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Gastrocnemius muscle fascicle behavior during stair negotiation in humans

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Spanjaard M, Reeves ND, van Dieën JH, Baltzopoulos V, Maganaris CN. Gastrocnemius muscle fascicle behavior during stair negotiation in humans. *J Appl Physiol* 102: 1618–1623, 2007. First published December 21, 2006; doi:10.1152/japplphysiol.00353.2006.—The aim of the present study was to establish the behavior of human medial gastrocnemius (GM) muscle fascicles during stair negotiation. Ten healthy male subjects performed normal stair ascent and descent at their own comfortable speed on a standard-dimension four-step staircase with embedded force platforms in each step. Kinematic, kinetic, and electromyographic data of the lower limbs were collected. Real-time ultrasound scanning was used to determine GM muscle fascicle length changes. Musculotendon complex (MTC) length changes were estimated from ankle and knee joint kinematics. The GM muscle was mainly active during the push-off phase in stair ascent, and the muscle fascicles contracted nearly isometrically. The GM muscle was mainly active during the touch-down phase of stair descent where the MTC was lengthened; however, the GM muscle fascicles shortened by ~7 mm. These findings show that the behavior and function of GM muscle fascicles in stair negotiation is different from that expected on the basis of length changes of the MTC as derived from joint kinematics.

biomechanics; muscle mechanics; ultrasound; musculotendon complex; tendon

STAIRS ARE REGULARLY ENCOUNTERED in daily life and negotiating stairs is a more physically demanding task than level walking (25, 27). The demands placed on the musculoskeletal system when ascending or descending stairs are not fully understood despite some research on stair negotiation (1, 12, 13, 19, 21, 25, 26, 28, 29). The ankle and knee extensor muscles are very important in stair negotiation, because they provide the moments and power needed to perform an ascent and to control a descent (1, 12, 13, 19, 21, 25, 26, 28, 29). In stair descent, the joint moment at the ankle can be as high as ~75% of a maximal voluntary contraction (MVC), whereas this is only ~30% at the knee (24). Also, during stair ascent, the ankle joint appears to play a key role, with moments in ascent of comparable magnitude to descent (19).

At ankle plantar flexor moments higher than 70% of MVC, the soleus muscle is maximally activated (17), and thus only the gastrocnemius muscle allows further modulation of the plantar flexor moment. Hence, gastrocnemius muscle function may be crucial in stair negotiation. This is supported by the strong modulation of the electromyographic (EMG) amplitude of the medial gastrocnemius (GM) muscle, compared with a much less pronounced modulation of the EMG amplitude of the soleus muscle in both ascent and descent (19). McFadyen and Winter (19) stated that the ankle extensor muscles act eccentrically in stair descent to dissipate a substantial amount of energy and act concentrically in ascent to produce a major part of the positive work required. However, because of the biarticular nature of the gastrocnemius musculotendon complex (MTC), it is difficult to predict its function. Furthermore, even when the kinematics of both the knee and ankle joints are taken into account to estimate gastrocnemius MTC length changes (5, 20), this may not adequately reflect the behavior of the contractile machinery. Because of elastic tendon structures and muscle pennation, the muscle fascicles do not necessarily undergo the same length changes as the whole MTC (4, 11, 15).

Real-time ultrasonography allows reliable and noninvasive dimensional measurements of intact human fascicles (10, 18, 23). Using this technique, it has been shown, that, in level walking, the GM muscle fascicle length stays relatively constant when the muscle is active during single support, while the tendon is being stretched to release elastic energy during push-off (4). This behavior is preserved when walking up and down slopes of 10% (15). Thus, across different modes of locomotion, this muscle acts more or less isometrically, which has been suggested to be energetically efficient (4). In the modes of locomotion studied heel landing is common, whereas in stair negotiation forefoot landing is commonly observed. This may imply that the previous findings on GM muscle behavior do not generalize to stair negotiation, which might account in part for the demanding nature of this activity.

