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In vivo maximal fascicle-shortening velocity during plantar flexion in humans

Hugo Hauraix,[1] Antoine Nordez,[1] Gaël Guilhem,[2] Giuseppe Rabita,[2] and Sylvain Dorel[1]

[1]*University of Nantes, UFR STAPS, Laboratory "Movement, Interactions, Performance", Nantes, France; and* [2]*French National Institute of Sport (INSEP), Research Department, Laboratory Sport, Expertise and Performance (EA 7370), Paris, France*

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Hauraix H, Nordez A, Guilhem G, Rabita G, Dorel S. In vivo maximal fascicle-shortening velocity during plantar flexion in humans. *J Appl Physiol* 119: 1262–1271, 2015. First published October 1, 2015; doi:10.1152/japplphysiol.00542.2015.—Interindividual variability in performance of fast movements is commonly explained by a difference in maximal muscle-shortening velocity due to differences in the proportion of fast-twitch fibers. To provide a better understanding of the capacity to generate fast motion, this study aimed to *1*) measure for the first time in vivo the maximal fascicle-shortening velocity of human muscle; *2*) evaluate the relationship between angular velocity and fascicle-shortening velocity from low to maximal angular velocities; and *3*) investigate the influence of musculo-articular features (moment arm, tendinous tissues stiffness, and muscle architecture) on maximal angular velocity. Ultrafast ultrasound images of the gastrocnemius medialis were obtained from 31 participants during maximal isokinetic and light-loaded plantar flexions. A strong linear relationship between fascicle-shortening velocity and angular velocity was reported for all subjects (mean $R^2 = 0.97$). The maximal shortening velocity (V_{Fmax}) obtained during the no-load condition (NLc) ranged between 18.8 and 43.3 cm/s. V_{Fmax} values were very close to those of the maximal shortening velocity (V_{max}), which was extrapolated from the F-V curve (the Hill model). Angular velocity reached during the NLc was significantly correlated with this V_{Fmax} ($r = 0.57$; $P < 0.001$). This finding was in agreement with assumptions about the role of muscle fiber type, whereas interindividual comparisons clearly support the fact that other parameters may also contribute to performance during fast movements. Nevertheless, none of the biomechanical features considered in the present study were found to be directly related to the highest angular velocity, highlighting the complexity of the upstream mechanics that lead to maximal-velocity muscle contraction.

maximal unloaded velocity; muscle-tendon unit; muscle mechanics; muscle architecture; stiffness; ultrasound

THE CAPACITY OF HUMAN SKELETAL muscle to achieve maximal power production is functionally very important during ballistic movements such as sprinting or jumping. The maximal angular velocity an individual can produce represents one of the key determinants of this ability and hence of human performance in various explosive tasks such as a sprint while running or cycling (31, 57). In the literature, this ability to reach extreme angular velocities in unloaded conditions is related mainly to a higher proportion of fast-twitch fibers (5, 11, 56) or a longer fascicle length, or both, which implies a higher number of sarcomeres in series (9, 53). These considerations suggest that subjects who are able to produce high velocity at the joint level should also be able to develop high muscle fascicle-shortening velocity. Consequently, the muscle-shortening velocity should be a key determinant of the ability to perform very-high-velocity movements.

To our knowledge, no previous study has measured actual maximal fascicle-shortening velocity in vivo in humans. Although measurement of fascicle-shortening velocity is classically performed using ultrasound (13), the sampling frequency of conventional devices (i.e., the number of images per second, typically 30–170 Hz) limits the investigations to relatively slow motion, far from the maximal velocities reached during human movements. In this context, ultrafast ultrasound (14, 55) could be used to overcome this limitation and analyze very fast movements (17, 29, 47). Using this technique, we measured fascicle-shortening velocity during maximal isokinetic plantar flexions performed at various submaximal preset angular velocities, from 30°/s up to 330°/s (29). Nevertheless, because the torque was higher than 0 at 330°/s [about 30% of MVC], this highest-tested velocity remained far below the maximal angular velocity measured with, for example, the slack-test method [i.e., about 493 ± 149°/s at 60% of maximal voluntary contraction before release on the same muscle group (52)]. Nonetheless, in the study by Hauraix et al. (29) it was interesting to note that the increase in fascicle-shortening velocity in this range seemed proportional to the increase in angular velocity. In addition, a high interindividual variability of fascicle-shortening velocity was found, indicating that various individual fascicle-shortening velocities could be observed for the same preset angular velocity.

The relationship between fascicle-shortening velocity and angular velocity should be influenced by a number of biomechanical features. First, Lee and Piazza (41) showed that elite sprinters possess a small Achilles tendon moment arm, promoting an increase in angular velocity for the same fascicle-shortening velocity. Thus a shorter moment arm could be considered a mechanical advantage for producing higher maximal joint angular velocities. Second, muscle gearing (i.e., the variation of the pennation angle during contraction) should also play an important role in global muscle shortening (4, 49). Third, few studies (10, 21, 29) have highlighted the significant contribution of tendinous tissues to the total shortening velocity of the muscle-tendon unit even when the latter contracts in a concentric way (i.e., produces positive mechanical work). Therefore, the mechanical properties of tendons would also influence the relationship between fascicle-shortening velocity and angular velocity. These elements overall suggest that the relationship between fascicle-shortening velocity and angular velocity could be relevant in exploring the biomechanical efficiency of the musculo-articular complex in performing fast motions.

To provide a better understanding of the ability to produce high angular velocity movements, this study aimed to measure,

Address for reprint requests and other correspondence: Antoine Nordez, Univ. of Nantes, Laboratory "Movement, Interactions, Performance" (EA 4334), 25 bis boulevard Guy Mollet, BP 72206, 44322 Nantes cedex 3, France (e-mail: antoine.nordez@univ-nantes.fr).

for the first time in vivo, the maximal shortening velocity of human muscle using ultrafast ultrasound. The second objective was to analyze the relationship between fascicle-shortening velocity and angular velocity from very low to maximal achievable velocity. An additional purpose was to investigate the link between the ability to produce maximum joint angular velocity, maximal shortening velocity of muscle fascicles, and some biomechanical parameters (i.e., moment arm, tendon stiffness, and muscle architecture characteristics). We expected that fascicle velocity would change linearly with the increase in joint angular velocity up to very high velocities. A second hypothesis was that maximal angular velocity would be related to both maximal fascicle-shortening velocity and biomechanical features. A large sample of subjects with various sport practices and levels was recruited to further analyze interindividual variability in fascicle-shortening velocity.

