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A Micromechanical Model of Skeletal Muscle to Explore the Effects of Fiber and Fascicle Geometry

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Abstract

Computational models of muscle generally lump the material properties of connective tissue, muscle fibers, and muscle fascicles together into one constitutive relationship that assumes a transversely isotropic microstructure. These models do not take into account how variations in the microstructure of muscle affect its macroscopic material properties. The goal of this work was to develop micromechanical models of muscle to determine the effects of variations in muscle microstructure on the macroscopic constitutive behavior. We created micromechanical models at the fiber and fascicle levels based on histological cross-sections of two rabbit muscles, the rectus femoris (RF) and the soleus, to determine the effects of microstructure geometry (fiber and fascicle shapes) on the along-fiber shear modulus of muscle. The two fiber-level models predicted similar macroscopic shear moduli (within 13.5% difference); however, the two fascicle-level models predicted very different macroscopic shear moduli (up to 161% difference). We also used the micromechanical models to test the assumption that the macroscopic properties of muscle are transversely isotropic about the fiber (or fascicle) direction. The fiber-level models exhibited behavior consistent with the transverse isotropy assumption; however, the fascicle-level models exhibited transversely anisotropic behavior. Micromechanical models, combined with fiber and fiber bundle mechanical experiments, are needed to understand how normal or pathological variations in microstructure give rise to the observed macroscopic behavior of muscle.

Keywords

muscle mechanics; micromechanical modeling; homogenization; muscle microstructure; transverse isotropy; fascicle and fiber geometry

1. Introduction

Skeletal muscle has a complex hierarchical structure. Muscle fibers are surrounded by connective tissue (endomysium) and are arranged into fascicles. Fascicles are also

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surrounded by connective tissue (perimysium). Several studies have shown that the shapes and geometrical arrangements of muscle fibers, fascicles, and connective tissues vary significantly across muscles (Purslow, 2002) and are often altered by disease (Briguet et al., 2004; Lieber et al., 2003). However, the effects of these variations on the macroscopic properties of muscles are not well understood.

Computational models of muscle generally lump the material properties of connective tissues, muscle fibers, and muscle fascicles together into one constitutive relationship that assumes a transversely isotropic microstructure (e.g. Johansson et al., 2000; Lemos et al., 2004). These constitutive relationships ignore the effects of the hierarchical nature of muscle structure and therefore cannot be used to examine the effects of variations in microstructure geometry.

Which aspects of the constitutive properties are affected by microstructure geometry? The along-fiber tensile properties of muscle can be predicted based on the volume fractions of fibers, fascicles, and connective tissues. However, the along-fiber shear modulus is additionally dependent on the cross-sectional shapes of the fibers and fascicles. The along-fiber shear modulus is a measure of the tissue's resistance to shear deformation along the fiber direction and plays an important role in lateral force transfer between neighboring fibers and the generation of muscle force (Huijing 1999a, Purslow 2002). To capture the dependence of the along-fiber shear modulus on microstructure geometry, a micromechanical model that explicitly represents the shapes and arrangements of fibers and fascicles is needed.

The goal of this work was to employ micromechanical modeling tools to uncover the effects of variations in muscle microstructure on macroscopic constitutive behavior. Specifically, we (i) developed a micromechanical modeling framework for skeletal muscle, (ii) created micromechanical models to determine the effects of microstructure geometry (fiber and fascicle cross-sectional shapes) on the along-fiber shear modulus of muscle, and (iii) used the micromechanical models to test the assumption that the macroscopic properties of muscle are transversely isotropic about the fiber direction. Our modeling framework makes use of the concepts of repeating unit cells (RUCs) and periodic boundary conditions (Drago and Pindera, 2007) in order to derive the macroscopic shear modulus of muscle from a finite element (FE) model of muscle microstructure. We created RUC meshes of muscle at the fiber and the fascicle levels from histological cross-sections of two rabbit muscles (the soleus and the RF). We performed FE simulations over a range of fiber, fascicle and connective tissue properties and determined the effects of microstructure geometry on the macroscopic shear modulus of the tissue.

