

## Effects of contraction intensity on muscle fascicle and stretch reflex behavior in the human triceps surae

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<sup>1</sup>Center for Sensory-Motor Interaction, Department of Health Science and Technology, Aalborg University, Aalborg, Denmark; and <sup>2</sup>Department of Biology of Physical Activity, University of Jyväskylä, Jyväskylä, Finland

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**Cronin NJ, Peltonen P, Ishikawa M, Komi PV, Avela J, Sinkjaer T, Voigt M.** Effects of contraction intensity on muscle fascicle and stretch reflex behavior in the human triceps surae. *J Appl Physiol* 105: 226–232, 2008. First published May 15, 2008; doi:10.1152/jappphysiol.90432.2008.—The aims of this study were to examine changes in the distribution of a stretch to the muscle fascicles with changes in contraction intensity in the human triceps surae and to relate fascicle stretch responses to short-latency stretch reflex behavior. Thirteen healthy subjects were seated in an ankle ergometer, and dorsiflexion stretches (8°; 250°/s) were applied to the triceps surae at different moment levels (0–100% of maximal voluntary contraction). Surface EMG was recorded in the medial gastrocnemius, soleus, and tibialis anterior muscles, and ultrasound was used to measure medial gastrocnemius and soleus fascicle lengths. At low forces, reflex amplitudes increased despite a lack of change or even a decrease in fascicle stretch velocities. At high forces, lower fascicle stretch velocities coincided with smaller stretch reflexes. The results revealed a decline in fascicle stretch velocity of over 50% between passive conditions and maximal force levels in the major muscles of the triceps surae. This is likely to be an important factor related to the decline in stretch reflex amplitudes at high forces. Because short-latency stretch reflexes contribute to force production and stiffness regulation of human muscle fibers, a reduction in afferent feedback from muscle spindles could decrease the efficacy of human movements involving the triceps surae, particularly where high force production is required.

stretch distribution; muscle spindle; short-latency reflex; ultrasound

IN THE HUMAN LOWER LIMB, SKELETAL muscle fibers are attached to bone via tendons. An externally imposed movement such as a stretch is not completely transferred to the muscle fibers and the associated muscle spindles, because some of this movement is attenuated due to the compliance of the tendon (10, 14, 44, 45, 59). The distribution of a stretch between muscle and tendinous tissues depends on their relative stiffnesses. For example, when a passive muscle-tendon unit (MTU) is stretched, most of the stretch occurs in the muscle fibers due to their greater compliance relative to the tendon at low forces (10, 46). Therefore, the muscle fascicles “see” more of the stretch and a greater proportion is transmitted to the muscle spindles. However, muscle stiffness increases with increasing force levels (8). In addition, tendon stiffness increases at low force levels, but it remains constant beyond the toe region of the force-length curve (43). Therefore, the relative increase in stiffness is greater in the muscle fibers than the tendon (46). Consequently, at high forces, the relative stiffness of muscle and tendon may

be approximately equal, as indicated by a progressive decline in muscle fiber stretch amplitude with increasing force levels in response to the same stimulus (46). Ishikawa and Komi (19) suggested that the stiffness of the muscle may even exceed that of the tendon at very high loads. Any relative increase in muscle fiber stiffness could decrease the muscle’s stretch response and thus affect the subsequent activation of the stretch reflex. As muscle spindles only “see” the movement of the muscle fibers in which they are situated, their view of a stretch depends on the distribution of the movement between muscle fibers and tendon (46). Furthermore, muscle spindles are highly sensitive to stretch velocity (e.g., Ref. 53). Consequently, a change in the velocity of stretch distributed to the muscle is likely to result in modulation of the stretch reflex.

From a control perspective, stretch redistribution from the muscle fibers and spindles toward the tendon would alter the afferent activity, decreasing the spindle afferent feedback and increasing the afferent feedback from Golgi tendon organs. The effect on the short-latency stretch reflex would depend on how the balance between excitatory and inhibitory inputs from these receptors affects the excitability of the motoneurons. During a static contraction, the spindle afferents are likely to dominate, resulting in a decreased short-latency stretch reflex response (45) as the spindle afferent feedback decreases. The short-latency stretch reflex has been shown to contribute to force enhancement in various activities such as running (19) and drop jumps (25), and it has an important role in stiffness regulation of muscle fibers (56, 59). Therefore, any changes in afferent feedback could compromise force production or stability during movement (19, 48, 59).

