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Distinct muscle-tendon interaction during running at different speeds and in different loading conditions

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Running head

Muscle-tendon mechanics under differing running constraints

Abstract

The interaction between the Achilles tendon and the triceps surae muscles seems to be modulated differently with various task configurations. Here we tested the hypothesis that the increased forces and ankle joint work during running under contrasting conditions (altered speed or load) would be met by different, time-dependent adjustments at the muscle-tendon level. Ultrasonography, electromyography, kinematics and ground reaction force measurements were used to examine Achilles tendon, gastrocnemius and soleus muscle mechanics in sixteen runners in four different running conditions, consisting of a combination of two different speeds (preferred and +20% of preferred speed) and two loading conditions (unloaded and +20% of body mass). Positive ankle joint work increased similarly (+13%) with speed and load. Gastrocnemius and soleus muscle fascicle length and peak velocity were not altered by either condition, suggesting that contractile conditions are mostly preserved despite the constraints imposed in this experimental design. However, at higher running speed, tendon length changes were unaltered but mean muscle electromyographic activity increased in gastrocnemius (+10%, $P<0.01$) and soleus (+14%, $P<0.01$). Conversely, when loading was increased, mean muscle activity remained similar to unloaded conditions but the mean velocity of gastrocnemius fascicles was reduced and tendon recoil increased (+29%, $P<0.01$). Collectively, these results suggest that the neuromuscular system meets increased mechanical demands by favoring economical force production when enough time is available.

New and Noteworthy

We demonstrate that muscle-tendon mechanics are adjusted differently when running under constraints imposed by speed or load, despite comparable increases in work. The neuromuscular system likely modulates the way force is produced as a function of availability of time and potential energy.

Keywords

Achilles tendon, running, load carriage, locomotion, muscle architecture

Introduction

Tendons play an essential role during locomotor tasks such as running (5, 22). During stance, tendons lengthen under load, uncoupling fascicle behavior from that of the muscle-tendon unit (MTU) and enabling elastic energy storage and release to accelerate the body forward during push-off. This mechanism offers several advantages, allowing muscle fascicles to operate under favorable conditions for force production, recycling mechanical energy and amplifying the MTU power output during recoil (28). Importantly, the interaction between muscle and tendon can be modulated according to external constraints, as previously demonstrated with a change in running slope (21) or in the transition from walking to running (9). When running conditions demand higher rate of force development and a larger ground reaction impulse, force and work production can be adjusted thanks to greater strains of elastic elements or heightened muscle activation and consumption of metabolic energy. Although triceps surae muscles may operate at shorter lengths and at higher activation levels with increasing running speed (16, 18), a greater stretch of the elastic elements seems to preserve their relative contribution to MTU work (19). Whether the relative contributions of muscle and tendon work are modulated differently as a function of stance duration, when work requirements increase, is currently unexplored.

Another paradigm to study MTU behaviour in response to increased ankle joint moments involves increasing inertial load. This experimental design is complementary to the approach of increasing speed, because it also requires an increase in ankle joint moment or positive work (23) but under different time and energy constraints. Contrary to conditions imposed by increasing speed, loaded running increases the availability of potential energy, prolongs ground contact time and increases peak forces (30), implying a greater ground impulse. During jumping, Wade and colleagues showed in an elegant study how the work contribution of the ankle joint remains constant when total work is increased via additional loading, whereas it is decreased when additional work is imposed by increasing jump height (32). The authors further suggested that the use of additional elastic strain energy stored in the Achilles tendon is prioritized over muscle work during submaximal jumps with loading (32). In a similar line of thought, running with additional load may provide a paradigm to investigate neuromuscular mechanisms when availability of potential energy and time to apply force are increased.

The aim of the present study was therefore to investigate the behavior of the triceps surae muscles and the Achilles tendon in response to a comparable increased demand for force production when running at higher speed or with additional loading. Based on findings from other locomotor tasks (9, 15, 32), we expected greater ankle joint moment and Achilles tendon force when speed or load increased, and therefore predicted a greater stretch of the Achilles tendon in both conditions. Although joint kinematics were not expected to change in either experimental condition (4, 25), we hypothesized that the contrasting change in ground contact duration imposed when speed or load increased would affect the MTU behavior differently. Namely, the time to produce ground reaction force would be reduced at higher running speed whereas it would be extended when load is added. The reduced time and the greater rate of force development required under the faster running condition were expected to induce faster fascicle shortening velocities and greater muscle activity to compensate for unfavorable conditions for force production. Contrarily, when running with load, we hypothesized that longer stance time would cause slower fascicle contraction, which would not require muscle activation to increase.

