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The differential response in fascicle behaviors of the individual plantarflexors to the post-activation potentiation

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ABSTRACT

We aimed to clarify whether post-activation potentiation (PAP) is associated with the amount of fascicle shortening of individual muscles during twitch and whether this relationship depends on muscle fiber composition in humans. Eighteen healthy young adults (four female) participated in this study. Single supramaximal electrical stimulations were applied to the tibial nerve to elicit plantarflexion twitch, involving the medial gastrocnemius (MG) with approximately 50 % Type I fibers and the synergist soleus (SOL) with more than 80 % Type I fibers. The stimuli were delivered before (Pre), immediately after (Post-0 min), 5 min after (Post-5 min), and 10 min after a 6-s maximal voluntary isometric plantarflexion contraction (MVC) and peak torque (PT) during twitch contraction were calculated. The instantaneous fascicle length of each muscle was measured using ultrasound B-mode images acquired at 125 fps during twitch contraction and the amount of fascicle shortening (ΔFL) was calculated. PT was greater after MVC than that at Pre ($P < 0.05$). The ΔFL of both MG and SOL were greater at Post-0 min and Post-5 min than at Pre ($P < 0.05$). PT and ΔFL at Post-0 min relative to values at Pre were positively correlated in the MG ($r = 0.624$, $P = 0.006$), but not in the SOL. These results suggest that the contribution to PAP of isometric plantarflexion is greater from the MG than that from the SOL, implying a dependence of PAP on muscle fiber composition.

1. Introduction

The enhancement of muscle force, usually measured from an electrical stimulation applied to the motor nerve or muscle following conditioning contractions at a high contraction level has been termed post-activation potentiation (PAP) (Baudry and Duchateau, 2004; Vandervoort et al., 1983). Since the enhancement of voluntary performance, known as post-activation-performance-enhancement (PAPE) (Cuenca-Fernández et al., 2017), could be more relevant to daily activities and sports performance and may be partially influenced by PAP (Blazevich and Babault, 2019), gaining a deeper understanding of PAP is essential as a foundation for its effective application in improving muscular performance. PAP is proposed to occur through an increase in myosin regular light chain (RLC) phosphorylation in response to conditioning contractions, which is considered as the most likely mechanism responsible for this phenomenon (Blazevich and Babault, 2019). High-intensity contractions, regardless of voluntary and electrically-induced contractions, can cause an increase in myosin RLC phosphorylation. Additionally, this response is thought to enhance subsequent contractions by increasing the sensitivity of actin-myosin to Ca^{2+} released from the sarcoplasmic reticulum, thereby increasing the likelihood of myosin cross-bridge interactions with actin. However, PAP demonstrates significant inter-individual variability, leaving its precise mechanisms and characteristics partially understood.

A possible mechanism underlying the high inter-individual variability of PAP could be individual differences in muscle fiber composition. Since Type II fibers have greater phosphorylation in RLC (Moore and Stull, 1984), Type II fibers would enhance force more than Type I

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fibers. Indeed, Hamada et al. (Hamada et al., 2003, 2000) demonstrated that participants with a higher PAP magnitude have a higher percentage of Type II fibers in their vastus lateralis muscle estimated by needle biopsy compared with participants with a smaller PAP magnitude. Seitz et al. (Seitz et al., 2016) also showed a close correlation between the percentage of Type II myosin heavy chain isoforms in the vastus lateralis muscle (estimated using needle biopsy) and PAP magnitude. However, although PAP magnitude was determined by the increase in net force of individual quadriceps femoris muscles after the conditioning contractions, they quantified muscle fiber composition solely from the vastus lateralis muscle. Therefore, the association between PAP and muscle fiber composition has not yet been fully clarified.

Miyamoto et al. (Miyamoto et al., 2010, 2009) demonstrated that differences in muscle fiber composition affect PAP using a non-invasive method. They used mechanomyography (MMG), which can measure the mechanical lateral expansion of individual muscles during contractions, to quantify the PAP magnitude of the medial gastrocnemius (MG) and soleus (SOL) muscles, which are synergists of plantarflexion with distinct different muscle fiber composition (Johnson et al., 1973) and can be simultaneously measured under the same experiment. The results demonstrated that the MG with ~ 50 % of Type I fibers showed a greater increase in MMG amplitude than the SOL with more than 80 % of Type I fibers (Johnson et al., 1973), after the conditioning contractions. These results imply that PAP depends on the muscle fiber composition. However, the MMG signal detected from a muscle could include cross-talk, where the mechanical lateral expansions are transmitted from the neighboring muscles through the common skin and connective tissues. Therefore, the dependence of PAP on muscle fiber composition in humans needs to be investigated using different noninvasive methods to overcome the limitations mentioned above.

The ultrasound B-mode imaging (ULS) technique non-invasively assesses the mechanical properties of individual muscles (Roberts and Dick, 2023), such as temporal changes in muscle fascicle length (FL), elongation of aponeurosis, and muscle thickness. Temporal FL changes during contractions detected by ULS could be similar to the force profile for individual muscles (Martinez-Valdes et al., 2022; Yoshitake et al., 2005). In this regard, Mayfield et al. (Mayfield et al., 2015) used the ULS technique to quantify the FL change in the triceps surae during contractions induced by electrical stimulation and showed different mechanical characteristics between synergistic plantarflexors. Hence, we assumed that the ULS technique can non-invasively and accurately quantify the contribution of individual muscles to the PAP magnitude at a joint, and verify whether PAP depends on muscle fiber composition.