Previous studies have identified decreases in stretch reflex amplitude (1, 5) and reflex-induced stiffness (50) at high preactivation force levels. However, it is unknown whether these phenomena are influenced by the stretch responses of the muscle fascicles. The aim of this study was to examine changes in the distribution of a stretch to the muscle fascicles with changes in contraction intensity in the human triceps surae using ultrasonography. Furthermore, fascicle stretch responses were examined in relation to EMG activity to make inferences about the effects of contraction intensity on muscle spindle activity and stretch reflex activation. It was hypothesized that with increasing contraction intensity, the amount of stretch and, more importantly, the velocity of stretch that was transferred to the muscle fascicles would decrease. Because stretch velocity is a potent stimulus to the muscle spindles, a decrease

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in fascicle stretch velocity would be expected to result in a decrease in stretch reflex amplitude.

## METHODS

**Subjects.** Thirteen healthy subjects (7 men, 6 women) aged 21–30 yr ( $25.7 \pm 2.8$  yr; mean  $\pm$  SD) volunteered to participate in this study. The subjects had no known history of musculoskeletal disorders. Before testing, subjects were fully informed of the procedures and risks, and each subject provided written informed consent. The study was approved by the local ethics committee, and was performed in accordance with the Declaration of Helsinki.

**Protocol.** Subjects were seated in an ankle ergometer (see Ref. 37), with the ankle ( $90^\circ$ ), knee ( $180^\circ$ ; full extension), and hip ( $120^\circ$ ) angles fixed. Two straps were applied to the foot and one to the thigh to minimize leg movement. The upper body was also strapped to the seat. Subjects initially performed three isometric plantar flexion maximal voluntary contractions (MVCs) with intertrial durations of 1–3 min, and each trial required the maximal moment to be maintained for  $\sim 3$  s. The trial exhibiting the highest peak moment value was selected as the MVC, and it was used to calculate the percentage increments for the stretch conditions (see below).

During isometric plantar flexion, it is inevitable that some activation of the tibialis anterior (TA) muscle will be present, and this will affect moment calculations. To take this into account, a series of trials were performed to estimate the contribution of TA coactivation to the moment values in the stretch conditions (28). First, the EMG from the selected MVC trial was visually examined. The EMG activity and the corresponding moment were then measured in three additional trials: 1) in passive conditions, 2) producing a dorsiflexion moment with a TA EMG amplitude below the maximal amplitude achieved during MVC, and 3) a second dorsiflexion with an EMG amplitude slightly above the maximal MVC amplitude. In the latter two trials, subjects held the moment level for 3 s, using real-time visual feedback. The three trials were repeated for three ankle positions from  $90^\circ$  to  $100^\circ$  in  $5^\circ$  intervals, to account for the possible range of ankle rotation during isometric contractions (28). Trials were separated by rest periods of 1–3 min, and the EMG electrodes on the soleus (Sol) and medial gastrocnemius (MG) muscles were used to exclude the possibility of coactivation. The moments recorded during the dorsiflexion trials were fitted by a linear regression curve as a function of the corresponding rectified and smoothed TA EMG values. This allowed the estimation of antagonistic moments for each force condition. Estimated TA moments were determined at the ankle angle nearest to the angle at which the required moment level was achieved. This value was then added to the moment value recorded at the ankle ergometer. A separate series of passive trials were performed to calculate the contribution of gravitational forces to the recorded moment values (see Ref. 2). The subjects completely relaxed the muscles of their right leg while seated in the experimental position. The foot was passively rotated at  $5^\circ/\text{s}$  in a range of motion between  $80^\circ$  and  $120^\circ$  ( $90^\circ$  = tibia perpendicular to foot;  $<90^\circ$  = dorsiflexion). After three cycles, data were captured during the passive movement, and the resultant force traces were averaged from three trials for each subject. The contribution of gravitational force to the measured moment for the studied angular position was then calculated by subtracting the passive values from the values recorded during isometric plantar flexion (3).

