the meshed surface area.

Predicted and observed fascicle lengths for the isometric contractions are shown in Fig. 7 for a representative muscle. Fascicle lengths for the activation phase were estimated using model A, and fascicle lengths for the deactivation phase were estimated using model D. The arrows indicate the progression in time of the force–fascicle length curves. The predicted results (black, thin lines) fit the observed results (gray, thick lines) well for all isometric contractions for the activation phases.

Theoretically predicted fascicle lengths were compared with the experimentally observed fascicle lengths for the dynamic protocols that approximated muscle– tendon length changes occurring during cat walking and trotting at 0.4, 0.8, 1.2, and 1.6 m/s (Fig. 8). Model A tended to overestimate fascicle lengths at any speed, while model D tended to underestimate them. Similar errors were also seen in the other muscles. The average error of model D was smaller than that of model A for all conditions, except for MG #3 at 1.6 m/s (Fig. 9). The maximum average error of model A was 22.3% and that



Fig. 6. The predicted fascicle length of MG #1 as a function of muscle force and muscle–tendon length. The curve in the muscle force–length plane represents the maximum isometric force–length relation.



Fig. 7. Muscle force–fascicle length curves of MG #3 during (a) the activation and (b) deactivation phase of all isometric contractions. The predicted fascicle lengths (black, thin lines) were compared with the observed lengths (gray, thick lines). The lengths during the activation phase were estimated by model A and those during the deactivation phase were estimated by model D. The arrows indicate the direction of the curves in time.

of model D was 8.5%. For most trials, the greatest errors were found during the swing phase of walking/ trotting. The best-fitting linear relationship between the predicted and observed fascicle lengths is shown in Fig. 10. As indicated in Table 1, correlation coefficients tended to increase with increasing speeds of contraction (i.e., increasing speeds of simulated locomotion) for both models.

4. Discussions

Knowledge of instantaneous fascicle lengths during dynamic contractions is essential for many muscle models because of the force–length and force–velocity properties of skeletal muscle (Gordon et al., 1966; Hill, 1938). However, direct, in vivo, dynamic fascicle length measurements are rare (Griffiths, 1989, 1991; Hoffer et al., 1989; Biewener et al., 1998a, b) and are limited to selected movement patterns. Theoretical models have been used frequently to determine fascicle (CE) length for dynamically contracting muscles (Pandy et al., 1990; Soest et al., 1993; Gerritsen et al., 1995; Hase and Yamazaki, 1997). In these models, fascicle lengths were estimated using muscle–tendon length and muscle force as the only input variables. Therefore, the basic question



Fig. 8. Comparison of observed fascicle lengths of MG #2 (gray line) with the predicted fascicle lengths (thin solid line for model A, fat solid line for model D) during the simulated step cycles at (a) 0.4 m/s, (b) 0.8 m/s, (c) 1.2 m/s, and (d) 1.6 m/s. The abbreviations, "st" and "sw" indicate the simulated stance and swing phase, respectively.



Fig. 9. Average errors of estimated fascicle lengths of (a) MG #1, (b) MG #2, and (c) MG #3 using models A and D during the stance and swing phase of simulated step cycles. The numbers in brackets indicate the number of steps used for analysis (these are total numbers of steps, not necessarily consecutive steps).



Fig. 10. Observed vs. predicted fascicle lengths of MG #2 using model D for each speed tested. Plots were made from the data of the entire step cycles (note that the lines are best fitting straight lines, but because of the variable density of data points, it may not appear that way).

arises: are total muscle-tendon length and muscle force good predictors of fascicle lengths? To our knowledge, this question has not been addressed previously.

Here, we demonstrate that fascicle lengths can be predicted adequately based on muscle-tendon length and force alone. Mean errors in fiber length predictions ranged from 2% to 14%, 1% to 6%, and 2% to 22% for MG #1, 2, and 3, respectively. More accurate predictions were not possible because of the following observations: (1) models A and D, derived from the activation and deactivation phase of isometric contractions (Fig. 4), gave different fascicle length predictions because there does not exist an absolute unique functional relationship between fascicle length and muscle force/length (e.g., Fig. 5); (2) fascicle lengths at a constant muscle-tendon length and zero force following a dynamic contraction do not stay constant as one would expect; and (3) there are distinct errors in fascicle length predictions when going from the (simulated) stance to the swing phase of the step cycles. These observations will be discussed in detail in the following.

(1) The difference in fascicle length predictions between models A and D indicates that instantaneous fascicle lengths are not a unique function of muscle force/length, since fascicle lengths behave in a different way in the activation and deactivation phase. Overall, model D provided better predictions (maximum average error = 8.5%; Fig. 9) than model A (maximum average error = 22.3%; Fig. 9). In order to identify the source for the greater errors in model A compared to those in

Table 1

| Speed (m/s) | MG #1 | | MG #2 | | MG #3 | |
|-------------|------------|------------|-----------|-----------|------------|------------|
| | Model A | Model D | Model A | Model D | Model A | Model D |
| 0.4 | 0.691 (6) | 0.701 (6) | 0.931 (6) | 0.937 (6) | 0.887 (12) | 0.884 (12) |
| 0.8 | 0.767 (9) | 0.799 (9) | 0.930 (8) | 0.931 (8) | 0.793 (12) | 0.812 (12) |
| 1.2 | 0.820 (10) | 0.889 (10) | 0.980 (9) | 0.983 (9) | 0.827 (14) | 0.838 (14) |
| 1.6 | 0.933 (2) | 0.952 (2) | 0.973 (8) | 0.982 (8) | 0.854 (19) | 0.901 (19) |