Materials and Methods

Subjects and experimental protocol

Data were collected from sixteen male distance runners (age = 27±4 years, height = 1.79±0.05 m, mass = 68±6 kg) who ran at least 40 km per week.

A warm up period of five minutes barefoot running on an instrumented treadmill (M-Gait, Motekforce Link, Amsterdam, The Netherlands) was used to determine the individual preferred speed of each subject. Thereafter the subjects were asked to run at their individual preferred speed and at increased speed (+ 20% of the preferred speed), with and without additional loads (+ 20% of body weight). Loading was achieved by means of one or two adjustable weighted vests containing up to 10 kg each. Data were recorded for at least 10 complete steps during each of the four conditions. Ultrasound, kinematic and kinetic data were synchronously collected from the right leg, while muscle activity was recorded from the left leg at the same time. All measurements were synchronized during acquisition with a trigger signal sent from the ultrasound apparatus. All tests were performed twice, to obtain ultrasound scans from the muscle fascicles and from the myotendinous junction. The protocol was approved by the ethical committee of the Norwegian School of Sport Sciences and all subjects gave written informed consent to participate in the study.

Joint mechanics

Eleven infrared cameras (Qualisys, Gothenburg, Sweden; 300 Hz) captured the three-dimensional position of 20 reflective markers, mounted on the right leg of the subjects. Reflective markers placed over relevant anatomical landmarks (right and left anterior and posterior iliac spine, medial and lateral condyles, medial and lateral malleoli, calcaneus, first, second and fifth metatarsal) were used to define the joint centers of the pelvis (3), the right knee and the right ankle. The same calibration markers were used to define local coordinate systems for the body segments (pelvis, thigh, shank and foot) during a static capture. While calibration markers of the pelvis and foot were also used as tracking markers, the movement of the shank and thigh were tracked with 4-marker clusters positioned mid-way along these segments. A force plate instrumented to the treadmill measured ground reaction forces during the running trials. Initial ground contact and toe-off were defined with a threshold of 25N. Inverse kinematic and dynamic calculations were performed for the right leg using Visual 3D (C-motion, Germantown, MD). Negative and positive ankle and knee joint work were calculated by integrating the negative and positive joint power using trapezoidal integration. Individual net work was calculated as the sum of negative and positive work for both joints. Joint angle data were used to estimate MTU lengths of gastrocnemius and soleus (12).

Muscle-tendon mechanics

Gastrocnemius and soleus muscle fascicles and the gastrocnemius muscle-tendon junction were imaged using an ultrasound linear array transducer (LV7.5/60/96Z LS128, Telemed, Vilnius, Lithuania). The transducer was secured to the leg in a custom-made holder with self-adhesive tape to avoid probe movement. Tape was also used to rigidly attach three kinematic markers to the transducer to track its position. B-mode images with a field of view of 60 mm were collected at 80 frames s^{-1}. To measure fascicle length and pennation angle, the transducer was placed over the gastrocnemius muscle belly and aligned with the azimuthal direction of fascicles. A semi-automated tracking algorithm was used offline to analyze fascicle lengths and pennation angles (6, 8). The image quality of the soleus scans of three subjects was insufficient for analysis. Consequently, data for this muscle are based on thirteen subjects instead of sixteen. Architectural gear ratio (AGR) was calculated as the ratio between muscle length change and fascicle length change during the stance phase, similarly to Hollville et al. (14). Muscle length change was defined as the vertical projection of fascicle length change.

