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Finite Element Modeling Reveals Complex Strain Mechanics in the Aponeuroses of Contracting Skeletal Muscle

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Abstract

A finite element model was used to investigate the counter-intuitive experimental observation that some regions of the aponeuroses of a loaded and contracting muscle may shorten rather than undergo an expected lengthening. The model confirms the experimental findings and suggests that pennation angle plays a significant role in determining whether regions of the aponeuroses stretch or shorten. A smaller pennation angles (25°) was accompanied by aponeurosis lengthening whereas a larger pennation angle (47°) was accompanied by mixed strain effects depending upon location along the length of the aponeurosis. This can be explained by the Poisson effect during muscle contraction and a Mohr's circle analogy. Constant volume constraint requires that fiber cross sectional dimensions increase when a fiber shortens. The opposing influences of these two strains upon the aponeurosis combine in proportion to the pennation angle. Lower pennation angles emphasize the influence of fiber shortening upon the aponeurosis and thus favor aponeurosis compression, whereas higher pennation angles increase the influence of cross sectional changes and therefore favor aponeurosis stretch. The distance separating the aponeuroses was also found to depend upon pennation angle during simulated contractions. Smaller pennation angles favored increased aponeurosis separation larger pennation angles favored decreased separation. These findings caution that measures of the mechanical properties of aponeuroses in intact muscle may be affected by contributions from adjacent muscle fibers and that the influence of muscle fibers on aponeurosis strain will depend upon the fiber pennation angle.

Keywords

Finite Element Modeling; Skeletal Muscle; Muscle-Tendon Complex; Muscle Fiber Contraction; Muscle Deformation

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1. Introduction

The complexity and diversity of skeletal muscle design and the challenge which these pose to our ability to understand muscle mechanics is well recognized (Gans, 1982; Otten, 1988). The lumped-parameter models for muscle-tendon complex (Bahler, 1968; McMahon, 1984; Zajac, 1989) widely used in many biomechanics applications do not take into account the material and geometric nonlinear behaviors (Epstein *et al.*, 2006). The assumptions in those models are not fully consistent with the recent experimental studies which have revealed non-uniform strains in muscle, aponeurosis and tendon structures (Finni *et al.*, 2003; Pappas *et al.*, 2002; Ahn *et al.*, 2003; Kinugasa *et al.*, 2008, Shin *et al.*, 2008). Our objective was to develop models of skeletal muscle and tendon with physics based analysis of numerical results for better understanding of the tissue organization and mechanics which brings about the observed deformations of muscle and tendon (Hodgson *et al.*, 2006; Narici, 1999; Otten, 1988; Gans, 1982). Of particular relevance to this paper are efforts to explain why slight differences in the conditions under which aponeurosis strains are measured using magnetic resonance imaging (MRI) and ultrasound produce apparently conflicting results, in one case indicating an expected stretch of the loaded tendon material, in the other case suggesting compression in some regions of the aponeurosis (Muramatsu *et al.*, 2002a, 2002b; Kinugasa *et al.*, 2008). A significant issue is if such discrepancies indicate errors in the experimental technique. The MRI data indicates that some regions of an aponeurosis may shorten during an isometric contraction, counter to the intuitive notion that a loaded elastic material should stretch. One motivation for this study was therefore to determine if a mechanical model could be developed to demonstrate the existence of conditions where some portions of a loaded aponeurosis may shorten and offer the explanation of this unexpected experimental observation. The observation of shortening in a loaded aponeurosis has important implications in relation to the storage and recovery of elastic energy in the passive elastic materials of the muscle (Morgan *et al.*, 1978; Sawicki, 2009). If true, the finding underlines deficiencies in many widely accepted muscle models and reinforces some more recent models which challenge the more traditional views and assumptions related to the nonuniformity of stress and strain in aponeurosis and muscle, even along the fiber direction of muscle (Yucesoy *et al.*, 2002; Epstein *et al.*, 2006).

