Passive knee movement-induced modulation of the soleus H-reflex and alteration in the fascicle length of the medial gastrocnemius muscle in humans

Junichi Ushiyama [a,*], Taku Wakahara [b], Kei Masani [c,d], Motoki Kouzaki [e], Tetsuro Muraoka [f], Tetsuo Fukunaga [g], Hiroaki Kanehisa [h]

[a] Institute of Physical Education, Keio University, Yokohama, Kanagawa, Japan
[b] Faculty of Sport Sciences, Waseda University, Tokorozawa, Saitama, Japan
[c] Rehabilitation Engineering Laboratory, Lyndhurst Centre, Toronto Rehabilitation Institute, Toronto, Ontario, Canada
[d] Rehabilitation Engineering Laboratory, Institute of Biomaterials and Biomedical Engineering, University of Toronto, Toronto, Ontario, Canada
[e] Graduate School of Human and Environmental Studies, Kyoto University, Sakyo-ku, Kyoto, Japan
[f] College of Economics, Nihon University, Chiyoda-ku, Tokyo, Japan
[g] National Institute of Fitness and Sports in Kanoya, Kanoya, Kagoshima, Japan
[h] Department of Life Sciences, Graduate School of Arts and Sciences, The University of Tokyo, Meguro-ku, Tokyo, Japan

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ABSTRACT

In humans, an inhibitory via Ia afferent pathway from the medial gastrocnemius (MG) to the soleus (SOL) motoneuron pool has been suggested. Herein, we examined the relation between MG fascicle length changes and the SOL H-reflex modulation during passive knee movement. Twelve subjects performed static and passive ($5° s^{-1}$) knee movement tasks with the ankle immobilized using an isokinetic dynamometer in sitting posture. The maximal H- and M-waves were measured at four target angles ($20°$, $40°$, $60°$, and $80°$ flexion from full knee extension). The MG fascicles length and velocity were measured using a B-mode ultrasonic apparatus. Results demonstrated that the SOL Hmax/Mmax; i.e., ratio of the maximal H- to M-waves, was attenuated with increasing MG fascicle length in static tasks. The SOL Hmax/Mmax at $20°$ was significantly attenuated compared with $60°$ and $80°$ with increasing MG fascicle length and lengthening velocity in passive knee extension. However, no significant differences in the SOL Hmax/Mmax were found across the target angles in the passive knee flexion task. In conclusion, as muscle spindles increase their discharge with lengthening fascicle velocity, but keep silent when fascicles shorten, our data suggest that lengthening the MG facilitates an inhibitory Ia pathway from MG to SOL, and modulates SOL motoneuron activity during movements.

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1. Introduction

The soleus (SOL) H-reflex represents the excitability of the motor neuron pool in the spinal cord. It is well established that the SOL H-reflex is modulated depending on the motor task including standing (Hayashi et al., 1992; Katz et al., 1988; Koceja et al., 1993) and gait (Capaday and Stein, 1986), and also depending on the phase during passive and dynamic cyclic movement such as bicycle pedaling or isolated joint rotations (Brooke et al., 1995; Cheng et al., 1995; Misiaszek et al., 1998). These task- and/or phase-dependant H-reflex modulations have been intensively studied with respect to the centrally regulated reciprocal inhibition between the dorsiflexor and the SOL (Schneider et al., 2000) or the

Ia afferent inhibition from the quadriceps muscle on the SOL (Brooke et al., 1995; Cheng et al., 1995; Misiaszek et al., 1998).

Interestingly, in humans an inhibitory neural pathway from the medial gastrocnemius (MG) to the SOL may be another source of modulation of SOL motoneuron activity (Mao et al., 1984; Gritti and Schieppati, 1989; Schieppati et al., 1990). Gritti and Schieppati (1989) demonstrated that a conditioning stimulation of the MG nerve resulted in a short-latency inhibition of the SOL H-reflex in sitting posture. As this inhibition was abolished with a long-term (25 min) vibration on the Achilles tendon, a method used to inactivate the Ia afferent nerve fibers, they concluded that there is an inhibitory pathway including the Ia afferents from the MG to the SOL. However, it is largely unknown how this inhibiting pathway actually contributes to the modulations of the SOL motoneuron activity during human movements.

The muscle spindles lie in parallel with muscle fibers, and sense muscle fiber length and velocity. This information is transmitted to the central nervous system by the Ia afferent nerve fibers (Proske

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et al., 2000). Considering the inhibitory Ia pathway from the MG to the SOL described above, it is hypothesized that the SOL H-reflex is modulated by MG length changes during passive knee movements; i.e., the amplitude of the SOL H-reflex is depressed when the MG is lengthened during passive knee extension, but is not when the MG is shortened during passive knee flexion.

Although previous studies demonstrated that length changes in bi-articular hip and knee muscles, such as the rectus femoris or semitendinosus, contribute to the phase-dependent H-reflex modulation during passive single and/or multi-joint pedaling movements (Brooke et al., 1995; Cheng et al., 1995; Misiaszek et al., 1998), the muscle length of the MG was not examined. Furthermore, those studies used the musculo-tendon complex (MTC) length estimated from the joint angle as a measure of muscle length, using the model described by Frigo and Pedotti (1978). However, Hoffer et al. (1989) reported that the behavior of muscle length estimated from the joint angle does not equally correspond to that of the muscle spindle in anesthetized cats. Since the muscle spindle is the sensor of muscle 'fiber' length (Proske et al., 2000), the muscle fiber length should be measured to describe the changes in Ia afferent discharge during movements. It is possible to directly measure muscle fascicle length that is proportional to the muscle fiber length in humans using a B-mode ultrasonic apparatus (Friedrich and Brand, 1990; Kawakami et al., 1998). However, there are no studies investigating the effect of muscle fascicle length directly measured using ultrasonic apparatus on the H-reflex modulation.

To investigate the effect of inhibitory Ia inputs from the MG on SOL motoneuron activity during movement, the present study tested the hypothesis that the movement-induced modulation of the SOL H-reflex is related to the MG fascicle length behavior; i.e., the amplitude of the SOL H-reflex is depressed when the MG fascicle is lengthened during passive knee extension, but is not when the MG fascicle is shortened during passive knee flexion.

2. Methods

2.1. Subjects

Twelve healthy male subjects participated voluntarily in the present study. Their age, height, and body mass ranges were 22–32 years, 1.655–1.782 m, and 58.0–82.4 kg, respectively. They had no history of neurological disorders. All subjects provided informed consent to participate in the present study after receiving a detailed explanation of the purpose, potential benefits, and risks involved. The experimental procedures used were in accordance with the ethical standards of the Committee on Human Experimentation at the Department of Life Sciences, The University of Tokyo.

2.2. Joint angles and surface EMG recordings

The subjects were comfortably seated on the chair of a dynamometer (model Myolet RZ-450; Asics, Kobe, Japan) with the hip flexed at 80° from full extension (Fig. 1). The axis of the lever arm of the dynamometer was visually aligned with the center of rotation of the knee joint. The upper body was strapped to the chair so that the subjects maintained a stable position throughout the measurements. The thigh was also strapped to prevent the knee joint from any circumnutation. The foot was attached firmly to a footplate mounted to the lever arm of the dynamometer in order to fix the ankle joint at 0° (neutral position) throughout the experiment.