Glossary

AGR	Architectural gear ratio
L_O	Optimal length of fascicle
L_F	Fascicle length
L_{FH}	Horizontal fascicle length
L_{MA}	Length of the triceps surae moment arm
L_{MTU}	Muscle-tendon unit length
L_{TT}	Tendinous tissues length
MVC	Maximum voluntary contraction
NLc	No-load condition
V_F	Fascicle shortening velocity
V_{Fmax}	Maximal fascicle velocity measured during no-load condition
V_{max}	Maximal fascicle velocity extrapolated from F-V curve
V_{TT}	Tendinous tissues shortening velocity
ω_{max}	Maximal articular velocity

MATERIALS AND METHODS

Participants

Thirty-one healthy men (age 23.3 ± 3.2 yr, height 180.8 ± 6.4 cm, weight 75.0 ± 8.9 kg) volunteered to participate in the study. All participants were engaged in physical activity, ranging from recreational to high-level competition (i.e., sprint running, basketball, soccer, gymnastics, badminton, taekwondo, dance, and tennis). The subjects were fully informed about the nature and aim of the study before giving their written informed consent to participate. The study was conducted in accordance with the Declaration of Helsinki and was approved by the local ethics committee.

Ergometers

Isokinetic plantar flexions were performed on an isokinetic dynamometer (Biodex 3 Pro; Biodex Medical, Shirley, NY), which measured ankle angle, angular velocity, and torque. Participants lay in a prone position with their legs fully extended and thighs and hips secured by adjustable belts. The right ankle was firmly attached to an appropriate attachment on the platform, and the ankle's axis of rotation was adjusted to the input axis of the dynamometer. Ankle angle, angular velocity, and torque provided by the dynamometer were converted to digital data by a 12-bit analog-to-digital converter (National Instrument; Delsys, Boston, MA), and sampled at 1 kHz (EMGWorks 3.1; Delsys).

High-velocity plantar flexions were performed on a specific ergometer composed of a rotational footplate and a bench (Bio2M, Compiègne, France) (40). The specific ergometer we used consisted of a rotational platform only (17) so as to reduce the moment of inertia as much as possible. Ankle angle was measured with an optical absolute encoder. An electromagnet was used to maintain the starting position in dorsiflexion. Three conditions were tested: one with no additional load and two loaded isoinertial conditions (1.3 kg and 2.6 kg applied to the back of the pedal, 25 cm from the axis of rotation). The ankle angle signal was sampled at a frequency of 2 kHz (EMGWorks 3.1; Delsys).

Ultrasound Measurements

An ultrafast ultrasound scanner (Aixplorer, Supersonic Imagine, Aix en Provence, France) was used to observe the behavior of muscle fascicles during plantarflexion. The probe (5–12 MHz, 55 mm) was placed on the skin surface over the gastrocnemius medialis belly at 30% of the distance between the popliteal crease and the center of the lateral malleolus (36). To minimize error due to the two-dimensional (2-D) measurement of 3-D phenomena (7), the probe was placed vertically at the midline of the muscle in the same plane of the muscle fascicles to obtain the longest fascicles (8). The investigator securely attached the probe to the leg with custom-made equipment and carefully ensured that the device was not displaced throughout the experimental protocol. The sampling frequency was adapted to the angular velocity (500 Hz, 1,000 Hz, and 2,000 Hz for angular velocity of 30–90°/s, 150–330°/s, and high-velocity conditions, respectively). Ultrasound measurements were synchronized with mechanical data using an external trigger of the ultrasound scanner sampled using the same device as the mechanical signals (EMGWorks 3.1; Delsys).

Measurement of Biomechanical Features

Moment arm. After a standardized warm-up (Fig. 1*A*), L_{MA} was measured using the tendon excursion method (1, 44). The probe was

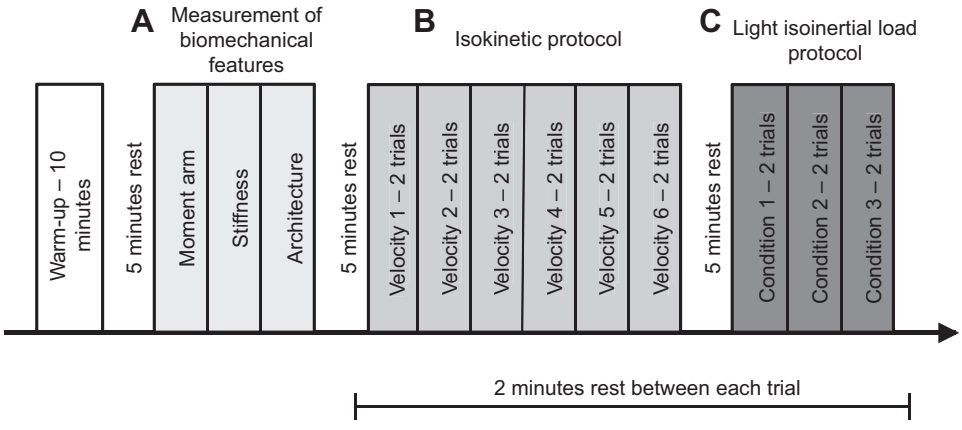

Fig. 1. The experimental protocol included three successive steps. Measurement of biomechanical features and isokinetic conditions were performed with an isokinetic ergometer, whereas the light-load isoinertial conditions were performed on a specific ergometer. The velocities (i.e., 30, 90, 150, 210, 270, and 330°/s) and isoinertial conditions (two isoinertial loads and no-load) tested were randomized.

placed over the myotendinous junction of the gastrocnemius medialis. The isokinetic dynamometer applied passive cycles at 5°/s (110°−60°, 90° corresponding to the foot perpendicular to the leg and a decreased angle for plantarflexion) during which the displacement of the myotendinous junction was assessed by ultrasound acquisition (100 Hz). L_{MA} was considered as the slope of linear regression between the myotendinous junction displacement and the change in ankle angle (100-70°).

Muscle architecture. Three measurements were made at rest. The ankle was placed at 90° and an ultrasound image was taken to measure fascicle length and pennation angle. Tendon length at rest was measured as the distance between the myotendinous junction of the gastrocnemius medialis and the proximal tendon insertion on the calcaneus localized using the ultrasound method.