The purpose of this study was to establish the behavior of the human GM muscle fascicles during stair negotiation. We hypothesized that GM muscle fascicles would remain at constant length while the muscle was active in both ascent and descent, and we examined the relation between muscle fascicle and MTC length changes.

METHODS

Subjects. Ten healthy young men [age 24.9 ± 3.2 yr; body mass 79.9 ± 9.1 kg; height 1.82 ± 0.06 m (means ± SD); leg length (distance between the medial malleolus and spina iliaca anterior superior) 95.7 cm, ranging from 86 to 102.5 cm] volunteered to participate in the experiment. All volunteers gave their written consent to participate after approval was gained from the ethics committee of the Institute for Biophysical and Clinical Research into Human Movement at the Manchester Metropolitan University.

Measurements. Subjects walked up and down a custom-built steel staircase of four steps (Fig. 1). The steps were independently mounted on the floor, and their dimensions were 170 mm (height) × 280 mm (length) × 900 mm (width).

Kinetic data during stair ascent and descent were collected using four force plates. Three force plates (model Z17068, Kistler; 270 ×

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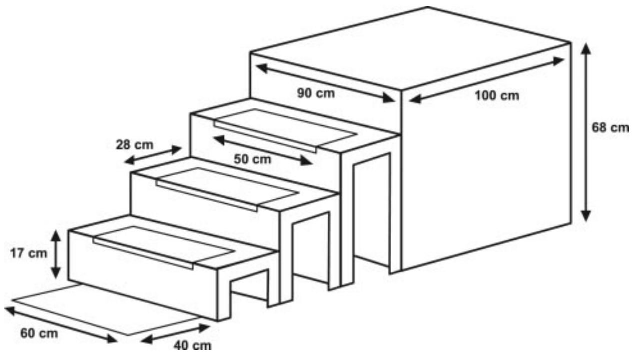

Fig. 1. The custom-built steel staircase with step dimensions. Force plates are embedded in the first 3 steps and in the floor in front of the staircase. The 4 steps are independently mounted in the floor.

500 mm) with built-in amplifiers were embedded in the first three steps (from the ground), and one force plate (model 9253A, Kistler; 400 × 600 mm) with an external amplifier (model 9865C, Kistler) was embedded in the floor, in front of the staircase.

Kinematic data were acquired using a nine-camera VICON 612 system (VICON motion systems, Oxford, UK). Retroreflective markers were placed on bony landmarks, directly on the skin, or on appropriate tight-fitting clothing using double-sided tape. In total, 34 markers were placed on the body according to the standard "plug-in-gait" model of the VICON system implemented in the Bodybuilder software module for three-dimensional segment modeling and calculation of upper and lower limb kinematics. Four markers were placed on the head: left and right temple, front of the head, and left and right on the back of the head (using a headband). Two markers were placed on the spinal column (C_7 and T_{10}), one in the center of the right scapula, and two on the sternum (1 cranial and 1 caudal). Three markers were placed on the pelvis, one on the sacrum and one on each spina iliaca anterior superior. Upper extremity markers were placed on the shoulder (acromion), elbow (brachial lateral epicondyle), two on the wrist (radial and ulnar directions using a wrist bar), and one on the hand (second metacarpal). Lower extremity markers were placed on the lateral thigh (extended from the thigh using a wand marker), knee (femoral lateral epicondyle), lateral side of the lower leg (extended using a wand marker), ankle (lateral malleolus), and foot (2 markers: 1 back of the heel and 1 on the second metatarsal bone). From the marker coordinates, knee and ankle joint angles were calculated. Knee joint angle was defined as the angle between the lower leg and a line through the thigh, so a straight leg corresponds to 0° knee joint angle. Positive angles indicated knee flexion. Ankle joint angle was defined as the angle of the foot with the lower leg, with 0° defined as the ankle at the neutral position. Positive angles indicated dorsiflexion, and negative angles indicated plantar flexion.

The GM muscle behavior was assessed in vivo from ultrasound scans recorded in real time during the stair negotiation trials. For these measurements, a linear 7.5-MHz probe (UST-579T-7.5, Aloka SSD-5000, Tokyo, Japan) with a 60-mm field of view was tightly secured around the left lower leg in the midsagittal plane of the GM muscle with a custom-built fixation device. The ultrasound scanning was synchronized with the kinematic and kinetic data using an external trigger.

