Intensitv- and muscle-specific fascicle behavior during human drop jumps

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Sousa F, Ishikawa M, Vilas-Boas JP, Komi PV. Intensity- and muscle-specific fascicle behavior during human drop jumps. J Appl Physiol 102: 382–389, 2007. First published October 26, 2006; doi:10.1152/japplphysiol.00274.2006.—The present study was designed to examine fascicle-tendon interaction in the synergistic medial gastrocnemius (MG) and soleus (Sol) muscles during drop jumps (DJ) performed from different drop heights (DH). Eight subjects performed unilateral DJ with maximal rebounds on a sledge apparatus from different DH. During the exercises, fascicle lengths (using ultrasonography) and electromyographic activities were recorded. The results showed that the fascicles of the MG and Sol muscles behaved differently during the contact phase, but the whole muscle-tendon unit and its tendinous tissue lengthened before shortening in both muscles. The Sol fascicles also lengthened before shortening during the ground contact in all conditions. During the braking phase, the Sol activation increased with increasing DH. However, the amplitude of Sol fascicle shortening was not dependent on DH during the same phase. In the MG muscle, the fascicles primarily shortened during the braking phase in the lower DH condition. However, in the higher DH conditions, the MG fascicles either behaved isometrically or were lengthened during the braking phase. These results suggest that the fascicles of synergistic muscles (MG and Sol) can behave differently during DJ and that, with increasing DH, there may be specific length change patterns of the fascicles of MG but not of Sol.

stretch-shortening cycle; ultrasound; biarticular muscle; elasticity; inhibition

FASCICLES OF SKELETAL MUSCLE consist of bundles of muscle fibers usually arranged in parallel. Ultrasonography is increasingly used in the assessment of superficially located soft tissue structures (fascicle and tendon), for example, during movements of major leg extensor muscles. Accordingly, the fascicle behavior of the triceps surae muscle group has received particular attention during human locomotion, from both neurophysiological and biomechanical points of view. These muscles are known to have either mono- [soleus (Sol) muscle] or biarticular (gastrocnemius muscle) structures, and they may consequently show different functional behavior. For example, the medial gastrocnemius (MG) and Sol muscles show similar patterns of H-reflex modulation during the ground contact of human hopping, but the amplitudes of the modulation are different between these muscles (22, 27). Consequently, it has been suggested that there are differences between the two muscles in the distribution of peripheral afferent feedback to their respective motoneuron pools (26). In line with this suggestion, Kokkorogiannis (17) reported that Sol possesses three times more spindles than gastrocnemius muscle. In human movements, Voigt et al. (27) reported that, during hopping, the movement-induced short-latency stretch reflex (SLR) was consistently observed in the electromyogram (EMG) of Sol, but not always in MG. However, Moritani et al. (22) reported that the amplitude of H-reflex modulation was greater in MG than in Sol during maximal effort hopping. The authors thus suggested that there is a preferential, movement-phase-dependent neuromuscular activation of the synergistic human ankle extensor muscles. Consequently, the modulation of muscle activation in MG and Sol may depend not only on the different distribution of muscle spindles, but also on mechanical effects, such as movement intensity. This suggestion is based on previous observations during high-intensity human stretch-shortening cycle (SSC) movements, whereby fascicle behavior was found to be dependent on the muscle (12, 13) and the movement intensity (10, 11, 13). One may question whether the fascicles of the MG and Sol muscles can behave differently during different intensity SSC movements. This question can be answered by performing real-time ultrasonographic scanning of fascicle and tendon behavior during human movements (5, 6), provided that the ultrasound scanning frequency is high enough to capture the high-speed movement (12, 13).

Repeated drop jumps (DJ) can be used to study fascicle behavior and are particularly suitable for investigating the utilization of tendinous tissue (TT) elasticity (10, 13). It has been suggested (13) that the fascicles of a biarticular muscle may not behave in the same way as those of a monoarticular muscle. However, this suggestion was based on a comparison between the MG and vastus lateralis (VL) muscles. During DJ, the relative muscle-tendon unit (MTU) lengthening of MG (5.2%) was less than that of VL muscle (11%).

