Muscle performance during maximal isometric and dynamic contractions is influenced by the stiffness of the tendinous structures

Jens Bojsen-Møller, S. Peter Magnusson, Lars Raundahl Rasmussen, Michael Kjaer, and Per Aagaard

Institute of Sports Medicine Copenhagen/Team Danmark Test Center, Bispebjerg Hospital, University of Copenhagen, Copenhagen, Denmark

Submitted 19 November 2004; accepted in final form 19 April 2005

Bojsen-Møller, Jens, S. Peter Magnusson, Lars Raundahl Rasmussen, Michael Kjaer, and Per Aagaard. Muscle performance during maximal isometric and dynamic contractions is influenced by the stiffness of the tendinous structures. J Appl Physiol 99: 986–994, 2005. First published April 28, 2005; doi:10.1152/japplphysiol.01305.2004.—Contractile force is transmitted to the skeleton through tendons and aponeuroses, and, although it is appreciated that the mechanocharacteristics of these tissues play an important role for movement performance with respect to energy storage, the association between tendon mechanical properties and the contractile muscle output during high-force movement tasks remains elusive. The purpose of the study was to investigate the relation between the mechanical properties of the connective tissue and muscle performance in maximal isometric and dynamic muscle actions. Sixteen trained men participated in the study. The mechanical properties of the vastus lateralis tendon-aponeurosis complex were assessed by ultrasonography. Maximal isometric knee extensor force and rate of torque development (RTD) were determined. Dynamic performance was assessed by maximal squat jumps and countermovement jumps on a force plate. From the vertical ground reaction force, maximal jump height, jump power, and force-velocity-related determinants of jump performance were obtained. RTD was positively related to the stiffness of the tendinous structures (r = 0.55, P < 0.05), indicating that tendon mechanical properties may account for up to 30% of the variance in RTD. A correlation was observed between stiffness and maximal jump height in squat jumps and countermovement jumps (r = 0.64, P < 0.05 and r = 0.55, P < 0.05). Power, force, and velocity parameters obtained during the jumps were significantly correlated to tendon stiffness. These data indicate that muscle output in high-force isometric and dynamic muscle actions is positively related to the stiffness of the tendinous structures, possibly by means of a more effective force transmission from the contractile elements to the bone.

ultrasonography; squat jump countermovement jump; connective tissue; rate of torque development

IT HAS PREVIOUSLY BEEN DEMONSTRATED that physiological mechanisms, such as neural activation and muscle structural properties, determine performance in human movements that involve maximal or near-maximal muscle force exertion (3, 20, 46, 49, 50). Contractile force is transmitted to the skeleton through connective tissue structures such as tendons and aponeuroses, and, although it is appreciated that the mechanical properties of the connective tissue play an important role for movement-performance with respect to energy storage and release (4, 13, 17, 26, 27, 54), the association between the mechanical properties of the connective tissue and contractile muscle output during maximal force exertion is not well understood. Recent developments in high-resolution ultrasonography have allowed the assessment of the connective tissue mechanocharacteristics in vivo (11, 18, 23, 32, 38, 40) and hence enabled further investigation of the relation between mechanical properties of the force-transmitting tissues and maximal force and power output of human skeletal muscle.

The methods to quantify contractile performance are copious, but may be classified based on the type of contraction, e.g., isometric or dynamic muscle actions. The rate of rise in contractile force [rate of force development or rate of torque development (RTD)] measured under isometric conditions has been identified as a key parameter that quantifies the ability of the neuromuscular system to exert so-called “explosive” muscle actions (3, 6, 20, 50, 53). RTD is, in part, influenced by muscular properties, such as muscle size, relative area of fast-twitch fibers, and myosin heavy chain isoform composition (19, 22), but also neural factors, such as the magnitude of efferent motoneuron output in the initial phase of contraction, exert strong, positive influence on RTD (1, 3, 20, 51). The work of Wilkie (55) indicated that contractile RTD is associated with the compliance of the force-transmitting structures, and such an association has, furthermore, been proposed in more recent studies (36, 39, 42, 44).