The electrical activity of the GM muscle of the left leg was recorded using a Bagnoli EMG system (Delsys, Boston, MA). The recording electrodes were placed proximal to the ultrasound scanning probe in the midsagittal plane of the muscle. The sampling frequency of the EMG recordings was 2,000 Hz.

To obtain an estimate of the magnitude of GM muscle EMG activity during stair negotiation relative to a plantar flexion MVC, we performed measurements in a subsample of six participants. EMG activity was recorded during stair negotiation and during MVC at 0° ankle joint angle. Participants performed five stair ascent and five stair descent trials on the previously described staircase, and they were then asked to perform MVCs while lying prone on the bench of an isokinetic dynamometer (Cybex Norm, New York, NY). For these measurements, EMG system, setup, and placement of electrodes were maintained constant.

Protocol. Before the experiment, a number of anthropometric measurements were taken for each subject to scale the generic human plug-in-gait model in the VICON software (Oxford Metrics). Subsequently, the markers and EMG electrodes were positioned, and data collection was initiated.

Subjects performed three trials of stair descent and three trials of stair ascent at a self-selected pace, barefoot, in a step-over-step fashion. Subjects stood still on top of the platform (stair descent), or on the ground just in front of the ground force plate (stair ascent), and started every trial with their right foot. The trial ended when the subject was on the top platform, or on the ground off the force plate, with the two feet together. All six trials were recorded, but only the last trial in each direction was analyzed to ensure that the subjects were familiarized with the tests.

Data analysis. The step between the first touch-down point of the left foot and the second touch-down point of the left foot (2 steps above/below) was considered a steady-state step (1). From marker positions and force plate data, VICON software was used to calculate kinematics and kinetics in three dimensions using the plug-in-gait model. The kinematic and kinetic data of the ankle and knee, from the steady-state step, were transported from VICON workstation software to Matlab (The Mathworks, Natick, MA).

The GM muscle fascicle lengths were measured from the sonographs recorded. On each ultrasound frame during the steady-state step, three points were located manually using Matlab: one point at the end of the fascicle on the superficial aponeurosis, a second point at the end of the same fascicle on the deep aponeurosis, and a third point along the deep aponeurosis to allow calculation of the pennation angle. From these three points, the fascicle length and pennation angle were calculated. The muscle fascicle length was measured using the assumption that the fascicular trajectory was linear. The pennation angle was the angle that the fascicle made with the deep aponeurosis. The fascicle length measured in a standing position was the reference length for each subject. To account for individual differences, the fascicle length change was calculated as the difference between the reference length and the measured fascicle length during the steady-state step.

The equations by Menegaldo et al. (20) were used to calculate the GM MTC length change (muscle plus free tendon and aponeurosis in both distal and proximal ends) using ankle and knee joint displacements. The difference between the MTC length change and the fascicle length change, taking the pennation angle into account, was calculated as an estimate of the whole tendon (free tendons plus aponeuroses) length change (Fig. 2).

The EMG signals were band-pass filtered (20–450 Hz) using the Delsys software, rectified, smoothed (using a 2nd-order low-pass 5-Hz bidirectional filter) and normalized to their own maximum (EMG_{max}) during the phase analyzed, using Matlab. To study muscle length changes during periods of muscle activity, we determined these from the EMG signal taking into account an electromechanical delay estimated at 24 ms (2, 22). Foot contact phases were separated by bilateral foot contact and lift-off events. The foot contact phase where the peak EMG amplitude was obtained was used to further analyze the fascicle length data. During this phase, the velocity of fascicle length changes was averaged. Averaged fascicle contraction velocities were compared with zero using a one-sample *t*-test to determine whether shortening or lengthening occurred.