The signal of the knee angle was recorded from the output of the dynamometer by a computer. The ankle angle was also
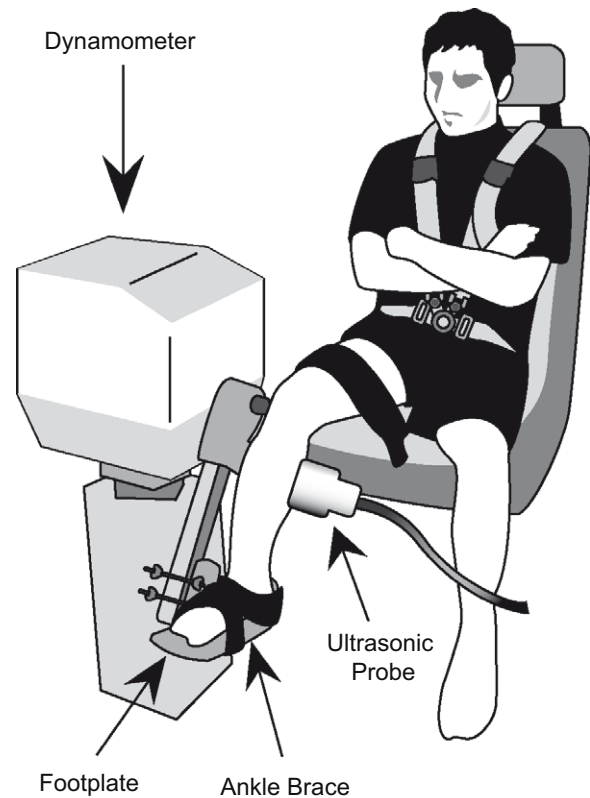

Fig. 1. Schematic of the setup used for measurement of H-reflexes and M-waves when the knee is held static and/or passively moved. The foot was fixed to a footplate mounted on the lever arm of the dynamometer. An ultrasonic probe was longitudinally attached to the dermal surface over the mediolateral center of the MG. See Section 2 for more details.

recorded using a goniometer (PH-412B; DKH, Tokyo, Japan) to check that it did not change throughout experiments. Surface EMG were recorded from the MG, lateral gastrocnemius (LG), SOL, tibialis anterior (TA), and biceps femoris longus over the muscle bellies using bipolar Ag–AgCl electrodes (diameter 5×10^{-3} m, inter-electrode distance 2×10^{-2} m). The reference electrode was placed on the medial malleolus. The EMG signals were amplified (model 1253A; NEC Medical Systems, Tokyo, Japan) with bandpass filtering between 5–1000 Hz. All electric signals were stored with a sample frequency of 2000 Hz on the hard disk of a personal computer using a 16-bit analog-to-digital converter (PowerLab/16SP; ADInstruments, Sydney, Australia).

2.3. Stimulation procedures

The stimulus for eliciting H-reflexes and M-waves from the SOL was delivered as a 1 ms rectangular pulse from a digital stimulator (SEN-7203; Nihon Koden, Tokyo, Japan) in series with a stimulus-isolation unit (SS-1963; Nihon Koden). The cathode, a 35×10^{-5} m^2Ag–AgCl surface electrode, was placed cutaneously over the tibialis nerve in the popliteal fossa. The anode, a 24×10^{-4} m^2 plate ground electrode, was placed on the ventral aspect of the knee, just proximal to the patella.

To select suitable stimulus intensities, static recruitment curves were obtained at each of four different target knee angles (20°, 40°, 60°, and 80° flexion from full extension) before starting the experiment. Recruitment curves were also recorded at each target angle during passive knee extension and flexion. The dynamometer was programmed to move the knee joint passively through 20° at an angular velocity of 5° s^{-1} starting at +10° from

the target angle for passive knee extension tasks, or at $-10°$ from the target angle for passive knee flexion tasks, respectively. For example, when the H-reflex was elicited at 20° during knee extension, the knee was moved from 30° to 10°. Since it was difficult to obtain the accurate ultrasonic images when the dynamometer was set at a faster angular velocity, we employed passive slow movement at an angular velocity of $5° \, s^{-1}$. Electrical stimulations were applied to the tibialis nerve when the knee was at the target angle (for the static tasks) or triggered as the knee passed the target angle (for the passive tasks). To record each recruitment curve of the H-reflexes and M-responses, the stimulus intensities were gradually increased from an initial value below the threshold of the H-reflex to the maximal M-responses. We repeated the same procedure twice, and determined the influence of possible variations in the effective stimulus intensity that likely resulted from alterations in the spatial relationship between the stimulation electrode and the tibialis nerve. Based on each recruitment curve, the stimulus intensity required to elicit the maximal amplitude of the H-reflex (Hmax) was identified within each target angle and action type (static or passive knee extension and flexion). To elicit the maximal amplitude of the M-wave (Mmax), the supramaximal stimulus intensity (approximately 120% of the intensity at which we first obtained the Mmax) was used for every task. The typical recruitment curves for each target angle during the static, passive knee extension, and passive knee flexion tasks are shown in Fig. 2.

2.4. Ultrasonography

The fascicle length of the MG was measured with a B-mode ultrasonic apparatus (SSD-2000; Aloka, Tokyo, Japan). An ultrasonic probe (UST-579T; Aloka) with a frequency of 7.5 MHz was longitudinally attached to the dermal surface over the mediolateral center of the MG (Fig. 3). The probe was carefully fixed to the skin surface with a specially designed supporting device and surgical tape, so as not to compress the tissue. During the measurements, the probe was also supported by the examiners' hand, such that images of the uniform longitudinal plane of the tissue could be obtained. When the knee joint was moved passively the examiner made an effort to obtain accurate images throughout the range of motion. Ultrasonic images were recorded as video signals at 30 Hz with a videotape recorder (HR-V; Victor, Yokohama, Japan). The images were then synchronized with the joint angle and EMG data by superimposing a clock timer. The ultrasonic images were stored on the hard disk of a personal computer using a digital video converter (ADVC-100; Canopus, Kobe, Japan).

2.5. Experimental protocol

In the static and passive tasks, five Hmax and three Mmax values were recorded at each of the four different target knee angles (20°, 40°, 60°, and 80° flexion from full extension). In passive tasks, the dynamometer was programmed as described under 'Stimulation
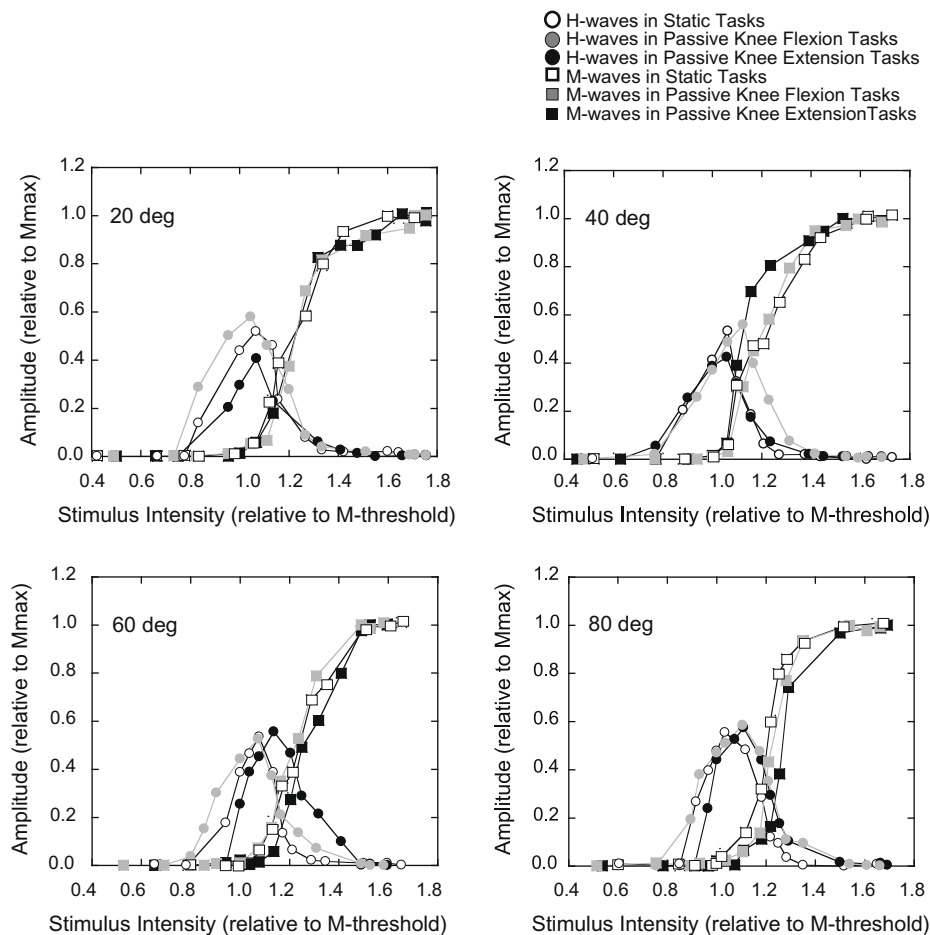

