【課程内】

博士（人間科学）学位論文

膝関節角度の異なる姿勢における腓腹筋の筋束動態

Fascicle behavior of the gastrocnemius muscle at different knee joint positions

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CHAPTER 1 Introduction

1-1. Preface

The gastrocnemius muscle is a bi-articular muscle crossing both knee and ankle joints. Hence, the gastrocnemius muscle fibers (fascicles) produce force during human movements with influences of the two joint angles. Also, the behavior of the fascicles are further complicated by the connection with long tendinous tissues (external tendon and aponeurosis) (Herbert et al. 2002), because tendinous tissues elongate with applied force (Butler 1978). In order to understand the gastrocnemius muscle mechanics, knowledge of fascicle behavior is essential since the force generating potential of a fascicle is dependent on its length (Gordon et al. 1966) and velocity (Hill 1938).

The fascicle behavior of the human gastrocnemius has been investigated under various conditions using ultrasonography (Narici et al. 1996; Fukunaga et al. 2001, Chino et al. in press). These studies examined how the fascicle behavior influences the mechanical output at the ankle joint. Although the gastrocnemius is one of the main ankle plantar flexors, its architecture (Kawakami et al. 1998) and activation (Cresswell et al. 1995) have been shown to be markedly influenced by knee joint angle. In prior studies, the influences of knee joint angle on the gastrocnemius fascicle behavior have not been clarified, especially in dynamic contractions. A detailed examination of this point will provide valuable information about the force generating properties of the bi-articular gastrocnemius muscle.

The general purpose of this thesis is to clarify 1) how the fascicle behavior of the gastrocnemius muscle changes in relation to knee joint angle and 2) how these changes influence on the force developed by the gastrocnemius. To this end, the effects of knee joint rotation on the architectural characteristics (fascicle length, pennation angle and external tendon length) of the gastrocnemius were firstly elucidated in passive conditions, and compared with those of the ankle joint rotation. Then, the effects of knee joint angle on the gastrocnemius fascicle behavior were investigated in static and dynamic plantar flexions.

1-2. Terminology

(i) Muscle fascicle

Muscle fascicle is a bundle of muscle fibers surrounded by connective tissue sheath known as perimysium. It has been reported that, in some muscles, the muscle fibers terminate intrafascicularly and do not extend from the proximal to distal aponeuroses (Trotter 1993). However, the fibers of the human triceps surae muscles have been shown to run between two aponeuroses (Kawakami et al. 2000). In the present thesis, therefore, the fascicle length of the medial gastrocnemius muscle (MG), which is the target muscle of the present thesis, is considered to be equal to the fiber length.

(ii) Pennation angle

Pennation angle is defined as the fascicle angle relative to the force-generating axis (Lieber 1992). However, it has been indicated that the aponeuroses in the intact MG were not so slanted to the axis due to the existence of adjacent muscles [e.g. soleus (SOL)] and bones (Kawakami et al. 1998). In this thesis, therefore, the pennation angle is measured as the angle between the fascicle and deep aponeurosis (Figure 1-1).

(iii) Tendinous tissues

The term "tendinous tissues" is used to describe both external tendon and aponeurosis in the present thesis. The length of distal external tendon is defined as the distance between muscle-tendon junction (MTJ) and Achilles tendon insertion point (Figure 1-1, Muramatsu et al. 2001).

(iv) Muscle contraction types

When a muscle is not activated, the muscle is in a passive condition. When a muscle is activated, but not allowed to lengthen or shorten, the contraction is referred to as a static contraction. The contraction that permits the muscle to shorten is referred to as a concentric contraction. On the other hand, when an active muscle is forced to lengthen by external load, the contraction is referred to as an eccentric contraction.

(v) Tendon force and MG force

In the present thesis, the force applied to the Achilles tendon is defined as the tendon force. The tendon force is calculated by dividing plantar flexion torque by the moment arm of the Achilles tendon. On the other hand, the sum of the force that generated by all MG fascicles and effectively transmitted to its tendinous tissues is defined as the MG force. The MG force is a component of the tendon force.

1-3. Anatomical and architectural features of the triceps surae muscles

The MG, lateral gastrocnemius (LG) and SOL are main synergists of ankle plantar flexion. Each of the muscles has different anatomical and architectural features as summarized in Table 1-1.

Both of the gastrocnemius muscles originate from the posterior and superior surfaces of medial (MG) and lateral (LG) femoral condyles, and thus they are bi-articular muscles, crossing knee and ankle joints. On the other hand, SOL is a mono-articular muscle, crossing only the ankle joint. All the three muscles have the common insertion (i.e. posterior surface of calcaneus). It has been observed that collagen structures connect the aponeuroses of gastrocnemius and SOL, and they increase distally to form the Achilles tendon (Bojsen-Moller et al. 2004, Figure 1-2). The SOL has the largest physiological cross-sectional area (PCSA) among three muscles. The PCSA of MG is approximately 2.5 times greater than that of LG. The MG fascicle is shorter, and its pennation angle is greater as compared to LG.

1-4. Brief history

The purpose of this thesis is to investigate 1) how the fascicle behavior of the gastrocnemius muscle changes in relation to knee joint angles and 2) how these changes influence on the force developed by the gastrocnemius. In this section, related studies are overviewed from following three viewpoints: 1) length changes of fascicle and tendinous tissues of the gastrocnemius by passive knee and ankle joint rotations, 2) gastrocnemius fascicle behavior in active conditions and 3) effects of knee joint angle on the electromyogram (EMG) of the gastrocnemius.

1-4-1. *Length changes of fascicle and tendinous tissues of the gastrocnemius by passive knee and ankle joint rotations*

Using human cadavers, some researchers have measured changes in the gastrocnemius muscle-tendon complex (MTC) length in relation to knee and ankle joint angles to obtain its moment arm (Grieve et al. 1978, Spoor et al. 1990, Visser et al. 1990). However, these studies did not focus on the length changes of fascicle or tendinous tissues, which compose an MTC. In 1992, Henriksson-Larsen et al. and Rutherford and Jones have used, one after another, B-mode ultrasonography as a method to visualize the muscle fascicles in vivo in humans. Since then, several attempts have been made to determine the length changes of fascicle and tendinous tissues with joint angles in passive conditions.

Narici et al. (1996) have applied the ultrasonography to MG and measured its fascicle length and pennation angle in vivo. They showed that when the ankle joint was plantar flexed at rest, the fascicle shortened and the pennation angle increased (Figure 1-3). Similar findings have also been presented by Maganaris et al. (1998). Kawakami et al. (1998) have found that the fascicle length and pennation angle of MG are altered not only by the ankle joint angle but also by the knee joint angle. Herbert et al. (2002) have determined MG fascicle length at various knee and ankle joint positions. From their findings, the fascicles took up by 27% of changes in MTC length, and thus much of the change occurred in the tendinous tissues primarily due to their high compliance at low force levels. Muraoka et al. (2002) have compared length changes of distal external tendon and deep aponeurosis of MG during passive ankle joint motions. They revealed a greater length change in the external tendon compared to the aponeurosis. Furthermore, De Monte et al. (2006) have investigated the lengths of MG fascicle, distal external tendon and deep aponeurosis during passive knee and ankle joint motions. Their results were consistent with those reported by Herbert et al. (2002) and Muraoka et al. (2002).

As described above, a number of studies have been made to examine the length changes of fascicle and tendinous tissues of the gastrocnemius with knee and ankle joint angles under passive conditions. However, it is unclear whether the knee and ankle joint rotations have the same effect on the length of each of fascicle and tendinous tissues. Bojsen-Moller et al. (2004) have reported that the distal external tendon of MG attaches to the tendinous tissues of SOL (Figure 1-2). Considering that the SOL architecture is independent of knee joint angle (Kawakami et al. 1998), the length of distal external tendon of MG may not be changed by the knee joint motion, although it was shown to be influenced by the ankle joint motion (Muraoka et al. 2002; De Monte et al. 2006).

1-4-2. *Gastrocnemius fascicle behavior in active conditions*

Since the force generating potential of a fascicle is dependent on its length (Gordon et al. 1966) and velocity (Hill 1938), many researchers has investigated the behavior of MG fascicles in the contracted conditions using ultrasonography. Narici et al. (1996) have determined the MG fascicle length and pennation angle during static plantar flexions. They revealed that, from rest to maximal voluntary contraction (MVC), the fascicle length and pennation angle gradually decreased and increased, respectively (Figure 1-4). Maganaris et al. (1998) have scanned the MG fascicles at nine sites over the muscle belly during static plantar flexions. Their results demonstrated that the changes of the fascicle length and pennation angle were consistent over a major part of the muscle. Kawakami et al. (1998) have measured the fascicle length and pennation angle of MG during static plantar flexions at various knee and ankle joint angles. From their findings, the fascicle lengths were shorter and the pennation angles were greater at the flexed knee positions than those at the extended position, indicating that the MG force decreased with knee flexion. Maganaris (2003) has associated the fascicle length during MVC with the mechanical output, and estimated the length-force relation of the MG fascicle. He suggested that MG fascicles operated on the ascending limb of the length-force relation (Figure 1-5).

Chino et al. (in press) have examined the fascicle behavior of MG during maximal concentric and eccentric plantar flexions. They found that the fascicle velocities were not identical to those of MTC, and much of MTC length change was accounted for by those of the tendinous tissues in both concentric and eccentric contractions. Kubo et al. (2000) have determined the MG fascicle length during cyclic ankle bending exercises. When the exercise was performed at higher frequency (1.0 Hz), the fascicle length was almost unchanged in the first half of the plantar flexion phase (Figure 1-6). They suggested that the fascicles could develop high force in relation to the velocity-force relationship due to the elongation of tendinous tissues. Kawakami et al. (2002) have demonstrated that the MG fascicle maintains an almost constant length when the ankle joint was dorsiflexed in a counter-movement exercise at the ankle joint. On the other hand, Sugisaki et al. (2005) have reported that the MG fascicle is lengthened during the dorsiflexion phase of rebound exercise at the ankle joint.

The MG fascicle behavior during multi-joint movements has also been studied. In the stance phase of walking, the MG fascicle maintained a near-constant length, while the MTC was elongated (Fukunaga et al. 2001; Ishikawa et al. 2005a; 2007; Lichtwark et al. 2007). During vertical (Kurokawa et al. 2001) and counter-movement jumping (Kurokawa et al. 2003), MG fascicle has been shown to be able to exert force with a relatively low velocity in the last part of push-off because of the elasticity of tendinous tissues. The MG fascicle during running has been demonstrated to shorten throughout the ground contact phase, while MTC is lengthened and subsequently shortened (Ishikawa et al. 2007; Lichtwark et al. 2007). Ishikawa et al. (2005b) have reported that MG fascicle continues to shorten during the ground contact of drop jumping from low height. They found that only when the drop height exceeded the optimal level, the fascicle was lengthened during the braking phase. On the other hand, the fascicle behavior of MG was compared with that of mono-articular SOL in walking (Ishikawa et al. 2005a) and drop jumping (Sousa et al. 2007). As a result, the patterns of fascicle length change were different between MG and SOL in both walking (Figure 1-7) and drop jumping (Figure 1-8).

In previous studies, MG fascicle behavior during active conditions has been examined and discussed in relation to the mechanical output at the ankle joint. As a consequence, the behavior of MG fascicle varies with the mode and intensity of the movements taken. This may be related to the bi-articular nature and long tendinous tissues (Herbert et al. 2002) of MG.

1-4-3. *Effects of knee joint angle on the EMG of the gastrocnemius*

As mentioned above, the MG fascicles gradually shorten from rest to maximal static plantar flexions (Figure 1-4, Narici et al. 1996). This finding suggests that muscle activation levels have a strong influence on the behavior of fascicles. Hence, it is necessary to consider muscle activation for interpreting the fascicle behavior.

Many studies have examined the effects of knee joint angle on MG activation levels by using EMG. Cresswell et al. (1995) have indicated that the EMGs of MG during maximal static plantar flexions gradually decrease as the knee joint is flexed (Figure 1-9). Similar findings were reported by other researchers (Miaki et al. 1999; Pinniger et al. 2000; Arampatzis et al. 2006; Shinohara et al. 2006). The MG EMGs during concentric plantar flexions have also been shown to decrease at flexed knee positions (Carpentier et al. 1999; Price et al. 2003). These findings were obtained using surface EMG. Hence, there is a possibility that the decrease in MG EMGs with knee flexion may be due to the impaired neuromuscular transmission or changes in electrode-muscle configuration (Cresswell et al. 1995). Even when fine-wire electrodes were applied, however, the EMGs were shown to be reduced with knee flexion (Cresswell et al. 1995). Furthermore, using a needle electrode, Kennedy and Cresswell (2001) have revealed that the activities of MG motor unit are inhibited at the flexed knee position. These findings suggest that the declined EMGs at flexed knee positions are attributable to the impairment of neuromuscular transmission rather than the change in electrode-muscle configuration. Consequently, it is likely that the activation levels of MG during static and concentric plantar flexions would be reduced at flexed knee positions as compared to extended ones.

1-5. Purpose

As mentioned in the Brief history, the architecture (Kawakami et al. 1998; Maganaris 2003) and EMGs (Cresswell et al. 1995; Arampatzis et al. 2006) of MG in static contractions are affected by the knee joint angle, and this results in the lower mechanical output at flexed knee positions. Hence, it may be expected that the fascicle behavior during dynamic contractions is also altered by the knee joint angle. However, the effects of knee joint angle on the MG fascicle behavior during dynamic contractions have not been examined so far. To clarify this point will provide valuable information on the force generating properties of the bi-articular MG.

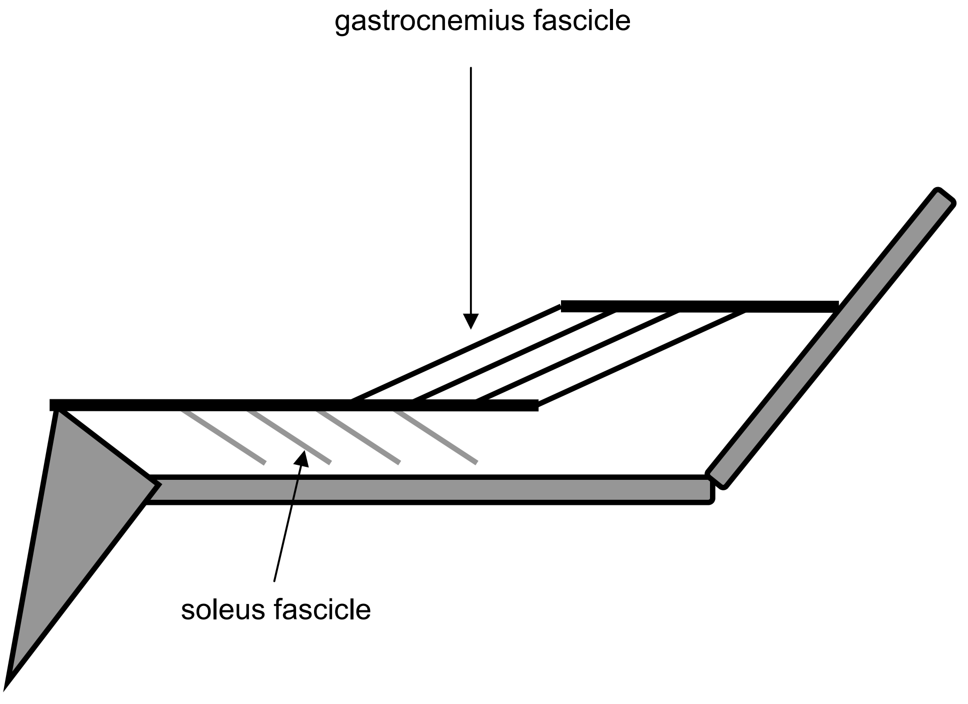
The general purpose of the present thesis is to examine 1) how the fascicle behavior of MG changes in relation to the knee joint angle and 2) how these changes influence on the force produced by the gastrocnemius. To this end, the effects of knee joint motion on the architectural characteristics (fascicle length, pennation angle and external tendon length) of MG were firstly clarified in passive conditions, and compared with those of the ankle joint motion. Then, the effects of knee joint angle on the MG fascicle behavior were investigated in static and dynamic plantar flexions. The outlines of each chapter are as follows.

In Chapter 2, the changes of architectural parameters of MG were determined during passive knee and ankle joint motions. The length changes of fascicle and external tendon for a certain length changes of MTC were compared between the knee and ankle joint motions.

In Chapter 3, MG fascicle length was determined during static and concentric contractions at extended and flexed knee positions. The effects of knee joint angle on the MG fascicle behavior during concentric contractions and its relevance to the tendon force were discussed.

In Chapter 4, MG fascicle length was determined during static and eccentric plantar flexions with the knee fully extended and flexed. The effects of knee joint angle on the MG fascicle behavior during eccentric contractions were clarified.

In Chapter 5, the effects of knee joint angle on the force generation of MG were firstly discussed. Secondly, several limitations that might affect the interpretation of the present results were addressed.



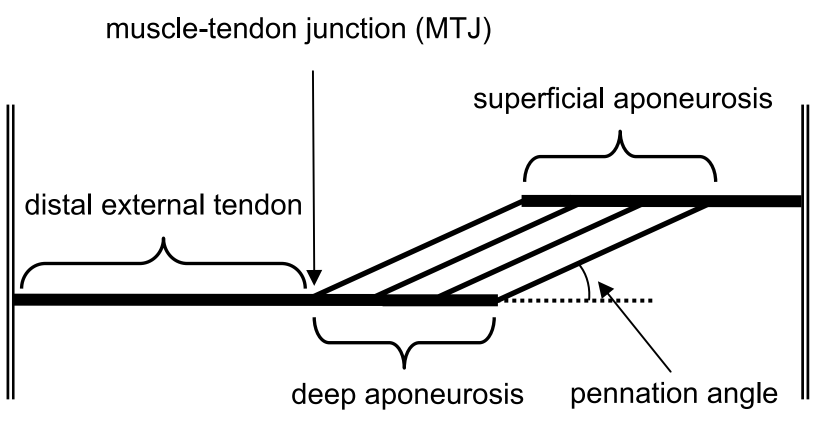


Figure 1-1. Schematic representation of the gastrocnemius muscle-tendon complex (MTC). The length of distal external tendon is defined as the distance between muscle-tendon junction (MTJ) and Achilles tendon insertion point.

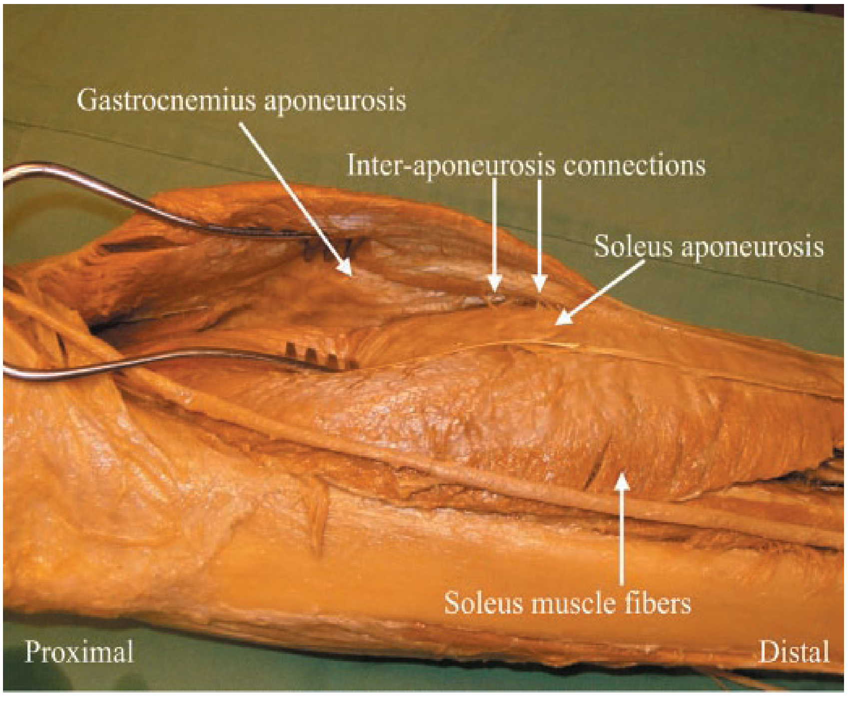


Figure 1-2. Medial view of a cadaver dissection of the gastrocnemius-soleus junction. The picture from Bojsen-Moller et al. (2004).