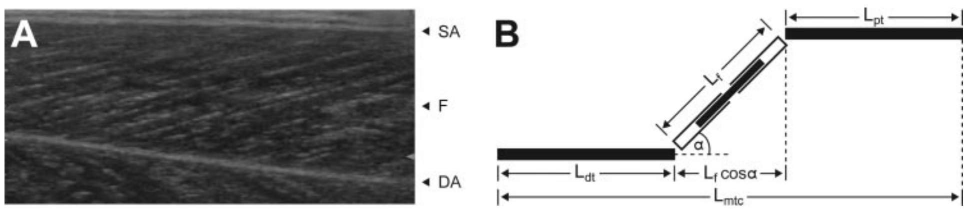

Fig. 2. *A*: typical sonograph of the medial gastrocnemius (GM) muscle during the stance phase of stair descent. GM muscle fascicles (F) lie in between and in parallel with thin white lines, which represent interfascicular tissue. GM muscle fascicles run between the superficial aponeurosis (SA) and the deep aponeurosis (DA). *B*: schematic representation of the musculotendon model used. L_f, fascicular length; α, pennation angle; L_{pt}, proximal tendon (free tendon and aponeurosis) length; L_{dt}, distal tendon (free tendon and aponeurosis) length; L_{mtc}, the musculotendon complex length. L_f and α are measured using ultrasound imaging (see *A*). L_{mtc} is calculated from the kinematic data from ankle and knee joint (see text). Total tendon length ($L_{pt} + L_{dt}$) is estimated by the length difference in L_{mtc} and $L_f$cosα. [Adapted from Fukunaga et al. (4).]

RESULTS

Stair ascent. Averaged stride cycle time for ascent was 1.3 s, ranging from 1.03 to 1.42 s. Results for the ascending trials are shown in Table 1 and Fig. 3. In the first part of the stance phase during double support, MTC length and fascicle length both increased slightly and in parallel, resulting in a zero length change of the tendon. After lift-off of the contralateral leg, in the first part of single support, the GM muscle fascicles lengthened, but not as much as the whole MTC, which lengthened due to knee extension. In the second part of single support stance, the GM muscle became active and the fascicle length remained constant, while MTC length increased even further, thus stretching the tendon. After the contralateral leg touched down again, the fascicles shortened rapidly, and so did the MTC, following the burst in GM muscle activity and the decrease in external force on the foot. This concentric activity resulted in a peak ankle moment, leading to push-off. During the swing phase, in the absence of external force on the foot, GM muscle fascicle shortening followed the MTC length change, until ankle dorsiflexion stretched the GM muscle fascicles.

The GM muscle activity peaked during the lift-off phase (second double support phase). While the EMG amplitude remained over 30% EMG_{max}, the GM muscle fascicles shortened by 0.02 cm per 1% of the stride cycle, which was, however, not significantly different from zero ($P = 0.14$). Hence, during lift-off, the GM muscle fascicles can be considered to have contracted almost isometrically.

Stair descent. Averaged stride cycle time for descent was 1.2 s, ranging from 1.15 to 1.45 s. Results for descending trials are shown in Table 2 and Fig. 4. During the first double support phase, immediately after touch-down, the GM muscle fascicles shortened rapidly, coinciding with a high level of GM muscle activity. At the same time, MTC length increased, resulting in a considerable tendon stretch. After lift-off of the contralateral leg, during the single-support phase, the muscle fascicles were elongated passively or with very low muscular activity (evidenced by low GM muscle EMG activity), while the tendon shortened. During the second double support stance phase, after touch-down of the contralateral leg, GM muscle fascicle length stayed relatively constant, while both the tendon and MTC length decreased slightly due to knee flexion. Toward lift-off, ankle dorsiflexion released the toe from the step. During the swing-phase the GM muscle fascicles shortened passively as the ankle joint rotated in the plantar flexion direction, following the MTC length, until just before touch-down, when the GM muscle became active and the GM muscle fascicles actively shortened.

The GM muscle was mainly active during the touch-down phase (first double-support phase). During this phase, the GM muscle activity remained over 43% EMG_{max} and the GM fascicles shortened by 0.05 cm per 1% of the stride cycle, which was significantly less than zero ($P < 0.005$). Hence, during touch-down, the GM muscle fascicles actively shortened even though the MTC lengthened.

