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Interaction between gastrocnemius medialis fascicle and Achilles tendon compliance: a new insight on the quick-release method

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[1]*Research Department, National Institute for Sports, INSEP, Paris;* [2]*AP-HP, Hôpital Rotschild, Department of Neuro-Orthopaedic Rehabilitation, Paris;* [3]*University Paris-Est, EAC CNRS 4396, Créteil; and* [4]*University of Nantes, Laboratory "Motricité, Interactions, Performance", EA 4334, Nantes, France*

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Farcy S, Nordez A, Dorel S, Hauraix H, Portero P, Rabita G. Interaction between gastrocnemius medialis fascicle and Achilles tendon compliance: a new insight on the quick-release method. *J Appl Physiol* 116: 259–266, 2014. First published December 5, 2013; doi:10.1152/japplphysiol.00309.2013.—The insufficient temporal resolution of imaging devices has made the analysis of very fast movements, such as those required to measure active muscle-tendon unit stiffness, difficult. Thus the relative contributions of tendon, aponeurosis, and fascicle to muscle-tendon unit compliance remain to be determined. The present study analyzed the dynamic interactions of fascicle, tendon, and aponeurosis in human gastrocnemius medialis during the first milliseconds of an ankle quick-release movement, using high-frame-rate ultrasonography (2,000 frames/s). Nine subjects performed the tests in random order at six levels of maximal voluntary contraction (MVC) (30% to 80% of MVC). These tests were carried out with the ultrasound probe placed on the muscle belly and on the myotendinous junction. Tendon, muscle fascicle, and aponeurosis length changes were quantified in relation to shortening of the muscle-tendon unit during the first few milliseconds following the release. The tendon was the main contributor (around 72%) to the shortening of the muscle-tendon unit, whereas the muscle fascicle and aponeurosis contributions were 18% and 10%, respectively. Because these structures can be considered in series, the quantified contributions can be regarded as relative contributions to muscle-tendon compliance. These contributions were not modified with the level of MVC or the time range used for the analysis between 10 and 25 ms. The constant contribution of tendon, muscle fascicle, and aponeurosis to muscle-tendon unit compliance may help to simplify the mechanism of compliance regulation and to maintain the important role of tendons in enhancing work output and movement efficiency.

ultrafast ultrasound; aponeurosis; interactions; compliance

THE CHARACTERIZATION OF THE mechanical properties of the series elastic element (SEE) is fundamental to a better understanding of its role in the whole muscle-tendon unit and the mechanisms responsible for muscle adaptation to modified functional demand (pathology or training) (23). According to the Hill's muscle model (31), the SEE represents the nonlinear spring elements in series with the contractile elements. Several authors have modified this model and specified the SEE location in the tendinous (tendon and aponeurosis) tissues and in the myofilaments (57, 61). To measure its compliance in humans, classical methods were adapted from isolated muscle techniques such as quick-release (QR), controlled-release, or short-range stretching methods. For instance, numerous studies have used QR to investigate changes in musculotendinous stiffness induced by training programs (26, 50), immobilization (43) or neuromuscular diseases (10, 11), or to compare musculotendinous stiffness between different populations (41, 44, 52, 53). This QR method consists of a sudden and fast release of the isometrically contracted muscle, as a "catapult-like" movement, using a specific ergometer (42, 59). Compliance is then calculated using the estimated ratio between the change in joint angle and the change in torque. In vivo, this methodology that only take into account the first few milliseconds after the release (classically 20–25 ms) provides the opportunity to specifically focus on the SEE (24, 33, 51, 59) based on the following assumptions: *1*) shortening velocity exceeds the maximal shortening velocity of the active part of the contractile element, and *2*) muscle activation is constant (3, 24). Nevertheless, only few studies quantified in vivo the QR movement characteristics with regard to the required velocity (33, 34), and, because of technological limitations, no study directly measured the shortening velocity of the muscle fascicles. In addition, the QR method alone does not allow for the differentiation of the relative contribution of the tendon, aponeurosis, and muscle fibers to the global stiffness of the SEEs.

In passive conditions, the relative contributions of tendon and fascicle to the muscle-tendon unit stiffness have been quantified using ultrasound in plantar flexors muscles (1, 29, 30). Contrary to previous considerations (22), these studies show that, even passively for the gastrocnemius muscle-tendon unit, the compliance of tendon structures is about 70% of the muscle-tendon unit compliance (29). Regarding active conditions, many studies (for review, see Ref. 13) focused on the interactions between muscle fascicle and tendinous tissues during dynamic activities such as walking (12, 45), running (37), or jumping (36). However, to the best of our knowledge, no investigation has quantified the relative contribution of tendon, aponeurosis, and fascicle to muscle-tendon unit compliance. This may be due, at least in part, to the technological limitations of imaging devices, especially insufficient temporal resolution, which make the analysis of very fast movements, such as those required for the stiffness measurement of SEEs, difficult. Recent technological innovation in ultrasound imaging presently allows for the study of tissue displacements during very fast human movement at up to 20,000 frames per second (15, 49). For example, Nordez et al. (49) used high-frame-rate ultrasound (4 kHz) to determine the relative contribution of the passive parts of the SEEs to the electromechanical delay that last around 10 ms.

