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Hauraix H, Nordez A, Dorel S. Shortening behavior of the different components of muscle-tendon unit during isokinetic plantar flexions. *J Appl Physiol* 115: 1015–1024, 2013. First published July 25, 2013; doi:10.1152/japplphysiol.00247.2013.—The torque-velocity relationship has been widely considered as reflecting the mechanical properties of the contractile apparatus, and the influence of tendinous tissues on this relationship obtained during in vivo experiments remains to be determined. This study describes the pattern of shortening of various muscle-tendon unit elements of the triceps surae at different constant angular velocities and quantifies the contributions of fascicles, tendon, and aponeurosis to the global muscle-tendon unit shortening. Ten subjects performed isokinetic plantar flexions at different preset angular velocities (i.e., 30, 90, 150, 210, 270, and 330°/s). Ultrafast ultrasound measurements were performed on the muscle belly and on the myotendinous junction of the medial and lateral gastrocnemius muscles. The contributions of fascicles, tendon, and aponeurosis to global muscle-tendon unit shortening velocity were calculated for velocity conditions for four parts of the total range of motion. For both muscles, the fascicles' contribution decreased throughout the motion (73.5 ± 21.5% for 100–90° angular range to 33.7 ± 20.2% for 80–70°), whereas the tendon contribution increased (25.8 ± 15.4 to 55.6 ± 16.8%). In conclusion, the tendon contribution to the global muscle-tendon unit shortening is significant even during a concentric contraction. However, this contribution depends on the range of motion analyzed. The intersubject variability found in the maximal fascicle shortening velocity, for a given angular velocity, suggests that some subjects might possess a more efficient musculoarticular complex to produce the movement velocity. These findings are of great interest for understanding the ability of muscle-tendon shortening velocity.

force-velocity relationship; ultrafast ultrasound; gastrocnemius; fascicles; tendons

THE FORCE-VELOCITY RELATIONSHIP of a muscle, characterized first on isolated samples (18, 27), depicts the increase in the force generated with a decrease in the shortening velocity and vice versa (23, 27). In this framework, the relationship is classically considered to correspond to the mechanical properties of the contractile apparatus (23, 52, 54). Based on these fundamental works, the force-velocity relationships of isolated muscles are classically considered as the major explanation of the hyperbolic or linear decrease in strength production with increased movement velocity reported during monoarticular (49) or polyarticular movements (42) for elderly subjects (47) or athletes (26).

However, in vivo, different structures of the musculoarticular complex (i.e., fascicles, aponeurosis, tendon, and joint) are involved in the production of joint motion. Accordingly, recent investigations using ultrasound have shown that the change in length of muscle fascicles differs greatly from the global change in length of the muscle-tendon unit [for review see Cronin and Lichtwark (13)]. This difference could be mainly explained by the influence of series elastic elements (tendons and aponeurosis) and the effect of the pennation angle (34, 41). Thus the influence of the series elastic component on the force-velocity relationship obtained during in vivo experiments remains to be determined.

Few studies have focused on the direct measurement of the fascicles' shortening velocity using ultrasound during isokinetic testing (11, 19, 32, 48). Ichinose et al. (32) performed measurements on the shortening velocity of vastus lateralis fascicles during an isokinetic leg extension and found that the shortening velocity increased with increased knee angular velocity from 30 to 150°/s. The second main result was demonstrating that the fascicles' shortening velocity does not exhibit any plateau throughout the isokinetic angular movement. Finni et al. (19) reproduced a similar experiment with a larger number of isokinetic velocities of up to 180°/s and established the force-velocity relationship of vastus lateralis fascicles. Finally, two recent studies have quantified the contribution of tendinous tissues to the total displacement of the muscle-tendon unit at different isokinetic velocities during a plantar flexor movement (11, 48). They reported that this contribution is important, confirming that series elastic elements are significantly involved and, hence, probably influence the concentric torque-velocity relationship obtained in vivo during a monoarticular movement.

As the participation of tendinous tissues should imply a storage restitution of elastic energy, it is probable that this contribution depends on the angular range of the movement used to perform the analysis. However, the studies cited used either data obtained at a specific joint angle (19, 32) or data corresponding to only the reach of maximum shortening velocity (48). To our knowledge, no study has determined the behavior of fascicles and tendinous tissues on the whole range of motion. Furthermore, previous studies focused on relatively low velocities (<200°/s) (13). However, many human movements are performed at movement velocities that induce significantly greater angular velocities, such as a vertical jump task [e.g., 650°/s in the study of Haguenauer et al. (25)], sprint running (6), or skating (30). Both drawbacks were probably due to the low ultrasound sampling frequency (limited to 20–100 Hz for conventional devices), which makes it difficult to measure the instantaneous shortening velocities of fascicles, aponeurosis, and tendon during dynamic contractions (17). Recently, an innovative ultrasound sequence was developed to achieve a sampling frequency of up to 10,000 Hz (15, 16). This could allow a precise characterization of the behavior of musculotendinous elements, especially during very fast move-

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ments (i.e., on a wider range of velocities) and hence a greater part of the force-velocity relationship.

Therefore, the aims of this study were *1*) to describe the pattern of the shortening of fascicles, tendon, and aponeurosis at different constant angular velocities, up to the highest reachable velocities during isokinetic protocols; and *2*) to assess the contributions of each of these different elements to the total shortening velocity production of the muscle-tendon unit on various angular ranges. For this purpose, the medial and lateral gastrocnemius muscle-tendon units were analyzed during isokinetic plantar flexions performed at six velocities using ultrafast ultrasound. We hypothesized that the contributions of tendinous tissues and fascicles to the muscle-tendon unit shortening velocity depend highly on the angular range analyzed. In addition, due to their viscoelasticity, the behavior of tendon and aponeurosis depends on the contraction velocity (22, 38). Therefore, we also hypothesized that the angular velocity has an influence on muscle-tendon interactions and hence on the contribution of the different elements.

MATERIALS AND METHODS

Participants. Ten men volunteered to participate in the present study (age 23.4 ± 4.8 yr; height 179.0 ± 7.8 cm; weight 73.2 ± 7.5 kg). Subjects were fully informed about the nature and aim of the study before signing a written, informed consent form. Approval for the project was obtained from the local ethics committee. All procedures used in this study were in conformity with the Declaration of Helsinki.

