Mapping of movement in the isometrically contracting human soleus muscle reveals details of its structural and functional complexity

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Finni, Taija, John A. Hodgson, Alex M. Lai, V. Reggie Edgerton, and Shantanu Sinha. Mapping of movement in the isometrically contracting human soleus muscle reveals details of its structural and functional complexity. J Appl Physiol 95: 2128–2133, 2003. First published July 11, 2003; 10.1152/japplphysiol.00596.2003.—It is becoming increasingly apparent that precise knowledge of the anatomic features of muscle, aponeurosis, and tendons is necessary for understanding how a muscle-tendon complex generates force and accomplishes length changes. This report presents both anatomic and functional data from the human soleus muscle acquired by using magnetic resonance imaging. The results show a strong relationship between the complex three-dimensional structure of the muscle-tendon system and the intramuscular distribution of tissue velocities during in vivo isometric contractions. The proximal region of the muscle is unipennate, whereas the midregion has a radially bipennate hemicylindrical structure, and the distal region is quadrupennate. Tissue velocity mapping shows that the highest velocity regions overlay the aponeuroses connected to the Achilles tendon. These are located on the anterior and posterior surfaces of the muscle. The lowest velocities overlap the aponeuroses connected to the origin of the muscle and are generally located intramuscularly.

MATERIALS AND METHODS

Anatomic and functional MR images were acquired from 11 volunteers (4 women, 7 men; 28 ± 6 yr, 75 ± 13 kg, 173 ± 8 cm). Subjects signed an informed consent approved by the University of California-Los Angeles Institutional Review Board. Detailed anatomic images were taken from the lower leg with the subject relaxed. The functional images were then acquired during isometric contractions at 20 and 40% of a maximal voluntary contraction. During the measurements, the ankle joint of the subject was immobilized at an angle of 90° with a posterior half of a fiberglass cast. A strain gauge (Fabry-Perot interferometer, Fiberscan 2000, Luna Innovations) was embedded in the sole of the cast to measure the level of plantarflexion torque.

The anatomic images were acquired in the axial plane by using proton density fast spin echo sequence with a slice thickness of 7 mm and slice spacing of 8.5 mm. These images were used for three-dimensional volume renderings of major connective tissues in the triceps surae (Vitrea 2 image processing workstation, Vital Images, Minneapolis, MN). The velocity of the tissues during isometric contractions was acquired separately by using cine phase-contrast (PC) MR imaging (4) with a field of view of 32 cm and pixel resolution of 1.25 mm. In this method, the velocity of protons is quantified by means of the phase dispersion that they generate. This procedure also provides corresponding anatomic images, showing the position of the limb at each time interval of the cine sequence (≈75 ms). During the PC-MR acquisition,
the subjects were required to perform ~70 isometric contraction-relaxation cycles 40 times/min timed to an audio cue. The initial rise in torque in each contraction cycle was programmed to trigger the MR acquisition. The velocity images were processed by using in-house software (LabView IMAQ environment, National Instruments). Validation and calibration of these procedures have been described previously (5).

Sagittal PC-MR images were taken at a similar mediolateral location from all subjects. Two overlapping images were required to reconstruct the entire Achilles tendon-soleus muscle complex by using the 32-cm field of view. In the first slice, the calcaneus was visible, and in the second slice the origin of the soleus was visible. In addition, PC-MR images were taken from several sagittal and axial sections from two subjects and from a coronal section from one subject to confirm and complete the functional map of the soleus muscle. The anatomic images were also taken from overlapping locations along the length of the leg. The excursion of the ankle due to the design of our apparatus in these isometric contractions was measured from the PC-MR images and was on average 3 and 5 mm in 20 and 40% contractions, respectively.

RESULTS

During the attempted isometric contractions, the soleus muscle shortened as the Achilles tendon stretched. The distribution of velocities within the soleus muscle corresponded closely to the structural anatomy of the muscle fibers, aponeuroses, and tendons. There were intersubject variations in the velocity patterns in the selected sagittal slice, but these corresponded with the variations in the anatomy between individuals. Regardless of the individual anatomy, however, the fastest velocities were found in close proximity to the aponeurosis of insertion. The points of insertion of the soleus fibers are located at the distal ends of the pennate tendons. They make contact with an aponeurosis of insertion lying over the posterior surface of the soleus muscle and with a median septum located within the anterior compartment of the muscle (Fig. 1) (11). The points of origin of the soleus fibers are located at the proximal ends of the fibers where they contact the intramuscular aponeurosis separating the anterior and posterior compartments. This corresponds to the anterior aponeurosis described by Chow et al. (3).