Fig. 2. Representative examples of the recruitment curves of the H-reflexes and M-waves at each knee angle (upper left, 20°; upper right, 40°; lower left, 60°; lower left, 80°). White circles, gray circles, black circles, white squares, gray squares, and black squares indicate H-reflexes in the static tasks, H-reflexes in the passive knee flexion tasks, H-reflexes in the passive knee extension tasks, M-waves in the static tasks, M-waves in the passive knee flexion tasks, and M-waves in the passive knee extension tasks, respectively. Amplitude of the H- and M-waves and stimulus intensity are represented as a percentage of the amplitude of Mmax and the motor threshold (M-threshold), respectively.
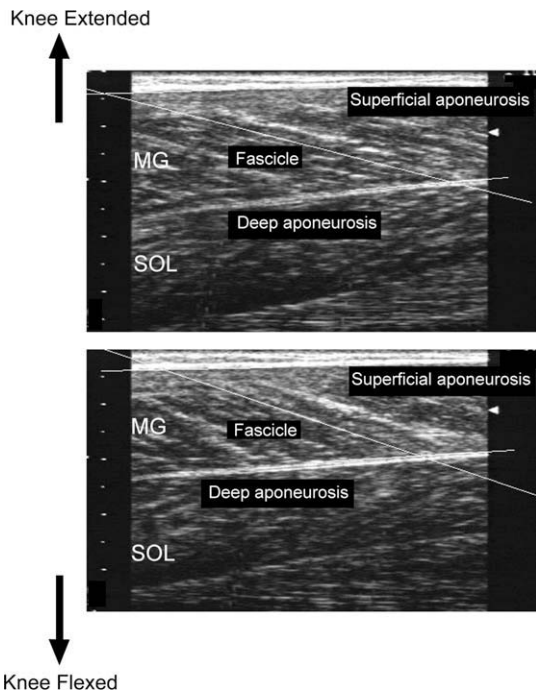
Fig. 3. Ultrasonic images of longitudinal sections of the MG when the knee is in the extended position (upper) and flexed position (bottom). The superficial aponeurosis, deep aponeurosis, and fascicle can been seen in each image. The MG fascicle is shorter in the knee-flexed position than in the knee-extended position. The fascicle length was determined as the length of echoes from the fascicles.

procedures'. Electrical stimulation of the tibialis nerve was triggered as the knee passed the target angle. A sufficient interval (at least 30 s) was given between consecutive tasks. During passive tasks, the subjects were instructed to relax their thigh and leg, and the examiner checked that no EMG activity was found in their muscles. The order of the action types and target angles was randomized among the subjects. Changes in the MG fascicle length were also measured using ultrasonography with respect to static and passive angular variations of the knee joint, separately from the recordings of H- and M-waves.

2.6. Data analysis

The peak-to-peak amplitude was determined for all H and M potentials. The averages of the five Hmax and three Mmax were calculated for each task, followed by calculation of the Hmax/Mmax ratio. In addition, we also determined the amplitudes of M-waves when we elicited the Hmax, and calculated the ratios of the averages of these five small M-waves to the averaged Mmax (M/Mmax) to ascertain the stability of recording conditions.

The fascicles were traced in ultrasonic images, and their length was determined using a software package for image processing and analysis (Image J; National Institute of Health, Bethesda, MD, USA). For static tasks, the fascicle length was determined at the four different target angles. For passive tasks, the changes in fascicle length were measured every 1° over the entire range of motion in each task. Fascicle length data were low-pass-filtered by a three-point moving average method, and differentiated to calculate the fascicle velocity when the knee passed each target angle. From the knee joint angle and the leg length data, the length of the MG musculo-tendon complex (MTC) was estimated using the model described by Frigo and Pedotti (1978), which has been widely utilized in studies concerning the movement-induced H-reflex modulation (Brooke et al., 1995; Cheng et al., 1995; Misiaszek et al.,

1998). Data from the goniometer were also calculated every 1° over the entire range of motion, and the SE was determined in each task.

2.7. Reproducibility of the fascicle length measurements

The reproducibility of the fascicle length measurements was evaluated on the basis of the coefficient of variation (CV) (SD × 100/mean) (Narici et al., 1996; Fukunaga et al., 1997; Muraoka et al., 2003). We calculated the reproducibility of the fascicle length at each target angle across three action types during two procedures: (1) the averaged CV value of three different trials for every experimental condition, which was determined for one subject, was 1.5%; and (2) the averaged CV value of digitizing the ultrasonic images, which was repeated three times on the same image for all subjects, was 1.8%. These values are within the ranges of the reproducibility previously reported (Narici et al., 1996; Fukunaga et al., 1997; Muraoka et al., 2003).

2.8. Statistical analysis

The effects of knee angle and action type on Hmax/Mmax, M/Mmax, and fascicle length were analyzed by two-way ANOVA (four target knee angles × three action types) with repeated measures. The effects of knee angles on the fascicle velocity were analyzed in each task by one-way ANOVA with repeated measures. An alpha level of 0.05 was chosen for all statistical analyses with post hoc comparisons (Tukey's test) when appropriate. All statistical analyses were performed using Statistica software (StatSoft Japan, Tokyo, Japan).

3. Results

3.1. H-reflexes and M-waves at different knee angles

Representative examples of the Hmax and corresponding M-waves at each target angle during the static, passive knee extension, and passive knee flexion tasks are shown in Fig. 4A. The group data (mean ± SE) of the Hmax/Mmax and M/Mmax for all the subjects and for all tasks, i.e., static, passive extension, and flexion tasks, are shown in Fig. 4B. Note that the plots for the values of Hmax/Mmax and M/Mmax of static tasks were identical between the areas of flexion and extension movements. M/Mmax remained consistent in both passive and static tasks; i.e., the main effects of task ($F_{2,6} = 0.05$, $P = 0.948$) and knee angles ($F_{3,6} = 0.45$, $P = 0.721$) were not significant in M/Mmax values (Fig. 4B).

