Muscle-tendon interaction and elastic energy usage in human walking

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In human locomotion, there are two fundamental concepts for different energy-conserving mechanisms. First, mechanical energy stored in the elastic elements of muscle can be recovered as both kinetic and gravitational energy (spring-like bouncing mechanism). Second, gravitational potential energy is converted to kinetic energy as the leg swings in a pendulum-like mechanism. Both of these mechanisms are important for the mechanics and energetics of locomotion (5, 17, 19). In running or jumping, it has been proposed that skeletal muscle stores energy by the active stretching due to inertial, gravitational, or any other external forces during the first half of the stance phase of the step cycle and then immediately returns this energy effectively over the later part of the stance phase (34, 42) as a spring-like bouncing mechanism (2, 17). On the fascicle level, the gastrocnemius muscle fascicles have been shown to contract isometrically or shorten throughout the stance phase (34, 42) as a spring-like bouncing mechanism (2, 17). These findings suggest that the elastic recoil takes place not as a spring-like bouncing but as a catapult action in natural human walking. These findings suggest that the elastic recoil takes place not as a spring-like bouncing but as a catapult action in natural human walking.

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lacks reports that have examined interaction between fascicle-TT during the natural walking on level ground.

In the present study, we used novel in vivo techniques to measure Achilles tendon force (ATF) and fascicle lengths for two muscles [medial gastrocnemius (MG) and soleus (Sol)] during natural human walking on level ground. The present study was designed to explore how the interaction between the fascicles and TT is involved in storage and utilization of elastic energy during human walking with a natural cadence. We hypothesized that the elastic bouncing may not be the most important way to utilize elastic energy. Instead, it is believed that the specific interaction between fascicle and TT allows elastic energy to be utilized for energy saving. This possible mechanism may not, however, appear similarly in MG and Sol muscles. One of the possible candidates for this mechanism is a catapult action introduced by Alexander and Bennet-Clark (6).

METHODS

Subjects and experimental procedure. Eight male subjects, age 28.4 yr (SD 5.0), height 171.8 cm (SD 4.3), body mass 71.7 kg (SD 7.2), participated in the study after giving informed consent of the procedures and risks associated with the study according to the Declaration of Helsinki. The study was approved by the Ethics Committee of the University of the Jyväskylä.

The subjects walked with a natural cadence, speed 1.4 m/s (SD 0.1) and ground contact time 640 ms (SD 50), on a unique 10-m-long force platform system with two separate rows of force plates (Raute; Fig. 1) starting from 5 m before. The horizontal and vertical ground reaction forces were recorded separately (right and left sides). In the present study, the ultrasonographic apparatus (SSD-2000, 5500; Aloka) were used to measure fascicle length in the MG and Sol muscles during walking (50 and 96 images/s, a linear array probe with scanning frequency of 5–10 MHz, Aloka) (25, 34–36, 39). In the present study, the width and depth resolution of our high-speed scanning ultrasonography were 0.45 and 0.36 mm, respectively. The ultrasound apparatus was pushed on the side of the force platform at the subjects’ walking speed. Simultaneously, an optic fiber transducer passed transversely through the Achilles tendon was used to measure the tensile stress within the Achilles tendon. The use of optic fiber as a transducer for tendon stress is based on the modulation occurring in a micro-deformable optic fiber. The light signal detected by the receiver unit is converted to analog signal and further to force using calibration curves and equation of balance of the moments (see Refs. 9, 22, 38 for details). Surface bipolar electromyographic (EMG) electrodes were used to record the Tibialis anterior, MG, and Sol muscle activities (Ag/AgCl miniature surface bipolar electrodes, diameter of 5 mm, interelectrode distance of 20 mm; Beckman skin electrode 650437). The midbellies of the muscles were confirmed from B-mode ultrasonographic images, and care was taken not to place the electrodes over the peripheries of muscles to minimize EMG cross talk between muscles. EMGs were amplified (input impedance of >25 MΩ, common mode rejection ratio >90 dB) and sent telemetrically to the recording computer (12-bit analog-to-digital converter) with a sampling frequency of 1 kHz. Care was taken that the interelectrode resistance was below 5 kΩ. The goniometers were used to record the angular position of the hip, knee, and ankle joints. The output signal triggered from the vertical ground reaction force of the right leg side was used to synchronize the signal and ultrasound data. Ground reaction forces, ATF, EMGs, and angular data were sampled at 1,000 Hz simultaneously.