The shape and thickness of the tendon-aponeurosis at the most distal end of the soleus muscle varied considerably in a given cross section between and within the individuals. In all subjects, a portion of the posterior aponeurosis protruded anteriorly into the distal soleus muscle. As we have noted previously, the location and shape of the protrusion varied significantly among the subjects studied (see Figs. 8 and 9 in

![Fig. 1.](image-url)

Fig. 1. A: cross-sectional magnetic resonance (MR) images of the leg. The soleus muscle is outlined (thin line), and the location of the aponeurosis of insertion in C is shown (thick lines). The 2 compartments of the soleus are present in the proximal image. B: schematic drawing of the soleus anatomy in an axial plane. Muscle fiber orientation is shown with arrows pointing proximally toward the aponeurosis of origin (gray lines). In the distal image, the median septum migrates anteriorly, and in the proximal muscle it is located in the middle of the anterior compartment of the soleus. C: virtual dissection of the Achilles tendon-aponeurosis complex from the axial MR images in A. The horizontal arrows point to the central tendon that has separated from the posterior aponeurosis. D: schematic drawing of the aponeurosis of insertion illustrating the connection (hatched area) of the central tendon (thick black line) to the posterior aponeurosis in the distal muscle.
The anterior protrusion eventually separated from the posterior aponeurosis and became the median septum as it progressed proximally. This median septum extended throughout the anterior compartment of the soleus muscle (Fig. 1). Thus the median septum is an anterior projection of the Achilles tendon, serving as the tendon of insertion for the muscle fibers of the anterior soleus compartment. The median septum seems to have a continuous connection to the anterior edge of the muscle, but the level of continuity was less obvious in some individuals. The anterior soleus fibers were arranged radially around the median septum. The fiber arrangement was also radial in the superior portion of the posterior soleus (Fig. 1B). These fiber arrangements are based on the three-dimensional structure and velocity map of the entire soleus muscle and were later confirmed from cadavers and a threedimensional reconstruction of the Visible Human Dataset (loaded under license from National Library of Medicine ftp site, available at http://www.nlm.nih.gov/research/visible/visiblehuman.html).

In each cross-sectional image, the highest velocities during an isometric contraction were always found in close proximity to the posterior aponeurosis and median septum, which we now define as an aponeurosis of insertion based on our anatomic and functional observations (Fig. 2). In Fig. 2B, the anatomic landmarks of cortical bones and major aponeurosis structures were extracted from high-resolution MR images taken in the relaxed condition and superimposed onto the velocity image taken at early force rise. Because the shape of the muscles changed during contraction, the anatomic landmarks, especially in the posterior aponeurosis, do not coincide exactly with the highest velocity region. However, the lower-resolution anatomic images acquired simultaneously with the velocity images enabled us to conclude that the high-velocity areas are located at the site of the aponeurosis of insertion.

The same interpretation was made on the basis of the sagittal and coronal PC-MR images. A velocity map of the soleus muscle revealed high velocities, especially in the posterior edge of the muscle, where the posterior aponeurosis lies (Fig. 3). In the anterior border, the velocities were not as consistently high because the orientation of the slice greatly affected the velocity pattern in the sagittal images (see below). Between the high-velocity regions in the mid-muscle lies the aponeurosis of origin that separates the anterior and posterior compartment of the soleus. The aponeurosis of origin had velocities near zero, but sometimes it was observed to move distally during a contraction, presumably because it was stretched during the contraction (Fig. 2B). The velocity profiles across the soleus in both the 20 and 40% maximal voluntary contraction clearly illustrate this phenomenon (Fig. 3E). The posterior aponeurosis and anterior border of the soleus muscle moved proximally, but the mid-muscle moved slightly distally. The velocity gradient between the aponeurosis of origin and insertion reflects the relative sliding of the two aponeuroses and rotation of the muscle fibers during contraction. The schematic drawing in Fig. 3F illustrates aponeurosis movement and fiber orientation. If the aponeurosis of origin is considered to be fixed at its proximal end, the distal movement along the length of the structure suggests some strain during contraction. However, determination of the magnitude and possible nonuniformity of the strain in the aponeurosis of origin requires further measurements with different slice positioning and orientations.

The velocities in the posterior aponeurosis of the soleus insertion displayed some nonuniformity along the length of the soleus muscle (Fig. 3, C and D). In these panels, a single time point at the beginning of the contraction is represented. Similar relationships occurred at all time points. Regions of higher and lower velocities can be seen along the length of the posterior aponeurosis. These differential velocities parallel our
earlier observations of nonuniform movement and strain in the soleus aponeurosis during isometric contractions (5). We have suggested that these nonuniformities could be due to the presence of active and passive motor units along the length of the muscle or due to the influence of the median septum transferring strain from the anterior compartment to the posterior aponeurosis. Elucidation of these, or alternative mechanisms, must await more detailed studies.

The velocity pattern in the sagittal images was dependent on the individual anatomy and the slice location relative to that muscle anatomy. For example, if...