Using a high-frame-rate ultrasound scanner, the present study was designed to characterize the dynamic interactions between the gastrocnemius medialis fascicle, aponeurosis, and the Achilles tendon during a QR movement. Its originality

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resides in the fact that the experimental conditions allow quantifying, on the basis of the length variation of each structure, the relative contributions of their respective compliance with respect to the compliance of the global muscle-tendon unit. As the commonly used model is based on the assumption that the three structures are placed in series (61), the force variations were equivalent among the structures. Consequently, the contribution in length variation of each structure refers to its contribution in compliance. Considering that fascicles are stiffer during contractions, it was hypothesized that the contribution of tendinous tissues (i.e., tendon and aponeurosis) to muscle-tendon unit compliance would be higher than during passive conditions (i.e., about 70%) (29) and that this contribution increases with the level of muscle force.

MATERIALS AND METHODS

Participants

Nine healthy males volunteered to participate in the study. Their physical characteristics were as follows (means ± SD): age 25.0 ± 8.4 yr; height 175.7 ± 7.7 cm; body mass 67.7 ± 3.0 kg. They had no history of neurological or musculoskeletal pathology. Informed consent, in accordance with the approval of the local ethical committee, was obtained from all subjects before the experiment. This study was conducted according to the Helsinki Statement (last modified in 2004).

Materials

Ergometer. The ankle ergometer used in this study has been described in details previously (42). Briefly, it comprises a bench and an adjustable rotational footplate. Angular displacement was measured with an optical absolute encoder. Isometric force was obtained using an S-type load cell connected to an electromagnet, ensuring the isometric conditions of the muscles. Specific software digitally recorded the ankle angle and isometric force (10,000-Hz sampling frequency) via an acquisition card (type ATMIO16, National Instrument) driven by a commercialized software (Daqware, National Instrument). A computer provided the subjects and the experimenters with visual feedback of torque developed as a percentage of the maximal contraction.

Ultrasonography. An ultrafast ultrasound scanner (US, Aixplorer, Supersonic Imagine), coupled with a linear transducer array (4–15 MHz, SuperLinear 15–4, Vermon) was used. Ultrasonic raw data (i.e., RF signals) obtained at 2 kHz using the very-high-frame-rate ultrasound device were used to create echographic images by applying a conventional beam formation, i.e., applying a time-delay operation to compensate for travel time differences. A trigger out was used to synchronize ultrasound and ergometer data via the above-mentioned acquisition card.

Experimental Protocols

During the experimentations, the participants lay prone on a table with the knee fully extended and the ankle joint in a neutral position (foot-leg angle: 90°). The participants were positioned so that the bimalleolar axis of the ankle was aligned with the ergometer rotation axis.

After a standardized warm-up, two plantar flexion maximal voluntary contractions (MVC) in isometric conditions were performed. The best performance was considered as the MVC. Second, QR tests were performed at 30, 40, 50, 60, 70, and 80% of MVC in random order. The QR test consisted of a sudden and fast release of the actuator while the subject performed an isometric plantar flexion with the foot perpendicular to the shank. Isometric contractions were sustained at a given percentage of the MVC using visual feedback displayed to the experimenter and to the subject. To avoid any subject anticipation that could affect the neural drive, the timing of release was unknown from the subject. For each torque level, QR tests were performed twice in a random order, i.e., with the ultrasound probe placed over the muscle belly and the myotendinous junction (MTJ). During muscle trials, the ultrasound probe was maintained over the gastrocnemius medialis muscle parallel to the muscle fascicles and perpendicular to the skin, as described in Blazevich et al. (7). Appropriate probe alignment was achieved when several fascicles could be traced without interruption across the image. During the tendon trials, the probe was maintained on the distal MTJ (48). A pilot study was performed to ensure that the fastening system did not induce any movement of the probe over the skin.

Data Analyses

Data were processed offline with Origin 8.5 (OriginLab) and Matlab (The Mathworks) software.

Ergometer mechanical parameters. A zero-phase low-pass filter (100 Hz) was applied to the angle data θ_a and its derivative θ'_a. For each QR trial, the following parameters were analyzed: *1*) isometric torque just before the release (T_{iso}); *2*) changes in ankle angular position ($\Delta\theta_a$), and changes in angular acceleration ($\Delta\theta_a''$, obtained as second derivative of $\Delta\theta_a$ and filtered at 100 Hz low-pass) within the first 25 ms from maximal acceleration after the beginning of the QR movement; *3*) inertia (I) calculated by considering the transition between the static and dynamic phases, where acceleration is maximal ($\theta_a''_{max}$) and instantaneous torque is theoretically equal to the isometric torque ($I = T_{iso}/\theta_a''_{max}$) (51, 59). The maximum of the acceleration was then considered in the analysis of ultrasound data as the onset of the release (i.e., time = 0). Angular musculotendinous stiffness (K_{MT}) was measured according to the formula: $K_{MT} = I\Delta\theta_a''/\Delta\theta_a$.

Ultrasound images. The tracking of the distal MTJ was done manually using a specific Matlab script. It consisted of marking the position of the junction on each image. For each test, the procedure was performed four times, so we could calculate the mean displacement over time of the junction, D_{MTJ}, which represents the length variation of the muscle (Fig. 1). A 150-Hz low-pass filter was applied to D_{MTJ}.