Vertical jumping on a force platform has been widely applied as a functional approach to assess contractile performance during maximal muscle actions due to the involvement of dynamic muscle contractions (10, 15, 34, 45). Although recent studies have investigated the relation between the mechanical properties of the connective tissue and jump performance (i.e., maximal jump height), no direct relationship has been observed (32, 34), which may pertain to the complexity of the jump movement. However, the vertical ground reaction force (Fv) during a push-off phase yields detailed information about the mechanical execution of the jump, such as peak force and the ability of the involved muscles to generate mechanical power on the body center of mass (CM) (15, 45). These parameters have not previously been investigated in relation to the mechanical properties of the force-transmitting tissues despite the fact that such an analysis may increase the understanding of the determinants for jump performance. The purpose of the present study was, therefore, to investigate the relation between mechanical properties of the quadriceps [i.e., vastus lateralis (VL)] tendon-aponeurosis complex and contractile muscle performance in maximal isometric and dynamic muscle actions quantified by 1) maximal isometric contraction force [maximum voluntary contraction (MVC)], 2) RTD, and 3) jump height and the mechanical power output of the leg.
extensor muscles during maximal vertical jumping. The hypothesis was that contractile RTD measured under isometric conditions, as well as maximal jump performance, is positively related to the stiffness of the tendon-aponeurosis complex measured in vivo by ultrasonography.

MATERIALS AND METHODS

Sixteen healthy men (age: 26 ± 2 yr, body weight: 78.6 ± 8.5 kg) participated in the study. Subjects were recruited among highly trained, competitive volleyball players (n = 8) and cyclists (n = 8). This configuration of subjects was chosen for two reasons: 1) to obtain a certain spectrum in tissue mechanical properties that was assumed to exist between these groups due to the different daily loading pattern that jumpers and cyclists experience; and 2) to ensure that subjects were accustomed to high knee extensor loads and maximal force exertion. Before inclusion, all subjects filled out a questionnaire regarding current training status and medical history. Subjects were excluded if current lower extremity or lower back pain was reported or in case of previous injury to any of the leg joints. The local ethics board approved the experimental procedures, and written, informed consent was obtained from the subjects.

Study Design

Each subject was required to participate on 3 separate days: 1 familiarization day and test days 1 and 2. On all days, a similar experimental protocol was conducted, and one session consisted of 1) assessment of isometric knee extensor MVC and RTD, 2) measurement of mechanical properties of the VL tendon-aponeurosis complex, and 3) force plate analysis of squat jumps (SQJ) and countermovement jumps (CMJ) (see detailed description below). The duration of one session was ~75 min and involved in total 7–9 maximal knee extension efforts and 10 maximal vertical jumps. Testing was completed for each subject within 12 days, and sessions were separated by at least 72 h.

Experimental Procedures and Data Analysis

After careful preparation of the skin by light abrasion and cleansing with alcohol, pregelled bipolar Ag-AgCl surface electrodes (type QN-10-A, Medicotest, Ølstykke, Denmark) were placed over the muscle bellies of the VL, vastus medialis, rectus femoris, and biceps femoris. Electrodes were positioned in parallel to the approximated fiber direction with a 2-cm interelectrode distance (3). A reference electrode was placed over the facies medialis of the tibia.

Isometric force measurements. Following a 10-min warm-up on a bicycle ergometer, subjects were strapped to a custom-made rigid chair in a seated position with 90° of flexion at the hip and knee joints (Fig. 1). The setting was individually adjusted to ensure minimal hip and knee joint movement and to minimize vertical displacement between the lower back and the backrest during muscular force exertion. A rigid leg cuff was mounted on the lower leg ~3 cm above the medial malleolus, which was connected to a strain-gauge load cell (Bofors KRG-4, Bofors, Sweden) through a stiff steel rod. The cuff and steel rod were adjusted such that the direction of force was perpendicular to the longitudinal axis of the lower leg. To ensure identical cuff placement between sessions, and furthermore, to obtain the external knee joint moment arm, the distance from the cuff to the knee joint line was measured. Following three to five submaximal contractions, the subjects performed three MVCs, each separated by a 2-min rest period. The subjects were carefully instructed to contract as fast and forceful as possible on a given signal from the test leader (8, 47), and attempts that displayed a visible countermovement (precontraction force in the direction of knee flexion) were immediately discarded. The force signal was recorded at 1 kHz during MVCs and stored on a personal computer (PC) using an external analog-to-digital (A/D) converter (DT 2801A, Data Translation).