After the passive trials, the ankle ergometer was programmed to apply dorsiflexion stretches of  $8^\circ$  amplitude at a velocity of  $250^\circ/\text{s}$  (49) to the triceps surae at different moment levels: 0, 20, 40, 60, 80, and 100% of MVC. The order of the preactivation conditions was randomized, and a minimum of three trials were obtained at each moment level. Before each trial, the ankle axis of rotation was carefully aligned with the ankle ergometer axis. In all contractions, subjects increased the plantar flexion effort up to the required moment level and maintained this level for  $\sim 1$  s before the stretch was elicited.

This allowed greater accuracy when digitizing muscle fascicle data (21), and it also enabled the moment level and fascicle length to stabilize before the stretch. During all conditions, a high-speed video camera (200 frames/s; Peak Performance, Englewood, CO) was used to record changes in ankle joint angle. The camera was positioned on the subjects' left side, perpendicular to the line of motion. Reflective markers were placed over the center of rotation of the knee, medial malleolus, heel, and first metatarsal head. After the stretch trials, another series of passive trials were performed, and three trials were obtained for each subject. This enabled a comparison of the passive muscle behavior before and after the stretch trials to ensure that the intervention did not cause any changes in passive muscle properties that could influence the stretch responses.

**EMG.** EMG activities of the MG, Sol, and TA muscles were recorded from the right leg using bipolar surface electrodes with a 5-mm diameter and a 20-mm fixed interelectrode distance (model 650437 skin electrode, Beckman). In Sol and TA, EMG electrodes were positioned in accordance with SENIAM guidelines (16). In MG, the electrodes were placed slightly lateral to the muscle midbelly to accommodate the ultrasound probe. Before electrode placement, the skin was shaved, abraded, and cleaned with alcohol to ensure an interelectrode resistance value below 5 k $\Omega$ . The EMG signals were amplified and band-pass filtered at 20 Hz to 1 kHz, and they were rectified and low-pass filtered at 20 Hz (Butterworth 1st-order digital filter). Stretch reflex amplitude and onset latency were then calculated visually. Onset latency was identified as the first major deflection in the EMG record following the perturbation (13, 34), which was also used to quantify reflex amplitude. Background EMG was averaged over 30 ms from the point of stretch onset (49), and stretch reflex amplitude was then calculated by subtracting the background EMG from the short-latency reflex peak. All EMG and moment data were collected at a sampling frequency of 2 kHz.

**Ultrasound measurements.** Two-dimensional fascicle lengths of the MG and Sol muscles of the right leg were determined using a B-mode ultrasound apparatus (7.5-MHz probe; model SSD-5500, Aloka, Tokyo, Japan) with a scanning frequency of 96 Hz. The probe was positioned over the midbelly of the MG muscle, and the optimal depth was adjusted to enable the visualization of fascicles in both MG and Sol. This location was chosen to standardize the probe position between subjects. To position the probe accurately, the medial and lateral borders of the MG muscle were identified, and the midpoint between the two borders was marked on the skin. Sagittal-plane scans were then taken at the heel to identify the insertion point of the Achilles tendon on the calcaneus, which was also marked on the skin. A straight line was drawn between the two points, and this line was assumed to be the operating axis of the MTU (31). The probe was secured with a custom-made support device to minimize any probe movement relative to the muscle. The superior and inferior aponeuroses were identified, and fascicle length was defined as the length of the fascicle between the two aponeuroses. Pennation angle was defined as the angle between the fascicle and the deep aponeurosis in MG, and between the fascicle and superficial aponeurosis in Sol. Fascicle velocities were calculated by differentiating fascicle stretch amplitudes with respect to time. Ultrasound scanning is a valid and reliable method of measuring muscle fascicle lengths (e.g., Ref. 6). In the present study, the reliability of this method of fascicle length calculation was determined by calculating the coefficient of variation between three different trials at each contraction intensity and in each subject. The mean value was 5%, which is within the range of values reported previously (between 0 and 6%; Refs. 18, 22, 24, 27).