The position of the muscle-tendon junction was tracked from the displacement of the closest visible fascicle insertion in the two-dimensional ultrasound images (Tracker 4.95; www.physlets.org/tracker/). Applying previously obtained calibration of the image coordinate system and the transducer coordinate system, the position of the muscle-tendon junction was reconstructed into the three-dimensional coordinate system of the laboratory (20). Thus, the distance between the gastrocnemius muscle-tendon junction and a reflective marker over the osteotendinous junction on the calcaneus was defined as Achilles tendon length. The position of the osteotendinous junction of the Achilles tendon was previously identified using ultrasound. The shortest perpendicular distance between the force vector of the Achilles tendon and the ankle joint center was defined as the tendon moment arm at each time point (26). Thus, Achilles tendon force was estimated by dividing the ankle moment by the moment arm of the tendon.

Muscle activity

Muscle activity of gastrocnemius, soleus and tibialis anterior was measured with a wireless electromyography (EMG) system (TeleMyo DTS, Noraxon U.S.A. Inc., Scottsdale, AZ, USA) and recorded in Qualisys. Surface electrodes were placed on the muscle belly following SENIAM guidelines (13), after the recording sites were shaved and cleaned. EMG signals were collected at 1500 Hz and processed using a bandpass filter (20 – 450 Hz), rectified and low-pass filtered (10 Hz). For each subject and muscle, EMG data were normalized to the highest values recorded during the control trials (i.e. without added mass and at preferred speed).

Data processing and statistics

Kinematic, kinetic, ultrasound and EMG data were acquired during ten steps and at least eight steps were included in the analysis for each subject and each condition (9.5 ± 0.6 steps). All data were visually inspected to identify and exclude steps when their pattern or excursions departed from most other steps. A bidirectional second order Butterworth filter with a 15 Hz cut-off was applied to all raw data (except EMG, see above). Velocities of relevant variables were calculated as their time differential. Data were synchronized and resampled to 101 data points per full step cycle starting with the right heel strike, to calculate means across each percentage of the step for individual subjects and conditions.

Descriptive statistics were calculated for main outcome variables (Achilles tendon length, fascicle velocities and muscle activity) and for other variables related to muscle-tendon behavior (MTU length, stance duration, joint kinematics and kinetics). Differences between conditions were tested with two-way repeated-measures ANOVAS (factors: speed and load) and Sidak multiple comparison tests as appropriate. For all statistical tests, alpha was set to 0.05.

Results

The average preferred and increased running speeds were 3.1 (± 0.3) m s^{-1} (± 0.3) and 3.7 (± 0.3) m s^{-1}, respectively. Step cycle (from right foot touch-down to the following right foot touch-down) and stance phase durations (from touch-down to toe-off of the right foot) were affected by load and speed conditions. When speed increased, cycle duration decreased in both the unloaded and loaded conditions (-4 to -6%). Adding load also resulted in a reduction of cycle duration at increased speed (-3%) but not at preferred speed (**Table 1**). Stance duration decreased when running speed was increased, with or without additional load. On the contrary, stance duration was longer when the subjects ran with added mass at either speed (**Figure 1A**). Stance duration did not differ between running at increased speed with load and running at preferred speed unloaded. For this reason, average stance durations for these two conditions are indicated with the same shade of grey in the figures.

More positive and negative work was done by the ankle joint at higher speed in both loading conditions and with increased loading in both speed conditions. The positive work performed at the knee joint also increased when subjects were loaded (irrespective of speed), whereas speed did not have a statistically significant effect on positive knee work. Ankle and knee joint net work did not change in any condition (**Table 1**).

Peak ankle and knee joint angles were consistent across speed and loading conditions and, accordingly, no differences were found in MTU peak lengths for gastrocnemius (interaction $P = 0.33$, speed $P = 0.11$ and load $P = 0.47$) and soleus (interaction $P = 0.33$, speed $P = 0.06$ and load $P = 0.44$). Likewise, the shortening magnitude of both MTUs before toe-off was similar across all speed and mass conditions ($P > 0.12$ in all comparisons). However, maximum MTU shortening velocities increased with speed, regardless of loading conditions (**Table 1, Figure 1F**). At preferred speed, load carrying significantly reduced MTU velocities, whereas no difference was present at increased speed.

Mean length changes of the MTUs during a step cycle are presented for all modalities of speed and mass in **Figure 2**.