2. Methods

Overview of the micromechanical modeling approach

We employed the concept of an RUC and periodic boundary conditions (Drago and Pindera, 2007) to derive the macroscopic along-fiber shear modulus from an FE model of the microstructure. The assumption behind this concept is that the composite material (in this case muscle) is spatially periodic. The material can be thought of as the many repetitions of a periodic unit cell that remains periodic while deforming. The macroscopic stress and deformation tensors at a particular point in the tissue are the averages of stress and deformation over the volume of the RUC (Drago and Pindera, 2007; Smit et al., 1998). These assumptions are consistent with the asymptotic expansion homogenization theory that was initially derived for linear materials and infinitesimal strains (Hollister and Kikuchi, 1992) and expanded to apply to finite strain analysis (Ohno et al., 2002; Takano et al., 2000).

Creation of RUC models from histological cross-sections

Samples were obtained from rabbit RF and soleus muscles, in accordance with a protocol approved by the Animal Care and Use Committee at the University of Virginia. Samples were fixed in formalin, sectioned, and stained with Hematoxylin and Eosin for characterization of fiber and fascicle morphology. For each cross-section, we obtained a rectangular image at 20× magnification that contained several fibers and an image at 10× magnification that contained several fascicles. Each of these images was the foundation of an RUC. To create the RUCs, we outlined the fiber and fascicle boundaries using a series of line segments (Fig. 1). The edges of each image were then manipulated in order to provide a periodic geometry, while leaving the original geometry as unchanged as possible. Hexahedral meshes were created based on these outlines in Ansys 11 (Ansys, Inc. Canonsburg, PA) (Fig. 2). The meshes were one element thick in the direction out of the plane.

Definition of the constitutive model used in the models

We used a hyperelastic, nearly incompressible, transversely isotropic constitutive model to represent the behavior of the fibers in the fiber-level RUCs, the fascicles in the fascicle-level RUCs, and the connective tissues in all models. This constitutive model uses an uncoupled form of the strain energy to simulate the nearly incompressible behavior of muscle tissue. This uncoupled form additively separates the dilatational and deviatoric responses of the tissue, giving rise to the following strain energy function (W) (Blemker et al., 2005):

$$W(\lambda, \psi, \beta, J) = W_\lambda(\lambda) + W_\psi(\psi) + W_\beta(\beta) + W_J(J), \quad (2.1)$$

where λ is the along-fiber stretch, ψ is along-fiber shear, β is cross-fiber shear, and J is the relative change in volume. The “fiber” direction in the constitutive model is the axis of transverse isotropy for muscle fibers, fascicles, and connective tissues, which we have assumed is collinear with the direction of muscle fibers and fascicles for all these tissues. We have adopted the following functional forms for W_ψ , W_β , and W_J :

$$W_\psi = G_\psi \psi^2, \quad W_\beta = G_\beta \beta^2, \quad W_J = \frac{K}{2} \ln J^2, \quad (2.2)$$

where G_ψ is the along-fiber shear modulus, G_β is the cross-fiber shear modulus, and K is the bulk modulus. $W_\lambda(\lambda)$ is represented by a piecewise exponential (Blemker et al., 2005).

Measurements do not currently exist for the shear moduli of fibers, fascicles, or connective tissues and these values likely vary across muscles. Therefore, we ran simulations over a large range of fiber shear moduli (G_ψ^{fiber}), fascicle shear moduli (G_ψ^{fascicle}), endomysium shear moduli (G_ψ^{endo}), and perimysium shear moduli (G_ψ^{peri}).