Measurements. An isokinetic dynamometer (Biodex medical, Shirley, NY) was used to perform isokinetic movements and to measure the torque produced, ankle joint angle, and angular velocity. Subjects were lying prone, legs fully extended with the thighs, and the hip and the shoulders secured by adjustable lap belts and held in position. The right ankle was firmly fixed in an appropriate accessory. The input axis of the dynamometer was carefully adjusted to the axis of rotation of the right ankle joint. Ankle angle, angular velocity, and torque signals were recorded at a sampling frequency of 4,000 Hz (Delsys, Boston, MA).

An ultrafast ultrasound scanner (Aixplorer, Supersonic Imagine, Aix en Provence, France) was used, with a sampling frequency adapted to the isokinetic velocity (100, 500, and 1,000 Hz for preset angular velocity of 30, 90, and 150–330°/s, respectively). For ultrasound measurements performed on the medial and lateral gastrocnemius, the probe (5–12 MHz; 55 mm) was placed at 30% of the distance between the popliteal crease and the center of the lateral malleolus. The probe was aligned vertically to the midline of the muscle so as to be in the same plane as the muscle fascicles, to obtain the longest possible fascicles (7) and to minimize measurement error (5). For ultrasound measurements performed on the myotendinous junction of the medial and lateral gastrocnemius, the probe was placed on the most distal region of the junction, aligned with the calcaneus (46). The ultrasound probe was fixed to the subject's leg using custom-made equipment. Raw ultrasound signals obtained with the ultrafast scanner were synchronized with the mechanical data using an external trigger of the ultrasound system recorded on the acquisition system of mechanical data (Delsys).

Protocol. Subjects performed six bouts of three maximal contractions, at six different isokinetic angular velocities (30, 90, 150, 210, 270, and 330°/s), with 2 min of rest between each bout. This protocol was repeated four times (i.e., four series) to record the ultrasound data on the different sites. Each series corresponded to a probe location on the triceps surae: on the belly of the muscle, and on the myotendinous junction of both medial and lateral gastrocnemius. Both bouts with various velocities and series with various probe locations were performed in a randomized order.

Before each bout, the experimenter placed a subject's ankle in a maximal dorsiflexion position at rest (i.e., without any preactivation). Then the subject performed three successive maximal plantar flexions according to the predetermined maximal range of motion of each subject. This corresponded to 118.8 ± 5.8° in dorsiflexion and 52.0 ± 5.8° in plantar flexion (with 90° corresponding to the foot being perpendicular to the leg and a decreased angle for the plantar flexion). The subject started the first maximal plantar flexion contraction after a countdown of 3-s duration and was encouraged to produce the fastest contraction as possible to reach the preset velocity. When the plantar flexion was completed, the dorsiflexion was actively performed by the subject (submaximally at 30°/s) to return to the initial dorsiflexed position of the foot. Immediately after this dorsiflexion movement, the subjects performed the second maximal plantar flexion without any delay. The data analysis focused on the second plantar flexion.

Data analysis. The analysis was performed using standardized Matlab Scripts (The Mathworks, Natick, MA). Ankle angle, angular velocity, and torque signals were filtered using a low-pass (20 Hz) zero-phase second-order Butterworth filter. The ankle angle specific moment arm and the length (Fig. 1*A*) of the gastrocnemius muscle-tendon unit were estimated according to the model of Grieve et al. (24) from the knee and ankle angles (28). The torque measured by the dynamometer was corrected for inertia and the weight of the dynamometer attachment to obtain the external torque at the ankle joint. The total plantar flexion force was calculated from the torque divided by the Achilles tendon moment arm (32).

Figure 1 depicts typical changes in length and the shortening velocity of fascicle and muscle used to calculate change in length and shortening velocity of tendon and aponeurosis. First, ultrasonic raw data (i.e., RF signals) obtained 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 the travel time differences. The automatic fascicle tracking method proposed by Cronin et al. (12) was then used to follow displacements of fascicles, deep aponeurosis, and superficial aponeurosis (Matlab, Mathworks) (Fig. 1*C*). When the fascicle was not fully visible, then its length was interpolated as the length of the straight line between the superficial and deep aponeurosis (19, 48). The angle between the fascicle and the deep aponeurosis corresponded to the pennation angle (1, 8). The horizontal fascicle shortening was calculated as the fascicle shortening divided by the cosine of the pennation angle. Manual processing was performed to track the displacements of the myotendinous junction that corresponded to the change in length of muscle (Fig. 1*B*). The change in length of the Achilles tendon was calculated from the difference between the change in length of the muscle-tendon unit and the displacement of the myotendinous junction (i.e., change in length of muscle, Fig. 1*D*) (14). The change in length of the aponeurosis was calculated as the difference between the change in length of the muscle and the horizontal changes in length of the fascicles (Fig. 1*E*). The length of tendinous tissues was taken as the sum of the Achilles tendon length and the aponeurosis length (33). Then the temporal derivative of the changes in length of each element was calculated to obtain the shortening velocity of each element.

The percent contributions of fascicles, tendon, and aponeurosis to global muscle-tendon unit shortening velocity were analyzed on an area of interest corresponding to the great midrange of the total movement (110–70°), where the movement velocity was closest to the preset velocity and the muscle activation is presumably maximal. Therefore, these contributions were calculated for each velocity conditions for four ankle ranges of motion (110–100, 100–90, 90–80, and 80–70°, with 90° corresponded to foot perpendicular to the leg and a decreased angle for the plantar flexion) by using the mean

