The role of the stretch reflex in the gastrocnemius muscle during human locomotion at various speeds

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Ishikawa M, Komi PV. The role of the stretch reflex in the gastrocnemius muscle during human locomotion at various speeds. J Appl Physiol 103: 1030–1036, 2007. First published July 12, 2007; doi:10.1152/japplphysiol.00277.2007.—In the present study, the fascicle length (Lfa) of the human medial gastrocnemius (MG) muscle was monitored to evaluate possible input from the short-latency stretch reflex (SLR) during the stance phase of running and to examine its timing at various running speeds. Eight subjects ran at 2.0, 3.5, 5.0, and 6.5 m/s. The Lfa was measured with the high-speed ultrasound fascicle scanning together with kinematics and myoelectrical activities. The amplitudes and onset latency of SLR activities were determined. During ground contact, the sudden MG fascicle stretch occurred during the early contact at all running speeds. This was followed by the fascicle shortening. The timing of fascicle stretch depended on running speed and type of foot contact. In slower speed conditions (2.0, 3.5, 5 m/s), the MG fascicle stretch and the corresponding SLR activities occurred during the middle of the braking phase. In fast-speed running (6.5 m/s), however, the MG fascicle stretch occurred later compared with the lower speed. The corresponding SLR activities occurred significantly later at the end of the braking phase. In addition to the clear demonstration of the different timings of SLR in MG during ground contact of running, the results imply that the role of the MG SLR during the stance phase of running can be different between fast- and slow-speed running conditions.

IN LOCOMOTION, HUMAN (and animal in general) skeletal muscle produces force and movement by utilizing the combination of preactivation and subsequent eccentric and concentric actions. This is described as the concept of the stretch-shortening cycle (SSC) (see Ref. 28 for a review). One important function during SSC movements is the appearance of stretch reflex, which can be evoked by the forced lengthening of the skeletal muscle at the beginning of SSC, for example in running (7) and drop jumps (28). Thus it is possible that similarly to the isolated neuromuscular preparation studies (18, 34), the stretch-induced reflex activities can play an important role in regulating the stiffness of muscle fibers also in human running.

However, there are several doubts regarding the possible contribution of stretch reflex in SSC movements, especially for the rapid SSC movements (38). The first issue is the question of the fascicle behavior during the eccentric phase. It has been suggested that this behavior takes place as the concerted fascicle action (1, 16). In this action, the length of the contractile component is thought to be maintained constant (optimal working range of sarcomeres) so that it stretches tendinous tissues effectively while the muscle-tendon unit (MTU) is forced to lengthen during the eccentric phase of SSC. Several studies have reported this behavior for the medial gastrocnemius (MG) muscle during animal and human walking (11, 13, 19), running (31, 36), and low-intensity plantar flexion SSC movements (24). Consequently, this would mean that there is no lengthening of muscle fascicles to stretch the muscle spindles and thus trigger the stretch reflex (10). However, and in contrast to these reports, the recent high-speed (97 Hz) ultrasound scanning measurement has demonstrated a clear short-duration stretching of the MG fascicles during the very early phase of the ground contact in the slow-speed running (21), supporting the appearance of stretch reflex activities during human locomotion (7, 28). We were, therefore, curious to see whether this similar fascicle lengthening during the ground contact can be observed at different speeds of running. It is reportedly known that the MG fascicles during SSC movements can behave differently depending on the intensity and type of the SSC movements (20, 21, 23, 37). When this is complemented with the knowledge that the precontact activation can be dependent on the running speed (29), the nature of the fascicle behavior during running may appear rather complex. We believe that by using the high-scanning ultrasound technique we may get more direct and exact records of the fascicle (and spindle) behaviors compared with either low-scanning ultrasound measurements (31) or estimations based on a series of assumptions (e.g., Ref. 40).