Description of the boundary conditions

The periodicity assumption of our approach necessitates that opposite boundaries of the RUC (faces 1+ and 1-, 2+ and 2-, 3+ and 3- in Fig. 3A) be compatible (Smit et al., 1998). Displacement boundary conditions were defined such that the shapes of opposite faces of the RUC remain periodic while the average deformation of the RUC is equal to $\mathbf{F}^{\text{macro}}$, a given macroscopic deformation. These boundary conditions can be formulated as follows:

$$\mathbf{x}(\mathbf{X}_0 + \mathbf{d}) = \mathbf{x}(\mathbf{X}_0) + \mathbf{F}^{\text{macro}} \bullet \mathbf{d}, \quad (2.3)$$

where $\mathbf{X}_0$ and $\mathbf{X}_0 + \mathbf{d}$ are the initial positions of two mirror points on two opposite faces of the unit cell, whose coordinates in the final configuration are $\mathbf{x}(\mathbf{X}_0)$ and $\mathbf{x}(\mathbf{X}_0 + \mathbf{d})$ (Appendix 1).

In order to test the validity of the transverse-isotropy assumption, we analyzed the along-fiber shear behavior of the RUCs in both the 2-3 and 1-3 planes, where direction 3 (Figs. 1-3 and 5) is the direction of muscle fibers (and fascicles). If the along-fiber shear moduli determined from these two analyses are the same, then we conclude that the transverse isotropy assumption is valid; if not, then the transverse isotropy assumption is invalid.

For along-fiber simple shear in the 2-3 and 1-3 planes (Fig. 3A and B):

$$\mathbf{F}_{2-3}^{\text{macro}} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & k & 1 \end{bmatrix} \text{ and } \mathbf{F}_{1-3}^{\text{macro}} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ -k & 0 & 1 \end{bmatrix}, \quad (2.4)$$

where k is the tangent of the shear angle (Fig. 3).

Substituting (2.4) into (2.3) produces the appropriate boundary conditions for 2-3 and 1-3 shear respectively:

$$u_3^{(\text{face}^{2+})} = u_3^{(\text{face}^{2-})} + kl_2 \text{ and } u_3^{(\text{face}^{1+})} + kl_1 = u_3^{(\text{face}^{1-})}, \quad (2.5)$$

where $u_i^{(\text{face}^{j+/-})}$ are displacements of points on the j^{th} face along the i^{th} direction, and l_i is the length of the RUC along the i^{th} direction (Fig. 3). All other displacements were constrained to be equal to each other on opposite boundaries of the RUC. One point (point P in Fig. 3) was constrained to zero displacements in all directions to adequately constrain the model. The boundary conditions described here were implemented in the nonlinear FE solver, NIKE3D (Puso, 2006).

The periodic boundary conditions further require that the traction forces on mirror points on two opposite boundaries of the RUC be equal and opposite (Drago and Pindera, 2007; Smit et al., 1998). This condition holds, as the constraint forces applied to enforce the periodic displacement conditions are equal and opposite for each two mirror points, giving rise to periodic tractions.

Determination of the macroscopic along-fiber shear properties

For each of the simulations, the volume average of stress, $\sigma_{\text{RUC}}^{\text{ave}}$ was calculated as

$$\sigma_{\text{RUC}}^{\text{ave}} = \left(\sum_i \sigma^{(i)} V_i \right) / \left(\sum_i V_i \right), \text{ where } V_i \text{ is the volume of the } i^{\text{th}} \text{ element and } \sigma^{(i)} \text{ is the (local microscopic) stress value for the } i^{\text{th}} \text{ element. These calculations were performed using the post-processing software, Postview (Musculoskeletal Research Laboratories, Salt Lake City, UT). We then determined the macroscopic along-fiber shear moduli in the 2-3 and 1-3 planes (} G_{23}^{\text{macro}} \text{ and } G_{13}^{\text{macro}}, \text{ respectively):}$$

$$G_{23}^{\text{macro}} = \frac{\sigma_{23}^{\text{ave}}}{2k} \text{ and } G_{13}^{\text{macro}} = \frac{\sigma_{13}^{\text{ave}}}{2k}, \quad (2.6)$$

where σ_{i3}^{ave} is the $i3$ component of the average stress in the RUC (Appendix 2). In order to test the assumption of transverse isotropy, we compared G_{23}^{macro} and G_{13}^{macro} . If the assumption of transverse isotropy were valid, our simulations would predict $G_{23}^{\text{macro}} = G_{13}^{\text{macro}}$.