Although finite element (FE) methods have been employed to analyze a wide variety of engineering and scientific problems for decades, most of the materials in these problems exhibit passive behaviors. The analysis of skeletal muscles, on the other hand, requires consideration of both passive and active stresses in the materials (van Leeuwen and Spoor, 1992). Zajac (1989) considered the passive part of stress to be dependent on the strain along the fiber direction while the active stress in fibers to be a function of the activation level, the fiber length and the fiber shortening velocity. These FE simulations of muscle contraction were based on Hill-type models (Bahler, 1968; Hill, 1970). More recently, a linked fiber-matrix FE mesh has been proposed to study force transmission between the matrix and fibers (Yucesoy, 2002, 2006). The two-state Huxley model (Huxley, 1957), which considers molecular operations in the fiber contraction, also has been employed in a FE continuum model by Oomens *et al.*, (2003).

This paper introduces a nonlinear FE model which takes into account voluntary contraction of fibers and passive deformation of muscle matrix and tendon with specifically defined geometry and boundary conditions for evaluation of important mechanical properties of muscle. In this paper, we restrict our major interest to the properties of the aponeuroses with the goal of demonstrating that the observed shortening of a loaded aponeurosis can be explained with physics principles applicable to the mechanics of skeletal muscle.

2. Methods

2.1. Transversely isotropic hyperelastic model

We consider an anisotropic strain energy density function W as follows:

$$W = W_{matrix}(\bar{I}_1, \bar{I}_2, J) + W_{fiber}(\lambda). \quad (1)$$

where W_{fiber} representing the strain energy stored in the fibers will be discussed in Section 2.2, and W_{matrix} is

$$W_{matrix}(\bar{I}_1, \bar{I}_2, J) = \bar{W}_{matrix}(\bar{I}_1, \bar{I}_2) + \tilde{W}_{matrix}(J), \quad (2)$$

where $\bar{W}_{matrix}$ and $\tilde{W}_{matrix}$ are the deviatoric and volumetric parts of W_{matrix} , respectively, $\bar{I}_i$ are the reduced invariants of the Cauchy-Green deformation tensor $\mathbf{C}$ defined as $\bar{I}_1 = J^{-2/3}$

$I_1, \bar{I}_2 = J^{-4/3} I_2, I_1 = \text{tr}(\mathbf{C}), I_2 = \frac{1}{2} [\text{tr}(\mathbf{C})^2 - \text{tr}(\mathbf{C}^2)]$, $J = \det(\mathbf{C})^{1/2}$, $\mathbf{C} = \mathbf{F}^T \cdot \mathbf{F}$, and $\mathbf{F}$ is the deformation gradient. We adopt a quadratic polynomial type function for W_{matrix} :

$$W_{matrix} = \underbrace{\sum_{i+j=1}^2 C_{ij}(\bar{I}_1 - 3)^i (\bar{I}_2 - 3)^j}_{\bar{W}_{matrix}} + \underbrace{\frac{K}{2}(\ln(J))^2}_{\tilde{W}_{matrix}} \quad (3)$$

where C_{ij} and K are material constants. Although the isotropic strain energy density function for muscle matrix is used, the contribution of fiber stress to be discussed in Section 2.2 introduces anisotropy to this material model. The material constants for W_{matrix} were calibrated from the reported experimental data in (van der Linden, 1998) as given in Table 1.

The tendon and the aponeurosis were modeled by an isotropic cubic hyperelastic model of which the strain energy density function is given as:

$$W_{tendon} = \underbrace{C_{10}(\bar{I}_1 - 3) + C_{20}(\bar{I}_1 - 3)^2 + C_{30}(\bar{I}_1 - 3)^3}_{\bar{W}_{tendon}} + \underbrace{\frac{K}{2}(J - 1)^2}_{\tilde{W}_{tendon}} \quad (4)$$

where C_{10}, C_{20}, C_{30} , and K are material constants, and $\bar{W}_{tendon}$ and $\tilde{W}_{tendon}$ denote the deviatoric and volumetric parts of W_{tendon} , respectively. The material constants given in Table 2 were calibrated from the experimental data (Shin *et al.*, 2007) shown in Fig. 1(a). The stress-strain relations of the matrix, fiber and tendon obtained from the strain energy density functions are given in Appendix A.