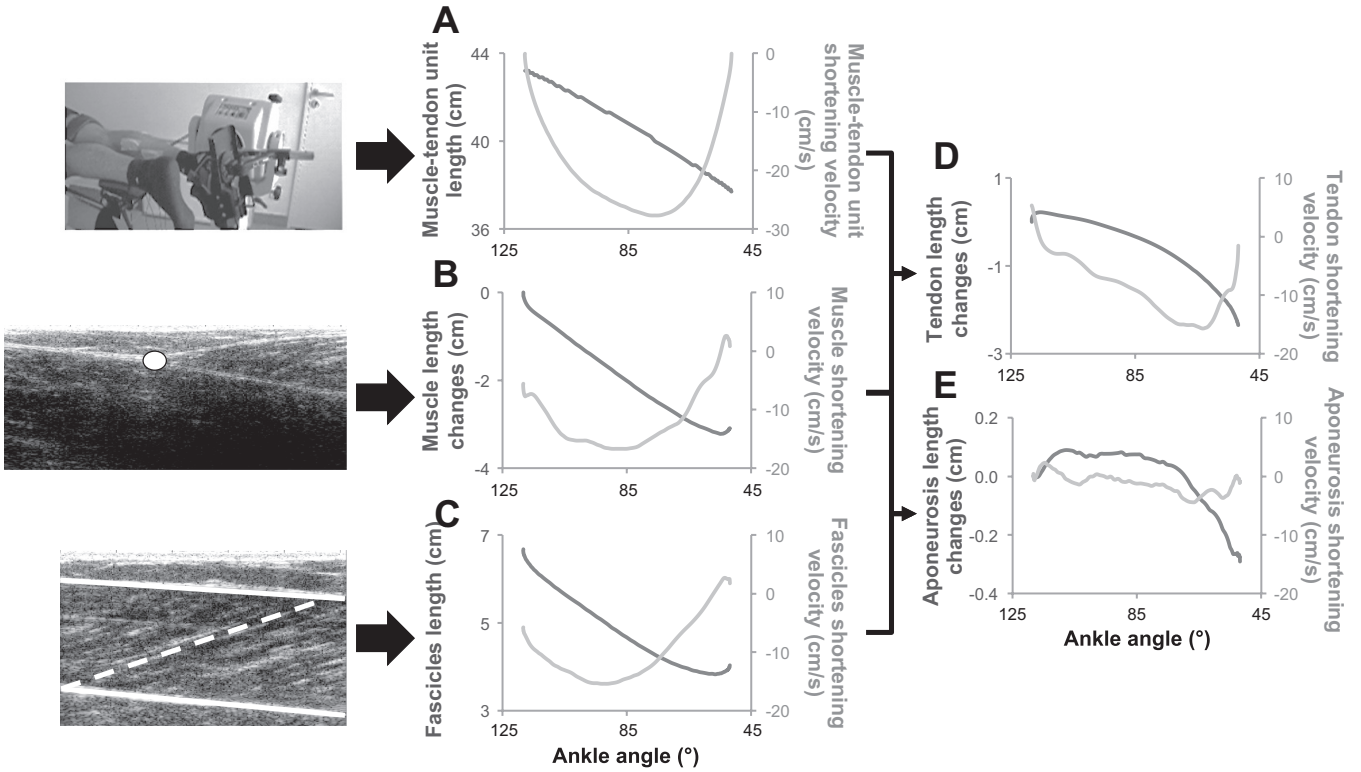

Fig. 1. Individual examples of lengths and velocities measurements at an isokinetic velocity of 330°/s. *A*: the isokinetic dynamometer was used to measure ankle angle and angular velocity, and the muscle-tendon unit (MTU) length was estimated using the model of Grieve et al. (24). *B*: the ultrasound scanner was used to manually track the myotendinous junction (white point), to estimate the change in length of the muscle. *C*: the ultrasound scanner was also used to measure the fascicle length change (white dotted line) and the aponeurosis behavior (white line) using the automatic tracking procedure of Cronin et al. (12). *D*: the tendon length change was estimated as the MTU length change minus the muscle length change. *E*: the aponeurosis length change was estimated as the muscle length change minus the horizontal fascicle length change. The temporal derivative of the changes in length was calculated to obtain the shortening velocity of each element.

values of shortening velocity on these angular sectors. The contribution of fascicles was calculated using the horizontal projection of the fascicle shortening velocity. The force-velocity relationship was established at different levels of the musculoarticular system: muscle-tendon unit, fascicle, tendon, and aponeurosis for these four ankle ranges of motion. The maximal shortening velocity of fascicles was calculated as the highest shortening velocity obtained by fascicles at each preset velocity for gastrocnemius medialis and lateralis.

Statistical analysis. After checking the normal distribution of data using a Shapiro-Wilk test, parametric statistical tests were performed using Statistica software (Statsoft, Tulsa, OK).

Coefficient of variation (CV) and standard error of measurement (SE) were calculated to evaluate the repeatability between the four series of the mean torque produced on the four angular ranges of the ankle range of motion (110–100, 100–90, 90–80, and 80–70°).

One four-way multivariate ANOVA (muscle × velocity × angular range × element) was performed to assess the statistical changes of contribution of elements (fascicles, aponeurosis, and tendon) to muscle-tendon unit shortening velocity. One two-way ANOVA (muscle × velocity) was performed to assess the statistical changes of the fascicles maximum shortening velocity. A Newman-Keuls post hoc analysis was conducted when appropriate. In each statistical analysis, the level of significance was set to $P < 0.05$.

RESULTS

Repeatability. The results of torque repeatability between each series are shown in Table 1. The CV ranged between 4.5 and 12.2, 3.8 and 9.4, 3.2 and 9.3, and 2.8 and 7.6% for ankle ranges of motion of 110–100, 100–90, 90–80, and 80–70°, respectively. Due to a lower repeatability, the first angular range (110–100°) was not considered in the results and in the statistical analyses.

Behavior of musculotendinous elements. The shortening patterns of muscle-tendon unit, fascicles, tendon, and aponeurosis are shown for the medial gastrocnemius (Fig. 2) and the lateral gastrocnemius (Fig. 3) muscles. At low speeds, the mean force generated is higher and then decreased with increase in the angular velocity (Figs. 2*A* and 3*A*). The shortening pattern of the muscle-tendon unit reflected the angular velocity with the influence of moment arm and exhibited an approximately constant shortening velocity on the isokinetic plateau (Figs. 2*B* and 3*B*). The fascicles exhibited a quite different behavior in shortening velocity compared with muscle-tendon unit (Fig. 2*C* and Fig. 3*C*). Overall, the fascicles shortening velocity increased rapidly in the first phase of the range of motion (i.e., until a maximal value reached between 95 and 115°), then it decreased more or less rapidly during the second phase, depending on the preset angular velocity. During the initial force development, the tendon stretches (positive velocity), while the fascicles shorten. Later in the movement, when force begins to decline, the tendon begins to shorten (negative velocity) along with the fascicles (Figs. 2*D* and 3*D*). At the end of motion, the tendon continues to shorten the muscle-tendon unit, while lengthening the muscle (Fig. 1). The participation of the aponeurosis was low, regardless of the considered angular velocity (Figs. 2*E* and 3*E*).