This study aimed to clarify whether PAP depends on muscle fiber composition using the ULS technique. To this end, we measured the temporal FL behaviors during twitch contractions to explore the contributions of the MG with ~ 50 % Type I fibers and SOL with > ~ 80 % Type I fibers to PAP. We hypothesized that the increase in fascicle shortening of the MG during twitch contraction after conditioning contraction was greater than that of the SOL.

2. Method

2.1. Participants

The mean (± SD) age, height, and body mass of eighteen (4 female, 14 male) participants were 22.2 ± 0.8 yrs, 168.2 ± 7.4 cm, and 59.1 ± 7.6 kg, respectively. All participants declared no history of neuromuscular disorders and were asked to avoid performing exercise one day before the experiment. Participants provided informed consent after receiving a detailed explanation of the purpose, potential benefits, and risks involved in the study. The study protocol was approved by the Ethics Committee for Human Experiments of Shinshu University, Japan (No. 240).

2.2. General experimental procedures

Throughout the experiments, including twitch and maximal voluntary contractions (MVC), participants lay in the prone position on a bed with a fully extended left knee joint and a neutral ankle joint angle (Fig. 1). The bare sole of the entire foot was attached to a flat-foot pedal (i.e., base metal plate). The exact position of the foot and the apparatus attached to the torque dynamometer (Contrex, CMV AG, Switzerland) were carefully adjusted so that the axes of the ankle and footplate were aligned for each participant. The bottom end of the footlever plate had a semicircular attachment that surrounded and secured the heel. A single electrical stimulation at the supramaximal level was delivered to the tibial nerve of the left leg to evoke plantarflexion twitch torque (Fig. 1). By monitoring the signal of the surface electromyogram (EMG) from the SOL, special care was taken to keep the participants in a relaxed condition throughout the twitch measurements to avoid unwanted muscle activity (see below for details). Three single electrical stimuli with ~ 10-sec rest in between were delivered before (Pre), immediately after (Post-0 min), 5 min after (Post-5 min), and 10 min after (Post-10 min) performing MVC.

2.3. Single electrical stimulation

A single square-wave pulse with a width of 1-ms was delivered to the tibial nerve to evoke isometric twitch torque of the plantarflexion (Fig. 1A). An anode (8-mm diameter Ag-AgCl, Kendall, CardinalHealth, Shizuoka, Japan) was positioned ~ 2 cm proximal to the horizontal skin crease overlying the popliteal fossa, and a cathode (8-mm diameter Ag-AgCl) was positioned in the popliteal fossa. A pen-type electrode mounted into a wand was used to find the appropriate position that induced both the maximal amplitude of EMG (mass action potential; M–wave) in the SOL and twitch torque. Before the measurements, the stimulus current was gradually increased until the M–wave amplitude and twitch torque did not further increase and was further increased by 20 % to ensure that maximal activation was achieved. Then, the electrode was fixed and fastened using an surgical tape.

2.4. MVC task

The MVC task involved a gradual increase in plantarflexion from baseline to maximum in ~ 3 s, which was then sustained for ~ 6 s. The timing of the task was based on a verbal count given at 1 s intervals, with persistent encouragement from the investigator when the force began to plateau.

2.5. Surface EMG

Surface EMG (sEMG) was measured from the SOL to measure the M–wave amplitude to determine the placement of the cathode electrode, electrical stimulation intensity, and the effect of M–wave amplitude on PAP. Moreover, sEMG was used to ensure that unwanted activation of the calf muscle during electrical stimulation did not occur. sEMG with a double-differential configuration was detected using a linear array of three circular electrodes placed along the approximated fascicle orientation of the SOL (3-mm diameter, 6-mm inter-electrode distance, FWS-SWMG1; 4Assist Inc., Tokyo, Japan) (Suzuki et al., 2021; Washino et al., 2017). The ground electrode was attached to the pedicle of the right fibula head using a disposable electrode (10-mm diameter Ag–AgCl, Kendall, CardinalHealth, Shizuoka, Japan). The skin surface was abraded with fine sandpaper and wiped with alcohol cotton before attaching the electrodes. The electrode on the skin surface of the SOL was connected to a differential amplifier with a bandpass filter of 5–4,000 Hz (× 1000, FWS-8ABX, 4Assist Inc., Tokyo, Japan).