A software developed by Cronin et al. (12) was used to track the muscle fascicle and superficial and deep aponeurosis (Figs. 2 and 3). Because the complete fascicle was not always visible, the change in the length of the fascicle was calculated by the extrapolation of aponeurosis and fascicle. We multiplied L_f by the cosines of the angle of pennation α to obtain the horizontal length variation of the muscle. The shortening velocity (in cm/s) of the fascicles was obtained as first

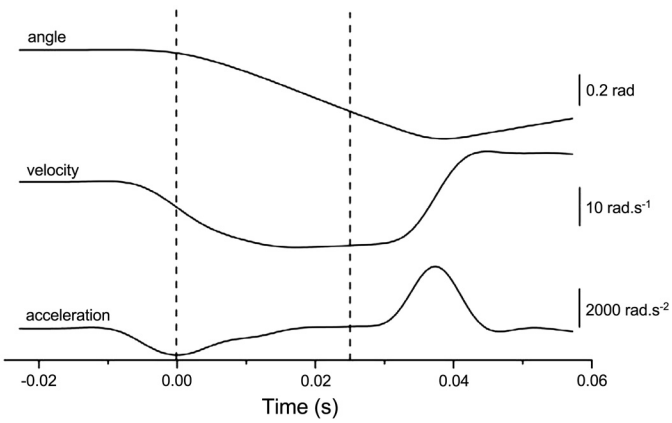


Fig. 1. Typical example of instantaneous ankle angle, angular velocity, and angular acceleration during a quick-release (QR) movement performed at 70% of maximal voluntary contraction (MVC). The vertical dashed lines represent the 25-ms window analysis from the maximal acceleration (t_0).

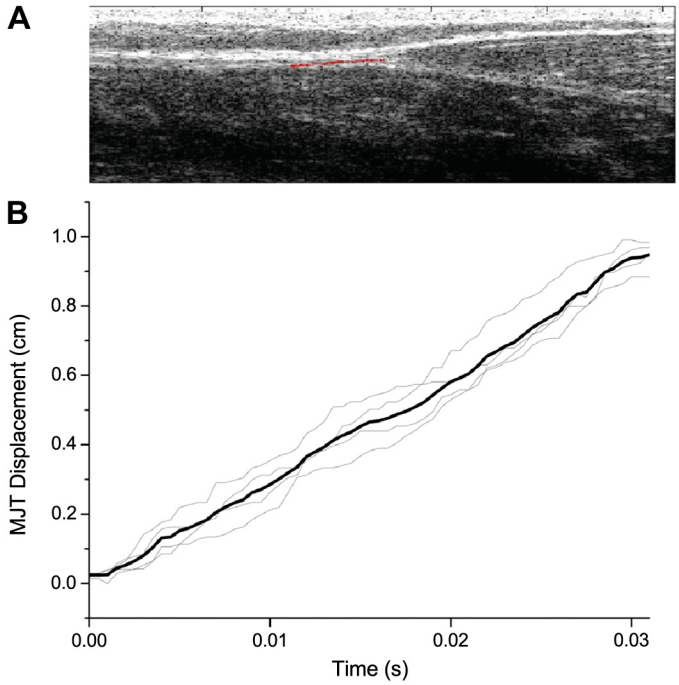


Fig. 2. *A*: typical example of ultrasound image analysis used for quantifying the myotendinous junction (MTJ) displacement. The red circles represent the successive positions of the MTJ during the QR movement. For each QR trial, this analysis was repeated 4 times by the experimenter. *B*: MTJ displacement (in cm) represented over the time (in seconds). The gray lines represent the 4 repeated measurements, and the black line corresponds to their mean values.

derivative of the fascicle length. To also express the shortening velocity in fiber length/s (*FL*/s), based on previous studies (33, 38), the gastrocnemius medialis fascicle length at rest (l_0) was estimated to be equal to 5 cm.

We used the following formula (25) to calculate the instantaneous length of the gastrocnemius medialis muscle-tendon unit (L_{MTU}) at any position of the ankle during the QR movement: $L_{MTU} = l_{ref} + (A0 + A1 \cdot \theta_a + A2 \cdot \theta_a^2 + K0 + K1 \cdot \theta_k + K2 \cdot \theta_k^2)l_s/100$, where l_{ref} is the reference length of gastrocnemius, l_s is the length of the shank, θ_a is ankle angle, and θ_k is knee angle ($\theta_k = 0$ when the thigh and leg are parallel). The parameter l_{ref} is the length measured between the lateral epicondyle of the femur and the tip of the lateral malleolus when the knee and ankle are both at 90°. The parameter l_s is defined as the distance between the centers of rotation of the knee and ankle joints. The instantaneous ankle angle θ_a during the QR movement was obtained from the optical absolute encoder. The coefficients A0, A1, and A2 are respectively, −22.18468, 0.30141, and −0.0006, and the coefficients K0, K1, and K2 are respectively, 6.46251, −0.07987, and 0.00011. To combine the analysis of the various parameters, the mechanical angle data were resampled to correspond to the ultrasound images for each trial.

The distal tendon length was calculated by subtracting the MTJ displacement from the muscle-tendon unit length. The aponeurosis length was calculated by subtracting the distal tendon length and the muscle fascicle horizontal length from the muscle-tendon unit length. The relative contribution of each element was obtained calculating the ratio between the length of each element and the muscle-tendon unit length. Change in length of the various elements was calculated from the maximum of the acceleration of the ankle angle (i.e., time = 0) until the end of the plantar flexion. Then, to match the time of all the results, the data were interpolated throughout the range of motion at 100 equally spaced points.

Statistical Analysis

To assess the repeatability of mechanical data between both conditions (muscle and tendon), the intraclass correlation coefficient (ICC), standard error of the mean (SE), and coefficient of variation (CV) were calculated (35) for K_{MT} obtained at the different torque levels.

To evaluate the effect of *1*) the structure (tendon, muscle fascicle and aponeurosis), *2*) the level of torque (30, 40, 50, 60, 70, and 80% of MVC), and *3*) the time range (5, 10, 15, 20, 25 ms) from the maximal acceleration (t_0) on the contribution of the muscle-tendon unit shortening, a three-way, repeated-measures ANOVA was carried out (Statistica). A post hoc analysis (Newman-Keuls) was performed when appropriate. The critical level of significance in the present study was set at $P < 0.05$.

