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Interaction between fascicles and tendinous structures during counter movement jumping investigated in vivo

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Submitted 3 March 2003; accepted in final form 2 July 2003

Kurokawa, Sadao, Tetsuo Fukunaga, Akinori Nagano, and Senshi Fukashiro. Interaction between fascicles and tendinous structures during counter movement jumping investigated in vivo. J Appl Physiol 95: 2306–2314, 2003.—Behavior of fascicles and tendinous structures of the m. gastrocnemius medialis (MG) was quantitatively examined during human jumping in vivo. Eight male subjects performed maximal-effort counter movement jumping (CMJ) motions. Kinematic and kinetic data were obtained using a high-speed camera and a force platform. Behavior of fascicles and tendinous structures was determined using ultrasonography and electromyography. Although the muscle-tendon complex (MTC) shorted only by 1.6% during the downward phase of the counter movement, fascicles shortened as much as 10.4%. This shortening of fascicles caused elongation of tendinous structures by 2.2%. Although the MTC remained at almost constant length during the upward-I phase (−250 to −100 ms before toe-off), fascicles shortened by 19.2% of the initial length with an elongation of tendinous structures by 4.4%. The MTC shortened rapidly by 5.3% of the initial length during the upward-II phase (−100 to 0 ms), whereas fascicles shortened slightly during the first half of this phase and contracted in a quasi-isometric manner during the latter half of this phase. These findings implied that elastic energy was stored in tendinous structures throughout the latter half of the downward phase (1.0 J) and upward-I phase (5.6 J), which was thereafter rapidly released during the upward-II phase (3.8 J). It was found that muscle fibers of the MG were not stretched during counter movement; therefore, stretch reflex and potentiation of the contractile component of the MG might not contribute to the work enhancement in CMJ. It was suggested that the interaction between fascicles and tendinous structures was essential in a generation of higher joint power during the late push-off phase. This behavior of the MTC of the MG in CMJ was quite similar to what was observed in squat jumping performed without counter movement.

ultrasonography; elastic energy; vertical jump

NATURAL AND COMPLEX HUMAN movements, such as running, jumping, and throwing, are generated as a combination of joint actions. Joint moments are caused by tensi-
nous structures behave during human natural and complex movements in vivo.

Muscle fibers are packed in fascicles that attach to proximal and distal tendinous tissues on either end. Intrafascicle muscle fibers are serially connected to compose one functional unit, whose length is identical to that of fascicles, although some muscle fibers taper off to a point and terminate midfascicularly (35). Thus a change of fascicle length corresponds to a change of muscle fiber length. Recently, using ultrasonography, we succeeded in determining the muscle architecture (length and angle of fascicles) and elongation of tendinous structures of human muscles in vivo (20, 22, 35). Kurokawa et al. (39) applied this methodology to investigate the behavior of the m. gastrocnemius media-

\[\text{sis (MG)}\] during human SJQ. They reported that fascicles shortened and tendinous structures were stretched during the first phase of take-off and that fascicles generated force quasi-isometrically, although the MTC shortened rapidly during the last phase of take-off. They concluded that the compliance of tendinous structures, together with no yielding of muscle fibers, allowed the MTC to effectively generate relatively large power at the high joint angular velocity region during the last part of push-off.

The purpose of this study was to quantitatively de-

\[\text{termine the mechanical output of fascicles and tendi-}

\[\text{nous structures of the human MG during counter movement vertical jump and to discuss the mechanism of performance enhancement in CMJ compared with SQJ (39).}\]

METHODS

Subjects and experimental protocol. Eight healthy male subjects [age 23 ± 5 yr old; height 1.72 ± 0.10 m; body mass 68 ± 11 kg; shank length (measured from the lateral malle-

\[\text{olus to lateral epicondyle) 0.40 ± 0.03 m (means ± SD)}\] participated in this study. All subjects gave an informed consent to participate in the study. This study was approved by the Ethics Committee of the University of Tokyo. After warming-up, subjects were asked to jump vertically as high as possible, with a counter movement starting from an erect standing position. Their hands were kept on the hips throughout the movement. Kinematic, kinetic, ultrasonogra-

\[\text{phy, and electromyography (EMG) data were obtained from lower leg muscles during movements and at an erect standing position.}\]