Analyses

Each repeating unit cell was subjected to boundary conditions described in equations (2.5) and macroscopic shear moduli were calculated for the 2-3 and 1-3 planes, respectively. In what follows, the macroscopic shear modulus G_{i3}^{macro} , $i=1,2$, can be thought of as the shear modulus of a bundle of fibers in the context of the fiber-level models (fiber-level macroscopic shear modulus), and the shear modulus of a bundle of fascicles in the context of the fascicle-level models (fascicle-level macroscopic shear modulus). Measurements for the shear moduli of fibers, fascicles, perimysium, and endomysium are nonexistent. Moreover, endomysium and perimysium are known to have different compositions and structures (Purslow, 2002) and likely have different shear moduli. We therefore ran a number of simulations where we changed the fiber and fascicle shear moduli, G_{ψ}^{fiber} and $G_{\psi}^{\text{fascicle}}$, and the connective tissue shear moduli, G_{ψ}^{endo} and G_{ψ}^{peri} , up to several orders of magnitude. We found that for different values of G_{ψ}^{fiber} and G_{ψ}^{endo} (or $G_{\psi}^{\text{fascicle}}$ and G_{ψ}^{peri}), but the same ratios of $G_{\psi}^{\text{fiber}}/G_{\psi}^{\text{endo}}$ (or $G_{\psi}^{\text{fascicle}}/G_{\psi}^{\text{peri}}$), the strain distributions remain constant for a given macroscopic shear deformation $\mathbf{F}^{\text{macro}}$. Moreover, the ratio of the macroscopic shear modulus to connective tissue shear modulus, $G_{i3,i=1,2}^{\text{macro}}/G_{\psi}^{\text{endo}}$ (or $G_{i3,i=1,2}^{\text{macro}}/G_{\psi}^{\text{peri}}$) stays constant. This finding allows us to present our results by normalizing both the fiber (or fascicle) modulus and the macroscopic modulus by the connective tissue shear modulus, G_{ψ}^{endo} (or G_{ψ}^{peri}). This normalization simplifies the presentation of our results as it eliminates the need for three dimensional plots of the fiber-level (or fascicle-level) macroscopic shear modulus against the fiber (or fascicle) shear modulus, G_{ψ}^{fiber} (or $G_{\psi}^{\text{fascicle}}$), and the connective tissue shear modulus, G_{ψ}^{endo} (or G_{ψ}^{peri}). We analyzed the relationship between the ratio of the macroscopic shear modulus to the connective tissue shear modulus, $G_{i3,i=1,2}^{\text{macro}}/G_{\psi}^{\text{endo}}$ (or $G_{i3,i=1,2}^{\text{macro}}/G_{\psi}^{\text{peri}}$), and the ratio of fiber (or fascicle) shear modulus to connective tissue shear modulus, $G_{\psi}^{\text{fiber}}/G_{\psi}^{\text{endo}}$ (or $G_{\psi}^{\text{fascicle}}/G_{\psi}^{\text{peri}}$). For these analyses, the ratio of fiber (and fascicle) shear modulus to connective tissue shear modulus, $G_{\psi}^{\text{fiber}}/G_{\psi}^{\text{endo}}$ (and $G_{\psi}^{\text{fascicle}}/G_{\psi}^{\text{peri}}$), was varied between 0.1 and 500. This was done for shear in the 2-3 and 1-3 planes for RF and soleus fiber-level and fascicle-level models (Fig. 4A-D).