RESULTS

The main data relative to the ankle angular and muscle fascicle shortening velocities are presented in Fig. 4 and Table 1. For QR trials carried out at 30 and 80% MVC, the ankle angular velocity reached 12.02 ± 1.24 and 23.12 ± 1.40 rad/s, respectively. For these trials, the associated maximal shortening velocity of muscle fascicles ranged from 14.03 ± 1.40 to 23.19 ± 10.97 cm/s, respectively.

The repeatability of mechanical data, especially K_{MT}, between the two sets of QR measures on muscle belly and tendon, respectively, is shown in Table 2. The mean ICC is 0.90, and the mean CV is 5.03%.

The shortening of the whole muscle-tendon unit and of each of its components (tendon, muscle fascicle, and aponeurosis) during the QR movement is shown in Fig. 5. The change in length of the tendon was about four times higher than muscle

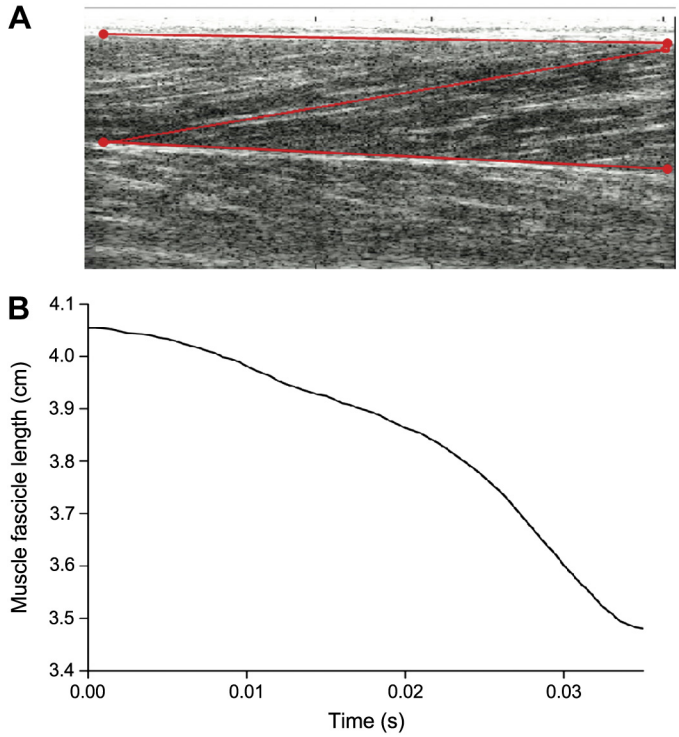


Fig. 3. *A*: example of muscle fascicle length analysis using ultrasound images using the software of Cronin et al. (11). *B*: typical example of instantaneous muscle fascicle length (in cm) represented over the time (in seconds) during a QR.

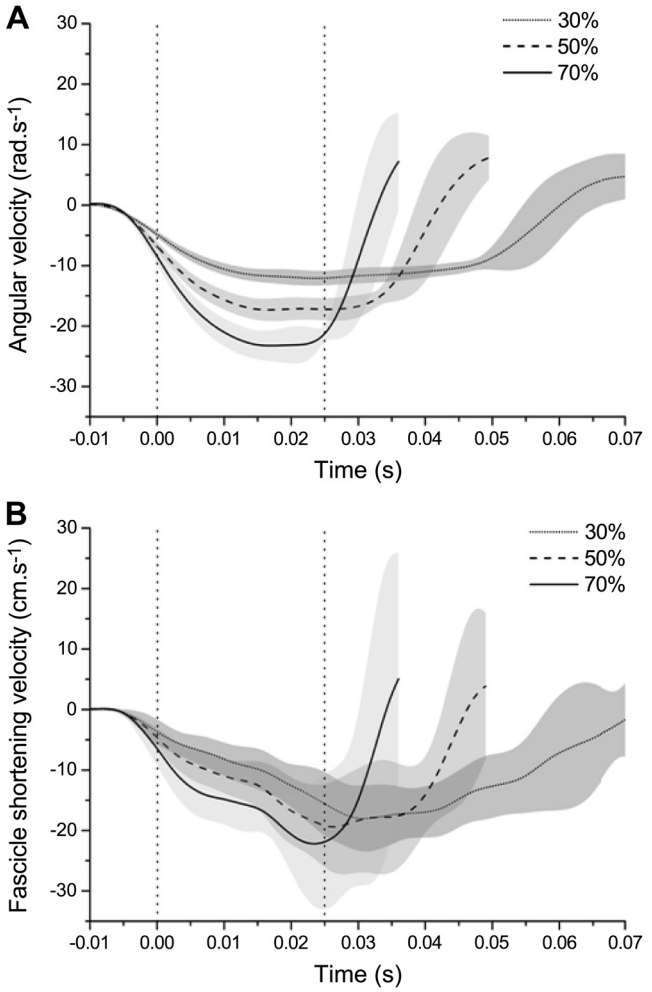


Fig. 4. Mean values (± SD) of ankle angular velocity (in rad/s) during QR experiments carried out at 30 (gray line), 50 (dashed line), 70 (black line) % of MVC (*A*) and fascicle shortening velocity (in cm/s) of the gastrocnemius medialis (*B*) during QR experiments carried out at 30 (gray line), 50 (dashed line), 70 (black line) % of MVC. The vertical dashed lines represent the 25-ms window analysis from the maximal acceleration (t_0).

fascicle and seven times greater than aponeurosis. The relative contributions of each structure to the muscle-tendon shortening are represented over time in Fig. 6.