2.2. Stresses in Muscle Fibers

The force-stretch characteristics of muscle fibers have been characterized by experiments (Zajac, 1989; Fung, 1981) and can be related to the strain energy density function as:

$$\lambda \frac{\partial W_{fiber}}{\partial \lambda} = \sigma_{fiber} \quad (5)$$

where σ_{fiber} is the component of Cauchy stress along fiber direction. Blemker *et al.* (2005) expressed the stress in muscle fibers in the following form:

$$\sigma_{fiber} = \sigma_{max} f_{fiber}^{total} \cdot \lambda / \lambda_0, \quad (6)$$

where σ_{max} is the maximum isometric stress which occurs at the optimal fiber stretch λ_0 , and f_{fiber}^{total} is the normalized fiber force, which is assumed to be the combination of the normalized active and passive fiber forces in the following form:

$$f_{fiber}^{total} = a \cdot f_{fiber}^{act} + f_{fiber}^{pass}, \quad (7)$$

where a is the muscle activation function, and f_{fiber}^{active} and f_{fiber}^{pass} are the normalized active and passive fiber forces, respectively. The explicit forms of f_{fiber}^{active} and f_{fiber}^{pass} are listed below and plotted in Fig. 1(b) based on $\gamma_1 = 0.05$, $\gamma_2 = 6.6$, $\lambda_0 = 1.4$, and $\sigma_{max} = 30 \text{ N/cm}^2$ (Gordon *et al.*, 1966; Blemker *et al.*, 2005, 2006).

$$\begin{cases} f_{fiber}^{pass} = 0 & \lambda^* \leq 1 \\ f_{fiber}^{pass} = \gamma_1 (e^{\gamma_2 (\lambda^* - 1)} - 1) & 1 < \lambda^* \leq 1.4 \\ f_{fiber}^{pass} = (\gamma_1 \gamma_2 e^{0.4 \gamma_2}) \lambda^* + \gamma_1 (e^{0.4 \gamma_2} - 1) & \lambda^* > 1.4 \end{cases} \quad (8)$$

$$\begin{cases} f_{fiber}^{act} = 9(\lambda^* - 0.4)^2 & \lambda^* < 0.6 \\ f_{fiber}^{act} = 1 - 4(1 - \lambda^*)^2 & 0.6 < \lambda^* \leq 1.4, \\ f_{fiber}^{act} = 9(\lambda^* - 1.6)^2 & \lambda^* > 1.4 \end{cases} \quad (9)$$

where λ^* is the normalized stretch defined as $\lambda^* = \lambda / \lambda_0$. The abovementioned material models were implemented into ABAQUS 6.5 (Abaqus Inc., Providence, RI, 2004).

In this study, we consider only quasi-static cases and neglect the velocity dependency. Thus, graphs of muscle properties versus activation represent a series of isometric contractions at different activation levels acting uniformly throughout all of the fibers of the muscle. It should be noted that the major conclusions of the paper are based upon comparisons between relaxed and fully activated muscle. The inclusion of data for sub-maximal activation may not be a true representation of the distribution of stress in a sub-maximally activated muscle, but we felt that such information was invaluable in providing some indications of how a muscle may behave when activated sub-maximally.

