

maximal performance in the drop jump for each subject due to methodological limitation, i.e., used load and drop height (the details are discussed below). The other reason was the difference in exercise modes. During running and hopping, the stretch-shortening cycle of muscles is repeated any number of times, while the jumping tests in the present study consisted of a single trial. Therefore, it seems that joint stiffness would be related to performance during repetitive stretch-shortening cycle exercises (i.e., running and hopping) but not to that in a single movement.

Another interesting finding of this study was that there was no significant correlation between tendon stiffness and joint stiffness (Fig. 3). In respect of the mechanical properties of lower limb in sprinters, a group of elite sprinters had a higher leg stiffness during the eccentric phase compared to less skilled sprinters (Mero and Komi 1986). On the contrary, we observed that the tendon structures in knee extensors were more compliant in sprinters than in untrained subjects, and thus tendon stiffness was inversely correlated to sprint time among sprinters (Kubo et al. 2000a). On the other hand, some previous investigators showed that repeated stretch-shortening cycle exercises caused a reduction in joint stiffness, as well as jump performances and maximal voluntary contraction (Kuitunen et al. 2002a). Inversely, our recent study showed that repeated drop jump exercises decreased muscular functions without changing tendon properties (Kubo et al. 2005b). Therefore, it is reasonable to assume that the joint stiffness is related to the properties of muscle (active cross-bridge) but not to tendon properties.

In the present study, the employed load (50% of the body mass) and drop height (20 cm) were decided based on the results of a preliminary experiment. However, to exert maximal power during jumping, the optimal load for each subject should be used according to the force–velocity relationship of muscles (Beker et al. 2001; Stone et al. 2003). In many previous studies using vertical jump tests (e.g., Bosco et al. 1982; Bobbert et al. 1996), the body mass of each subject corresponded to the load. Therefore, we may say that this decision of the load was justified at least for studying inter-subject variability. On the other hand, some previous studies indicated that the optimal drop height during the drop jump differed due to the characteristics of each subject (Asmussen and Bonde-Peterson 1974). Considering this point, there was no conclusive proof that each subject in the present study exerted maximal performance during DJ. In addition, this may have caused the large variability observed in the relationship between pre-stretch augmentation and measured parameters.

Regardless, further investigations are needed to clarify this point.

In addition, the resultant ankle joint torque during jumping should be calculated from not only the vertical ground reaction force and ankle joint but also all three components of ground reaction force, the inertial and gravitational forces. In the present study, however, a simple model was used according to the previous findings (Kawakami et al. 2002; Kubo et al. 2000a, b). In particular, we examined the validity of the simple model for calculating ankle joint torque comparing with data obtained using standard inverse dynamics (Kubo et al. 2000a, b). As a result, the values and pattern of torque development during exercise was similar between the two calculations. Therefore, we considered that the use of a simple model would be valid to elucidate the present purpose.

We must draw the attention to the limitation and assumption of the *in vivo* approach of this study followed. To estimate the tendon force, the moment arm length was estimated from the lower leg length of each subject. According to the previous studies (e.g. Maganaris et al. 1998), however, this assumption was not always true. The moment arm length changes of each subject during the measurement of tendon properties would be necessary for an accurate absolute tendon force determination. In the present study, however, we aimed to study whether the tendon and/or joint stiffness was related to the jump performances. Furthermore, there was any difference in the condition between the jump tests (dynamic) and tendon measurement (static). However, it would be impossible to measure the tendon properties during the dynamic movements, i.e. jump. It appeared that the tendon properties affected the speed of force increase to the maximum. Previously, we confirmed that there were no significant differences in the tendon stiffness values among the contraction times (3, 5 and 10 s) during an increasing force level (Kubo et al. 2002). In future studies, the difference in the tendon properties between the dynamic and static conditions should be tested. Considering these points, the authors considered that this tendon force and stiffness calculations in the present study would be valid to investigate the stiffness and measured variables.

In conclusion, the present results showed that pre-stretch augmentation in both CMJ and DJ was related to tendon stiffness, but not to joint stiffness. Concretely, the greater jump height in CMJ could be explained by both the tendon elasticity and the increased activation level of muscle, whereas tendon elasticity plays a more significant role in the enhancement of jump height during DJ.

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In vivo fascicle behavior of synergistic muscles in concentric and eccentric plantar flexions in humans

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Abstract

Ultrasonography was used to directly measure *in vivo* fascicle behavior of the medial gastrocnemius (MG) and soleus (SOL) muscles while the subjects ($n = 6$ men) performed maximal voluntary concentric and eccentric plantar flexions at 60, 120, 180 and 240 deg/s. Fascicle shortening and lengthening velocities of MG, obtained from fascicle length changes over time, were significantly higher than those of SOL at ± 120 , ± 180 and $+240$ deg/s, possibly reflecting physiological and mechanical differences between these muscles. On the other hand, the effective fascicle shortening and lengthening velocities, defined as the velocities in the longitudinal direction of muscle belly, were not significantly different between MG and SOL. This could be due to difference in fascicle architecture and/or the existence of mechanical linkages between these muscles. Moreover, when the contribution of tendinous tissues to muscle-tendon complex length change was determined from fascicle length, pennation angle, moment arm and joint angle, it accounted for approximately 50% in both concentric and eccentric trials, but showed considerable intra-subject variations. This result quantifiably demonstrates the importance of tendinous tissues in isokinetically controlled joint movements.

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1. Introduction

Plantar flexors make an important contribution to human locomotion and jumping by controlling ankle movement through concentric and eccentric contractions (Fukashiro and Komi, 1987; Fukunaga et al., 2001; Johnson and Buckley, 2001). The gastrocnemius and soleus muscles are the largest synergists among plantar flexors

(Fukunaga et al., 1992), but have different architectural properties such as fascicle length and pennation angles (Kawakami et al., 1998). Moreover, the number of in-series sarcomeres in a gastrocnemius fascicle is larger than that in a soleus fascicle (Wickiewicz et al., 1983; Huijing, 1985; Kawakami et al., 2000). In addition, the soleus muscle is mainly composed of slow-twitch fibers, while the gastrocnemius muscle contains more fast-twitch fibers (Johnson et al., 1973; Saltin and Gollnick, 1983). The larger number of in-series sarcomeres and greater proportion of fast-twitch fibers in the gastrocnemius suggest that the gastrocnemius is designed to develop a higher shortening velocity

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compared to the soleus muscle. It is therefore possible that even in isokinetically controlled plantar flexions performed in many previous studies (e.g. Fugl-Meyer et al., 1979; Wickiewicz et al., 1984; Svantesson et al., 1994; Ferri et al., 2003), fascicle behaviors differed between these muscles. The possibility of inconsistent fascicle behavior of synergistic muscles was pointed out in previous studies that measured fascicle or tendinous tissue length changes during isokinetic joint movement with ultrasonography (Ichinose et al., 2000; Kawakami et al., 2002a). However, a satisfactory quantification and understanding of the differences between synergistic muscles has yet to be performed.

In previous animal studies, it has been shown that fascicles do not necessarily experience the same length changes as that of the muscle–tendon complex, due to the length changes of series elastic components (Hoffer et al., 1989; Griffiths, 1991; Zuurbier and Huijing, 1992). Griffiths (1991) evaluated fascicle length change in the medial gastrocnemius muscle of anesthetized cats by an ultrasound technique that measured the distance between pairs of piezoelectric crystals implanted at each end of a fascicle. It was reported that the fascicle shortened during the stance phase of normal walking while the muscle–tendon complex lengthened. Zuurbier and Huijing (1992) determined the shortening velocities of the fiber, aponeurosis and muscle–tendon complex during isokinetic concentric contraction in the medial gastrocnemius muscle of anesthetized rats by cinematography, and showed that due to substantial aponeurosis shortening velocity, the shortening velocity of the fiber was lower than that of the muscle–tendon complex. *In vivo* human studies using ultrasonography have also shown the importance of tendinous tissues in various types of joint movements (Fukunaga et al., 2001; Kawakami et al., 2002a,b; Kurokawa et al., 2003; Herbert et al., 2002; Reeves and Narici, 2003). Herbert et al. (2002) measured fascicle length changes of medial gastrocnemius and tibialis anterior muscles during passive joint movement, and reported that the medial gastrocnemius and tibialis anterior fascicles contributed 27% and 55% of total length change in muscle–tendon complex, respectively. This result clearly pointed to the fact that the fascicle length change is not equivalent to that of the muscle–tendon complex. Since the tension imposed on tendinous tissues during active muscle contraction is larger than that during passive joint movement, more difference in length change between fascicles and muscle–tendon complex is expected during active muscle contractions. Moreover, the interaction between fascicles and tendinous tissues would have a considerable contribution to the fascicle behavior of the gastrocnemius and soleus muscles, because the Achilles tendon connecting these muscles is the largest tendon in the human body (Mazzone and McCue, 2002), and is much longer than the muscle fascicles themselves (Walmsley and Proske, 1981; Biewener and Roberts, 2000).

In the present study, the fascicle behavior of the medial gastrocnemius (MG) and soleus (SOL) muscles were directly measured *in vivo*. To estimate the length changes

of the muscle–tendon complex, the Achilles tendon moment arm length was also measured for each subject. The purpose of this study was to investigate the fascicle behavior of these synergistic muscles and the contribution of the length change of tendinous tissues to that of the muscle–tendon complex (MTC) in isokinetically concentric and eccentric joint movements. We hypothesized that the fascicle behavior would differ between these synergistic muscles in isokinetic plantar flexions, and that length changes of the tendinous tissues would make an important contribution to isokinetic plantar flexion.