The three-way ANOVA showed nonsignificant time × torque × structure, time × torque, and structure × torque interactions ($P > 0.05$). However, the ANOVA showed a main effect for structure ($P < 0.0001$) and a significant time × structure interaction ($P < 0.0001$). Figure 7 shows the mean contribution of each structure (tendon, muscle fascicle, aponeurosis) to the shortening of the muscle-tendon unit for all levels of torque and during the 25-ms window from maximal acceleration. Tendon was the main contributor (72.5 ± 9.5%) of the shortening of the muscle-tendon unit, whereas muscle fascicle and aponeurosis contributed about 17.7 ± 5.3% and 9.7 ± 8.6%, respectively.

The post hoc time × structure interaction showed no significant difference between the relative contributions measured at 25 ms for each structure and their respective contribution at 5, 10, 15, and 20 ms ($P > 0.05$), except for aponeurosis between the contribution at 25 ms and 5 ms ($P < 0.01$; Fig. 8).

Table 1. *Ankle angular and muscle fascicle shortening velocities*

Torque, % of MVC	30	80
Ankle velocity, rad/s		
Mean velocity, 0–25 ms	10.21 ± 0.98	21.97 ± 1.84
Maximal velocity, 20–25 ms	12.02 ± 1.24	23.12 ± 1.40
Fascicle-shortening velocity, cm/s		
Mean velocity, 0–25 ms	9.32 ± 2.81	17.89 ± 5.15
Maximal velocity, 20–25 ms	14.03 ± 4.43	23.19 ± 10.97
Fascicle-shortening velocity, length/s with theoretical l_0=5 cm		
Mean velocity, 0–25 ms	1.86 ± 0.56	3.57 ± 1.03
Maximal velocity, 20–25 ms	2.80 ± 0.88	4.63 ± 2.19

Values are means ±SD in ankle angular, fascicle-shortening velocity in cm/s, and fascicle-shortening velocity in length/s during the quick-release movement measured over the entire analysis window (0–25 ms; mean velocity) or over the last 5 ms (20 and 25 ms; maximal velocity). The value of 5 cm was used as a theoretical gastrocnemius medialis length l_0 for calculation of fascicle-shortening velocity in length/s (40'). MVC, maximal voluntary contraction.

DISCUSSION

The ultrafast ultrasound scanner allowed us to quantify the length changes in medial gastrocnemius fascicle, tendon, and aponeurosis during a QR of the contracted plantar flexors. Considering that fascicle, aponeurosis, and tendon are placed in series, their length changes were used to assess the relative contributions of their compliance to the muscle-tendon unit compliance. The main results were that, inside a 25-ms window following the release, *1*) the tendon contributes on average to around 72% of the muscle-tendon unit compliance, whereas the fascicle and aponeurosis contributions are only about 18% and 10%, respectively; *2*) the structure contributions do not depend on the contraction level between 30 and 80% of MVC; and *3*) these contributions are constant over time after 5 ms.

Ankle joint and gastrocnemius fascicle shortening velocities were measured to discuss whether applying the QR method in vivo gives the possibility to evaluate the SEE properties excluding any contribution of the contractile elements. For that purpose, the above-mentioned underlying assumption implies that the muscle-shortening velocity is higher than the maximal velocity of the contractile elements.

For the first time, the shortening velocity of the muscle fascicles were measured during QR experiments. However, the comparison with the actual muscle maximal shortening velocity (V_{max}) is complex, especially because a direct measurement is not possible in vivo in human. In addition, in vitro measure-

Table 2. *ICC and CV values for musculotendinous stiffness and length changes*

Torque,% MVC	30	40	50	60	70	80	Mean
Stiffness							
ICC	0.84	0.90	0.94	0.90	0.83	0.96	0.90
CV	5.7	4.3	4	5.1	6.5	4.6	5.03
MTU Length Changes							
ICC	0.77	0.82	0.91	0.89	0.97	0.98	0.89
CV	6.4	6.6	4.2	5.9	3.3	2.3	4.7

Intraclass correlation coefficient (ICC) and coefficient of variation (CV) values for the musculotendinous stiffness and length changes calculated with the two sets of quick-release measures (muscle belly and myotendinous junction) for each level of torque. MTU, muscle-tendon unit.