Kinematic and kinetic data collection. Retroreflective markers were placed over the following anatomic landmarks on the right side of the subjects: the fifth metatarsophalan-

\[\text{geal joint, the lateral malleolus, the lateral epicondyle of the knee, the tip of the trochanter major, and the glenohumeral joint. Four body segments, i.e., feet, shanks, thighs, and HAT (head, arms, and trunk), and angles of the joints connecting those segments were identified with reference to these land-}

\[\text{marks. During CMJ, subjects were filmed at 200 Hz from the right side of the body (perpendicular to the sagittal plane) with a digital high-speed video camera (MEMRECAM-5’s, NAC). Vertical and fore-aft components of the ground reaction force, as well as the location of the center of pressure of this force under the feet, were determined using a force platform (Type 9281B, Kistler Instruments AG). These data were stored into a personal computer system through an analog-to-digital converter (MacLab/8s, AD Instruments) at a sampling frequency of 1 kHz.}\]

Location of the five anatomic landmarks was automati-

\[\text{cally digitized using a motion analyzer software package (Frame-DIAS, DKH). Digitized coordinates were low-pass filtered at 8 Hz (bidirectional Butterworth digital filter) (47). After synchronization of kinematic and kinetic data, instantaneous net joint moments around the ankle and knee joints were calculated through inverse dynamics (49). Joint net moments in the direction of plantar flexion and in the direc-

\[\text{tion of knee extension were defined as positive and were referred to as “plantar flexion moment” and “knee extension moment,” respectively. Net joint power output was calculated by multiplying net joint moment and joint angular velocity.}\]

Ultrasonography. A real-time B-mode computerized ultrasonic apparatus (SSD-2000, Aloka) was used with an electronic linear array probe of 7.5-MHz wave frequency (UST 5710–7.5, Aloka) to obtain longitudinal ultrasonic images of the MG during CMJ. The probe was fixed at a proximal part of the lower leg (30%) between the popliteal crease and the center of malleolus, at the midpoint of the mediolateral width of the MG. The probe was carefully fixed on the skin surface with a specially designed supporting device and elastic tape to minimize noisy fluctuations. During CMJ (from 1,150 ms before the toe-off to 100 ms after the toe-off), longitudinal ultrasonic images of the MG were stored consecutively in the cine-memory of the ultrasonic apparatus at 40 Hz. The ultrasonic images were synchronized with kinematic and kinetic data using a specially constructed trigger controller. With these arrangements, it was possible to obtain echoes reflected from interspaces among fascicles and from the superficial and deep aponeuroses of the MG on ultrasonic images. These images were stored frame by frame into a personal computer equipped with a video card.

Fascicle length was measured as the length of the echo image that runs diagonally from the superficial to the deep aponeurosis along the direction of fascicles (39). Fascicle angle was determined as the average value of two angles; i.e., the angle between the deep aponeurosis and the line drawn tangentially to the fascicle (\(\theta_{\text{apap}}\)) and the angle between the superficial aponeurosis and the tangential line to the fascicle (\(\theta_{\text{apap}}\)). These measurements were performed frame by frame by means of an image processing and analysis application software package [National Institutes of Health (NIH) image 1.60b, NIH]. The reproducibility of fascicle length and angle determination has been evaluated in a preceding study (34, 35, 39). Measurements of fascicle lengths and angles were repeated for three times on each ultrasonic image, and the average value of the three measurements was used to repre-

\[\text{sent the image. Coefficients of variation (CV) of three mea-

\[\text{surements were in the range of 0–4%}.}\]

EMG. Surface EMG was obtained from the MG, m. gas-

\[\text{trocnemius lateralis (LG), m. soleus (Sol), and in some trials m. tibialis anterior using bipolar Ag/AgCl electrodes (NEC Medical System) with a constant interelectrode distance of 20 mm from the muscle belly. The electrodes were connected to a preamplifier and a differential amplifier with a bandwidth between 5 Hz to 1 kHz (1253A, NEC Medical System). EMG signals were analog-to-digital converted at a sampling frequency of 1 kHz (MacLab/8s, AD Instruments) and stored into a personal computer system for further analyses. Raw EMG signal was high-pass filtered at 20 Hz, low-pass filtered at 500 Hz, full-wave rectified, and smoothed using a bidirec-