Tendon stiffness. Two MVCs were performed at 90° of ankle angle. The subjects performed a progressive isometric ramp plantarflexion from 0 to 90% of MVC (5 s), during which the displacement of fascicle insertion on the deep aponeurosis (i.e., aponeurosis displacement) was observed by ultrasound acquisition (37). The stiffness of tendinous tissues corresponded to the ratio between the change in force (in N) and the displacement of the aponeurosis (in mm) between 50% and 90% of MVC. Because a slight detachment of the heel may occur during isometric plantarflexion (3, 45), a correction was performed according to the method proposed by Magnusson et al. (45).

Protocol

Isokinetic conditions. Subjects performed two trials of maximal plantarflexion over a 56° range of motion (i.e., 110° to 54°) at six different isokinetic angular velocities (30, 90, 150, 210, 270, and 330°/s) in randomized order, with 2 min of rest between each trial (Fig. 1*B*). Before each trial, the investigator placed the subject's ankle in dorsiflexion (i.e., 110°). Then, after a 3-s countdown, the subjects performed maximal plantarflexion contraction while the investigator simultaneously released the ankle. The subjects were instructed to contract "as strong and as fast as possible."

Light-load isoinertial conditions. The subjects were asked to move toward the specific ergometer (Fig. 1*C*). The ankle was then placed in the same starting position as in the isokinetic condition (i.e., dorsiflexion at 110°) using an electromagnet. The resistance of the electromagnet was adjusted to compensate for the passive torque produced, and hence to allow the subject to initiate the movement immediately at the start of maximal muscle contraction. For each isoinertial condition performed in randomized order (i.e., no load, light load, and medium load), the subjects performed two trials separated by 2 min of rest. Again, the subjects were instructed to contract "as strong and as fast as possible."

Data Processing

The data were analyzed using custom Matlab scripts (The Mathworks, Natick, MA). The mechanical data (i.e., ankle angle, angular velocity, and torque) were low-pass filtered (20 Hz) using a zero-phase second-order Butterworth filter. L_{MTU} was calculated using the anthropometric model proposed by Grieve et al. (24) from the knee and ankle angles. The torque measured by the isokinetic dynamometer was corrected for inertia and gravity to obtain external torque at the ankle joint. On the specific ergometer system (light-load isoinertial conditions), the moment of inertia (i.e., foot, footplate, and additional loads) was estimated using quick-release protocol (17). Torque was calculated as the moment of inertia multiplied by the acceleration of the ankle angle and corrected for weight (foot and additional loads).

The ultrasonic raw data obtained using the ultrafast ultrasound scanner were used to create B-mode images by applying a conventional beam formation (i.e., applying a time-delay operation to compensate for travel time differences). The behavior of muscle fascicle and deep and superficial aponeurosis were obtained using the automatic tracking method proposed by Cronin et al. (12). When the fascicle was not fully visible, an extrapolation of the length was performed using trigonometry (19, 49). The pennation angle corresponded to the angle formed between the fascicle and deep aponeurosis. L_F and pennation angle were low-pass filtered using a zero-phase, second-order Butterworth filter, depending on the movement's duration (20, 30, and 40 Hz for 30°/s, 90–330°/s, and isoinertial conditions, respectively). Raw signals were quite smooth, but filtering was required to calculate the derivative. A pilot analysis showed that the filter used did not alter the signals. L_{FH} was calculated as fascicle length multiplied by the cosine of the pennation angle. L_{TT} (that is, tendon and aponeurosis) was considered to be the difference between L_{MTU} and L_{FH} (Fig. 2).

V_F and V_{TT} corresponded to the first-time derivatives of L_F and L_{TT}, respectively. The higher instantaneous fascicle-shortening velocity and angular velocity were considered as the peak values of V_F and ω, respectively. AGR was calculated as the ratio between horizontal fascicle velocity and absolute fascicle-shortening velocity (4, 49). Total plantar flexion force was calculated from the torque divided by the Achilles tendon moment arm (33). Fascicle force was calculated from the gastrocnemius medialis muscle force [i.e., 15.9% of total plantar flexion force (23)], divided by the cosine of the pennation angle. A previous study (29) showed that ultrasound measurements are reliable in the central part of the range of motion. Thus the analysis focused on the 100° to 70° range of motion for each condition. Angular velocity, fascicle-shortening velocity, and fascicle force were averaged over this range and used to obtain the angular velocity-fascicle velocity relationship and the force-velocity relationship at the fascicle level. This force-velocity relationship was fitted using a hyperbolic equation proposed by Hill (30): $(F + a)(V + b) = c$, where F and V are fascicle force and velocity; and a, b, and c are constants. The maximal theoretical velocity of fascicle was considered as the force-velocity curve x-intercept (V_{max}).

Statistical Analysis

Because all data were normally distributed (via a Shapiro-Wilk's test), one-way ANOVA was performed to assess the statistical

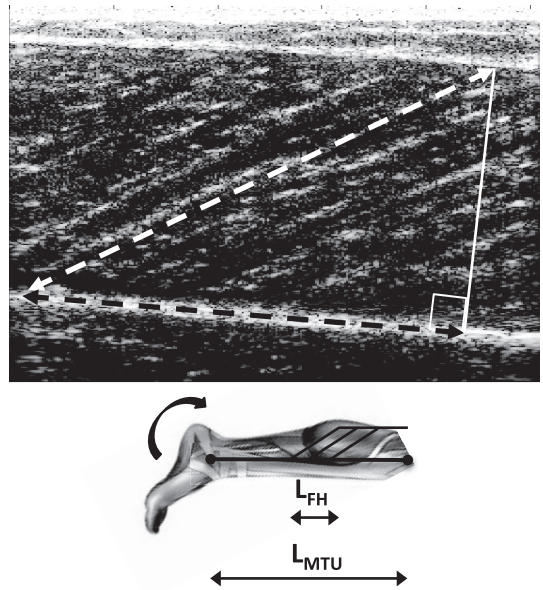

Fig. 2. *Top*: B-mode image of the gastrocnemius medialis during plantarflexion contraction. Fascicle length change was measured by an automatic tracking method (white dotted line). The horizontal projection of fascicle length is represented by the black dotted line. The tendinous tissues length was calculated as the muscle-tendon unit length minus the horizontal fascicle length. *Bottom*: the AGR corresponded to the horizontal fascicle shortening velocity divided by the fascicle's direction shortening velocity.

changes in angular and fascicle-shortening velocities according to the velocity condition (i.e., nine conditions). A Newman-Keuls post hoc analysis was conducted when appropriate. A linear regression model and the corresponding coefficient of determination were used to evaluate the linearity of the relationship between the mean fascicle-shortening velocity and the mean angular velocity for each subject. Hill's hyperbolic model was fitted to the fascicle force-velocity relationship (least-squares method). The Bravais-Pearson correlation coefficient (r) was calculated to describe the relationship between biomechanical features, fascicle-shortening velocity, tendinous tissues shortening velocity, and angular velocity during the no-load condition (NLc). In each statistical analysis, the level of significance was set to $P < 0.05$.