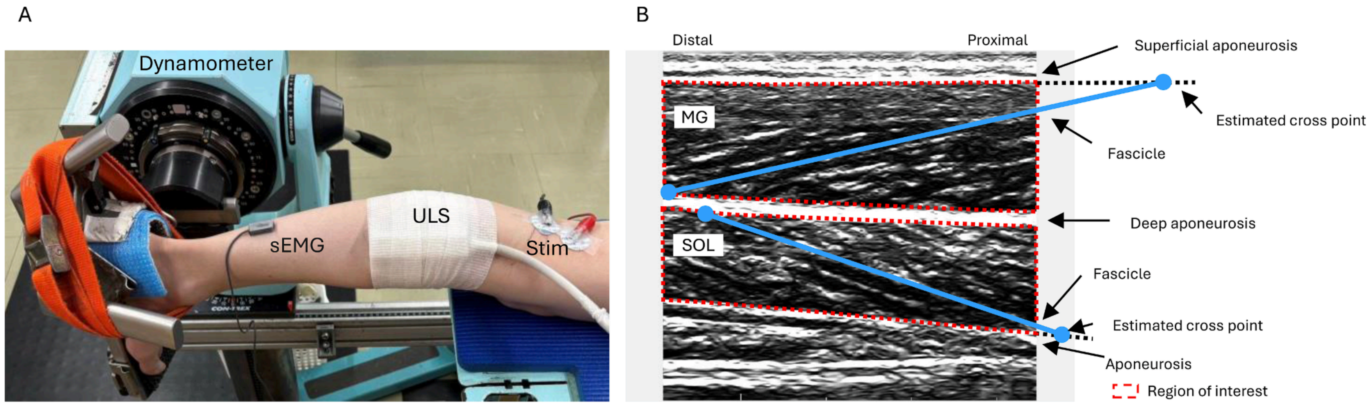

Fig. 1. A) Schematic diagram of measurement. B) A representative ultrasound B-mode image showing region of interest and defined fascicle length of the medial gastrocnemius (MG) and soleus (SOL) muscles. For determination of the entire length of the fascicle, the distal endpoint of a fascicle in each muscle at the cross point between the aponeurosis and fascicle using an image at rest was defined first. In this case, the proximal cross point of the fascicle was occasionally not visualized within the image as this image; thus, we estimated the cross point by linear extrapolation of the aponeurosis (black dotted lines) and fascicle (blue lines) (see a movie in the *Supplementary Material* for more details). The optical flow utilized for fascicle tracking in the current study can be determined at any point relative to the region of interest, and therefore the entire fascicle in successive images (during twitch) can be tracked correctly. Dynamometer, torque motor system to measure the plantarflexion torque; sEMG, surface electromyogram from SOL; ULS, the probe for ultrasound B-mode images; Stim, anode and cathode electrode for electrical stimulation to the tibial nerve.

2.6. Ultrasound

A PC-based ULS system (ArtUs EXT-1H, Telemed, Vilnius, Lithuania) was used to visualize and acquire two-dimensional longitudinal images of the MG and SOL. A flat, 96-element, linear, multi-frequency transducer (LF11-5 N60-A3) was fixed over the midbelly of the MG using double-sided tape and surgical tape (Fig. 1). B-mode (6–7 MHz) images were acquired at a rate of 125 fps with a field of view of 48 mm and an image depth of 40 mm. The placement of the ultrasound probe allowed both the MG and SOL to be visualized simultaneously in one imaging plane.

2.7. Data collection and analysis

The torque and sEMG signals were stored in a personal computer with a sampling frequency of 8,000 Hz using 16-bit Power 1401 and Spike2 software (Cambridge Electronic Design, Cambridge, UK). TTL pulses representing the time of each ultrasound image generated by the ULS system were also stored using Power 1401 to synchronize with the time-series data of fascicle length for subsequent analysis. The torque and sEMG signals obtained during the single-twitch were used to quantify the maximal single-twitch torque (PT), rate of torque development (RTD), contraction time (CT_{Torque}), half-relaxation time (HRT), and peak-to-peak amplitude of the M–wave (PP_M) using custom-made MATLAB scripts (MATLAB R2023b, The MathWorks, Inc., Natick, MA, USA). PT was determined as the peak value of the single-twitch torque. RTD was calculated as the slope within 100 ms from the onset of torque (Tillin et al., 2021). CT_{Torque} was defined as the time interval between the onset of torque and PT. HRT was defined as the time interval between PT and 50 % decline in PT.

To confirm the absence of muscle activation during measurements, the root mean square (RMS) amplitude of sEMG for 2 s just prior to electrical stimulation was calculated and normalized (%EMGmax) to the maximal RMS value that was calculated over a 500-ms window centered at the time at which peak torque was attained during MVC task.

The instantaneous FL was determined for each frame of the ULS through the implementation of a custom-written automatic tracking algorithm (Brennan et al., 2017; Cronin et al., 2011; Gillett et al., 2013) in MATLAB, which enables the reliable detection of changes in FL with sub-millimeter resolution during relatively static tasks (Day et al., 2013). FL was defined as the linear distance between the origin and insertion of the fascicle at the superficial and deep aponeuroses. A fascicle recorded within the middle of the image was selected for analysis. In this event, the entire length of the fascicle could not be visualized within the field of view, and the fascicle end-point (s) were extrapolated according to the orientation of the aponeurosis (see Fig. 1B). The amount of shortening FL (ΔFL) and strain in MG and SOL were calculated to assess the effect of PAP on changes in muscle geometry during contractions. To clarify the difference in muscle fiber composition between MG and SOL, we calculated CT of individual muscles, which was determined as the time interval between the onset of FL change and peak ΔFL of MG (CT_{MG}) and SOL (CT_{SOL}).

2.8. Statistical analysis

All data are presented as mean ± standard deviations (SDs). A linear mixed model with fixed effects for time periods (Pre, Post-0 min, -5 min, and -10 min) was used to compare the variables, including PT, RTD, ΔFL, strain, CT_{Torque}, HRT, CT_{MG}, CT_{SOL}, and PP_M. The relative values of ΔFL and strain of MG and SOL after MVC to those at Pre were compared using a linear mixed model with fixed effects for muscle (MG vs. SOL) or period. When a significant interaction was detected, post-hoc multiple comparisons were performed to identify pairwise differences using paired t-tests with Bonferroni correction. We conducted an a priori power analysis for the interaction term in the linear mixed model using the 'simr' package in R (Green and Macleod, 2016). The simulation was performed based on pilot data (n = 6) with 1,000 iterations under scenarios in which the sample size was progressively increased to generate a power curve. As a result, 80 % power was achieved with a sample size of eight; therefore, our sample size (n = 18) was considered sufficient.