In the triceps surae muscle group, only one study has shown that fascicles of the synergistic MG and Sol muscles behave differently during human walking (12). The MG fascicles were stretched during the early single-stance phase and then remained isometric during the late single-stance phase. In contrast, the Sol fascicles were lengthened throughout the single-stance phase. During this long contact phase of slow walking, the peak Achilles tendon load was quite low (<1,600 N). It is believed that this low-impact condition cannot be used to generalize the fascicle behavior of these muscles, as slow speed walking clearly differs from other forms of movement. Consequently, there is a need for a greater understanding of muscle-specific fascicle behavior during SSC movements that involve higher Achilles tendon loads.

The objectives of the present study were to investigate fascicle-TT interaction in a synergistic pair of muscles (MG and Sol) during DJ of different impact loading conditions. We hypothesized that, during the braking phase, the MG fascicles would shorten with low-impact loads. However, as the impact...
load increased [higher drop heights (DH) in DJ], the MG fascicles would shorten less during the braking phase and actually lengthen when the impact load was extremely high. In the Sol muscle, on the other hand, the fascicles were always expected to lengthen, regardless of the stretch (impact) condition. Both of these hypotheses suggest that, during high-impact SSC movements, the MG muscle is much more sensitive than the Sol muscle to variations of the impact load. It must be emphasized that, to the best of our knowledge, with the exception of human walking (12), the Sol fascicle-TT interaction has not previously been studied under natural stretch (impact) conditions, while simultaneously studying the MG muscle.

METHODS

Subjects and experimental procedure. Eight physically active subjects, age 26.6 yr (SD 2.8), height 170.1 cm (SD 6.8), and body mass 61.9 kg (SD 9.9), participated in this study. Before testing, subjects were familiarized with the sled DJ exercises and provided written, informed consent. The study was approved by the Ethics Committee of the University of Jyväskylä.

The lowest position of the sled seat was determined at rest with knee and ankle angles of 50 and 85°, respectively (0° is full extension). The subjects then performed several unilateral (right leg) maximum DJ from different DHs on the sled apparatus (9–11, 21) to decide the optimal DH for each subject. This was determined by dropping the subject from different heights to find the greatest rebound height of the center of gravity (13, 19). Thereafter, subjects performed the DJ with maximal rebounds from four individually predetermined DHs: 50, 75, 100, and 120% of the optimal DH (DJ1, DJ2, DJ3, and DJ4, respectively), in a random order. Unilateral jumps were chosen to ensure a higher relative impact load compared with bilateral jumps. To obtain the same condition bilaterally would not have been possible using our sled apparatus. In the present study, the sled inclination was set to 43° above the horizontal position. The subjects then performed several unilateral (right leg) predetermined DHs: 50, 75, 100, and 120% of the optimal DH (DJ1, DJ2, DJ3, and DJ4, respectively), in a random order. Unilateral jumps were chosen to ensure a higher relative impact load compared with bilateral jumps. To obtain the same condition bilaterally would not have been possible using our sled apparatus. In the present study, the sled inclination was set to 43° above the horizontal position. During the jumping tasks, the lowest sled seat position (see above) and maximal jump height were confirmed by monitoring signals of the position sensor attached to the sled seat during trials. Three successful trials were required for each task.

Reaction forces [vertical force (Fv); parallel to the movement plane of the sled seat], sled displacement, velocity of sled displacement, and EMG activity of the MG and Sol muscles of the right leg were stored simultaneously on a personal computer via an analog-to-digital converter (sampling rate 2 kHz; Power 1401, Cambridge Electronics Design). Surface bipolar EMG electrodes were used to record the MG and Sol muscle activities (Ag-AgCl miniature surface bipolar electrodes, interelectrode distance of 20 mm; Beckman skin electrode 650437). To place the EMG electrodes on the muscle belly, B-mode ultrasound images were used to precisely locate the MG muscle midbelles for each subject.

EMG signals were amplified (input impedance 25 MΩ, common mode rejection ratio >90 dB) and then sent telemetrically to the analog-to-digital converter. The skin was lightly treated with sandpaper to secure an interelectrode resistance value <5 kΩ.