\[\text{tional low-pass Butterworth digital filter with a cut-off fre-

\[\text{quency of 7 Hz to yield smoothed-rectified EMG (EMG}_{

\[\text{SSR}}\). EMG}_{

\[\text{SSR}}\text{ values were subsequently normalized relative to the maximum value attained during CMJ.}\]
MTC length, tendon length, and moment arm length. Instantaneous length of the MTC of the MG (L\textsubscript{MTC}), i.e., the distance between the origin and insertion, was calculated by substituting instantaneous ankle and knee joint angles into the equations developed by Grieve et al. (26). Instantaneous length of tendinous structures was determined based on a geometrical MTC model proposed by Allinger and Herzog (2). Properties of the fascicles and tendinous structures were assumed to be uniform along the length of the MTC. It was also assumed that all fascicles were parallel. Length of the tendinous structures (L\textsubscript{TTS}) was defined according to the following equation.

\[
L_{TTS} = L_{MTC} - L_{\text{fascicle}} \cdot \cos \alpha
\]

where \(L_{\text{fascicle}}, \alpha, \) and \(L_{MTC}\) are fascicle length, fascicle angle, and MTC length, respectively. Instantaneous moment arm length of the MG at the ankle joint was calculated by referring to Bobbert et al. (11).

Fascicle and tendon force. Force applied to the Achilles tendon was calculated as the quotient of plantar flexion moment generated by a single leg and the moment arm length of the MG at the ankle joint. It was assumed that relative contribution of the force developed by the MG on the Achilles tendon force was equal to the relative physiological cross-sectional area (PCSA) of the MG among all plantar flexors, represented as \(c.\) Also, it was assumed that the ratio of tendon cross-sectional area of the MG in the Achilles tendon can be represented by \(c.\) According to Fukunaga et al. (23), averaged relative PCSA of the MG was 15.4\% of the total plantar flexors (\(c = 0.154\)). Instantaneous tendon force developed by the MG (\(F_{\text{tendon MG}}\)) and tendinous force of fascicles of the MG (\(F_{\text{fascicles MG}}\)) were calculated as follows.

\[
F_{\text{fascicles MG}} = c \cdot (M_{\text{ankle}} \cdot d^{-1})
\]

\[
F_{\text{tendon MG}} = F_{\text{tendon MG}} \cdot \cos \alpha^{-1}
\]

where \(M_{\text{ankle}}\) and \(d\) indicate the plantar flexion moment generated by a single leg and the moment arm length of the MG at the ankle joint, respectively.

Usually, the muscle stress component perpendicular to the line of action of a muscle is not taken into account when considering Hill’s muscle model. Additionally, the tensional external mechanical work is not affected by this perpendicular component. Therefore, this muscle stress component was not considered in this study.

Velocity, power, and work outputs of fascicles and tendon. Velocity of the MTC, fascicles, and tendinous structures was calculated by numerically differentiating the corresponding length value with respect to time. Shortening direction of the MTC, fascicles, and tendinous structures was defined as positive. Mechanical power generated by the MTC and tendinous structures was calculated as a product of \(F_{\text{tendon MG}}\) and shortening velocity of the MTC and tendinous structures, respectively. \(F_{\text{fascicles MG}}\) was multiplied with the velocity of fascicles to calculate mechanical power generated by fascicles. Negative and positive mechanical work outputs performed by the MTC, fascicles, and tendinous structures were calculated by numerically time integrating the corresponding power values.

Statistical analysis. After synchronization of the variables obtained as described previously, mean curve (±SE) of each variable was calculated for the group of subjects.

RESULTS

Ankle and knee joint angles decreased gradually until 175 and 225 ms before toe-off, respectively, and then rapidly increased (Fig. 1). On the other hand, the change in plantar flexion moment generated by both legs was small during the downward movement phase. Subsequently, plantar flexion moment increased gradually (peak value: 226 ± 22 N·m at −85 ms) and thereafter rapidly decreased. Plantar flexion moment changed in synchronization with the EMG activity of plantar flexor muscles (peak of EMG of Sol was observed at around −175 ms). Peak joint power of the ankle generated by both legs (1,950 W) was observed at −45 ms, whereas angular velocity of the ankle joint was 81\% of the peak value (14 rad/s) at that instant.

In the present study, three phases were distinguished during CMJ based on the movement of the mass center of the body (MCB) and MTC (Fig. 2): downward phase, from the start of downward movement of the MCB (−800 ms) to the start of the upward movement of the MCB (−250 ms); upward-I phase, from the start of the upward movement of the MCB to the start of rapid shortening of the MTC (−100 ms); and upward-II phase, from the start of rapid shortening of the MTC to toe-off (Fig. 2).