2. Materials and methods

2.1. Subjects

Six healthy males voluntarily participated in the present study. The average (\pm SD) age, height and body mass of the subjects were 32.5 ± 9.4 years, 173.9 ± 4.5 cm and 66.3 ± 7.5 kg, respectively. Before the experiment, subjects were fully informed of the experimental protocol as well as the purpose of the study, and their informed consent to participate in the experiment was obtained. This study was approved by the ethical review board of Waseda University.

2.2. Experimental set-up

An isokinetic dynamometer (CON-TREX MJ, CMV AG Switzerland, Switzerland) was used to attain isokinetic joint movements. The reliability and validity of the dynamometer have been confirmed in a previous study (Cotte and Ferret, 2003). Previous studies (Muramatsu et al., 2001; Maganaris et al., 2002) reported that large torque production induced inevitable rotation in the plantar flexion direction during isometric plantar flexion. Considering such discrepancy between the movements of ankle joint and footplate of the dynamometer, the angle and angular velocity of ankle joint were evaluated with an electrical goniometer (Biometrics, UK) attached on the lateral side of right ankle joint. The subjects were tested in a seated position with the knee fully extended and the thigh–trunk angle at 110° . The trunk and right thigh were fastened with belts and a strap, respectively. The footplate of the dynamometer was adjusted to align the center of rotation of the right ankle joint with the rotational axis of the dynamometer. The right foot was tightly fixed to the footplate by using a non-elastic strap to minimize heel lift during plantar flexions.

Surface electromyograms (EMGs) were recorded from the MG and SOL as an indication of muscle activation. After careful preparation of the skin by light abrasion and cleaning with alcohol, bipolar Ag/AgCl electrodes with a diameter of 5 mm and an inter-electrode distance of 20 mm were placed on the bellies of these muscles. The reference electrode was placed on the patella. The EMG signals were amplified (MEG-6100, Nihon Kohden, Japan) with bandpass filtering between 5 Hz and 1 kHz. The torque, ankle joint angle and EMG signals were analog-to-digital converted (Power Lab/16SP, AD Instruments, Australia) at a sampling rate of 2 kHz and stored on a computer for subsequent analyses.

Longitudinal images of the MG and SOL during isokinetic trials were continuously captured with a real-time B-mode ultrasound apparatus (SSD-5500, Aloka, Japan) (Fig. 1). A linear

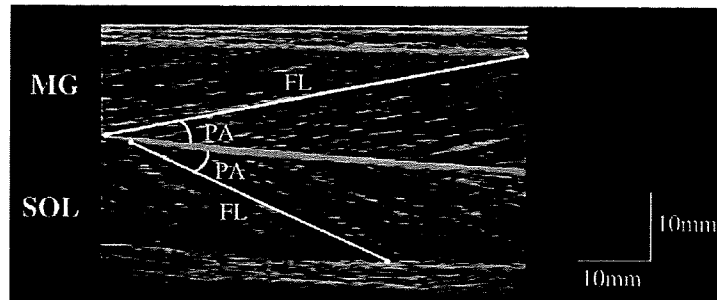


Fig. 1. A typical ultrasound image of the medial gastrocnemius (MG) and soleus (SOL) muscles. The lines correspond to the fascicle lengths (FL) of each muscle. Pennation angles (PA) were determined as angles at which fascicles arose from deep (MG) and superficial (SOL) aponeuroses.

array probe with a scanning frequency of 7.5 MHz was positioned onto the midbelly of MG identified by both cross-sectional and longitudinal ultrasound images. A custom-built instrument was used to fix the probe firmly in position. The raw data were sampled synchronously with the torque, joint angle and EMG data at 78 Hz with the use of an electrical timing switch, and then stored to computer. The fascicle lengths and pennation angles of the MG and SOL were measured by using digitizing software (ImageJ 1.32, National Institutes of Health, Bethesda, MD).

2.3. Experimental protocol

Maximal voluntary concentric and eccentric plantar flexions were randomly performed at pre-set angular velocities of ± 60 , ± 120 , ± 180 and ± 240 deg/s (positive and negative velocities indicate concentric and eccentric movements, respectively). The ranges of motion were set from -15° (dorsiflexed direction) to $+15^\circ$ (plantar flexed direction) for 60–180 deg/s and from -20° to $+20^\circ$ for 240 deg/s. These ranges were determined to secure constant angular velocities for the range under analysis, considering acceleration and deceleration of the dynamometer. The isokinetic movement immediately followed maximal voluntary isometric plantar flexion for about 1 second. Maximal voluntary isometric plantar flexions for about 4 s were performed with the ankle at 0° (anatomical position) to obtain reference data for normalizing torque and EMG values during isokinetic trials. Each isokinetic and isometric trial was performed a minimum of twice, and the trial with the larger torque value was selected for further analysis. In order to minimize fatigue effects, the rest period between trials at a given velocity was 3 min or more, and each tested velocity was separated by 5 min or more rest.

2.4. Calculation of the Achilles tendon moment arm

To measure the Achilles tendon moment arm during maximal voluntary isometric plantar flexion in each subject, sagittal magnetic resonance images (MRIs) [Signa CV/I 8.4 (1.5 T), GE Medical Systems, Milwaukee, WI, USA] of the right leg were taken at the level of the ankle (Fig. 2). With the subjects in the supine position, MRIs were taken at foot positions of -20° , -15° , -10° , 0° , $+15^\circ$, $+30^\circ$. Specially handmade mechanical stops and strap were used to secure the ankle joint in position. All MRIs were obtained by Fast Gradient Echo sequence at a flip angle of 90° . The imaging parameters used were as follows: repetition time, 10 ms; echo time, 4.2 ms; imaging matrix, 128×256 ; field of view, 24 cm; number of excitations, 1.0; slice thickness, 5 mm; and slice gap, 1 mm. The scanned sections were determined prior to data

collection by using a real-time mode in which instantaneous images were obtained every 1 s. Because some degree of non-sagittal plane movement of the ankle joint occurred by developing plantar flexion torque, three images were taken within a 4 s maximal isometric plantar flexion. One image was taken at the midpoint between the medial and lateral malleoli in the sagittal plane, with the second and third images taken medially and laterally to the first image, respectively. The clearest image of the tibia, talus and Achilles tendon was then selected for further analysis.

Achilles tendon moment arm lengths were determined according to the procedure described in Rugg et al. (1990). By using the Reuleaux graphical analysis, ankle joint instant centers of rotation of -10° , 0° and $+15^\circ$ were identified for ankle angle rotations from -20° to 0° , from -15° to $+15^\circ$ and from 0° to $+30^\circ$, respectively. A straight line drawn through the middle of the Achilles tendon was considered to represent the tendon action line. The distance between the center of rotation and the Achilles tendon action line, i.e. Achilles tendon moment arm length (Fig. 2), was measured by a vernier micrometer. The angle between the longitudinal axis of the tibia and the sole of the foot was measured in the MRI, and was determined as the ankle joint angle during isometric plantar flexion (Fig. 2). To predict the moment arm lengths for each angle, a linear regression equation for each subject was obtained by the moment arms at -10° , 0° , $+15^\circ$.

2.5. Data analysis

Isokinetic torques, ankle joint angles and ultrasound images were analyzed in the range from -5° to $+5^\circ$. In this range, the angular velocities of ankle joint were constant, i.e. isokinetic joint movement trials were satisfied in all trials. Isometric trials were analyzed over a 1 s period of stable torque output. Two different fascicles in the same ultrasound image were measured and averaged to determine fascicle lengths and pennation angles. The coefficient of variation (CV) for these two fascicle lengths or pennation angles was under 5% in all trials. When fitting the time-course data during the analyzed range of ankle joint angle and fascicle lengths of the MG and SOL to a linear regression equation, the correlation coefficient of all regression equations was more than 0.98 ($p < 0.05$) for ankle joint angle and 0.94 ($p < 0.05$) for fascicle length of both muscles. As a consequence, the slopes of the linear regression equations represent the angular velocities of the ankle joint, and the fascicle shortening and lengthening velocities, respectively. The “effective fascicle velocity”, representative of the velocity in the longitudinal direction of the muscle

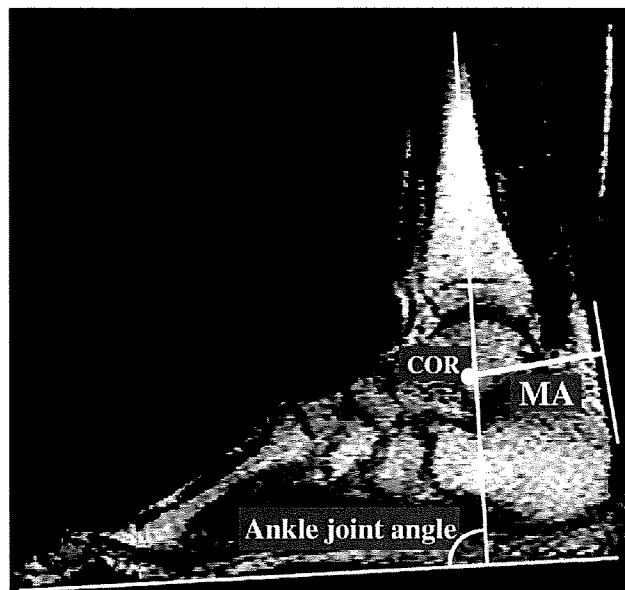


Fig. 2. A typical magnetic resonance image of the ankle joint. Achilles tendon moment arm (MA) was determined by the distance between the center of rotation (COR) and the line through the middle of Achilles tendon. The ankle joint angle was defined as the angle formed by the longitudinal axis of the tibia and sole of the foot.

belly, was also obtained. The “effective length” was calculated by multiplying fascicle length by the cosine of the pennation angle. The effective fascicle velocity was obtained by fitting the time-course data of effective length changes to a linear regression equation. The correlation coefficients of the linear regression were more than 0.93 ($p < 0.05$) for effective fascicle length of both muscles in all trials. To control for the influence of electromechanical delay, the EMG data were analyzed 50 milliseconds earlier than the torque data (Cavanagh and Komi, 1979). The EMG signals were full-waved rectified, and the mean EMG amplitude (mEMG) in each isokinetic trial was normalized by isometric mEMG value.