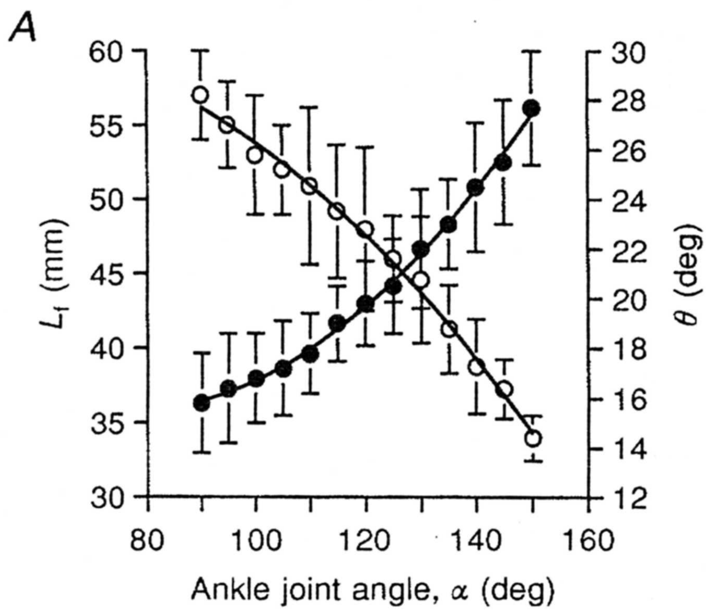


Figure 1-3. The fascicle length (L_f, ○) and pennation angle (θ, ●) of the medial gastrocnemius (MG) as a function of ankle joint angle at rest. An increase of ankle joint angle means plantar flexion. Data from Narici et al. (1996).

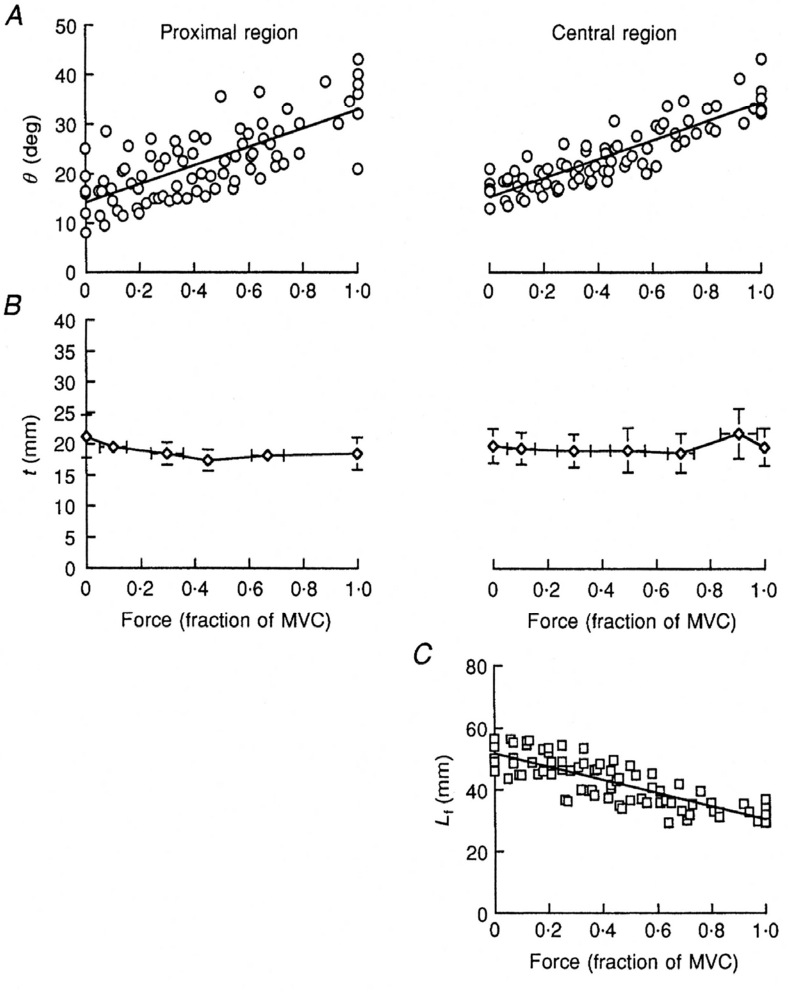


Figure 1-4. The pennation angle (θ, ○, upper), muscle thickness (t, ◇, middle) and fascicle length (L_f, □, lower) of the medial gastrocnemius (MG) as a function of exerted force. Left and right graphs show the data obtained from proximal and central region of MG muscle belly, respectively. Data from Narici et al. (1996).

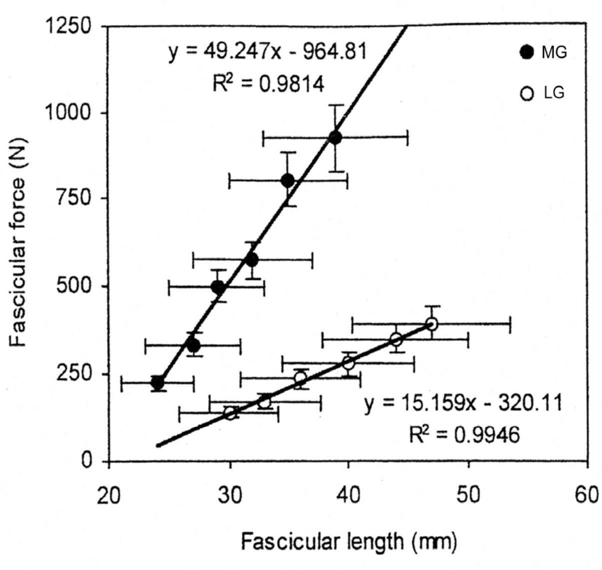


Figure 1-5. Length-force relation of muscle fascicle for the medial gastrocnemius (MG, ●) and lateral gastrocnemius (LG, ○). Data from Maganaris (2003).

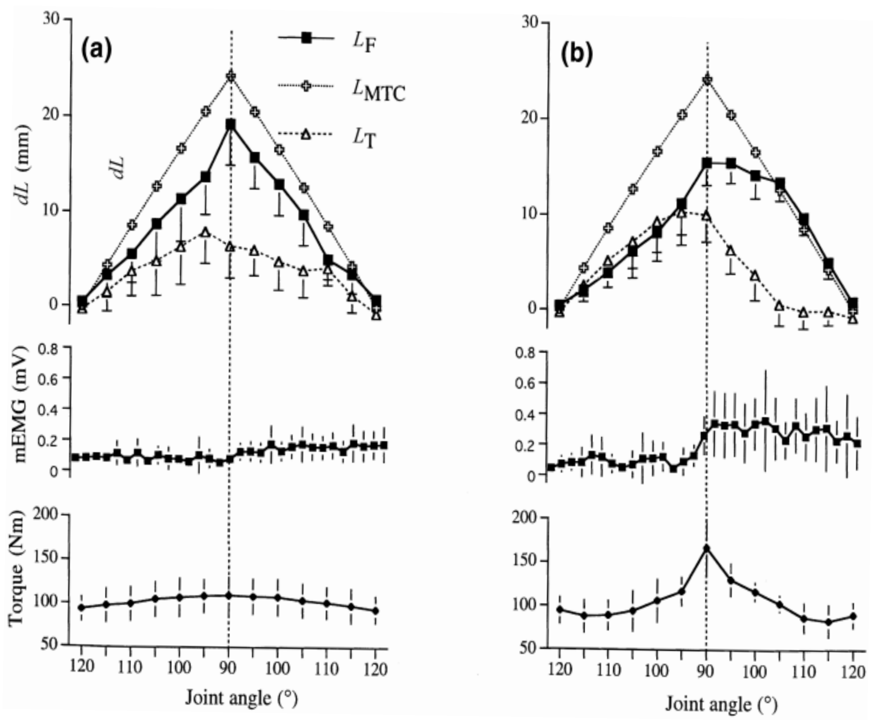


Figure 1-6. The fascicle length (L_F), tendinous tissue length (L_T), muscle-tendon complex (MTC) length (L_{MTC}), electromyograms (EMG) and ankle joint torque against ankle joint angles during slow (a; 0.3 Hz) and fast (b; 1.0 Hz) ankle bending exercises. Data from Kubo et al. (2000).

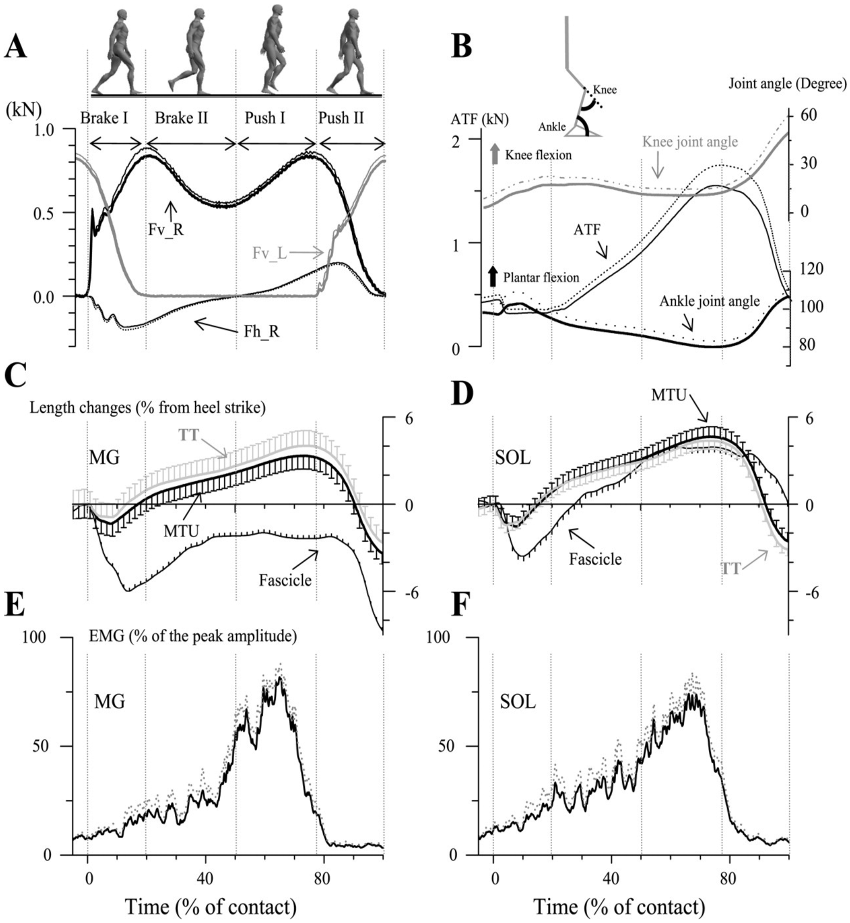


Figure 1-7. Time courses of the vertical reaction force right (Fv_R) and left (Fv_L) legs and horizontal ground reaction force of right leg (Fh_R) (A), Achilles tendon force (ATF) and joint angles (B), length changes of muscle-tendon complex (MTU), fascicle and tendinous tissues (TT) [medial gastrocnemius (MG, C) and soleus (SOL, D)] and electromyogram (EMG) of MG (E) and SOL (F) during walking. Data from Ishikawa et al. (2005a).

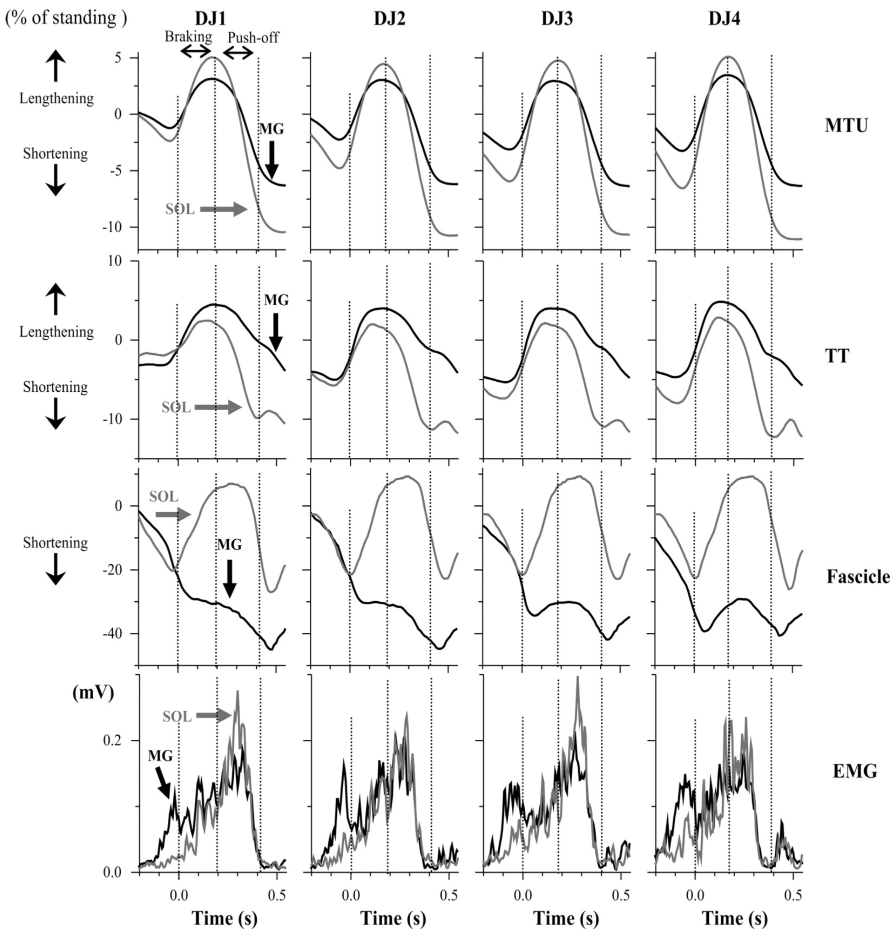


Figure 1-8. Typical example of the time courses of length changes of muscle-tendon complex (MTU), tendinous tissues (TT) and fascicle, together with the electromyogram (EMG) for the medial gastrocnemius (MG) and soleus (SOL) muscles during drop jumps. Dropping heights were increased from DJ1 to DJ4. Vertical dotted lines show the moment of the contact, end of the braking phase and take-off. Data from Sousa et al. (2007).

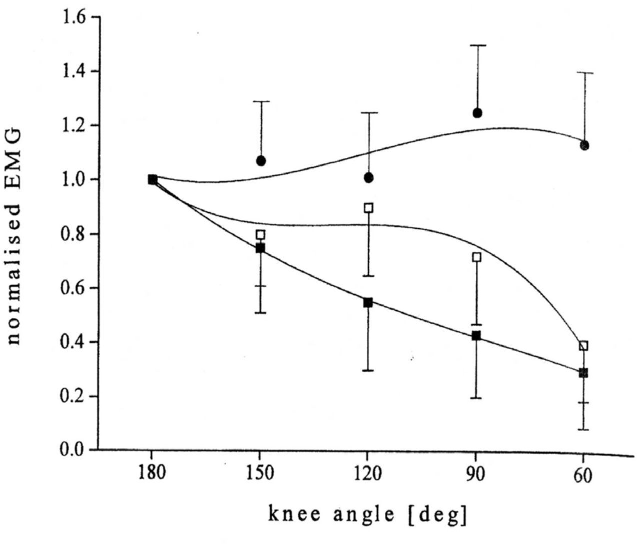


Figure 1-9. The electromyogram (EMG) of the medial gastrocnemius (MG, ■), lateral gastrocnemius (LG, □) and soleus (SOL, ●) during maximal static plantar flexions as a function of knee joint angle. An increase of knee joint angle means knee joint flexion. Data from Cresswell et al. (1995).

Table 1-1.
Anatomical and architectural features of the triceps surae muscles from the literature

	MG	LG	SOL	reference
Origin	Posterior/superior surfaces of medial femoral condyles	Posterior/superior surfaces of lateral femoral condyles	Posterior proximal surface of fibula	a
Insertion	Posterior surface of calcaneus	Posterior surface of calcaneus	Posterior surface of calcaneus	a
Muscle volume (cm^3)	243.7 ± 33.0	140.8 ± 27.7	489.1 ± 64.5	b
Maximum ACSA (cm^2)	16.5 ± 2.1	11.2 ± 1.6	30.0 ± 3.7	b
PCSA (cm^2)	68.3 ± 7.3	27.8 ± 4.2	230.0 ± 36.7	b
Muscle length (mm)	248.3 ± 17.1	216.7 ± 18.8	309.5 ± 2.1	c
Fascicle length (mm)	35.3 ± 3.5	50.6 ± 9.7	19.5 ± 0.7	c
Pennation angle (°)	16.7 ± 7.6	8.3 ± 2.9	25.0 ± 7.1	c

Values are means ± standard deviations (SDs). a: Lieber (1992), b: Fukunaga et al. (1992), c: Wickiewicz et al. (1983), MG: medial gastrocnemius, LG: lateral gastrocnemius, SOL: soleus, ACSA: anatomical cross-sectional area, PCSA: physiological cross-sectional area

CHAPTER 2 Length changes of fascicle and tendinous tissues of the gastrocnemius during passive knee and ankle joint motions

2-1. Introduction

Several studies have examined the architectural changes of MG in relation to knee and ankle joint angles under passive conditions (Narici et al. 1996; Kawakami et al. 1998; Herbert et al. 2002; Muraoka et al. 2002; De Monte et al. 2006). However, it is unclear whether the knee and ankle joint motions have the same effect on the lengths of fascicle and tendinous tissues. Bojsen-Moller et al. (2004) have reported that the distal external tendon of MG attaches to the tendinous tissues of SOL, which crosses only the ankle joint. Considering that the SOL architecture is independent of knee joint angle (Kawakami et al. 1998), the length of distal external tendon of MG may not be altered by the knee joint rotation, although it has been demonstrated to be influenced by the ankle joint motion (Muraoka et al. 2002; De Monte et al. 2006).

This chapter aimed to clarify the architectural changes of MG during passive knee and ankle joint motions. The length changes of fascicle and distal external tendon of MG during passive knee joint motions were compared with those during ankle jont motions.

2-2. Methods

(i) Subjects

Seven healthy men voluntarily participated in this study. Means ± standard deviations (SDs) of their age, height and body mass were 24.4 ± 2.0 years, 170.3 ± 4.5 cm and 66.7 ± 6.0 kg, respectively. All subjects had no disability in their right leg. The subjects gave their written informed consent to participate in the study. This study was approved by the Human Research Ethics Committee in the Faculty of Sport Sciences, Waseda University.

(ii) Experiment protocol

The subjects lay prone on a test bench with the knee fully extended (0°). The right foot of the subject was strapped to an attachment of a dynamometer (Model VEL-016, VINE, Japan) with an ankle joint angle at 0° (neutral position, negative and positive values denote dorsiflexion and plantar flexion, respectively). The rotation axis of the ankle joint was aligned with that of the dynamometer. After a warm-up exercise with submaximal effort, the subjects exerted maximal static plantar flexion and dorsiflexion torque. They performed two maximal trials for each contraction with a rest of more than 1 min between them. The trial with the greater torque was used for further analysis.

In the measurement of knee joint motion, the subjects were instructed to extend slowly the knee joints from 90° flexed position to 0° with a fixed ankle joint angle at 0° (Figure 2-1). The knee joint angles were measured with a goniometer (SG150, Biometrics, UK) and visually fed back to the subjects by a monitor set in front of them. With this feedback, each subject could extend his knee joints so as not to exceed the angular velocity of more than 5°/s. The subjects were instructed to extend the knee joints using the hip joints and arms with leg muscles completely relaxed in order to accomplish a passive knee joint motion for MG.