Several studies have shown that muscle contractions at presumed fixed joint positions are not truly isometric (e.g., Refs. 29, 32, 47) and that the heel lifts off of the dynamometer footplate. In the present study, movement of the heel relative to the dynamometer footplate was recorded by positioning a high-speed camera (200 frames/s; model HDR-HC3, Sony, Tokyo, Japan) directly below the dynamometer footplate. Reflective markers were placed over the Achilles

tendon point of insertion and on the ergometer pedal so that calcaneal displacement could be calculated relative to the pedal. A digital pulse was used to synchronize the kinetic, kinematic, EMG, and ultrasound data.

**Data analysis.** Repeated-measures ANOVA was used to detect differences between different moment levels, and least significant difference post hoc tests were used to identify the levels between which differences were observed. Dependent samples *t*-tests were used to examine the prestretch-poststretch differences between passive force trials, as well as the differences between torque levels in terms of the stretch that was imposed at the ankle joint. Pearson's product-moment correlation coefficient was used to determine relationships between variables. All video data were digitized automatically using Motus software (Peak Performance). For each subject and each moment level, data from all accepted trials were averaged. These data were then pooled to calculate mean values for the whole group of 13 subjects. In all tests, statistical significance was set at  $P < 0.05$ . Data are reported as means  $\pm$  SD where appropriate.

## RESULTS

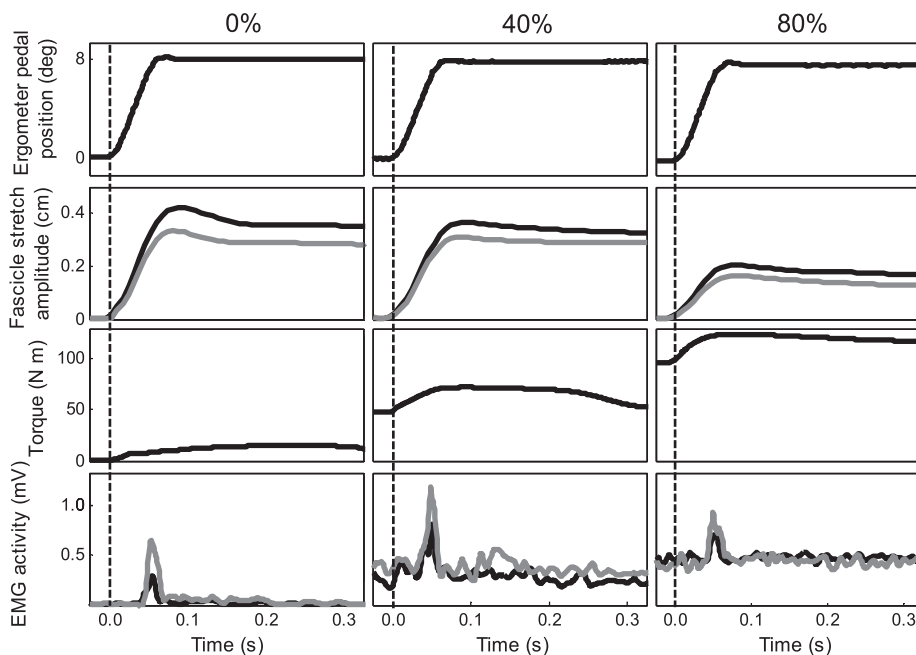
The voluntary plantar flexion moment produced during MVC was  $139.2 \pm 43.4$  N·m. All moment values were corrected for the influence of gravity, which accounted for  $2 \pm 2\%$  of the total moment, and the estimated influence of TA coactivation. The latter equated to  $8 \pm 6$ ,  $6 \pm 5$ ,  $4 \pm 3$ ,  $4 \pm 3$ , and  $4 \pm 3\%$  of the total moment between the 20 and 100% conditions. In each trial, subjects produced a target moment level before the stretch. The actual levels achieved for the 20, 40, 60, 80, and 100% conditions were the following:  $19.7 \pm 0.9$ ,  $38.6 \pm 1.7$ ,  $57.5 \pm 2.7$ ,  $76.8 \pm 3.1$ , and  $92.4 \pm 6.4\%$ , respectively. The force data from the passive trials were analyzed at four different time periods, and no significant prestretch-poststretch differences were found, suggesting that the intervention did not cause any lasting mechanical changes in the muscle.