The contribution of tendinous tissues to MTC in each concentric and eccentric trial was estimated by dividing the length change of tendinous tissues by that of MTC. The MTC length change was calculated as follows: (1) Achilles tendon moment arm lengths at both end positions of the analyzed range for ankle joint angle and ultrasound images ($\pm 5^\circ$) were obtained from the relationship between ankle joint angle and Achilles tendon moment arm length, (2) the difference between the two joint angle ($10^\circ = 0.17$ rad) was multiplied by the averaged moment arm at these joint angles, to obtain the MTC length change during the analyzed range (Kawakami et al., 2002a). The tendinous tissues length change in the MG and SOL was determined by subtracting the MTC length change from the effective fascicle length change of each muscle (Herbert et al., 2002).

2.6. Statistics

Descriptive data are presented as means \pm SDs. The CV was calculated by dividing the SD by the data mean (Chilibeck et al., 1994). Statistical analyses were performed by Statistica software (StatSoft, USA). The effect of the angular velocities on torque was tested for significance by a one-way analysis of variance

(ANOVA) with repeated measures. The mEMG values were analyzed by using a two-way ANOVA (8 pre-set velocities \times 2 muscles) with repeated measures. A Tukey's post-hoc test was used for inter- and intra-muscle comparison, when appropriate. Fascicle shortening and lengthening velocities, effective fascicle shortening and lengthening velocities, and tendinous tissue contribution to MTC length change were separately analyzed by using a two-way ANOVA (8 pre-set velocities \times 2 muscles) with repeated measures. Since there was no interaction between the muscles and angular velocities, the differences in these variables between MG and SOL at corresponding pre-set velocities were tested by a Student's paired t -test. $P < 0.05$ was considered significant.

3. Results

3.1. Relationships between angular velocity and torque

Fig. 3 illustrates typical time-course data of ankle joint torque, ankle joint angle, rectified EMG, fascicle length and pennation angle during a concentric plantar flexion at 60 deg/s. The relationships between ankle joint angular velocity and angle-specific torque are shown in Fig. 4. Isometric torque was significantly higher than concentric torques at 120, 180 and 240 deg/s, and concentric torques at 60 and 120 deg/s were higher than that at 240 deg/s. Eccentric torques showed little change among angular velocities and were not significantly different from the isometric torque value.

3.2. EMG activities in isokinetic trials

The mEMG values of MG and SOL at each angular velocity are presented in Fig. 5. There was a significant difference in MG and SOL activation between 60 and 240 deg/s. The SOL showed no significant differences between eccentric and concentric activation levels at corresponding pre-set angular velocities. Whereas, MG showed a significant difference between the activations at +240 and -240 deg/s. There were no significant differences between MG and SOL at any of the corresponding pre-set angular velocities.

3.3. Shortening and lengthening velocities of MG and SOL

The fascicle shortening and lengthening velocities of MG was significantly higher than that of SOL at ± 120 , ± 180 and $+240$ deg/s (Fig. 6). However, the effective fascicle shortening and lengthening velocities did not significantly differ between MG and SOL in any of the angular velocity conditions (Fig. 7).

3.4. Contributions of tendinous tissues to MTC length change

The averaged contributions of tendinous tissues to MTC length change are shown in Fig. 8. The averaged contributions of MG tendinous tissues were $49 \pm 15\%$ for concentric

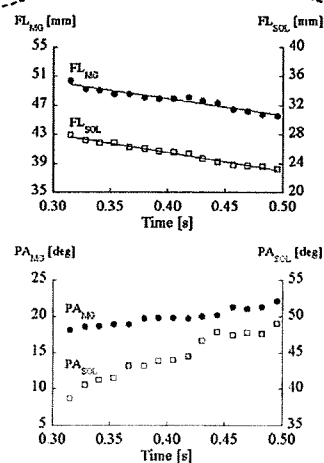
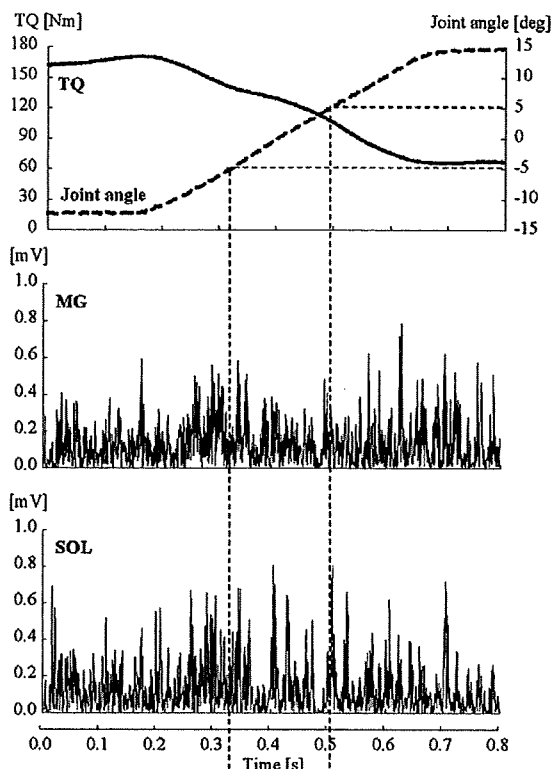


Fig. 3. From top, a typical time-course of ankle joint torque (TQ), joint angle and rectified EMG from the medial gastrocnemius (MG) and soleus (SOL) muscles with fascicle lengths (FL) and pennation angles (PA) of the MG and SOL. The data are from one subject performing a concentric plantar flexion at 60 deg/s. For fascicle lengths and pennation angles (bottom 2 graphs), only the data within the analyzed range of $\pm 5^\circ$ from neutral ankle angle are shown. Regression lines highlight the linear nature of the fascicle length changes in the MG and SOL.

trials and $45 \pm 22\%$ for eccentric trials. For the SOL, tendinous tissues accounted for $55 \pm 17\%$ and $52 \pm 23\%$ of the MTC length change, respectively. The averaged contributions were not significantly different between MG and SOL at any corresponding pre-set velocities. Large intra-subject variability was observed in both muscles.

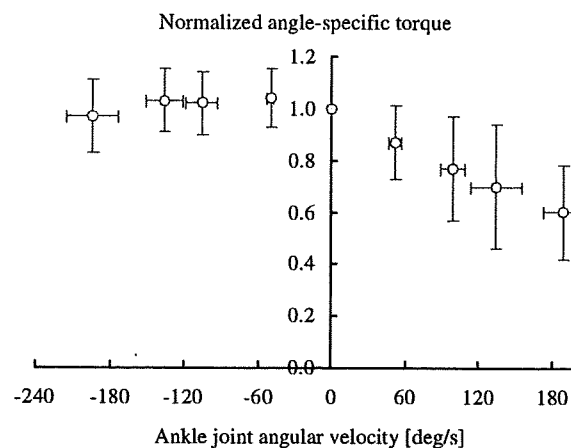


Fig. 4. Torque–angular velocity relationship in plantar flexors. Ankle joint angular velocities were not measured by isokinetic dynamometer, but by electrical goniometer positioned onto the ankle joint. Isokinetic torques were averaged in the range from -5° to $+5^\circ$, and each torque was normalized by the isometric value at 0° .

4. Discussion

There are two main findings in the present study that we wish to highlight. Firstly, significantly higher fascicle shortening and lengthening velocities of the MG compared to the SOL were observed at ± 120 , ± 180 and $+240$ deg/s, but there were no significant differences between these muscles in effective fascicle shortening and lengthening velocities at any of the tested angular velocities. Secondly, the contributions of tendinous tissues to MTC length change accounted for approximately 50% in both concentric and eccentric trials on average, but showed large intra-subject variability. The finding that fascicle behavior differed between these synergistic muscles supports our hypotheses, but no significant differences between the MG and SOL in the longitudinal direction of muscle belly is a surprising result. As expected, tendinous tissues made a large contribution to MTC length change during isokinetic joint movement. However, it is unexpected that the contributions of tendinous tissues showed large intra-subject variability.