In the measurement of ankle joint motion, the ankle joint was passively changed by the dynamometer from maximally dorsiflexed to plantar flexed position (Figure 2-1). Angular velocity was set to keep below 5°/s, so as not to provoke stretch reflex (Hufschmidt and Mauritz 1985; Nicol and Komi 1999). The subjects were instructed to relax the leg muscles completely during the passive ankle joint motion.

(iii) Data acquisition

The fascicle and MTJ of MG during the passive knee and ankle joint motions were visualized using a B-mode ultrasonic apparatus (SSD-6500, Aloka, Japan). An electronic linear array probe (UST-5712, 10 MHz wave frequency, Aloka, Japan) was placed on the muscle belly and MTJ along the longitudinal direction of MG, and fixed on the skin using surgical tapes. Echo jelly was applied on the surface of the probe. When the probe was applied on MTJ, a water bag (MP-2463, Aloka, Japan) was attached to it. A marker was placed between the water bag and the skin, and fixed on the skin. Ultrasound images were recorded on a videotape (S-VHS) at 30 Hz via a video timer (VTG-55, FOR-A, Japan) for synchronization.

Recorded images were digitally converted using a media converter (ADVC-500, Canopus, Japan) and transferred to a computer. An image processing program (Image J, National Institute of Health, USA) was used to measure the fascicle length, pennation angle and MTJ displacement. The analysis was conducted at every 1° of angle change in the knee and ankle joints during passive knee and ankle joint motions, respectively. The fascicle length was measured as the distance from the intersection points of fascicle and deep and superficial aponeuroses (Figure 2-2A). The pennation angle was determined as the angle between fascicle and deep aponeurosis. The MTJ was determined as the intersection point of the most distal fascicle and deep aponeurosis (Figure 2-2B). The MTJ displacement was defined as its horizontal displacement relative to the marker.

Surface EMGs were recorded from MG, LG, SOL and tibialis anterior (TA) muscles. After the preparation of the skin, pairs of electrodes (Blue Sensor, Ambu A/S, Denmark, sensor: Ag/AgCl, measuring area: 154 mm^2) were placed at the belly of each muscle with an inter-electrode distance of 20 mm. The reference electrode was placed at the medial malleolus of the left foot. The EMG signals were amplified (input impedance >10 MΩ, common mode rejection ratio >80 dB, time constant: 0.03 s, hi-cut filter: off) with a multi telemeter system (WEB-5000, NIHON KOHDEN, Japan).

The ankle joint angle was measured with a goniometer (SG110/A, Biometrics, UK). The joint angle and EMG signals were digitally converted using an A/D converter (PowerLab/16SP, AD Instruments, Australia), and sampled at 1 kHz.

(iv) Data processing

The joint angles were processed with a Butterworth-type low-pass filter of the fourth order (cutoff frequency: 20 Hz). By using the knee and ankle joint angles and leg length (distance between the knee and ankle joint centers) of each subject, the length change of MG MTC (ΔL_{MTC}) was calculated (Grieve, et al., 1978) with reference to the knee and ankle joint angles at 0°. The length change of the distal external tendon was calculated as the difference between the displacement of MTJ and Achilles tendon insertion (Muraoka et al. 2002) (Figure 1-1). In the passive knee joint motion, because the ankle joint was fixed, the displacement of Achilles tendon insertion was hardly observed. Therefore, changes in the external tendon length during the passive knee joint motion were determined by defining the proximal and distal displacement of MTJ as lengthening and shortening, respectively. In the passive ankle joint motion, the displacement of Achilles tendon insertion was regarded as identical to ΔL_{MTC}, because the knee joint was fixed.

The EMG data were full wave rectified. In the maximal static plantar flexion and dorsiflexion, the mean amplitude of EMG was calculated during a 0.5-s period when the exerted torque reached a steady state. The mean amplitude was calculated every 0.5 s during passive joint motions and normalized to the value in the maximal static contractions.

(v) Statistical analysis

Descriptive data were presented as means ± SD. A two-way analysis of variance (ANOVA) [2 test conditions (knee and ankle joint motions) × 6 ΔL_{MTC} (–25, –20, –15, –10, –5, 0 mm)] with repeated measures was used to test the effects of the test condition and ΔL_{MTC}. When the interaction between the two factors was significant, a one-way ANOVA was conducted on every group categorized by the two factors, followed by Bonferroni post hoc tests. Statistical software (SPSS 12.0J, SPSS Japan, Japan) was used for all analyses.

Statistical significance was set at $P < 0.05$.

2-3. Results

The angular velocity during passive knee joint motion ranged from 1.6°/s to 4.2°/s. The ankle joint angle that all the subjects achieved in the passive ankle joint motion ranged from –9° to 35°. The EMG activities of MG were less than 1.7 ± 1.7% and 0.4 ± 0.6% of those during maximal static plantar flexions, for the passive knee and ankle joint motions, respectively.

The passive knee joint motion from 90° to 0° lengthened the fascicle from 39.4 ± 4.5 mm to 61.7 ± 4.6 mm and decreased the pennation angle from 24.4 ± 2.2° to 20.5 ± 1.9° (Figure 2-3 left). The MTJ displacement in the knee joint motion was only –0.2 ± 1.3 mm. The passive ankle joint motion from –9° to 35° shortened the fascicle from 66.5 ± 5.9 mm to 44.6 ± 4.7 mm, and increased the pennation angle from 18.9 ± 1.6° to 26.3 ± 1.5° (Figure 2-3 right). In the passive ankle joint motion, MTJ moved to distal (4.1 ± 1.1 mm) by dorsiflexion and moved to proximal (–17.5 ± 1.9 mm) by plantar flexion, as compared to the neutral position.

The two-way ANOVA indicated that the fascicle length was affected by the test condition and ΔL_{MTC} ($P < 0.01$) with an interaction ($P < 0.01$, Figure 2-4). The fascicle lengths changed with the MTC length both in passive knee and ankle joint motions. However, the fascicle lengths at ΔL_{MTC} of –25, –20, –15 and –10 mm were different between the knee and ankle joint motions.

The effects of the test condition and ΔL_{MTC} on the length change of the external tendon were significant ($P < 0.01$) with an interaction ($P < 0.01$, Figure 2-5). With shortening of MTC, the external tendon length decreased during the passive ankle joint motion, but that during the knee joint motion was almost constant. The length changes of external tendon were different between knee and ankle joint motions at ΔL_{MTC} of –25, –20, –15 and –10 mm.

2-4. Discussion

The present study aimed to investigate the length changes of fascicle and external tendon of MG during passive knee and ankle joint motions. The main findings of this study were 1) the MG fascicle length at a given ΔL_{MTC} differed between the passive knee and ankle joint motions (Figure 2-4), and 2) the external tendon length changed by the passive ankle joint motion, but not by the passive knee joint motion (Figure 2-5). Using a planimetric model (Huijing and Woittiez 1984; 1985), these results can be expressed by a schematic view as shown in Figure 2-6. The model indicates the MTC at the knee flexed position (A), with knee and ankle joint angles at 0° (B), and at the plantar flexed position (C). Although the length change of MTC induced by knee joint motion (A-B) is identical with that induced by ankle joint motion (B-C), the lengths of fascicle and external tendon are different between A and C. The present results indicate that the difference in the joint to move (i.e. proximal or distal) is a factor that affects the length changes of the fascicle and external tendon under passive conditions.

The present result that MTJ did not move during the passive knee joint motion (Figure 2-3) is inconsistent with the report of De Monte et al. (2006). In their study, the MTJ moved by approximately 5 mm during passive knee joint motions from 114.5° to 6.3°. This discrepancy can be explained by the difference between the body postures taken in the two studies. In the passive knee joint motion executed by De Monte et al. (2006), subjects lay prone, and the leg was rotated with the trunk and thigh fixed. In this case, the effects of the gravity acting on the muscle would vary depending on the knee joint angle. This may change the MTJ position relative to the ultrasound probe during the passive knee joint motion. In support of this, my preliminary experiments showed that about 7 mm of MTJ displacement was observed during passive knee joint motion when the subjects sat with the trunk and thigh fixed, and the leg was rotated. On the other hand, the leg was unchanged in the present experiments, and the trunk and thigh were moved to rule out the possible effects of the gravity on MTJ displacement. Therefore, it is reasonable to assume that the present results would properly reflect the MTJ displacement during passive knee joint motions.

The length changes of the fascicle and external tendon were different between the passive knee and ankle joint motions (Figure 2-4, 2-5). The phenomena would be related to the fact that the distal external tendon of MG attaches to the tendinous tissues of SOL (Bojsen-Moller et al. 2004). The SOL is a mono-articular muscle which crosses only the ankle joint, and thus its architecture has been shown to be not altered by knee joint angle (Kawakami et al. 1998). This suggests that the tendinous tissue length of SOL is also independent of the knee joint angle. Therefore, the length change of distal external tendon of MG would be limited by its connection with SOL tendinous tissues, when the knee joint was passively extended (Figure 2-6 A-B). On the other hand, when the ankle joint was passively rotated, the changes in the passive force altered the external tendon length of MG (Muraoka et al. 2002) as well as SOL architecture (Kawakami et al. 1998). These different length changes of external tendon would result in the difference in the fascicle length at a given MTC length.

Another possible explanation for the different length changes of the fascicle and external tendon is the influences of viscosity of MTC. The present study analyzed the lengthening and shortening phases of MG MTC in the passive knee and ankle joint motions, respectively (Figure 2-1). There is a possibility that the length changes of fascicle and tendinous tissues may not be the same for lengthening and shortening phases because of their viscosity (Lieber et al. 1991). Moreover, the velocity of MTC was not identical in the knee and ankle joint motions. Hence, the difference in the velocity of MTC may also affect the present results, since the influence of viscosity depends on the velocity of length change (Hubbard and Soutas-Little 1984; Danto and Woo 1993). In the passive knee and ankle joint motions, however, the velocities of MTC were calculated to be 0.2 ± 0.1 %/s and 0.9 ± 0.1 %/s, respectively. The velocities of MTC (Heerkens et al. 1987; Syme 1990) and tendon (Herrick et al. 1978; Ker 1981) occurred in the locomotion have a small influence on their viscosity.

Considering these points into account, it seems that the viscosity of MTC would not have a substantial influence on the behavior of the fascicle and external tendon in the present experiments.

In summary, the present study showed that the length changes of MG fascicle and external tendon relative to a given MTC length differed between the passive knee and ankle joint motions. This difference may be related to the fact that the external tendon of MG attaches to SOL tendinous tissues.

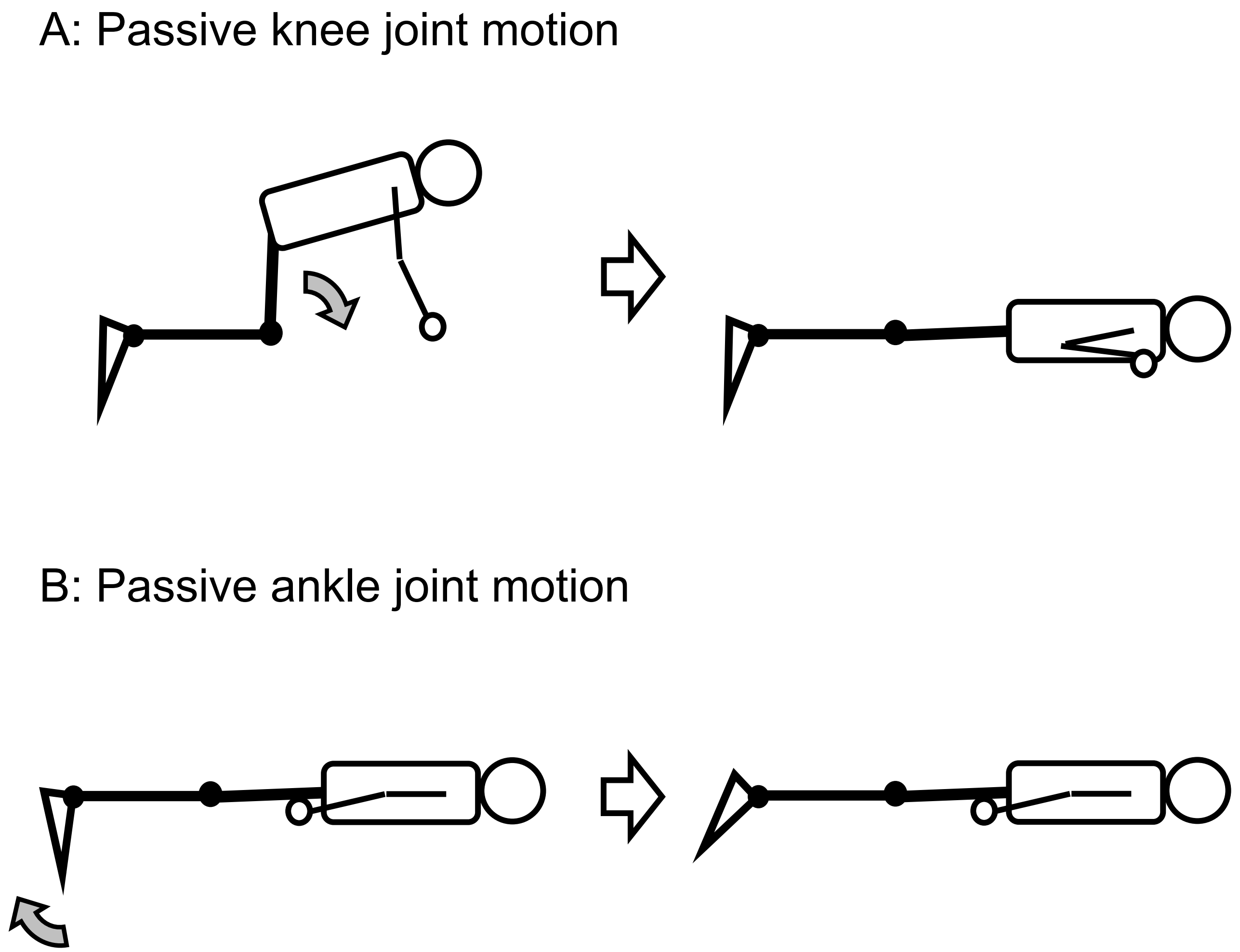


Figure 2-1. Schematic drawings of the passive knee (A) and ankle (B) joint motion. A: The subjects slowly extended their knee joints from 90° (left) to 0° (right) with the leg muscles completely relaxed. B: The ankle joint was passively moved from maximal dorsiflexed position to maximal plantar flexed position.

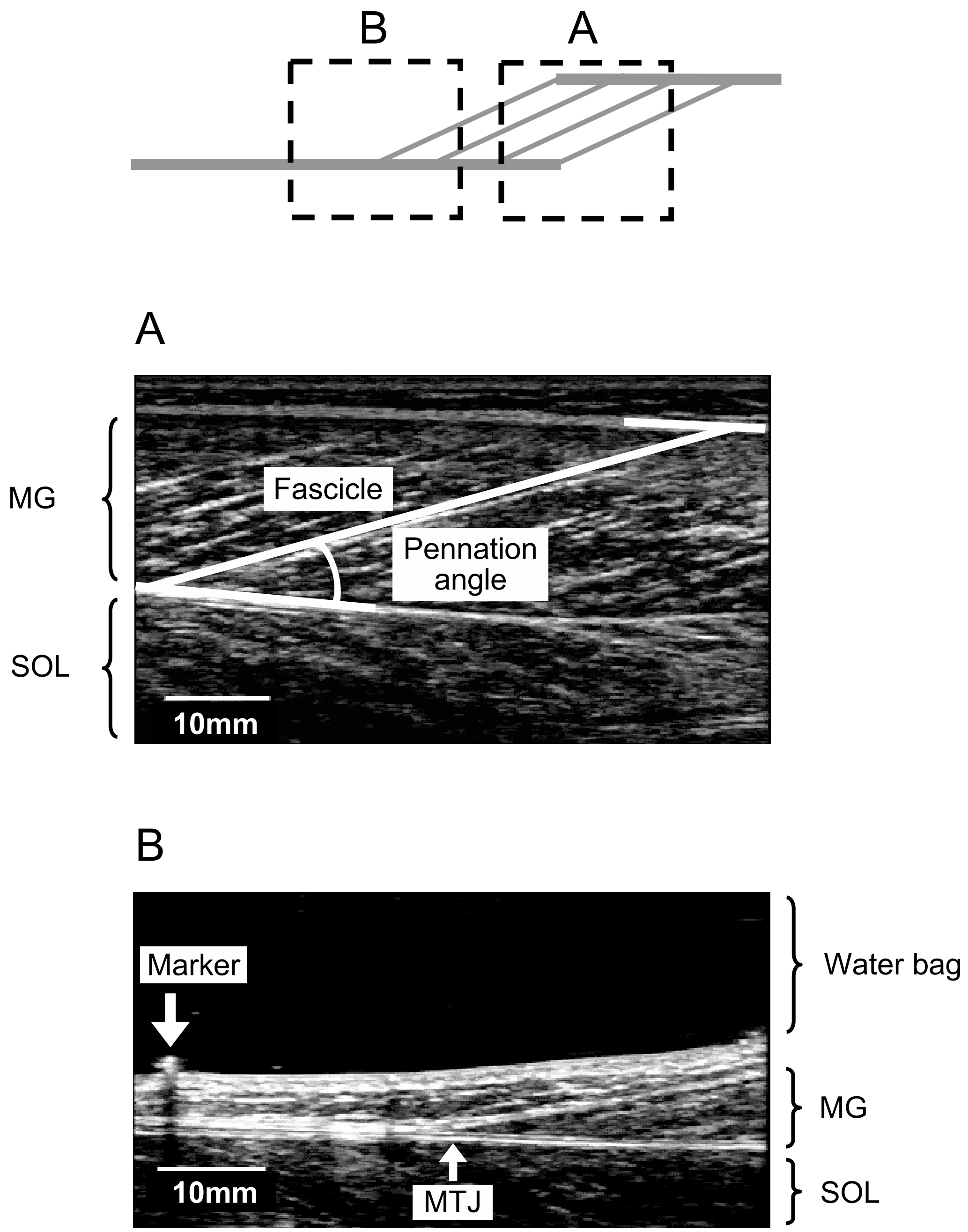


Figure 2-2. Typical ultrasound images of muscle belly (A) and around distal edge (B) of the medial gastrocnemius (MG). A: The fascicle length and pennation angle were measured at every 1° of knee or ankle joint angles. B: Horizontal displacement of muscle-tendon junction (MTJ) was determined relative to the marker. SOL: soleus.