3. Results

For all analyses, the shapes of the normalized macroscopic shear modulus relationships were similar (Fig. 4). For a given connective tissue shear modulus, the macroscopic shear modulus first increased monotonically with increasing fiber (or fascicle) shear modulus but gradually plateaued. In the plateau region, as $G_{\psi}^{\text{fiber}}/G_{\psi}^{\text{endo}}$ (or $G_{\psi}^{\text{fascicle}}/G_{\psi}^{\text{peri}}$) increased,

$G_{i3,i=1,2}^{\text{macro}}/G_{\psi}^{\text{endo}}$ (or $G_{i3,i=1,2}^{\text{macro}}/G_{\psi}^{\text{peri}}$) remained relatively constant. Moreover, the macroscopic shear moduli are close to one another for all models for values of $G_{\psi}^{\text{fiber}}/G_{\psi}^{\text{endo}}$ (or $G_{\psi}^{\text{fascicle}}/G_{\psi}^{\text{peri}}$) smaller than one or close to one, but the differences become pronounced as these ratios increase, so that for ratios considered for this analysis the maximum differences occurred at $G_{\psi}^{\text{fiber}}/G_{\psi}^{\text{endo}}$ (or $G_{\psi}^{\text{fascicle}}/G_{\psi}^{\text{peri}}$)=500.

The macroscopic shear moduli at the fiber level were similar for both muscles and for both the 2-3 and 1-3 planes (Fig. 4A and B). In the 2-3 plane, the difference between the soleus and the RF fiber-level models was 13% for $G_{\psi}^{\text{fiber}}/G_{\psi}^{\text{endo}}$ =500; in the 1-3 plane, this difference was less than 1%.

By contrast, the macroscopic shear moduli at the fascicle level showed large variations between muscles and between the 1-3 and 2-3 planes. In the 2-3 plane, the macroscopic shear modulus of the RF fascicle-level model was 161% higher than that of the soleus fascicle-level model for $G_{\psi}^{\text{fascicle}}/G_{\psi}^{\text{peri}}$ =500 (Fig. 4C); in the 1-3 plane, the soleus fascicle-level model had a 57% higher shear modulus than the RF fascicle-level model for $G_{\psi}^{\text{fascicle}}/G_{\psi}^{\text{peri}}$ =500 (Fig. 4D). The distributions of shear strain at the fascicle level were also highly variable between muscles and between the 1-3 and 2-3 planes.

4. Discussion

The purpose of this work was to develop micromechanical models of muscle to explore the effect of microstructure geometry on the macroscopic along-fiber shear modulus of muscle. We studied fiber and fascicle geometries of the rabbit RF and soleus muscles. We created models of the fiber and fascicle geometries of each muscle. Similarity of fiber shapes between the two muscles resulted in similar fiber-level macroscopic shear moduli. We observed a greater variation between fascicle shapes, which resulted in larger differences in the fascicle-level macroscopic shear moduli. The fascicle-level models, unlike the fiber-level models, demonstrated significant transverse anisotropy in shear. This result is consistent with the observation that fascicle cross-sections, unlike fibers, appear highly anisotropic. Our results challenge the assumption of transverse isotropy implicit in most FE models of muscle (Blemker et al., 2005; Johansson et al., 2000; Lemos et al., 2004; Oomens et al., 2003).

The examination of fascicle strains in the fascicle-level models revealed that, if the fascicle shear modulus is higher than that of the perimysium (Fig. 5 and Table 1), lower fascicle strains correspond to lower macroscopic shear moduli. Lower fascicle strains translate to higher shear strains within the perimysium. Therefore, in general, fascicle geometries that allow most of the shear deformation in a given plane of shear to be concentrated within the perimysium have the lowest shear modulus in that plane (soleus fascicles in the 2-3 plane) and the highest shear modulus in the transverse plane orthogonal to it (soleus fascicles in the 1-3 plane). We hypothesize that the variation of fascicle geometry across muscles may therefore be due to each muscle's need to accommodate greater or lesser shear deformation in a given plane, which is dependent on the muscle's macroscopic architecture (e.g. Blemker et al., 2005; Purslow, 2002). Our hypothesis would indicate that muscles that must undergo large amounts of shear strain due to their macroscopic architecture would have fascicle microstructures that accommodate those shear deformations.