Table 1. *Repeatability of torque measurements between each bout obtained on four angular ranges (110–100, 100–90, 90–80, 80–70°)*

Range of Motion, °	Preset Angular Velocity, °/s	SE, N·m	CV, %
110–100	30	11.5	12.2
	90	8.3	8.6
	150	5.3	5.5
	210	4.4	4.5
	270	4.6	4.7
	330	5.1	5.2
100–90	30	8.9	9.3
	90	9.0	9.4
	150	4.5	4.6
	210	4.2	4.3
	270	3.7	3.8
	330	4.3	4.4
90–80	30	5.9	6.1
	90	8.9	9.3
	150	4.5	4.6
	210	4.1	4.2
	270	3.2	3.2
	330	3.2	3.3
80–70	30	6.6	6.8
	90	7.3	7.6
	150	5.2	5.3
	210	4.1	4.2
	270	6.2	6.4
	330	2.8	2.8

SE, standard error in measurement; CV, coefficient of variation.

Contribution of fascicles, aponeurosis, and tendon to muscle-tendon unit shortening velocity. Considering the four-way ANOVA (muscle × velocity × angular range × element), the main effects of "element" were significant, whereas no main effects of "muscle," "velocity," and "angular range" were found. Interactions "angular range × element," "velocity × element," and "velocity × angular range × element" were found, contrary to the other interactions. As no significant effect of muscle was found, the results described below were obtained for both muscles pooled together.

The main effect of element ($P < 0.001$) indicated that, whatever the velocity condition, contribution of aponeurosis (5.9 ± 21.7%) to muscle-tendon unit velocity was significantly lower ($P < 0.001$) than fascicle and tendon contribution (respectively, 53.7 ± 26.4 and 40.3 ± 20.1%). No significant difference of contribution was found between fascicles and tendon ($P > 0.05$).

The significant interaction ($P < 0.001$) between angular range and element factors is described in Fig. 4. For fascicles, a significant decrease in contribution to muscle-tendon unit velocity was observed during the motion (73.5 ± 21.5, 54.1 ± 20.8, and 33.7 ± 20.2% for angular ranges 100–90, 90–80, and 80–70°, respectively, $P < 0.001$). For tendon, a significant increase in contribution was observed during the motion (25.8 ± 15.4, 39.6 ± 15.9, and 55.6 ± 16.8% for angular ranges 100–90, 90–80, and 80–70°, respectively, $P < 0.001$). For aponeurosis, a significant increase of contribution was observed between the first and the third angular range (0.7 ± 23.9, 6.3 ± 21.3, and 10.7 ± 18.6% for angular ranges 100–90, 90–80, and 80–70°, respectively, $P < 0.01$).

The significant interaction ($P < 0.001$) between velocity, element and angular range factors is described in Fig. 5. For the first angular range (Fig. 5*A*), no significant difference of contribution was found between each movement velocity for fascicles and aponeurosis. In this range, the tendon contribution at 90°/s is significantly lower than at 330°/s (17.1 ± 17.6 vs. 33.4 ± 10.4%) ($P < 0.05$). For the second and third angular range (Fig. 5, *B* and *C*), the contribution at low movement velocity (30°/s) is significantly different than at other velocities for fascicles and tendon elements ($P < 0.05$).

Force-velocity relationship. The force-velocity relationships are shown in Fig. 6. For the angular range 100–90° (Fig. 6*A*), the fascicles are primarily responsible for the muscle-tendon unit shortening. Then the contribution of tendon increased for

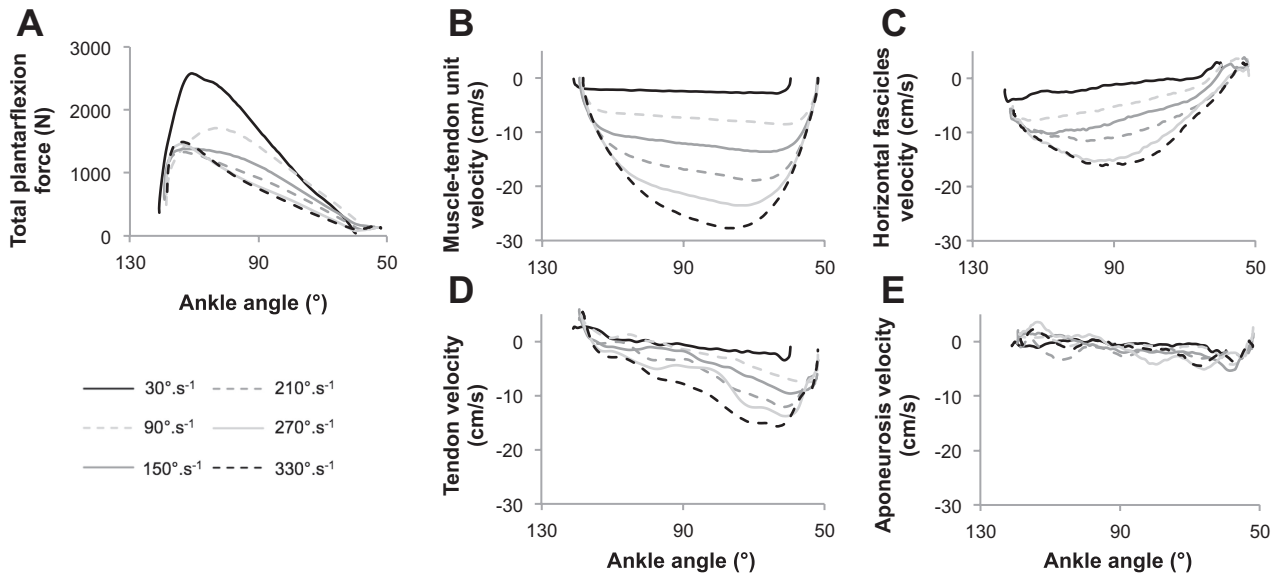

Fig. 2. Patterns of shortening velocity of musculotendinous elements measured during plantar flexions at different movement speed for the gastrocnemius medialis. *A*: total plantar flexion force. *B*: MTU velocity. *C*: horizontal fascicles velocity. *D*: tendon velocity. *E*: aponeurosis velocity. Error bars were omitted for clarity.