4.1. Difference in fascicle shortening velocity between MG and SOL

In concentric trials, the fascicle shortening velocity of the MG was significantly higher than that of the SOL at 120, 180 and 240 deg/s (Fig. 6). In humans, the MG and SOL contain 1.72×10^4 and 1.34×10^4 in-series sarcomeres, respectively (Kawakami et al., 2000). Moreover, the MG and SOL are composed of 36–50% and 20–30% fast-twitch fibers, respectively (Saltin and Gollnick, 1983). These data indicate that the MG is better suited for developing higher fascicle shortening velocity than the SOL. Then, we sought to control MG and SOL fascicle shortening velocities due to difference in the number of in-series sarcomeres. This was achieved by normalizing the fascicle shortening

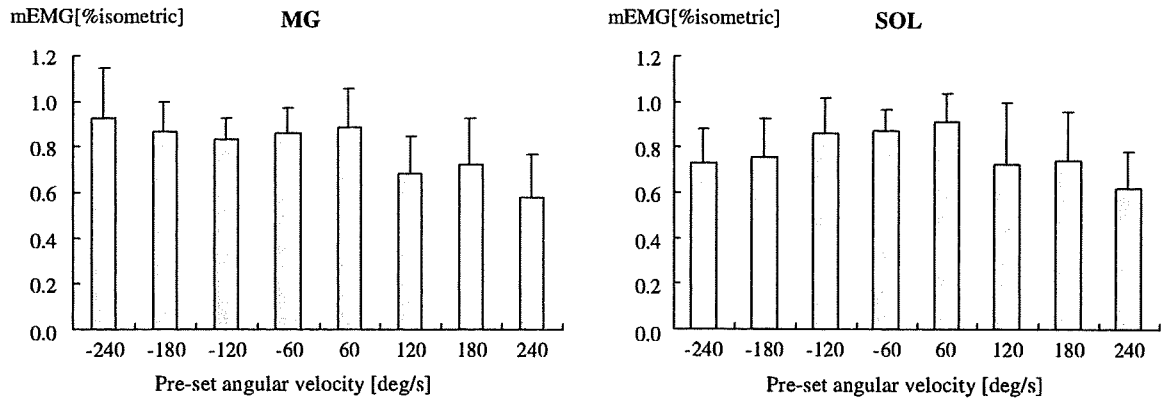


Fig. 5. Full-wave rectified amplitude-averaged electromyograms (mMGs) of the medial gastrocnemius (MG) and soleus (SOL) muscles. EMG values were normalized by isometric trial data for each muscle.

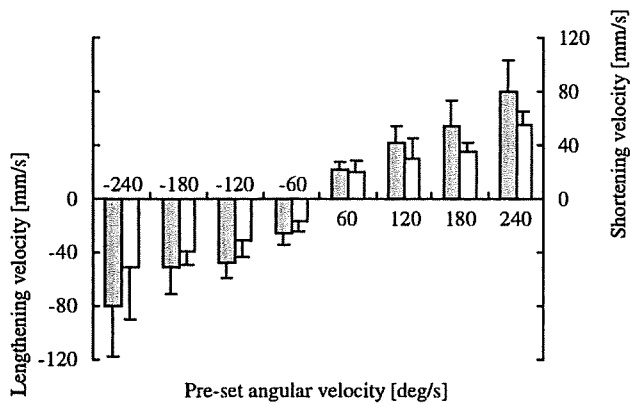


Fig. 6. Shortening and lengthening velocities of the medial gastrocnemius (MG, solid bars) and soleus (SOL, open bars) fascicles. Significant differences were found between the MG and SOL at ± 120 , ± 180 and $+240$ deg/s.

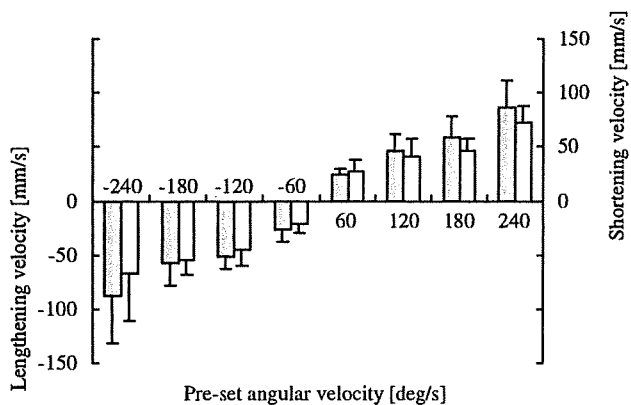


Fig. 7. Effective shortening and lengthening velocities of the medial gastrocnemius (MG, solid bars) and soleus (SOL, open bars) muscle bellies. The effective fascicle shortening and lengthening velocities were determined from the effective fascicle length corrected for pennation angle. No significant differences between the MG and SOL were found at any of the measured velocities.

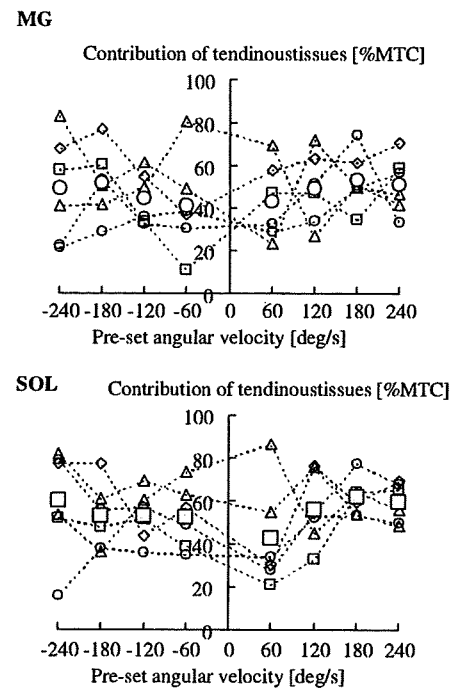


Fig. 8. Contributions of tendinous tissues to muscle-tendon complex (MTC) length change in isokinetic trials. Individual values of six subjects (opened symbols) and group averaged values (closed squares) are shown. The contributions of tendinous tissues amounted for about 50% on average, but large intra-subject variation was observed.

velocities by the estimated optimal fascicle length of each muscle. The optimal fascicle lengths of MG and SOL were estimated by multiplying the optimal sarcomere length ($2.81\mu\text{m}$; Herzog et al., 1990) by the number of in-series sarcomeres of each muscle (MG; 1.72×10^4 , SOL; 1.34×10^4 ; Kawakami et al., 2000). As a result of this normalization, the significant differences in the fascicle shortening velocities between the MG and SOL at 120, 180 and 240 deg/s were eliminated. Spector et al. (1980) measured force-velocity characteristics of cat MG and SOL in situ. In contrast to our results, they reported that even

if the number of in-series sarcomeres of each muscle was considered, great difference in shortening velocities between these muscles was observed. This inconsistency between studies may be due to differences in fiber composition between species. The cat SOL is composed entirely of slow-twitch fibers, and the MG contains 75% fast-twitch fibers (Ariano et al., 1973), whereas the human MG and SOL are composed of 36–50% and 20–30% fast-twitch fibers, respectively (Saltin and Gollnick, 1983). Thus, the heterogeneous fiber composition of the human triceps surae muscle may minimally affect the fascicle shortening velocities of MG and SOL, whereas the homogeneous fiber composition of the cat may significantly affect the shortening velocities of these muscles. However, since inter-subject difference in the number of in-series sarcomeres was not considered in our study, we cannot completely rule out the possibility of the influence of fiber composition on fascicle shortening velocity. Duchateau et al. (1986) reported that integrated EMG activity of the MG increased and the SOL decreased as the speed of cycling changed from 30 to 170 rpm under constant load. In our study, the mEMG values of SOL were not significantly different between 120, 180 and 240 deg/s, and were similar to those of the MG at corresponding pre-set angular velocities (Fig. 5). Although surface EMG would be only an approximation of muscle activation, we feel it justified to consider that the activation levels during concentric movements were not substantially different among angular velocities or between these muscles. Consequently, we conclude that the differences in fascicle shortening velocities between the MG and SOL observed in the present study were related to inherent physiological characteristics of each muscle, rather than different neural commands among the tested velocities or between these muscles.

4.2. Difference in fascicle lengthening velocity between MG and SOL

In eccentric trials, fascicle lengthening velocity significantly differed between the MG and SOL at -120 and -180 deg/s (Fig. 6). Nardone and Schieppati (1988) demonstrated activation of the gastrocnemius muscle and deactivation of the SOL in lengthening contractions. However, the MG and SOL showed similar activation regardless of lengthening velocities in our study (Fig. 5). Petit et al. (1990) compared the tension change during forced stretching between the motor units of different types in peroneus longus muscle of cats, and reported that slow type units produced a resistance to stretch comparable with or greater than that of fast units. As the SOL contains a higher percentage of slow-twitch fibers than MG (Saltin and Gollnick, 1983), SOL was expected to exhibit a slower lengthening velocity than MG. Moreover, some previous studies have described that rigor force is proportional to the total number of interacting sites between the actin and myosin filaments (Fink et al., 1986; Stephenson and Williams, 1981; Wilson et al., 1991). To obtain the aver-

aged sarcomere lengths of MG and SOL in the eccentric trials, the averaged fascicle lengths within the analyzed range (MG: 44 ± 6 mm, SOL: 27 ± 3 mm) were divided by the number of in-series sarcomeres of each muscle (MG; 1.72×10^4 , SOL; 1.34×10^4 ; Kawakami et al., 2000). The sarcomere lengths of both MG and SOL were calculated to be on the ascending limb of the length-force relationship (1.64 – 2.64 μm ; Herzog et al., 1990) excluding a few exceptions, so it was concluded that MG and SOL had the same number of the interaction filaments in one sarcomere. However, due to the larger number of in-series sarcomeres in one MG fiber (Kawakami et al., 2000), the total number of interacting filaments in a MG fiber would be larger than that in a SOL fiber. On the other hand, due to the much larger physiological cross-sectional area of SOL than MG (230.02 cm^2 vs. 68.34 cm^2 ; Fukunaga et al., 1992), SOL would contain more muscle fibers than MG. It is not therefore clear which muscle has a larger number of interacting sites between the actin and myosin filaments. When considering both fiber composition and actomyosin site interaction, it is not possible to clearly predict which muscle would show higher fascicle lengthening velocity. Our results which demonstrate no clear differences in fascicle lengthening velocities between the MG and SOL could be a result of an intricate interaction of the above factors and highlight the need for future research in this area.