All DJs were recorded with a high-speed video camera (200 frames/s; Peak Performance) 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 the center of rotation of the shoulder, 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 (cut-off frequency: 8 Hz). Longitudinal images of the MG and Sol muscles of the right leg were obtained during movement using a real-time B-mode ultrasound apparatus (SSD-5500, Aloka). An adhesive silicon pad was placed between the skin and the ultrasound probe to avoid any movement of the probe relative to the muscle belly. The probe was fixed securely with a special support device made of polystyrene. The ultrasound apparatus was used to measure two-dimensional fascicle lengths (Lfa) in the MG and Sol muscles during the DJ (96 images/s, 6-cm linear array probes with scanning frequency 10 MHz; Aloka) (7, 12, 13). The width and depth (thickness) of the scanning images were 5.91 cm (330 pixels) and 5.38 cm (248 pixels), respectively. The superior and inferior aponeuroses, and the MG and Sol fascicles, were identified and digitized in each image (7, 12, 13, and 14) (Fig. 1). The reliability of the ultrasound method of Lfa calculation has been established elsewhere, with a coefficient of variation ranging between 0 and 6% (6, 14, 15, 16, 20). An electronic pulse was used to synchronize the EMG, kinetic, kinematic, and ultrasonographic data.

Analyses. The model of Hawkins and Hull (8) was used to estimate MTU length (LMTU) changes in MG and Sol muscles from the joint angular data. The LMTU data acquired at 96 Hz were interpolated to 100 Hz. After the LMTU of MG and Sol data were resampled at 100 Hz, the length changes of TT were calculated by subtracting the horizontal length component of the identified MG and Sol fascicle from the LMTU (7, 12, 13, 20):

\[ L_{TT} = L_{MTU} - L_{fa} \cos \alpha \]

where \( L_{TT} \) is the TT length, and \( \alpha \) is the angle between the fascicle line and the aponeurosis (pennation angle). The TT strain was esti-
mated from the length change of TT from the moment of contact to the moment of peak $L_{TT}$, divided by the $L_{TT}$ at the moment of contact. EMG signals were full-wave rectified and low-pass filtered at 75 Hz (Butterworth type fourth-order low-pass digital filter). The filtered EMG signals were integrated and then averaged (aEMG) individually and separately for the following three phases during the ground contact of DJ: preactivation, braking, and push-off. The preactivation phase was defined as the 100-ms period preceding ground contact. The transition from the braking phase to the push-off phase was determined while the sledge was at its lowest position.

**Statistics.** Values are presented as means and SDs, unless otherwise stated. To analyze the differences between the different DH conditions for the sledge speed and $F_v$, a repeated-measures one-way ANOVA was used, with a post hoc least significant difference multiple comparison. A multivariable ANOVA was used to assess the differences in the EMG and length data, as well as interactions of the DH intensity with each muscle, and of the DH intensity with each phase. If interactions were present, a post hoc Tukey was used to test the difference between them. Spearman’s rank correlation coefficient for polynomial regression analysis of variables was used to calculate the statistical significance of the relationship between the dropping sledge speed and the fascicle stretch amplitude. The probability level accepted for statistical significance was $P < 0.05$.

**RESULTS**

**Changes in mechanical parameters.** As shown in Table 1, the sledge jump performances were in accordance with our hypotheses: the peak $F_v$ and the peak dropping speed increased significantly from DJ1 to DJ4, and the corresponding peak rebound speeds increased until DJ3 (optimal DH). DJ4 was intended to represent an excessive DH (prestretch speed), and the resulting peak rebound speed of 1.13 ± 0.09 m/s showed no significant increase compared with DJ3 (1.20 ± 0.11 m/s). Although there was no significant change in total contact time, the duration of the braking phase decreased in DJ3 and DJ4 compared with DJ1 (Table 1).

**Changes in EMG activity.** The SSC action can be divided into three important phases: preactivation, braking, and push-off (18). Accordingly, EMG signals were analyzed for these phases during the four DH conditions (DJ1, DJ2, DJ3, and DJ4). These results are shown in Fig. 2. When a significant interaction ($P < 0.01$) was found between a muscle and a particular phase, the effects of DH were examined for each muscle. The most obvious finding was the significant increase in preactivation of MG and Sol muscles as a function of DH. In addition, in the braking phase, the DJ3 condition showed higher aEMG values of both muscles compared with DJ1 (Fig. 2). Between DJ3 and DJ4, the Sol aEMG increased in the braking phase. This was not the case for the MG muscle, although its aEMG at DJ4 was still higher than at DJ1 ($P < 0.05$). When comparing the MG and Sol muscles, significant differences were observed from DJ1 to DJ3, but this significance disappeared at DJ4. In both muscles, EMG amplitudes were similar in the push-off phase, regardless of the DH.