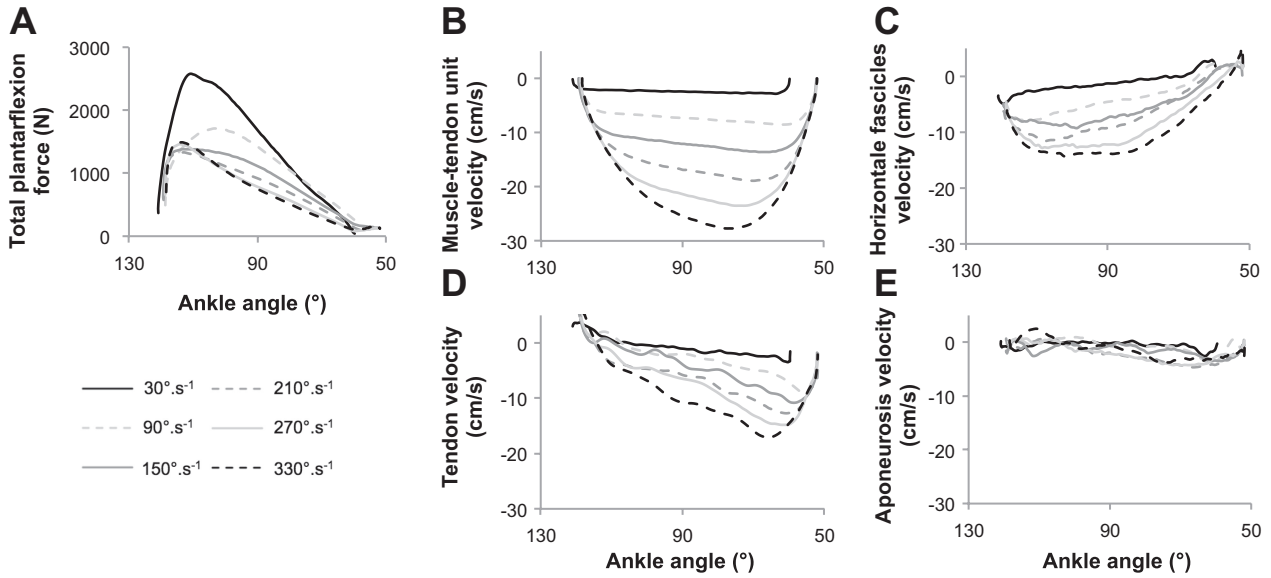

Fig. 3. Patterns of shortening velocity of musculotendinous elements measured during plantar flexions at different movement speed for the gastrocnemius lateralis. *A*: total plantar flexion force. *B*: MTU velocity. *C*: horizontal fascicles velocity. *D*: tendon velocity. *E*: aponeurosis velocity. Error bars were omitted for clarity.

the second angular ranges (90–80°, Fig. 6*B*) and reached a similar contribution to fascicles on the third range (80–70°, Fig. 6*C*).

Maximal shortening velocity of fascicles. Considering the two-way ANOVA (muscle × velocity), there was no muscle effect on the maximal shortening velocity of fascicles ($P = 0.72$) and no muscle-velocity interaction ($P = 0.10$). A main effect of the movement velocity was observed ($P < 0.001$), indicating that the maximal shortening velocity of fascicles increased with increasing of movement speed (Fig. 7). The standard deviation results show an important intersubject variability (between 45.8 and 16.1% for 30 and 330°/s, respectively).

DISCUSSION

The aims of the present study were to describe the shortening patterns of fascicles, tendon, and aponeurosis for gastrocnemius lateralis and medialis and to determine their relative contributions to the global muscle-tendon unit shortening velocity during plantar flexions performed at different isokinetic angular velocities. The pattern of fascicles shortening velocity differed from the behavior of the muscle-tendon shortening. In the first phase of the plantar flexion, fascicles are the primary contributor to the shortening velocity of the muscle-tendon unit (Figs. 2*C* and 3*C*), while the tendon contribution becomes greater during the second phase (Figs. 2*D* and 3*D*). Therefore, the contribution of tendon to muscle-tendon shortening velocity was significant, but depends highly on the considered range of motion (Figs. 4 and 5). The velocity contribution of each tendon and fascicle was relatively constant in the different isokinetic conditions, except at the slowest velocity (i.e., 30°/s, Fig. 5). The maximal shortening velocity increased with increasing angular velocity; however, a high intersubject variability was found.

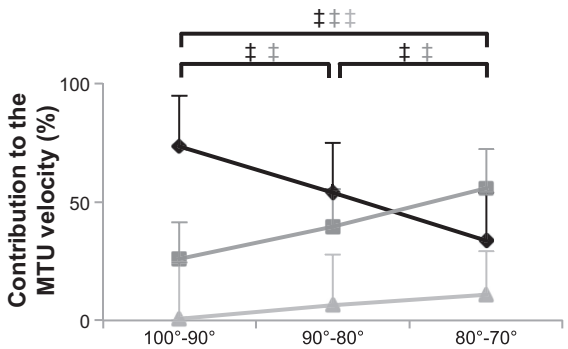

Fig. 4. Relative contributions of elements (fascicles: solid diamonds; tendon: medium-shaded squares; aponeurosis: light-shaded triangles) to global MTU velocity on the different angular range (100–90°, 90–80°, 80–70°). ‡Significant difference with the other angular ranges of the element considered ($P < 0.001$).