During the downward phase, the MTC shortened by only 1.6\% (7 mm) of the initial length, whereas fascicles shortened by 22.5\% (15 mm) of the initial length, and the tendinous structures were lengthened by 2.2\% (8 mm) of the initial length. Especially this elongation of tendinous structures occurred predominantly in the latter half of the downward phase, where fascicles shortened actively by 12.1\% of the initial length with EMG activities of plantar flexor muscles. Shortening of fascicles during the first half of the downward phase was 10.4\% of the initial fascicle length, which was accompanied by small EMG activity of the plantar flexors.

During the upward-I phase, the MCB was raised by 0.12 m. MTC length remained at an almost constant value of 0.423 m, whereas fascicles were further shortened by 19.2\% (13 mm) of the initial length, and the tendinous structures were further stretched by 4.4\% (16 mm) of the initial length. During the upward-II phase, the MCB continued moving upward and the MTC shortened rapidly by 5.3\% (22 mm) of the initial length, whereas fascicles shortened by 5.2\% (4 mm) of the initial length. As a consequence, tendinous structures rapidly shortened by 5.2\% (19 mm) of the initial length. Especially during the latter half of this phase, only a small amount of shortening of fascicles was observed. Shortening of fascicles was accompanied by an increase of fascicle angle.

Shortening velocity of MTC was almost zero (i.e., constant length) during the downward phase and upward-I phase because of the interaction between shortening of fascicles and lengthening of tendinous structures (Fig. 3). During the upward-II phase, shortening velocity of fascicles decreased gradually to zero, and the behavior of tendinous structures changed from...
lengthening to shortening. Tendinous structures, which were prestretched throughout the downward phase and upward-I phase, began shortening rapidly with a maximum value of 0.35 m/s at -25 ms. Tendon force corresponding to the tension of MG fibers attained the minimum value of 30 N at -550 ms and then increased to the peak value of 500 N at -100 ms and thereafter rapidly decreased during upward-II phase. Time history of the force generated by fascicles was similar to that of tendon force. The difference between fascicle and tendon forces was remarkable around -100 ms because of the relatively large fascicle angle.

During the downward phase, mechanical power generated by the MTC was almost zero. During upward-I phase except for the last 25 ms, mechanical power of the MTC remained near zero, because mechanical power output of fascicles was approximately opposite to that of tendinous structures (similar magnitude, opposite sign). During upward-II phase, mechanical power of fascicles decreased gradually and reached zero in the latter half of this phase. Mechanical power of tendinous structures and the MTC rapidly increased and attained the peak value of 72 and 83 W, respectively, at -50 ms.

Table 1 shows average mechanical work outputs performed by the MTC, fascicles, and tendinous structures of the MG during three phases in CMJ. Absolute value of work performed by tendinous structures during downward phase was small (1.0 J) compared with work performed during upward-I phase (5.6 J) and upward-II phase (3.8 J). Work performed by the MTC during the downward phase was even smaller (0.3 J), which was equivalent to the sum of positive work performed by fascicles and negative work performed by tendinous structures.

DISCUSSION

The purpose of this study was to determine quantitatively the mechanical behavior (force and length changes) of the MTC of the MG during CMJ compared with SQJ (39). CMJ is a typical SSC exercise (38). It has been generally considered in CMJ that agonist MTCs are stretched through counter movement. The MTC length of the biarticular MG is determined as a result of interaction between ankle dorsi flexion and knee flexion during downward phase (Fig. 1). In this study, the biarticular MG shortened by 1.6 and 22.5% of the initial length of MTC and fascicles in the downward phase, respectively (Fig. 2). Fascicle shortening of the MG during the downward phase might be caused through the following mechanism. At the erect standing position, fascicles might have already been in a stretched position without elongation of tendinous structures because of the relatively lower stiffness of fascicles than that of tendinous structures (45). Active shortening of fascicles associated with the increase of joint moment during the downward phase, where length of the MTC remained almost constant, occurred due to the compliant nature of tendinous structures.