By contrast, main effects of task ($F_{2,6} = 8.32$, $P = 0.0020$) and knee angle ($F_{3,6} = 6.64$, $P = 0.0012$) were highly significant in Hmax/Mmax values. As there was a significant interaction between knee angle and task ($F_{6,66} = 4.58$, $P = 0.0006$), one-way ANOVA was performed prior to post hoc analysis. Since the ANOVA result was significant ($F_{11,121} = 6.40$, $P < 0.0001$), we conducted the post hoc analysis. During static task, post hoc analysis showed that the Hmax/Mmax at 20° (0.474 ± 0.042) was significantly lower than at 60° (0.558 ± 0.054; difference 13.4 ± 5.6%, $P = 0.0005$) and at 80° (0.572 ± 0.056; difference 15.2 ± 5.7%, $P = 0.0001$). During the passive knee extension task, Hmax/Mmax at 20° (0.428 ± 0.042) was also significantly lower than at 60° (0.549 ± 0.061; difference 21.0 ± 5.6%, $P = 0.0025$) and at 80° (0.590 ± 0.052; difference 26.4 ± 6.3%, $P = 0.0001$), and Hmax/Mmax at 40° (0.479 ± 0.057) was significantly lower than at 60° (difference 13.7 ± 5.0%, $P = 0.0010$) and at 80° (difference 19.2 ± 6.6%, $P = 0.0002$). On the other hand, no significant differences were found across the target angles in the passive knee flexion task (20° vs. 40°, $P = 0.999$; 20° vs. 60°, $P = 0.936$; 20° vs. 80°, $P = 0.098$; 40° vs. 60°, $P = 0.985$; 40° vs. 80°, $P = 0.150$; 60° vs. 80°, $P = 0.851$). Furthermore, when we

compared the Hmax/Mmax at a certain angle among tasks, there was a significant difference between passive knee extension and flexion at 20° ($P = 0.0001$).

3.2. Length and velocity of the MG fascicle and the MG MTC at different knee angles

The ankle angle was determined using the goniometer in each task. The small averaged SE value of the ankle angle (0.19°) implied that no changes in the SOL fascicle length occurred through-

out the experiments. The MG fascicle length and velocity in both static and passive tasks are shown in Fig. 5A and B, respectively. The curved plot of MG fascicle length (Fig. 5A) indicates that the alteration of fascicle length was not uniform, despite the isokinetic property of the dynamometer. Indeed, the MG fascicle velocity was clearly not constant (Fig. 5B); i.e., the fascicle velocity became slower when the knee was flexed deeper than 70°. During passive knee extension, the fascicle velocity differed significantly between 20° (1.68 ± 0.32 mm s^{-1}) and 80° (0.55 ± 0.15 mm s^{-1}; $P = 0.019$; Fig. 5B). Furthermore, during passive knee flexion, the
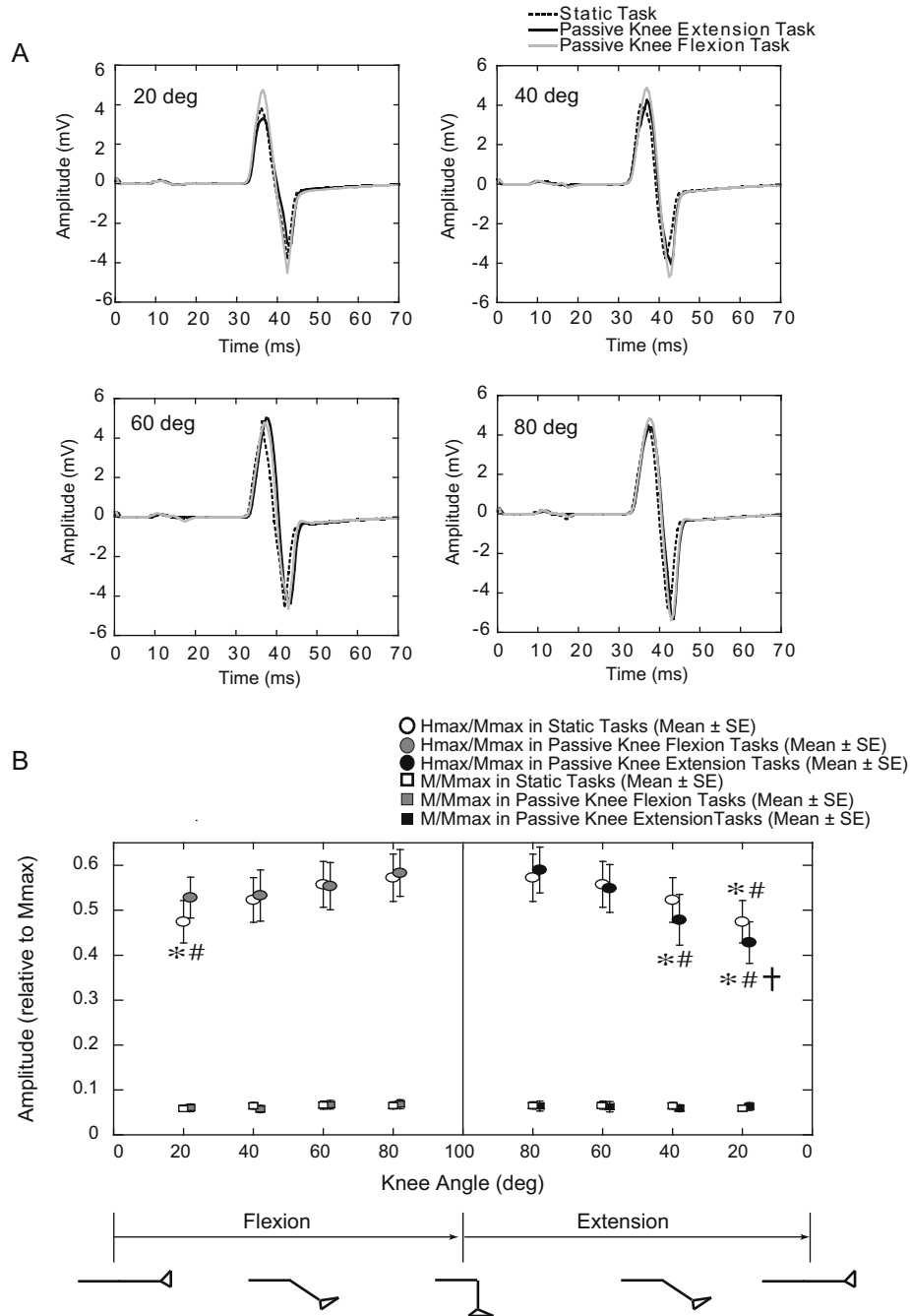