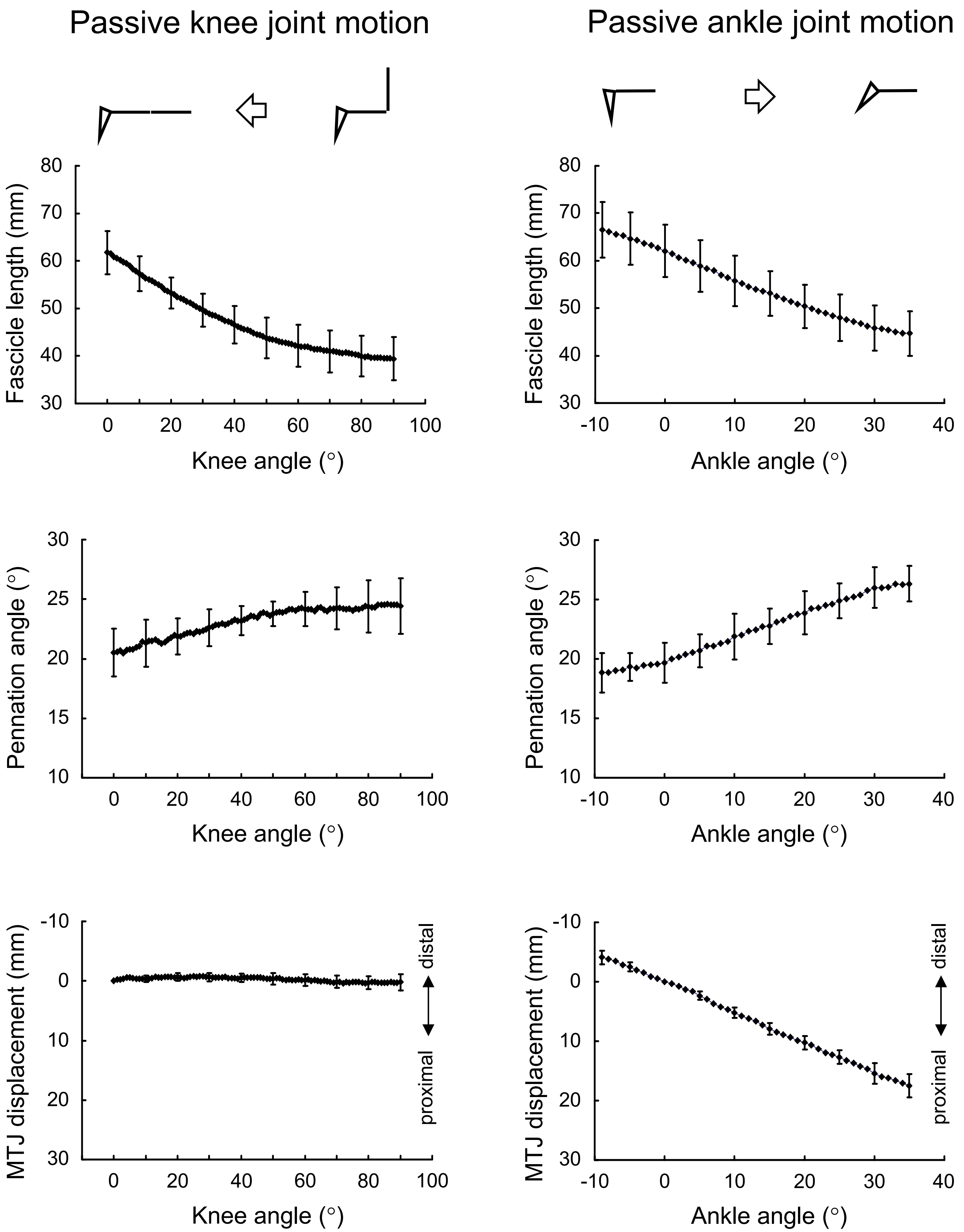


Figure 2-3. The fascicle length (upper), pennation angle (middle) and muscle-tendon junction (MTJ) displacement (lower) during passive knee (left) and ankle (right) joint motions. The MTJ displacement was calculated with reference to the knee and ankle joint angles at 0°.

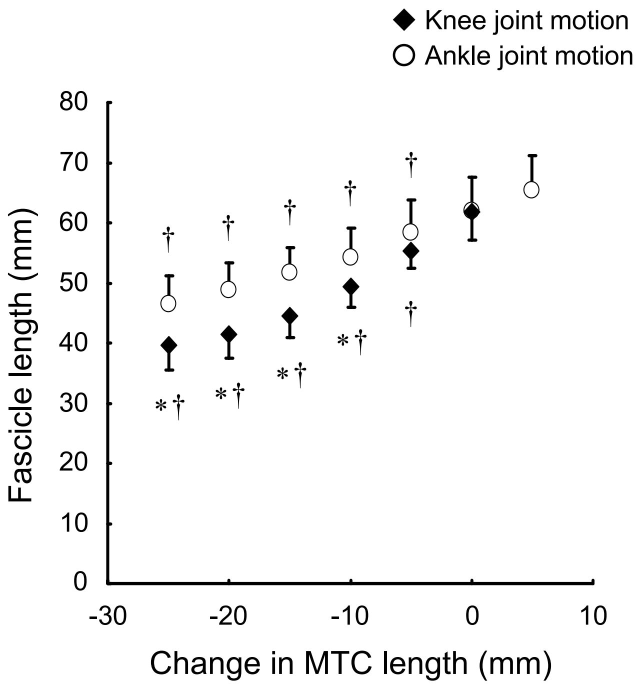


Figure 2-4. Relationship between the change in muscle-tendon complex (MTC) length and fascicle length. * denotes that the difference between knee and ankle joint motions is significant. † denotes that the value is significantly different from that at ΔL_{MTC} of 0 mm.

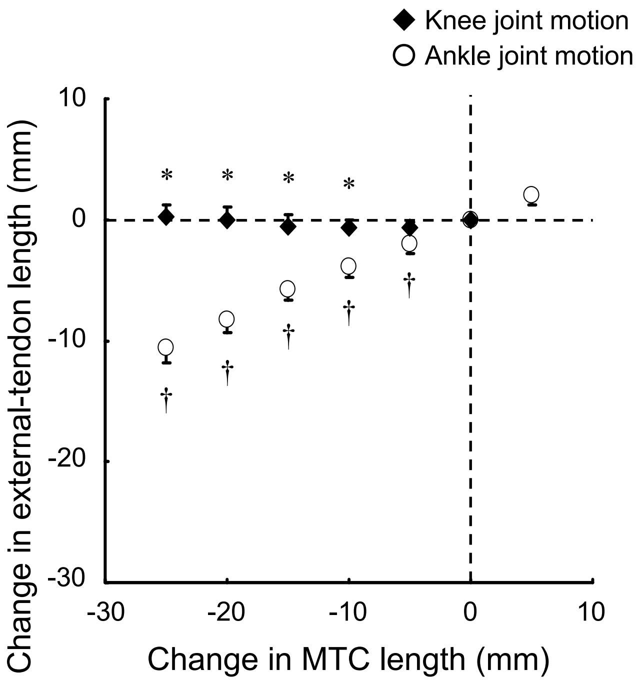


Figure 2-5. Relationship between the length change in muscle-tendon complex (MTC) and external tendon. * denotes that the difference between knee and ankle joint motions is significant. † denotes that the value is significantly different from that at $\triangle L_{MTC}$ of 0 mm.

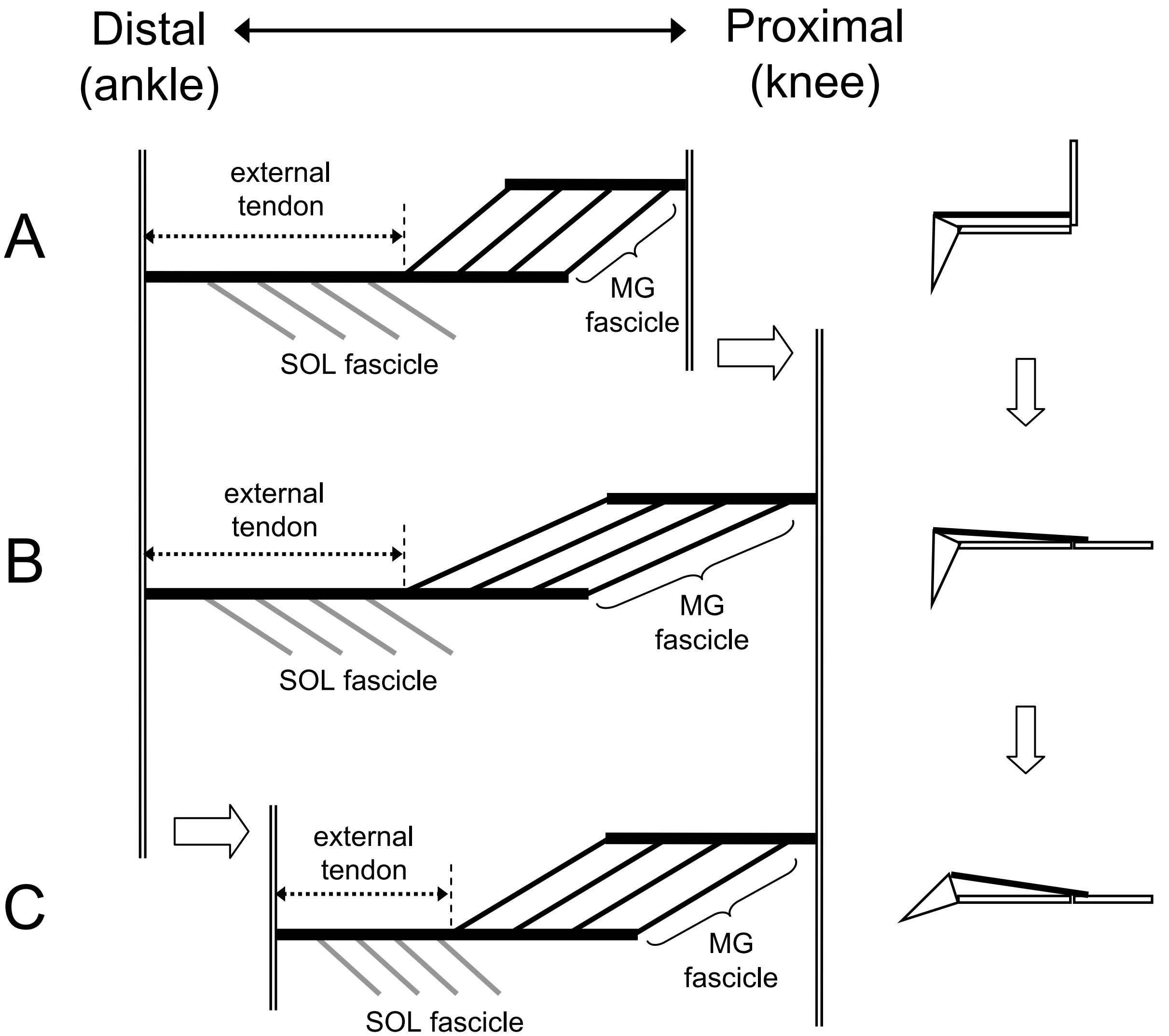


Figure 2-6. A schematic view of the present results. The models show the muscle-tendon complex (MTC) at the flexed knee position (A), with knee and ankle joint angles at 0° (B) and at the plantar flexed position (C). MG: medial gastrocnemius, SOL: soleus.

CHAPTER 3 Effects of knee joint angle on the fascicle behavior of the gastrocnemius during concentric plantar flexions

3-1. Introduction

In Chapter 2, the architectural changes of MG induced by passive knee and ankle joint motions were investigated. As a result, the length changes of MG MTC by the knee joint motion had a greater influence on the fascicle length than those by the ankle joint motion. Considering the decrease of MG EMG with knee flexion (Cresswell et al. 1995; Arampatzis et al. 2006) as well as the architectural changes by knee joint rotation observed in Chapter 2, the MG fascicle behavior during active conditions can be different depending on the knee joint angles. Some previous studies have determined the effects of knee joint angle on the MG fascicle length and pennation angle during static plantar flexions (Kawakami et al. 1998; Maganaris et al. 2003). However, it is unclear how the MG fascicle behavior during dynamic contractions is influenced by the knee joint angle.

The purpose of this experiment was to examine how MG fascicle behavior during concentric plantar flexions changes with knee joint positions. The relevance of the observed fascicle behavior to the tendon force was discussed.

3-2. Methods

(i) Subjects

Seven healthy men (age, 23.9 ± 3.1 years; height, 170.5 ± 3.5 cm; and body mass, 63.8 ± 5.5 kg; mean ± SD) participated as subjects. They were instructed about the aims and procedures of the study. Written informed consent was obtained from all subjects. This study was approved by the Human Research Ethics Committee in the Faculty of Sport Sciences, Waseda University.

(ii) Experimental setup

Subjects lay supine on a test bench of a dynamometer (CON-TREX, CMV AG, Switzerland). They performed maximal static and concentric plantar flexions at two knee joint positions [fully extended (K0) and 45° flexed (K45)] (Figure 3-1) in a randomized order. The right thigh was secured to the bench in K0 and to a pad in K45 to prevent knee joint rotations. The foot was firmly strapped to the footplate of the dynamometer. In static contractions, the ankle joint was fixed at 0° (neutral position). In concentric contractions, the range of motion of the ankle joint was from –10° (dorsiflexed) to 30° (plantar flexed). The subjects were completely relaxed at –10° and then asked to exert the maximal plantar flexion torque until the end of the movements. Angular velocities of the dynamometer were set at 30°/s (slow) and 350°/s (fast). To familiarize the subjects with the testing procedures, two or three trials were performed for each contraction with submaximal and maximal effort. Following a 2-min rest interval after completion of the warm-up, the subjects performed two maximal trials for each contraction. In each of the contractions, the trial in which the greater peak torque was recorded was used for further analysis.

In the fast concentric contractions, the angular velocity of the ankle actually did not reach 350°/s, possibly due to the limited range of motion of the joint (40°). However, the time courses of angle and angular velocity of the ankle joint were almost the same between K0 and K45. In the fast concentric contractions, therefore, the measurement conditions for the subjects were considered to be comparable for the two knee joint positions.

(iii) Torque and angle measurements

Plantar flexion torque was measured with the dynamometer. The ankle and knee joint angles were determined with goniometers (ankle, SG110/A; knee, SG150; Biometrics, UK). The torque and angle signals were sampled at 1 kHz with a 16-bit A/D converter (PowerLab/16SP, ADInstruments, Australia) and transferred to a computer. The data were filtered with a Butterworth-type low-pass filter of fourth order. The cutoff frequency of the filter was 13 Hz, which was determined by residual analysis (Winter 1990).

Passive plantar flexion torque was subtracted from the measured torque to obtain the torque exerted actively by the plantar flexors. The relationship between the ankle joint angle and the passive plantar flexion torque was determined during passive ankle joint motion at a 5°/s in each of K0 and K45. Achilles tendon force was calculated by dividing the active torque by the moment arm of the tendon. The moment arm was calculated by differentiating the length change of MG MTC (Grieve et al. 1978) with respect to the ankle joint angle (radians).

(iv) Ultrasonographic measurements

An ultrasonic apparatus (SSD-6500, Aloka, Japan) was used to visualize the MG fascicle during each contraction. A 10-MHz, linear-array probe (UST-5712, Aloka, Japan) was longitudinally placed to the belly of MG and secured to the skin. Ultrasound images were recorded on a videotape at 30 Hz in the static and slow concentric contractions. In the fast concentric contractions, the images were stored in the computer memory of the apparatus at 95 Hz. An electric signal was superimposed on the images to synchronize them with the torque, joint angles and EMGs.

The ultrasound images were A/D converted (ADVC-500, Canopus, Japan) and stored on a computer. Fascicle lengths and pennation angles were measured using ImageJ software (National Institute of Health, USA). The measurements were performed two times for the same images, and the mean values were used for further analysis. The coefficients of variation in the two measurements were lower than 6.8% and 8.5% for the fascicle length and pennation angle, respectively. The intraclass correlation coefficients were more than 0.997 and 0.991 for the fascicle length and pennation angle, respectively. In the fast concentric contractions, the data obtained with the ultrasonography were interpolated every 10 ms with a cubic spline. The shortening velocity of fascicle was determined as the first derivative of its length changes with respect to time, and expressed as positive values.

(v) EMG recordings

Surface EMGs were recorded from MG, LG, SOL and TA muscles using bipolar Ag/AgCl electrodes (Blue Sensor, Ambu A/S, Denmark, measuring area: 154 mm^2) with an inter-electrode distance of 20 mm. The EMG signals were amplified with a telemeter system (WEB-5000, NIHON KOHDEN, Japan; time constant: 0.03 s, hi-cut filter: off) and stored on the computer after A/D conversion at 1 kHz of sampling frequency (PowerLab/16SP, ADInstruments, Australia). The EMG data were full-wave rectified and averaged over a 0.5-s period in the static contractions and over the entire movement in the concentric contractions.

(vi) Statistics

Values were presented as means ± SDs. A two-way ANOVA (2 knee joint angles × 3 angular velocities for the ankle joint angle at the time of peak tendon force and EMGs of each muscle) with repeated measures was used to determine the effects of the knee joint angle and angular velocity of the ankle. The ANOVA was followed by Bonferroni post hoc tests. As a result of the ANOVA, the ankle joint angle at the time of peak tendon force was affected by angular velocities (Table 3-1, $P < 0.01$). Since the tendon force, fascicle length, pennation angle and fascicle velocity can be influenced by the ankle joint angle (Kawakami et al. 1998), the differences of these parameters between knee joint angles were tested by paired t-test with a Bonferroni correction for each angular velocity. Statistical software (SPSS 12.0J, SPSS Japan, Japan) was used for all analyses. Statistical significance was set at $P < 0.05$.

3-3. Results

Figure 3-2 shows typical examples of the time courses of the ankle joint angle, tendon force, fascicle length, pennation angle, fascicle velocity and EMG of MG in each concentric contraction. The tendon force peaked along the time course of the contractions. From the beginning to the end of the contractions, the fascicle shortened and pennation angle increased.

The peak values of tendon force during static contractions were lower in K45 than in K0 by 21.5 ± 6.1% ($P < 0.01$, Figure 3-3). On the other hand, there was no significant difference between knee joint positions in the peak tendon forces of slow and fast concentric contractions. The peak tendon forces in K45 during each of the slow and fast concentric contractions corresponded to 87.4 ± 18.0% and 107.6 ± 10.6% of those developed in K0, respectively.

The ankle joint angles at the time of peak tendon force were affected by knee joint angle ($P < 0.05$) and angular velocity of the ankle ($P < 0.01$, Table 3-1). At the corresponding time, the MG fascicle lengths were longer in K0 than in K45 for each contraction ($P < 0.05$ for the slow concentric contractions and $P < 0.01$ for the static and fast concentric contractions, Figure 3-4). The pennation angles were smaller in K0 than in K45 for the static ($P < 0.01$) and fast concentric ($P < 0.05$) contractions. The pennation angles during the slow concentric contractions were not different between knee joint positions. The fascicle velocities in the slow concentric contractions tended to be higher in K0 as compared to K45 ($P < 0.1$). The fascicle velocities in the fast concentric contractions were higher in K0 than in K45 ($P < 0.05$).

The two-way ANOVA revealed that EMGs of MG were influenced by the knee joint angle and angular velocity with an interaction ($P < 0.01$). The MG EMGs during the slow and fast concentric contractions were higher in K0 than in K45, whereas those during the static contractions were not different between knee joint angles (Table 3-1). Both knee joint angle and angular velocity had main effects on the LG EMGs with no interaction. The LG EMGs were higher in K0 than in K45. The EMGs of SOL were influenced by angular velocity ($P < 0.05$), but not by knee joint angle with no interaction. The effects of knee joint angle and angular velocity on the EMGs of TA were not significant.

3-4. Discussion

The peak tendon forces during the slow and fast concentric contractions were not different between extended and flexed knee positions, while those in the static contractions decreased at the flexed knee position (Figure 3-3). This result was consistent with the reports of previous studies that examined the effects of knee joint angle on the plantar flexion torque during static (Sale et al. 1982; Arndt et al. 1998) and concentric (Fugl-Meyer et al. 1979; Svantesson et al. 1991) contractions. However, the discrepancy between static and concentric torques has not been elucidated in these studies. In the present study, the ankle joint angles at the time of peak tendon force were different between knee joint angles (Table 3-1). However, the mean differences of the ankle angles were small: 0.8, 3.5 and 3.6° in the static, slow concentric and fast concentric contractions, respectively. Therefore, the differences in the ankle joint angles would not be a critical factor for the present results of the tendon force. Instead, the differences in the fascicle lengths, pennation angles, fascicle velocities and EMGs between the extended and flexed knee positions (Figure 3-4, Table 3-1) would be related to the discrepancy in the tendon forces between the static and concentric contractions.

The MG fascicle lengths were different between knee joint angles when the tendon force peaked (Figure 3-4). From the fascicle lengths, the sarcomere lengths were estimated by dividing the fascicle lengths by the number of sarcomeres in series within MG fascicle [17,600; Huijing (1985)], because the sarcomere length is a major determinant of muscle force-generating potential (Gordon et al. 1966). The estimated sarcomere lengths were superimposed onto the length-force relationship of human sarcomere (Walker and Schrodt 1974) (Figure 3-5). In the static contractions, the sarcomere lengths of both knee positions reached the ascending limb, and thus the sarcomere in K0 had greater force potential than in K45. Similarly, the force-generating potential of sarcomere in the slow concentric contractions was greater in K0 than in K45. In the fast concentric contractions, however, the sarcomere in K45 had higher force potential than that in K0. Therefore, the differences in the fascicle lengths between the two knee joint angles could be a factor explaining the similar tendon forces in the fast concentric contractions.