3. Implementation of the model

We introduce the geometry of the muscle-tendon complex widely adopted in the lumped-parameter models (Zajac, 1989) shown in Fig. 2(a) and (b) and consider material and geometry nonlinearities. In our model, we assume that the material is nearly incompressible (Baskin and Paolini, 1967), the material properties are homogeneous, and the muscle fibers are straight and parallel to each other. The models in Fig. 2(a)–(b) are discretized by finite elements with a bilinear displacement field and constant pressure field, and the plane strain condition with a thickness of 3 cm is considered. Since the thickness of 3 cm is of the same

order as the width of 4 cm of the muscle, and the prescribed boundary conditions are in the in-plane directions, plane strain condition is assumed. The two end points of the tendons are fixed to simulate isometric conditions for the muscle-tendon unit. Two simulation models, with fiber pennation angles of $\theta = 25^\circ$ and 47° were considered. Two pennation angles were chosen to sample different values in the range of pennation angles encountered in normal muscle activities and to study if pennation angle has a significant impact on distribution of strain in the muscle. As will be seen in the Results Section and explained in the Discussion Section using Mohr's circle analogy, the sign of strain along the tendon-aponeurosis axes induced by the fiber contraction is determined by whether twice the pennation angle is greater or smaller than 90° . This is the reason that we choose two pennation angles of $\theta = 25^\circ$ and 47° in this study. In addition, we compared the behavior of the models with, and without lateral constraints which prevented movement of the tendon or aponeurosis in the x-axis direction. This was done to evaluate the possible differences between a constrained and an unconstrained muscle and also to directly compare our model with the constrained, lumped parameter model (Zajac, 1989). A convergence study on the FE mesh has been made by comparing the load-displacement responses of the analysis by fixing one end of tendon at point A and pulling the other end of the tendon at point F in the vertical direction using 3 mesh refinements with 145, 341, and 1360 elements. The load-displacement curves in Fig. 2(c) indicated that the models with 1360 elements as shown in Fig. 2(a) and (b) were sufficient to obtain reliable numerical solutions.

A two-stage simulation was implemented to investigate the possible mechanisms underlying the influence of muscle fiber pennation angle upon aponeurosis strain as discussed in Section 4.1. We considered two competing factors that contribute to the deformation of muscle-tendon assembly under contraction, (1) active muscle contraction, and (2) the isometric condition. In the first stage, muscle contraction without the isometric constraint was simulated, thus allowing the model to shorten and deform independently of any external forces. In the second stage, we reimposed the isometric condition by maintaining the activation of the muscle while pulling the two ends of the tendons to their original positions.

4. Results

The maximum principal strain contours for four cases when muscle fully activated are given in Fig. 3. The figure illustrates that muscle and aponeurosis strains and strain distributions are influenced by the pennation angle as well as the lateral constraints. Corresponding displacement and strain distributions along the tendon-aponeurosis axis (point A to B in Fig. 3) are given in Fig. 4. The progressive increase in displacement from the end of the tendon (point A) to almost the opposite extremity of the aponeurosis (approaching point B) illustrates an overall extension of the tendon-aponeurosis complex of approximately 0.6 cm, compatible with the expected elongation of the loaded tendon and aponeurosis (Fig. 4a). The reverse of this trend near point B in the 25° model indicates a compression of the aponeurosis in this region. These observations are further clarified by calculating the strain along the tendon and aponeurosis (Fig. 4b). It is unlikely that these figures represent precise distribution of displacement and strain along the aponeurosis, since these would depend upon a precise anatomic representation of the muscle, tendon and aponeurosis, but it suffices to illustrate that muscle fiber pennation angle may influence the mechanical response of the muscle and that, under some circumstances, negative aponeurosis strains are theoretically possible in a contracting muscle. This will be further analyzed in Section 4.1 using a two-stage analysis approach. It should also be noted that, despite regions of negative strain in the 25° pennation angle model, the overall length of the aponeurosis still increased when the muscle contracted.

4.1. Positive and negative aponeurosis strain in contracting muscle

To further investigate the mechanisms underlying the regional positive and negative strains along the aponeurosis components, we then divided our simulation into two stages. In the first stage we considered the role of active muscle contraction without the isometric constraint. The maximum principal strain contours of the two muscle geometries following the first stage are given in Fig. 5. The isometric condition was then added by pulling the two ends of the tendons to their original positions while the muscle remained fully activated. The final deformations and strain contours are shown in Fig. 5(b) and are identical to Fig. 3(a) and (b).