The ultrasound scanner used in the present study had a higher sampling frequency (i.e., number of frames acquired per second) compared with a standard device (13, 17, 50). This advantageous innovation (15, 16) was required to accurately determine the patterns of shortening velocity of fascicles, tendon, and aponeurosis. On the other hand, we did not estimate the fascicle force, because this estimation would be significantly less precise for at least two reasons. First, the torque measured is the result of the force produced by both the plantar flexors and the coactivation of the antagonist muscles. Second, in many studies (4, 17, 21, 32, 38, 39, 43), the muscle force is estimated using the torque, the moment arm, and a relative contribution of each muscle. This contribution is classically determined using literature values of the mean relative physiological cross section of each muscle (20). Thus the intersubject variability is not considered. Further investigations are needed to improve the force estimation used to establish the force-velocity relationship of fascicles.

We excluded the angular range 110–100° of our results and statistical analysis, because it presented a lower repeatability with CV that reached values higher than 10%. The aponeurosis length changes were calculated as the difference between changes in

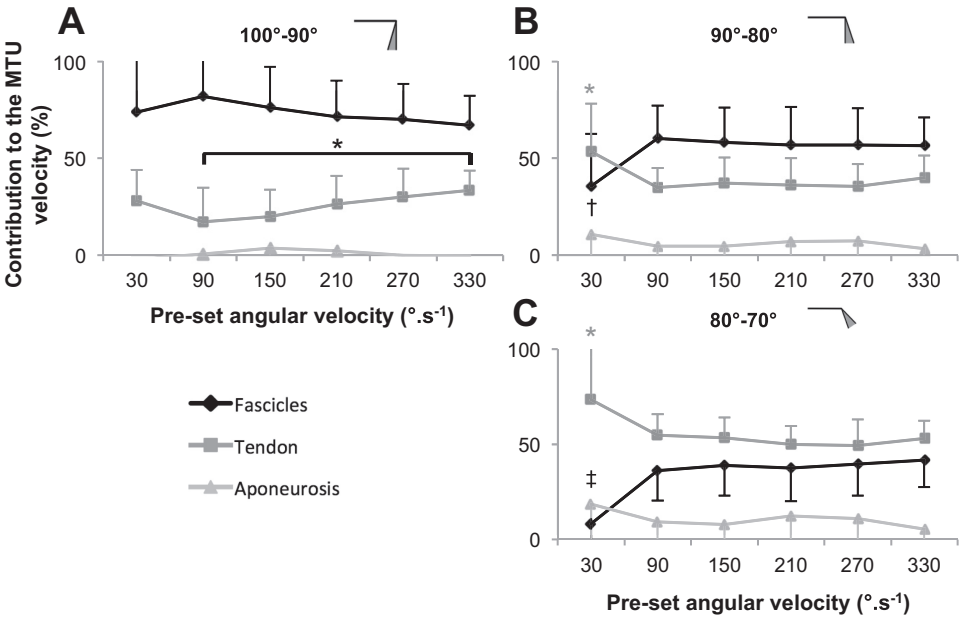

Fig. 5. Relative contributions of elements (fascicles: solid diamonds; tendon: medium-shaded squares; aponeurosis: light-shaded triangles) to the global MTU velocity in isokinetic trials, on three angular ranges [100–90° (*A*), 90–80° (*B*), 80–70° (*C*), with 90° corresponding to the foot being perpendicular to the leg and a decreased angle for the plantar flexion]. Significant difference between the considered angular velocity and the fastest angular velocity: $*P < 0.05$, $\dagger P < 0.01$, and $\ddagger P < 0.001$. All of the other contributions were not significantly ($P > 0.05$) different from the contribution of the same element at the fastest velocity.

length of the muscle minus the changes in length of fascicles (Fig. 1). As two different trials were used (due to the replacement of the probe), a good repeatability was required. Therefore, the estimation of aponeurosis length changes could be incorrectly estimated on this range. This angular range is a phase where the movement remains accelerated for some time, because the subjects do not reached the preset velocity in all conditions. Therefore, the CV could be higher, because it is more difficult to produce a similar acceleration between each bout.

Visually, the shapes of the curves describing the changes in length and shortening velocities of fascicles, tendon, and aponeurosis were similar between gastrocnemius medialis (Fig. 2) and gastrocnemius lateralis (Fig. 3). This observation was statistically confirmed, as the contributions of the various elements and the maximal fascicles shortening velocity were not significantly different between both muscles whatever the condition. These results can be explained by the facts that the Achilles tendon is common to both muscles (11), and that these synergistic plantar flexor muscles showed a mechanical interaction via the shared epimysium (31). Moreover, gastrocnemius muscles have been demonstrated to have similar typologies (35) and architecture (53). Consequently, the lack of differences between gastrocnemius medialis and gastrocnemius lateralis observed in the present study can be explained by several links and similar physiological characteristics between these muscles.

In accordance with Ichinose et al. (32), the pattern of fascicle shortening velocity is different compared with the behavior of the muscle-tendon shortening (Figs. 2 and 3). The specific pattern of the fascicles results from concomitant influences of the associated pennation angle, the change in the moment arm