4.3. Difference in effective fascicle velocity between MG and SOL

The effective fascicle shortening and lengthening velocities were calculated to investigate the fascicle behavior along the longitudinal axis of the muscle belly. There were no significant differences between the MG and SOL at each of the tested velocities (Fig. 7). This result could be attributed to the following three architectural properties. Firstly, there could have been a pennation effect. This has been described as the displacement of the aponeurosis insertion being greater than the absolute length change of the fascicle due to pennation angle (Gans and Gaunt, 1991). The averaged pennation angle of the SOL within the analyzed range was significantly larger than that of the MG at all corresponding angular velocities, thus the pennation effect would be more pronounced in the SOL. Secondly, the MG and SOL merge via each aponeurosis into a common Achilles tendon. Thirdly, intermuscular myofascial force transmission; i.e. interaction between adjacent muscle bellies during contraction (Maas et al., 2001), could have existed between the MG and SOL. A previous study on human cadavers by Bojsen-Moller et al. (2004) observed that collagen structures connected the gastrocnemius and SOL aponeuroses, and the interaponeurosis became increasingly connected toward the distal common junction. Moreover, Denny-Brown (1929) reported that the tension of the SOL developed by a maximal stimulation to the popliteal nerve was altered by a section of fascia along the

medial border of the SOL. Based on these previous investigations, it is quite possible that the MG and SOL interacted with each other during contraction via adjacent muscle bellies, which could account for the similarity between the two muscles in our study.

4.4. Contribution of tendinous tissues to MTC length change

In numerous studies (e.g. Fugl-Meyer et al., 1979; Wickiewicz et al., 1984; Westing et al., 1990; Svantesson et al., 1994; Ferri et al., 2003), isokinetic dynamometry has been used to measure the force–velocity relationship in intact human muscle. Although there are no problems in obtaining a force-velocity relationship of skeletal muscle *in vitro*; strictly speaking, only the entire joint torque–angular velocity relationship can be determined under *in vivo* conditions (Gulch, 1994). In order to regard the torque–angular velocity relationship as the force–velocity relationships of skeletal muscle, certain assumptions are necessary. One of the major assumptions is the equivalency of constant angular limb velocity and constant muscle velocity (Westing et al., 1990). To confirm the validity of this assumption, it is necessary that the contributions of tendinous tissues are identical between all trials. As shown in Fig. 8, however, the contributions of tendinous tissues to MTC length change were not always identical, but showed large intra-subject variation. From this result, it is shown that the contribution of tendinous tissues greatly affects fascicle behavior even in isokinetically controlled joint movements. Previous human studies have reported the importance of tendinous tissues not only during isokinetic joint movement (Kawakami et al., 2002a; Reeves and Narici, 2003) but also during walking (Fukunaga et al., 2001) and jumping (Kawakami et al., 2002b; Kurokawa et al., 2003).

The contributions of tendinous tissues to MTC length change during concentric and eccentric movements amounted to approximately 50% (Fig. 8), while Herbert et al. (2002) reported that the contribution of MG tendinous tissues during passive movement was 72%. This discrepancy could be partly due to the fact that in our study the pennation effect was taken into consideration, while in the previous study it was not. By not considering the pennation effect, overestimation of the contribution of tendinous tissues can be as great as 14.4% (Herbert et al., 2002). Changes in the mechanical properties of the tendinous tissues upon contraction could also affect these figures during active and passive movements. It was reported that tendon compliance decreased as the applied tension increased (Viidik, 1973; Bennett et al., 1986). Moreover, Lieber et al. (2000) measured the load-strain properties of frog semitendinosus tendon and aponeurosis, and reported that the strain during active contraction was smaller than that during passive loading. From these studies, it has been shown that the elasticity of tendinous tissues during active movements decreases compared to passive movements.

5. Conclusions

Fascicle shortening and lengthening velocities were significantly higher in the MG compared to the SOL at ± 120 , ± 180 and $+240$ deg/s, which could reflect differences in the number of in-series sarcomeres, muscle-fiber composition and/or resistance to stretch. However, the effective fascicle shortening and lengthening velocities showed no consistent variation between the MG and SOL at any of the tested velocities. This could be due to differences in fascicle architecture and/or the existence of mechanical linkages between these muscles. The length change of tendinous tissues in both concentric and eccentric trials contributed as much as 50% to total changes in MTC length, but there was considerable intra-subject variability. From these results, it would be concluded that the assumption that angular velocity of limb movement can be used to calculate muscle velocity should be carefully reconsidered.

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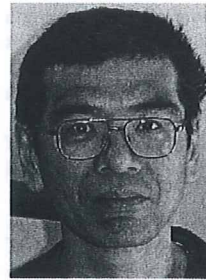
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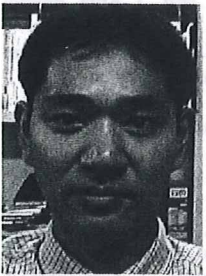
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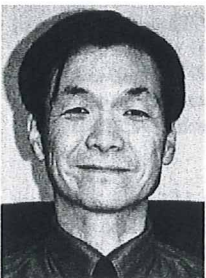
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In vivo behavior of muscle fascicles and tendinous tissues of human gastrocnemius and soleus muscles during twitch contraction

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Abstract

The present study investigated the differences between the human medial gastrocnemius (MG) and soleus (SOL) muscles in length changes of muscle fascicles and tendinous tissues during twitch contraction induced by an electrical nerve stimulus. Also, the time-course characteristics of twitch torque were related with changes in the length of muscle fascicles and tendinous tissues. No significant difference was observed between MG and SOL in contraction and half relaxation times of the changes in lengths and velocities of both muscle fascicles and tendinous tissues. The time-course of changes in twitch torque was nearly identical to that of the length of muscle fascicles and tendinous tissues. It was suggested that the behavior of MG and SOL during twitch contraction is practically similar in spite of their known physiological and architectural differences, and that the time-course of twitch torque is greatly influenced by the changes in the length of muscle fascicles and tendinous tissues.

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Keywords: Twitch time-course characteristics; Shortening velocity of muscle fascicles; Elongation of tendinous tissues; Ultrasonic images; Force transmission

1. Introduction

The time-course of twitch torque or force (e.g. contraction and half relaxation times) induced by a single electrical stimulus has been well utilized to investigate the muscle contractile properties of mammalian species (Close and Hoh, 1968; Cooper and Eccles, 1930; Ranatunga, 1977). In human muscles *in vivo*, many attempts (Belanger and

McComas, 1985; Davies et al., 1987; McComas and Thomas, 1968; Pääsuke et al., 1999; Rice et al., 1988; Sale et al., 1982; Vandervoort and McComas, 1983) have been made to determine the time-course of twitch contraction by examining the triceps surae as the greatest contributor to plantar flexion torque. These weight-bearing muscles have important roles in various human movements; e.g. bipedal locomotion (Fukunaga et al., 2001; Hof et al., 2002) and stabilization of the body mass during quiet stance (Masani et al., 2003).

The triceps surae comprises the gastrocnemius (GAS) and the soleus (SOL). Although GAS and SOL are synergistic muscles as plantar flexors, they differ considerably in muscle fiber composition (Johnson et al., 1973), architecture (Fukunaga et al., 1992; Kawakami et al., 1998; Wickiewicz et al., 1983), and contractile properties (Vandervoort

Abbreviations: B-mode, brightness mode; GAS, the gastrocnemius muscle; MG, the medial gastrocnemius muscle; M wave, muscle compound action potential; SOL, the soleus muscle; FL, fascicle length; FV, fascicle velocity; TE, elongation of tendinous tissues; TV, lengthening velocity of tendinous tissues.

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and McComas, 1983; Widrick et al., 1999; Widrick et al., 2001). The proportion of type I fibers in GAS is smaller than SOL (Johnson et al., 1973) and hence GAS has shorter contraction time compared with SOL (Vandervoort and McComas, 1983). In addition, SOL has larger pennation angles than GAS (Kawakami et al., 1998). In spite of these differences, most previous studies have only focused on the contractile properties of the triceps surae as a whole, not as each of GAS and SOL. No study has ever tried to determine the *in vivo* behavior of muscle fascicles and tendinous tissues in GAS and SOL during twitch contractions. The present study aimed to investigate the differences between GAS and SOL in the time-course characteristics of changes in the length of muscle fascicles and tendinous tissues (Achilles tendon and aponeuroses) and in their velocities during twitch contractions. In addition, how the changes in muscle fascicles and tendinous tissues relate with the time-course characteristics of twitch torque was also examined. For these purposes, the sequences of changes of length in muscle fascicles and tendinous tissues were determined directly and non-invasively using an ultrasonic apparatus (e.g. Fukunaga et al. (1997), Herbert and Gandevia (1995), Kawakami et al. (1998), Rutherford and Jones (1992)). Our hypothesis was that the time-course characteristics and the velocity of GAS would differ from those of SOL during twitch contractions because of their physiological and architectural differences.