Which aspects of the fascicle microstructures gave rise to differences in the predicted macroscopic shear moduli and shear strains between the two muscles? The key differences

between the RF and soleus fascicle microstructures include: (i) the relative thickness of perimysium concentrated in each direction, (ii) the staggering of the fascicles with respect to one another, and (iii) the elongation of fascicles in a given direction. To examine the potential effects of differences in perimysium thickness, we calculated the relative thickness of perimysium in each direction for each of the fascicle RUCs. This calculation was made by measuring the width of each fascicle and the thickness of its surrounding connective tissue, where the measurements were taken along directions 1 and 2 passing through the centroid of each fascicle (shown for a soleus fascicle in Fig. 6). Based on these measurements, we calculated the ratio of the thickness of perimysium along each direction to the width of the fascicle in that direction and averaged this ratio across all fascicles for both the soleus and the RF fascicles. For the soleus this ratio was greater in direction 2 (0.1220) than in direction 1 (0.0672). For the RF, the ratios were more similar to each other, but also greater in direction 2 (0.0648) than in direction 1 (0.0492). This observation is consistent with our result that both muscles have a lower fascicle-level macroscopic shear modulus in the 2-3 plane. The relative thickness is predictive of transverse anisotropy in shear; however it does not adequately explain the differences between the shear moduli of the two muscles. If the relative thickness alone were a predictive measure, then the RF fascicle-level shear modulus would be higher than the soleus in the 1-3 plane.

The staggering or offset of fascicles with respect to one another prevents the layers of perimysium from being aligned (Fig. 6) in a way that allows for shear strain to be relieved through the perimysium. Qualitatively (Figs. 1-2 and 6), we observed that the perimysium layers in the soleus are aligned in direction 1, which indicates shear in the 2-3 plane can easily be relieved through the perimysium, resulting in a lower G_{23}^{macro} . Elongation of fascicles in a given direction influences the extent of staggering between fascicles. As a result, the direction in which fascicles are more elongated corresponds to the direction of highest shear modulus. Both fascicle geometries, especially the soleus, are more elongated in direction 1, and both muscles, especially the soleus, have higher shear moduli in the 1-3 plane compared to the 2-3 plane.

While the qualitative assessments of microstructure given above provide general insight into how the differences in geometry gave rise to the observed differences in macroscopic shear moduli, at this point we cannot generalize these findings to other muscles. In order to generalize these results, it would be necessary to create models of fascicle cross-sections from a large number of muscles. Based on this type of analysis, concrete metrics of the microstructure could be established and used to predict how muscle tissue properties vary across muscles. Similarly, the metrics could be further expanded to predict how pathological alterations in fascicle microstructure affect macroscopic muscle properties.

The micromechanical models presented here can be used to derive a macro-scale constitutive model for muscle from the geometry and properties of the microstructure. To this end new experimental techniques must be developed that enable measurements of the shear moduli of fibers and fascicles, in both active and passive conditions. Since these data are currently lacking, we performed simulations over a large range of fiber, fascicle, and connective tissue shear moduli. It has been observed that shear strains are largely concentrated within the perimysium when rigor muscle is subjected to shear (Purslow, 2002). This observation suggests that in fully activated muscles, fascicles are much stiffer

than the perimysium ($G_{\psi}^{\text{fascicle}}/G_{\psi}^{\text{peri}} \gg 1$). This relationship may not hold for passive or partially activated muscle (i.e., the fascicle modulus might be the similar or less than the perimysium modulus under these conditions). In this case, the macroscopic shear moduli would be similar between the muscles and nearly transversely isotropic due to the fact that $G_{\psi}^{\text{macro}}/G_{\psi}^{\text{peri}}$ is similar between the muscles for $0 < G_{\psi}^{\text{fascicle}}/G_{\psi}^{\text{peri}} \leq 1$.