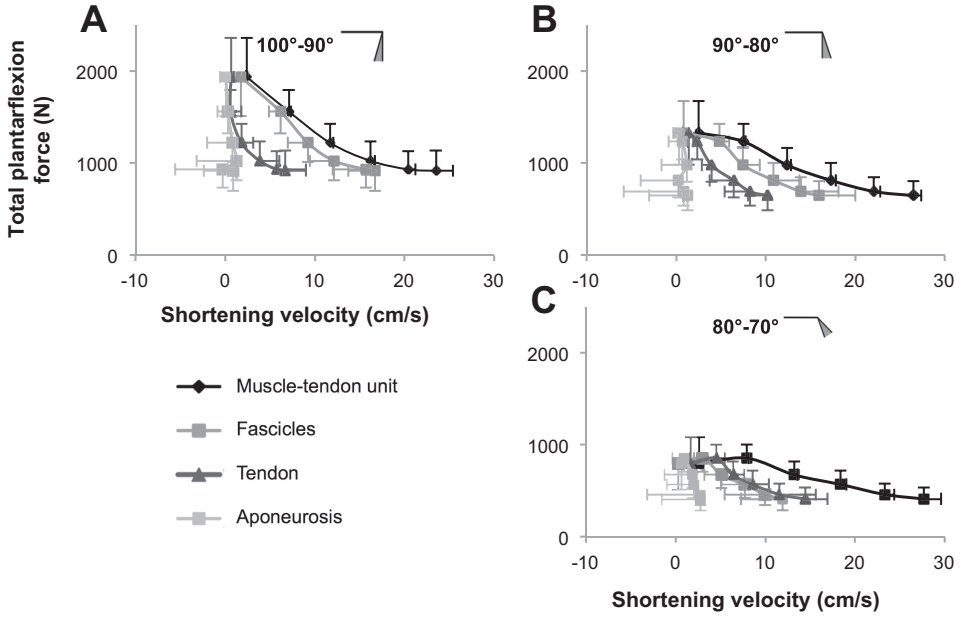

Fig. 6. Force-velocity relationships of the MTU, fascicles, tendon, and aponeurosis on the three considered angular range of motion [100–90° (*A*), 90–80° (*B*), 80–70° (*C*), with 90° corresponding to the foot being perpendicular to the leg and a decreased angle for the plantar flexion].

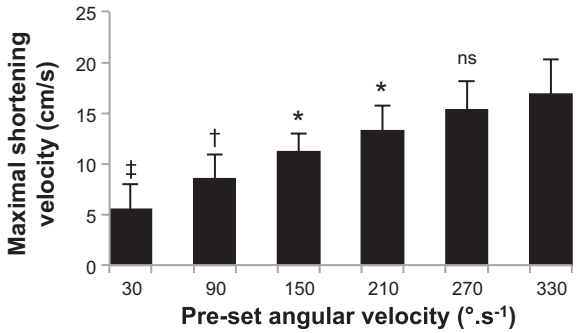

Fig. 7. Maximal shortening velocity of fascicles for each preset angular velocity. Significant differences between the considered velocity and the higher velocity: *$P < 0.05$, †$P < 0.01$, and ‡$P < 0.001$. ns, Nonsignificant.

length, and also the interaction with the behavior of tendinous tissues (32). The fascicle contribution is reduced as the force drops (Figs. 2*C* and 3*C*), which occurs partly because of the fascicle shift down the ascending limb of the length-tension relationship (and possibly due to reduced neural drive) (3). The drop in force means the tendon must shorten to release elastic energy, and hence the contribution increases the more the force drops through the range (Figs. 2*D* and 3*D*). Hence, mechanical interaction means that the tendon releases energy through the range after initial storage (10). Indeed, the initial ankle dorsiflexion position at the beginning of contraction induced stretching of the muscle-tendon unit. Then, by shortening to return the energy stored (36), the tendon significantly participates in the muscle-tendon unit shortening velocity and thereafter allows reduction of the fascicle contribution (38). The importance of tendinous tissues has already been demonstrated in the literature during stretch-shortening cycle eccentric exercise (19, 33, 38) and locomotion tasks (34, 41). On the other hand, it has been studied to a lesser degree during a concentric contraction typically used to draw the torque-velocity relationship and hence to characterize the contractile properties of muscle. In the present study, the lengthening phase of plantar flexors (during the dorsiflexion) was performed by the antagonist muscles (i.e., dorsiflexors), and therefore these plantar flexors were almost passive during this phase preceding the concentric contraction. Thus this sequence of contractions remains different from the typical stretch-shortening cycle task (37) during which the plantar flexor muscles act eccentrically during the lengthening phase (dorsiflexion). Nonetheless, possible stretch-reflex may induce a residual eccentric contraction of plantar flexors during the dorsiflexion. Thus we conducted additional analysis to determine the influence of the active vs. passive dorsiflexion on the behavior of musculotendinous elements during the following plantar flexion. Two starting positions were performed: *1*) with an active dorsiflexion as in the present study; and *2*) with a passive dorsiflexion performed by the experimenter combined with a static starting position. Similar behavior of musculotendinous elements was found for both starting positions (Fig. 8). Thus it can be concluded that contractions analyzed were close to concentric contractions started in a significant passive stretching state.

To our knowledge, no previous study has determined the influence of contraction velocity on the contributions of fascicles, aponeurosis, and tendon to muscle-tendon unit shortening velocity. Figure 5 shows that the contribution of fascicles and tendon to the global shortening velocity of the muscle-tendon unit were, respectively, lower and higher at 30°/s compared with the other velocities on the second and third angular range (90–80° and 80–70°). The tendon contribution at 90°/s was lower than at 330°/s on the first angular range (100–90°). On the other hand, no significant effects were found for higher velocities, indicating that these contributions remain similar for preset velocities higher than 90°/s. Two main reasons can be proposed to explain this velocity effect. First, due to the classical force-velocity relationship of the muscle, the stress applied to tendinous tissues is different at the various velocities (as shown in Figs. 2, 3, and 6), implying that the strain of these structures is also different. As expected, the force of the plantar flexor muscles is significantly higher at 30°/s compared with the other velocities (Figs. 2 and 3), matching the velocity effect depicted in Fig. 5. Second, tendinous structures possess viscous properties that imply a strain-rate dependence and a loading rate effect on the tendon strain (22).

The force-velocity relationships obtained for the muscle-tendon unit and fascicles (Fig. 6) are in agreement with those found in the literature (19, 32). Describing the force-velocity relationship of