The pennation angles of MG were higher in K45 than in K0 for the static and fast concentric contractions (Figure 3-4). However, they were not different between knee joint positions for the slow concentric contractions. In a pennate muscle, the force exerted by a muscle fascicle is transmitted to the tendinous tissues by a factor of the cosine of the pennation angle (Gans and Gaunt 1991). Hence, higher pennation angle in K45 would reduce the force effectively transmitted to the tendinous tissues in the static and fast concentric contractions. Also, no difference in the pennation angle in the slow concentric contractions is one of the reasons for the finding that the peak tendon forces in the slow concentric contractions were not different between knee joint positions.

The fascicle velocities were lower in K45 than in K0 when the tendon force peaked, although the difference in the slow concentric contractions did not reach statistical significance (Figure 3-4). As shortening velocity of fascicles increases, the force-generating potential of a muscle decreases (Hill 1938). Thus, the lower fascicle velocities in K45 would be advantageous for generating force. Possible explanations for the different fascicle velocities despite similar angular velocities of ankle are the velocity of tendinous tissues (Zuurbier and Huijing 1992) and/or angular effects (Gans and Gaunt 1991; Zuurbier and Huijing 1992), the latter of which is the increase of muscle velocity along the line of action due to changes in pennation angle. To examine this supposition, the angular effects were calculated as follows.

$$AE = [(FL_2 \times \cos\alpha_2 - FL_1 \times \cos\alpha_1) - (FL_2 - FL_1)] / dt$$

where AE is the angular effects, FL is the fascicle length, α is the pennation angle and subscripts 1 and 2 denote right before and after the time of peak tendon force, respectively. As a result, the angular effects were not different between knee joint angles (Table 3-2). This implies that the differences in the fascicle velocities might arise from the tendinous tissue velocities, not from the angular effects. In any case, further investigation is required to clarify the exact mechanisms for the different fascicle velocity with knee joint angles.

The MG EMGs during the slow and fast concentric contractions were lower in K45 than in K0 (Table 3-1). This agrees with the earlier reports (Carpentier et al. 1999; Price et al. 2003) that examined the EMGs of MG in concentric contractions. In the case of surface EMG, the decrease in MG EMGs with knee flexion may be explained by the impaired neuromuscular transmission or changes in electrode-muscle configuration (Cresswell et al. 1995). However, the EMGs recorded by fine-wire electrodes were also shown to decrease with knee flexion (Cresswell et al. 1995). Furthermore, Kennedy and Cresswell (2001) revealed that the MG motor unit activities measured by a needle electrode were inhibited at the flexed knee position. These findings suggest that the decline in the MG EMGs with knee flexion was not due to the change in electrode-muscle configuration, but due to the impairment of neuromuscular transmission. Therefore, the present result on EMG indicates that the activation levels of MG during the concentric contractions decreased with knee flexion.

Taken together, the difference in the tendon forces during the static contractions could be attributed to the lower force potential due to the shorter fascicle length and the higher pennation angle of MG in K45. In the slow concentric contractions, the force generating potential related to the fascicle length and the EMGs of MG were lower in K45 than in K0. However, no difference in the pennation angle and lower velocity of MG fascicle in K45 would be related to the fact that the peak tendon forces were not different between knee joint positions in the slow concentric contractions. In the fast concentric contractions, the MG force potential, based on the length and velocity of fascicle, was greater, but its pennation angle was higher and the EMGs were lower in K45 than in K0. The interaction of these four factors could account for the similar tendon forces in the fast concentric contractions.

The LG and SOL as well as MG contribute to the development of tendon force, and thus the influences of these muscles should be considered when the changes in the tendon force by the knee joint angle were interpreted. The PCSA of LG is only about 40% of that of MG (Table 1-1, Fukunaga et al. 1991). In addition, the EMGs of mono-articular SOL were not affected by knee joint angles (Table 3-1). Accordingly, the forces developed by LG and SOL could not explain the differences observed in the tendon force between extended and flexed knee positions. This issue will be discussed in more detail in Chapter 5.

In summary, the present study showed that the tendon forces in concentric contractions did not decrease with knee flexion, but those in the static contractions were reduced. This phenomenon could be explained by the length-force and velocity-force characteristics, pennation angle and EMGs of MG.

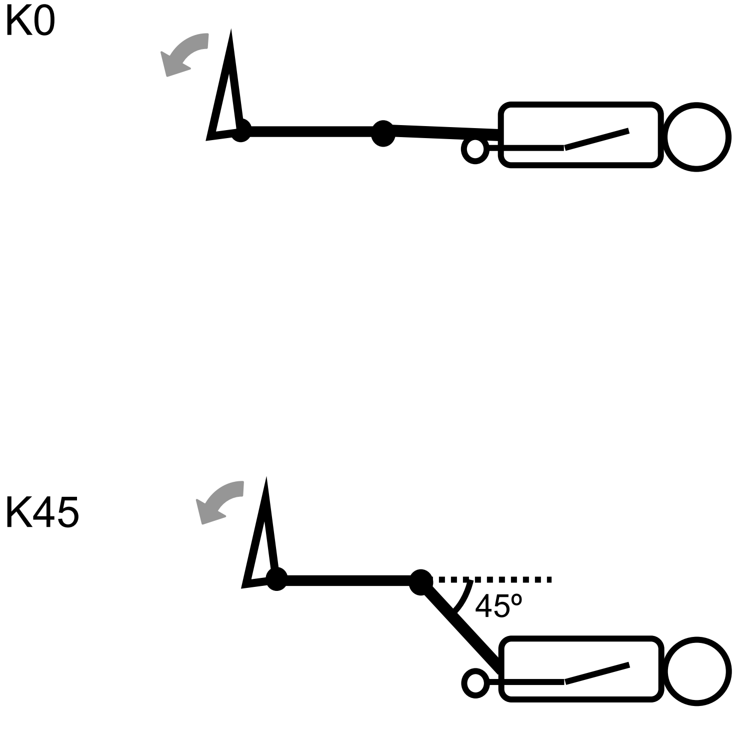


Figure 3-1. Schematic illustrations of the experimental setup. Subjects performed maximal voluntary plantar flexions with knee fully extended (K0, upper) and 45º flexed (K45, lower) positions.

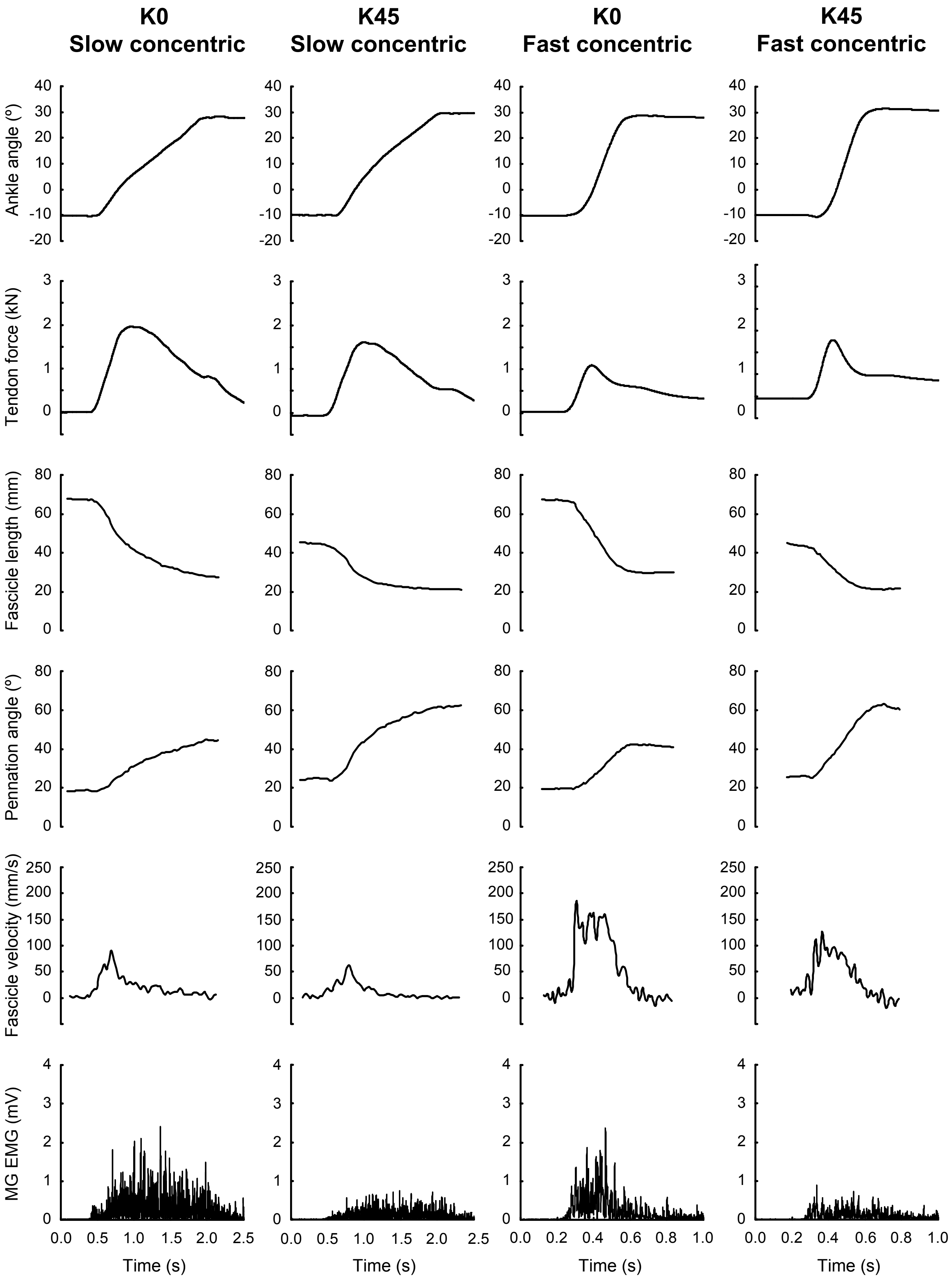


Figure 3-2. Typical examples of the ankle joint angle, tendon force, fascicle length, pennation angle, fascicle velocity and electromyogram (EMG) of the medial gastrocnemius (MG) during each of the concentric contractions. K0: knee joint angle at 0º. K45: knee joint angle at 45º.

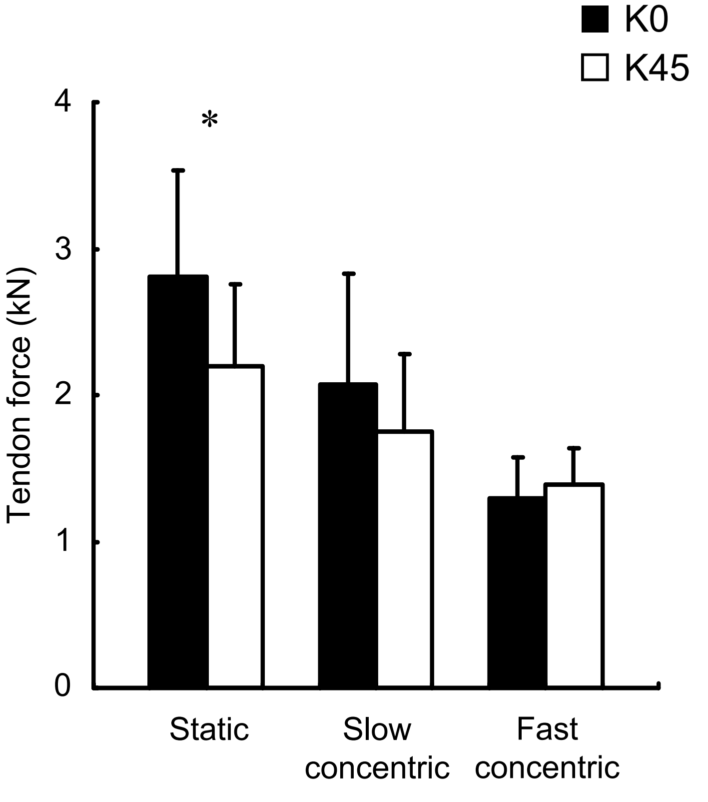


Figure 3-3. Peak values of tendon force in each contraction. Means and standard deviations (SDs) of seven subjects are presented for the knee joint angle at 0º (K0, filled bars) and at 45º (K45, open bars). * denotes that the difference between K0 and K45 is significant.

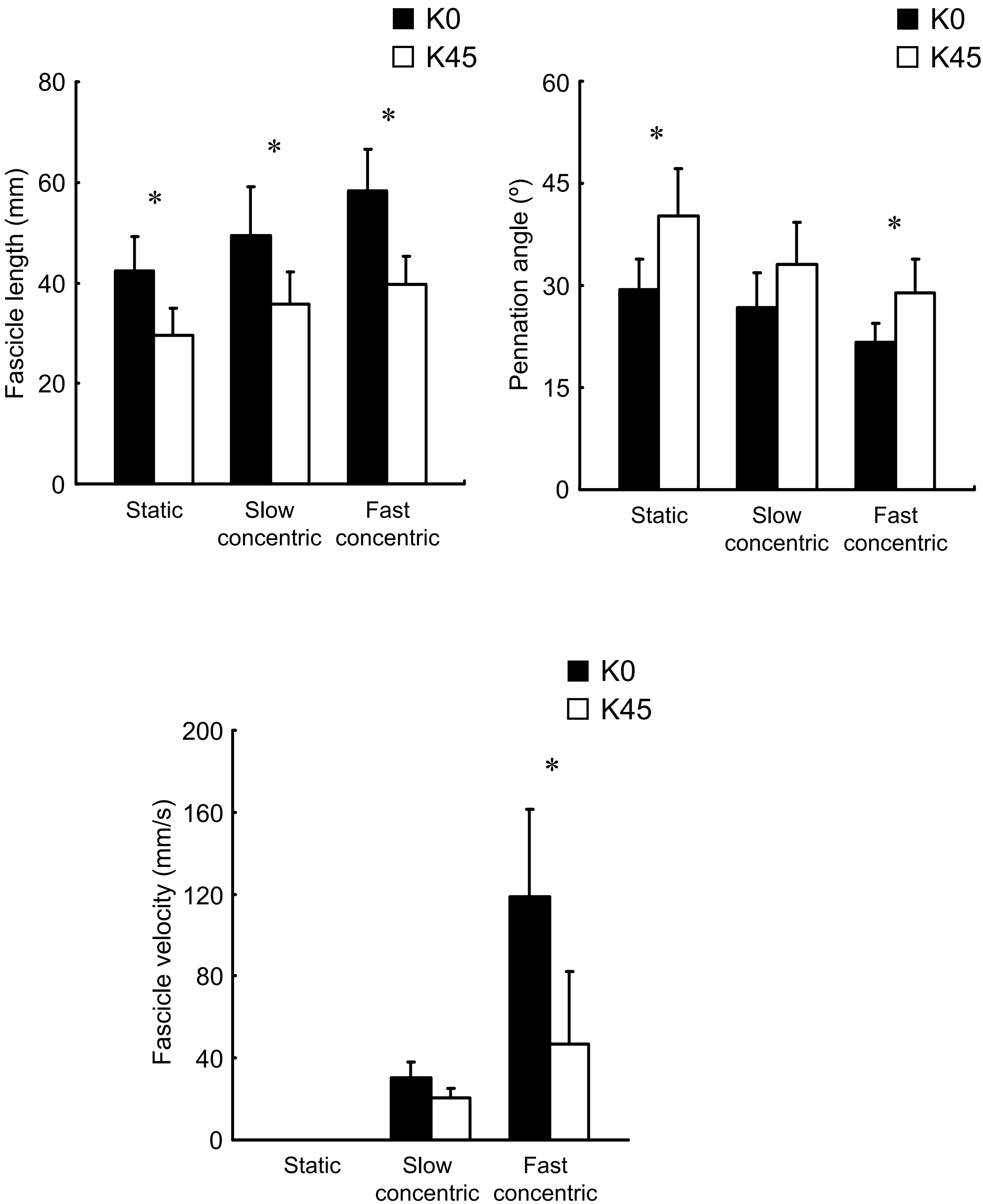


Figure 3-4. The fascicle length, pennation angle and fascicle shortening velocity of the medial gastrocnemius (MG) at the time of peak tendon force. Means and standard deviations (SDs) of the subjects are presented for the knee joint angle at 0º (K0, filled bars) and at 45º (K45, open bars). * denotes that the difference between K0 and K45 is significant.

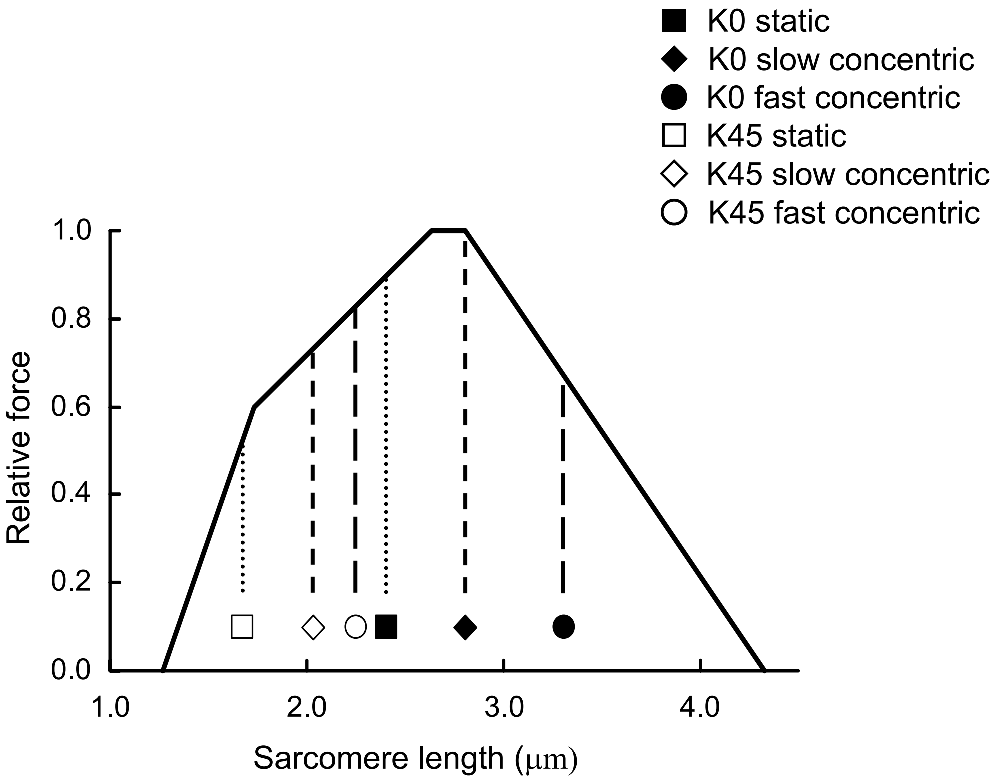


Figure 3-5. Estimated sarcomere lengths of the medial gastrocnemius (MG) at peak tendon force. The length-force relationship of human sarcomeres is derived from data of Walker & Schrodt (1974). The intersection points of the length-force relationship and vertical lines mean the force-generating potential of sarcomere at each length. K0: knee joint angle at 0º. K45: knee joint angle at 45º.

Table 3-1.