During subsequent data analysis, the force signal was digitally low-pass filtered by using a fourth-order zero-lag Butterworth filter, 15-Hz cutoff frequency (3). MVC was defined as the peak isometric torque (N·m) exerted within the entire contraction phase. In accordance with the procedures of Aagaard et al. (3), contractile RTD was calculated as the average slope of the torque-time curve (N·m·s⁻¹) in time intervals of 0–30, 50, 100, and 200 ms after onset of contraction (time = 0). Peak RTD was defined as the maximal tangential slope of the torque-time curve derived over any 2-ms time period during the initial 200 ms of contraction. Onset of contraction was defined as the time point where the knee extensor torque exceeded baseline + 7.5 N·m (3). On each day, MVC and RTD parameters were averaged from the two trials that exhibited the highest MVC, and these values were used for the analyses of repeatability.

Assessment of the mechanical properties of the tendon-aponeurosis complex. A flexible electrical goniometer (Penny & Giles, Bio-metrics, Gwent, UK) was mounted laterally across the knee joint, and an ultrasound probe (7.5-MHz linear array B-mode, width, and depth resolution; 0.51 and 0.34 mm, 14 frames/s; Sonoline Sienna, model no. GM 6600A2E00, Siemens, Erlangen, Germany) was fitted into a custom-made rigid cast that was secured to the skin of the subjects at ~50% of the distance between the proximal border of the patella and the greater trochanter of the femur (11). The ultrasound image was 58 × 50 mm, and the apparatus was set to “one focal zone,” corresponding to the site of the aponeurosis. The probe was positioned so that the VL insertion aponeurosis and inserting fascicles could be visualized during rest and contraction, and care was taken to ensure uniform placement of the transducer on successive sessions. In accordance with previous reports (38, 40), the ultrasound probe did not shift position during contractions.

Two submaximal 10-s graded contractions served as practice and preconditioning trials before actual data collection (41). Following a
brief rest period in which the passive trial was performed (see below), the subjects performed two isometric ramp contractions (trials 1 and 2) by gradually increasing knee extensor force over a 10-s period from a relaxed state to maximal effort. During the force ramps, the subjects received an audiovisual signal to ensure a linear force ramp, and the trials were separated by a 3-min rest period.

A separate experiment was performed in which the leg was passively extended (passive trial), by an investigator, from 90 to 75° immediately before trial 1 to account for aponeurosis displacement due to angular knee joint movement (40). Online evaluation of the electromyogram (EMG) signals ensured that no muscle activation occurred during the passive trial.

To assess the level of antagonist coactivation during the graded knee-extensor contractions, the subjects performed two knee flexion MVCs, enabling concurrent measurement of force and EMG (40). Each knee flexion effort lasted ~5 s, separated by a 2-min rest period.

During ramp contractions and passive trials, force and joint angle data were sampled at 50 Hz to match the frequency of the US S-VHS video frame capturing (see below). For subsequent analysis, the force and goniometer data were stored on a PC using an external A/D converter (DT 2801A, Data Translation). EMG activity was registered by using custom-made amplifiers with a frequency response of 10 Hz to 10 kHz and 1:1 preamplifiers. The EMG signals were full-wave rectified, integrated, and averaged with a time constant of 200 ms online (7), A/D converted, and sampled at 50 Hz on a PC (40). The ultrasound S-VHS video images obtained during ramp and passive trials were sampled on a separate PC at a rate of 50 Hz, utilizing frame-by-frame capturing software (Matrox Marvel G400-TV, Dorval). The two sampling computers were interconnected to enable synchronous sampling of all data, using a custom-built trigger device that provided a visual marker on the ultrasound video image and simultaneously initiated sampling of the force, EMG, and goniometer signals (11, 42).

In the subsequent data analysis, the following procedures were adopted. On the ultrasound images, the VL insertion aponeurosis is visible as two parallel hyperechoic lines lying profound in the muscle (Fig. 1). Echoes corresponding to the muscle fascicles of the VL and the vastus intermedius can be observed in the classical pennate pattern inserting at the aponeuroses at which interfascicle connective tissue can be defined as hyperechoic aponeurosis fixed points. The longitudinal displacement of such fixed points during graded contractions was considered to represent the magnitude of deformation of the combined aponeurosis and free tendon distal to this point (11, 18, 23, 40, 42). Before analysis of the displacement, each video sequence was carefully evaluated to identify five to nine high echogenic fixed points that were observable throughout the entire ramp contraction, and the video sequence exhibiting the most clearly visible fixed points was selected for further analysis. Aponeurosis displacement was measured with automated tracking software by using a pyramidal implementation of the Lukas-Kanade feature tracking (14), which provided frame-by-frame displacement data of the defined fixed points, as previously described and evaluated in detail elsewhere (11, 12, 21, 42). The selected ultrasound video sequence was analyzed three times for aponeurosis displacement using dissimilar fixed points. Values from the two analyses sequences that yielded the greatest maximal displacement (11) were averaged and used for the subsequent calculation of aponeurosis-tendon stiffness.