In both muscles, a short-latency stretch reflex could usually be identified in all conditions, occurring at a mean latency of  $44.2 \pm 3.1$  ms in Sol and  $39.5 \pm 2.9$  ms in MG (Fig. 1).

Although it was also possible to identify the long-latency component of the stretch reflex in some subjects (not shown in Fig. 1), this response is not discussed here, because its latency is too long to affect the fascicle stretch responses that were examined. In the 100% condition, it was not possible to clearly identify a short-latency stretch reflex in two subjects in the MG muscle. Consequently, the mean data for this condition are based on reflex responses from 11 subjects. As shown in Fig. 2, stretch reflex amplitudes significantly increased between rest and activation, peaked between 40 and 60%, and thereafter declined in both muscles. At 100% of MVC, the stretch reflex amplitude did not significantly differ from the resting stretch reflex amplitude (0%) in either muscle. In MG, background EMG increased between 0 and 100% ( $P < 0.001$ ). In Sol, background EMG increased up to 60% and remained constant thereafter. Second-order polynomials were applied to the reflex amplitudes plotted against background torque (Fig. 3). Reflex modulation across the entire torque range was well described by a quadratic relation in MG but not in Sol.

Between the 0 and 100% conditions, mean MG pennation angle increased from  $27 \pm 8$  to  $36 \pm 12^\circ$  ( $P < 0.05$ ), and prestretch fascicle length decreased from  $5.74 \pm 0.89$  to  $3.94 \pm 0.83$  cm ( $P < 0.01$ ), with a total fascicle shortening of  $1.80 \pm 0.58$  cm. In Sol, pennation angle increased from  $23 \pm 4$  to  $36 \pm 5^\circ$  ( $P < 0.001$ ). Prestretch fascicle length decreased between 0 and 60% of MVC ( $P < 0.05$ ), but no further shortening occurred above this level. The total shortening was  $0.86 \pm 0.40$  cm ( $4.23 \pm 1.0$  to  $3.37 \pm 0.68$  cm). The mean fascicle stretch amplitudes and velocities in response to stretch are shown in Fig. 4. Between the 0 and 100% conditions, fascicle stretch velocity decreased by  $61 \pm 12$  and  $56 \pm 14\%$  in MG and Sol, respectively (Fig. 2). The horizontal heel displacement throughout the force development phase that preceded each stretch was as follows: 20,  $0.82 \pm 0.71$ ; 40%,  $2.31 \pm 1.71$ ; 60%,  $3.59 \pm 2.31$ ; 80%,  $3.62 \pm 2.91$ ; 100%,  $4.44 \pm 2.51$  mm. The concurrent changes in ankle angle were

Fig. 1. Typical responses of a single subject to an  $8^\circ$  stretch at the 0, 40, and 80% conditions. A: position of the ankle ergometer pedal. B: fascicle stretch responses of the medial gastrocnemius (MG; black lines) and soleus (Sol; gray lines) muscles. C: torque responses. D: EMG activity in the MG (black lines) and Sol (gray lines) muscles, showing a clear short-latency reflex component at  $\sim 40$  ms. Vertical lines represent the stretch onset.