Fig. 1. Mean time history of joint angles (A), joint angular velocities (B), joint moments (C), joint powers (D), moment arm length of the gastrocnemius medialis (MG) at the ankle joint (E), as well as normalized electromyography (EMG) activity from lower leg muscles (F). Positive joint moment around the ankle joint and the knee joint indicates ankle plantar flexion moment and knee extension moment, respectively. Time is expressed relative to the instant of toe-off (time = 0). Thin vertical bars indicate SE for 8 subjects. Sol, soleus; LG, gastrocnemius lateralis; TA, tibialis anterior.
Fig. 3. Mean time history of force (B), velocity (A), and mechanical power of the MTC, fascicles, and tendinous structures during counter movement jumping (CMJ; C). Shortening of the MTC, fascicles, and tendinous structures was defined as positive. Left vertical dotted lines represent the start of the downward movement of the MCB. Middle vertical dotted lines represent the start of upward movement of the MCB. Right vertical dotted lines indicate the start of the rapid shortening of MTC. Time is expressed relative to the instant of toe-off (time = 0). Thin vertical bars indicate SE for 8 subjects.

Fig. 2. Mean time history of vertical displacement of mass center of the body (MCB; A), muscle-tendon complex (MTC) length (B), fascicle length (C), length of tendinous structures (D), and fascicle angle (E). Left vertical dotted lines represent the start of the downward movement of the MCB. Middle vertical dotted lines represent the start of the upward movement of the MCB. Right vertical dotted lines indicate the start of the rapid shortening of the MTC. Three phases were defined as downward phase, upward-I phase, and upward-II phase. Time is expressed relative to the instant of toe-off (time = 0). Thin vertical bars indicate SE for 8 subjects.
MUSCLE-TENDON COMPLEX DESIGNED FOR COUNTER-JUMPING

Table 1. Mechanical work output performed by the MTC, fascicles, and tendinous structures of the MG during 3 phases in CMJ

<table>
<thead>
<tr>
<th></th>
<th>CMJ Downward</th>
<th>SQJ</th>
<th>CMJ Upward-I</th>
<th>SQJ</th>
<th>CMJ Upward-II</th>
<th>SQJ</th>
</tr>
</thead>
<tbody>
<tr>
<td>MTC</td>
<td>Mean SE</td>
<td></td>
<td>Mean SE</td>
<td></td>
<td>Mean SE</td>
<td></td>
</tr>
<tr>
<td>Fascicles</td>
<td>0.3 0.08</td>
<td></td>
<td>0.3 0.17</td>
<td>0.2 0.04</td>
<td>4.8 0.38</td>
<td>5.1 0.12</td>
</tr>
<tr>
<td>Tendinous</td>
<td>-1.0 0.10</td>
<td></td>
<td>-5.6 0.86</td>
<td>-4.9 0.23</td>
<td>3.8 0.42</td>
<td>4.3 0.40</td>
</tr>
</tbody>
</table>

Values are mean and SE; n = 8. MTC, muscle-tendon complex; MG, gastrocnemius medialis; CMJ, counter movement jumping; SQJ, squat jumping. Work measured in joules (J). Styles: CMJ and SQJ. Phases: downward, upward-I, and upward-II.

(Figs. 1 and 2). These results agreed well with those of previous animal and human experiments (22, 27, 35). It can be stated that neither MTC nor fascicles of the MG had a stretching phase during the downward phase in CMJ. In the previous study that investigated SQJ, Kurokawa et al. (39) reported that the MTC and fascicles of the MG shortened by 5 and 26% of the initial length of the standing position. The shortening of the MTC and fascicles in CMJ were quite similar to those of SQJ. Because the MG is a biarticular muscle, it can be stated that its behavior during movements is similar in both SQJ and CMJ.

Several possible mechanisms have been proposed to account for the performance enhancement through making a counter movement. The first one is that counter movement results in the development of a higher level of muscular force preceding the start of concentric action (9). The second one is that active muscles prestretched during the counter movement store elastic energy, which is reused during the following concentric action (4, 8, 31, 38). The third one is that prestretching of active muscle during the counter movement alters the properties of the contractile machinery through the mechanism called “potentiation” (13, 14, 17, 18), by which force generation by active muscle is enhanced. The fourth one is that prestretching of active muscle during counter movement triggers spinal reflexes (16, 46) as well as longer latency responses (42) that help increase muscle stimulation during concentric action to the maximal level. To induce potentiation of the contractile machinery and/or stretch reflex, muscle fibers have to be stretched during counter movement.