Fig. 4. (A) Representative examples of the Hmax and corresponding M-waves at each knee angle (upper left, 20°; upper right, 40°; lower left, 60°; lower left, 80°). Dotted line, gray line, and black line indicate the signals in the static tasks, those in the passive knee flexion tasks, and those in the passive knee extension tasks, respectively. (B) Effects of changes in the knee angle on the SOL Hmax/Mmax and M/Mmax. White circles, gray circles, black circles, white squares, gray squares, and black squares indicate mean ± SE values of the SOL Hmax/Mmax in the static tasks, Hmax/Mmax in the passive knee flexion tasks, Hmax/Mmax in the passive knee extension tasks, M/Mmax in the static tasks, M/Mmax in the passive knee flexion tasks, and M/Mmax in the passive knee extension tasks, respectively. $^{*}P < 0.05$, significant difference from the value at 80° in the same task. $^{\#}P < 0.05$, significant difference from the value at 60° in the same task. $^{\dagger}P < 0.05$, significant difference between passive knee extension and flexion at the same knee joint angle.
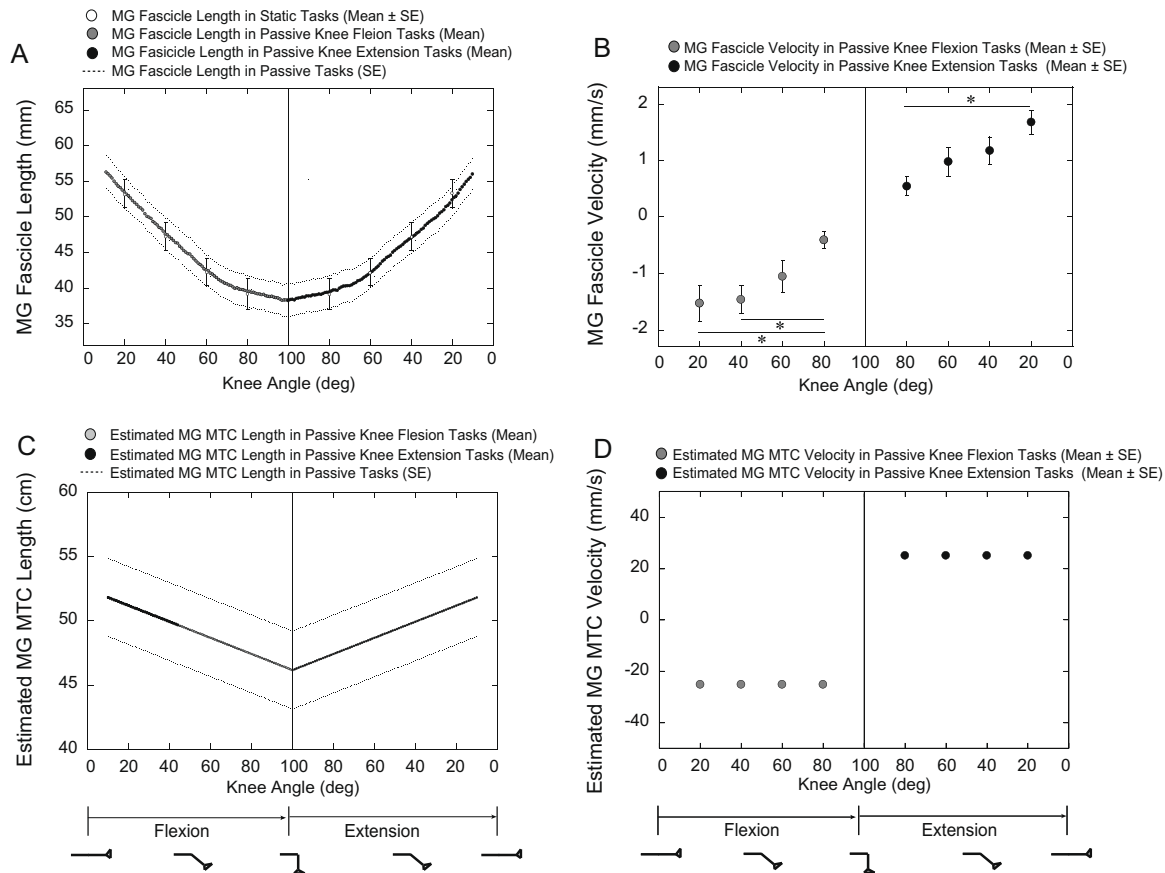
Fig. 5. (A) Changes in the MG fascicle length during static and passive tasks. White circles are mean ± SE values of the MG fascicle length in static tasks. Gray and black squares with dotted line indicate mean ± SE values of the MG fascicle length in the passive knee flexion tasks and in the passive knee extension tasks, respectively. (B) Changes in the MG fascicle velocity in the passive tasks. Gray and black squares indicate mean ± SE values of the MG fascicle velocity in the passive knee flexion tasks and in the passive knee extension tasks, respectively. (C) Changes in the MG MTC length during passive tasks estimated from the knee joint angle and the leg length using the model described by Frigo and Pedotti (1978). Gray and black squares with dotted line indicate mean ± SE values of the MG MTC length in the passive knee flexion tasks and in the passive knee extension tasks, respectively. (D) Changes in the MG MTC velocity during passive tasks. Gray and black squares indicate the value of the estimated MG MTC velocity in the passive knee flexion tasks and in the passive knee extension tasks, respectively. Note that as the MG MTC velocity values were estimated as equal for all subjects, there is no SE bar in this figure. $^{*}P < 0.05$, significant difference from the fascicle velocity at 80° during the same task.

fascicle velocity at 80° (-0.41 ± 0.17 mm s^{-1}) was significantly slower than at 20° (-1.53 ± 0.21 mm s^{-1}; $P = 0.010$) and 40° (-1.46 ± 0.24 mm s^{-1}; $P = 0.016$; Fig. 5B). On the other hand, when we estimated the MG MTC length and velocity using the joint angle, the MG MTC velocity was constant. The MG MTC length and velocity are shown in Fig. 5C and D, respectively. Note that we plotted one mark because the estimated MTC behaviors were the same in all tasks (as they depend on the knee joint angle only). Since the model we used to estimate the MTC length changes depended on the knee angle only and assumed a constant moment arm of MG over knee joint angles, the MG MTC length was changed constantly within the range of motion due to the isokinetic property of the dynamometer, while the MG MTC velocity was kept constant. These data indicate that the behavior of the MG MTC estimated using the joint angle is different from that of the actual MG fascicle.

3.3. Relationship between the muscle behavior and Hmax/Mmax

The relationship between the MG fascicle length and Hmax/Mmax in static and passive tasks is shown in Fig. 6A. Results demonstrated that in the static task, the longer the length of the MG fascicle, the smaller the SOL Hmax/Mmax. This tendency was more prominent during passive knee extension, but was diminished during passive knee flexion. Note that the Hmax/Mmax in the passive flexion task was not significantly different across the knee joint an-

gles. The relationship between the MG fascicle velocity and Hmax/Mmax during passive tasks is shown in Fig. 6B. During passive knee extension, the SOL Hmax/Mmax was attenuated with increasing fascicle-lengthening velocity of the MG, while the SOL Hmax/Mmax was not significantly influenced by the fascicle shortening velocity of the MG during passive knee flexion. The relationships between the MG MTC length and the SOL Hmax/Mmax in static and passive tasks, and between the MG MTC velocity and the SOL Hmax/Mmax during passive tasks, are shown in Fig. 6C and D, respectively. Although there is a similar tendency in Fig. 6C compared with Fig. 6A, there is a clear difference in Fig. 6D compared with Fig. 6B. We could not identify the effect of the MG muscle behavior on the SOL Hmax/Mmax in Fig. 6D as the MG MTC velocity was constant due to the isokinetic property of the dynamometer.

4. Discussion

Using direct measurement of MG fascicle behavior with an ultrasonic apparatus, the results of the present study demonstrated that: (1) the SOL Hmax/Mmax was attenuated with increasing MG fascicle length in static tasks; (2) the SOL Hmax/Mmax was more attenuated with increasing MG fascicle length and lengthening velocity in the passive knee extension tasks; and (3) the SOL Hmax/Mmax was almost constant irrespective of the MG fascicle length and length change in the passive knee flexion tasks.

4.1. Effect of MG fascicle length changes on SOL H-reflex

In the present study, the SOL Hmax/Mmax was attenuated with decreasing knee joint angle and with increasing MG fascicle length in static tasks. These data suggest that increasing muscle length due to knee joint angle difference facilitates the inhibitory neural pathway including the Ia afferent from the MG to the SOL (Gritti and Schieppati, 1989), and inhibits the motor neuron excitability of the SOL. Furthermore, the magnitude of the SOL H-reflex attenuation was larger in the passive knee extension task than in the static task, suggesting that the inhibitory neural pathway from the MG to the SOL is more facilitated in the passive knee extension task. This is in agreement with a previous study showing that activity of the primary endings of muscle spindles was lower during static stretch than during passive stretching movement in the cat SOL muscle (Houk et al., 1981).