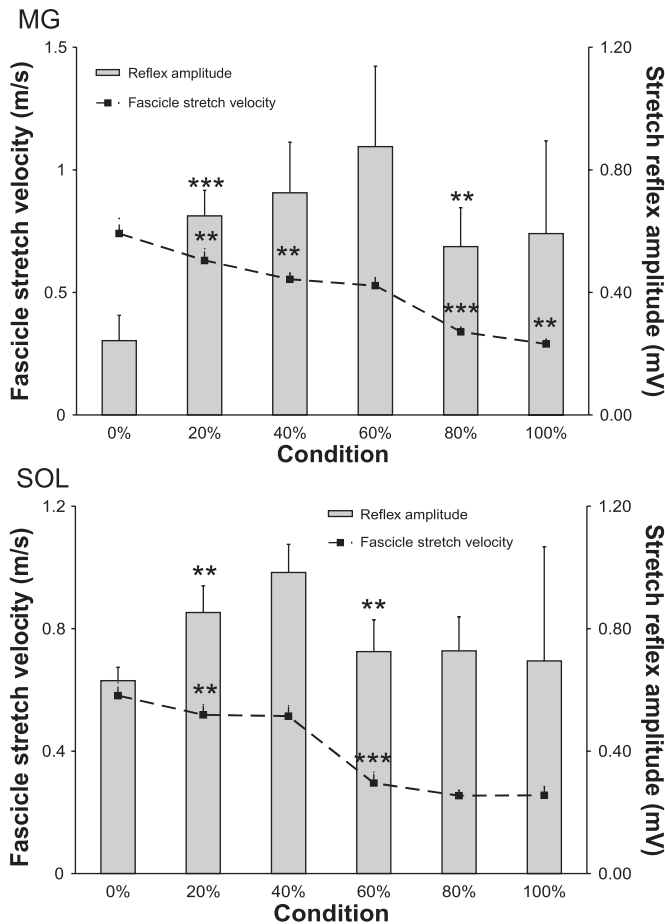


Fig. 2. Fascicle stretch velocity and stretch reflex amplitude in the MG (top) and Sol (bottom) muscles. Significant difference from the preceding condition: \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

as follows:  $3.4 \pm 1.8$ ,  $6.0 \pm 2.2$ ,  $7.1 \pm 2.6$ ,  $7.3 \pm 3.3$ , and  $8.5 \pm 4.1^\circ$ . Analysis of the force pedal potentiometer data confirmed that pedal movement was minimal during isometric contractions ( $0-0.6^\circ$ ). To ensure that a constant stretch was induced at the ankle joint between torque levels, the slope of the pedal displacement curve and the amplitude of the stretch were compared between the 0 and 100% conditions, and no differences were found in either variable ( $P = 0.114$  and  $P = 0.396$ , respectively).

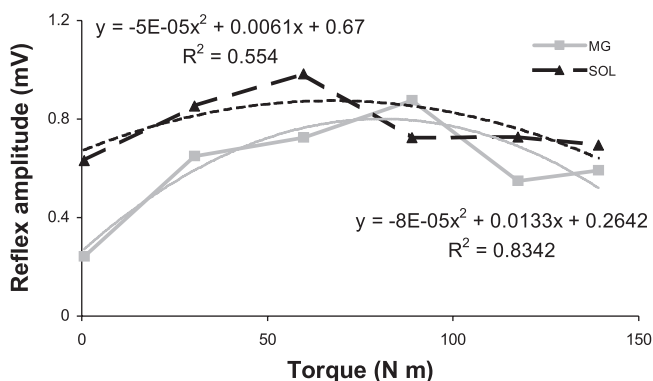


Fig. 3. Stretch reflex amplitude as a function of background torque. Second-order polynomials were fitted to the data and the coefficients are displayed.