RESULTS

Velocity Patterns of the Ankle Joint and Muscle-Tendon Unit, Fascicle, and Tendinous Tissues of the Gastrocnemius Medialis

Figure 3 presents fascicle-shortening velocity, horizontal fascicle-shortening velocity, tendinous tissues-shortening ve-

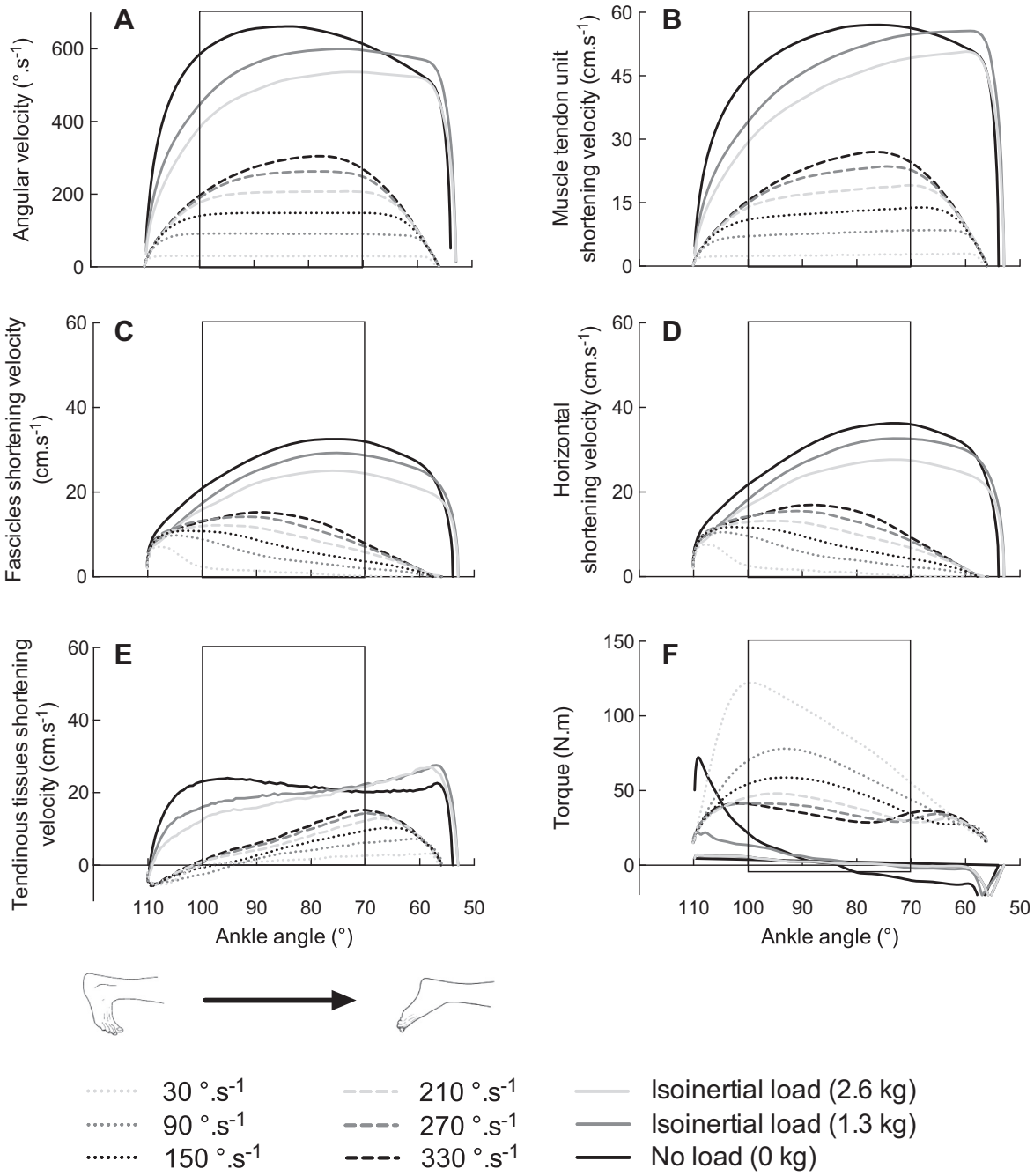

Fig. 3. Angular velocity (*A*), muscle-tendon unit shortening velocity (*B*), fascicle shortening velocity (*C*), horizontal fascicle shortening velocity (D), tendinous tissues shortening velocity (*E*), and torque (*F*) patterns measured during maximal plantar flexions at various isokinetic preset velocities and during light-load isoinertial conditions. Data were averaged across participants. The black frame represents the range of motion of interest for further analysis. Note that the starting position (i.e., 110° = 20° of dorsiflexion) corresponds to a significant initial muscle-tendon stretch.

locity, muscle-tendon unit shortening velocity, and angular velocity patterns for all tested conditions. We observed an increase in fascicle-shortening velocity with the increase in angular velocity over the entire range of motion (Fig. 3*C*). The patterns of fascicle-shortening velocity and horizontal fascicle-shortening velocity were similar, whereas the latter was higher than the absolute shortening velocity due to the effect of pennation (+10.4% on average, Fig. 3, *C* and *D*). The angular velocity and muscle-tendon unit shortening velocity patterns were almost similar (Fig. 3, *A* and *B*), whereas fascicle-shortening velocity patterns were quite different from the patterns of muscle-tendon shortening velocity, particularly in relation to the significant contribution of tendinous structures (Fig. 3*E*). Nonetheless, the change in muscle-tendon unit was accounted for mainly by fascicle shortening, with a relative contribution that amounted to between 58% and 66% (except at 30°/s, Fig. 4). Finally, the 100° to 70° range of motion of interest used for all tested conditions consistently encompassed the peak instantaneous fascicle and joint velocity reached in the no-load condition.