The additional facilitation of the inhibitory neural pathway may be accounted for by the MG fascicle velocity, as SOL Hmax/Mmax was attenuated with the increasing fascicle lengthening velocity of the MG. The Ia afferent usually provides a continuous discharge during passive lengthening (Al-Falahe et al., 1990), and its discharge frequency increases with increasing velocity of muscle lengthening (Prochazka et al., 1979; Proske et al., 2000). Thus, in passive knee extension, the Ia afferent of the MG is more activated, which facilitates the inhibitory neural pathway from the MG to the SOL. The amplitude of the SOL H-reflex was not significantly modulated during passive knee flexion, even though MG fascicle length was almost equal among the tasks. Al-Falahe et al. (1990) reported that Ia afferents show no

discharge during passive shortening, irrespective of muscle length and velocity. Thus, it is likely that the Ia discharge is not evoked when the MG fascicle is passively shortened, such that the amplitudes of the SOL H-reflex are less changed during passive knee flexion tasks.

Interestingly, although we employed isokinetic movements, fascicle velocity was not constant within the range of joint motion. This is likely due to the following: (1) the muscle moment arm changes depending on the joint angle (Spoor et al., 1990); (2) the length of the tendinous tissue changes even during passive joint movement (Herbert et al., 2002), and this tendency is non-linear (Muraoka et al., 2002); and (3) the pennation angle changes depending on the joint angle (Narici et al., 1996; Kawakami et al., 1998). Since the model we used to estimate the MTC behavior (Frigo and Pedotti, 1978) was quite simple, i.e., it depended on knee angle only and assumed a constant moment arm of the MG over knee joint angle, the estimated MTC behavior was very different from that of the MG fascicle. Furthermore, the behavior of the MG MTC does not account for the observed difference in H-reflex modulation between static and knee extension tasks. These data demonstrate the advantage of the ultrasonic measurements with respect to movement-induced modulation in neural pathways.

4.2. Other potential contributors to movement-induced modulation of the SOL H-reflex

We determined the amplitudes of small M-waves when we elicited the Hmax. M/Mmax remained consistent in both passive and
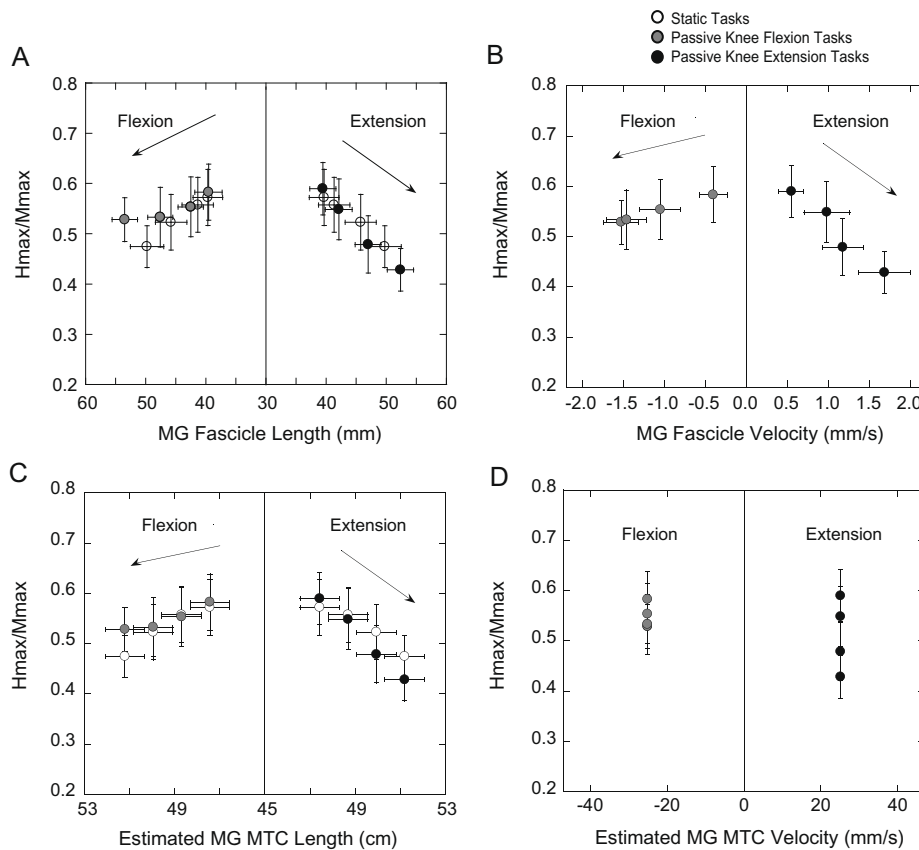

Fig. 6. (A) Relationship between the MG fascicle length and the SOL Hmax/Mmax during static, passive knee extension, and flexion tasks. (B) Relationship between the MG fascicle velocity and the SOL Hmax/Mmax during passive knee extension and flexion tasks. (C) Relationship between the MG MTC length and the SOL Hmax/Mmax during static, passive knee extension, and flexion tasks. (D) Relationship between the MG MTC velocity and the SOL Hmax/Mmax during passive knee extension and flexion tasks. White, gray, and black circles indicate mean ± SE values of the SOL Hmax/Mmax in the static tasks, Hmax/Mmax in the passive knee flexion tasks, and passive knee extension tasks, respectively.

static tasks (Fig. 4B), confirming that there were no alterations in the spatial relationship between the stimulation electrode and the tibialis nerve within each experimental paradigm.

Since the SOL is a single-joint plantar flexor, changes in the knee angle do not influence the SOL fascicle length (Kawakami et al., 1998). In the present study, the stability of the ankle angle was determined using the goniometer in every task. Since the averaged SE value of the ankle angle was 0.19°, no changes in the SOL fascicle length would have occurred throughout the experiments, and the potential for an influence of homonymous Ia afferent activities on the observed H-reflex modulations can be excluded.

Ib afferent activities are known to respond to changes in muscle tension (Houk and Henneman, 1967) and contribute to the reflex inhibition of several muscles (Pratt, 1995). Indeed, Pierrot-Deseilligny et al. (1981) suggested that the inhibition of the SOL H-reflex induced by the MG nerve stimulation is mainly Ib afferents in origin. However, Ib afferents are more influential during active movements than for passive movements (Burg et al., 1973; Jami, 1992). Since the slow passive movement used in the present study did not evoke any EMG activity in any of the muscles, the contribution of the Ib afferent activities to the observed SOL H-reflex modulations was assumed to be not so large.

It was previously reported that the majority of joint receptors are silent within the range of natural movement during slow passive movements that do not force extreme rotation of the knee joint (Burgess and Clark, 1969; Ferrell et al., 1986; Johansson et al., 1991). Further, Hultborn et al. (1996) reported that applying a tourniquet at ankle angle, which induces an ischemic block of the sensory inputs from cutaneous mechanoreceptors, does not alter the H-reflex modulation patterns following passive dorsiflexion. Thus, it is unlikely that discharge of the cutaneous mechanoreceptors was responsible for the observed H-reflex modulations. In several previous studies reporting H-reflex modulations during passive bicycle pedaling, the Ia afferent activity of bi-articular muscles crossing both the knee and hip joints, i.e., the rectus femoris muscle (RF), was considered a powerful source of the phase-dependent H-reflex modulations (Brooke et al., 1995; Cheng et al., 1995; Misiaszek et al., 1998). However, in the present study, the SOL H-reflexes were attenuated, especially in knee extension tasks. Thus, it is unlikely that the observed H-reflex modulations were due to changes in Ia afferent input from the RF, as the RF is shortened during knee extension. Throughout our experiments the subjects were seated on the chair with their hip at 80° flexion from full extension. In this position, the RF might be insufficiently stretched to reinforce the Ia afferent activity levels within the range of motion, which would explain why movement-induced modulations of the SOL H-reflexes were observed only in passive knee extension tasks.