Analyses. The contact phase of the step cycle was subdivided into four different phases based on the ground reaction forces curves (brake I and II, push I and II; see Fig. 2A for detail). During the contact of walking, the model of Hawkins and Hull (28) was used to estimate length changes in MTU from the ankle (Sol and MG) and knee joint angular (MG) position. The muscle fascicle length of both MG and Sol muscles were measured from each ultrasonographic image during walking (Fig. 1B). The MG and Sol fascicles were identified in each image along their length from the superficial and deep aponeuroses (Fig. 1B). These fascicles were then tracked continuously frame by frame using Motus software (Peak Performance Technologies). The fascicle angles in the MG and Sol muscles were determined as the angle between the aponeurosis and the line drawn tangentially to the fascicle (see Fig. 1B). The analyzed ultrasound data were interpolated at 100 Hz. The length of TT ($L_{TT}$) in both muscles were calculated from the following equation (25, 34, 39)

$$L_{TT} = L_{MTU} - L_{fascicle} \cdot \cos \alpha$$

where $L_{fascicle}$, $\alpha$, and $L_{MTU}$ are fascicle length, fascicle angle, and MTU length, respectively.
The velocities of MTU, fascicle, and TT were calculated by the weighted quadratic polynomial differentiation (5 discrete points) of the corresponding length value. Shortening direction was defined as positive. The reliability and reproducibility of the fascicle length measurement with the ultrasound method has been confirmed elsewhere (23, 25, 36, 39).

From the direct ATF during walking, ATF was further reduced to the relative physiological cross-sectional area of the MG and Sol in the Achilles tendon (24). The mechanical power was calculated by velocities of the length changes (MTU and TT) and tendon forces in the MG and Sol muscles, respectively (34, 39).

In each subject, the signal data of 8–10 steps were averaged (after the EMG signals were full-wave rectified), and then eight subjects’ data were averaged. For the ultrasound data, the three steps were averaged for each subject, and then eight subjects’ data were averaged.

Statistics. Values are presented as means and standard deviations unless stated otherwise. Statistical analysis was performed using the two-tailed paired Student’s t-test for the comparison between MG and Sol muscles. The Wilcoxon signed rank test was used for the comparison of the fascicle lengthening between MG and Sol because the normality test was failed. A two-way ANOVA was used to analyze the difference in the averaged EMG amplitude and fascicle length changes during the brake I and push I phases. The probability level for statistical analysis was set at $P < 0.05$.

RESULTS

Figure 2 presents the time course-averaged data during the contact of walking, where changes in ground reaction forces, joint angular data, ATF, length changes, and EMGs are shown. As expected from previous experiments (22, 37), ATF demonstrated a sudden decrease on heel strike during walking on ground in all subjects (Fig. 2B). Similar reductions in the MTU, fascicle, and TT lengths in both muscles were observed due to the rapid ankle plantar flexion during the brake I phase (Fig. 2). In the subsequent brake II phase, the vertical ground reaction force in the right leg decreased but ATF started to increase after the first peak vertical ground reaction force in the right leg (Fig. 2, A and B). The ATF and EMGs (MG and Sol) increased with a simultaneous lengthening of MTU, fascicles, and TT in both muscles in varying degrees (Figs. 2 and 3). Increase of ATF took place until the beginning of the push II phase (Fig. 2B). Thereafter, it decreased but much later than the corresponding EMG activities of the MG and Sol muscles (Fig. 2).

The MTU and TT in both muscles lengthened slowly during the brake II and push I phases, and then they recoiled rapidly during the push II phase in all subjects (Fig. 2B). However, the pattern and amplitude of the fascicle length changes were different between muscles. MG fascicles were stretched during the brake II phase and then remained isometrically during the push I phase. In contrast, Sol fascicles continued lengthening during the push I phase. In both cases, the fascicles shortened with the low EMG activities during the push II phase (Fig. 2).
Figure 3A shows the peak-to-peak amplitudes of lengthening and shortening in MTU, fascicle, and TT during the right-leg contact of walking. Compared with MG, Sol MTU lengthened relatively more. The difference was not, however, statistically significant. Similarly, there was no significant difference between both muscles in the MTU shortening amplitude. On the fascicular level, however, not only the patterns of the fascicle length but also the lengthening amplitudes were different between muscles (Fig. 3B). The fascicle lengthening amplitude was greater in Sol than in MG ($P < 0.05$). In contrast, the shortening was greater in MG than in Sol ($P < 0.05$). On the TT level, the lengthening and shortening amplitudes did not show any significant difference between the two muscles (Fig. 3C).