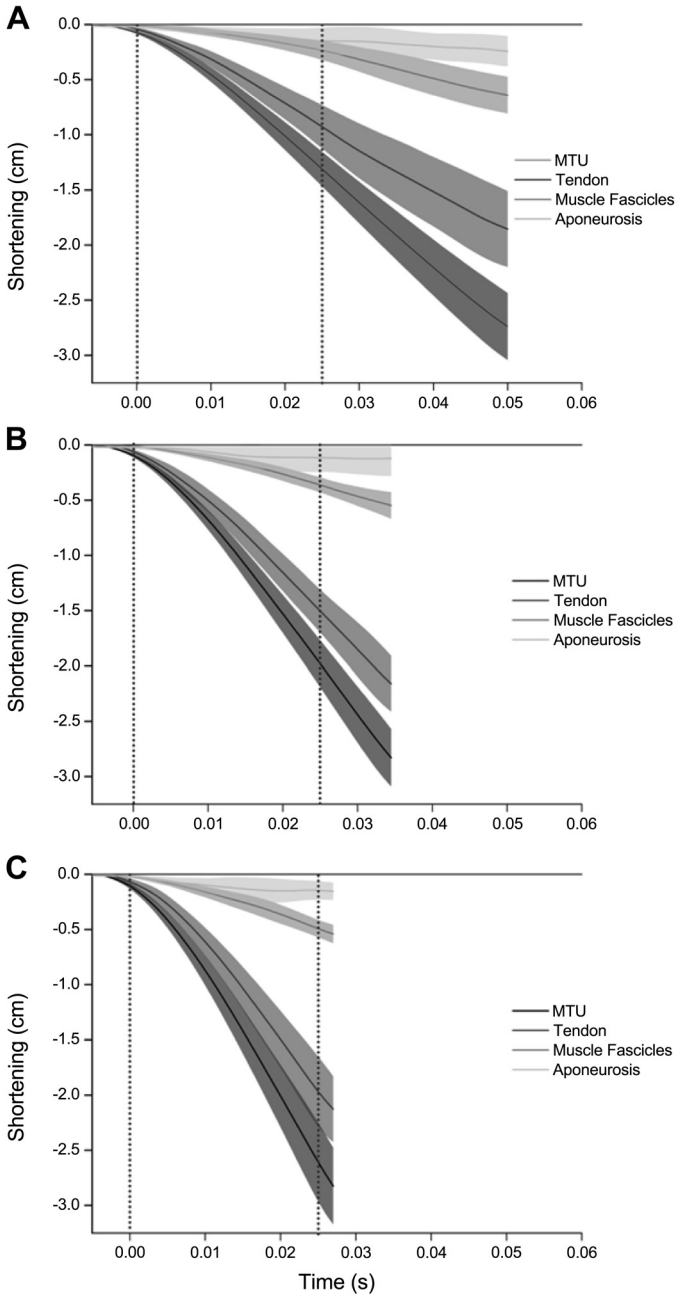


Fig. 5. Mean values (± SD) of the shortening patterns of the different structures [muscle tendon unit (MTU), muscle fascicles, tendon, and aponeurosis] during QR experiments imposed at 30% (*A*), 50% (*B*), and 70% (*C*) of MVC. The vertical dashed lines represent the 25-ms window analysis from the maximal acceleration (t_0).

ments in human from biopsy investigations present a wide range of maximal shortening velocity. Indeed, maximal shortening velocities were reported from lower than 0.5 to about 1.5 *FL*/s (type I fibers, 8, 16, 20, 29, 47, 10, 21, 26, 69), and from 0.5 to about 4 *FL*/s (type IIa, IIax, or IIx fibers, 8, 16, 10, 21, 20, 29, 47, 69, 16, 50, 53). With consideration of the size principle (27, 28), type I fibers mainly contribute to the steady-state contraction before the release (14, 40) for lowest contraction intensity. Thus, for low contraction levels, such as for higher contraction levels, shortening velocities (from about 2.80 ± 0.88 *FL*/s for 30% of MVC to about 4.63 ± 2.19 *FL*/s for 80% of MVC) could be slightly higher than the maximal shortening velocities. However, this comparison at the fascicle level with in vitro measurements is quite speculative.

At a joint level, the threshold classically used in the literature is about 10 rad/s (33). All the experiments performed in the present study induced angular velocities higher than this threshold. Interestingly, Sasaki and Ishii (56) have quantified in vivo the maximal shortening velocity on the basis of the time

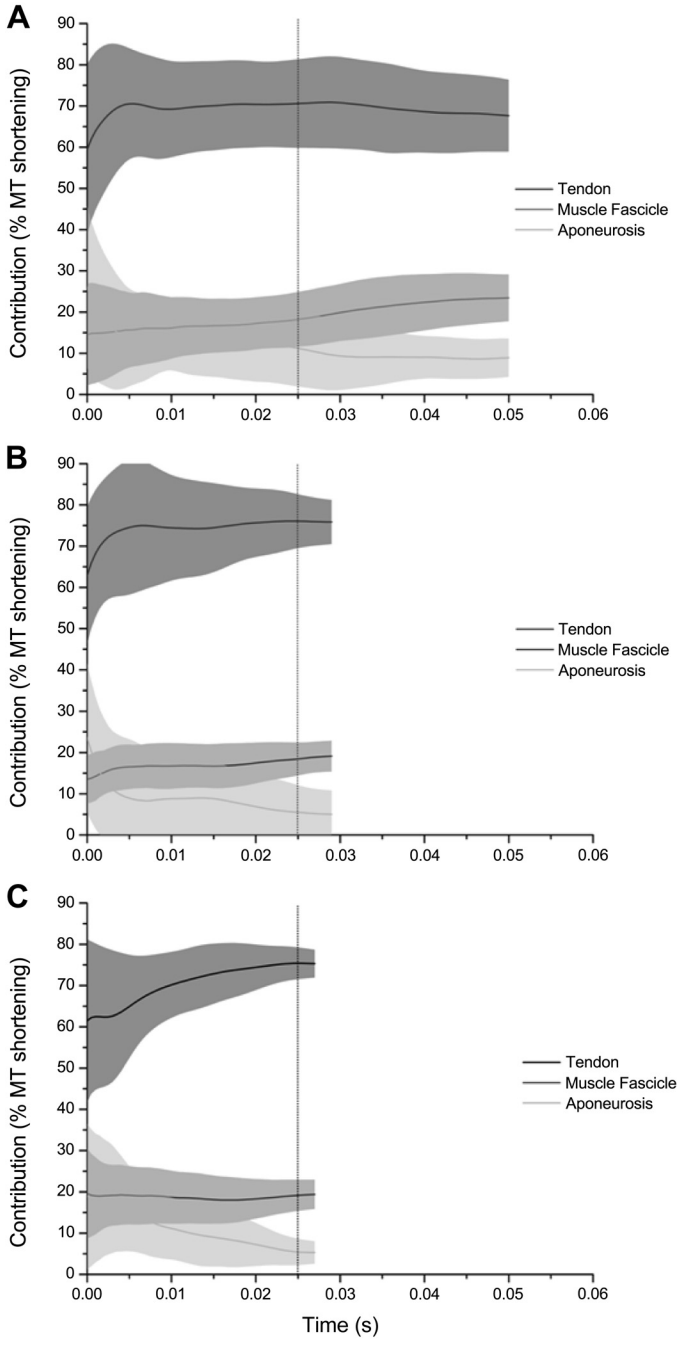


Fig. 6. Mean values (± SD) of the shortening contribution of the different structures (muscle fascicles, tendon, and aponeurosis) on the shortening of the whole muscle-tendon (MT) unit during QR experiments imposed at 30% (*A*), 50% (*B*), and 70% (*C*) of MVC. The vertical dashed lines represent the 25-ms window analysis from the maximal acceleration (t_0).