Speed and load effect on tendon behavior

Achilles tendon lengthening and tendon peak length were unaffected by increases in speed or load ($P > 0.05$ in all comparisons). However, a significant increase in tendon shortening amplitude (i.e. recoil) was found when running with load (**Figure 1B**, load effect $P = 0.01$), independently of speed ($P < 0.01$ at preferred and increased speed). Mean lengths of the Achilles tendon during the step cycle are presented for all modalities of speed and mass in **Figure 2**. Peak Achilles tendon force increased with speed in both loading conditions, and with loading at both speeds (**Table 1**). Achilles tendon work loops for all four conditions are presented in **Figure 3**.

Speed and load effect on muscle fascicle behavior

Neither speed nor mass had a substantial influence on changes in gastrocnemius (interaction $P = 0.55$, speed $P = 0.66$ and load $P = 0.80$) or soleus ($P = 0.60$ and $P = 0.52$) fascicle length. Mean fascicle length during the stance phase, fascicle shortening and peak fascicle shortening velocity did not vary across speed and loading conditions for either muscle ($P > 0.05$ for all variables). Loading had a main effect on mean gastrocnemius fascicle velocity during stance. Multiple comparison tests showed that mean fascicle velocity was reduced at preferred speed (post-hoc comparison $P = 0.01$) but not at increased speed (post-hoc comparison $P = 0.26$), whereas soleus mean shortening velocity was similar across conditions (**Table 1**). Changes in pennation angle during stance were similar under all conditions in both muscles (all $P > 0.05$). Gastrocnemius AGR during stance was also unchanged when speed or load increased (**Table 1**).

Speed and load effect on muscle activity

Running at higher speed increased mean muscle activity of the gastrocnemius and soleus during stance, in both loading modalities (interaction $P < 0.01$ for gastrocnemius and $P = 0.04$ for soleus, speed $P < 0.01$ for both muscles). Post-hoc comparisons indicated that mean EMG during the stance phase increased with speed with or without loading. There was no main effect of loading on muscle activity ($P = 0.61$) (**Figure 1D, E**). There were no interaction effects for time integral activity (reflecting the total amount of muscle activity) but we observed a main effect of loading for gastrocnemius ($P < 0.01$) and soleus ($P = 0.04$). Additionally, speed did not affect time integral activity of the gastrocnemius, whereas it was increased for soleus ($P = 0.04$). Activity of the antagonist tibialis anterior peaked during the swing phase in all conditions. However, the mean activity of this muscle during the stance phase increased with speed in both loading conditions, whereas load carrying did not affect tibialis anterior activity. The activity of all three muscles during the whole step cycle is presented in **Figure 4**.

Discussion

The present study examined the effect of increased mechanical demand of running on human triceps surae muscle-tendon behavior, when either speed or loading was altered. Based on the different availability of potential energy and time to produce force imposed by the two conditions, it was hypothesized that plantarflexion force would be produced via distinct adjustments of muscle-tendon interaction. Consistent with predictions from the literature, higher running speed reduced the stance duration while stance was prolonged with loading. In addition, both conditions required more mechanical work at the ankle joint (as previously shown in 23). Kinematic data showed little variation, which resulted in similar MTU stretch and shortening amplitudes across all conditions. However, the analysis of muscle and tendon mechanics also showed that the greater force requirements were met by different muscle-tendon behavior in the speed and loading conditions.

When speed was increased, the strain patterns of the Achilles tendon and muscle fascicles remained similar. The higher force produced during a shorter stance duration is therefore attributed to the greater muscle activity of the gastrocnemius and soleus. Additional loading did not affect tendon stretch either, but greater recoil was observed. Overall fascicle behavior remained similar, but in contrast to the increased speed condition, a reduction in mean fascicle shortening velocity was observed in the gastrocnemius when running at preferred speed with load. Hence, the increased work and impulse produced with added loading may be attributable to more favorable contractile conditions, and possibly result from a greater return of elastic energy due to the configuration of the running task.