**DISCUSSION**

The results of the present study demonstrated that, during walking on level ground and with a natural cadence, TT elasticity can be utilized. TT of both MG and Sol muscles were stretched slowly during the single support phase and then dramatically recoiled during the end of the contact phase. In contrast to TT, the fascicles behaved differently during the contact phase of walking. In addition, the fascicle and TT length patterns did not follow the ATF patterns. These results clearly indicate the existence of specific interactions between fascicles, TT, and ATF during walking. Furthermore, we have provided evidence that the two muscles (MG and Sol) that are commonly accepted as synergists do not have similar mechanical behavior of fascicles during walking.

Utilization of elasticity in walking. The fascicle length and ATF measurements used in this study indicated that TT was stretched slowly throughout the brake II and push I phases and subsequently recoiled rapidly (Fig. 2). The stretched TT amplitudes from the heel strike in both MG (4.2 ± 1.5%) and Sol (4.3 ± 1.4%) muscles are consistent with similar values reported previously in animal walking (2–6%) (8, 20). In the present study, however, these TT behaviors during the contact of walking do not follow the spring-like bouncing concept, in which the tendons store energy in the first half of the step and then return this energy in the second-half phase (2). According to our interpretation of several studies that have examined stretch-shortening cycle in both animals (42) and humans (34, 36, 39), the concerted fascicle action seems to refer to favoring of the effective spring-like bouncing of TT during the ground contact. In running and jumping, for example, the elastic energy comes mainly from the initial negative work. But in walking with a natural cadence, ATF is low during the brake I and II phases (Fig. 2B). Therefore, TT cannot be stretched under the spring-like bouncing concept during the brake I and II phases. To support this suggestion, the TT stretching curves in both MG and Sol did not follow the ATF development slope during contact of walking (Fig. 2). These results clearly indicate existence of an alternative way for the spring-like bouncing concept to utilize elasticity.

The question may be asked which mechanism would cause utilization of elastic energy during the slow stretching and rapid recoiling of TT during the ground contact of walking. The natural candidate for this behavior is the concept of a catapult action (6, 11, 12), in which the spring stretches slowly and recoils rapidly. In this action, the power output can be amplified by the rapid positive work against the negative work done during the slow stretch, as demonstrated in insect jumping (11, 12). The mechanical power curves of the present study also showed a similar catapult behavior to amplify MTU power production during the end of the ground contact (Fig. 4). To the best of our knowledge, this has not been demonstrated earlier in human locomotion. These catapult and spring-like bouncing actions have a common feature of the dramatic TT shortening. But the catapult action is fundamentally different from the spring-like bouncing behavior of TT that is observed during running (42) and in short contact jumps (34). In the catapult action, which we now suggest to take place during human walking, elastic energy is not provided directly from initial negative work. Instead, it can be mainly provided by muscle action. This does not exclude the possibility to utilize simultaneously the pendulum and energy transfer mechanisms.

Benefits of catapult action in walking. The spring-like bouncing behavior of TT observed during running (42) and in short-contact jumps (34) can be advantageous for effective utilization of elasticity. However, the concerted contraction for the spring-like bouncing is not necessarily economical to achieve the highest possible positive work. In the natural cadence walking performed in the present study, however, it can be assumed that the energy expenditure can be lower compared with other speeds of walking (15). Our data indicate that the MG and Sol TT can act as a catapult action to amplify muscle power production. The observed interaction between