Moreover, to estimate the contribution of each muscle to PAP, a linear correlation analysis was conducted between the relative values in PT and ΔFL and strain for MG and SOL at Post-0 min. These statistical analyses mentioned above were performed using R (Version 4.4.0). Statistical significance was set at $P < 0.05$.

3. Results

3.1. sEMG amplitude just prior to applied stimulation

The sEMG amplitude for 2 s just prior to applied stimulation was less than 5 %EMGmax across all trials (ranged from 0.0 % to 4.9 % EMGmax).

3.2. Peak torque (PT) and rate of torque development (RTD)

PT and RTD increased after MVC trial, and the aftereffects of PT and RTD remained for 10 min after MVC trial (Figs. 2 and 3). A linear mixed model showed a significant main effect of time ($P < 0.05$). While there were multiple significant differences in PT and RTD between periods, post-hoc tests revealed that PT and RTD were greater in the following order; Post-0 min > Post-5 min > Post-10 min > Pre ($P < 0.05$). Note that PT at Post-10 min was greater than that at Pre for both variables ($P < 0.05$). When compared to the value at Pre, PT was greater in Post-0 min by ~ 55 %, Post-5 min by ~ 20 %, and Post-10 min by ~ 10 % (Fig. 3).

3.3. Contraction time (CT) and half relaxation time (HRT) estimated from torque and fascicle length (FL) of each muscle

In time-related variables measured from torque, a linear mixed model showed that CT_{Torque} and HRT were smaller at Post-0 min than these at any time period ($P < 0.05$, Table 1). CT of individual muscles, which was calculated from FL changes for each muscle, was smaller at Post-0 min than at other time periods ($P < 0.05$, Table 1). When comparing muscles, CT_{MG} was smaller than CT_{SOL} at Pre and Post-0 min ($P < 0.05$, Table 1).

3.4. Peak to peak amplitude of M–wave

A linear mixed model showed no significant main effect of time ($P > 0.05$, Table 1).

3.5. Fascicle length and strain

With respect to ΔFL and strain (Fig. 4), there was a main effect of time on MG and SOL ($P < 0.05$). For MG, similar to PT, ΔFL and strain increased after the MVC trial, and the aftereffect of ΔFL and strain remained for 10 min after the MVC trial (Fig. 4). While there were multiple significant differences in ΔFL and strain between periods, post-hoc tests revealed that ΔFL and strain were greater in the following order; Post-0 min > Post-5 min > Post-10 min > Pre ($P < 0.05$). For SOL, ΔFL and strain increased after the MVC trial (Fig. 4). Post-hoc tests revealed that ΔFL and strain at Post-0 min was greater than that at any periods ($P < 0.05$). With respect to strain, there was a main effect of muscle ($P < 0.05$). When collapsed across time periods (averaging strain values across all post-MVC time periods), the strain of SOL was smaller than that of MG ($P < 0.05$).

When normalizing ΔFL and strain of individual muscles to the values at Pre (the relative values), a linear mixed model revealed a significant interaction between the muscles and time. Post-hoc tests showed that the relative values of ΔFL and strain were greater in the MG than in the SOL at all time periods ($P < 0.05$) (Fig. 5).

There was a significant positive correlation between the relative value of PT and the relative value of ΔFL ($r = 0.624$, $P = 0.006$) and strain ($r = 0.585$, $P = 0.011$) in the MG, whereas no correlation was found in the SOL ($r = 0.239$ for ΔFL, $r = 0.240$ for strain, $P > 0.05$) (Fig. 6).

4. Discussion

The major findings of the current study were that 1) the changes in the degree of fascicle shortening (ΔFL) of the MG were greater than those of the SOL during twitch contraction after MVC, and 2) the change in ΔFL and strain of the MG after MVC was correlated with the increase in PT, whereas there was no correlation between the change in ΔFL and strain of SOL and PT. The contraction time (CT) calculated from the ΔFL at Pre was significantly smaller in the MG than in the SOL. These findings suggest that the magnitude of PAP of isometric plantarflexion is attributed to the MG than the SOL, implying the dependence of PAP on