**Changes in fascicle-TT behavior.** As the major purpose of the present study was to compare the fascicle behavior between the two muscles (MG and Sol), Fig. 3 was designed to give a representative example of changes in the examined parameters during the contact phase (DJ1, DJ2, DJ3, and DJ4). The curves were averaged from three repetitions, with the first contact with the force plate used as a trigger point for averaging. As shown in Fig. 3, and also verified for the entire sample group, the MG and Sol muscles both exhibited similar MTU behavior across all jumping conditions. In all DJs, the MTU of the two muscles demonstrated typical SSC behavior: stretch before shortening during contact with the force plate. This SSC behavior was also observed in the TT of both muscles. The amplitudes of the respective stretch and shortening of the MTU and TT, in the braking and push-off phases, are shown in Fig. 4. The stretch amplitudes of the two muscles increased as a function of DH, and the amplitudes of shortening remained constant across all conditions in both muscles. The effects of DH on TT strain are displayed for both muscles in Fig. 5. There was a significant interaction between DH and the Sol muscle ($P < 0.05$), and subsequent analysis of the effects of DH showed that the TT strain of Sol increased with increasing DH ($P < 0.05$). This was not the case for MG (Fig. 5).

The situation became more complicated when $L_{TT}$ changes were compared. As already shown in Fig. 3, different fascicle behavior was observed between the two muscles when the DH was increased. Until the point of contact, the fascicles of both muscles shortened, but thereafter the behavior patterns differed. After the initial contact, the Sol fascicles began lengthening before shortening in all subjects (Table 2), thus following the SSC concept. However, the MG fascicles continued shortening during the early braking phase in all DH conditions and in all subjects (Fig. 3 and Table 2). Thereafter, the MG fascicle behavior differed during the late-braking phase, depending on the DH condition. In DJ1 and DJ2, the MG fascicles shortened further or remained the same length during the late-braking phase. In DJ4, which represents very high stretch loads upon impact, a sudden stretch of the MG fascicles was observed 30–60 ms after ground contact in all subjects (also in DJ3 in some subjects). In the subsequent push-off phase, the MG fascicles shortened again in all subjects (Fig. 3 and Table 2).

### Table 1. Peak and rebound speeds, peak reaction force, and contact times for all dropping conditions (DJ1, DJ2, DJ3, and DJ4)

<table>
<thead>
<tr>
<th></th>
<th>DJ1</th>
<th>DJ2</th>
<th>DJ3</th>
<th>DJ4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Drop speed, m/s</td>
<td>0.48 (0.15)</td>
<td>0.76 (0.05)$^b$</td>
<td>0.94 (0.07)$^{b,d}$</td>
<td>1.15 (0.12)$^{b,d,e}$</td>
</tr>
<tr>
<td>Rebound speed, m/s</td>
<td>0.95 (0.17)</td>
<td>1.07 (0.16)</td>
<td>1.20 (0.11)$^b$</td>
<td>1.13 (0.09)$^a$</td>
</tr>
<tr>
<td>Peak $F_v$, N</td>
<td>786.1 (101.5)</td>
<td>854.9 (137.6)</td>
<td>918.9 (129.6)</td>
<td>1,060.1 (242.3)$^{b,c}$</td>
</tr>
<tr>
<td>Contact time, ms</td>
<td>453 (56)</td>
<td>432 (51)</td>
<td>420 (43)</td>
<td>410 (49)</td>
</tr>
<tr>
<td>Braking phase</td>
<td>236 (36)</td>
<td>215 (27)</td>
<td>207 (24)$^a$</td>
<td>195 (27)$^b$</td>
</tr>
<tr>
<td>Push-off phase</td>
<td>217 (28)</td>
<td>217 (27)</td>
<td>213 (25)</td>
<td>215 (27)</td>
</tr>
</tbody>
</table>

Values are means (SD); $n = 8$. $F_v$, vertical force; DJ1, DJ2, DJ3, and DJ4: drop jumps at 50, 75, 100, and 120% of optimal drop height, respectively. Significantly different from DJ1 at $^aP < 0.05$ and $^bP < 0.01$. Significantly different from DJ2 at $^cP < 0.05$ and $^dP < 0.01$. $^e$Significantly different from DJ3 at $P < 0.01$. 