Second, it has been shown that the H-reflex excitability is lower during locomotion than during rest and that it is even lower during running (6). This would indirectly imply that also the stretch reflex is less important during running. Nonetheless, the rate of stretch experienced by muscles in many SSC movements does seem to evoke a stretch reflex of sufficient magnitude to influence the force exerted by muscle (35, 40). In addition, it has been reported that the hopping training could improve the amplitudes of short-latency stretch reflexes (SLR) during hopping exercises (39). Consequently, there is no reason to believe that the stretch reflex would not participate in the extensor activity during the functional contact phase, such as the stance phase of running.

The purpose of the present study was to provide evidence of SLR responses during human running while the MG fascicle stretching was observed. It was hypothesized that the stretch timing of the MG fascicles would be changed because of the increased preactivation with higher speed of running. Timing of these SLR activities would then be expected to significantly influence the rate of the force production and the fascicle stiffness during the ground-contact phase of running.

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METHODS

Subjects and experimental procedure. Eight physically active male subjects [age 25.2 (SD 3.8) yr, height 171.1 (4.8) cm, and body mass 62.9 (8.9) kg] participated in this study. Subjects were fully informed of the procedures and risks associated with the study according to the Declaration of Helsinki. The study was approved by the local ethics committee.

The subjects run at four different speeds (Jog 2.0, Slow 3.5, Mid 5.0, High 6.5 m/s) in a random order on a motorized treadmill (0 grades, 4 m long, and 2 m wide; Telinehtyma, Kotka, Finland). Subjects were asked to run on the heel contact in Jog and to run on the ball of the foot in the other conditions. After the target speeds were reached, the 8–10 steps were collected for each subject.

Measured parameters. In the present study, the real-time B-mode scanning of ultrasonic apparatus (SSD-5500m and Alpha-10, Aloka, Tokyo, Japan) was used to measure the fascicle length in the MG muscle of the right leg during running (96–169 images/s, a 6-cm-width linear array probe with scanning frequency of 10 MHz; Aloka). The total weight of the tip of the ultrasound probe and the supporting device made of the polystyrene is less than 130 g. The scanning image sampling was changed individually depending on the depth of the MG muscle. The width and depth (thickness) of the scanning images were at least 5.91 (330 pixels) and 5.38 (248 pixels) cm, respectively. The superior and inferior aponeuroses and the MG fascicles were identified and digitized in each image (see references cited in reviews; Refs. 12, 25) (Fig. 1B). The normalized two-dimensional cross-correlation coefficient was used to show the reproducibility of the ultrasound images during contact between two steps. The correlation coefficient for images during contact was, on average, 0.83 ± 0.03. The reproducibilities for the fascicle length measurements during dynamic movements have been reported by the several groups (e.g., Refs. 21, 24).

Electromyographic (EMG) signals of the MG and soleus (Sol) muscles of the right leg (Ag-AgCl miniature surface bipolar electrodes, interelectrode distance of 20 mm; skin electrode 650437, Beckman, Fullerton, CA) were amplified (input impedance 25 MΩ, common-mode rejection ratio > 90 dB) and then sent telemetrically to the analog-to-digital converter (Sampling rate 2 kHz; Power 1401, Cambridge Electronics Design, Cambridge, UK). To place the EMG electrodes on the muscle belly, B-mode ultrasound images were used to precisely locate the MG muscle midbellies for each subject (Fig. 1A). The skin was lightly treated with sandpaper to secure an inter-electrode resistance value below 5 kΩ. The insole foot touch sensor was used to determine the exact contact timing for aligning the EMG signals and synchronizing the EMG signal, ultrasound data, and kinematics.

All running movements were recorded with a high-speed video camera (200 frames/s; Peak Performance, Englewood, CO) from the subjects’ right side, perpendicular to the plane of motion, to calculate the joint angles of the lower limb (knee and ankle). Reflective markers were placed over trochanter major, center of rotation of the knee, lateral malleolus, heel, and fifth metatarsal head. The markers were then digitized automatically using Peak Motus software (Peak Performance). The transformed coordinates were digitally filtered with a Butterworth fourth-order zero-lag low-pass filter (cutoff frequency: 8 Hz).