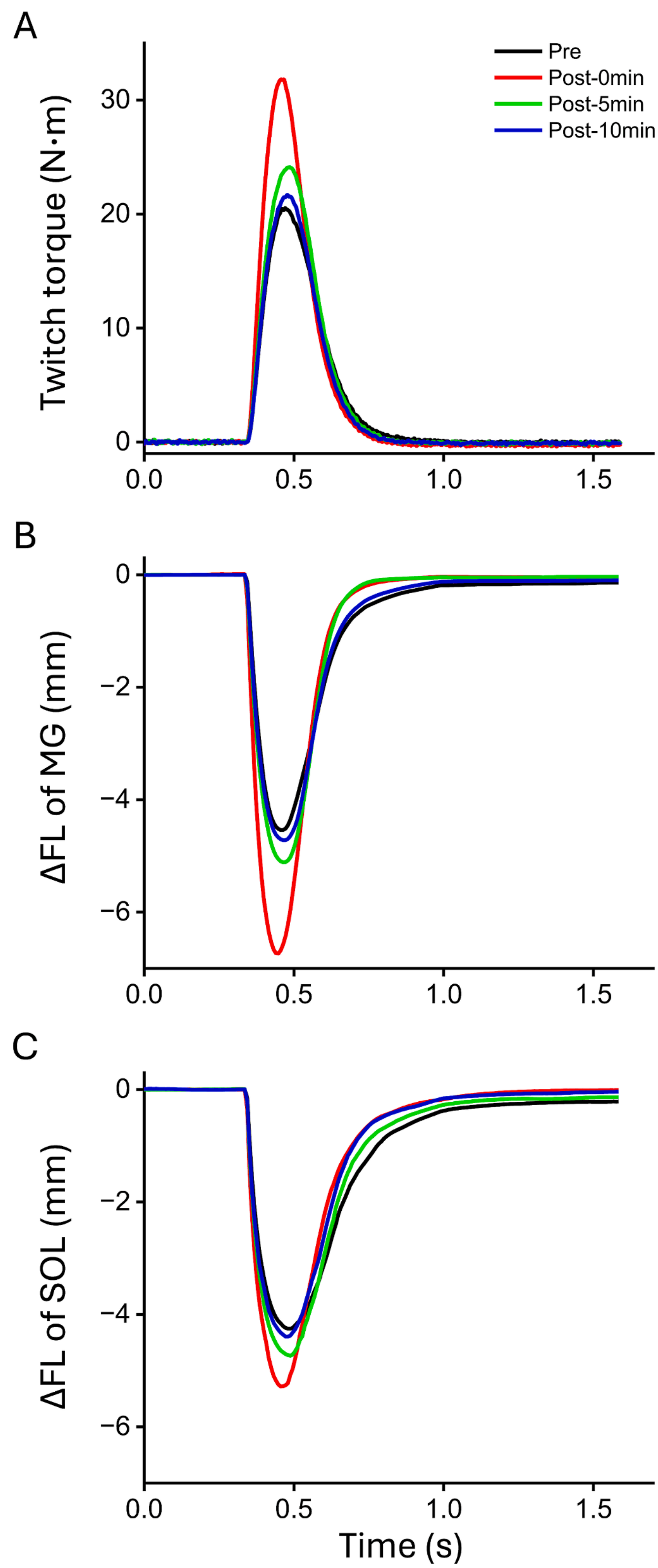

Fig. 2. Representative plantarflexion torque (A) and the medial gastrocnemius (B, MG) and soleus (C, SOL) fascicle length (FL) change (fascicle shortening) during twitch contractions before (Pre, black), immediately after (Post-0 min, red), 5 min after (Post-5 min, light-green), and 10 min after (Post-10 min, blue) a 6-s maximal voluntary plantarflexion. Ultrasound and torque data were sampled simultaneously.

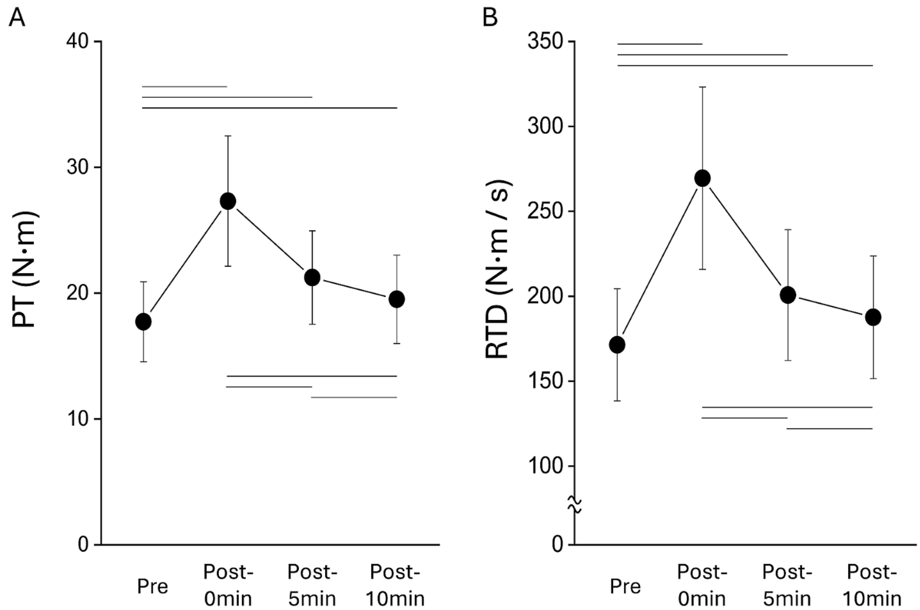

Fig. 3. Peak torque (PT) (A) and rate of torque development (RTD) (B) during twitch contraction before (Pre), immediately after (Post-0 min), 5 min after (Post-5 min), and 10 min after (Post-10 min) a 6-s maximal voluntary plantarflexion. The horizontal lines represent a significant difference between periods ($P < 0.05$).

Table 1
Contractile property during twitch contractions at each measurement time.