The strain distributions along the tendon-aponeurosis axis in the two-stage simulation are given in Fig. 6. Intriguingly, the strain along the aponeurosis axis during the first stage deformation is entirely in compression (negative strain) for the 25° pennation angle model, whereas for the 47° pennation angle case it is entirely in tension (positive strain). We will provide the explanation of these very distinct strain distributions in the two models in the Discussion Section. The strain distributions along the tendon-aponeurosis axis at the end of the stage 2 deformation are also shown in Fig. 6 and are identical to the strain distributions plotted in Fig. 4(b). The influence of the isometric condition on the tendon-aponeuroses deformation can be depicted by subtracting the curve “stage 1” from the curve “stage 2” in Fig. 6. The “difference” curve in Fig. 6 indicated that the isometric condition induces a tensile deformation to the tendon-aponeurosis axis in both muscles. For the 47° pennation angle case, the combined deformation of the two stages is tension along the tendon-aponeurosis since the strains along tendon-aponeurosis axis induced in both stages are positive. However, for the 25° pennation angle case, a large compressive deformation exists near point B when the muscle contracts in stage 1 (similarly for point E due to symmetry). The addition of tensile deformation caused by the return to the isometric condition in stage 2 results in a progressive transition from tensile deformation to compressive deformation along the tendon-aponeurosis axis.

4.2. Deformations and strains of muscle

The muscle length change, defined as the distance change between point C, D in Fig. 2(a) (b), and the muscle width change, defined as the distance change between point B, E in Fig. 2(a)(b), are plotted against normalized force (reaction force divided by its maximum value) in Fig. 7(a) and (b), respectively. They indicate that the muscle belly is getting shorter (~4%) and fatter (~20%) as load develops under isometric conditions, although there is only a slight change in aponeurosis separation (Fig. 8). The distance between the aponeuroses, d_a , can be calculated directly by measuring the closest distance between the two aponeuroses. The calculated results are given in Fig. 8. The numerical calculations of the changes in aponeurosis separation range between 3% for the 25° case and -5% for the 45° case with some influence of muscle locations in both cases, which qualitatively agree with previous observations (Otten, 1988). A further notable observation from these data are that the relationship between aponeurosis separation and activation level may not be monotonic. The 25° case illustrates a rise in aponeurosis separation for low levels of activation, reaching peak separation in the mid-range of activation levels, then declining again with increased levels of activation.

5. Discussions

Recent work, using MRI techniques has hinted at a distribution of strains over muscle aponeurosis with some regions evidently shortening as load increases, which appear contrary to intuition (Finni *et al.*, 2003; Kinugasa *et al.*, 2008). Other direct observations of

contracting rat medial gastrocnemius muscle suggest that some areas of the surface of the muscle shorten during a contraction (Zuurbier and Huijing, 1992).

The modeling data presented here clearly predict regions of negative strain in the aponeurosis of contracting muscle giving some credence to the above observations. We have identified the two competing factors that contribute to the deformation of muscle-tendon assembly under contraction: (1) active muscle contraction, and (2) isometric condition. The two-stage simulation suggests that the active muscle contraction yield compressive deformation only for muscle with certain pennation angles and tensile deformation for muscles with other pennation angles. The isometric condition adds tensile stresses to modify the deformations due to active muscle contraction. The combined effects yield the tension-compression deformation along the tendon-aponeurosis axis. More specifically, this analysis shows that the regions of negative strain in the aponeurosis of contracting muscle exist only in the model with certain pennation angle, at 25° amongst our two tested models at 25° and 47° .