Results of the present study exhibited that fascicles shortened by 22.5% of the initial length during counter movement. Furthermore, enhancement of muscle stimulation in the MG was not observed in CMJ. It was suggested that potentiation and/or stretch reflex induced by prestretch did not contribute to work enhancement through making a counter movement. Thus, these two mechanisms (potentiation and stretch reflex) might contribute to work enhancement through counter movement only in the monoarticular plantar flexor muscles (not in the biarticular MG) and more proximal knee and hip extensor muscles.

Many researchers asserted that storage and reutilization of elastic energy help to enhance the maximum work produced during the following concentric action (4, 38, 44). A major part of series elastic component is located in tendinous structures (32). As shown in Fig. 2 and Table 1, only a little lengthening (8 mm) and storage of elastic energy (0.3 J) were found in the tendinous structures during the downward phase. Fukashiro and Komi (21) as well as Bobbert et al. (9) indicated that there was no substantial difference of plantar flexion moment between CMJ and SQJ and that joint moments peaked almost at the same time during those motions. Table 1 summarizes the mechanical work outputs of the MTC, fascicle, and tendinous structure of the MG in CMJ compared with those of SQJ (39) (in Ref. 39, the identical subjects as were recruited in this study performed squat jumping motions under the identical experimental setup in the same day). Positive work performed by the MTC, fascicles, and tendinous structures was calculated to be 5.4, 8.0, and 3.8 J in CMJ, and 5.3, 5.5, and 4.3 J in SQJ, respectively. On the other hand, negative work of them was calculated to be 0, 0, and −6.6 J in CMJ, and 0, 0, and −4.9 J in SQJ, respectively. Considering this study and our previous study (39), total elastic energy stored in, and released from, tendinous structures during CMJ was qualitatively (Fig. 2) and quantitatively (Table 1) very similar to that of SQJ (P > 0.1). In the MG, therefore, this mechanism may not contribute to work enhancement through counter movement. Work enhancement by making a counter movement in CMJ might be mainly attributed to enhancement of muscular work output from monoarticular muscles.

On the other hand, it has been suggested that knee extensors and plantar flexors during SSC exercise (such as hopping and running) may behave in the manner of concerted contraction, i.e., a contraction where the MTC is lengthened but muscle fibers remain isometric or even shortened during counter movement (5, 29, 33). Thus, if concerted contraction could occur in monoarticular muscles, there might be no work enhancements induced by potentiation and/or stretch reflex. Storage and reutilization of elastic energy by tendinous structures were expected as the result of concerted contraction. Further studies need to focus on the behavior of fascicles and tendinous structures of monoarticular muscles such as Sol, vastus lateralis, and gluteus maximus muscle during human natural/complex movements.

According to kinetic analysis, increase of MCB velocity during the upward-II phase was closely related to...
higher ankle joint power output (Fig. 1), i.e., a combination of high angular velocity of the ankle joint with relatively large ankle plantar flexion moment (11). This implies high shortening velocity of the MG with large MTC force. This high-power output around the ankle joint in upward-II phase is obtained as an interaction between the force-length-velocity relationship of fascicles, tendon, and MTC. It is commonly known that the length of sarcomere in vertebrate striated muscle fascicles, tendon, and MTC. It is commonly known that the length of sarcomere in vertebrate striated muscle is determined by the PCSA, muscle activation, and shortening velocity. Additionally, the muscle architecture (e.g., fiber length/tendinous length ratio) might affect the force-generating properties of the generate relatively high force, which is required to accelerate the MCB during the latter half of the push-off phase, despite the slightly lower maximum force generation at the initial length.

On the other hand, it is well known that force generation capability of muscle fibers decreases with increasing shortening velocity of muscle fibers. During upward-II phase, where relatively large force was required, shortening velocity of fascicles began decreasing and became near zero (Fig. 3). This is realized as an effect of the compliant nature of tendinous structures, which allows fascicles to generate large force. Also, high shortening velocity of the MTC during upward-II phase predominantly comes from shortening of tendinous structures, of which peak shortening velocity was three times as high as the corresponding velocity of fascicles. This high shortening velocity of the tendinous structures was realized by elastic recoil (Figs. 2 and 3) so called “catapult action” (30). Thus, interaction between fascicles and tendinous structures is essential in building up a combination of high shortening velocity of the MTC with relatively large fascicle force. It can be stated that the behavior of the MTC during CMJ was mechanically quite similar to that of SQJ (39).