Fascicle-Shortening Velocity for the Various Conditions

The one-way ANOVA showed a main significant effect of velocity condition ($P < 0.001$), indicating that fascicle-shortening velocity increased with the increase in angular velocity. Individual relationships between fascicle-shortening velocity and angular velocity were very well fitted by the linear model (Fig. 5, mean $R^2 = 0.97 \pm 0.01$, range 0.93–0.99).

Individual force-velocity relationships for the muscle fascicles were nicely fitted by the hyperbolic Hill model (Fig. 6, mean $R^2 = 0.94 \pm 0.05$, range 0.78–0.99) and then allowed to confidently extrapolate the maximal theoretical velocity of fascicles (by Hill's equation) (30). This maximal theoretical fascicle-shortening velocity reached 30.8 cm/s on average (range 19.4–43.4 cm/s, Table 1) and was significantly higher than the fascicle-shortening velocity measured during NLc ($P = 0.003$, mean 29.4 cm/s, range, 18.8–43.3 cm/s, Table 1). However, a significant correlation was found between the theoretical maximal fascicle-shortening velocity and maximal fascicle-shortening velocity obtained during NLc ($P < 0.0001$, $r = 0.84$).

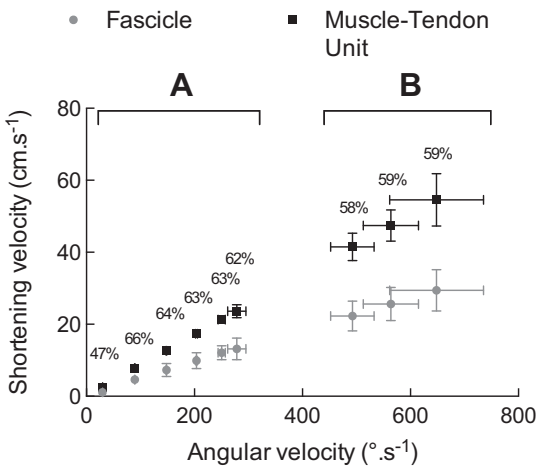

Fig. 4. Mean ± SD fascicle shortening velocity and muscle-tendon unit shortening velocity (100° to 70°) are displayed for each of the six isokinetic velocities (*A*) and the three light-load isoinertial conditions (*B*). The average relative contributions of fascicle shortening velocity to muscle-tendon unit shortening velocity are expressed as percentages (horizontal fascicle shortening velocity + tendinous tissues shortening velocity = 100%).

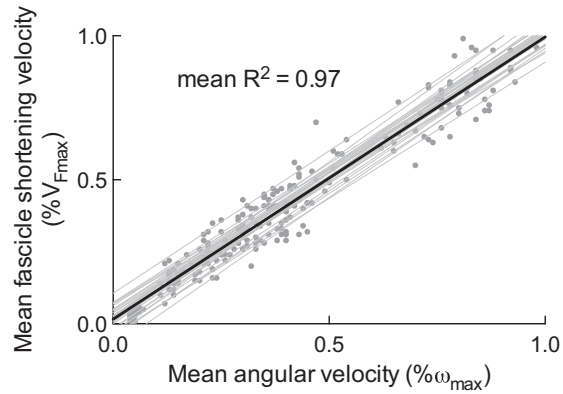

Fig. 5. Mean fascicle shortening velocity in relation with mean angular velocity (over a 100° to 70° range of motion) for all trials. Fascicle shortening velocity and angular velocity in each condition were normalized to maximal values (V_{Fmax} and ω_{max}, respectively). Gray lines (individual models) and the black line (mean trend curve; $n = 31$) are shown for information and clarity purposes.

Maximal Angular Velocity and Muscle Dynamics in the No-Load Condition

The angular velocity reached during NLc was largely higher than the tested isokinetic velocities (at least twice as high compared with the 330°/s isokinetic condition, Table 1, Fig. 4) and exhibited a high degree of interindividual variability. Table 1 shows the corresponding shortening velocities reached by muscle fascicle during NLc. Fascicle-shortening velocity was significantly correlated with angular velocity during NLc (mean values over the 100° to 70° range of motion, $P < 0.001$, $r = 0.57$, Fig. 7). A significant correlation was also obtained between angular velocity and tendinous tissues-shortening velocity ($P = 0.011$, $r = 0.45$). Although the angle of pennation varied on average by 5.9° throughout the range of motion of interest (1.6° to 13.3°), during this maximal contraction in NLc, the AGR was not correlated with the angular velocity ($P = 0.93$, $r = 0.016$).

Maximal Angular Velocity in NLc and Biomechanical Features

Table 2 depicts the values of biomechanical features measured on the gastrocnemius medialis and the Achilles tendon. None of these variables was significantly correlated ($P > 0.05$) with the mean angular velocity (100° to 70°) reached during NLc.

DISCUSSION

The present study contributes to the literature by describing fascicle-tendon interactions during single-joint ballistic concentric plantar flexion contractions, and determining for the first time the maximal achievable shortening velocity in human muscle in vivo. Interestingly, both muscle fascicles and tendinous tissues contributed to muscle-tendon shortening velocity (i.e., 60% and 40%, respectively). According to our first hypothesis, fascicle-shortening velocity increased linearly with the increase in angular velocity to reach extremely high values

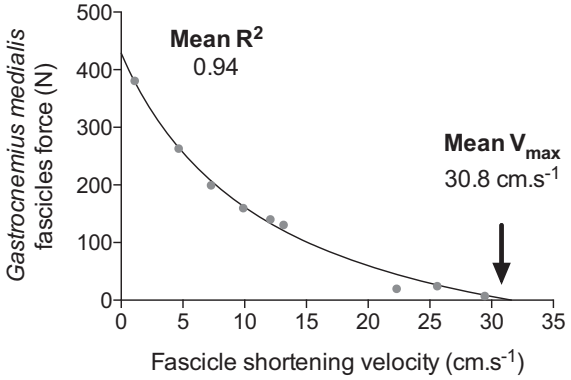

Fig. 6. Averaged relationship between force and fascicle shortening velocity based on mean values of all subjects (gray circles) on the range of motion of interest (100° to 70°). Each individual force-velocity curves were fitted by the hyperbolic equation proposed by Hill (30). The means of individuals R^2 and V_{max} correspond to the values obtained from all subjects (n = 31). The mean curve is shown for clarity purposes.