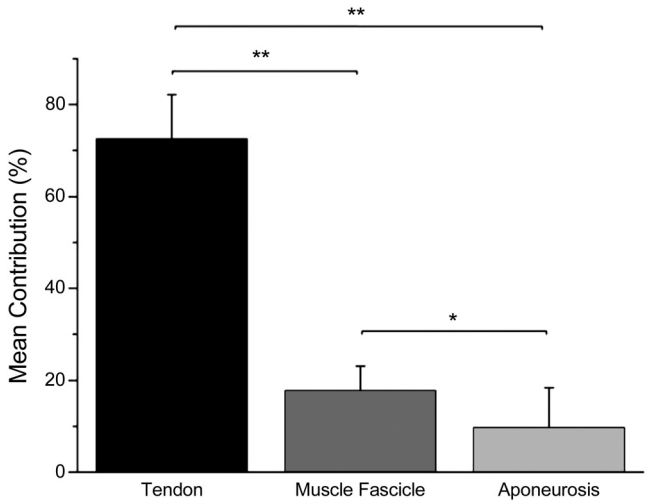


Fig. 7. Mean contribution (± SD) of tendon, muscle fascicle, and aponeurosis to the MTU compliance during the 25-ms window analysis from the maximal acceleration (t_0) of the QR and for all levels of torque. Significant difference between the structures at $^*P < 0.05$ and $^{**}P < 0.01$, respectively.

to torque redevelopment carried out by the contractile elements after QR experiments. In the same initial condition as in the present study, their slack test carried out on the human triceps surae muscles showed a mean maximal velocity of 8.6 ± 2.6 rad/s. This angular velocity is lower than the maximal ankle speed obtained in the present study, even at the lowest torque level (i.e., 30% of MVC; 12.02 ± 1.24 rad/s; 80% of MVC; 23.12 ± 1.40 rad/s). Therefore, these considerations at the ankle joint level suggest that, in our experiment, the contribution of contractile element to the shortening could be minor.

Furthermore, because shortening velocities increased gradually to reach the maximal values around 20–25 ms (Fig. 4), a higher proportion of the contractile element would have participated to the fascicle shortening during the first few milliseconds. However, no significant change between the contributions of fascicles and tendinous tissues were observed over time between 5 and 25 ms of the analysis window. Taken together, these arguments, without excluding the participation of the contractile element, suggest that its contribution to the fascicle shortening is limited compared with the contribution due to the SEE. Further studies are needed to directly and individually demonstrate the effective contribution of both parts to the muscle-tendon unit shortening.

The present study shows that the shortening of the tendon was on average around four times greater than muscle fascicle and seven times greater than aponeurosis length variations. These results are consistent with previous in vitro investigations, which have shown that tendinous tissues are mainly implied during the first phase of a "catapult-like" movement (4, 55, 60). Astley and Roberts (4), in frog jumping, observed that the plantaris longus muscle, which was shortened without ankle movement during the preload phase, only exhibited a minimal shortening in the first few milliseconds of the ankle extension despite a high angular acceleration of the joint. This indicates a substantial contribution of tendinous recoil to powering ankle movement. These findings are also in line with human studies that examined tendinous tissues (tendon and aponeurosis) and fascicle behavior in running (37) or jumping (36), which showed major participation of the tendinous tissues during the shortening of the plantar flexors muscle-tendon unit. Functionally, it is well-known that, during rapid release, the tendon operates as a power amplifier to enhance muscle-powered acceleration (8), as it is not bound by the constraints on shortening velocity that limit power output of muscle contractile elements (2, 32). The high contribution of tendon compliance of the active muscle-tendon unit optimizes this phenomenon in a catapult-like movement.

As detailed above, numerous studies have analyzed the dynamic interaction between tendon and muscle fascicles with an ultrasound system, especially by measuring the changes in the length of each structure during movement (21, 36, 37, 45). However, the methodology used here allowed us to assess for the first time, in active conditions, the compliance of these structures and their respective contributions to the whole muscle-tendon unit compliance. To our knowledge, this has only been studied previously in a passive condition. Herbert et al. (29, 30) have shown that, during imposed ankle mobilization, tendinous tissues (tendon and aponeurosis), albeit intrinsically less compliant than muscle, contribute to about 70% of the passive compliance of the gastrocnemius medialis. They explained this result by the fact that the Achilles tendon is about 10 times longer than the medial gastrocnemius fascicle. In the present study, a higher contribution of tendon and aponeurosis (around 82%) was observed. This can be explained by higher fascicle stiffness in active rather than passive conditions. It could be noticed that this result is only applicable to the QR movement. Regarding the dynamics of the system, the tendon can variably contribute to the overall length changes of the muscle-tendon unit depending on the force applied and the activation level (36, 37, 42).