It has been reported that passive angular joint movement results in considerable aponeurosis displacement (40, 42, 48). Thus, if any knee joint extension should occur during the ramp contractions, the observed aponeurosis displacement would be attributed to both joint angular rotation and contraction-related tissue deformation. To correct for contamination of the measured displacement due to joint movement, individual ratios of the aponeurosis displacement relative to joint angular movement (mm°2) were obtained from the passive trial, by plotting fascicle displacement as a function of knee joint angle (11, 40, 42). This correction procedure could not be performed for four subjects due to erroneous goniometer data, and these subjects were assumed to exhibit zero joint angular movement during ramp contractions.

Total knee extensor muscle force was determined by dividing the externally measured torque (calculated as load cell force multiplied by the external moment arm length) by the internal knee moment arm, which was derived from Visser et al. (53a). To correct for the force contributed by coactivation of the antagonist muscles (knee flexors) during the graded contractions (40, 42), the antagonist muscle force was estimated from the magnitude of knee flexor EMG during ramp contractions, assuming a linear relation between the recorded EMG amplitude and muscle tension (37, 56).

The aponeurosis displacement (corrected for joint movement) was plotted against total knee extensor muscle force (corrected for antagonist activity), and connective tissue stiffness was derived using a linear least squares curve fit between 50 and 90% MVC, in accordance with previously reported procedures (11, 32–34). To yield additional information with respect to understanding the mechanical function of the tendinous structures, the energy absorption by the connective tissue during the graded contractions was estimated as the integrated area below the entire force-deformation curve from 0 to 90% MVC (32).

Due to technical issues, the US video sequences were corrupted for one subject, and, therefore, all data reported with respect to connective tissue stiffness and energy absorption pertain to n = 15 subjects.

**Jump mechanography.** The electrodes, goniometer, and the US transducer were removed, and a dynamic warm-up was conducted consisting of 5–10 submaximal vertical jumps. Hereafter, the subjects performed five maximal SJQ succeeded by five maximal CMJ on a force plate (AMTI R6-5-1000, Watertown, MA). From upright standing position, the subjects performed a CMJ by rapidly moving downward (knee and hip flexion combined with dorsiflexion at the ankle), immediately followed by a fast upward movement. The SJQ was performed as a maximal vertical jump from an initial static position of 90° knee flexion controlled by an external goniometer. The subjects were instructed to jump vertically for maximal jump height, to land approximately at the takeoff site, and to maintain arms akimbo. In SQJ, the subjects were instructed to avoid any counter-movement, and attempts that displayed reduced ground reaction force values before movement onset were immediately discarded. The order of the jumps was similar in all sessions, and all jumps were separated by at least 90 s. The Fz signal was sampled on a separate PC at a sampling rate of 1 kHz (DT 2801A, Data Translation).

The analysis of jump data was performed in accordance with the procedures of Caserotti et al. (15). Maximal jump height was determined for CMJ and SJQ by time integration of the Fz signal (Fig. 2). The two CMJ and two SJQ from each test day that exhibited the greatest jump heights were selected for further analysis. To investigate the potentiating effect of a stretch-shortening cycle (SSC) (16, 34), augmentation in jump height from SJQ to CMJ was determined as the maximal SJQ height subtracted from that of the CMJ ($\Delta Fz$-height$_{CMJ}$). During the push-off phase, the vertical velocity of the CM was determined by integration over time of the acceleration, which, in turn, was calculated from the ground reaction force signal. The position of the CM was determined by time integration of the vertical velocity. To compare the two jump types, only their respective concentric phases were considered. In the CMJ, the concentric phase was defined as the time period of upward movement of the CM, while this phase constituted the entire push-off phase in the SJ. Peak force in the concentric phase was determined, and instantaneous vertical takeoff power was calculated as the product of force and CM velocity. Peak power and mean power were determined in the concentric phases of both jump types, and force and velocity at the instant of peak power were registered.