Ankle joint angles at peak tendon force and electromyograms (EMGs) of each muscle

		Static	Slow concentric	Fast concentric
Ankle joint angle (º)	K0	5.8 ± 3.7 †	6.3 ± 3.6 †	-2.9 ± 1.8
	K45	5.0 ± 2.7 * †	1.8 ± 4.1 * †	-5.5 ± 1.4 *
EMG amplitude (mV)				
MG	K0	0.22 ± 0.08 †	0.28 ± 0.09 †	0.38 ± 0.13
	K45	0.17 ± 0.06	0.15 ± 0.04 *	0.19 ± 0.06 *
LG	K0	0.19 ± 0.10 †	0.21 ± 0.09 †	0.32 ± 0.10
	K45	0.14 ± 0.06 * †	0.17 ± 0.06 * †	0.23 ± 0.09 *
SOL	K0	0.16 ± 0.02	0.14 ± 0.03 †	0.19 ± 0.04
	K45	0.15 ± 0.04	0.14 ± 0.03 †	0.17 ± 0.03
TA	K0	0.03 ± 0.01	0.03 ± 0.01	0.04 ± 0.01
	K45	0.04 ± 0.04	0.03 ± 0.01	0.03 ± 0.01

Values are means and standard deviations (SDs). K0: knee joint angle at 0º. K45: knee joint angle at 45º. MG: medial gastrocnemius, LG: lateral gastrocnemius, SOL: soleus, TA: tibialis anterior. * denotes that the difference between K0 and K45 is significant. † denotes that the mean value is significantly different from that in the fast concentric contraction.

Table 3-2.

Angular effects due to pennation angle in concentric contractions

		Slow concentric	Fast concentric
Angular effects (mm/s)	K0	2.3 ± 2.3	9.5 ± 6.5
	K45	3.3 ± 2.4	8.1 ± 7.3

Values are means and standard deviations (SDs). K0: knee joint angle at 0º. K45: knee joint angle at 45º.

CHAPTER 4 Effects of knee joint angle on the fascicle behavior of the gastrocnemius during eccentric plantar flexions

4-1. Introduction

In Chapter 3, the length and shortening velocity of MG fascicle were different between the extended and flexed knee positions, despite identical ankle joint actions. The fascicle behavior during the fast concentric contractions was shown to be related to the similar tendon forces at the two knee joint positions. However, it is unclear how the knee joint angle influences the MG fascicle behavior during eccentric contractions. It has been shown that the force during eccentric contractions is greater and less affected by changes in the velocity as compared with that during concentric contractions (Joyce et al. 1969; Scott et al. 1996). If the tendon force during eccentric contractions is also reduced by knee flexion, this change will affect MG fascicle behavior, because the tendinous tissues are lengthened with applied force (Trestik and Lieber 1993). The purpose of the study is to investigate the effects of knee joint angle on the fascicle behavior of MG during maximal eccentric plantar flexions.

4-2. Methods

(i) Subjects

Eight healthy men (age, 25.6 ± 3.0 years; height, 172.9 ± 6.2 cm; and body mass, 66.9 ± 7.3 kg; mean ± SD) voluntarily participated in the present study. Written informed consent was obtained from each subject. This study was approved by the Human Research Ethics Committee in the Faculty of Sport Sciences, Waseda University. The subjects were highly motivated and had previously attended the laboratory on at least one occasion to become familiarized with the testing procedures.

(ii) Experimental protocols

The subjects lay prone on a bench of an isokinetic dynamometer (CON-TREX, CMV AG, Switzerland) with the knee fully extended (K0) and 90° flexed (K90) (Figure 4-1). In K0, the trunk was tightly fastened to the bench with belts. In K90, wooden blocks were placed in front of the thigh to prevent knee joint movements during contractions. The rotation axis of the right ankle was aligned with that of the dynamometer, and the foot was firmly strapped to a footplate. After a warming-up period, maximal voluntary static and eccentric plantar flexions were performed at each of the two knee joint positions mentioned above. The ankle joint angle in the static contraction was set at slightly dorsiflexed position (–10° ~ –3°) from the anatomical neutral position (0°), so that it would reach 0° at the time of peak torque, since the exertion of plantar flexion toque involved the ankle joint displacement (Muramatsu et al. 2001; Karamanidis et al. 2005). The extent of dorsiflexion was previously determined for each subject in the familiarization session. Indeed, 9.8 ± 3.4° and 3.9 ± 1.9° of angular displacement occurred in K0 and K90, respectively. As a result, the means ± SDs of the ankle joint angle were 0.1 ± 3.4° in K0 and –0.4 ± 2.2° in K90 at the time of peak toque. In the eccentric contractions, the angular velocities of the ankle were set at 30°/s (slow) and 150°/s (fast). The range of ankle joint motion was from 30° (plantar flexion) to –15° (dorsiflexion). The eccentric contractions were preceded by about 2 s of static phase with the ankle angle at 30°. The subjects were instructed to sustain their maximal effort from the static phase to the end of the movement. The static and eccentric contractions were performed at the two knee joint positions in a randomized order. Two trials were conducted for each contraction, and a 2-min rest period was provided between the trials. In each of the test conditions, the trial with the greater peak torque was chosen for subsequent analyses. The maximal voluntary static dorsiflexion was performed at the ankle angle of 0° in K0.

(iii) Torque and joint angle measurements

Plantar flexion torque was measured with the dynamometer. The ankle and knee joint angles were determined with electrical goniometers (ankle joint, SG110/A; knee joint, SG150; Biometrics, UK). Torque and joint angle signals were sampled at 2 kHz using a 16-bit A/D converter (PowerLab/16SP, ADInstruments, Australia) and stored on a computer. These data were processed by using a fourth-order zero-lag Butterworth filter with a cutoff frequency of 17 Hz. The cutoff frequency was determined by a residual analysis (Winter 1990). Passive plantar flexion torque was subtracted from the measured torque to obtain the torque exerted actively by the plantar flexors. In each of K0 and K90, relationships between the ankle angle and the passive plantar flexion torque were determined during passive ankle joint motion at 5°/s. Tendon force was computed by dividing the active plantar flexion torque by the moment arm of the Achilles tendon. The moment arm was estimated as the first derivative of the length change of MG MTC, which was derived from a previous report (Grieve et al. 1978), with respect to ankle joint angle (radians).

(iv) Ultrasonographic measurements

Longitudinal sectional images of MG were obtained using a B-mode ultrasound apparatus (SSD-6500, Aloka, Japan) with a linear-array probe (10 MHz wave frequency, UST-5712, Aloka, Japan). The probe was placed over the midbelly of MG and fixed to the skin using elastic tapes. Ultrasound images were stored on computer memory of the apparatus at 36 Hz in the static and slow eccentric contractions, and at 96 Hz in the fast eccentric contractions. An electrical signal was superimposed on the images to synchronize them with other data (torque, angle and EMG). The fascicle length and pennation angle of MG were measured frame by frame using an image processing program (Image J, National Institute of Health, USA). The measurements were performed two times for each image, and the mean values were used for further analyses. The coefficients of variation of the two measurements were less than 3.6% and 5.5% for fascicle length and pennation angle, respectively. The intraclass correlation coefficients of the measurements were more than 0.962 and 0.939 for fascicle length and pennation angle, respectively. The lengthening velocity of fascicle was determined as the first derivative of its length changes with respect to time, and expressed as negative values.

(v) EMG recordings

Surface EMGs were recorded from MG, LG, SOL and TA muscles. After careful preparation of the skin, pairs of Ag/AgCl electrodes (Blue Sensor P-00-S, Ambu A/S, Denmark, measuring area: 154 mm^2) were placed over the belly of each muscle with an inter-electrode distance of 20 mm. A reference electrode was placed on the medial malleolus of the left foot. The EMG signals were collected telemetrically (WEB-5000, NIHON KOHDEN, Japan; input impedance > 10 MΩ, common mode rejection ratio > 80 dB, time constant: 0.03 s, hi-cut filter: off) with a sampling frequency of 2 kHz. After full-wave rectification, EMGs were averaged over a 0.5-s period around the peak tendon force for the static contractions and over the entire range of motion for the eccentric contractions, respectively.

(vi) Statistics

Values were expressed as means ± SDs. A three-way ANOVA (2 knee joint angles × 4 ankle joint angles × 2 angular velocities for the tendon force, fascicle length and pennation angle, 2 knee joint angles × 3 ankle joint angles × 2 angular velocities for the fascicle velocity) with repeated measures was used to determine the effects of the knee joint angle, ankle joint angle and angular velocity of the ankle. The tendon force at an ankle angle of 0° and EMGs were tested by using a two-way ANOVA (2 knee joint angles × 3 angular velocities, in which the static contraction was included as 0°/s) with repeated measures. The ANOVAs were followed by Bonferroni post hoc tests. Statistical significance was set at $P < 0.05$. All analyses were performed with a statistical software (SPSS 12.0J for Windows).

4-3. Results

The three-way ANOVA revealed that the knee and ankle joint angles had a main effect on the tendon force ($P < 0.01$), but the angular velocity did not (Figure 4-2). An interaction between knee and ankle joint angles ($P < 0.05$) indicated that the tendon forces were not different between knee joint angles at the ankle angle of 30°, but were higher in K0 than in K90 at 0°, 10° and 20°. Also, an interaction between ankle joint angle and angular velocity ($P < 0.05$) indicated that the tendon forces were higher in the slow than in the fast eccentric contraction at 0° in K0, whereas those were not different between angular velocities at any other ankle joint angles. The two-way ANOVA demonstrated that the tendon force at the ankle angle of 0° was decreased in K90 than in K0 ($P < 0.01$) but not affected by angular velocity with no interaction (Table 4-1).

The fascicle length and pennation angle of MG during the eccentric contractions were affected by knee and ankle joint angles ($P < 0.01$) (Figure 4-3). However, no main effect of angular velocity was found on either the fascicle length or pennation angle. There was a significant interaction between knee and ankle joint angles ($P < 0.01$), indicating that the fascicle lengths and pennation angles in K0 were elongated and decreased as the ankle was dorsiflexed, respectively, while those in K90 did not show any difference among the ankle joint angles. The lengthening velocity of MG fascicle was influenced by all three factors (knee and ankle joint angles and angular velocity; $P < 0.01$). An interaction between knee joint angle and angular velocity ($P < 0.01$) indicated that the fascicle velocities were not altered by knee joint angle in the slow eccentric contractions, whereas those during the fast eccentric contractions were faster in K0 than in K90. There was also an interaction between ankle joint angle and angular velocity ($P < 0.01$), indicating that the fascicle velocities were not different between any ankle angles in the slow eccentric contractions, but became faster with dorsiflexion in the fast eccentric contractions.

The mean EMGs of MG ($P < 0.01$) and LG ($P < 0.05$) were higher in K0 than in K90, but were not affected by angular velocity without interaction (Table 4-1). On the other hand, neither the knee joint angle nor the angular velocity had an effect on SOL EMGs. The mean EMGs of TA were relatively low in all contractions (7~18% of those during maximal static dorsiflexion).

4-4. Discussion

The present results demonstrated that the knee joint angle affects the length change of MG fascicle during the eccentric plantar flexions with respect to the ankle joint angle, but the angular velocity did not. In K0, the MG fascicle length was elongated as the ankle was dorsiflexed, but it was almost constant in K90 (Figure 4-3). These were essentially consistent with the findings in Chapter 3. Namely, the MG fascicle velocity was slower at the flexed knee position than at the extended. Thus, the present data extend the findings in Chapter 3 to the fascicle behavior during maximal eccentric contractions.

The tendon forces during the eccentric contractions were lower in K90 than in K0 (Figure 4-2). This result would be attributable to the lower force of MG in K90 according to the following three factors; 1) fascicle length, 2) pennation angle and 3) activation levels. Firstly, MG fascicle lengths were shorter in K90 as compared to K0 (Figure 4-3). These length ranges corresponded to the ascending limb of the length-force relation of MG fascicle for both knee positions, on the assumption that the number of sarcomeres in series within MG fascicle is 17,600 (Huijing 1985), and the optimal length of the human sarcomere ranges from 2.64 to 2.81 μm (Walker and Schrodt 1974). Thus, it is most likely that the shorter MG fascicle in K90 had lower potential for generating force than in K0. Secondly, the pennation angles of MG were different between knee joint positions throughout the range of motion (Figure 4-3). The higher pennation angles in K90 probably reduced the force transmitted to the tendinous tissues. Thirdly, the EMGs of MG in K90 were lower than those in K0 (Table

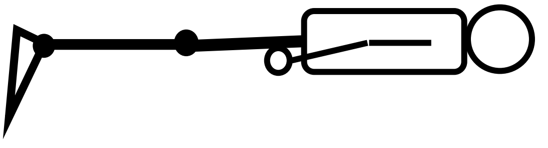
4-1). However, the SOL EMGs were not different between the two knee joint angles. Taken together, the lower tendon forces in K90 compared to K0 would be due to the decrease in the force exerted by MG.

During the eccentric plantar flexions, the MG fascicle was lengthened to a different extent between K0 and K90 (Figure 4-3), despite the identical range of ankle motion. A possible explanation for this phenomenon is the non-linear length-force relations of tendinous tissues, i.e., the tendinous tissues are more compliant at low force levels and gradually become stiffer as the applied force increases (Trestik and Lieber 1993). The force developed by MG was reduced with knee flexion. In K90, therefore, a slight increase in the force would result in the greater deformation of compliant tendinous tissues. On the other hand, it is likely that higher levels of force in K0 limited the tendinous tissue elongation with increasing force, and consequently the fascicle was lengthened. Another explanation is that the slackness of tendinous tissues was not fully taken up by the force during the pre-static phase in K90. Although the subjects performed the static plantar flexion with their maximal effort, there is a possibility that the fascicles might be close to their active slack length, and thus they could not remove a greater amount of slack at the extremely shortened MTC length. In any case, the differences in the elongation of MG fascicle would be related to the mechanical properties of tendinous tissues at lower force levels.

The length changes of MG fascicle with respect to ankle joint angle were not influenced by the angular velocity, although the lengthening velocities of fascicle were different between the slow and fast eccentric contractions in K0 (Figure 4-3). Previous animal experiments have shown that the eccentric force increases up to 1.7-2.0 times as high as static force with increasing lengthening velocity (Lombardi and Piazzesi 1990; Krylow and Sandercook 1997). In addition, the tendinous tissue elongation has been shown to be partly dependent on the strain rate (Hubbard and Soutas-Little 1984; Danto and Woo 1993), because of their viscoelastic properties. These findings imply that force production during eccentric contractions increases as the angular velocity increases, and thus the length changes of fascicle is also affected by the angular velocity. However, the present study could not find the difference in the tendon force between angular velocities (Figure 4-2). This result may be due to a neural inhibitory mechanism that restricts excessive muscle force production during eccentric contractions to avoid injuries (Dudley et al. 1990; Westing et al. 1990). On the other hand, the effects of strain rate on the elongation of tendinous tissues are still controversial (Wren et al. 2001). Some studies (Hubbard and Soutas-Little 1984, Danto and Woo 1993) found significant effects of strain rate on the elastic modulus of tendinous tissues, while others (Herrick et al. 1978; Ker 1981; Wren et al. 2001) did not. Taken together, similar forces between the slow and fast eccentric contractions would have resulted in analogous length change patterns of fascicle.

In summary, the present study demonstrated that knee joint angles and corresponding differences in the force, not the angular velocity, have influences on the length change of MG fascicle during the maximal eccentric plantar flexions. The results were probably due to the non-linear length-force relation and/or the slackness of tendinous tissues.

K0



K90

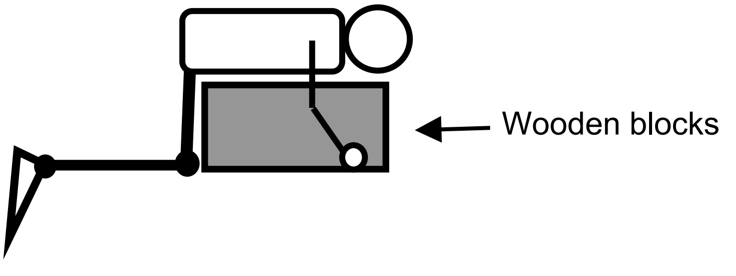


Figure 4-1. Schematic illustrations of the two testing positions. The subjects performed static and eccentric plantar flexions with the knee fully extended (K0, upper) and 90° flexed (K90, lower).

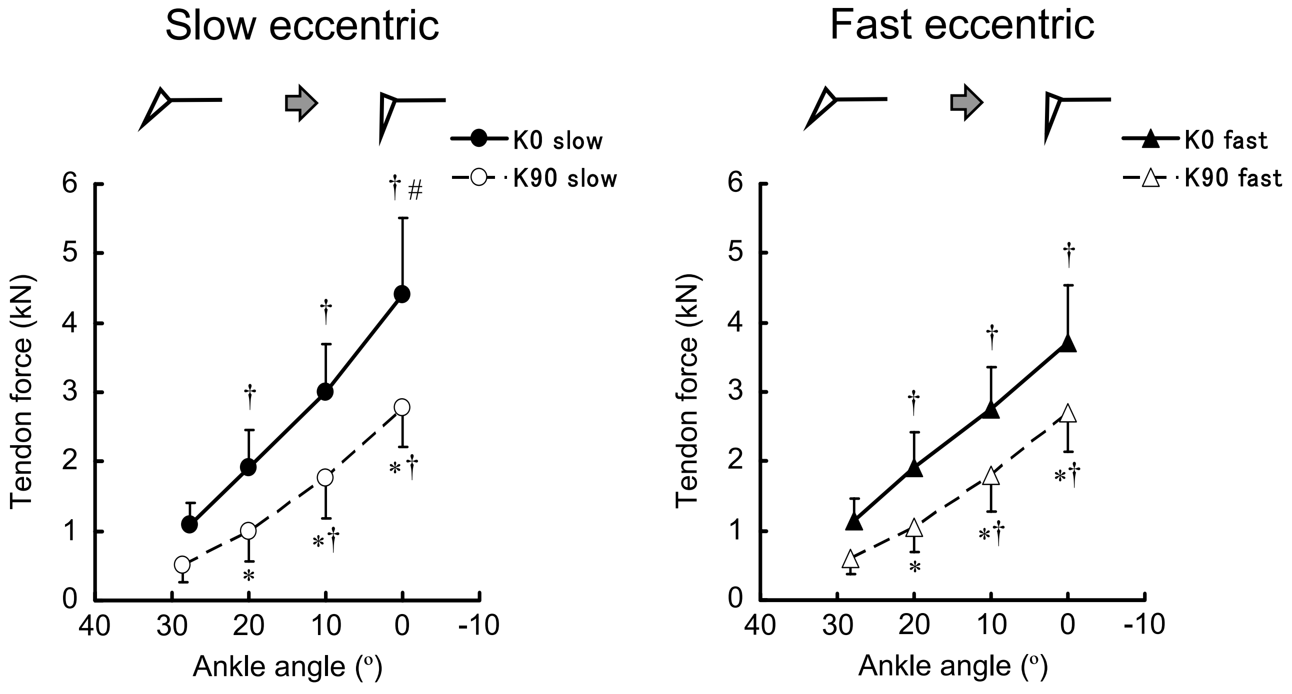


Figure 4-2. Means and standard deviations (SDs) of the tendon forces during slow (left) and fast (right) eccentric contractions. Closed and open symbols denote the data at the knee joint angle of 0º (K0) and 90º (K90), respectively. * denotes that the difference between knee joint angles is significant. † denotes that the value is significantly different from that at the ankle joint angle of 30º. # denotes that the difference between angular velocities is significant.