Electromyographic (EMG) signals of the MG and soleus (Sol) muscles of the right leg (Ag-AgCl miniature surface bipolar electrodes, interelectrode distance of 20 mm; skin electrode 650437, Beckman, Fullerton, CA) were amplified (input impedance 25 MΩ, common-mode rejection ratio > 90 dB) and then sent telemetrically to the analog-to-digital converter (Sampling rate 2 kHz; Power 1401, Cambridge Electronics Design, Cambridge, UK). To place the EMG electrodes on the muscle belly, B-mode ultrasound images were used to precisely locate the MG muscle midbellies for each subject (Fig. 1A). The skin was lightly treated with sandpaper to secure an inter-electrode resistance value below 5 kΩ. The insole foot touch sensor was used to determine the exact contact timing for aligning the EMG signals and synchronizing the EMG signal, ultrasound data, and kinematics.

Fig. 1. A: schematic presentation of the experimental setup. B: serial ultrasound images of medial gastrocnemius (MG) muscle as measured during running. A: subjects ran at 4 different speeds on the treadmill. Ultrasonographic images for the fascicle length of MG were taken simultaneously with EMG activities of the MG and soleus (Sol) muscles as well as kinematics (ankle and knee joint angles). Inset: position of the ultrasound probe and EMG electrodes. B: parts of a longitudinal sequence of ultrasonographic images of MG during running. Images were recorded at 150 Hz in this particular example. Line of MG fascicles in each image is drawn between the superficial and deep aponeuroses. Time is expressed relative to the ground contact.

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Analyses. The joint angles of ankle and knee were calculated by the obtained kinematic data (Fig. 1A). The model of Hawkins and Hull (15) was used to estimate MTU length ($L_{MTU}$) in MG muscle from the joint angular data and the shank length. During the ground-contact phase, the braking and push-off phases were determined by the transition point from the stretching to shortening of MTU. The muscle fascicle length of MG muscle ($L_{fa}$) was analyzed from the each ultrasonographic image during running. The MG fascicle was identified in each image along its length from the superficial and deep aponeuroses (Fig. 1B). This fascicle was then tracked continuously frame by frame. Then the $L_{fa}$ data acquired at 96–169 Hz were interpolated to 200 Hz. For the kinematics and the ultrasound data, the two steps were analyzed and averaged for each subject. This is because the limitation of the memory capacity of our high-speed ultrasound scanning device. The velocities of the MG fascicles were calculated by the quadratic polynomial differentiation. Shortening direction was defined as positive.

After EMG signals were band-pass filtered (5–500 Hz) and then full-wave rectified, the EMG signal data of 8–10 steps were averaged in each condition and in each subject. These EMG signals were integrated and then averaged (aEMG) individually and separately for the following two phases during running: preactivation and ground-contact phases. The preactivation phase was defined as the 100-ms period preceding ground contact (29). The stretch-induced SLR activities and onset latency of the MG muscle were determined by visual inspection using a cursor on the display (7, 9, 27, 38). The SLR amplitude and latency were defined as the peak amplitude after the first major deflection in the EMG record following the MG fascicle stretch during the ground contact (9) (Fig. 2).

Statistics. Values are presented as means and standard deviations (SD) unless otherwise stated. A one-way repeated-measures ANOVA with a post hoc Fisher’s least significant difference multiple comparison were used to assess the differences between the different running speed conditions for the EMG and length data. The probability level accepted for statistical significance was $P < 0.05$.