Possible effects of Ia afferent activities of other knee flexors cannot be excluded, as it was previously shown that the stretch of the hamstrings evokes strong H-reflex depression in the alpha-chloralose-anesthetized cat (Enríquez-Denton et al., 2002). On the other hand, Iles and Roberts (1987) demonstrated that vibration-induced H-reflex inhibition was stronger when the vibration was applied to anatomically closer flexors; i.e., inhibition from the MG to the SOL is greater than that from the biceps femoris to the SOL. Therefore, although we cannot exclude the contribution of the inputs from the hamstrings, the Ia discharge of the MG may have had a stronger influence on the observed H-reflex modulations. Of course, it is also possible that the Ia afferent activity of the LG is related to the observed H-reflex modulations, since the behavior of the LG would be similar to that of the MG during passive knee movement. However, there are no studies describing the effects of Ia afferent activities of the LG to the SOL motoneurons. Further studies are required to clarify the neural transmission between the LG and the SOL.

4.3. Functional significance of an inhibitory pathway via the Ia afferent from the MG to the SOL for human locomotion

There is a species variation in the neural pathway patterns between the MG and the SOL. In cats, Ia afferent activity of the MG facilitates the majority of SOL motoneurons (Eccles et al., 1957; Scott and Mendell, 1976), whereas in baboons the facilitatory effects are weaker (Hongo et al., 1984). On the other hand, several studies have suggested that in humans the Ia afferent of the MG terminates to SOL motoneurons via inhibitory interneurons (Mao et al., 1984; Gritti and Schieppati, 1989; Schieppati et al., 1990). With respect to species variation in locomotion patterns, as the knee and ankle are flexed and extended together during the locomotion in four-footed animals (Engberg and Lundberg, 1969), facilitatory effects of Ia afferent activity of the MG on the SOL would be reasonable. In humans, on the other hand, when the MG is lengthened as the knee extends in the swing phase of walking, the ankle remains in dorsiflexion and the MG fascicles continue to lengthen (Fukunaga et al., 2001). If Ia afferent activity of the MG also facilitates SOL motoneurons in this phase in humans, it would become difficult to accomplish smooth heel-contact. Indeed, Capaday and Stein (1986) demonstrated that the amplitude of the SOL H-reflex is small in this phase. Thus, it is reasonable to assume that Ia afferent activity of the MG induced by the fascicle lengthening in the swing phase of walking would contribute to the inhibition of the SOL motoneuron activity.

With respect to the mechanisms of phase-dependent H-reflex modulations, Schneider et al. (2000) suggested that the central organs mainly regulate these phase-dependent reflex modulations during functional tasks such as gait. On the other hand, it was also suggested that stretch-evoked Ia afferent activity, especially from the quadriceps muscle, contributes to the gain modulation of the SOL H-reflexes during gait (Brooke et al., 1995; Cheng et al., 1995; Misiaszek et al., 1998). Of course, since the tasks employed in the present study were not considered functional tasks such as gait, we cannot conclude that an Ia afferent input from the MG is the main contributor of the modulation of the SOL motoneuron activity during locomotion. However, as the SOL H-reflexes were attenuated with increasing MG fascicle length and its velocity during passive knee extension, it is likely that an inhibitory pathway via the Ia afferent from the MG to the SOL can, at least partly, contribute to the phase-dependent modulation of the SOL motoneuron activity during locomotion.

5. Conclusion

We demonstrated that the amplitudes of the SOL H-reflexes were: (1) depressed with increasing MG fascicle length in the static task; (2) strongly depressed with increasing MG fascicle length and lengthening velocity in the passive knee extension tasks; and (3) unchanged in the passive knee flexion tasks. These data suggest that lengthening the MG facilitates an inhibitory neural pathway via the Ia afferent from the MG to the SOL in static and passive knee extension tasks, and modulates SOL motoneuron activity. The larger inhibition in the passive knee extension task than in the static task is accounted for by a large lengthening velocity of the MG fascicle. The activity of this inhibitory pathway can, at least partly, account for the modulation of SOL motoneuron activity during human locomotion. Finally, our data also demonstrate the advantage of ultrasonic measurements in the study of movement-induced modulation in neural pathways.

References

Al-Falahe NA, Nagaoka M, Vallbo AB. Response profiles of human muscle afferents during active finger movements. Brain 1990;113:325–46.

Brooke JD, Cheng J, Misiaszek JE, Lafferty K. Amplitude modulation of the soleus H reflex in the human during active and passive stepping movements. J Neurophysiol 1995;73:102–11.

Burg D, Szumski AJ, Struppler A, Velho F. Afferent and efferent activation of human muscle receptors involved in reflex and voluntary contraction. Exp Neurol 1973;41:754–68.

Burgess PR, Clark FJ. Characteristics of knee joint receptors in the cat. J Physiol 1969;202:317–35.

Capaday C, Stein RB. Amplitude modulation of the soleus H-reflex in the human during walking and standing. J Neurosci 1986;6:1308–13.

Cheng J, Brooke JD, Misiaszek JE, Staines WR. The relationship between the kinematics of passive movement, the stretch of extensor muscles of the leg and the change induced in the gain of the soleus H reflex in humans. Brain Res 1995;672:89–96.

Eccles JC, Eccles RM, Lundberg A. The convergence of monosynaptic excitatory afferents on to many different species of alpha motoneurons. J Physiol 1957;137:22–50.

Engberg I, Lundberg A. An electromyographic analysis of muscular activity in the hindlimb of the cat during unrestrained locomotion. Acta Physiol Scand 1969;75:614–30.

Enríquez-Denton M, Morita H, Christensen LOD, Petersen N, Sinjaer, Nielsen JB. Interaction between peripheral afferent activity and presynaptic inhibition of Ia afferents in the cat. J Neurophysiol 2002;88:1664–74.

Ferrell WR, Nade S, Newbold PJ. The interrelation of neural discharge, intra-articular pressure, and joint angle in the knee of the dog. J Physiol 1986;373:353–65.

Friedrich JA, Brand RA. Muscle fiber architecture in the human lower limb. J Biomech 1990;23:91–5.

Frigo C, Pedotti A. Determination of muscle length during locomotion. In: Amussen E, Jorjensen K, editors. Biomechanics VI, Univ. Park Press, Baltimore, MD; 1978. p. 355–60.

Fukunaga T, Ichinose Y, Ito M, Kawakami Y, Fukashiro S. Determination of fascicle length and pennation in a contracting human muscle in vivo. J Appl Physiol 1997;82:354–8.

Fukunaga T, Kubo K, Kawakami Y, Fukashiro S, Kanehisa H, Maganaris CN. In vivo behavior of human muscle tendon during walking. Proc Roy Soc Lond B Biol Sci 2001;268:229–33.

Gritti I, Schieppati M. Short-latency inhibition of soleus motoneurons by impulses in Ia afferents from the gastrocnemius muscle in humans. J Physiol 1989;416:469–84.

Hayashi R, Tako K, Tokuda T, Yanagisawa N. Comparison of amplitude of human soleus H-reflex during sitting and standing. Neurosci Res 1992;13:227–33.

Herbert RD, Moseley AM, Butler JE, Gandevia SC. Change in length of relaxed muscle fascicles and tendons with knee and ankle movement in humans. J Physiol 2002;539:637–45.

Hoffer JA, Caputi AA, Pose IE, Griffiths RI. Roles of muscle activity and load on the relationship between muscle spindle length and whole muscle length in the freely walking cat. Prog Brain Res 1989;80:75–85.

Hongo T, Lindberg A, Phillips CG, Thompson RF. The pattern of monosynaptic Ia connection to hindlimb motor nuclei in the baboon: a comparison with the cat. Proc Roy Soc Lond B Biol Sci 1984;221:261–89.

Houk J, Henneman E. Responses of Golgi tendon organs to activate contractions of the soleus muscle of the cat. J Neurophysiol 1967;30:466–81.