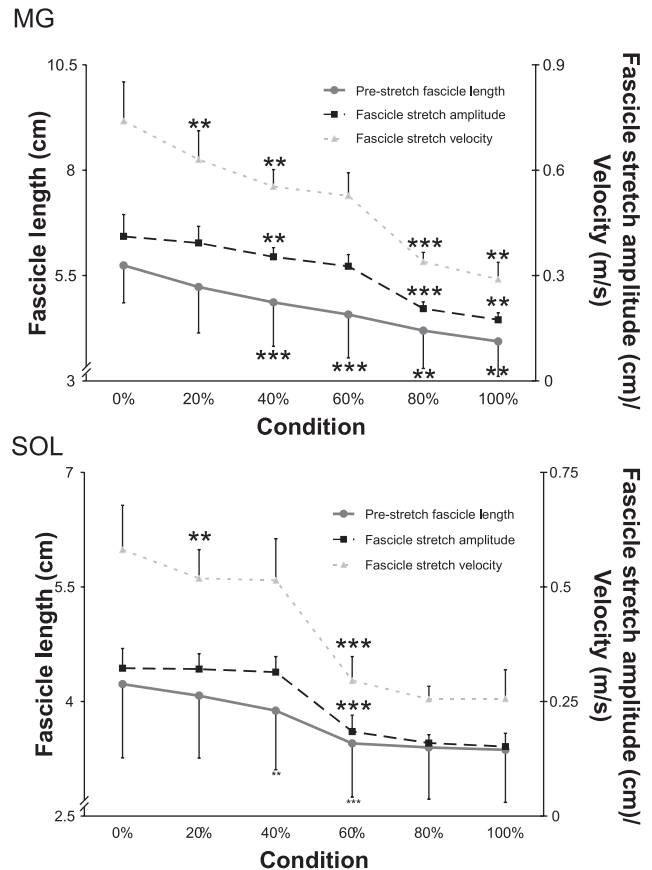


Fig. 4. Fascicle behavior in the MG (top) and Sol (bottom) muscles. Fascicle stretch amplitude and velocity are plotted against the right y-axis, and pre-stretch fascicle length is plotted on the left y-axis. Significant difference from the preceding condition: \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

## DISCUSSION

In the present study, stretch reflex amplitudes peaked at low to intermediate force levels and subsequently declined in MG and Sol. At low force levels, reflex amplitudes increased despite a lack of change or even a decrease in fascicle stretch amplitudes and velocities. At high force levels, however, lower velocity, and smaller amplitude fascicle stretch responses coincided with smaller stretch reflex amplitudes. These findings clearly show that stretch distribution is modulated between muscle and tendinous tissues with variations in contraction level. Furthermore, the velocity at which muscle fascicles were stretched dramatically decreased at high force levels. This can ultimately lead to a reduction in reflex amplitude due to a decreased stimulus to the muscle spindles and thus a decrease in afferent activity (45).

It should be noted that there are some methodological considerations associated with this study. For example, the method used to examine fascicle lengths in this study was able to account for fascicle curvature (e.g., Ref. 36); however, an alteration in additional planes (58) during contraction could not be taken into account. Nonetheless, because of the similar joint configuration between each condition, this factor is unlikely to have significantly influenced the results. Because this is the first study to examine fascicle stretch responses during active contractions, it is unknown whether the fascicle responses are uniform within different parts of the muscle. Numerous studies



in animals and humans have reported uniform fascicle behavior within a muscle during a contraction (23, 30, 35, 51). Notwithstanding, further investigation is required to resolve whether this is also true for stretch responses. During the performance of isometric contractions, rotation of the knee joint was not recorded in this study. However, previous studies have identified that knee joint rotation is insignificant ( $<1^\circ$ ) during maximal isometric plantar flexion, and its effect can thus be neglected (15, 21). To control that the stretch induced at the ankle joint was constant across all torque levels, a comparison was performed between the 0 and 100% conditions, and no differences were observed in the slope of the ankle angular displacement curves or the amplitude of stretch. This confirms that the applied stretch was constant between torque levels.

It is well established that the magnitude of the neural stretch reflex response increases with muscle contraction level up to intermediate force levels (e.g., Ref. 11). However, very few studies have examined stretch reflex responses above 50% of MVC. Toft et al. (55, 56) and Cathers et al. (5) reported a plateau in reflex magnitude in the human TA and Sol muscles, and in the flexor carpi radialis, respectively, at  $\sim 50\%$  of MVC. These findings are consistent with the results obtained here in the soleus and gastrocnemius muscles. Furthermore, previous authors have reported a quadratic relation between reflex torque (or gain) and background torque in the knee extensors (34) and flexor carpi radialis (5). A qualitatively similar relation was observed between reflex amplitude and preactivation torque in the MG muscle in this study. The relation was far weaker in Sol, which may be due to differences in the range of reflex amplitudes between the two muscles, as well as differences in contractile properties of slow- and fast-twitch muscle fibers (e.g., Ref. 26). Differences in contractile behavior between these two muscles have been observed previously in terms of length changes during dynamic activities (20, 52) and shortening behavior during isometric contractions (31).