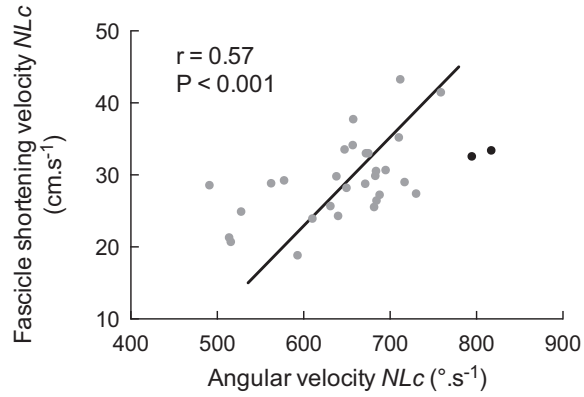

Fig. 7. Correlation between fascicle shortening velocity and angular velocity reached during NLc (n = 31, mean values over a 100°-to-70° range of motion). Linear regression is represented by a black line, gray points represent individual values and black points represent the two subjects that reached the highest angular velocity.

in the NLc (almost 6 L_O/s, on average). Moreover, maximal angular velocity achieved in the NLc was significantly related to the maximal fascicle-shortening velocity, but contrary to our second hypothesis, none of the biomechanical features nor the change in fascicle pennation angle during contraction was significantly correlated with this maximal angular velocity.

Relationship Between Fascicle-Shortening Velocity and Angular Velocity

Some previous studies have demonstrated that fascicle-shortening velocity increased with an increase in angular velocity during maximal plantar flexions performed up to 330°/s (10, 29). One of the main results of the current study is that fascicle-shortening velocity continues to increase along with angular velocity up to extreme values (445 to 816°/s, Fig. 5). Moreover, this relationship can be very well fitted by a linear model (i.e., mean R^2 = 0.97). Recently, Fontana Hde et al. (21) demonstrated that the fascicle-shortening velocity of vastus lateralis reached a plateau at velocities above 240°/s despite the increase in muscle tendon unit velocity up to 500°/s. The authors explained this finding by showing a potential growing contribution of tendinous tissues to muscle tendon unit shortening as angular velocity increases (i.e., 89% at 500°/s). In the present study, significant contributions of tendinous tissues were also observed but were lower and almost constant regardless of the velocity considered (i.e., 34% to 42% from 90°/s to 654.3°/s, on average, Fig. 4). Two factors could explain such differences between studies. First, it is well known that vastus lateralis and gastrocnemius medialis muscles do not have the same muscle fiber type repartition and architecture (35, 38), and that the Achilles tendon is much longer than the quadriceps tendon. Although different tendon length could influence fascicle-tendon interactions, it did not contribute to higher contribution of fascicle velocity in the present study. Second, conventional ultrasound with low-acquisition frequency (42–49 Hz) to compare fascicle length at the beginning and end of the range of motion, and thus evaluated the mean shortening velocity, whereas ultrafast ultrasound (up to 2,000 Hz) allowed for the tracking of the instantaneous behavior of the fascicles throughout the entire movement. Further studies performed on the vastus lateralis using ultrafast ultrasound are required to better explain the different results obtained by Fontana Hde et al. (21).

Table 1. *Angular and fascicle shortening velocities during no-load condition*

	Mean ± SD	Maximum	Minimum
Articular Velocity, °/s			
Mean, NLc, 100°-70°	648.3 ± 86.9	816.9	445.4
Peak, NLc, peak value	701.2 ± 80.2	864.8	534.3
Fascicle shortening velocity, cm/s			
V_{Fmax}, NLc, 100°-70°	29.4 ± 5.7	43.3	18.8
V_{max}, NLc, 100°-70°	30.8 ± 5.8	43.4	19.4
V_{Fmax} peak, NLc, peak value	34.7 ± 6.4	49.6	24.2
Fascicle shortening velocity, L_0/s with L_0 = 5 cm			
V_{Fmax}, NLc, 100°-70°	5.9 ± 1.1	8.7	3.8
V_{max}, NLc, 100°-70°	6.2 ± 1.2	8.7	3.9
V_{Fmax} peak, NLc, peak value	6.9 ± 1.3	9.9	4.8
Gear ratio	1.08 ± 0.04	1.21	1.01

Measurement of Maximal Fascicles Shortening Velocity In Vivo

Muscle fascicle shortening velocity has previously been appraised in various conditions (e.g., plantar flexions or knee extensions) at different preset velocities between 2 and 20.5 cm/s (corresponding to 0.4 and 4.1 L_O/s) during strictly concentric contractions (10, 19, 21, 29, 33, 49, 50). In the present study, the peak instantaneous fascicle-shortening velocity reported during NLc ranged between 24.2 and 49.6 cm/s (corresponding to 4.8 and 9.9 L_O/s), with corresponding maximal angular velocities ranging from 534 to 865°/s. To date, such

Table 2. *Biomechanical features*

Feature*	Mean ± SD	Max	Min	r (P)
Fascicle length, cm	5.9 ± 0.9	7.7	4.5	0.05 (0.80)
Pennation angle, degrees	23.9 ± 2.8	30.1	18.1	0.03 (0.88)
Moment arm, cm	3.1 ± 0.4	4.4	2.3	0.12 (0.51)
Tendon stiffness, N/mm	295 ± 112	584	124	0.31 (0.09)
Tendon length, cm	19.4 ± 2.1	25.5	15.5	0.23 (0.22)

*n = 31.

extremely fast contraction velocities had never before been measured directly in vivo.

Although we acknowledge that the present experimental protocol did not impose strict unloaded conditions, some considerations strongly suggest that maximal shortening velocities of fascicles reached during the NLc should be very close to the actual maximal value. First, the mean torque produced over the range of motion during NLc was 2.4 N/m, corresponding to only 1.7% of MVC. Second, the force-velocity relationship was analyzed over the entire range of velocities (Fig. 6) to avoid unrealistic estimation of maximal shortening velocity (15, 22). Thus we were able to confidently extrapolate a realistic maximal shortening velocity using the Hill equation (Fig. 6). Interestingly, a visual inspection of Figure 6 demonstrated that V_{Fmax} was very close to the value obtained for V_{max} from the force-velocity relationship. In addition, although V_{max} was significantly higher than V_{Fmax} (i.e., 30.8 vs. 29.4 cm/s, or 6.2 vs. 5.9 L_O/s), a strong correlation was found between these two methods used to determine maximal velocity ($P = 0.003$). Therefore, we believe that for the first time, a direct measurement of the maximal shortening velocity of the human muscle fascicles in vivo was carried out.