	Pre			Post-0 min			Post-5 min			Post-10 min		
CT_{Torque} (ms)	120.3	±	10.4	107.6	±	11.1*	129.4	±	11.5	123.8	±	8.5
HRT (ms)	109.4	±	15.6	94.4	±	12.9*	101.7	±	11.8	102.8	±	11.9
CT_{MG} (ms)	112.0	±	13.1†	101.7	±	12.3*†	124.2	±	11.0	117.6	±	11.5
CT_{SOL} (ms)	129.9	±	18.6	117.6	±	19.2*	132.4	±	14.1	127.5	±	12.8
PP_M (mV)	5.6	±	2.2	5.5	±	2.3	5.5	±	2.3	5.4	±	2.3

CT_{Torque}, contraction time estimated by torque; HRT, half relaxation time; PP_M, peak to peak amplitude of M wave; CT_{MG} and CT_{SOL}, contraction time of the medial gastrocnemius and soleus estimated by behaviors of the fascicle length change, respectively. *$P < 0.05$ from other time periods. †$P < 0.05$ between muscles in the same time period.

muscle fiber composition.

The amount of PAP, which was evaluated by the relative value of PT immediately after brief MVC to the value at Pre (~155 %, see Figs. 3 and 5), was comparable to that reported previously. For example, previous studies focused on the PAP of plantarflexion with similar experimental setups and protocols (MVC for ~ 6 s to ~ 10 s, single twitch stimulation, ankle joint angle, etc.) and showed an approximately 140–200 % increase in PT after MVC (Bourgeois et al., 2022; Fukutani et al., 2013; Gago et al., 2017; Miyamoto et al., 2010, 2009). We found that brief MVC decreased CT_{Torque} and HRT, as previously observed for twitch in this muscle group (Bourgeois et al., 2022), indicating that PAP was not due to prolonged muscle activation. Furthermore, the absence of a change in the amplitude of the M–wave after brief MVC, as demonstrated in a previous study (Bourgeois et al., 2022), indicates that PAP was not induced by changes in neuromuscular propagation. The results showed that EMGmax immediately before the application of a single electrical stimulus was consistently less than 5 % throughout the electrically induced twitch contractions, indicating that unwanted EMG activity did not occur at any time period. Hence, muscle activation did not contribute to the increase in PT.

In the current study, the time-course changes in ΔFL and strain corresponded well with an increase in PT during a single twitch (Fig. 5). In brief, the degree of increase in PT relative to that before MVC was greatest immediately after MVC, and this enhancement declined with time, while the degree of ΔFL and strain mirrored the changes in PT. Bourgeois et al. (Bourgeois et al., 2022) demonstrated a similar result, in that the changes in ΔFL obtained using the same ultrasound imaging technique showed similar time trends to PT. While this previous study focused on only MG but not other plantarflexor muscles, we measured the FL of SOL as well as MG and indicated that the characteristics of PT were better associated with that of ΔFL and strain in MG than in SOL (Fig. 6). The physiological cross-sectional area (PCSA), which is the determinant of muscle strength, was much smaller in the MG (21.1 ± 5.7 cm^2; ~16 % of the total plantarflexors) than in the SOL (51.8 ± 14.9 cm^2; ~57 % of the total plantarflexors) (Fukunaga et al., 1996; Ward et al., 2009). Also, the PCSA of SOL is the largest among human skeletal muscles (Ward et al., 2009). Hence, it is clear that SOL is the major determinant of plantarflexor torque, but the results of the current study demonstrate that the MG plays a greater role in enhancing the post-MVC force than the SOL.

In this study, we interpreted greater fascicle shortening (ΔFL or strain) as indicative of a greater PAP-induced force increase in individual muscles. However, this interpretation is based on the assumption that ΔFL directly reflects the changes in muscle force. Given that the MG and SOL have different aponeurotic structures and potentially different series elastic compliance, ΔFL may not directly correspond to force changes. Although the MG showed a greater increase in ΔFL after MVC, we acknowledge that ΔFL does not directly quantify muscle force and is influenced by muscle–tendon compliance and architectural factors. Given that the SOL has a much larger PCSA, it may still generate a greater absolute force increment during PAP, despite showing smaller relative ΔFL changes. Our findings should therefore be interpreted as indicating that the MG shows a more pronounced relative PAP response in fascicle behavior, which was significantly associated with individual