Fig. 3. Cine phase-contrast MR images provide both anatomy (A) and velocity (B) image sequences. These sagittal images (and data in C–E) were taken from the beginning of the contraction during early force rise. In B, the dark and light gray shades represent high velocities in the proximal and distal direction, respectively. Contour velocity maps of the soleus during 20 (C) and 40% (D) MVC further illustrate the velocity distributions and their dependence on load. The negative velocities represent movement proximally. Positive velocities are not shown in these plots for clarity. E: velocity distribution across the soleus muscle taken from midmuscle at the level of the diamond arrows shown in B–D. The midmuscle moves distally, whereas the anterior and posterior edges of the muscle move proximally. F: a simple model of part of the soleus muscle in relaxed and contracted conditions illustrating the relative movement of the aponeuroses (thick arrows) and consequent rotation of the muscle fibers. Rotation of the fibers while the interaponeuroses distance is kept constant results in a smaller change in fiber length (ΔL_f) than in tendon length (ΔL_t). Force vectors placed on the anterior soleus (relaxed scheme) illustrate the idea that longitudinally (F_L) and laterally (F_La) transmitted forces relative to the fiber orientation produce a net force (F_net) in the proximal direction to produce proximal tissue movements that supplement fiber length changes in shortening contractions. Force vectors placed on the posterior soleus show that the intramuscular pressure (F_imp) counteracts the fiber force component (F_f) that would move the aponeuroses closer together.
vertical (sagittal) lines are drawn 1 cm apart through the axial image in Fig. 2, the velocity pattern would be very different in each slice. A slice bisecting the tibia would have low velocities at the anterior border of the soleus coinciding with the origin of the muscle with progressively higher velocities toward the distal aponeurosis. However, a slice bisecting the median septum would have high velocities at the anterior border, a low velocity located near the origin in the midmuscle, and then higher velocities at the posterior aponeurosis (Fig. 2). An anatomic sagittal slice along the length of the leg was rarely oriented along a constant plane relative to the three-dimensional structure of the aponeuroses. Consequently, the effect of slice orientation and location must be taken into account when muscle behavior is compared between individuals, and the slice must be selected specifically for a given study purpose.

The compartmentalization of the soleus into anterior and posterior portions was evident in all subjects. However, instead of a unipennate posterior compartment and a bipennate anterior compartment, a human soleus muscle can contain two bipennate compartments or just one unipennate compartment (13). We hypothesize that the compartmentalization of the soleus reflects fundamental architectural design principles, which enable thousands of very short fibers (~3 cm long) to generate force effectively within a very large muscle (~30 cm long). It is well known that the soleus muscle has short fibers and that these fibers are arranged in a pennate fashion that contributes to a large physiological cross-sectional area and, consequently, to a high maximum force (15). Theoretically, the pennation angle reduces the potential force output of the muscle to the cosine of the total force exerted by the muscle fibers (6). Rotation of fibers during a contraction increases this effect but also suggests a remarkable adaptation, which provides some explanation of how the soleus muscle accomplishes shortening distances of the entire muscle belly that represents a very large proportion of the fiber lengths. Fiber rotation implies an intramuscular force, such as intramuscular pressure, which opposes the inward force component exerted by the muscle fibers so that the aponeuroses of origin and insertion are prevented from moving closer together. The result is a fiber rotation where the proximal movement of the muscle insertion is greater than the shortening of the muscle fibers (Fig. 3F).

Preliminary observations that the aponeurosis of origin moves proximally during shortening contractions under moderate loading suggest that the muscle mechanics are somewhat more complex than present models predict or assume. Lateral force transmission between muscle fibers would provide the net component of force to accomplish such a movement, even where the fibers attach to the aponeurosis of origin (Fig. 3F). Some recent literature has placed considerable emphasis on the lateral force transmission from sarcomeres to the intrafiber matrix in addition to longitudinal force transmission along the muscle fibers (see Refs. 1, 7, 9, 12). Although the details of this lateral force transmission remain poorly understood, it has been clear for many years that there are transverse connections that can bear a significant amount of the active force (14). Tight lateral connections via Z and M lines and connections between muscle fibers via transmembrane proteins can contribute to the apparent uniformity of contraction along the length of the muscle (in regard to the observed velocity pattern) even during very low-level submaximal contractions, where the fibers from active motor units are in contact with passive fibers from other units (2). However, although the lateral force transmission paradigm is consistent with results that the maximum force increases as a function of fiber radius, not fiber length (1), further research efforts need to clarify its significance.

These results demonstrate that the human soleus muscle consists of multiple components that act in parallel but also are highly interactive in their dynamics. These results also demonstrate that the fastest velocities during isometric contraction occur in the region most adjacent to the aponeurosis of insertion and that this velocity contains subtle nonuniformities throughout its length. The heterogeneity in the dynamics is probably due to a combination of an uneven spatial distribution of the motor units that are recruited and the physical structures within the muscle. Certainly, the heterogeneity parallels the three-dimensional structure of the muscle-tendon unit, suggesting that further detailed studies of muscle structure and function are essential to a better understanding of muscle function. The general implication of these observations is that modeling or assuming muscle fiber function within a large composite muscle based on joint motion is insufficient to fully understand the in vivo dynamics of force and velocity of large muscles.

DISCLOSURES

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