Speed and load effect on muscle fascicle behavior and activity

In the present study, gastrocnemius and soleus fascicle peak shortening velocities and operating lengths were similar between loading conditions. Unchanged AGR and angular excursion of fascicles during stance further suggest that loading had little effect on contractile conditions. Yet gastrocnemius mean shortening velocity was reduced when running at preferred speed with loading, which may be associated with the longer duration of the stance phase. The inconsistency of the effect of loading on mean fascicle velocity across speeds suggests that a shorter stance phase duration may abolish the possibility to reduce contractile velocity when running with load. Regardless of running speed, unaltered or reduced contraction velocities observed with increased loading constitute advantageous conditions for increased force production while limiting the need to increase the mean level of activation. Further investigation is required to explain the different adjustments of gastrocnemius fascicle velocity when loading is added at different speeds. However, differences between the present results and a similar experiment on an animal model (25) are noteworthy. The initial stretch of fascicles measured in guinea fowl running with a similarly heavy load did not occur in humans in this study. Although the loading was similar, relative to body mass (22% vs 20% of body mass), load may have been higher relative to the gastrocnemius muscle force for the guinea fowl than for humans (i.e. because of different force/bodyweight ratios), or the relative tendon stiffnesses of guinea fowls may have been higher due to calcifications. If this were the case, it can be speculated that a similar fascicle stretch as in the guinea fowls could have been observed in humans at loads higher than in this study. Finally, loading conditions and contractile behavior may simply differ between humans and guinea fowls, because of the foot posture of the birds.

Despite the reduced ground contact duration at higher running speed, fascicles maintained the same shortening velocities (peak and mean), lengths and AGR seen at preferred speed. This may seem counterintuitive but is in line with previous work examining gastrocnemius (9, personal communication) and soleus (18, personal communication) fascicles within similar speed ranges. However, *in silico* data have shown that fascicle shortening velocities are higher at higher running speeds (3.5 - 8 m/s) than those used in this study (3.1 and 3.7 m/s) (7). Hence, the present data may either indicate that fascicles only maintain their contraction velocities within certain speed ranges or that our methods lack the resolution to detect smaller differences.

The unchanged operating length of fascicles in this study contrasts with the shift towards shorter operating lengths observed by others in the gastrocnemius (16) and soleus (18) muscles at higher running speeds. This inconsistency may again partly be due to differences in speed increment between previous studies (e.g. 33% between 3 and 4 ms^{-1} (18)) and our protocol (20%, between 3.1 and 3.7 ms^{-1}). Despite the good reliability of the method to track fascicle behavior (11), small changes induced within our speed conditions may have gone undetected due to insufficient sensitivity of ultrasound measurements. Nonetheless, the advantage conferred to the triceps surae muscles by operating towards the top of the ascending limb of the force-length relationship seems to be maintained at the speeds used in the present protocol.

While fascicle operating range was preserved when running at increased speed, mean muscle activity of gastrocnemius and soleus increased, regardless of the loading condition. The observation of increased muscle activity at higher running speed is consistent with previous reports (17, 18), and reflects a higher magnitude of activation. Despite the shorter stance phase, a faster rate of muscle activation also resulted in an increase in total amount of activity (i.e. time integral EMG) of the soleus. Conversely, when additional load was added to the runners at preferred speed, the longer duration of the stance phase resulted in an increase in time integral EMG but mean EMG activity was reduced. The post-hoc analysis further indicated that mean EMG increased with loaded running at higher speed, confirming that time availability is a critical factor driving the modulation of muscle activity when the mechanical demand increases. The advantage of the greater time availability may be linked to the way mechanical resonance of the system was altered when adding mass. In vitro data suggest that spring-like limb behavior during locomotion may be naturally regulated, by matching muscle strain patterns to the resonance frequency of the MTU (29). Hence, by increasing body mass without increasing running speed, the neuromuscular system may adopt an activation pattern in resonance with a lower natural frequency, maximizing force production and utilization of elastic energy.

With the exception of mean gastrocnemius fascicle shortening velocity decreasing with loading at preferred running speed, and the greater time integral of soleus EMG with loading at faster running speed, the adjustments in fascicle behavior and muscle activity observed between conditions were similar overall (e.g. peak fascicle velocity, fascicle operating length or mean EMG amplitude), for the gastrocnemius and soleus. Hence, different adjustments reflecting anatomical specificities of these muscles were largely missing here, although they may appear with larger increments in speed or load.

Collectively, the findings discussed above indicate that the system tends to meet an increased mechanical demand by modulating contraction velocity or muscle rate of activation as a function of time availability.