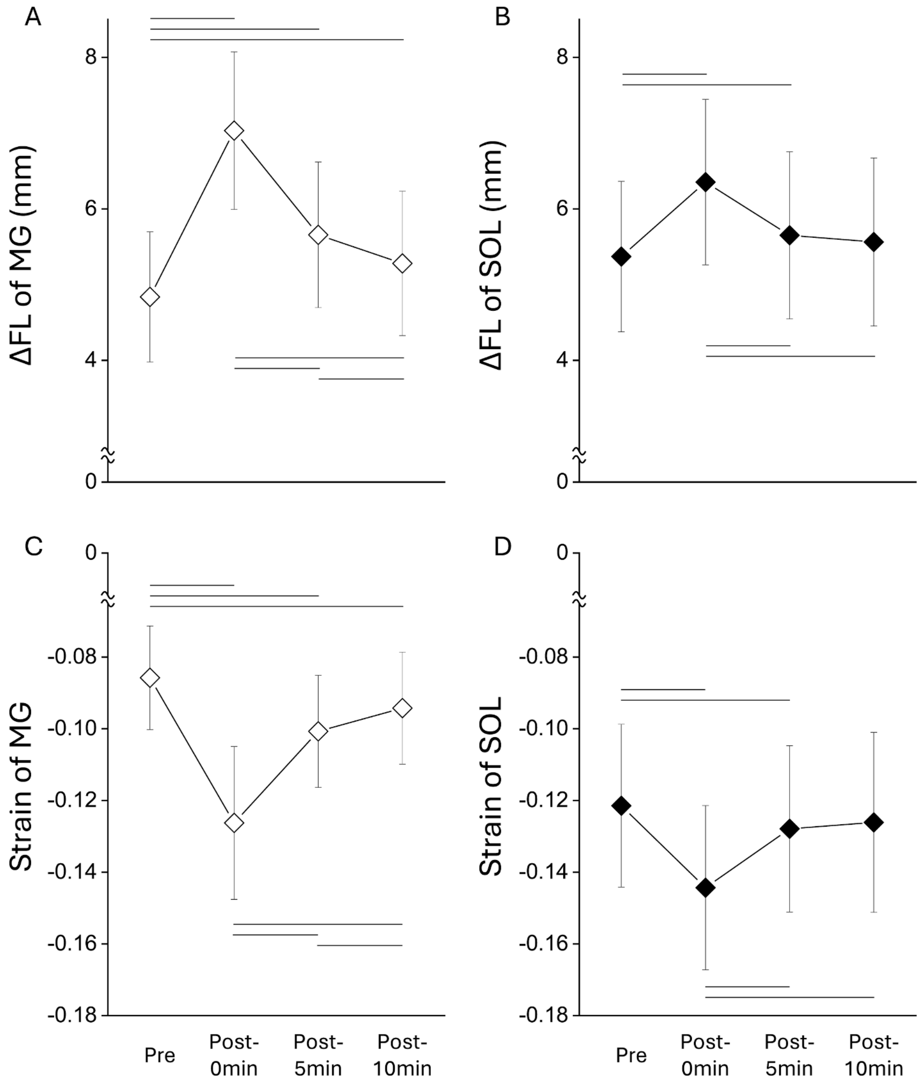

Fig. 4. The amount of fascicle shortening (ΔFL, top) and strain (bottom) of MG (left column, open diamond) and SOL (right column, closed diamond) during twitch contraction before (Pre), immediately after (Post-0 min), 5 min after (Post-5 min), and 10 min after (Post-10 min) a 6-s maximal voluntary plantarflexion. The horizontal lines represent a significant difference between periods ($P < 0.05$).

differences in net plantarflexor torque, rather than implying that the MG produces more force than the SOL. Furthermore, while our analysis focused on the relative changes in PAP (i.e., percentage increase), we did not assess the absolute magnitude of the force contribution from each muscle. Based on the PCSA, even a smaller percentage increase in force in the SOL may result in a larger absolute increment in torque. Therefore, our findings should be interpreted as reflecting relative contributions to PAP, not absolute torque output from each muscle.

In the current study, it is unclear why fascicle shortening behavior in the MG was more strongly associated with PT than in the SOL. Despite obvious technical limitations, Hamada et al. (Hamada et al., 2003, 2000) demonstrated that the vastus lateralis muscle, with a higher percentage of Type II fibers, induces greater enhancement of PT. High-intensity contractions, regardless of voluntary and electrically-induced contractions, can cause an increase in myosin RLC phosphorylation. Additionally, this response is thought to enhance subsequent contraction by increasing the sensitivity of actin-myosin to Ca^{2+} released from the sarcoplasmic reticulum, thereby increasing the likelihood of myosin cross-bridge interactions with actin. Since Type II fibers have greater phosphorylation in RLC (Moore and Stull, 1984), the distribution of Type II fibers within a muscle would therefore be correlated with PAP (Hamada et al., 2003, 2000; Seitz et al., 2016). In the current study, we estimated the CT of individual muscles, which reflects the muscle fiber composition, using fascicle shortening during twitch contractions and found smaller CT_{MG} compared with CT_{SOL} measured before MVC (see Table 1). These results imply that MG has a greater percentage of Type II fibers than the SOL in the current study, as reported by Johnson et al. (Johnson et al., 1973). Hence, our data obtained by non-invasive ultrasound imaging techniques support the notion that the magnitude of PAP depends on the muscle fiber composition. However, based on the moderate correlations between PT and ΔFL and strain in MG, the interindividual differences in muscle fiber composition as well as the ratio of PCSA among the plantarflexor muscles potentially affect the results of the current study. The mixed gender of the participants could also be attributed to inter-individual differences. Further studies are needed to clarify these factors.

This study had some limitations. As stated, we did not consider the interindividual difference in muscle morphology, which strongly affects the muscle force, because of the absence of measurement of the muscle PCSA. As the MG and SOL are adjacent structures, individual muscle forces may be transmitted laterally between these muscles (Bojsen-Møller et al., 2010). Therefore, the shortening fascicle of a muscle might be accompanied by that of the other muscle, potentially resulting in an error in estimating the individual muscle force using fascicle shortening.