**Corrections to body size.** Based on dimensional theory (5, 24) and on the empirical annotations of Markovic and Jaric (43), the present data were expressed relative to body mass using the allometric...
parameters listed in Table 1. The following equation was used to obtain the normalized parameter $P_n$:

$$P_n = P / BM^{ap}$$

where $P$ is the respective uncorrected parameter, BM is body mass, and $ap$ is the allometric parameter. To enable comparison to previous studies where normalization has not been performed, selected parameters are reported in Table 2 with no correction to body size, and, furthermore, additional correlations with absolute values are reported in Table 4. Statistics

For all parameters, a systematic bias between days was assessed with a Student’s $t$-test. Interday reproducibility was investigated by using coefficient of variance for duplicate measures (52) and linear regression analysis. Differences between jump types were investigated by using a paired $t$-test.

To determine associations between relevant parameters, linear regression analyses was performed, and Pearson product-moment correlations were computed, in which an $\alpha$-level of $P < 0.05$ was considered significant. For the correlation analyses, data of days 1 and 2 were averaged for all relevant parameters. Below, data are presented as means (SD) of test days 1 and 2.

RESULTS

Maximal isometric knee-extension torque (MVC) was 2.82 N·m$^{-1}$·kg$^{-1}$ (SD 0.51). Peak RTD and RTD at 0–30, 50, 100, and 200 ms (0 ms = onset of contraction) were 104.7 (SD 26.6), 55.8 (SD 19.9), 71.9 (SD 21.5), 63.5 (SD 14.4), and 45.0 (SD 8.3) N·m$^{-1}$·s$^{-1}$·kg$^{-0.67}$, respectively.

The stiffness of the VL aponeurosis-tendon structure at 50–90% MVC was 165.3 N·mm$^{-1}$·kg$^{-0.33}$ (SD 64.0), and the energy stored during ramp contractions (0–90% MVC) amounted to 253.8 mJ/kg (SD 83.5).

Maximal jump height was significantly greater for CMJ compared with SQJ [33.5 (SD 6.1) vs. 27.4 (SD 5.2) cm, $P < 0.01$], yielding a $\Delta$jump-height$\text{CMJ-SQJ}$ of 6.0 ± 3.0 cm (Table 3).

The mean power of the CM in the concentric phase of the CMJ was elevated ~55% compared with that of the SQJ [116.0 (SD 18.9) and 74.9 (SD 12.5) W/kg$^{0.67}$, $P < 0.01$], while peak power was similar between the two jump types [203.4 (SD 30.1) and 203.5 (SD 31.4) W/kg$^{0.67}$]. Similarly, peak $F_z$ in the concentric phase of the CMJ and in the SQJ was similar [102.4 (SD 13.7) and 105.9 (SD 10.8) N/kg$^{0.67}$]. $F_z$ and CM velocity at the instant of peak power were significantly different between jump types ($P < 0.01$) and amounted to 82.3 N/kg$^{0.67}$ (SD 6.7) and 2.5 m/s (SD 0.2) for the CMJ and 94.7 N/kg$^{0.67}$ (SD 9.0) and 2.2 m/s (SD 0.2) for the SQJ, respectively (Table 3).

Isometric RTD at 0–100 and 200 ms was positively related to the stiffness of the VL aponeurosis tendon complex ($r = 0.54$, 0.56, $r^2 = 0.30, 0.31, P < 0.05$) (Fig. 3), and a significant positive correlation was observed between maximal jump height in both jump types and stiffness ($r = 0.64, r^2 = 0.41, P < 0.05$ for SQJ and $r = 0.55, r^2 = 0.30, P < 0.05$ for CMJ) (Fig. 4). No correlation was observed between $\Delta$jump-height$\text{CMJ-SQJ}$ and stiffness or energy stored (Fig. 5).

Peak power and mean power exerted in the concentric phase of the CMJ and the SQJ were significantly correlated to connective tissue stiffness (Table 4), and, furthermore, a correlation was observed between stiffness and CM velocity at the instant of peak power for both types of jumps (Table 4). The correlation analysis between stiffness and $F_z$ at the instant of peak power reached significance for the SQJ and exhibited a trend toward a positive relation for the CMJ (Table 4). Peak force exerted in the concentric phase of the SQJ was significantly related to connective tissue stiffness, whereas, in the CMJ, only a tendency was observed (Table 4).