Houk JC, Rymer WZ, Cargo PE. Dependence of dynamic response of spindle receptors on muscle length and velocity. J Neurophysiol 1981;46:143–66.

Hultborn H, Illert M, Nielsen J, Paul A, Ballegaard M, Wiese H. On the mechanism of the post-activation depression of the H-reflex in human subjects. Exp Brain Res 1996;108:450–62.

Iles JF, Roberts RC. Inhibition of monosynaptic reflexes in the human lower limb. J Physiol 1987;385:69–87.

Jami L. Golgi tendon organs in mammalian skeletal muscle: functional properties and central actions. Physiol Rev 1992;72:623–66.

Johansson H, Sjolander P, Sojka P. Receptors in the knee joint ligaments and their role in the biomechanics of the joint. Crit Rev Biomed Eng 1991;18:341–68.

Katz R, Meunier S, Pierrot-Deseilligny E. Changes in presynaptic inhibition of Ia fibres in man while standing. Brain 1988;111:417–37.

Kawakami Y, Ichinose Y, Fukunaga T. Architectural and functional features of human triceps surae muscles during contraction. J Appl Physiol 1998;85:398–404.

Koceja DM, Trimble MH, Earles DR. Inhibition of the soleus H-reflex in standing man. Brain Res 1993;629:155–8.

Mao CC, Ashby P, Wang M, McCrea D. Synaptic connections from large muscle afferents to the motoneurons of various leg muscles in man. Exp Brain Res 1984;56:341–50.

Misiaszek JE, Cheng J, Brooke JD, Staines WR. Movement-induced modulation of soleus H reflexes with altered length of biarticular muscles. Brain Res 1998;795:25–36.

Muraoka T, Muramatsu T, Tachi M, Kawakami Y, Kanehisa H, Fukunaga T. Non-invasive estimation of the joint torque of the vastus lateralis during pedaling based on tendon elongation. Jpn J Biomec Sport Ex 2003;7:214–21.

Muraoka T, Muramatsu T, Takeshita D, Kawakami Y, Fukunaga T. Length change of human gastrocnemius aponeurosis and tendon during passive joint motion. Cells Tissues Organs 2002;171:260–8.

Narici MV, Binzoni T, Hiltbrand E, Fasel J, Terrier F, Cerretelli P. In vivo human gastrocnemius architecture with changing joint angle at rest and during graded isometric contraction. J Physiol 1996;496:287–97.

Pierrot-Deseilligny E, Morin C, Bergego C, Tankov N. Pattern of group I fibre projections from ankle flexor and extensor muscles in man. Exp Brain Res 1981;42:337–50.

Pratt CA. Evidence of positive force feedback among hindlimb extensors in the intact standing cat. J Neurophysiol 1995;73:2578–83.

Prochazka A, Stephens JA, Wand P. Muscle spindle discharge in normal and obstructed movements. J Physiol 1979;287:57–66.

Proske U, Wise AK, Gregory JE. The role of muscle receptors in the detection of movements. Prog Neurobiol 2000;60:85–96.

Schieppati M, Romano C, Gritti I. Convergence of Ia fibers from synergistic and antagonistic muscles onto interneurones inhibitory to soleus in humans. J Physiol 1990;431:365–77.

Schneider C, Lavoie BA, Capaday C. On the origin of the soleus H-reflex modulation pattern during human walking and its task-dependent differences. J Neurophysiol 2000;83:2881–90.

Scott JG, Mendell LM. Individual EPSPs produced by single triceps surae Ia afferent fibers in homonymous and heteronymous motoneurons. J Neurophysiol 1976;39:679–92.

Spoor CW, van Leeuwen JL, Meskers CG, Titulaer AF, Huson A. Estimation of instantaneous moment arms of lower-leg muscles. J Biomech 1990;23:1247–59.

Junichi Ushiyama received the B.A. degree in Environmental Information from Keio University, Kanagawa, Japan, in 2000, the M.Sc. degree in Life Sciences from The University of Tokyo, Tokyo, Japan, in 2002, and the Ph.D. degree in Life Sciences from The University of Tokyo in 2005. He is currently a research associate in Institute of Physical Education, Keio University. His research interest is to understand neural mechanisms underlying human motor control from a view point of sensory–motor interaction. He is a member of several academic organizations, including Society for Neuroscience, American College of Sports Medicine, Japanese Society of Biomechanics, Japanese Society of Physical Fitness and Sports Medicine, Japan Society of Exercise and Sports Physiology, and Japan Society of Physical Education, Health and Sport Sciences.

Taku Wakahara received the Ph.D. degree from Waseda University, Saitama, Japan, in 2008. He is currently a research associate at the Faculty of Sport Sciences, Waseda University. His research interest is the muscle mechanics in vivo in humans. He is a member of three professional societies.

Kei Masani received the B.Ed. in physical education from The University of Tokyo, Tokyo, Japan, and the M.Ed. and the Ph.D. in physical and health education from The University of Tokyo. He was an Assistant Professor (Jyosyu) in the Department of Life Sciences, The University of Tokyo. He is currently a Scientist in the Rehabilitation Engineering Laboratory at Toronto Rehab. His research interests include balance control during standing and gait, motion fluctuation, and control rules of complex motion-how humans execute complex movements in daily life. He received the Young Investigator Award of Japanese Society of Biomechanics in 2000, and is a member of several academic organizations, including the International Society of Biomechanics, Society for Neuroscience, the American College of Sports Medicine, the International Functional Electrical Stimulation Society, and the Japanese Society of Biomechanics.

Motoki Kouzaki received the Ph.D. degree in 1999 from the Department of Life Science, The University of Tokyo, Tokyo, Japan. From 1999 to 2007, he was an assistant Professor of the Department of Life Science, The University of Tokyo. In 2007, he was appointed as an Associate Professor of the Graduate School of Human and Environmental Studies, Kyoto University, Kyoto, Japan, where he is currently Director of the Laboratory of Neurophysiology. His major research interests focus on neural mechanisms underlying human motor control as related to muscle fatigue, especially "alternate muscle activity of synergistic muscles".

Tetsuo Fukunaga received the Ph.D. degree from The University of Tokyo, Tokyo, Japan, in 1973. He worked as a research assistant in The University of Tokyo from 1971 to 1973; as an associate professor in Chukyo University, Aichi, Japan, from 1973 to 1980; as an associate professor and a full professor in The University of Tokyo, from 1980 to 2002; as a full professor in Waseda University, Saitama, Japan, from 2002 to 2008. He is currently a president of National Institute of Fitness and Sports in Kanoya, Kagoshima, Japan. His research over the years as well as his current interests includes many aspects of Biomechanics, Exercise Physiology and Training Sciences, particularly on human skeletal muscle in vivo. He has served as president of Japanese Society of Biomechanics, and as a council member of two professional societies.

Tetsuro Muraoka received the Ph.D. degree from The University of Tokyo, Tokyo, Japan, in 2002. He is currently an associate professor in College of Economics, Nihon University, Tokyo, Japan. His research interest is to understand control mechanisms of a coordinated multi-limb movement. He is a member of several academic organizations, including Society for Neuroscience, Japanese Society of Biomechanics, Japanese Society of Physical Fitness and Sports Medicine, Japan Society of Exercise and Sports Physiology, and Japan Society of Physical Education, Health and Sport Sciences.

Hiroaki Kanehisa received the Ph.D. degree (education) from The University of Tokyo, Tokyo, Japan, in 1992. Currently, he is a full professor in the Department of Life Sciences, The University of Tokyo, Tokyo, Japan. His major area of research is the growth and aging of human skeletal muscles with special emphasis on the influences of physical training on the morphological and functional profiles of muscles. He is a member of two professional societies.