RESULTS

The MTU behavior. A representative example of changes in the $L_{MTU}$ during the contact phases is shown in Fig. 3A. In Jog, because of the heel contact, the MTU of MG initially shortened at the ground-contact moment and then behaved as SSC. At the contact point, the $L_{MTU}$ was significantly shorter in High than other conditions (Fig. 4A). The $L_{MTU}$ stretching amplitudes from the lowest length to the peak length during contact were

Fig. 3. Examples of length of the muscle-tendon unit (MTU) and fascicle ($L_{MTU}$ and $L_{fa}$, respectively) of the MG muscle during running. $L_{MTU}$ (A) and $L_{fa}$ (B) of the right leg during the ground contact are shown for 4 different running speeds. 0 represents the moment of ground contact. End of the MTU stretching.

Fig. 4. Comparison of the $L_{MTU}$ (A) and the $L_{fa}$ (B), stretch length changes (C), and stretch velocities of the MG fascicle (D) for different running speeds. $L_{MTU}$ (A) and $L_{fa}$ (B) are shown at the point of the initial ground contact of running. Amplitudes of the stretching of MTU and fascicle (C) were calculated from the shortest length during the braking phase to the peak length and the corresponding stretch velocities (D). *Significant differences between conditions, $P < 0.05$. **Significant differences between conditions, $P < 0.01$. 
smaller in Mid than in other conditions (Fig. 4C), but the differences were not statistically significant. At the toe-off moment, the \( L_{\text{MTU}} \) did not show any significant differences between all running conditions [Jog 45.8 (2.0), Slow 45.5 (2.2), Mid 45.8 (2.1), High 45.6 (2.0) cm].

**Fascicle Behavior.** At the ground-contact point, the \( L_{\text{fa}} \) was significantly shorter in Mid and High compared with the other conditions (Fig. 4B). After ground contact, the MG fascicles shortened initially and thereafter were stretched suddenly at the different timing during the braking phase (Fig. 3B). The sudden \( L_{\text{fa}} \) stretch timing after ground contact was significantly shorter in Mid compared with that in Jog and Slow (\( P < 0.05 \)) as well as that in High (\( P < 0.05 \)) (Table 1). After the sudden fascicle stretch, the MG fascicles shortened throughout the contact (Fig. 3B). The amplitudes and the peak stretch velocities of the sudden stretch of the MG fascicles were significantly greater in Mid than in Jog and High (Fig. 4, C and D). After the ground contact, the \( L_{\text{fa}} \) at the initial lowest point in High was significantly shorter than that in Slow (\( P < 0.05 \)) and Jog (\( P < 0.05 \)) (Table 2). The \( L_{\text{fa}} \) at the end of the braking phase (end of the MTU stretching) was significantly shorter in High than in Slow (\( P < 0.05 \)) and in Jog (\( P < 0.05 \)), and that at the toe-off moment was significantly shorter in High than in Mid (\( P < 0.05 \)), Slow (\( P < 0.05 \)), and Jog (\( P < 0.05 \)) (Table 2).

**EMG Changes and SLR Responses.** The aEMGs of MG and Sol in the preactivation and contact phases were significantly higher in High than in the other conditions (Fig. 5, A and B). The aEMG ratio (aEMG in MG divided by aEMG in Sol) during the preactivation phase was significantly greater in High than the other conditions (Fig. 5C), indicating that MG became relatively more active than Sol in higher running speed. During the contact phase, however, the aEMG ratio was significantly smaller in High than in Mid (Fig. 5D). The SLR amplitude in MG was significantly greater in Mid than in the other conditions (Fig. 6). The timing of the peak SLR in MG after ground contact was significantly earlier in Mid than in Jog and in High (Table 1, Fig. 2), and that in Sol was significantly later in Jog than in the other conditions and did not show any significant difference between Slow, Mid, and High (Table 1, Fig. 2). The duration between the MG fascicle stretch and the peak SLR in MG did not show the significant difference across all running conditions (Table 1). The ground-contact time and the timing of the end of the braking phase, which is the end of the MTU stretching, were significantly shorter and earlier with higher running speed (Table 1). The timing of the peak SLR was significantly earlier than the timing of the end of the braking phase in Jog, Slow, and Mid but not in High (Table 1).