Table 1. Corrections to body size

<table>
<thead>
<tr>
<th>Variable</th>
<th>Unit</th>
<th>Allometric Parameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stiffness</td>
<td>N/mm</td>
<td>0.33</td>
</tr>
<tr>
<td>Energy</td>
<td>mJ</td>
<td>1.00</td>
</tr>
<tr>
<td>MVC</td>
<td>N·m</td>
<td>1.00</td>
</tr>
<tr>
<td>RTD</td>
<td>N·m$^{-1}$·s$^{-1}$</td>
<td>0.67</td>
</tr>
<tr>
<td>Jump height</td>
<td>cm</td>
<td>0.00</td>
</tr>
<tr>
<td>Jump power</td>
<td>W</td>
<td>0.67</td>
</tr>
<tr>
<td>Jump force</td>
<td>N</td>
<td>0.67</td>
</tr>
<tr>
<td>Jump velocity</td>
<td>m/s</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Allometric parameters were used to express the present data relative to body mass. MVC, maximum voluntary contraction; RTD, rate of torque development. The following equation was used to obtain the normalized parameter $P_n$: $P_n = P / BM^{ap}$, where $P$ is the respective parameter, BM is body mass, and ap is the allometric parameter.
Jump mechanography correlation analysis between change in stiffness and RTD in declines in stiffness and RTD have been reported, albeit previously (31, 44). With prolonged bed rest, simultaneous increase in RTD following a training intervention; however, no direct correlation was observed between isometric RTD and connective tissue stiffness in vivo. For dynamic muscle actions, an association was observed between maximal jump height and the stiffness of the force-transmitting tissues. Furthermore, the connective tissue stiffness was associated with muscular power, F
\text{\textsuperscript{\text{\textdegree}}}
, and CV values within the range of 0.81–0.98 and 1.4–4.3%, respectively.

**DISCUSSION**

The main findings of the present study were that a positive correlation was observed between rapid muscle force exertion characteristics (RTD) and connective tissue stiffness measured in vivo. For dynamic muscle actions, an association was observed between maximal jump height and the stiffness of the force-transmitting tissues. Furthermore, the connective tissue stiffness was associated with muscular power, F
\text{\textsuperscript{\text{\textdegree}}}
, and CV values within the range of 0.81–0.98 and 1.4–4.3%, respectively.

During isometric contractions, it has previously been observed that RTD (rise of isometric tension) decreases when a compliant structure is inserted between the subject and the force transducer (55). These data suggest that the compliance or stiffness of the force-transmitting structures (i.e., tendons and aponeuroses) is associated with explosive force exertion. More recent studies have observed concurrent gains in connective tissue stiffness (estimated by ultrasonography) and isometric RTD following a training intervention; however, no direct correlation analysis has, to our knowledge, been performed previously (31, 44). With prolonged bed rest, simultaneous declines in stiffness and RTD have been reported, albeit correlation analysis between change in stiffness and RTD in that study did not reveal any significant relation, which may, as pointed out by the authors, be due to the limited number of subjects (28). These observations have prompted the suggestion that increased tendon-aponeurosis stiffness augments the ability of the connective tissue to transmit contractile forces effectively (36, 39, 42), and the presently observed correlation between isometric RTD and connective tissue stiffness in well-trained individuals supports this proposal.

Other than effective force transmission, an additional physiological mechanism that may explain the present findings is the apparent change in muscle fiber length as a result of the deformation of the connective tissue during contraction. During maximal isometric contractions, the muscle fibers shorten considerably due to connective tissue compliance (23), and a high compliance of the force-transmitting tissues (i.e., low stiffness) likely results in a rightward shift on the force-velocity curve, yielding a potentially lower maximal force and thus RTD.

Previous work (1, 3, 46, 50, 51) has indicated that neural activation properties, such as motor unit firing frequency and motorneuron recruitment, influence the magnitude of RTD. Furthermore, muscle structural properties, such as the distribution of muscle fiber types, have influence on the ability of skeletal muscle to exert high peak force and rate of force development (2, 22, 49). Neural and muscle structural properties likely play the imperative role for RTD; however, the present data extend previous results by suggesting that the mechanical properties of connective tissue may account for up to ~30% of the variance in isometric RTD during maximal knee extensor contraction.

In contrast to previous observations (34), the present data revealed a positive correlation between VL connective tissue stiffness and jump performance (maximal jump height). These diverging results may relate to different methods of assessing jump height. In the present study, maximal jump height was determined by integration of the vertical force signal, whereas Kubo et al. (34) utilized “flight-time” analysis, which introduces potential error if the body segment position at landing (especially ankle and foot configuration) is different from that at takeoff. Albeit speculative, differences in subject training status may also play a role in the design of the present study were highly trained and accustomed to high knee extensor force exertion, which was presumably not the case in the previous study (training status was not reported).