Significant Correlations between the observed and estimated fascicle lengths during entire step cycles (p < 0.001)

The numbers in brackets show the number of step cycles.

model D, the parameter constants of model A in Eqs. (1) and (5) were exchanged with the corresponding constants in model D. We found that the predicted results of the modified model A (using constants from Eq. (1)) were not substantially different from the original results. However, the modified model A gave much improved results when using the constants from Eq. (5). This result suggests that the use of the maximum fascicle length from the activation phase gives large errors in the prediction of instantaneous fascicle lengths. The result makes sense in so far as the maximum fascicle lengths at rest (i.e., before activation) are always considerably greater than the corresponding maximum fascicle lengths for the deactivation phase (i.e., immediately after zero force is reached after deactivation; Fig. 4). It appears that considerable time is required following force production for a fiber to return to its resting length. Therefore, during repeated contractions (as done here to simulate consecutive step cycles), there is not sufficient time to reach the large fascicle lengths observed at rest, therefore, fascicle lengths are consistently overestimated with model A.

(2) For slow simulated walking (0.4 m/s), both models predicted a constant fascicle lengths during part of the swing phase (Fig. 8) when force was zero and muscletendon length was kept constant. The experimentally observed fascicle lengths increased gradually during that period. The predicted fascicle lengths during this zero force period are a function of muscle-tendon length exclusively (Eq. (7)). Therefore, if muscle-tendon length remains constant in this phase, fascicle length is predicted to be constant, too. However, the experimentally observed fascicle lengths increased indicating that at least a small portion of fascicle length changes cannot be predicted accurately with a model that is based on muscle force and muscle-tendon length exclusively. This history-dependent fascicle length behavior was small relative to the fascicle length behavior as a function of muscle-tendon length and force, and therefore, the predictions of the model presented here were still adequate (i.e., the maximum average error in fascicle length prediction was 8.5%). However, this historydependent fascicle length behavior should be investigated to identify its source.

(3) A distinct and consistent error in fascicle length predictions was found at the transition from the stance to the swing phase at all speeds of simulated locomotion (arrows; Fig. 8). This error is caused by the great sensitivity of normalized fascicle lengths to force at low force levels (Fig. 5). For example, if muscle force drops from 0.2 to 0 in the deactivation model (Fig. 5b), fascicle length increases from 0.3 to 1. Obviously, the isometric relationship between fascicle length changes occurring in the deactivation phase of the dynamic contractions, hence the large error at the transition from stance to swing.

The change in pennation angle for the unipennate cat MG is substantial. The average relaxed pennation angle depends on muscle-tendon length and is about $30-40^{\circ}$, while the average pennation angle during contraction is about 40–60 $^{\circ}$ (Carvalho, 2000). Thus, changes in the pennation angle from a zero to a full active state may reach in excess of 20° during isometric contractions. Therefore, changes in pennation angle might affect muscle force production. However, pennation angles are typically assumed to be constant or negligible in muscle models (Zajac, 1989; Brown et al., 1996). Moreover, pennation angles, like fascicle length, seem to have a history-dependent behavior. For example in Fig. 4, the pennation angle is different at the beginning and end of the contraction, where force is zero and muscle-tendon length is the same (Fig. 4). This difference in pennation angle at the beginning and end of contraction is consistent for all muscles.

Two sources of experimental error should be mentioned here. First, the absolute magnitude of fascicle lengths depends on the assumed speed of ultrasound transmission (1540 m/s according to our measurements). The effect of a change in the ultrasound speed (possible range of 1520–1560 m/s) on fascicle length is about 1%. Second, relative movements of corresponding crystal pairs will produce an error in fascicle length measurement (i.e., crystals 3 and 4 in our analysis, Fig. 1). The crystals were embedded and fixed in light silicon tubing and were sutured to the fascia using separate sutures arranged in a triangular pattern. Therefore, relative movements of the transducers were assumed to be < 0.5 mm. For fascicle lengths of about 20 mm (on average), such relative movements of the crystals would produce an error of about 2.5%. Therefore, measurement errors would likely have influenced the exact absolute fascicle lengths in this study, but the errors were likely too small to affect the conceptual results and conclusions presented here.

5. Conclusions

Experimental evidence obtained in this study shows that muscle fascicle length is not a unique function of muscle force and muscle-tendon length. Nevertheless, a suitable relationship between fascicle length and muscle force/length could be derived from data of the deactivation phase of isometric contractions covering the approximate physiological range of muscle-tendon lengths. It should be noted that the relationship is much more complex than those typically found in Hill-type models of muscle function. Therefore, we must conclude that although a feasible relationship could be derived between fascicle lengths and muscle force/length during dynamic contractions, it is unlikely that an adequate relationship could have been obtained without the corresponding experimental observations. Fascicle lengths in the cat MG scale highly non-linearly with muscle-tendon length alone and with muscle force alone. Capturing these relationships in muscles other than the cat MG and without the use of experimental measurement of all the variables involved appears virtually impossible. We conclude that it is likely that models estimating fascicle lengths that are not based on experimentally observed fascicle lengths and muscle force/length may contain great errors and should be considered with caution.

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