Normalization of EMG data to MVC showed that peak EMG value was 64% of MVC during stair ascent and 50% of MVC during stair descent.

DISCUSSION

The aim of the present study was to establish the behavior of human GM muscle fascicles during stair negotiation. The two main findings of the study are the near isometric behavior of the GM muscle fascicles during stair ascent and the shortening of the GM muscle fascicles during stair descent. Both findings are in contrast to our hypothesis and show that the length change of muscle fascicles does not follow the MTC length change.

Table 1. *Gastrocnemius muscle fascicle length during stair ascent*

	Percentage of Stride Length*				
	0%	14%	50%	63%	100%
Muscle fascicle length, cm	5.0±0.7	5.1±0.7	5.7±0.8	5.2±0.8	4.9±0.8
Muscle fascicle length change, cm†	−1.5±0.3	−1.3±0.4	−0.8±0.6	−1.2±0.6	−1.5±0.5
MTC length change, cm	−1.4±0.2	−1.2±0.2	−0.1±0.2	−0.6±0.2	−1.5±0.2
Tendon length change, cm	−0.1±0.2	−0.0±0.2	−0.6±0.4	−0.5±0.4	0.1±0.3

Values are means ± SD. MTC, musculotendon complex. *0, 14, 50, 63, and 100% correspond, respectively, to touch-down of the analyzed leg, lift-off of the contralateral leg, touch-down of the contralateral leg, lift-off of the analyzed leg, and touch-down of the analyzed leg. †Difference between measured fascicle length during stair negotiation and measured fascicle length during stance.