Previous reports have noted that with increasing force levels, there is a decline in the amount of stretch that reaches the muscles fibers (45). This is because of a greater relative increase in muscle stiffness compared with the tendinous tissues (46). Consequently, the amount of stretch that is transferred to the muscle progressively declines. In the present study, this may have been exacerbated by the observed increase in fiber pennation angle with increasing force, which augments tendon excursion relative to fascicle length change (22). An interesting consequence of the shift in stretch distribution from the muscle toward the tendon at high torque levels is that Golgi tendon afferent feedback is likely to increase (1, 7). One could argue therefore that during the present experiments where the activity of the Golgi tendon organs is assumed to have had an inhibitory effect, this mechanism may have contributed to the decline in stretch reflex amplitudes at high torque levels. However, previous studies have suggested that pre- and postsynaptic sources of inhibition are independent of contraction intensity (40). Therefore, although we are unable to completely rule out a contribution of this mechanism, its influence is likely to have been minimal. Conversely, during walking where the input from Golgi tendon organs to the motoneurons through spinal interneurons is likely to have an excitatory effect (9, 17, 39), the consequences of the shift in stretch distribution from the muscle toward the tendon may

well be quite different from those observed during the sitting experiments in this study.

In addition to a decline in stretch amplitude, our results also revealed a dramatic decline in fascicle stretch velocity between passive conditions and maximal contraction intensity of 61 and 56% in MG and Sol, respectively. Because stretch velocity is known to be a more potent stimulus to muscle spindles than stretch amplitude (53), this decline would decrease the afferent activity and thus decrease the reflex response (45). Previous studies have reported a similar decrease in reflex amplitude at high force levels (1, 5), although these studies did not examine changes in mechanical stretch responses. Several possible explanations for the decline in reflex amplitude have been presented. According to Matthews (33), if reflex-evoked synaptic drive decreased with motoneuron size, as happens for Ia monosynaptic input (41), then a reduction in reflex output from the motoneuron pool would be expected at higher contraction levels as larger motor units are recruited. However, previous authors have noted a positive correlation between H-reflex amplitude and contraction intensity up to 60% MVC in Sol, beyond which no change in H-reflex amplitude was observed. Furthermore, in MG, H-reflex amplitude reportedly increased throughout the entire force range (4). These results suggest that motoneuron excitability remains constant (Sol) or even increases (MG) between  $\sim 50$  and 100% of MVC. Consequently, our finding of a decrease in stretch reflex amplitudes in both muscles at high torque levels is likely to be at least partly due to the decreased fascicle stretch velocity, which would decrease the stimulus to the muscle spindles.

Although this explanation may be accurate at high force levels, significant increases in reflex amplitude were observed in both muscles at low forces (0–40%), despite a constant or even decreased fascicle stretch velocity. Gregory et al. (12) suggested that the increase in stretch reflex size produced by low-level voluntary contraction is due to  $\alpha$ - $\gamma$  coactivation, whereby slack is removed from both extrafusal and intrafusal muscle fibers. This mechanism may explain our findings, because the fascicles progressively shortened with increasing contraction intensity. Furthermore, there is good evidence for  $\alpha$ - $\gamma$  coactivation during voluntary isometric contractions (57, 60). Because the fusimotor system has been suggested to be fully activated by 20–25% of maximum strength (e.g., Ref. 42), any additional increase in reflex amplitude above this force level may be due to the removal of slack from extrafusal muscle fibers and tendinous tissues. This mechanism could conceivably elevate muscle spindle sensitivity (38, 54), which may compensate for the constant or slightly decreased fascicle stretch velocity at low force levels.

In conclusion, the results of this study demonstrate a decline in fascicle stretch velocity of over 50% between passive conditions and maximal force levels in the major muscles of the triceps surae. This is likely to be an important factor with regards to the decline in stretch reflex amplitudes at high force levels, and it may also be at least partly responsible for the decline in reflex-induced stiffness of the dorsiflexors that our laboratory has observed previously (50). Because short-latency stretch reflexes play an important role in force production (19) and stiffness regulation (56) in the ankle extensor muscles, a change in reflex sensitivity, and thus muscle spindle afferent feedback (and perhaps Golgi tendon organ feedback), could

decrease the efficacy of human locomotion (19, 48, 59), particularly where high force production is required.

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