The question remains as to why a muscle contraction in stage 1 yields a completely opposite sign of strain in some regions of the tendon-aponeurosis axis for the 25° and 47° pennation angle models. When a muscle fiber contracts, it attempts to shorten, thus inducing a compressive deformation along the fiber direction. In order to maintain a constant muscle fiber volume, the cross sectional area of a shortening fiber must increase, thus adding a tensile deformation in the direction perpendicular to the fiber due to the Poisson effect. In the present model, the plane strain assumption requires the area of the muscle plane to remain constant, rather than the muscle volume. Thus, the magnitude of the tensile strain in the lateral direction is about the same as the magnitude of compressive deformation in the fiber direction. Using this strain state in the fiber direction, the strain state of the material in any orientation can be obtained by means of a Mohr's circle as shown in Fig. 9, which is a graphical representation of the strain rotational transformation formula. Let ε_y denote the normal strain in the fiber direction and ε_x denote the normal strain in the direction perpendicular to the fiber (Fig. 9(a)). The origin of the Mohr's circle is located at $(\varepsilon_x + \varepsilon_y)/2$ and its radius is $(\varepsilon_x - \varepsilon_y)/2$. As shown in Fig. 9(b), one rotates from point A by the angle 2θ (twice the pennation angle, θ) to obtain the strain component ε'_y and ε''_y which are the strains along the tendon-aponeurosis axes for $\theta = 25^\circ$ and $\theta = 47^\circ$ cases, respectively. Using the Mohr's circle calculation, we conclude that the strain along the tendon-aponeurosis axes is negative for $\theta = 25^\circ$ (ε'_y) and is positive for $\theta = 47^\circ$ (ε''_y) as shown in Fig. 9(b). This explains our finding in the stage 1 finite element strain distribution results shown in Fig. 6. Although this example uses a plane strain model, the case is easily extrapolated to a 3-dimensional model. A similar result would be predicted, although the strains perpendicular to the long axis of the muscle fibers will change slightly.

Ultrasound measurements performed at maximum voluntary contractions produce large changes in fiber pennation angles, likely producing aponeurosis lengthening (Maganaris *et al.*, 1998), while those with MRI performed at low submaximal levels produce much smaller pennation angle changes and thus may favor some regional aponeurosis shortening. Thus, we have demonstrated that our experimental observations of negative aponeurosis strains are theoretically possible and explainable. Furthermore, we suggest that such observations are entirely compatible with ultrasound measurements which measure strain over larger regions of the aponeurosis and thus average out the regional variations that we have observed using finer resolution measurements.

It is widely accepted that the distance between aponeuroses in a contracting muscle remains constant, even though muscle fiber force is exerted in a way that may be expected to bring

them closer together (reviewed in Otten, 1988). One way to meet this condition in models has been to apply a constraint which forbids such movement of the aponeurosis (Zajac, 1989). Our models achieve the similar effect without such constraints. Active muscle fibers exert a force along their axis which tends to pull the aponeuroses together, and this is balanced in part by the hydrostatic pressure generated due to incompressibility in the muscle matrix. The material incompressibility also forces the muscle to deform in shear and thus prevent aponeurosis horizontal movement. Our results thus also provide a mechanical explanation for the maintenance of a relatively constant aponeurosis separation and further present the possibility that the precise mechanics of aponeurosis separation may depend upon fiber pennation angle. An additional influence upon aponeurosis separation seems to be the level of activation of the muscle (Fig. 8). Here we see an initial increase of aponeurosis separation with increasing activation of the 25° case followed by a reduction in aponeurosis separation at higher levels of activation. This observation provides a glimpse of the complex environment of a muscle contraction where there is a constant interplay between altered loading and tissue deformation. In this case, loading increases the pennation angle of the muscle fibers, thus transitioning from the properties of a muscle with a low pennation angle to those of a muscle with a higher pennation angle.

The heterogeneous strain along the aponeuroses in Fig. 6, despite a constant fiber pennation angle along its length, can be explained by a change in the regional mix of aponeurosis and muscle materials as well as the boundary and geometry effects. These findings suggest that even simple models of muscle, composed of homogenous contractile and passive materials, may exhibit complex mechanical responses to contraction.