2. Methods

Six healthy males (age 30.3 ± 8.6 years, height 175.9 ± 5.0 cm and weight 70.2 ± 9.1 kg; means \pm SD) participated voluntarily in the present study. The participants were fully informed of the procedures to be utilized as well as the purpose of this study. Written consent was obtained from each subject.

3. Experimental design

The subject was seated on the bench of a joint torque measurement system (CON-TREX Multi Joint, CON-TREX, Switzerland), with the knee fully extended and the hip flexed at 110° (180° : full extension). The right foot was secured to an adjustable footplate by non-elastic straps at the neutral joint position (90°) (Fig. 1). A twitch contraction was induced by applying a supramaximal electrical stimulus to the tibial nerve. Along with the twitch torque, we measured electromyogram, muscle fascicle length and elongation of tendinous tissues in each of GAS and SOL.

4. Electrical stimulus

4.1. Setting and stimulus

A twitch contraction of the triceps surae muscles was induced by a supramaximal electrical stimulus with a 100- μ s duration using a high-voltage stimulator (SEN-

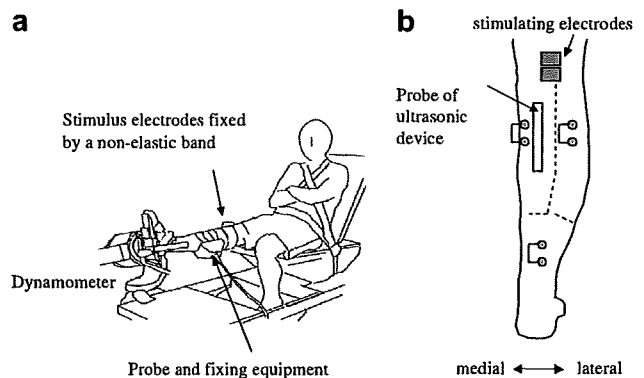


Fig. 1. Experimental set up. (a) The ankle joint was fixed at the neutral position, with the knee fully extended and hip flexed at 110° (180° : full extension). Electrical stimulus to the tibial nerve was applied from the right popliteal fossa. (b) The linear-array probe of the ultrasonographic device was held in place on the mid-belly of the medial gastrocnemius muscle at the 30% proximal level of the lower leg length. The stimulating and recording electrodes were placed on right popliteal fossa and mid-belly of each muscle, respectively.

3301, with a specially modified isolator; SS-1963, Nihon Koden, Japan). The stimulus was applied to the tibial nerve. Cathode and anode electrodes (square sheet: 5 cm \times 3 cm) were placed on the right popliteal fossa and oriented longitudinal to the estimated pass of the tibial nerve with the anode distal (Kawakami et al., 2000). The stimulating electrodes were placed on the position where maximal twitch peak torque and maximal muscle compound action potential (M wave) amplitude of SOL were evoked by submaximal intensity with the minimal M wave from the tibialis anterior muscle. Then, the stimulus intensity was increased to the supramaximal level at which no further increase in M wave amplitudes of SOL and the medial head of gastrocnemius (MG) was observed. Prior to the test, five repeated twitches were induced to avoid the staircase effect in which twitch peak torque increases gradually with repeated stimuli. Subsequently, twitch contractions were induced twice or three times at 3-min intervals.

4.2. Measurements of electromyograms

To confirm the position and intensity for the stimulus, the M wave was recorded using surface electrodes. The recording electrodes (Ag-AgCl electrodes, diameter: 5 mm, inter-electrode distance: 20 mm), were placed on the mid-bellies of MG, SOL and the tibialis anterior muscle of the right leg, after the electrode site had been cleaned with alcohol and shaved. The mid-bellies of the muscles were identified using a brightness mode (B-mode) ultrasonic apparatus (SSD5500, Aloka, Japan) as described in a prior study (Kawakami et al., 1998). M wave signals (Fig. 2) were amplified for gain of 60 dB, with a band-pass of 10–1000 Hz, and A/D converted at a sampling rate of 2 kHz (MacLab/8, type ML780, ADInstruments, Australia) for storing in a personal computer.

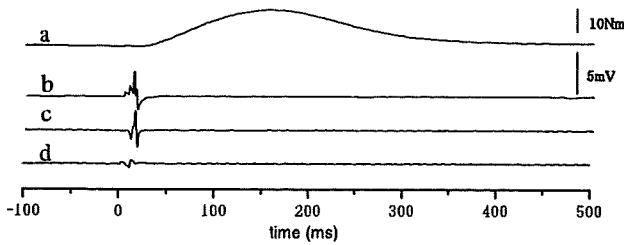


Fig. 2. Raw data of measured torque and electromyograms. Measured torque (a), and electromyogram from the medial gastrocnemius (b), soleus (c) and tibialis anterior (d) muscles are shown as a typical example from one subject.

4.3. Measurements of ultrasonic images and plantar flexion torque

A real-time B mode ultrasonic apparatus (SSD-5500, Aloka, Japan) with an electronic linear-array probe (7.5 MHz wave frequency with 60 mm scanning length; UST 5047-5, Aloka, Japan) was used to obtain a longitudinal ultrasonic image of MG and SOL at the level of 30% of the lower leg length; i.e. from the popliteal crease to the centre of the lateral malleolus (Kawakami et al., 1998). The width and depth resolution of the images was 0.16 mm. The probe position and imaging plane were confirmed to obtain the echoes from the aponeuroses of both

MG and SOL. The ultrasonic images were stored in computer memory at 77.8 Hz and later transferred to a personal computer. The plantar flexion torque measured using a joint torque measurement system was A/D converted and stored synchronizing with the stimulus signal and electromyogram for subsequent analyses.

5. Data analysis

The muscle fascicle length and elongation of tendinous tissues were measured using NIH Image (1.62/ppc, National Institutes of Health). In the present study, we assumed that the behavior of MG represented that of the entire GAS. A trial clearly showing cross points at which fascicles attached to the superficial and deep aponeuroses of both MG and SOL was selected for analysis. The cross points between fascicles and aponeuroses were digitized from the serial ultrasonic images during twitch contraction (Fig. 3). Fascicle length was defined as the distance between the proximal and distal ends of the fascicle without consideration of the fascicle’s curvature. The minimal and maximal length, and the contraction and half relaxation times were determined from the time-course of changes in fascicle length. The contraction time and the half relaxation time were defined as the time from stimulus to minimal fascicle length and the time of half decline in maximal fascicle length, respectively (Pääsuke et al., 1999). The elongation

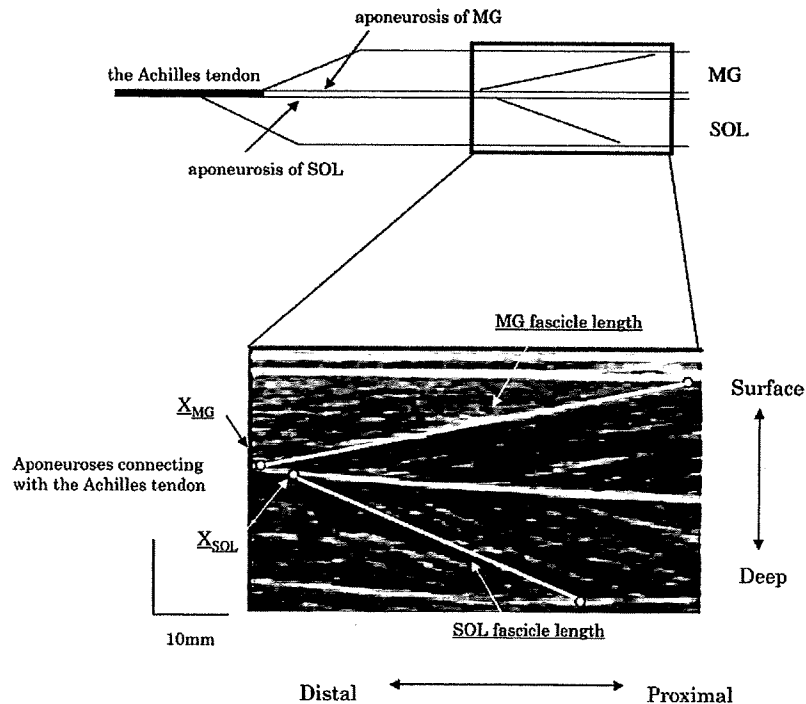


Fig. 3. Ultrasonic images of longitudinal sections of the medial gastrocnemius and soleus muscles. A real-time B mode ultrasonic apparatus with an electronic linear-array probe was used to obtain a longitudinal ultrasonic image of the medial gastrocnemius and soleus muscles at the level of 30% of the lower leg length. Fascicle length and elongation of tendinous tissues were defined as the distance between the proximal and distal ends of the fascicle without consideration of the fascicle curvature and as the movement of cross points between a muscle fascicle and aponeurosis connecting to the Achilles tendon (X_{MG} and X_{SOL}), respectively.

of tendinous tissues of MG and SOL was measured using the method described by Kubo et al. (2002). Briefly, the elongation was determined from the movement of cross points between a muscle fascicle and aponeurosis connecting to the Achilles tendon. The maximal elongation and the contraction and half relaxation times were determined in the same way as the muscle fascicles. The measurements of muscle fascicle length and elongation of tendinous tissues were performed three times and the mean value was calculated as descriptive data. The coefficient of variation of digitized values from three trials was $2.0 \pm 1.6\%$ for the muscle fascicle length and $17.9 \pm 15.4\%$ for the elongation of tendinous tissues. The larger coefficient of variation for the latter is due to very small amplitude of elongation of tendinous tissues (3.4–8.6 mm). Additionally, maximal velocity for length change of each of muscle fascicles and tendinous tissues was calculated. The time-course data of the length of muscle fascicles and tendinous tissues were filtered using three-point moving averaging, and then the maximal velocity was selected from the time-course of velocity calculated from the filtered data. The contraction and half relaxation times of torque were defined in the same way as the length changes of muscle fascicles and tendinous tissues.