It has previously been discussed whether the increase in jump height that occurs when an eccentric contraction precedes the concentric push-off phase (i.e., difference in jump height in SQJ vs. CMJ) is due to “elastic energy recoil” by means of release of energy stored in the connective tissue during the
eccentric phase (16, 26), or whether jump height enhancement occurs due to a potentiating effect on joint torque in the initial concentric phase resulting from the preceding eccentric contraction (10, 59). In the present study, this issue was addressed by correlating the enhancement in jump height from SQJ to CMJ to the elastic properties of the tendinous structures expressed as stiffness (determined from 50–90% MVC) and the energy storage during the entire ramp contraction (0–90% MVC). No relation was observed between Δjump-height\textsubscript{CMJ-SQJ} and the elastic properties of the aponeurosis-tendon structures, indicating that, at least for the knee extensor muscles, the increase in jump height with CMJ is mainly associated with the increased force output in the initial push-off phase that is a result of the preceding eccentric loading phase, which thus optimizes the kinetic impulse in the push-off phase. This observation is in line with the observations of Zajac (59) that, despite the fact that energy is stored and released in the connective tissue during a SSC, the gain in elastic recoil that would occur with a compliant tendon-aponeurosis complex is offset by the decreased ability to develop force fast. Previous studies based on similar methodology (32, 34) have reported an inverse correlation between stiffness and so called “prestretch augmentation” (determined as the difference in jump height between the two jump types relative to SQJ height). An additional correlation analysis for the present data where pre-stretch augmentation was calculated, according to the previous method, did not reveal a significant relation, and as such the results seem contradictory. However, the study of Kubo et al. (32) demonstrated that this relation was less strong in well-trained, long-distance runners compared with untrained subjects, and therefore the apparent disparity between study data may be explained by differences in subject training status. Albeit speculative, present and previous results suggest that the stiffness of the VL tendon-aponeurosis structures increases with daily loading (training), and, although additional factors such as rebound resilience determines the magnitude of energy that is returned when a system under tension is released, an increased stiffness implies a decreased ability to store and release energy during SSC-type movement tasks. It seems plausible, however, that, despite a high training load, other muscle groups (e.g., triceps surae) may contribute to substantial elastic energy storage and release due to a large tendon-to-muscle fiber length ratio. Previous studies have proposed that, for any muscle-tendon unit, a “trade-off” exists with respect to “position control” vs. “energy storage” that is directly related to the design of the tendon (thick and short vs. long and thin) (9, 25, 59) and that proximal leg extensors mainly exhibit the ability to control position (or force transmission), which is thus consistent with the present findings.

Jump performance is logically evaluated by jump height, but, because jumping is a highly complex movement task, the ground reaction force signal was examined in detail to elucidate the mechanical characteristics of the jump (15, 45). Maximal jump height is mainly determined by the power generated by the knee extensor muscles during the concentric push-off phase, which was confirmed by a strong relation between jump height in both jump types and mean and peak power in the concentric phase (r = 0.84–0.94). The jump
power generated in the push-off phase is composed of the $F_z$ and CM velocity, and, in both jump types, positive relations were observed between velocity at peak power and stiffness, whereas force at peak power and stiffness was associated only for SQJ while approaching significance for CMJ. The jump height was associated with connective tissue stiffness, and, combined with the observed relations between jump height and force and velocity, it seems that also in complex movement tasks that include dynamic muscle actions such as jumping, the ability of the connective tissue to transmit force effectively (i.e., stiffness) from the contracting elements to the bone has importance for optimal jump performance. Previous studies have emphasized the importance of correcting for scale when comparing measures of physical performance to avoid influence of body size. The present data were normalized to body mass based on an allometric approach that has recently been evaluated (24, 43). Previous studies in the present field have not applied such normalization, which probably also contributes to the diverging results discussed above. The present data were also analyzed without normalization for body size, and, although somewhat stronger correlations occurred for some parameters, the overall pattern remained similar to that of the normalized parameters (Table 4).