**DISCUSSION**

The results presented in this paper demonstrate clear and rapid fascicle stretch of the MG muscle during the early contact phase of running. This stretch resulted in occurrence of the SLR in this muscle. It is of interest to note that the timing of the \( L_{\text{fa}} \) stretch was different depending on the running speed and on the type of foot contact. However, the time interval between the onset of the MG fascicle stretch and the peak SLR in MG remained constant across all running conditions. Consequently, the role of the MG SLR during the stance phase of running can be different between fast- and slow-speed running conditions.

**Timing of the Fascicle Stretching.** A short-lasting sudden fascicle stretch of MG during the MTU stretching phase and the corresponding SLR were observed in all running conditions (Figs. 2 and 3B). After this stretch, the MG fascicles shortened throughout contact. These results are in agreement with those of the previous slow-running study (21), but they are in disagreement with the findings of another running study (31). The different observations may be related to the differences in the ultrasound image sampling frequency (>96 vs. 25 Hz) and the problem of the image smoothing processing because of the low ultrasound image sampling.

We have now observed further that the timing and amplitudes of the MG fascicle stretch after ground contact were different between the different running speed conditions and between the types of foot contact, but the duration from the MG fascicle stretch to the timing of the SLR in MG remained constant (Table 1). In Jog, the MG fascicle stretch after ground contact occurred later than in Slow and in Mid (Table 1). This delay can be explained by the delayed MTU stretch in MG due to the heel contact in Jog. Also, the timing of the MG fascicle stretch occurred differentially between Slow, Mid, and High, although these running conditions were performed on the ball of foot contact (Table 1). The slacking of tendon and fascicles and the rate of the Achilles tendon (AT) force development can

### Table 1. Timing and duration of the various parameters from the beginning of the ground contact

<table>
<thead>
<tr>
<th></th>
<th>Jog</th>
<th>Slow</th>
<th>Mid</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Timing of ( L_{\text{fa}} ) stretch, ms</td>
<td>37 (9)</td>
<td>29 (9)*</td>
<td>21 (9)*†</td>
<td>31 (4)‡</td>
</tr>
<tr>
<td>Timing of the peak SLR in MG, ms</td>
<td>83 (10)</td>
<td>72 (12)*</td>
<td>64 (13)†</td>
<td>76 (11)‡</td>
</tr>
<tr>
<td>Timing of the peak SLR in Sol, ms</td>
<td>78 (12)</td>
<td>52 (8)*</td>
<td>50 (8)*</td>
<td>50 (7)*</td>
</tr>
<tr>
<td>Duration between ( L_{\text{fa}} ) stretch and SLR response, ms</td>
<td>46 (5)</td>
<td>43 (9)</td>
<td>43 (10)</td>
<td>45 (9)</td>
</tr>
<tr>
<td>Timing of end of braking</td>
<td>143 (13)</td>
<td>123 (10)*</td>
<td>100 (17)*</td>
<td>79 (9)*‡</td>
</tr>
<tr>
<td>Contact time, ms</td>
<td>264 (63)</td>
<td>215 (28)*</td>
<td>168 (24)*</td>
<td>149 (17)*‡</td>
</tr>
</tbody>
</table>

Values are means (SD) for 8 subjects. \( L_{\text{fa}} \), fascicle length; SLR, short-latency stretch reflex; MG, medial gastrocnemius; Sol, soleus. *Significant difference from Jog, \( P < 0.05 \). †Significant difference from Slow, \( P < 0.05 \). ‡Significant difference from Mid, \( P < 0.05 \). Significant difference of timing between the peak SLR and the end of braking phase, \( P < 0.05 \).