6. Synchronization between the torque and data from ultrasound images

To synchronize the torque and ultrasound data, we assumed that the time lag from stimulus to onset of contraction (onset of muscle fascicle length change) was 10 ms, as reported by Rasch and Burke (1959). The onset of contraction was defined as the first point at which the change in fascicle length exceeded by 2-fold the standard deviation of the mean fascicle length determined for the 300 ms before the stimulus.

7. Statistics

Descriptive data were presented as means \pm standard deviations. A paired *t* test was used to analyze the difference between MG and SOL in the contraction and half relaxation times of both muscle fascicles and tendinous tissues, and the difference in the time-course changes among torque, muscle fascicles and tendinous tissues. The level of significance was set at $P < 0.05$.

8. Results

Fig. 4 shows a typical example of the time-course of changes in the twitch torque, fascicle length, elongation of tendinous tissues and velocities of muscle fascicles and tendinous tissues. The muscle fascicles in MG and SOL initially shortened and then lengthened with similar magnitude, which corresponded with the time course of change in twitch torque. The tendinous tissues elongated and then shortened with a similar time-course as the changes in muscle fascicle length.

Descriptive data on the measured variables are summarized in Table 1. Fascicle length at rest and minimal length during contraction were significantly longer for MG than SOL. However, the contraction and half relaxation times of the muscle fascicles, tendinous tissues and their velocities did not differ significantly between MG and SOL. Furthermore, no significant difference among torque, fascicle length and elongation of tendinous tissues was found in neither the contraction nor half relaxation times.

9. Discussion

To our knowledge, the present study is the first report to describe the time-course of length changes in muscle fascicles and tendinous tissues during twitch contractions in human skeletal muscles *in vivo*. The main finding of the present study was that the contraction and half relaxation times and velocities of both muscle fascicles and tendinous tissues did not differ significantly between MG and SOL, whereas fascicle length at rest and minimal length differed significantly between the two muscles. Power analysis to the contraction and half relaxation times and velocities of both muscle fascicles and tendinous tissues showed that considerable number of subjects needs for detection of its statistically significant difference with $\alpha = 0.05$ and $1 - \beta = 0.90$ (even minimal $n = 27$ for elongation of tendinous tissues; and maximal $n = 1282$ for half relaxation time of fascicles), which is practically impossible in the present study. We can only conclude that the parameters were not statistically different between MG and SOL, although the possibility of type II error cannot be excluded. Thus, the present result suggested that the time-course of the change in length of both muscle fascicles and tendinous tissues are nearly identical between MG and SOL during twitch contraction induced by an electrical nerve stimulus, although muscle fiber composition (Johnson et al., 1973) architecture (Fukunaga et al., 1992; Kawakami et al., 1998; Wickiewicz et al., 1983) and contractile properties (Vandervoort and McComas, 1983; Widrick et al., 1999; Widrick et al., 2001) differ between the two muscles.

It has been considered that the time-course characteristics of twitch torque reflect the duration of Ca^{2+} transients (release and re-uptake) by the sarcoplasmic reticulum (Kugelberg and Thornell, 1983), which is shorter in fast fiber compositions than slow fiber compositions. Thus, muscles that have higher percentages of fast fiber compositions have shorter contraction and half relaxation times (Harridge et al., 1996). Previous studies have reported that MG and SOL have a substantial fiber type difference; i.e. MG and SOL contain type I fiber of 44.0–54.4 and 74.5–98.4%, respectively (Johnson et al., 1973). When we started the present study, therefore, we expected the contraction and half relaxation times of MG to be shorter than those of SOL. In fact, Vandervoort and McComas (1983) stimulated individual muscle bellies of MG and SOL separately

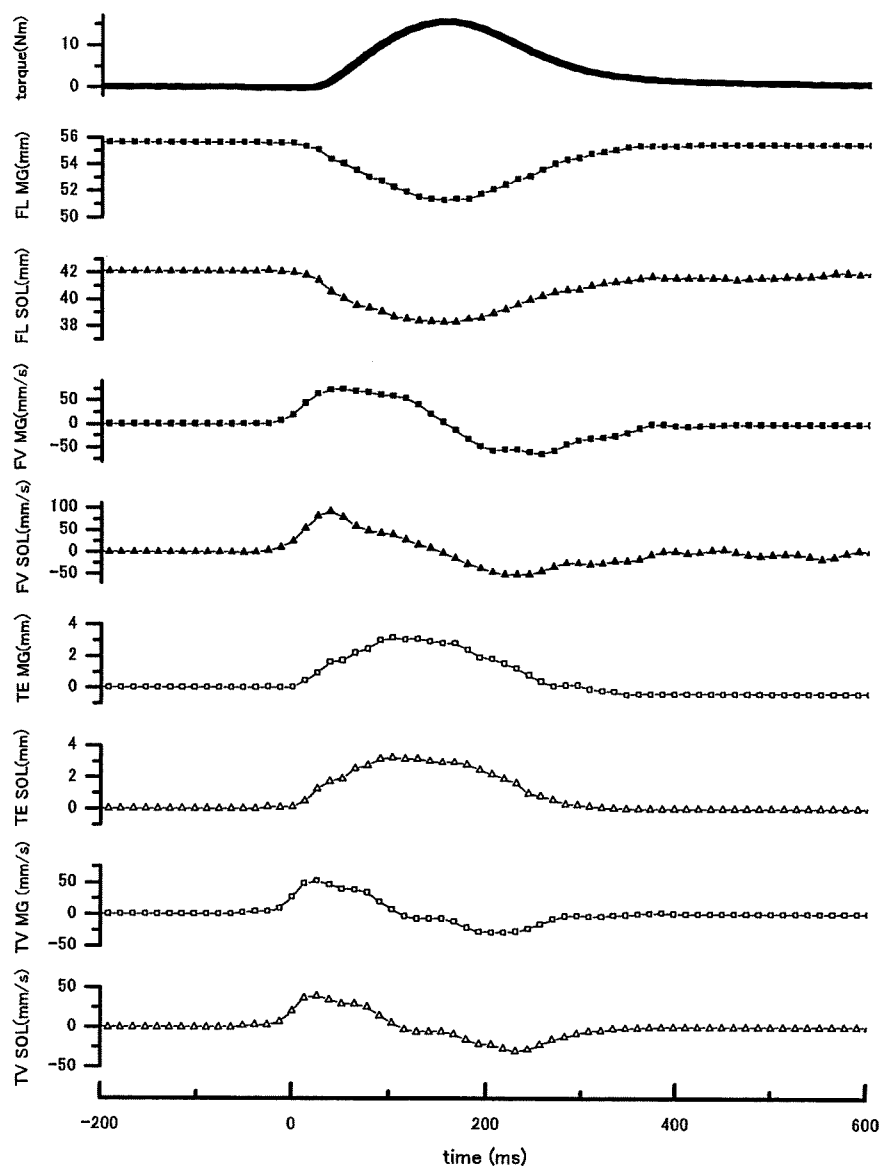


Fig. 4. A typical example of the time-course of change in plantar flexion torque, fascicle length (FL), fascicle velocity (FV), elongation of tendinous tissues (TE) and lengthening velocity of tendinous tissues (TV). Zero on the horizontal axis indicates the moment at which the electrical stimulus was delivered. Fascicle length in the medial gastrocnemius and soleus muscles initially shortened and then lengthened with similar magnitude, which corresponded with the time course of twitch torque. The tendinous tissues of the two muscles were elongated and then shortened with similar timing as the changes in muscle fascicle length. The velocities of muscle fascicles and tendinous tissues showed maximal value in the early phase of contraction. Note that fascicle shortening velocities start to increase before the stimulus due to the filtering effect of moving average.

and found short contraction and half relaxation times of twitch force for MG compared with SOL (114 ms and 110 ms for MG and 157 ms and 152 ms for SOL, respectively). In addition, it has been considered that MG muscle fascicles contract faster than SOL due to a larger number of sarcomeres in series as compared with SOL (Wickiewicz et al., 1983). Considering these differences, it would be reasonable to assume that the contraction and half relaxation times are shorter and the contractile velocity higher in MG than SOL. However, the present results did not support this assumption.