Speed and load effect on tendon behavior

Contrary to our expectations, tendon strain pattern was not affected when running speed increased, while a simulation study, conversely, predicted an increased elastic contribution to the positive work of the soleus and gastrocnemius MTUs when running speed increased from 2.1 to 9 ms^{-1} (19). However, the same study also suggested that the contribution of elastic strain energy of the gastrocnemius MTU would remain unchanged at intermediate speeds (19). Our Achilles tendon length results support the latter, by showing that neither tendon strain nor recoil changed at speeds lower than 4 ms^{-1}. This unchanged tendon behavior is consistent with the unchanged fascicular behavior and suggests a rather constant contribution of elastic energy within the studied range of speeds.

On the other hand, loading affected the Achilles tendon behavior through an increased recoil (but not stretch) amplitude, irrespective of the speed conditions. The apparent disagreement between the unaltered tendon stretch during the first part of the stance phase and the changes in recoil during the push-off is surprising and may have been caused by several factors. Firstly, methodological issues may have limited the precision of Achilles tendon length measurements (24, 31). To assess this possibility, we measured the inter-day variability of tendon strain measurements on a separate set of data collected for another project (n = 10, unpublished), using the same protocol as for the control running condition of the present study. We found a coefficient of variation of 10%, which in regards to sought differences in strain below 10% likely limited the sensitivity of our measures. Yet the reason why it would have affected tendon stretch and recoil differently remains unexplained. Aside from methodological explanations, the effective stiffness of the aponeurosis may have changed due to the influence of transverse strain. Farris and colleagues (10) established that a considerable amount of strain takes place transversely in the gastrocnemius aponeurosis during isometric contractions, which concurrently reduced longitudinal strain in the Achilles tendon. In addition, aponeurosis stiffness seemingly increases proportionally with contraction force because of radially expanding muscle fascicles (1, 2), and possibly also increases with MTU length (27). In the present case, a higher aponeurosis stiffness may have limited longitudinal tendon strain, in particular at the high Achilles tendon forces occurring at long MTU length measured at mid-stance when running with load. The hypothesis of additional energy being stored through transverse strain is also compatible with the unchanged joint kinematics and muscle operating conditions observed under loading. This may be seen as an advantageous way to increase tendon work when required, while allowing the subjects to run with the same joint coordination as in unloaded conditions and at preferred speed. Finally, the mismatched changes in tendon stretch and recoil with loading may also have been caused by the longer duration of the ground contact in this condition. By allowing a larger proportion of the tendon recoil to take place before the onset of the swing phase, the greater contact time would result in an increased impulse. This hypothesis would additionally be consistent with the observed faster velocities of tendon recoil.

Regardless of the factors explaining the lack of change in tendon stretch, the greater magnitude of tendon recoil arguably occurred while force was still being transmitted. Although certain methodological simplifications (as suggested by Matijevich et al. (24)) may give the impression of a continued tendon recoil while slackness has in fact been reached, we contend that this is not the case here. Firstly, tendon shortening continues after toe-off, when there is no longer any tension. Secondly, measurements obtained with shear wave elastography indicate that the gastrocnemius MTU is only slack beyond an ankle plantarflexion angle of 25°, which exceeds the angular range measured for this joint during running. We acknowledge, however, that tension and slackness levels cannot be inferred from the present data. For this reason, interpreting the larger recoil measured when running with load (e.g. in relation to energy return) can only be done with caution.

Conclusion

The present study shows distinct triceps surae muscle-tendon interaction in response to increased requirements for force and work at the ankle joint during running when speed or load increased. When ground contact time could be prolonged (i.e. with load), fascicle contractile velocity was preserved or lower and force was produced over a longer period of time. When running at increased speed and with shorter contact times, additional force was produced by greater muscle activation. These findings indicate that during running, the neuromuscular system meets increased mechanical demands by favoring economical force production when enough time is available.