### Table 2. Fascicle length at each point during running

<table>
<thead>
<tr>
<th></th>
<th>Jog (1.04)</th>
<th>Slow (1.04)</th>
<th>Mid (1.04)</th>
<th>High (1.03)</th>
</tr>
</thead>
<tbody>
<tr>
<td>At ground contact</td>
<td>7.32</td>
<td>7.16</td>
<td>6.87</td>
<td>6.83</td>
</tr>
<tr>
<td>At initial lowest</td>
<td>6.85</td>
<td>6.64</td>
<td>6.31</td>
<td>6.04</td>
</tr>
<tr>
<td>At peak</td>
<td>7.21</td>
<td>7.15</td>
<td>6.95</td>
<td>6.58</td>
</tr>
<tr>
<td>At end of MTU stretch</td>
<td>6.18</td>
<td>5.98</td>
<td>5.80</td>
<td>5.60</td>
</tr>
<tr>
<td>At toe-off</td>
<td>5.93</td>
<td>5.74</td>
<td>5.70</td>
<td>5.58</td>
</tr>
</tbody>
</table>

Values are means (SD) for 8 subjects. MTU, muscle-tendon unit. Significant differences between conditions are given in the text.
affect these different stretch timings. Generally, the rate of At force development increased with higher running speeds (26). Furthermore, the $L_{fa}$ just before the ground contact is shorter because of the higher preactivation at higher running speeds (Figs. 4B and 5A), resulting in the reduction of the fascicle and tendon slack. Consequently, the stretch timing of the MG fascicles can occur earlier with higher running speed (e.g., from Slow to Mid). In High, however, the fascicle stretch was delayed because the MG fascicle shortening immediately after ground contact lasted longer (Table 1). This is because the MG preactivation still increased in High (Fig. 5A), although the highest maximum AT force can be attained already at a speed of 6 m/s and the rate of AT force also showed similar trend in the direct AT force measurements (26). Thus it is possible that the MG fascicle stiffness increased in High and that the $L_{fa}$ was shorter immediately after the ground contact in High (Table 2). Consequently, the fine interaction between the fascicle stiffness due to the preactivation and the AT loading as well as type of foot contact are likely to influence the fascicle stretch timing.

It is also interesting that the SLR timing varied in MG, but not in Sol, with different running speeds (Table 1, except for Jog). These different SLR timings can be possible because the fascicle behavior can be different between MG and Sol during SSC movements (22, 37). The future work should test these points more thoroughly.

Fascicle behavior during running. It has been proposed recently that the concerted action defined in the introduction cannot occur in the short-contact (17, 21) and/or long-contact SSC movements (22). Instead, it has been proposed that the MG $L_{fa}$ can be modified to match the time of tendon oscillation (SSC) effectively with the contact time of locomotion (21, 22). In the present study, the MG $L_{fa}$ at the initial ground contact was shorter with higher running speeds (Table 2) together with increasing preactivation (Figs. 2 and 5). The MG fascicles continued shortening after the initial contact, except for the sudden fascicle stretching 20–40 ms after the ground contact. This shorter MG $L_{fa}$ and greater MG fascicle shortening at higher running speed can favor increase of the tendon stretch rates and amplitudes. These greater stretch rates of tendon may reduce the time of tendon oscillation (SSC) due to the viscoelastic material of tendon (3), implying increment of the resonant frequency of the elastic component in the human ankle extensors. Consequently, the tendon can be stretched rapidly and subsequently shortened even in the short contact running by variations of fascicle behavior.

Fig. 5. Comparison of EMG in the MG and Sol muscles at 4 different running speeds. Averaged EMG in the MG and Sol muscles of the right leg were analyzed for the preactivation (100 ms) and contact phase of running. MG-to-Sol ratio was calculated by dividing the MG averaged EMG over the Sol averaged EMG. *Significant differences between conditions, $P < 0.05$. **Significant differences between conditions $P < 0.01$.