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DISCUSSION

Previous investigations have suggested that the patterns of Lfa change during SSC exercises are muscle and intensity (DH and rebound effort) specific (10, 11, 13). The present work represents the first attempt to compare the fascicle behavior in synergistic muscles (MG and Sol) during different SSC exercises, including very high-impact load (DH) conditions. In the present DJ movements, different patterns of Lfa changes were observed between the MG and Sol muscles. The Sol fascicles demonstrated SSC behavior during the contact phase of all DJ conditions. Moreover, with increasing DH, where the peak Fa increased and the contact time during the braking phase decreased, the amplitude of Sol fascicle stretch showed no clear difference, while EMG activation increased. The MG fascicles exhibited comparatively different behavior during the DJ (Fig. 3), especially during the late-braking phase. With increasing DH, which represents much higher impact loads than those measured during walking (12), the MG fascicles exhibited less shortening during the late-braking phase, until they were suddenly stretched in DJ4 (also DJ3 in some subjects) (Fig. 3, Table 2). The present results thus emphasize that MG fascicle behavior varies during the braking phase of DJ, depending on DH, and that the fascicles of MG and Sol muscles show different behavior during the braking phase of DJ. This is despite the fact that the EMG activation of both muscles tended to increase similarly from DJ1 to DJ3 (Fig. 2). These results thus clearly indicate the existence of muscle-specific fascicle behavior (MG and Sol) that is also dependent on DH.

To enable examination of the influence of DH on Lfa changes during the braking phase, Fig. 6 plots these attributes against each other for this particular phase. The length change patterns tend to have an opposite quadratic relationship with the prestretch intensity (dropping speed). In the MG muscle, there may be a critical level of the stretch load (DH), beyond which the MG fascicles lose their ability to tolerate the imposed load (Fig. 6A). It is interesting to note that the result shown in Fig. 6A is almost identical to that presented in a previous report (13), despite the fact that the SSC exercise differed between these studies. These results further emphasize the difference in fascicle behavior of MG and Sol during DJ and again suggest that there may be specific length-change patterns of the MG and Sol fascicles, depending on the DH.

The observed difference in fascicle behavior between the two muscles is interesting from several points of view. One may initially think that the results can be explained in terms of pure anatomical differences between the muscles. The MG is a biarticular muscle and performs unique functions, such as transferring energy and power flow from one joint to another during human locomotion (c.f., Refs. 4, 24, 25). The results presented in Figs. 3 and 4 highlight the differences between mono- and biarticular muscles, whereby the stretched LMTU was significantly shorter in MG than in Sol for all DH conditions (Figs. 3 and 4). At the fascicle level, the stretched Lfa was also shorter in MG than in Sol (Fig. 3, Table 2). Figure 7 shows the relation between the absolute/relative MTU and fascicle stretch amplitudes from contact to the end of the braking phase in both muscles. If the MTU stretch is measured in absolute terms, then the fascicles are less stretched in MG than in Sol (Fig. 7). However, it may be possible that the fascicles behave in a similar way if the relative values are considered (Fig. 7B). Consequently, these results cannot confirm that the smaller MTU stretch in the MG muscle is a significant factor regarding MG fascicle behavior during DJs.

The functional difference between the MG and Sol muscles warrants further attention based on the present results. In the present study, the TT stretch amplitudes were greater in MG than in Sol. In addition, in Sol the TT stretch amplitudes were significantly smaller than the MTU stretch amplitudes in all DJ conditions. The MG muscle showed the opposite result in this regard (Fig. 4). This is in line with a previous study that compared MG and VL muscles (13). Furthermore, the present study showed that the difference between the TT and MTU stretch amplitudes in MG became smaller with higher DH conditions, but this was not the case in Sol (Fig. 4). In terms of the calculated TT strain during the contact of DJ, MG showed no significant variation between conditions, whereas Sol showed significantly higher strain values with increasing DH (Fig. 5). These results could be indicative of different roles that the MG and Sol muscles play during locomotion. For example, they may be related to the idea of biarticular muscle function proposed by van Ingen Schenau et al. (24), which suggests that a biarticular muscle may be involved in the fine regulation of net torque distribution over two joints, whereas monoarticular muscles act mainly as force or work generators.