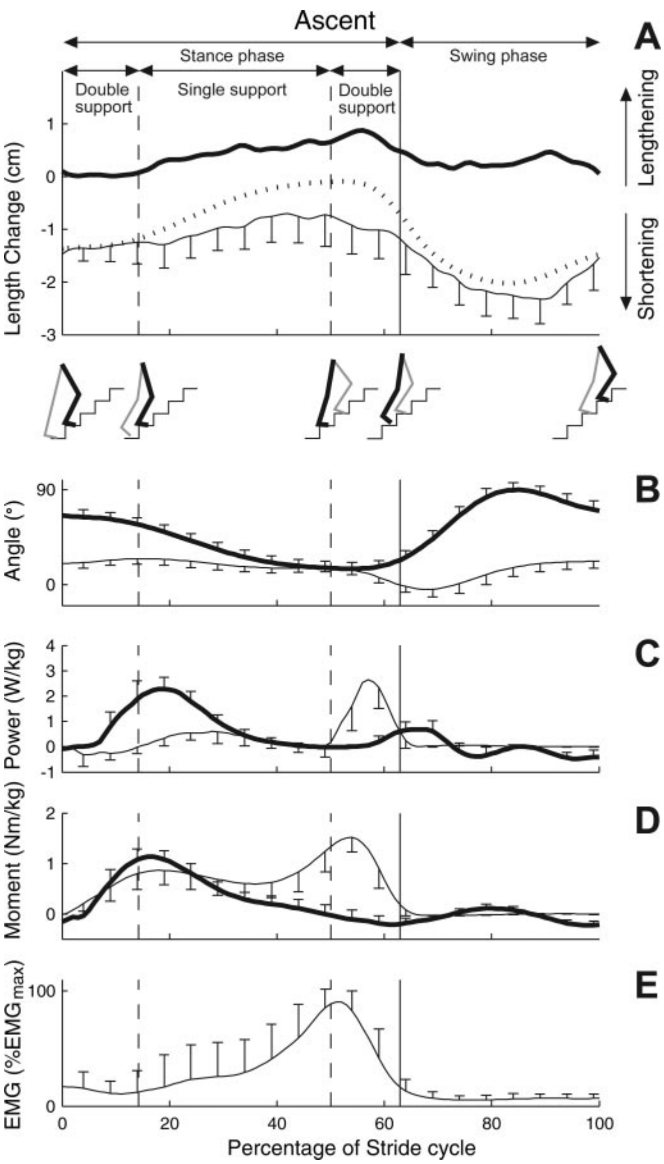

Fig. 3. *A*: mean changes in GM muscle fascicle length (thin line), musculotendon complex length (dashed line), and tendon length (thick line) during ascent ($n = 10$). SD of the changes in GM muscle fascicle length is shown by error bars. Values are relative to the reference position (standing still). Percentage of stride length is shown on the *x*-axis, beginning with touch-down of the left (analyzed) leg. *B*: mean ankle (thin line) and knee (thick line) joint angles during the same stride cycle ($n = 10$). *C*: mean ankle (thin line) and knee (thick line) power values during the same stride cycle ($n = 10$). *D*: mean ankle (thin line) and knee (thick line) moment values during the same stride cycle ($n = 10$). *E*: mean EMG of the GM muscle ($n = 9$) during the same stride cycle, normalized to the maximum value (EMG_{max}) reached during this stride cycle. EMG data from 1 subject are missing because offline analysis showed that the acquisition system failed during that trial. For clarity, error bars are pointing in 1 direction.

The kinematic results of both the ascending and descending trials show a very small intersubject variation and are in line with the results from other studies during stair negotiation (16, 19, 25, 30). Although the variation was larger for the kinetic results, both the ankle and knee joint moment and power values also are similar to the results from previous studies (19, 25). The variation in EMG results is rather large; however, the muscle activity bursts can be distinguished easily, and were, again, similar to the results of other studies (19, 29).

Stair ascent. It has previously been shown that during level walking and walking on an incline (+10%), GM muscle fascicles maintain a near-constant length during the phase in which this muscle is active (4, 8, 15). The present results show that the length modulation of the MTC (Fig. 3) is about twice as much as that of the muscle fascicles. Therefore, the MTC length change is not produced by GM muscle fascicle length change alone, and substantial tendon length changes occur. The results also show that, when the GM muscle becomes active around the second double-support phase during stair ascent, just before lift-off, the fascicles remain near isometric. This suggests that the GM muscle hardly produces any work. However, Fig. 3 shows a peak in ankle joint power during this phase. This suggests that other ankle plantar flexor muscles, most likely the soleus muscle, are responsible for this peak in ankle joint power. This is supported by McFadyen and Winter (19), who report soleus EMG activity during this part of the stride cycle. Another possibility is that the power at the knee, produced by the knee extensors, is transferred to the ankle through the biarticular GM muscle. Furthermore, the knee extensors likely produce work during the first double-support phase and early single-support phase. This notion is supported by the peak in knee joint power seen during the early single-support phase in the present study (Fig. 3) and the peak in vastus lateralis muscle activity around the same time reported in the literature (19, 29). During the landing phase of stair ascent, the foot is placed horizontally on the step, and hardly any plantar flexion power is produced until just before lift-off.

Stair descent. It is generally believed that muscles contract eccentrically and act as brakes to absorb energy during walking down a declined surface. However, Lichtwark and Wilson (15) showed that, when walking down a slope (−10%), the GM muscle fascicles contract nearly isometrically. The present results from stair descent show that although the MTC is stretched and thus absorbs energy as a whole, the GM muscle fascicles actually shorten considerably during touchdown and the first double-support phase. This active shortening of GM muscle fascicles will produce energy that will be stored in the tendon, producing an ankle joint moment sufficient to overcome the dorsiflexion acceleration caused by gravity.