It would be useful to compare this finding to that of the maximal shortening velocity measured in muscle fibers in vitro from biopsy investigations. This comparison is quite complex notably due to *1*) temperature dependence, because most of the available data were obtained from isolated muscle fibers placed at around 15°C; and *2*) the method of determination, because slack test measurements of maximal velocity (V_0) are usually 20–30% faster (43) than those determined from the F-V curve (V_{max}). Experiments performed at 15°C for MHC I and IIa myofibers reported maximal shortening velocity (V_{max}) ranging from 0.7 to 2.9 L_O/s [soleus and vastus lateralis muscles, (43)] and 0.9 to 3.0 L_O/s [for the gastrocnemius lateralis (27, 28)].

Considering a temperature coefficient of almost 4 to 5 corresponding to the increase from 15°C to 35°C (48), these V_{max} values measured in vitro would present a large range from approximately 3 to 15 L_O/s at a physiological temperature. They are in agreement with values obtained for direct measurements performed at 35°C on the soleus (slow twitch muscle) and extensor digitorum longus (fast-twitch muscle) of rats [7.02 to 13 L_O/s (48)]. In the present study, we found a maximal fascicle-shortening velocity ranging between 3.8 and 8.7 L_O/s [with a mean of 5.9 ± 1.1 L_O/s for V_{Fmax} and 6.2 ± 1.2 L_O/s for V_{max}; with $L_O = 5$ cm (32)]. The maximal shortening velocity properties of human muscle measured in vivo in the present study is within the lower range of values reported in vitro. It is not surprising to observe slightly slower shortening velocities in the present study compared with in vitro experiments. First, the small load applied in the NLc in the present study can reduce V_{max} values. Second, to establish force-velocity of fascicles, we made the choice to use mean values of fascicle velocity and force on an angular range (100° to 70°). However, the maximal instantaneous values of fascicle shortening velocity (ranged between 4.8 and 9.9 L_O/s, Table 1) were closer to values in vitro reported in the literature. Thus the method proposed in the present study represents a unique opportunity to directly measure the maximal muscle fascicle-shortening velocity of human muscles.

One study has examined the maximal unloaded shortening velocity (V_0) in vivo in triceps surae (52). Using the slack test applied, these authors obtained an ankle angular velocity of 492.9°/s in the unloaded condition with a preactivation level equal to 60% of MVC. This value is largely lower than the maximal angular velocity obtained in NLc in the present study (i.e., 654°/s). However, as mentioned above, the maximal angular velocity value obtained in this study included a significant contribution of tendinous tissues (Figs. 3 and 4), whereas Sasaki & Ishii (52) claimed to have measured only the unloaded shortening velocity that results from the contractile participation of muscle. It is interesting to note that considering a contribution of almost 60% of the fascicles to global joint angular velocity (Fig. 4), the maximal shortening velocity of fascicles in NLc in our study amounts 392°/s when expressed in ankle joint velocity. This value is closer than the previous reported V_0 value (52) and appears logically lower, keeping in mind that our measurement was equivalent to a V_{max} value. Further studies are needed to directly assess fascicle behavior during the slack test in vivo.

Taken together, these results suggest the maximal shortening velocities measured at the fascicle level in the present study should be very close to the actual maximal values. Therefore, the current methodological approach proposed to estimate the maximal shortening velocity (V_{Fmax}) on the basis that one trial in NLc may be used in practice in future studies and could be relevant for a better understanding of ballistic performance. Interestingly, it has been demonstrated that the ankle joint could reach the equivalent or even higher velocity in ballistic multijoint movements (e.g., vertical jump) than in monoarticular movements such as those the current study explores (25, 26, 51). Performance in multijoint movements is clearly enhanced by prestretching or the stretch-shortening cycle that involves an even larger contribution of tendinous tissues to angular velocity (34, 42). Therefore, it would be interesting to compare the maximal fascicle-shortening velocity obtained during both dynamic single-joint and multijoint tasks to appraise the respective roles of the different muscle-tendon unit components and to investigate the influence of V_{Fmax} on explosive performance.

Relationship Between Angular Velocity and Fascicle-Shortening Velocity in NLc

The second purpose of the present study was to analyze the factors that may be related to the capacity to achieve a maximum angular velocity (i.e., during NLc). Indeed, as expected, an important interindividual variability was observed in the capacity to reach a high angular velocity during NLc. In accordance with our hypothesis, the results showed that fascicle-shortening velocity was significantly correlated with angular velocity ($r = 0.57$, $P < 0.001$, Fig. 7), thereby confirming the primary importance of this muscular ability in fast-movement performance. Thus the factors that could influence this muscular property (e.g., fascicle length, muscle fiber type) are also essential in the ability to produce fast motion. In this context, it is interesting to note that fascicle length at rest (Table 2) was related to maximal fascicle-shortening velocity ($r = 0.52$, $P = 0.004$). This finding confirms those obtained on isolated fibers, reflecting a significant relationship between the number of sarcomeres in series and maximal fiber-shortening

velocity (16). Thorstensson et al. (56) raised a complementary explanation suggesting that subjects who possess a high percentage of fast-twitch fibers produce the highest maximal angular velocity. Thus we can assume that the proportion of fast-twitch fibers could partially explain the interindividual variability in fascicle-shortening velocity and hence the angular velocity in NLc. However, as in the other conditions, the contribution of tendinous tissues in NLc remains important (i.e., 41% of the muscle-tendon unit velocity). Despite an absence of preactivation and hence of an active stretch-shortening cycle before the start of contraction, the muscle tendon unit was substantially prestretched in the initial position (Fig. 3*E*). Such prestretching could induce the storage of elastic energy in the tendinous tissues that may subsequently contribute to movement generation. This can enhance the angular velocity at least at the start of the movement in NLc (Fig. 3*A*). Moreover, this contribution of tendinous tissues exhibited large variability between subjects (ranging from 18% to 57%), whereas a significant correlation was reported between maximal tendinous tissues velocity and maximal angular velocity ($r = 0.45$) during NLc. This result also highlights the importance of interactions between fascicle and tendon even during very fast concentric unloaded movements.