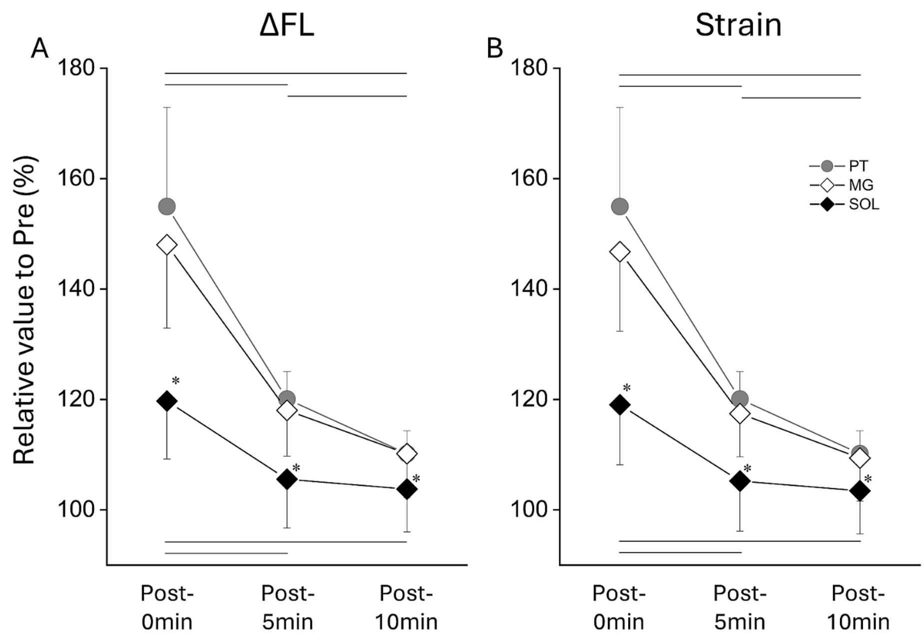

Fig. 5. Relative values of ΔFL (left column) and strain (right column) of MG (open diamond) and SOL (closed diamond) with PT (circle) to these values at Pre following a 6-s maximal voluntary plantarflexion. * indicates a significant difference between muscles at each period and the horizontal lines represent a significant difference between periods ($P < 0.05$).

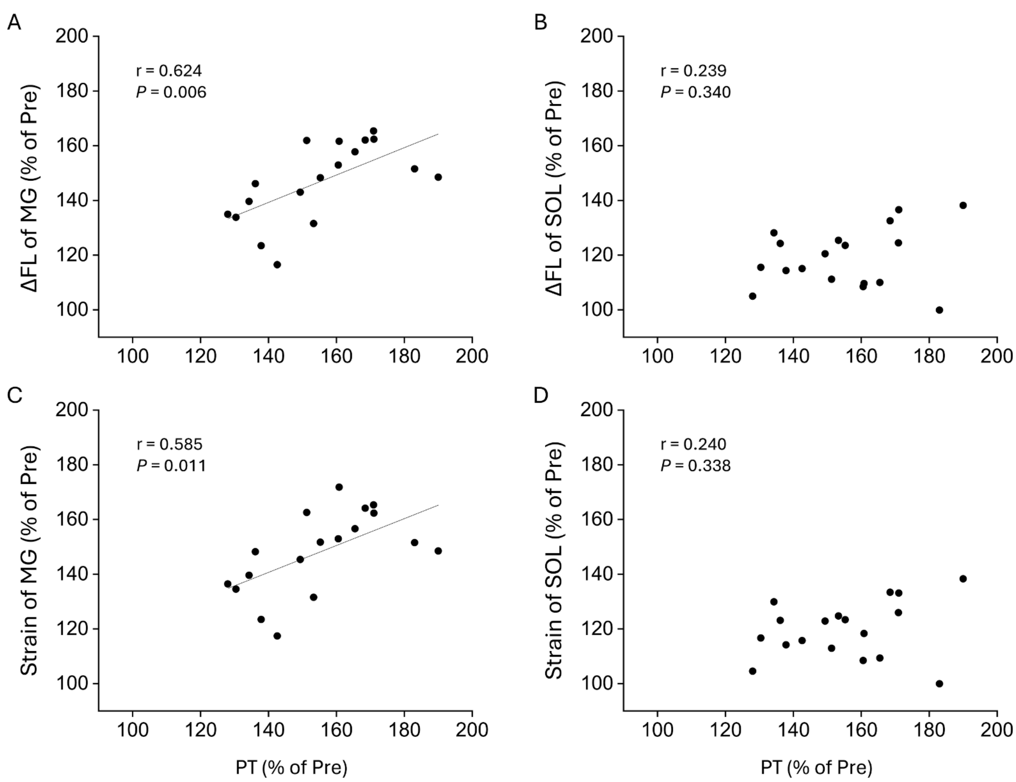

Fig. 6. The correlations between relative values of PT and ΔFL (top) and strain (bottom) of MG (left column) and SOL (right column) measured at immediately after a 6-s maximal voluntary contraction to these at Pre.

Despite this, an increase in fascicle shortening showed distinct differences between the MG and SOL (see Fig. 5), and the results suggest that the PAP magnitude was markedly different between the muscles. Meanwhile, twitch contraction by applying a single stimulus to the tibial nerve involves other plantarflexors, such as the lateral gastrocnemius muscle, which was not the focus of this study. However, the sum of the PCSA of the MG and SOL exceeds 70 % of that of the plantarflexors (Fukunaga et al., 1996). Hence, the findings regarding fascicle shortening would provide sufficient information on the contribution of PAP in the individual muscles to PAP, which has been evaluated using the net torque (plantarflexion torque).

In conclusion, the results of the present study suggest that the contribution to PAP of isometric plantarflexion is greater from the MG than that from the SOL, implying a dependence of PAP on muscle fiber composition.

CRediT authorship contribution statement

Kazuharu Kato: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sohei Washino:** Writing – review & editing, Writing – original draft, Investigation. **Patricio A. Pincheira:** Methodology, Software, Writing – original draft, Writing – review & editing. **Kosuke Hirata:** Writing – review & editing, Writing – original draft, Investigation, Data curation. **Yasuhide Yoshitake:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jbiomech.2025.112759.

Data availability

Data will be made available on request.

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