In conclusion, we demonstrate a possible explanation for the observation that some regions of aponeuroses compress during an isometric contraction and suggest that this phenomenon is dependent upon the pennation angle of the muscle fibers. Our model also predicts that aponeurosis separation may change slightly during a contraction and that the direction of this change may also vary with pennation angle. Finally, these findings suggest that the mechanical properties of aponeuroses in intact muscle may be modified by the mechanical properties of adjacent muscle materials, thus suggesting caution when attempting to infer aponeurosis mechanical properties from measures of aponeurosis strain in intact muscles.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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Fig. 1.
(a) Tendon force-displacement relationship. (b) Normalized Fiber Force-Length Properties. The activation level, a , is assumed to be one in this figure. The vertical dotted line shows the starting point and the shaded band indicates the range of fiber length change over which the model operates.

Fig. 2. Simplified muscle-tendon model and FE mesh

Two models were tested. The fibers were arranged at a pennation angle of 47° in (a) and at a pennation angle of 25° in (b). The fiber lengths of the two models were 4.375 and 7.572 cm respectively. The muscle thickness was set at 3 cm, giving PCSAs of 21.94 and 12.679 cm² respectively. Volumes were identical. (c) **Convergence study on the FE mesh.** The load-displacement curves indicate that the meshes with 1360 elements are sufficient to obtain reliable numerical solutions.

Fig. 3. Deformed geometries and maximum principal strain contours of muscle-tendon assemblies with different pennation angles and lateral constraints under isometric contraction
The maximum principal strain defines the maximum strain in each element regardless of orientation. (a) and (b) illustrate simulations of muscles with fibers at pennation angles of 47° and 25° when the muscles were allowed to move freely between the fixation points at the ends of the tendons. (c) and (d) illustrate similar simulations but under conditions where the aponeuroses were only allowed to move parallel to the vertical axis.

Fig. 4. Displacement (a) and strain distributions (b) along the tendon and aponeurosis of muscle-tendon assemblies with different pennation angles under isometric contraction

Fig. 5. Deformed shapes and maximum principal strains at two stages

(a) activation of the muscle without constraints, and (b) condition (a) followed by the two ends of the tendons pulled to their original positions

Fig. 6. Strain distribution along the tendon-aponeurosis axis at two stages of deformations
 The red line indicates the strain following stage 1, when the muscles were activated and allowed to shorten without load. The blue line indicates the strains when the ends of the tendons were forcibly returned to their starting positions with the muscle still active. The black dashed line plots the difference between the blue and red curves, thus isolating the contribution of the isometric loading to aponeurosis strain.

Fig. 7. Muscle length and width changes of muscle-tendon assemblies with different pennation angles under isometric contraction.

Fig. 8.
Separation of aponeurosis at the middle and bottom of muscle.

Fig. 9. Transformations of strain and Mohr's Circle

(a) Strains in reference coordinate, (b) Strains in fiber direction due to shortening of the actively contracting muscle ($-\epsilon_y$) and strains induced by Poisson effect in the direction perpendicular to the fiber (ϵ_x) for 25° and 47° pennation angle cases, (c) the strains transformed (rotated) to the aponeurosis axis. The fiber pennation angle determines the sign of strain along the aponeurosis axis. For the 25° pennation angle case, the rotated strain in the aponeurosis axis is negative, while it is positive for the 47° pennation angle case.

Table 1

Material Constants for Muscle Matrix

C_{10} (N/cm ²)	C_{01} (N/cm ²)	C_{20} (N/cm ²)	C_{11} (N/cm ²)	C_{02} (N/cm ²)	K (N/cm ²)
6.43	-3.80	0.94	-0.0043	0.0005	5×10^3

Table 2

Material Constants for Tendon and Aponeurosis

G_{10} (N/cm ²)	G_{20} (N/cm ²)	G_{30} (N/cm ²)	K (N/cm ²)
30	80	800	5×10^3