In the present study, we induced twitch contractions of GAS and SOL together by stimulating a nerve instead of individual muscle bellies. MG and SOL have the distal tendon common to the two muscles (the Achilles tendon), although they possess individual aponeurosis connecting to the Achilles tendon (Fig. 2). Thus, it is considered that the change in muscle fascicle length influences each other through the distal common tendon. In addition, there is evidence for extramuscular myofascial force transmission (Huijing, 2003; Huijing and Baan, 2001; Maas et al., 2003; Yucesoy et al., 2003) between adjacent muscles

Table 1
Data on muscle fascicles, tendinous tissues and plantar flexion torque
($N = 6$)

	MG		SOL	
<i>Muscle fascicles</i>				
Rest fascicle length (mm)	57.6 [*]	(2.7)	43.3	(4.1)
Minimal fascicle length (mm)	52.0 [*]	(2.4)	38.2	(3.9)
Contraction time (ms)	147.7	(33.0)	160.5	(20.5)
Half relaxation time (ms)	104.7	(33.6)	108.9	(17.7)
Maximal shortening velocity (mm/s)	68.0	(7.5)	78.2	(12.6)
<i>Tendinous tissues</i>				
Maximal elongation (mm)	6.1	(1.2)	6.8	(1.1)
Contraction time (ms)	134.7	(25.0)	143.6	(21.4)
Half relaxation time (ms)	111.6	(14.4)	117.8	(22.8)
Maximal velocity (mm/s)	70.6	(8.6)	78.9	(10.3)
<i>Plantar flexion torque</i>				
Peak (N)	19.3	(4.8)		
Contraction time (ms)	163.9	(5.1)		
Half relaxation time (ms)	100.3	(9.3)		

Data are the mean (SD). There were significant differences in only the rest fascicle length and the minimum fascicle length between the medial gastrocnemius (MG) and (SOL) muscles.

^{*} Significant difference from SOL ($p < 0.05$).

through their connective tissues. Huijing and Baan (2001) reported that extramuscular connective tissues transmitted the force to not only external tendons but also to synergist muscles. Yucesoy et al. (2003) also demonstrated that the length of contracting muscle influences the contractile properties of adjacent muscles (e.g. length–force characteristics) through extramuscular myofascial force transmission. These factors could induce mechanical linkage between MG and SOL, resulting in almost identical time-course characteristics and contraction velocities of the two muscles.

To observe the behavior of the tendon and aponeuroses, we determined the elongation of the tendinous tissues in both MG and SOL. We found that the contraction and half relaxation times and the maximal elongating velocities of the tendinous tissues did not differ significantly between MG and SOL (Table 1); i.e. MG and SOL were nearly synchronized at the level of tendinous tissues, as well as the muscle fascicles. Moreover, we carried out an additional experiment using separate stimulus to MG, to confirm the existence of mechanical linkage between MG and SOL. From four subjects out of the six subjects, the time-courses of changes in the lengths of muscle fascicles and tendinous tissues were measured during stimulus to muscle belly of MG. The stimulation intensity was carefully checked not to elicit EMG signals from SOL. Also in this experiment, the change of fascicle length of both MG and SOL was observed, and the time-courses of fascicle length change were similar between MG and SOL (Fig. 5). Similar tendency was observed in the time-courses of tendinous tissues. This phenomenon was apparent in all subjects, suggesting that fascicle length of SOL was passively altered by the shortening of fascicle of MG through a mechanical linkage between them. Hence, it is possible to conclude that the mechanical linkage that could be due to the Achilles tendon and extramuscular connective tissues, is an important factor indicating the observed similarity of time-course characteristics and contraction velocities in muscle fascicles of MG and SOL. The mechanical linkage would make interaction of length change of fascicles between synergist muscles, and thus affect the time-course of fascicle force in individual muscle during contraction.

The second purpose of the present study was to investigate how the length changes of muscle fascicles and tendinous tissues could be related to the twitch torque time-

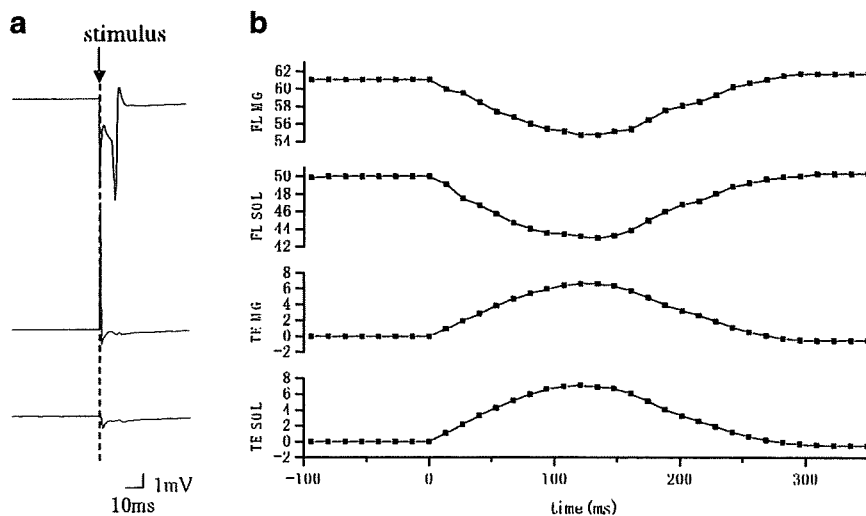


Fig. 5. A typical example of the additional experiment using separate stimulus to MG. (a) Electromyogram from the medial gastrocnemius (top), soleus (middle) and tibialis anterior (bottom) muscles. Only the medial gastrocnemius muscle was stimulated with stimulus to muscle belly. (b) A typical example of the time-course of change in fascicle length (FL) and elongation of tendinous tissues (TE). The changes in lengths of fascicles and tendinous tissues of both MG and SOL were observed, and the time-course changes were similar between them.

course characteristics. The contraction and half relaxation times did not differ significantly between the twitch torque and length change in each of muscle fascicles and tendinous tissues. This result suggests that there is little time lag among the peak torque, minimal muscle fascicle lengths and maximal elongation of tendinous tissues during twitch contraction. In other words, muscle fascicles shortened initially with elongating tendinous tissues, and the twitch force increased corresponding with the time-course of the shortening of muscle fascicles and elongation of tendinous tissues, and then the twitch torque peaked at the point of minimal muscle fascicle length and maximal elongation of tendinous tissues. At this moment, the shortening velocity of the muscle fascicles was zero, indicating that the maximal twitch torque was developed by MG and SOL which were contracting isometrically. However, there was a small time delay between the onset of the shortening of muscle fascicles and twitch torque output (see Fig. 4; this case 17 ms). This time delay may be due to the slackness of tendinous tissues (Cavanagh and Komi, 1979; Muraoka et al., 2004). In the initial phase of contraction, therefore, the coincidence between the time-courses of torque and muscle fascicle length is not high, although no significant difference was observed in contraction time between muscle fascicle length and resultant torque.

Finally, we should comment on the methodological limitations to this study. The sampling rate of 77.8 Hz for the ultrasonic images could have undetected the displacement by 12.82 ms. Similarly, time-course characteristics were determined only with the accuracy of 12.82 ms. Taking Nyquist theorem into consideration, the time resolution of the ultrasonic images become 25.64 ms. The time-course characteristics in Table 1 can thus contain errors caused from this sampling rate. It could be possible that the difference between MG and SOL in the time-course characteristics in the present study has gone undetected because of the time resolution of the displacement. However, the difference of time-course characteristics between MG and SOL using individual muscle belly stimulus in the previous study (43 ms for contraction time and 42 ms for half relaxation time (Vandervoort and McComas, 1983)) exceeded the time resolution in the present study. This indicates that the sampling rate in the present study does not affect the result on the similarity in the time-course characteristics between MG and SOL observed in the present study. Additionally, in the present study we investigated only one joint angle. Joint angle changes alter the contributions of agonist muscles for joint torque production, due to the length-force relationship (Kawakami et al., 2000). Hence, further studies are needed to investigate whether the present results are applicable to other joint positions.

In conclusion, the present study revealed that (1) there is no significant difference between MG and SOL in the contraction and half relaxation times of the change in muscle fascicle and tendinous tissue lengths and the velocities, whereas fascicle length at rest and minimal length differed significantly between the two muscles; (2) the

time-courses between the twitch torque and each length change of muscle fascicles and tendinous tissues did not differ significantly. These findings suggest that the behavior of *in vivo* MG and SOL during twitch contraction induced by an electrical nerve stimulus is nearly identical, in spite of their known differences in muscle fiber composition, architecture and contractile properties, and that the time-course of plantar flexion torque is greatly influenced by the length change of the muscle fascicles and the tendinous tissues.

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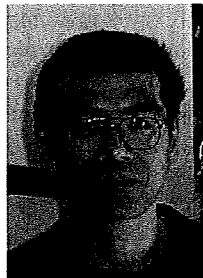
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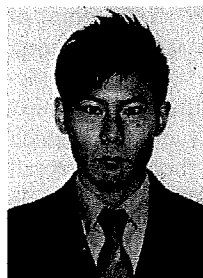
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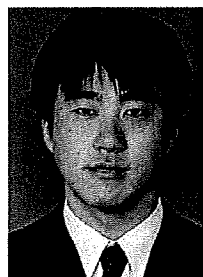
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