The results of the present study show that the aponeurosis weakly contributes to the compliance of the musculotendinous system (<10% in average). This observation was expected considering that the compliance of the aponeurosis is reduced during active contractions, compared with passive loading (5, 16, 46, 62). Furthermore, the relative proportion of maximal lengthening between the Achilles tendon and the aponeurosis

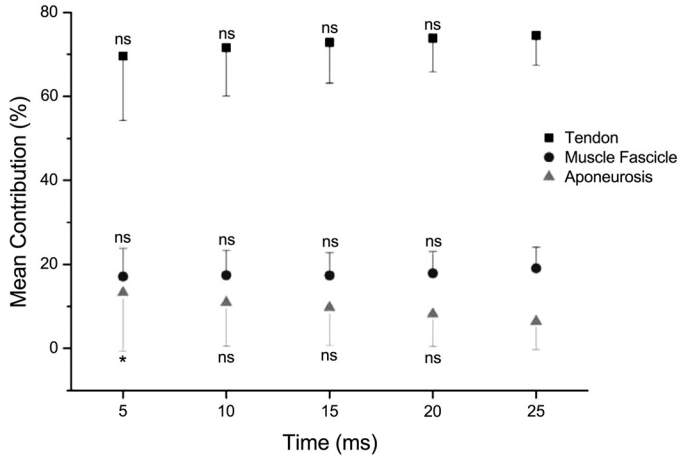


Fig. 8. Mean (± SD) values of the compliance contribution of each structure to the compliance of the muscle-tendon unit over time during the 25-ms window analysis from the maximal acceleration (t_0) of the QR and for all level of torque. *Significant difference with the data measured at 25 ms at $P < 0.01$. ns, nonsignificant difference.

mm) (39) was shown to be very close to the proportion of the shortening during the subsequent release phase. This suggests that, beyond intrinsic elastic properties, the lengthening during isometric contraction before the release plays a major role in the contribution of the compliance of each structure during the release. Taken together, these results partly explain why the aponeurosis compliance plays a minor role compared with tendon in the global compliance of the muscle-tendon unit in active conditions.

The second main result of the present study is that the relative contributions of the compliance of each structure to the whole muscle-tendon unit compliance were not influenced by the contraction intensity of the plantar flexors. In other words, tendon and muscle fascicle shortened in the same proportion when force increased, which meant that the ratio of tendon and fascicle length variation remained constant whatever the level of force. It has previously been observed that the presence of a compliant SEE presents a challenge to the motor control system, as the stretch of tendons decouples the length of muscle fascicle from the desired joint position (6, 54). From this point of view, the present results (constant ratio between the compliance of tendon, aponeurosis, and fascicle) reveal a mechanism that may help to simplify the control of compliance regulation while maintaining the important role of tendon in enhancing work output and movement efficiency. The implication for the motor control system has yet to be fully explored.

The third main result of the present study is the constant contribution of each structure to the total muscle-tendon unit shortening along the analysis time, except for the first 5 ms. This result is due to the proportional increase in the shortening of each structure over time. Thus, during this time, there are no mechanisms that induce a sudden and larger increase in the shortening of the muscle fascicle. This seems to be in agreement with the hypothesis that only the SEE contributes significantly to the acceleration of the ankle after the release (51, 59). This result also shows that, for in vivo QR experiments, an analysis time range that lasts between 10 and 25 ms (from the angular acceleration peak) can be taken into account in the analysis without any effect on the structure assessed. The statistical difference observed for the first 5-ms window should be considered with caution because the contribution was quantified for very small shortenings ($<$2–3 mm) of the tissues. The technique used here may be compared with the α-method (47) that has recently been adapted in vivo to estimate the stiffness of the active and passive part of the SEE of plantar flexors (9, 17, 19, 44, 58). This last method is mainly indirect because it calculates the stiffness of each part of the SEEs on the basis of only mechanical data (joint angle and external torque) and a model. This model is based on the assumptions that *1*) the stiffness of the active series elastic component is proportional to the torque (47) and *2*) the stiffness of the passive series elastic component is constant across the range of torque investigated. Experimental results obtained by Fouré et al. (18–20) support these hypotheses. On the other hand, because it was shown that contributions of fascicles and tendon to global compliance remain constant between 30% and 80% of the MVC during QR experiments, the results of the present study are not in accordance with the hypotheses of the α-method. The rationale for these discrepancies could be related to the main methodological differences between both methods (e.g., ms vs. 60 ms, and the analysis of one muscle-tendon unit vs. a global musculo-articular system, respectively). Further studies must be carried out to specifically characterize these dissimilarities.

The present study explored the dynamic interaction between tendon, muscle fascicle, and aponeurosis of the medial gastrocnemius during the first milliseconds of a QR movement and quantified the respective contributions to the global compliance of the muscle-tendon unit in active conditions. Tendon compliance was found to be the major contributor without any change in the level of force or time of analysis. Methodologically, the quantification of the compliance of tendon, muscle fascicle, and aponeurosis, combining both QR and ultrafast ultrasound system, opens clinical perspectives in the evaluation of pathologies that potentially alter muscle, tendinous, and/or aponeurosis mechanical properties.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Author contributions: S.F., A.N., S.D., P.P., and G.R. conception and design of research; S.F., A.N., S.D., H.H., and G.R. performed experiments; S.F. and H.H. analyzed data; S.F., A.N., S.D., P.P. and G.R. interpreted results of experiments; S.F. prepared figures; S.F., A.N. and G.R. drafted manuscript; S.F., A.N., S.D., P.P., and G.R. edited and revised manuscript; S.F., A.N., S.D., P.P., and G.R. approved final version of manuscript.

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