The models presented here provide a new paradigm for relating muscle microstructure to muscle function. In this study we focused on investigating variations in muscle microstructure in healthy muscle. This framework can also be used to study how pathological changes in muscle microstructure (e.g. Gosselin et al., 1998; Haus et al., 2007; Morgan et al., 1990) affect macroscopic properties.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1. Histological cross-sections taken from rabbit soleus and rectus femoris muscles. The rectus femoris and the soleus fibers (A and B) have similar shapes, while the rectus femoris and soleus fascicles have significantly different shapes (C and D).

Figure 2. Repeating unit cell (RUC) models created from the histological cross-sections. We created meshes of repeating unit cells for the fiber geometries of the rectus femoris (A) and soleus (B), as well as fascicle geometries of the rectus femoris (C) and soleus fascicle (D).

Figure 3. A repeating unit cell undergoing simple shear in the 2-3 plane (A) and in 1-3 plane (B). Fiber direction and the direction of the shear are both direction 3 in both (A) and (B).

Figure 4.

Macroscopic shear modulus derived from RUC models, plotted as a function of the fiber shear modulus for fiber-level models (A and B) and fascicle shear modulus for fascicle-level models (C and D). Both axes in each plot are normalized by the connective tissue shear modulus (endomysium for the fiber-level models (A and B) and perimysium for fascicle-level models (C and D)).

Figure 5.

The distribution of Green-Lagrange shear strains for the rectus femoris fascicles in 2-3 shear (A) and 1-3 shear (B), for the soleus fascicles in 2-3 shear (C) and 1-3 shear (D). These strain contour plots correspond to a ratio of 75 for the fascicle shear modulus to perimysium shear modulus and were obtained for a shear value of $k = 1$ (equations 2.4), corresponding to average Green-Lagrange strain components for the whole RUC of $E_{23} = 0.5$ and $E_{13} = 0.5$. The range of values of shear strains is only shown for fascicles in this figure. Shear strains are higher within the perimysium (Table 1).

Figure 6.

Geometric factors that affect the shear modulus, shown here for soleus fascicles. (i) In order to obtain an approximate measure of the relative thickness of perimysium concentrated in each direction, we calculated the area centroid of each fascicle (shown for one fascicle as point P) and drew lines passing through the centroid in directions 1 and 2 respectively. For example in direction 2 the relative ratio is calculated as $(d+w)/h$. If the fascicles are stiffer than the perimysium, a higher ratio of $(d+w)/h$, translates to a lower shear modulus in the 2-3 plane. We calculated this ratio for all fascicles in both fascicle models and in both directions. Furthermore the alignment of the perimysium layers is pointed out. In direction 1, unlike direction 2, layers of perimysium are highly aligned (minimal staggering), which points to a higher shear modulus in 1-3 plane.

Table 1
Average fascicle and perimysium strains for each model shown in Fig. 5*

		average shear strain in the 2-3 plane (E_{23})	average shear strain in the 1-3 plane (E_{13})
rectus femoris fascicle model	fascicle strain	0.11	-0.19
	perimysium strain	5.02	-4.09
soleus fascicle model	fascicle strain	0.05	-0.26
	perimysium strain	2.88	-1.72

* The values shown correspond to RUC models with modulus ratios of $G_{\psi}^{fascicle} / G_{\psi}^{peri} = 75$, where the applied shear value is $k = 1$ (equations 2.4). This applied shear value corresponds to average Green-Lagrange strain components for the whole RUC of $E_{13} = 0.5$ and $E_{23} = 0.5$.