It has been argued that the rotation of fascicles during dynamic contractions is an interesting property that could enhance the shortening velocity of pennate muscle [i.e., the horizontal projection of fascicles, (4)]. The pennation angle varied from an average of 5.9° over the range of interest, which was sufficient to have a positive effect on horizontal fascicle-velocity, as can be seen in Fig. 3, *C* and *D*. In line with results reported in the literature on lower angular velocity (49), AGR was always higher than 1. It therefore confirmed the results reported by Azizi et al. (4), who argued that AGR could play an important role during high-velocity movements. On the other hand, although AGR allowed the enhancement of almost 10% of muscle-shortening velocity, no significant correlation was found between this criterion and the maximal angular velocity ($r = 0.01$).

Relationship Between Angular Velocity Reached in NLc and Biomechanical Features

Many studies have assumed that several additional characteristics and the biomechanical properties of the musculoarticular complex could influence muscle fascicle behavior (6, 20, 41, 54). Therefore, they can also affect the efficiency of muscle fiber dynamics by allowing a reduction of fascicle-shortening velocity to produce very high angular velocity, especially during human locomotion (running, jumping) (39). Thus according to the force-velocity relationship, muscle fibers could still produce higher force in these tasks (18). As was previously discussed, the contribution of the tendinous tissues and their significant influence on the maximal angular velocity reached in the NLc concurs with this statement. However, none of the numerous features measured in the present study (i.e., fascicle length, pennation angle, tendon length, length of moment arm, all measured at rest, and the tendinous tissues stiffness measured during isometric ramp contractions) were correlated with the maximal angular velocity in the NLc. Only an interesting significant correlation (previously discussed) was observed between fascicle length and maximal fascicle-shortening velocity (NLc). The lack of simple correlation could be explained by the possible compensations between the various biomechanical features. For example, a subject with a short moment arm of the triceps surae [i.e., a theoretical joint angular velocity advantage (41, 46)] could have short fascicle length (i.e., a theoretical disadvantage). Therefore, the velocity advantage allowed by one parameter could be partly canceled by the other. Interestingly, the two subjects who reached the highest maximal angular velocity (black points on Fig. 7) both presented higher values of fascicle-shortening velocity than the mean (6.5 L_O/s and 6.7 L_O/s) but were relatively far from the subject with the highest values (8.7 L_O/s). They also had much shorter fascicles than the subjects with the longest fascicle lengths (5.25 cm and 5.70 cm). However, this could be certainly compensated by a very short moment arm length (2.30 and 2.78 cm), both much shorter than the population mean (Table 2), which favors the production of high angular velocity (41). Therefore, we think that this lack of significant correlation with biomechanical features emphasizes that the maximal velocity is multifactorial.

Methodological Considerations

The results of the present study are based on the behavior of the gastrocnemius medialis only, whereas the triceps surae is composed of two other main muscles (i.e., the gastrocnemius lateralis, and the soleus). A previous study (29) of the gastrocnemii showed that fascicle-shortening velocity and muscle mechanics were not significantly different between gastrocnemius lateralis and gastrocnemius medialis. In addition, it is well established that the proportion of fast-twitch fibers is higher in the gastrocnemius medialis than in the soleus [49.2% and 12.3%, respectively (35)]. Thus the maximal fascicle-shortening velocity of the soleus should be significantly lower than that of the gastrocnemius medialis during NLc. Although it is not excluded that soleus muscle could act as a kind of slight load on the gastrocnemius muscles. Therefore, it can be assumed that the production of angular velocity at ankle level is mainly related to the gastrocnemii fascicle-shortening velocity measured in the present study. Additional measurements on the soleus are required to confirm this assumption.

The contraction duration in NLc was relatively short (106 ms on average) compared with what is needed to achieve maximum muscle force [>300 ms (56)]. However, Andersen et al. (2) showed that the time to peak velocity is less than 90 ms, indicating that the range of motion used in the present study was sufficient to achieve maximum angular velocity. In addition, the range of motion consistently encompassed the peak of fascicle-shortening velocity for all participants (Fig. 3*C*). Some studies have justified the use of preactivation conditions to avoid incomplete muscle activation during high-load concentric contractions (19, 21, 33). We deliberately chose to perform plantar-flexion contractions without preactivation so as not to be in a "quick-release" condition. Indeed, although such an experimental setup should induce an increase in angular velocity, quick-release movements largely increase the contribution of tendinous structures (17) and should notably alter the fascicle-tendon interaction (and length) at the beginning of the contraction. Consequently, these authors reported a lower maximal gastrocnemius medialis fascicle-short-

ening velocity in the quick-release condition than in the present study in NLc [4.6 L_O/s (17)].

Finally, although the starting position of the ankle was the same for all subjects, the stretching level of both fascicles and tendinous tissues before the contraction can differ due to individual passive muscle-tendon stiffness. The energy restitution of the parallel elastic component could thereby increase fascicle and tendinous tissues shortening velocities during NLc. Regarding the last two points, further studies should be conducted to *1*) analyze fascicle-tendon interactions during unloaded contractions performed without and with different levels of preactivation (as is performed during the slack test), and *2*) clarify how some parameters such as passive stiffness and starting angle are involved in the production of very high angular velocity.

Conclusion

The present study was the first to measure fascicle-shortening velocity during maximal plantar flexor contractions performed from very low to very high angular velocities and then to report a maximal shortening velocity of human muscle in vivo. The results demonstrate that fascicle-shortening velocity increases linearly with an increase in angular velocity, even at very high movement velocity. The higher shortening velocity obtained during NLc exhibited a high interindividual variability, corresponding to 3.8 to 8.7 L_O/s [with L_O = 5 cm (32)]. Several considerations suggest that these values are robust estimations of the theoretical maximal shortening velocity. The maximal angular velocity reached in NLc was related mainly to the maximal fascicle-shortening velocity (r = 0.57). Nonetheless, the substantial contribution of tendinous tissues also emphasizes the importance of the fascicle-tendon interaction during maximal concentric contractions. Despite their probable influence, the biomechanical features of the musculo-articular complex (e.g., moment arm length, muscle architecture, tendinous tissues stiffness, and AGR) failed to be correlated with the individual capacity to produce high angular velocity. The present experimental design should help to better understand and explain human muscle performance during dynamic single- and multijoint tasks.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

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

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