The possibility of energy storage in elastic structures has been discussed in the literature (1, 12, 28). Although this issue has been well documented for animals (7, 13), more speculative discussions have been reported for humans. In recent studies (15, 29, 31), series elastic stiffness of human plantar flexors was measured in vivo with the quick release method, and thereby elastic energy stored in the triceps surae was calculated during walking, running, and jumping. Hof (29) found a stretch of series elastic components corresponding to ~0.52 rad with a joint moment of 114 N·m, which is equivalent to a strain of 8% assuming a moment arm length of 50 mm and a total length of tendinous structures of 350 mm. De Zee and Voigt (15) also found a stretch of ~0.3 rad with a moment of 104 N·m, which is equivalent to a strain of 4.3% using the same assumptions. In this study, we found a strain of 6.6% with the peak plantar flexion moment of 113 N·m, which was generated by a single leg during CMJ. A strain value of 6.6% found during CMJ lay in the range between values reported in these preceding studies. Additionally, assuming that the distribution of muscle force among plantar flexors is proportional to their PCSAs, recalculation of the data reported by Hof (29, 31) revealed that the amount of elastic energy stored in the tendinous structures of MG in SQJ and slow running was roughly of the same magnitude as that during CMJ. The result of this study indicates that energy saving by elastic energy occurs during human natural jumping and running.

An unavoidable limitation of inverse dynamics is that MG, LG, Sol, and other plantar flexors cannot be considered separately. The force generated by the muscle fiber is determined by the PCSA, muscle activation, length, and shortening velocity. Additionally, the muscle architecture (e.g., fiber length/tendinous length ratio) might affect the force-generating properties of the
muscle (50). In this study, the information regarding the factors determining the force sharing among plantar flexors is not available except for the MG. Therefore, in this study, the force sharing among plantar flexors was determined simply according to the ratio of PCSA. This methodology has been commonly used in previous studies by many researchers (31). In reality, however, there is a possibility that the distribution of muscle forces among plantar flexor muscles might not be proportional to their PCSAs during push-off phase in jumping. The shortening velocity of the MTC of the m. gastrocnemius is lower than that of the MTC of the Sol during the upward-I and -II phases in jumping. This difference is caused by the reducing influence of knee extension on the shortening velocity of the particular m. gastrocnemius MTC. This influence might cause the shortening velocity of the muscle fiber of m. gastrocnemius to be lower than that of the muscle fibers of monoarticular plantar flexors such as the Sol. Therefore, there is a possibility that m. gastrocnemius could contribute relatively greater force during the upward-I and -II phases in jumping (i.e., using only the ratio of PCSA may lead to an underestimation of the force and power contribution of the MG during the upward-I and -II phases in jumping). On the contrary, during downward phase, the MTC of the Sol lengthened, whereas the MTC of the m. gastrocnemius shortened slightly. Furthermore, the m. gastrocnemius is more compliant than the Sol because of the higher tendinous structure length and muscle fiber length ratio in the MG (50). Hence, the muscle fibers of the m. gastrocnemius could contract faster than the muscle fibers of the Sol and other plantar flexors; thereby the contribution of muscle force generated by the m. gastrocnemius might be lower than that of Sol and other plantar flexors during the downward phase (i.e., using only the ratio of PCSA may lead to an overestimation of the force and power contribution of MG during the downward phase). However, as the length measurements are assumed to be reliable and the muscle force and tendon force are roughly equivalent, the general characteristics of Figs. 3 and 4 will remain unaltered. Consequently, the interpretation of the functional role of muscle fibers and tendinous structures will remain unchanged in the MG.

To summarize the findings of this study, mechanical power generated by fascicles of MG is absorbed in tendinous structures and stored in them as elastic energy during the downward phase and upward-I phase. Subsequently, this elastic energy is reused during upward-II phase where high peak power of tendinous structures and the MTC was observed. The rate at which elastic energy was released by tendinous structures during upward-II phase is higher than the rate at which it was stored into tendinous structures by shortening of fascicles during downward phase and upward-I phase. These results support the suggestion reported in previous studies (1, 8, 10, 30, 31, 41). Therefore, it follows from the present investigation that fascicles function as force generator and tendinous structures function not only as energy storage but also as power amplifier. The interaction between fascicles and tendinous structures has an essential role when considering the generation of higher joint power during late push-off phase.

REFERENCES