![Fig. 3. Relative changes of lengthening and shortening in MTU (A), fascicle (B), and TT (C) of MG and Sol muscles during the contact of walking (means ± SD; $n = 8$). Lengthening amplitude was calculated from the lowest point after the rapid plantar flexion (top right).](image-url)
fascicles and TT seems to be advantageous for utilization of elastic energy during human walking. The energy expenditure during the fascicle lengthening action can be less than that during an isometric or shortening action (1, 2, 29). Thus the fascicle lengthening can take advantage of energy-saving during the single-stance phase. The fascicle behavior from the treadmill walking (25), however, may stand in opposition to our findings, especially for the Sol muscle. Fukunaga et al. (25) suggested that if fascicles are lengthened instead of maintaining the same length, the stored elastic energy in TT will decrease during the single-stance phase. Consequently, additional metabolic energy will be required to make up for this loss. However, TT was not stretched during the brake II phase of natural human walking by the concerted fascicle action in the manner it may occur in the spring-like bouncing mechanism. This is because ATP cannot be high enough during the braking phase. In addition, the contact time during human walking does not match the cycle time of the resonant frequency of the elastic component in ankle extensors (10). This resonant oscillating frequency has a range of 2.6–4.3 Hz (10, 14, 18). This corresponds to the ground contact time between 233 and 385 ms. However, the contact time measured in the present study (640 ± 50 ms) was much longer than that of the resonant elastic frequency. It is also possible that the bouncing frequency of elastic component in ankle extensors can be modified for the spring-like bouncing action by the regulation of the ankle joint stiffness. To regulate the stiffness, one must activate more triceps surae muscle during the braking phase. This may cause an increase in vertical position of center of mass during the middle of the single-stance phase, but it may not contribute to any additional forward push during the middle of the double-stance phase. Thus it can be suggested that the consumption of minimal metabolic energy during human walking cannot be provided by the spring-like bouncing but more likely by the catapult action. Consequently, it can be speculated that, if the contact time is shorter with increasing the walking speed, the TT utilization process may shift from the catapult to the spring bouncing action during the contact of walking. This assumption needs to be verified in future studies.

Muscle-specific behavior. Another major finding of the present study was that MG and Sol fascicles behaved differently during the push I phase during human walking (Fig. 2, C and D). The MG fascicles remained at the same length during the push I phase after the lengthening during the brake II phase. However, the Sol fascicles were lengthened continuously during the brake II and push I phases. Generally, the biarticular MG muscle offsets the lengthening and shortening effects during human movements. During the single-stance phase of human walking, however, the knee joint is extended only slightly (Fig. 2B). This indicates that the fascicles in the biarticular MG muscle may not behave in the same way as in the monoarticular Sol muscle (34). This muscle specificity during human walking could be observed by the difference of the fascicle behavior related to the muscle activation from the end of the brake II phase to the push I phase (Fig. 5). The Sol fascicles lengthened (P < 0.05) with increasing muscle activation, but the MG fascicles remained at the same length or tended to shorten in the opposite direction. Alexander (3) was the first to report the different muscle behavior between hip, knee, and ankle joint muscles during the dog jumping. In addition, the present study shows that leg muscles, which are commonly accepted as synergists, do not have similar mechanical behavior of fascicles during human walking. These results highlight the fact that observations made from the fascicles of one muscle cannot necessarily be extended to other muscles during dynamic movements (33, 34) as well as in the static human movements (13). On the TT level, however, both muscles showed a similar length change pattern during the contact of walking. These results suggest that, although TT elasticity depends on the length and cross-sectional area (7), the manner of the TT behavior may be the same between different muscles. This certainly is still speculation and awaits further verification.

Fig. 4. Changes of the mechanical power (MTU, TT, and MTU – TT) in Sol during the contact of walking (n = 8). It was assumed that relative contribution of the force developed by Sol muscle on ATF was equal to the relative physiological cross-sectional area of Sol among all plantar flexors. Mechanical power was calculated by multiplying the velocity by force in MTU and TT, respectively. The plus and minus signs refer to shortening and lengthening powers, respectively.

Fig. 5. Relative changes in the fascicle length (■) and corresponding changes in the averaged EMG (aEMG) during the brake II and push I phases. ◦, corresponding changes in aEMG values of the MG (left) and Sol (middle) muscles. Right: to calculate the aEMG changes, the brake I phase was used as a reference value to obtain the relative aEMG values for the brake II and push I phases.
Methodological consideration. There are certain points in the methods that need to be addressed. The present study is perhaps the first in which fascicle length and ATF measurements were utilized simultaneously during human walking. During the ATF measurements, it is possible that the skin movement during walking may cause minor artifacts to signal. However, the ATF patterns measured with this technique (22) have been shown to be similar to those obtained with the buckle transducer method (37) during human walking. With regard to calculation of MG and Sol forces, we did not consider the activation level and energy transfer from the knee joints. This can naturally influence our power calculation data. However, we assume that these methodological problems in our force calculation are minor and did not have a serious effect on our results and interpretation.

Finally, the results of the present study cannot be generalized to apply to all speeds of walking. As Alexander (4) argued, elastic energy-saving mechanisms cannot be equal when walking speeds are changed. These points need to be examined in future studies.

In summary, the present results demonstrate the concept of elastic recoil by a catapult action in natural human walking. The interactions between the muscle fascicles and TT play an important role in the process of the economical storage and release of elastic energy, although the manner in which this action occurs may depend on the muscle that is studied.

REFERENCES