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Figure 1. *Group mean values (± s.d.) during the stance phase for key variables that vary with loading or speed (preferred (PS) compared to increased speed (IS)): stance phase duration (A), Achilles tendon (AT) shortening (B), AT velocity (C), gastrocnemius (GM) EMG (D), soleus (SOL) EMG (E) and muscle-tendon unit (MTU) velocity (F). *P<0.05 for main effects of mass, § P<0.05 for main effect of speed, and # P<0.05 for interaction effect*

Figure 2. *Instantaneous lengths of the gastrocnemius and soleus muscle-tendon unit (MTU) (A-B), fascicles (C-D) and the Achilles tendon (AT) (E) during a whole step cycle for running at two different speeds (preferred speed and preferred speed + 20%) and two loading conditions (unloaded and loaded with 20% of body mass). Data are time normalized to 101 points and displayed as group means. The shaded area represents the stance phase of the conditions BM IS as dark grey, BM PS and AM IS as medium grey, and AM PS as light grey.*

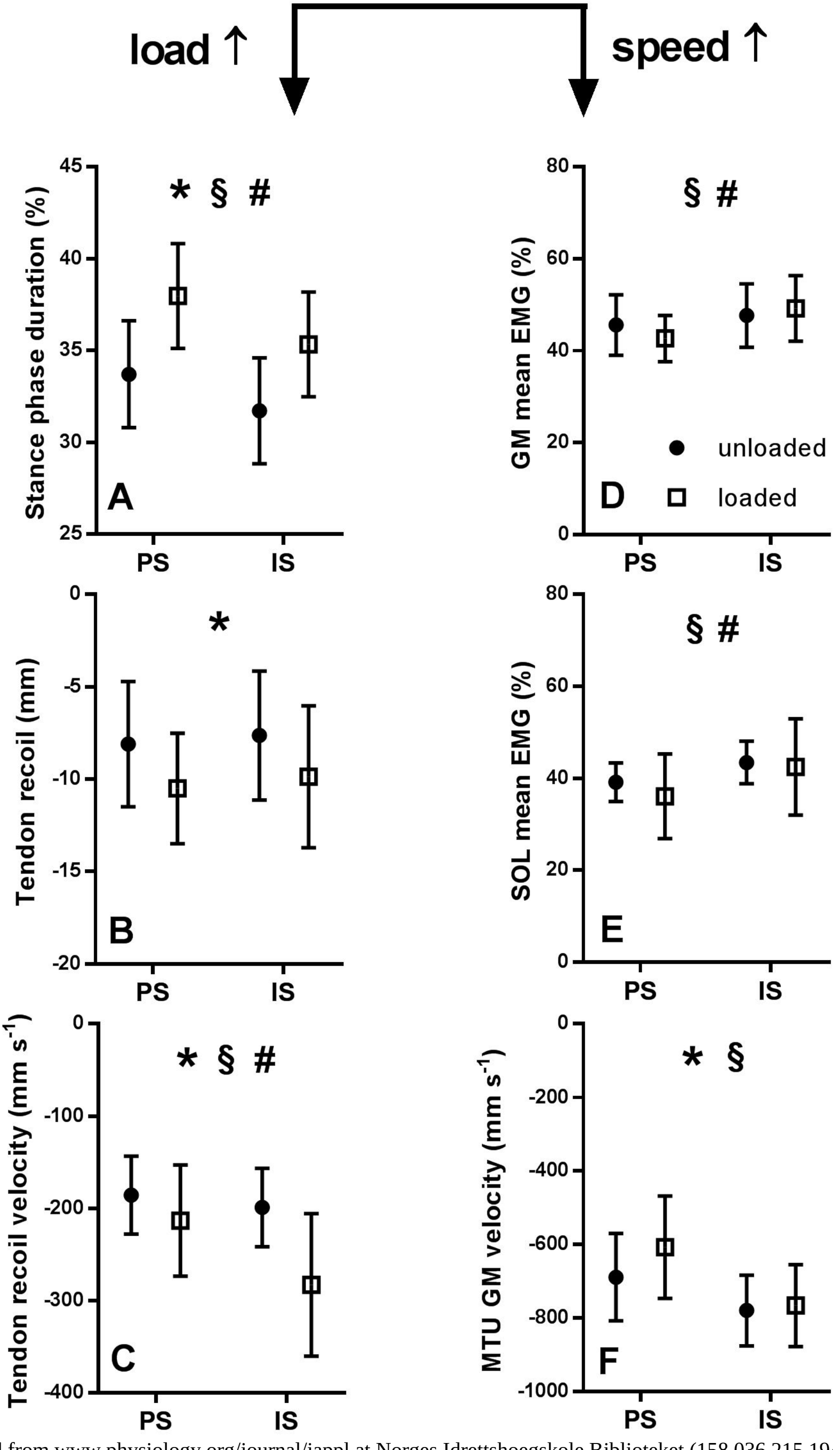
Figure 3. *Achilles tendon (AT) work loops during the stance phase of running unloaded and loaded (with 20% of body mass) at preferred and faster speed (preferred speed + 20%).*