The current method of assessing tissue mechanical properties has been evaluated previously and is well established (18, 23, 35, 38, 40); nonetheless, it is associated with inherent limitations. The calculation of mechanical properties remains an approximation, as it is not presently feasible to distinguish between the force contribution from VL vs. other muscle compartments, and as part of the measured deformation is related to total knee extensor muscle force, as previously discussed by Bojsen-Moller et al. (11). Furthermore, the method does not distinguish between aponeurosis and tendon deformation, respectively, and as such no inference can be made with the current method as to the respective roles of these tissues for contractile performance. Finally, it should be noted that, despite the fact that stiffness has been shown to be largely insensitive to strain rate (25, 57, 58), it cannot be discounted that the difference in strain rate between maximal vertical jumping and graded 10-s contractions may influence the results.

Albeit speculative, it may be suggested from the present and previous studies (28, 32) that training status and years of daily loading increase the stiffness of the aponeurosis-tendon structures. Also, training studies on humans have demonstrated increases in tendon stiffness; however, the findings are not consistent (21, 29–31, 44). Most training studies have been performed on untrained or elderly subjects, and it remains unsolved whether connective tissue stiffness plays a role with respect to training for athletic performance and whether specific performance gains can be achieved in individual sports disciplines. It appears, however, that, in the elderly population, the demand for a high RTD may be of importance, e.g., when an external perturbation entails a rapid postural correction (1), and the results of Reeves et al. (44), where a strength training regimen performed on elderly subjects yielded a great increase in tendon stiffness and RTD, may prove important for the

Table 4. Associations between stiffness and relevant parameters obtained during isometric and dynamic muscle actions

<table>
<thead>
<tr>
<th></th>
<th>Absolute Values</th>
<th>Normalized to Body Mass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r$</td>
<td>$r^2$</td>
</tr>
<tr>
<td>Isometric contractions</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RTD, 100 ms</td>
<td>0.65*</td>
<td>0.42</td>
</tr>
<tr>
<td>RTD, 200 ms</td>
<td>0.69*</td>
<td>0.48</td>
</tr>
<tr>
<td>CMJ</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jump height</td>
<td>0.55*</td>
<td>0.30</td>
</tr>
<tr>
<td>Peak force</td>
<td>0.54*</td>
<td>0.29</td>
</tr>
<tr>
<td>Concentric phase</td>
<td>0.65*</td>
<td>0.42</td>
</tr>
<tr>
<td>Peak power</td>
<td>0.60*</td>
<td>0.36</td>
</tr>
<tr>
<td>Concentric phase</td>
<td>0.51</td>
<td>0.26</td>
</tr>
<tr>
<td>Velocity at peak power</td>
<td>0.58*</td>
<td>0.34</td>
</tr>
<tr>
<td>SQJ</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jump height</td>
<td>0.65*</td>
<td>0.42</td>
</tr>
<tr>
<td>Peak force</td>
<td>0.60*</td>
<td>0.36</td>
</tr>
<tr>
<td>Mean power</td>
<td>0.63*</td>
<td>0.40</td>
</tr>
<tr>
<td>Peak power</td>
<td>0.67*</td>
<td>0.45</td>
</tr>
<tr>
<td>Force at peak power</td>
<td>0.55*</td>
<td>0.30</td>
</tr>
<tr>
<td>Velocity at peak power</td>
<td>0.57*</td>
<td>0.33</td>
</tr>
<tr>
<td>$\Delta$Jump-height$_{CMJ-SQJ}$</td>
<td>0.11</td>
<td>0.01</td>
</tr>
</tbody>
</table>

*Significant correlation between the stiffness of the tendon-aponeurosis structure and the respective parameter, $P < 0.05$. 

J Appl Physiol • VOL 99 • SEPTEMBER 2005 • www.jap.org
development of specific training recommendations to avoid fall-related injuries in this population.

In conclusion, the present data demonstrated that the ability for trained individuals to perform “explosive” knee extensor muscle contractions is related to the mechanocharacteristics of the tendon-aponeurosis complex. A positive correlation was observed between isometric RTD and connective tissue stiffness, and under dynamic conditions an association was observed between the stiffness of the force-transmitting tissue and jump performance and force- and velocity-related determinants of jump performance. These data indicate that muscle performance in high-intensity isometric and dynamic muscle actions relies in part on effective force transmission from the contractile elements to the skeleton.

ACKNOWLEDGMENTS
The authors express gratitude toward the staff at the Institute of Sports Medicine Copenhagen for valuable help.

GRANTS
This work was supported by the national Danish organization for elite sports; Team Danmark, the Danish Research Agency, The Danish Medical Research Foundation (22-01-0154), and Hovedstadsens Sygehusfællesskab Research Foundation.

REFERENCES