When a similar exercise protocol using different contact times (bilateral DJ) was used to observe MG fascicle behavior (13), the results were identical to those of the present study. However, the Sol muscle was not investigated in the previous...
In the present study, the behavior of Sol differed from MG in several ways. In the preactivation and braking phases, muscle activity tended to be higher in DJ4 than DJ3 in Sol, but not in MG (Fig. 2). At the end of the braking phase, the corresponding Sol $L_{fa}$ was shorter in DJ4 than in DJ3 (the only significant difference was between DJ2 and DJ4, Table 2). This suggests that the Sol muscle is still able to function “normally” without any additional rapid $L_{fa}$ changes (MG).

It would be beneficial to discuss the results from the perspective of neural influences. The results presented in Fig. 3 and Table 2 may help to clarify the findings obtained in studies in which running and various intensity hopping exercises were used. Voigt et al. (27) reported that, in the Sol muscle, the SLR in SSC is very apparent and easier to record than in the MG muscle during submaximal hopping. In contrast, Dietz et al. (2) observed the SLR responses in MG during running, and Moritani et al. (22) reported that the amplitude of H-reflex modulation was higher in MG than in Sol during maximal effort hopping. In the present study, the fascicles of MG shortened during the braking phase of the DJ1 and DJ2 conditions, whereas those of Sol were stretched (Fig. 3). However, with higher impact loads (DH), the MG fascicles were stretched during the late-braking phase (in DJ4) (Fig. 3), whereas the Sol fascicles exhibited similar behavior (stretching-shortening) in all DH conditions (Table 2). These results can partially explain the different results of Voigt et al. (27), Dietz et al. (2), and Moritani et al. (22, 23). One may conclude that, during the braking phase of DJs, DH- and muscle-specific $L_{fa}$ changes may influence the stretch-induced muscle activation.

It has been suggested that, in extremely high DJ exercises, inhibitory effects from the Golgi tendon organ may be operative. It would, therefore, be useful to know if there are any differences in inhibitory inputs to the two muscles in DJs. In the present results, the MG aEMG did not increase from DJ3 to DJ4 (Fig. 2) during the braking phase, but the MG fascicles were stretched during the braking phase in DJ4 (Figs. 3, 6, and 7). During the same phase in the Sol muscle, however, the aEMG increased, and the stretch amplitude of the Sol fascicles...
showed no difference between DJ3 and DJ4, or was actually lower in DJ4 (Figs. 6 and 7, Table 2). One may speculate that, while the MG muscle receives less facilitatory Ia afferent input [the muscle spindle content is greater in Sol than MG (17)], the same amount of Ib input would have greater inhibitory influences on the MG than on the Sol muscle. Therefore, the difference in muscle spindle content between the respective muscles may partially account for the observed differences in fascicle behavior in response to changes in DH. This assumption may also be influenced by additional unknown factors, such as the possibility that the induced stretch loads have equal excitatory effects on the activation of Ib afferents in both muscles. However, it is still difficult to explain how the possible inhibitory influences, for example, from the Golgi tendon organs, would operate differently between the two synergistic muscles.

In the previous study (13), our major argument was that the “yielding” that occurred in conjunction with fascicle lengthening was due to sudden cross-bridge detachment in high DH conditions. However, it is still difficult to explain how the possible inhibitory influences, for example, from the Golgi tendon organs, would operate differently between the two synergistic muscles.

### Table 2. The fascicle length at the contact, the end of the braking phase, and take-off moments during the contact of drop jumps