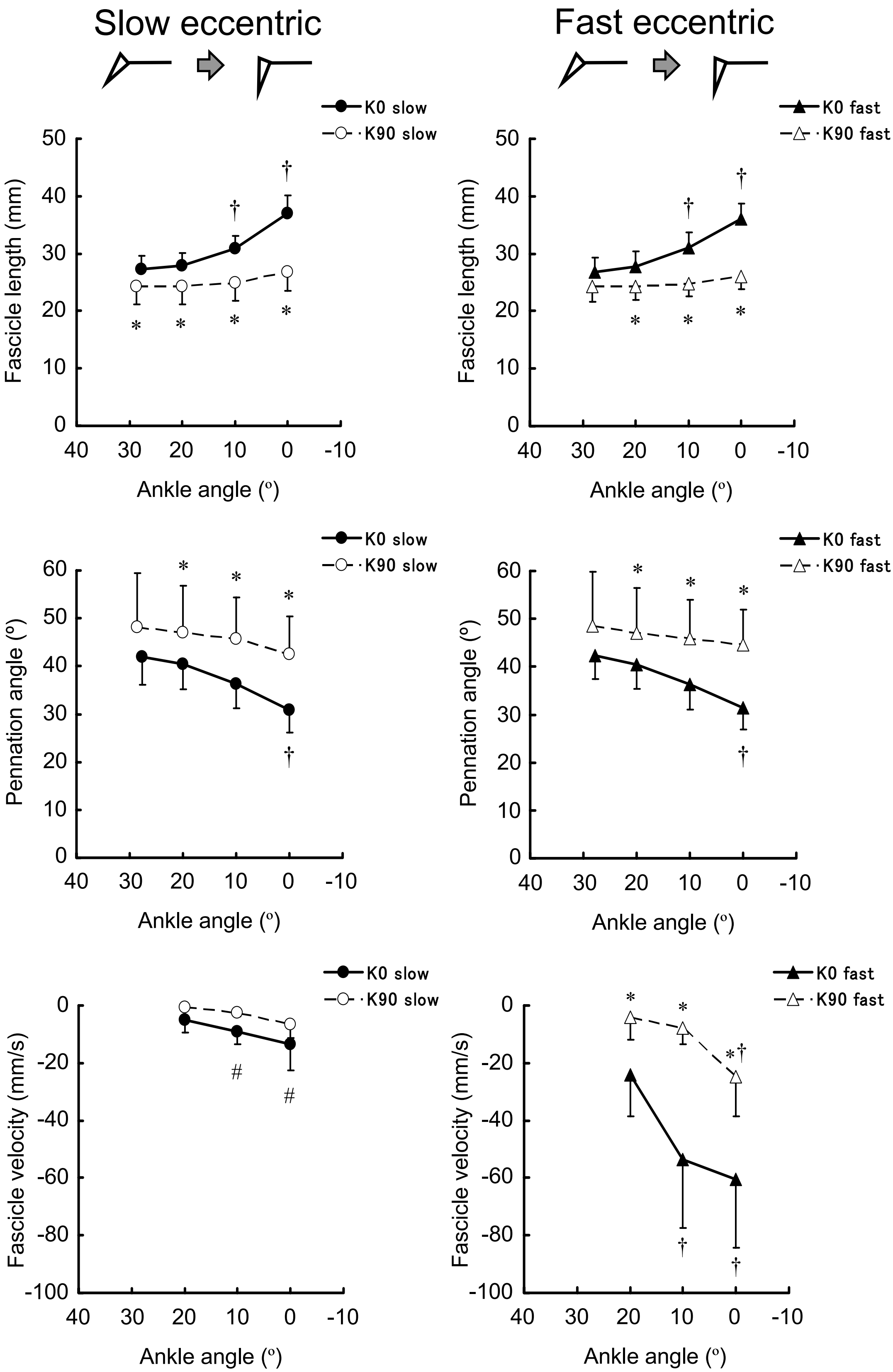


Figure 4-3. Means and standard deviations (SDs) of the fascicle lengths (upper), pennation angles (middle) and fascicle velocities (lower) of the medial gastrocnemius (MG) during slow (left) and fast (right) eccentric contractions. Closed and open symbols denote the data at the knee joint angle of 0º (K0) and 90º (K90), respectively. * denotes that the difference between knee joint angles is significant. † denotes that the value is significantly different from that at the ankle joint angle of 30º (20º for fascicle velocity). # denotes that the difference between angular velocities is significant.

Table 4-1.

Tendon forces at the ankle angle of 0º and electromyograms (EMGs) of each muscle

		Static	Slow eccentric	Fast eccentric	
Tendon force (kN)	K0	4.5 ± 1.2	4.4 ± 1.1	3.7 ± 0.8	*
	K90	3.0 ± 0.7	2.8 ± 0.6	2.7 ± 0.6	
EMG amplitude (mV)					
MG	K0	0.21 ± 0.07	0.18 ± 0.05	0.17 ± 0.04	*
	K90	0.13 ± 0.03	0.12 ± 0.04	0.13 ± 0.03	
LG	K0	0.23 ± 0.14	0.19 ± 0.09	0.19 ± 0.08	*
	K90	0.15 ± 0.08	0.15 ± 0.07	0.15 ± 0.06	
SOL	K0	0.20 ± 0.09	0.14 ± 0.05	0.13 ± 0.04	
	K90	0.16 ± 0.04	0.15 ± 0.03	0.17 ± 0.06	
TA	K0	0.05 ± 0.05	0.03 ± 0.01	0.03 ± 0.01	
	K90	0.04 ± 0.05	0.02 ± 0.01	0.03 ± 0.01	

Values are means and standard deviations (SDs). K0: knee joint angle at 0º. K90: knee joint angle at 90º. MG: medial gastrocnemius, LG: lateral gastrocnemius, SOL: soleus, TA: tibialis anterior. * denotes that the main effect of knee joint angle is significant.

CHAPTER 5 General discussion

Main findings of each chapter are summarized as follows.

1: The length changes of MG fascicle with respect to a certain length change of MTC were greater in the passive knee joint motion than in the passive ankle joint motion. The length of distal external tendon of MG was changed by the passive ankle joint motion, but not by the passive knee joint motion. These phenomena were related to the fact that the external tendon of MG attaches to SOL tendinous tissues (Chapter 2).

2: Peak tendon forces in the slow and fast concentric contractions were not different between the extended and flexed knee positions, while those in the static contractions decreased at the flexed knee position than at the extended. When the tendon force peaked, the fascicle lengths and pennation angles in each contraction (except for the pennation angle in the slow concentric contractions) and fascicle velocities in the fast concentric contractions were different between the knee joint positions. The EMGs during concentric contractions were higher at the extended knee position than at the flexed position. The results suggested that the discrepancy in the tendon forces between the static and concentric contractions could be explained by the length-force and velocity-force characteristics, pennation angle and EMGs of MG (Chapter 3).

3: The tendon forces during eccentric plantar flexions were influenced by the knee joint angle, but not by the angular velocity of the ankle. At the extended knee position, the MG fascicle length was elongated when the ankle dorsiflexed, but it was almost constant at the flexed knee position, despite the identical range of ankle joint motion. The different fascicle behavior between the knee joint positions was attributable to the non-linear length-force relations and/or slackness of tendinous tissues. The results suggested that the behavior of MG fascicle during eccentric plantar flexions was markedly affected by the knee joint angle (Chapter 4).

In this chapter, the effects of knee joint angle on the MG fascicle behavior and its force generation are firstly discussed. Secondly, several limitations that might be involved in the interpretation of the results are addressed.

5-1. *Effects of knee joint angle on the force generation of the gastrocnemius muscle*

On the basis of the results obtained in the static (Chapter 4), fast concentric (Chapter 3) and fast eccentric (Chapter 4) contractions, the effects of knee joint angle on the MG force are discussed from following four points; fascicle length, fascicle velocity, pennation angle and activation level. These are determinants of instantaneous force of MG.

Fascicle length

The force that a fascicle can develop is dependent on its length (Gordon et al. 1966; Rassier et al. 1999). The measured fascicle lengths of MG were superimposed on its length-force relation (Figure 5-1), which was estimated from the serial sarcomere number of MG fascicle (17,600; Huijing 1985) and the length-force relation of human sarcomere (Walker and Schrodt 1974). In the static contractions, MG fascicles at the extended and flexed knee positions reached the ascending limb of the length-force relation, when the tendon force peaked (Figure 5-1, upper). This was mainly due to the elongation of tendinous tissues. Thus, the knee flexion reduced MG force in maximal static contractions. In the concentric contractions, MG fascicles at the extended knee position were on the descending limb at the peak tendon force (Figure 5-1, middle), because the lower concentric force lengthened the tendinous tissues to a lesser extent than static contractions. On the other hand, the fascicles at the flexed knee position were on the ascending limb. As a result, the length-related force generating potential of MG fascicles in the concentric contractions was higher at the flexed knee position than at the extended. In the eccentric contractions, MG fascicles were operated on the ascending limb for both knee joint positions (Figure 5-1, lower). This resulted in the lower MG force at the flexed knee position. Accordingly, the effects of knee joint angle on the length-related force generating potential of MG were dependent on the contraction types.

Fascicle velocity

The force generated by a muscle fascicle is influenced by its velocity (Hill 1938). The MG fascicle velocities obtained in the fast concentric (Chapter 3) and eccentric (Chapter 4) contractions were superimposed on the estimated velocity-force relation (Figure 5-2). For the concentric part, the equation of Hill (Hill 1938) [$(P + a) \cdot V = (P_0 - P) \cdot b$, where P is the force at velocity V, P_0 is the maximal static force, a and b are constants] was used with following three assumptions; 1) $a/P_0 = 0.25$ (Faulkner et al. 1986), 2) L_0 (optimal length of MG fascicle) = 48 mm (Figure 5-1) and 3) the maximal shortening velocity of MG fascicle = $12.8 \cdot L_0$/s (Spector et al. 1980). For the part of eccentric contractions, the relationship between the force and fascicle velocity was estimated according to the reports of van Soest and Bobbert (1993) and Cole et al. (1996) (see appendix). In the Chapter 3, the shortening velocities of MG fascicles were lower at the flexed knee position than at the extended, despite identical angular velocity of the ankle. Hence, the lower fascicle velocities would be advantageous for generating force (Figure 5-2). The lengthening velocities of MG fascicles during the eccentric contractions were slower at the flexed than at the extended knee position(Chapter 4). However, the differences in the lengthening velocities of MG fascicles did not have a substantial effect on the MG force during eccentric contractions (Figure 5-2). Therefore, the decreases in the fascicle velocities by knee flexion had different effects on the MG force between concentric and eccentric contractions.

Pennation angle

The force developed by muscle fascicles transmitted to the tendinous tissues by a factor of cosine of the pennation angle in pennate muscles (Gans and Gaunt 1991). Within the range from 0° to 90°, a cosine of an angle decreases with increasing the angle. Therefore, an increase in the pennation angle leads to a decrease in the force that contributes to the tendon force. The pennation angle of MG increased as the knee joint was flexed in passive conditions (Chapter 2). In addition, the pennation angles were higher at the flexed knee position than at the extended knee position in each of the static, concentric and eccentric contractions (Figure 5-3), although the difference between the two knee joint positions was smaller in the concentric contractions. Therefore, the increase in the pennation angles induced by knee flexion reduced the force transmitted to the tendinous tissues, and this influence was prominent in the static and eccentric contractions.

Activation level

The averaged EMGs of MG were lower at flexed knee positions in each of the static, concentric and eccentric contractions (Figure 5-4). The decline in the MG EMGs with knee flexion has already been demonstrated by several researchers in static (Cresswell et al. 1995; Pinniger et al. 2000; Arampatzis et al. 2006) and concentric (Carpentier et al. 1999; Price et al. 2003) contractions. The present study is the first one that revealed the decrease in MG EMGs during eccentric contractions at the flexed knee position. In addition, Figure 5-4 points out that the effects of knee flexion on MG EMGs were remarkable in concentric contractions. This disagreed with the results of Chino et al. (in press), in which MG EMGs within a range from 5° dorsiflexion to 5° plantar flexion were not different among a total of eight eccentric and concentric velocities. The discrepancy may be related to the difference between the two studies in the operating ranges of MG fascicle (Figure 5-1) and/or no preactivation in the concentric contractions in the present study. In any case, the lower EMGs at flexed knee positions were a limiting factor for MG force, especially during concentric contractions.

The above discussions are summarized as shown in Figure 5-5. The size of arrows and values in parentheses (Figure 5-5) indicate relative changes of each of MG force determinants from extended to flexed knee positions. The changes of activation levels were calculated from EMG data on the assumption of a linear relationship between them (Lippold 1952). The MG force during the static contractions decreased by knee flexion primarily due to the decreases in the length-related force potential (–58%) and activation level (–39%). In the concentric contractions, the velocity-dependent force potential and activation level were greatly increased (+56%) and decreased (–51%), respectively, with knee flexion. This resulted in the similar MG force. The decrease in the MG force in the eccentric contractions by knee flexion was mostly attributable to the decline in the length-related force generating potential (–63%). Therefore, although the values in Figure 5-5 are just rough estimates of changes in the MG force potentials, their magnitudes and directions of effect strongly suggest the importance of MG fascicle behavior and EMG on the tendon force.

Several studies have already reported the effects of knee joint angles on the fascicle length, pennation angle and EMG of MG (Cresswell et al. 1995; Kawakami et al. 1998; Maganaris 2003). The present study firstly clarified that the fascicle velocity of MG was also affected by the knee joint angle. Furthermore, the difference in the MG fascicle velocity had a strong influence on the MG force in fast concentric contractions. The present finding suggests that the angles of each joint that the bi-articular muscle crosses have complex effects on its fascicle behavior. The effects would have to be taken into account to properly interpret the fascicle behavior of bi-articular muscle during multi-joint movements.

5-2. *Limitations of the experiments*

Contributions of other plantar flexors

In the Chapter 3 and 4, the results of the tendon forces were discussed in relation to the fascicle behavior and EMGs of MG. However, LG and SOL also contribute to the tendon force. Thus, the influences of these muscles should be considered.

The LG crosses knee and ankle joints. The physiological cross-sectional area of LG is reported to be only about 40% of that of MG (Table 1-1, Fukunaga et al. 1992). Also, although LG fascicles have more sarcomeres in series than MG fascicles (Huijing 1985), the moment arm of LG at the knee is shorter than that of MG (Spoor et al. 1990). Accordingly, the influence of a certain degree of knee flexion (45° and 90° in the Chapter 3 and 4, respectively) on the LG sarcomere length is expected to be smaller as compared to that for MG. Therefore, the difference of the LG force between extended and flexed knee positions would be smaller than that of MG force.

The SOL attaches to the common Achilles tendon with the gastrocnemius muscles. Hence, the difference in the tendon force between extended and flexed knee positions may cause a difference in the Achilles tendon elongation. If so, the behavior of SOL fascicles may not be identical at different knee joint positions. To confirm this point, SOL fascicle length and pennation angle were determined during maximal static plantar flexions (Figure 5-6) at knee fully extended (K0) and 90° flexed (K90) positions in six subjects. The experimental setup was almost the same as that in the Chapter 4.

As a result, the fascicle length and pennation angle of SOL were not different between K0 and K90, although the peak tendon force in K0 was higher than that in K90 ($P < 0.05$, Figure 5-7). The findings disagree with the hypothesis that the difference in the tendon force causes different length changes in the fascicles of SOL, whereas they are in accordance with Kawakami et al. (1998). The results obtained here suggest that the fascicle lengths of mono-articular SOL during the static contractions were independent of knee joint angle.

The difference in the tendon force between the extended and flexed knee positions was smaller in concentric contractions (Chapter 3) and similar in eccentric contractions (Chapter

4) as compared with that in static contractions. Hence, it is likely that the behavior of SOL fascicles during concentric and eccentric contractions would not be altered by knee joint position. In addition, SOL EMGs were not affected by the knee positions both in concentric (Chapter 3) and eccentric (Chapter 4) contractions. These findings suggest that SOL contributed to the tendon force to a similar extent regardless of knee joint positions. Consequently, it may be assumed that the differences in the tendon force between the extended and flexed knee positions would primarily be due to the differences in the MG force.

Number of sarcomeres within the MG fascicle

In the discussion of length-force relationship, a constant value of 17,600 (Huijing 1985) was applied for all subjects as the serial sarcomere number of MG. However, the mean number of sarcomeres in the human MG, which has been reported in previous studies, ranged from 15,333 to 18,500 [i.e.; 15,333: Wickiewicz et al. (1983); 16,614: Huijing (unpublished but cited by Out et al. 1996); 17,614: Huijing (1985); 18,400: Woittiez et al. (1985); 18,500: Vossen and Huijing (unpublished but cited by Bobbert et al. 1986)]. Hence, inter-individual variability in the sarcomere number may affect the discussion based on the estimated sarcomere length. In the present thesis, the value reported by Huijing (1985) was adopted, since it was obtained from a greater number of cadavers (n = 8) as compared with the other studies. Moreover, even if the other values were used, the relationship of the force generating potential between knee joint positions was not altered, except when the value of Wickiewicz et al. (1983) was used in slow concentric contractions. Therefore, the inter-individual variability in the number of sarcomeres would not affect greatly the discussion based on the estimation of the sarcomere lengths.

5-3. *Conclusion of the thesis*

The purpose of this thesis was to investigate 1) how the fascicle behavior of the gastrocnemius muscle changes in relation to knee joint angles and 2) how these changes influence on the force developed by the gastrocnemius. The main findings of this thesis are following three points. The first is that the length change of gastrocnemius muscle-tendon complex induced by passive knee joint motion had a greater effect on the fascicle length than that induced by passive ankle joint motion. Secondly, during fast concentric plantar flexions, the gastrocnemius fascicles at the flexed knee position were shorter and their velocities were lower than those at the extended position, and this could explain the similar tendon forces between the different knee joint potions. Thirdly, the gastrocnemius fascicles during eccentric plantar flexions were elongated at the extended knee position, but they were almost constant at the flexed knee position. These findings suggest that 1) gastrocnemius fascicle length is altered by knee joint angle, but its effects of knee joint angle on the length-related force generating potential of gastrocnemius are dependent on the contraction types, and 2) the knee flexion decreases the fascicle velocity of gastrocnemius both in concentric and eccentric contractions, but the decreased fascicle velocity have markedly different influences on the gastrocnemius force between the contraction types.

Appendix

The relationship between the force and velocity for the eccentric part was estimated from following equation (van Soest and Bobbert 1993; Cole et al. 1996).

$$V = L_0 \cdot \left(\frac{c_1}{\frac{F}{F_{\max} \cdot q} + c_2} - c_3 \right)$$

where $c_1 = 0.34$, $c_2 = -1.2$, $c_3 = -1.72$ (van Soest and Bobbert 1993; Cole et al. 1996), V is the lengthening velocity of MG fascicle, L_0 is the optimal length of MG fascicle [48 mm = 17,600 (series sarcomere number of MG fascicle, Huijing 1985) × 2.73 µm (optimal length of human sarcomere, Walker and Schrodt 1974)], F is the eccentric force, F_{max} is the maximal static force (= 1 in the present study) and q is the activation level (= 1 in the present study).