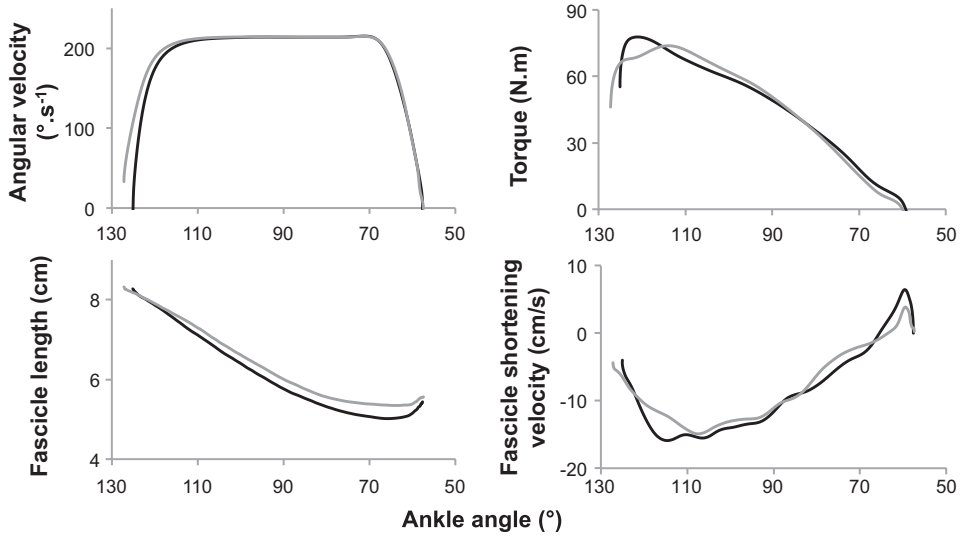

Fig. 8. Individual example of angular velocity, torque, and length and shortening velocity of fascicles at an isokinetic velocity of 210°/s between two start conditions: with an active dorsiflexion (solid line), and a dorsiflexion performed by the experimenter and with a started static position (shaded line).

tendon and aponeurosis is one of the original contributions of this study. While tendon and aponeurosis are passive structures that do not produce an active force, their elastic properties allow the production of an elastic force during the restitution of the energy stored (e.g., Refs. 34, 41, 44). In our experiment, some elastic energy is stored by tendinous tissues due to both the ankle angle at the beginning of the plantar flexion (i.e., 30° in dorsiflexion) and the contraction of the fascicles. A part of this energy is returned during the concentric contraction, which induces an important contribution of tendinous tissues to the total shortening. Finally, the establishment of the force-velocity relationship of muscle-tendon unit and their elements is another way to visualize the impact of tendinous tissues on the muscle-tendon shortening velocity (Fig. 6).

During this experiment, all subjects reached each preset angular velocities at least on part of the movement. The fascicle maximal shortening velocity increased with the increase of the angular velocity. According to Hoffman et al. (29), the optimal fascicle length (L_o) of the medial gastrocnemius is ~60 mm. Thus the fascicle maximal shortening velocity reached in the present study ranged between 0.9 ± 0.4 and 2.8 ± 0.6 L_o/s for 30 and 330°/s, respectively. These results are lower than estimated muscle maximal shortening velocity values found in the literature (55). Hence, much higher preset velocity would be required to achieve fascicle maximal shortening velocity. For a given preset isokinetic angular velocity, despite very similar angular velocity, patterns were observed between the subjects, which shows an important intersubject variability in the fascicle maximal shortening velocity. In other words, to produce the same angular velocity, subjects needed to shorten their fascicles more or less rapidly (i.e., standard deviation ranged from 16.1% for 150°/s to 45.8% for 30°/s). This point is of great interest, because it indicates that some subjects may benefit from a more efficient musculoarticular complex to produce a given velocity of motion. Indeed, the intrinsic factors that can explain this variability are *1*) the muscle architecture (i.e., fascicle length and pennation angle); *2*) the mechanical properties of tendinous tissues; and *3*) musculoarticular geometry (i.e., muscle-tendon moment arm). First, concerning the influence of muscle architecture, a large pennation angle increases the difference between the fascicle length and the horizontal fascicle length transmitted to the tendinous tissues. For the same fascicles length change, it is more efficient to have a low pennation angle to produce a given angular velocity. However, in our study it is interesting to note that the inter-subject variability of the horizontal shortening velocity is similar to that of the fascicle's shortening velocity (i.e., standard deviation ranged between 16.4% for 150°/s and 45.2% for 30°/s), indicating that the pennation angle cannot solely explain the interindividual variability. In addition, the fascicle shortening velocity can be affected by their length (number of sarcomeres in series) (1, 2, 9, 51). Nevertheless, even after a normalization of fascicle shortening velocity referring to the resting fascicle length, the intersubject variability of fascicle shortening velocity remains important (i.e., standard deviation ranged between 13.9% for 150°/s and 39.4% for 30°/s). Second, the viscoelasticity of tendinous tissues necessarily influence the amount of stretch of the tendon and thus the required shortening velocity of fascicles. In the present configuration, a stiffer tendon should be responsible for a greater and faster release of elastic energy and hence potentially induce a higher shortening velocity of the fascicles (38). It would be interesting to evaluate tendon stiffness concomitantly to these measurements to better understand the link between tendon characteristics and the fascicles shortening velocity. Third, the Achilles tendon moment arm length is the perpendicular distance from the Achilles tendon action line to the rotation center of the ankle joint (45). A smaller Achilles tendon moment arm length requires a lower muscle-tendon shortening velocity to reach the same angular velocity. Along this line, it has been recently shown that the Achilles tendon moment arm is lower for sprinters compared with control subjects (40). However, the moment arm was estimated in the present study using an anthropometric model (24), which cannot be applied to accurately determine the interindividual variability (28). Thus the intersubject variability in fascicle shortening velocity obtained in healthy and active young subjects seems to be mainly explained by musculoarticular geometry and the mechanical properties of tendinous structures rather than muscle architecture. Further studies should determine the contribution of both causes to further understand the ability of muscle-tendon shortening velocity production.

Conclusion and perspectives. In summary, we described the pattern of shortening of fascicles, tendon, and aponeurosis during isokinetic protocols. Results show the significant involvement of tendon even during a concentric contraction, but this contribution depends highly on the considered range of motion used for the analysis (i.e., 25.8 ± 15.4 to 55.6 ± 16.8% for angular ranges 100–90 and 80–70°, respectively). In addition, the velocity contribution of each tendon and fascicles was different at the slowest velocity (i.e., 30°/s); however, further investigation is required to further explain this velocity effect. Finally, a high intersubject variability was found in the maximal shortening velocity of fascicles required to reach a given angular isokinetic velocity. Further studies are needed to quantify the contributions of muscle-tendon moment arm and of tendon viscoelastic properties to this variability. These studies are of great interest for understanding the ability of muscle-tendon shortening velocity of healthy subjects and athletes.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

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

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