In stair descent, heel strike was absent and subjects landed on their forefoot, which makes it a different task than walking down a declined surface. As such, the landing phase of stair descent appears to some extent comparable to countermovement exercises, such as described by Kawakami et al. (11). These authors showed that during the plantar flexion countermovement, GM muscle fascicles acted almost isometrically, thus allowing storage of elastic energy in the tendon, consequent release of which would enhance exercise performance. However, during countermovements that are more strenuous, such as drop jumping, the GM muscle fascicles were found to shorten during the touch-down/push-off phase, while the MTC lengthened (9). This shortening of GM muscle fascicles during MTC stretch was also seen in in situ experiments in rat muscles (3) and in freely walking cats (6) and is similar to GM muscle fascicle behavior during the touch-down phase of stair descent as seen in the present study. However, this is not always the case. Ishikawa et al. (9) showed that the vastus lateralis muscle fascicles actively lengthened during MTC lengthening in drop

Table 2. *Gastrocnemius muscle fascicle length during stair descent*

	Percentage of Stride Length*				
	0%	13%	50%	63%	100%
Muscle fascicle length, cm	4.3±0.8	3.5±0.5	5.8±0.8	5.6±0.6	4.3±0.7
Muscle fascicle length change, cm†	−2.2±0.4	−2.9±0.2	−0.6±0.4	−0.8±0.4	−2.2±0.4
MTC length change, cm	−1.3±0.2	−0.4±0.1	−1.2±0.2	−1.9±0.1	−1.3±0.3
Tendon length change, cm	−0.9±0.2	2.5±0.1	−0.5±0.2	−1.1±0.2	0.8±0.1

Values are means ± SD. *0, 13, 50, 63, and 100% correspond respectively to touch-down of the analyzed leg, lift-off of the contra-lateral leg, touch-down of the contra-lateral leg, lift-off of the analyzed leg and touch-down of the analyzed leg. †Difference between measured fascicle length during stair negotiation and measured fascicle length during stance.