Fig. 6. Comparison of stretch-induced SLR amplitudes in the MG and Sol muscles at 4 different running speeds. Peak SLR amplitudes during the stance phase were analyzed for both MG and Sol muscles. *Significant differences between conditions, $P < 0.05$. **Significant differences between conditions, $P < 0.01$. 

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However, it is still an open question why $L_{el}$ appears to be shorter at high running speeds. As suggested in the previous study (21), the working range of sarcomeres in the force-length relationship can shift to a more ascending limb (from the plateau region) in running compared with walking. In the present results, the observed shorter $L_{el}$ at high running speed imply even further shifts to the left along the ascending limb. Interestingly, it is likely that the MG fascicles do not necessarily operate the plateau region of force-length relationship of sarcomeres to produce the maximal force during contact phase of running. A possible explanation for this specific MG fascicle modulation, which depends on the running speed, is to stretch and subsequently recoil the tendons effectively during the contact phase of running.

**Fascicle stretch and stretch reflex.** In previous studies, the modeling procedures of muscle fibre behavior have been based on a series of assumptions and data measured on cadavers (e.g., Ref. 40). Voigt et al. (40) reported that the SLR amplitude in Sol was negatively correlated with estimated peak muscle spindle stretch velocity. In the present study, however, it is likely that the SLR amplitudes were positively correlated to the fascicle stretch velocities and amplitudes in MG (Figs. 4, C and D, and 6). These differences may be explained by the idea of the preferential movement-phase-dependent neuromuscular activation during SSC movements (8, 33), in which two different synergistic muscles represent a functional specialization matched according to the demands of motor behavior (41).

Interestingly, the amplitudes of the SLR and the stretch $L_{el}$ decreased from Mid to High, although the MTU stretching amplitudes during the braking phase did not show any significant difference (Figs. 4C and 6). For running, a stiffer MTU would have positive implications, such as increased rate of force development at contact, resulting in decreased contact time and higher peak force. Stiffness of the MTU is enhanced by the preactivation (14) and the reflex activities (34). However, the timing of the peak SLR (76 ms) and the end of the braking phase (79 ms) were the same (Table 1). When we consider the electromechanical delay (10–15 ms) between the onset of EMG and mechanical response (35), the SLR activities contribute to the force enhancements during the push-off phase in High. When the running speeds are approaching maximum sprint running with contact time of 90 ms (32), the timing of the SLR and its contribution will change correspondingly to the end of the push-off phase. Consequently, these results suggest that the mechanical effect of the stretch reflex cannot contribute in the rate of the force production and the fascicle stiffness in the braking phase at higher running speed.

**Methodological considerations.** There are certain points in the methods that need to be addressed. To the best of our knowledge, this may be the first article to consider the different timing of the MG SLR activities together with the fascicle behavior during human running. Consequently, the present calculations of MG SLR can be under criticism. However, we assume that these methodological problems in the present study are minor and did not have a serious effect on our results and interpretation. Second, in some subjects, the MTU shortened immediately after ground contact not only in Jog. This is not due to the accuracy in synchronization but due to the plantar flexion and knee flexion movements immediately after the ground contact of running. The similar results were observed in another group (e.g., Staffilidis S and Arampatzis A, unpublished observation). Third, the kinematics and ultrasound data in our methods are two-dimensional information. These points also should be considered in the future study. Finally, the results of the present study cannot be directly applied to other muscles (e.g., Sol) with regard to timing differences of SLR activities. This is because the behavior of fascicles are muscle specific (21, 34).

With faster running speeds, the SLR activities in MG shifted more to the push-off phase influencing either the fascicle stiffness in the braking phase of slower running or the stretch-induced force potentiation during the push-off phase in the faster running. This delay of the MG SLR activities is likely related to interaction between the fascicle stiffness due to the preactivation and the tendon force development. Further study, particularly with faster running speed condition, is required to quantify the contribution of the stretch reflex response during the ground contact.

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