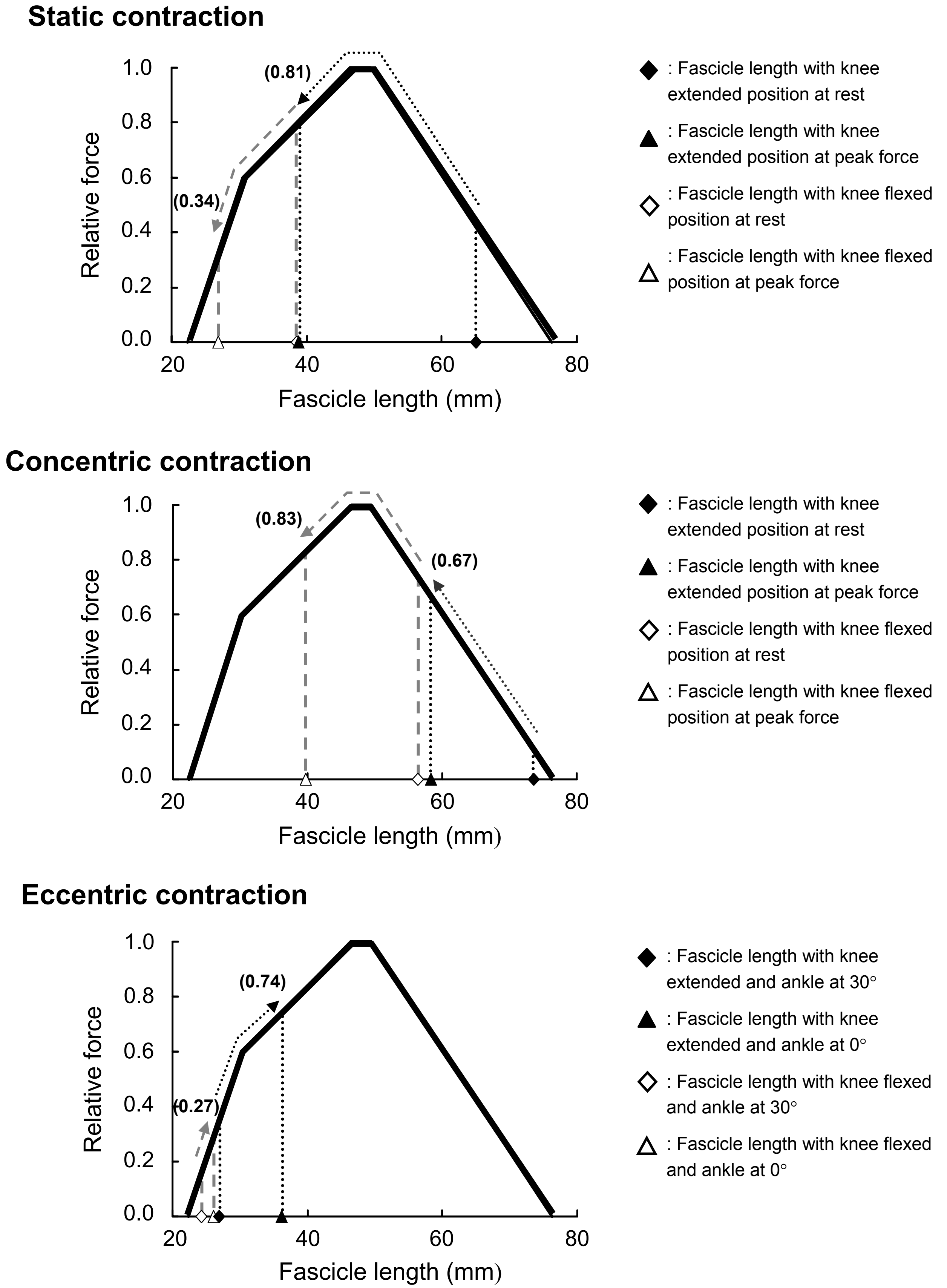


Figure 5-1. Operating ranges of the medial gastrocnemius fascicle in static (Chapter 4), fast concentric (Chapter 3) and fast eccentric (Chapter 4) contractions superimposed on the length-force relation obtained from humans (Walker and Schrodt 1974). The values in parenthesis mean the length-related force potential at the peak tendon force (static and concentric contractions) and at ankle joint angle of 0° (eccentric contractions).

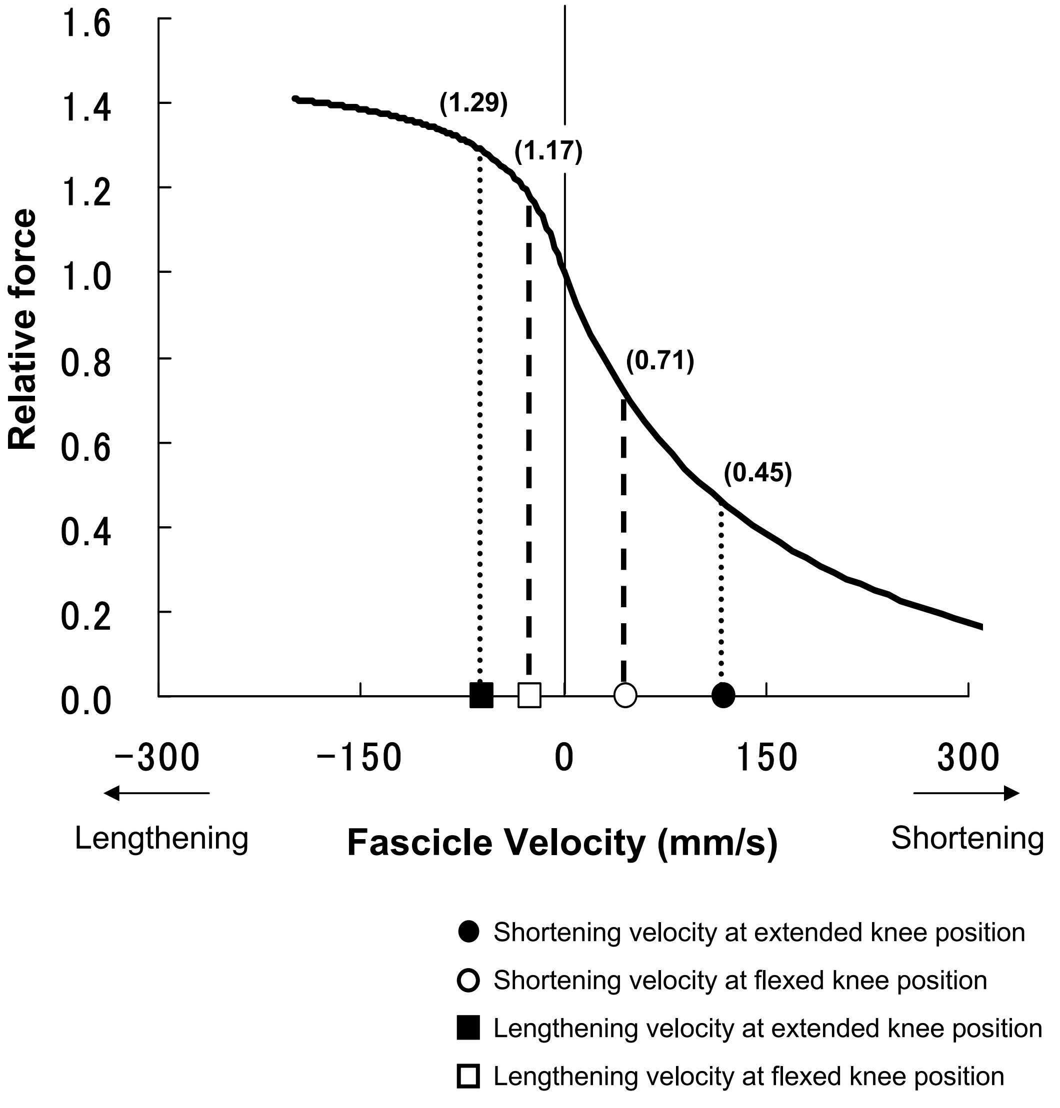


Figure 5-2. The fascicle velocity in fast concentric and eccentric contractions superimposed on the estimated force-velocity relation (Hill 1938; van Soest and Bobbert 1993; Cole et al. 1996). The values in parenthesis mean the velocity-related force potential at the peak tendon force for concentric contractions and at the ankle joint angle of 0° for eccentric contractions.

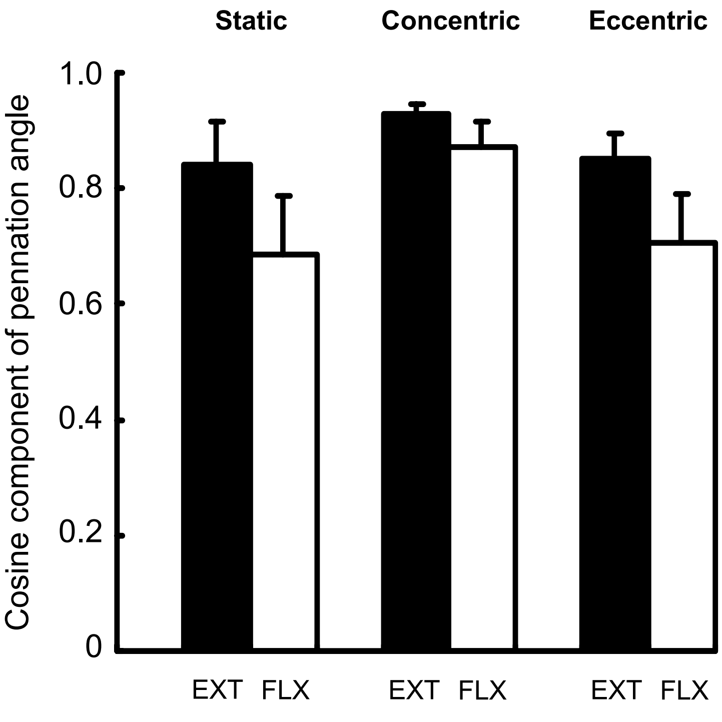


Figure 5-3. The cosine component of pennation angle in each of the static and fast concentric and eccentric contractions. The pennation angles at the peak tendon force (static and concentric contractions) and at the ankle joint angle of 0° (eccentric contractions) were used. EXT: extended knee position. FLX: flexed knee position.

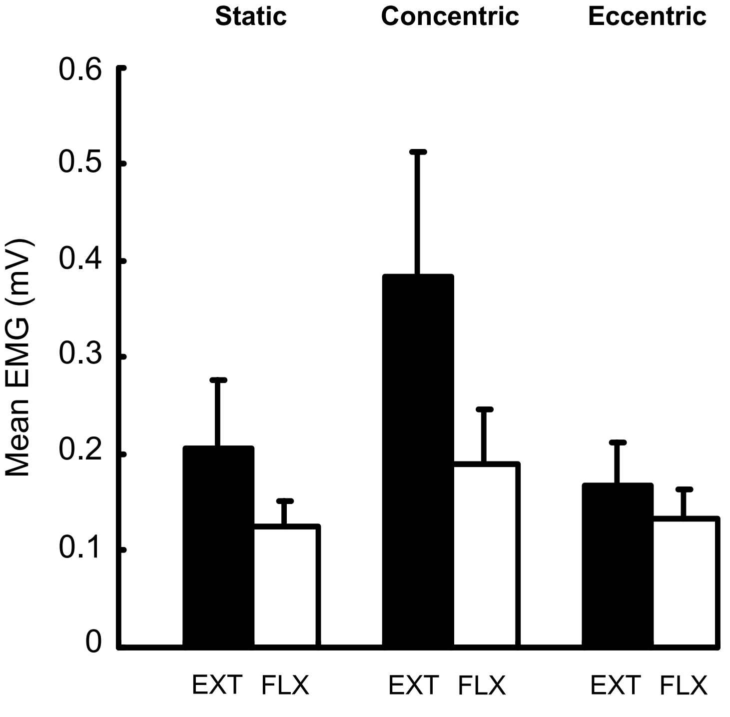


Figure 5-4. The averaged electromyograms (EMG) of medial gastrocnemius in each of the static and fast concentric and eccentric contractions. EXT: extended knee position. FLX: flexed knee position.

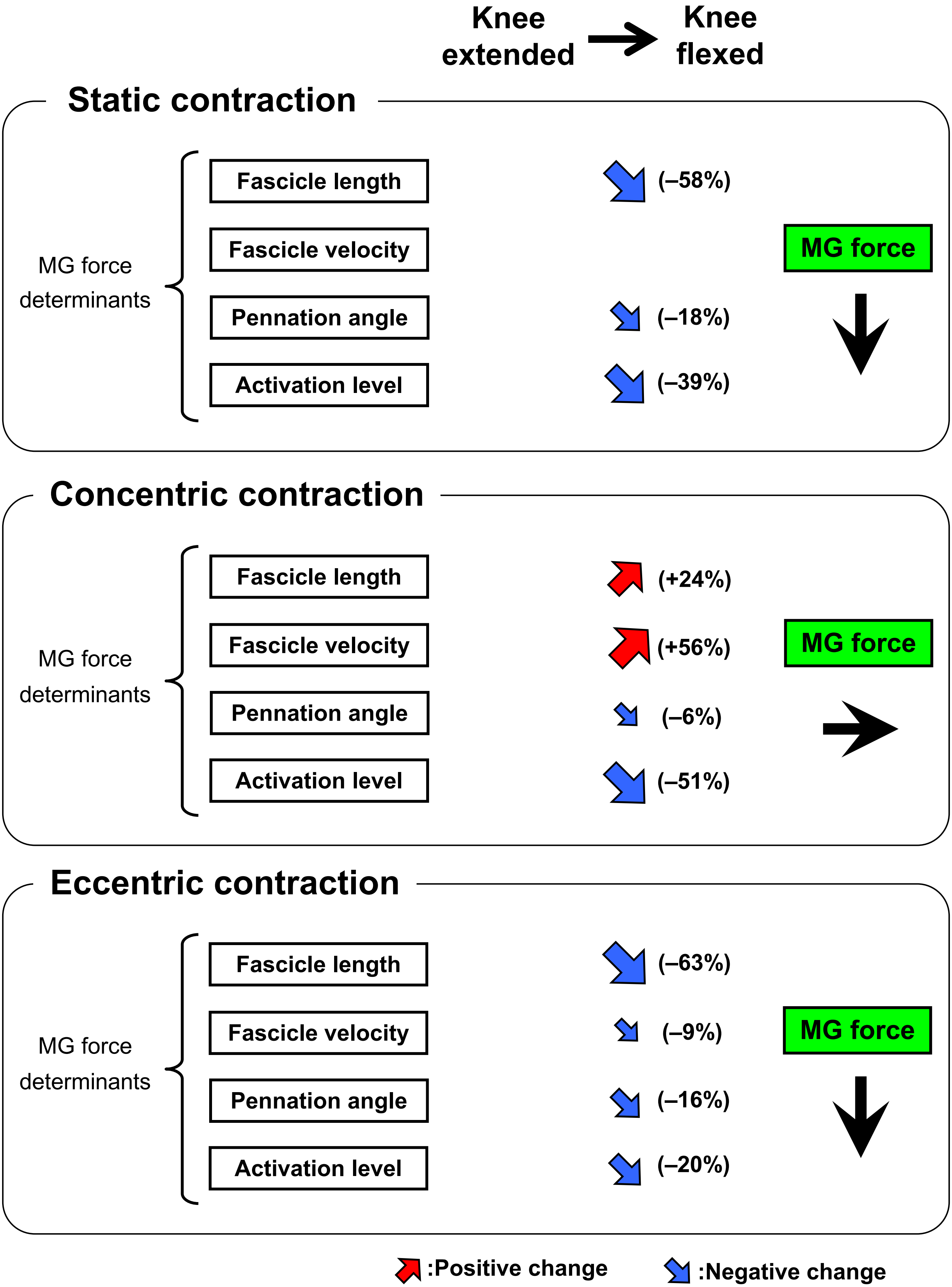


Figure 5-5. Summary of the present findings. Changes of the determinants of medial gastrocnemius (MG) force with knee joint flexion are demonstrated by the arrows and values in parentheses.

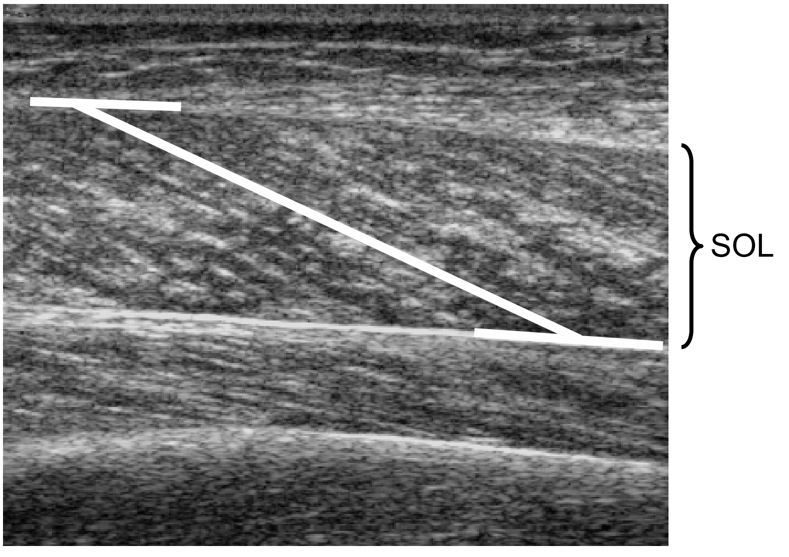


Figure 5-6. Typical ultrasound images of muscle belly of the soleus (SOL). The fascicle length and pennation angle were measured when the plantar flexion torque peaked.

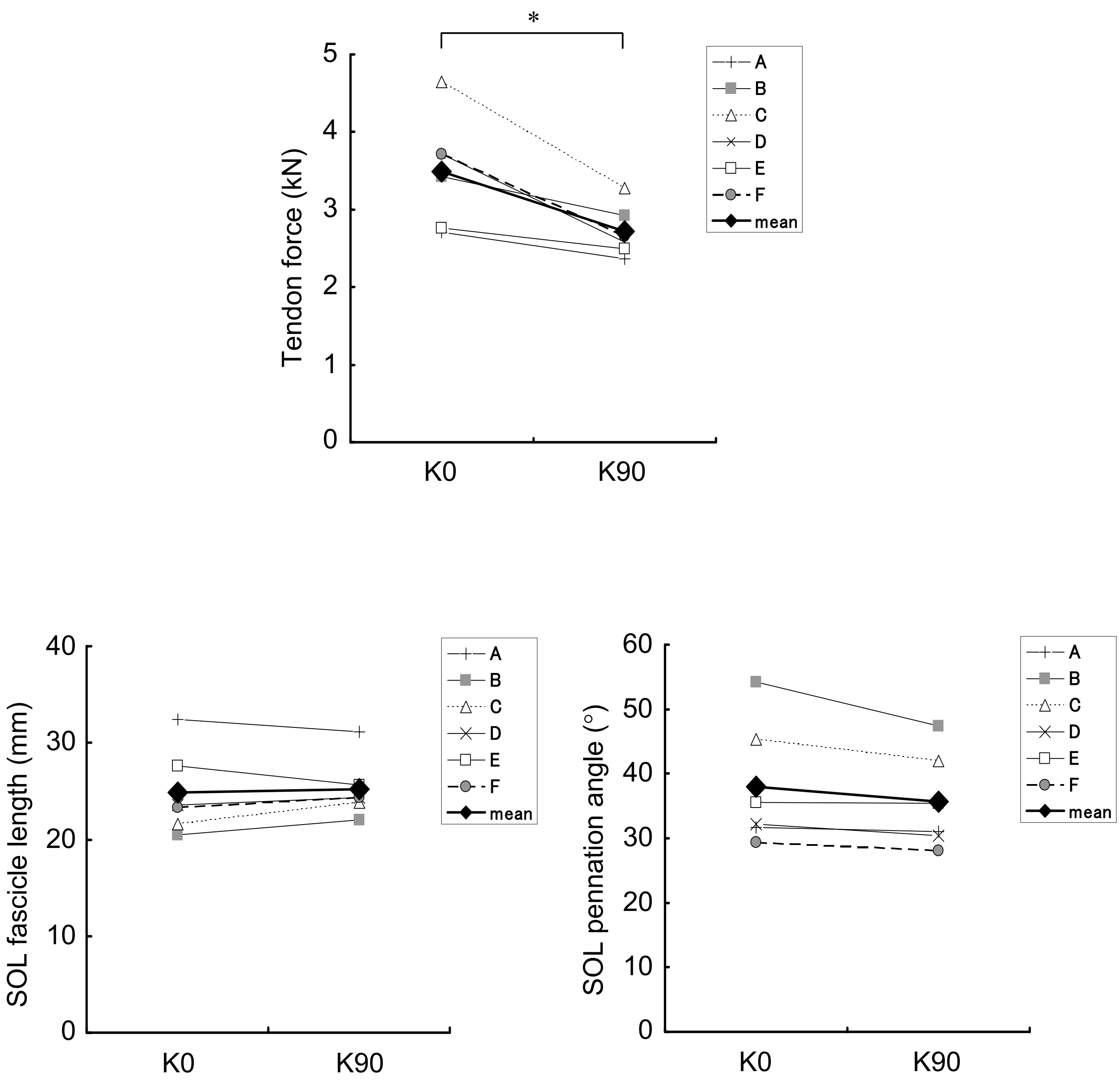


Figure 5-7. The tendon forces, fascicle lengths and pennation angles of the soleus (SOL) during maximal static plantar flexions with the knee fully extended (K0) and 90° flexed (K90) positions. * denotes that the difference between knee joint positions is significant.

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