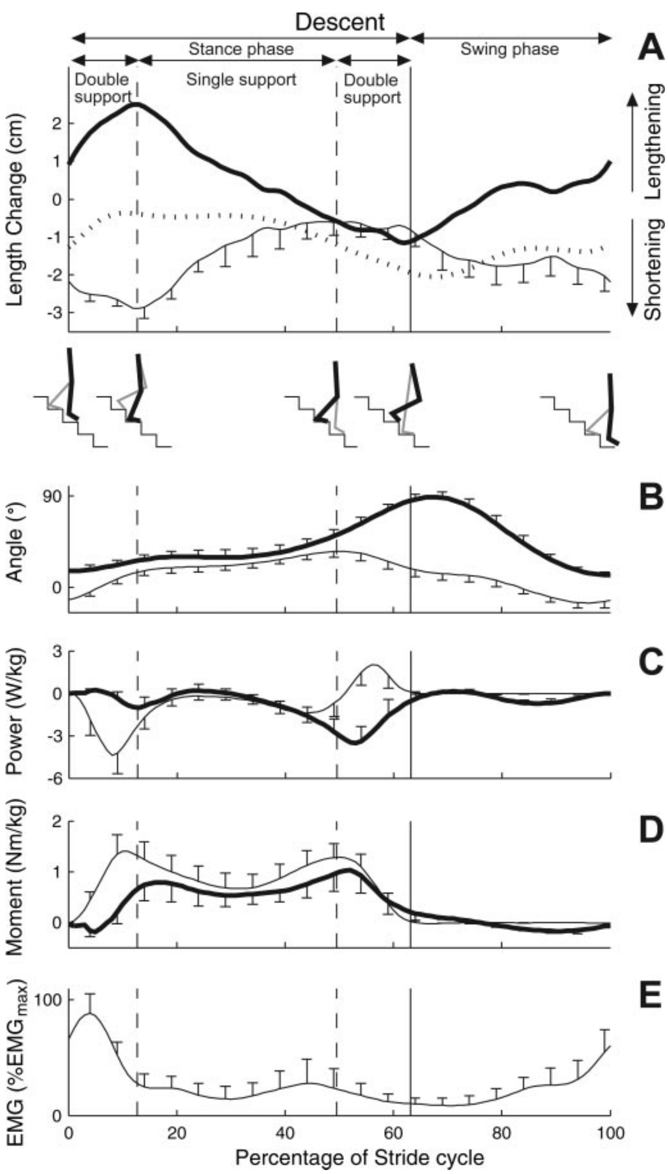

Fig. 4. *A*: mean changes in GM muscle fascicle length (thin line), musculotendon complex length (dashed line) and tendon length (thick line) during descent. SD of the changes in GM fascicle length is shown by error bars. Values are relative to the reference position (standing still). Percentage of stride length is shown on the x-axis, beginning with touch-down of the left (analyzed) leg. *B*: mean ankle (thin line) and knee (thick line) joint angles during the same stride cycle. *C*: mean ankle (thin line) and knee (thick line) power values during the same stride cycle. *D*: mean ankle (thin line) and knee (thick line) moment values during the same stride cycle. *E*: mean EMG of the GM muscle during the same stride cycle, normalized to the maximum value (EMG_{max}) reached during this stride cycle. For clarity, error bars are pointing in 1 direction (n = 10).

jumping, while the GM muscle fascicles shortened. In addition, it has been shown that fascicles of the soleus muscle behave in a different way than GM muscle fascicles during locomotion (8). It can be concluded that muscle fascicular shortening during MTC lengthening can occur during short, intense eccentric actions of muscles with a long compliant tendon. It might be that only biarticular muscles show this behavior, but more research is needed to confirm this. This concentric muscle fascicle behavior during an "eccentric" movement leads to internal energy losses and in this respect is less efficient than isometric behavior. However, the magnitude of the impact force during stair descent may not allow this efficient isometric strategy. It can, therefore, be hypothesized that the GM muscle is regulating the length of its tendon to provide the required stiffness around the ankle in the transition from foot down to single support. Apparently, stiffening of the ankle joint achieved through contracting the muscle is required for a controlled dorsiflexion, and this requirement probably dominates over (or cancels out) energetic efficiency criteria in performing the movement.

After touch-down, during single-support stance, the GM muscle fascicles are stretched while the EMG shows little or no activity. The energy that was stored in the tendon is probably dissipated here. Although muscle fascicles can produce considerable forces at low electrical activity when they are lengthened, the decreasing tendon length indicates that the ankle moment is low in this part of the stride cycle and force in the fascicles decreases. The knee extensors are active in this part of the stride cycle (19, 29), probably contracting eccentrically and also dissipating energy.

Methodological considerations in the study include the way that fascicular, tendon, and MTC lengths were obtained. The fascicular trajectory was approximated as a straight line, neglecting the slight curvature of the fascicles (18). The difference between the two measurement approaches is, however, small (<3%, as estimated in the present study) and falls within the variation of the measurements. Another methodological consideration is that fascicular recordings were taken from one region of the muscle only. However, ultrasound scanning of the gastrocnemius muscle in proximal, central, and distal regions during walking and running has shown that fascicle length changes in the central region approximate well the changes occurring throughout the muscle length (14). The calculation of the tendon length change depends on the MTC length change, which was calculated according to Menegaldo et al. (20) using data of knee and ankle joint angle changes. Other models for prediction of MTC length from joint angles can be found in the literature (5, 7, 31). In the phases of primary concern in the present study, (i.e., where the GM muscle was active), these alternative models yield similar predictions as the model used (i.e., tendon shortening late in the stance phase during ascent and tendon lengthening in early stance during descent). Only in the midstance phase during descent do predictions diverge. In this phase, the regression prediction model by Menegaldo et al. predicts MTC shortening, whereas the alternative models predict a near-constant length, which falls rapidly during the push-off phase. This disparity, in a phase of low GM muscle activity, does not largely affect the interpretations given above.

In conclusion, the present study shows that during stair ascent the GM muscle fascicles contract nearly isometrically during the push-off phase, suggesting that other leg muscles, such as the soleus and knee extensors, need to shorten to provide the work to elevate the body. During stair descent, the GM muscle fascicles are only active around touch-down and contract concentrically, not eccentrically as expected if the muscle operated as an energy-absorbing element. While other muscles, again such as the soleus and the knee extensors, may act eccentrically to decelerate the body, the present findings indicate that the GM tendon is stretched and hence stores energy, which is dissipated by the elongating muscle fascicles in a later phase. These findings are in contrast to what would be predicted from joint kinematics only.

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