<table>
<thead>
<tr>
<th></th>
<th>Contact</th>
<th>End of Braking Phase</th>
<th>Take-off</th>
</tr>
</thead>
<tbody>
<tr>
<td>MG</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DJ1</td>
<td>3.76 (0.39)*</td>
<td>3.54 (0.27)†</td>
<td>3.27 (0.60)‡§</td>
</tr>
<tr>
<td>DJ2</td>
<td>3.62 (0.40)*</td>
<td>3.51 (0.27)†</td>
<td>3.17 (0.40)‡§</td>
</tr>
<tr>
<td>DJ3</td>
<td>3.57 (0.41)*</td>
<td>3.48 (0.27)</td>
<td>3.21 (0.42)‡§</td>
</tr>
<tr>
<td>DJ4</td>
<td>3.25 (0.31)*</td>
<td>3.38 (0.28)†</td>
<td>3.17 (0.26)§</td>
</tr>
<tr>
<td>Sol</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DJ1</td>
<td>4.41 (0.99)</td>
<td>5.04 (0.96)†</td>
<td>4.29 (0.96)§</td>
</tr>
<tr>
<td>DJ2</td>
<td>4.35 (1.05)</td>
<td>5.05 (0.96)†</td>
<td>4.44 (0.95)§</td>
</tr>
<tr>
<td>DJ3</td>
<td>4.35 (1.06)</td>
<td>5.02 (0.94)†</td>
<td>4.43 (1.01)§</td>
</tr>
<tr>
<td>DJ4</td>
<td>4.34 (1.04)</td>
<td>4.97 (0.92)†</td>
<td>4.52 (0.84)§</td>
</tr>
</tbody>
</table>

Values are means (SD) in cm. MG, medial gastrocnemius; Sol, soleus.

*Significantly different from DJ1 to other DJs at $P < 0.05$.
†Significantly different from the contact at $#P < 0.05$ and $##P < 0.01$.
‡Significantly different from end of the braking phase to the take-off at $P < 0.05$. 
§Significantly different from DJ1 to all other DJs at $P < 0.05$. 
$\dagger$Significantly different from DJ1 to other DJs at $P < 0.05$. 
$\ddagger$Significantly different from the contact at $P < 0.05$. 
$\S$Significantly different from DJ1 to other DJs at $P < 0.05$. 

Fig. 4. Amplitudes of stretch (top) and shortening (bottom) in the braking and push-off phases for MTU and TT of the MG and Sol muscles, for all dropping conditions (DJ1, DJ2, DJ3, and DJ4). Significantly different between conditions at $*P < 0.05$ and $**P < 0.01$. Significantly different between MTU and TT at $#P < 0.05$ and $##P < 0.01$.

Fig. 5. Calculated peak TT strains of the MG and Sol during DJs under the different DH conditions. The bars show group means + SD. The strain was calculated from the length at the initial contact to the length at the peak TT stretch during contact divided by the TT length at the initial contact. There was a significant increase in the TT strain of Sol when the DH increased ($*P < 0.05$).
conditions. The present results show that the MG fascicles were stretched during the braking phase of DJ4 (Fig. 3). The contact times of the braking phase were twice as long in the present study (200 ms) compared with the previous one (130 ms). Therefore, the sudden cross-bridge detachment may not have occurred to the same extent as in the DJ condition of the previous study (13). This can be seen from the slopes of the fascicle stretch, which were approximately twice as steep in the previous study (13). It has been suggested that the reduction in DJ performance during the extremely high DH condition can be affected by neural inhibition, as well as by mechanical cross-bridge slipping (or detachment) (c.f., Ref. 13). In the present study, inhibitory effects from the Golgi tendon organ, if present, may have been mainly operative in the performance reduction that was observed in the long-contact, extremely high-DJ condition (DJ4).

Whatever the possible mechanism, the observed intermuscular differences in fascicle behavior are very important findings of the present study. The results suggest that the whole concept of the SSC of muscle function should be critically assessed, especially regarding the way in which fascicles interact with TT during normal locomotion. An equally important consideration is that the fascicle behavior is task dependent, at least in some muscles. For example, there is a preferential and movement-phase-dependent neuromuscular activation within the synergistic human ankle extensor muscles (23). In addition, and as shown in the present study, the preactivation may be DH dependent (see also Refs. 11, 13). There are, however, reports in the literature that question the interdependence of DH and EMG preactivation (1). Dietz (3), while supporting the idea of intensity-dependent preactivation, suggested that foot positioning and anticipation of the moment of ground contact may be critical factors for preactivation.
In summary, the results of the present study highlight differences in fascicle behavior of synergistic muscles (MG and Sol) during DJ exercises. Moreover, the fascicle behavior in response to changes in DH differed between the two muscles, whereas the EMG activities of these muscles showed a clear relationship with DH. Although some of these observations had been made previously to a certain degree (11, 13), the present comparison with simultaneous recording of two synergistic muscles serves to further emphasize the above-mentioned differences (4, 9, 21, 25).

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