Figure 4*. Electromyographic activity of gastrocnemius medialis (GM) (A), soleus (SOL) (B) and tibialis anterior (TA) (C) during a whole step cycle for running at two different speeds (preferred speed - PS and increased speed - IS) and mass (body mass - BM and added mass - AM) conditions. Time series are normalized to 101 points and EMG values are normalized to the maximum activity during unloaded running at preferred speed. Data are displayed as group means. The shaded area represents the stance phase of the conditions BM IS as dark grey, BM PS and AM IS as medium grey, and AM PS as light grey.*

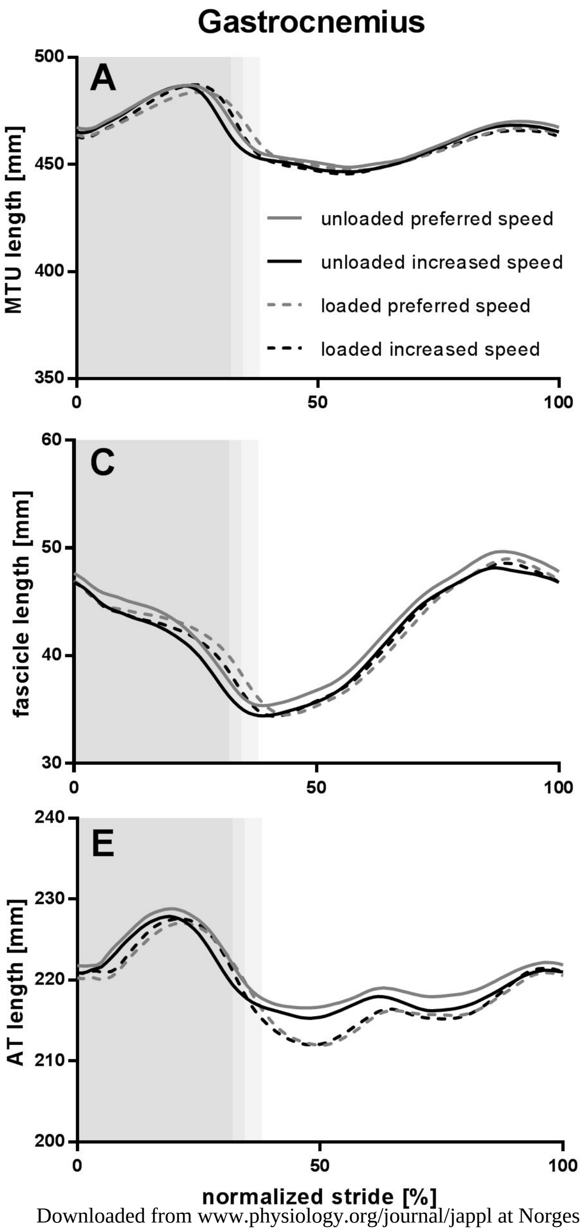
Table 1. Durations of step cycle and stance phase, positive work performed at the ankle and the knee, peak shortening velocities of the Achilles tendon, muscle-tendon units and fascicles, and AT forces, when running unloaded or loaded, at preferred speed or increased speed. Velocities were normalized to the respective mean length during stance.

			Unloaded		Loaded		ANOVA results		
			Preferred speed	**Increased speed**	**Preferred speed**	**Increased speed**	**Interaction effect**	**Main effect speed**	**Main effect load**
Duration [s]		**Cycle**	0.68 ± 0.04	0.66 ± 0.05*	0.68 ± 0.05	0.64 ± 0.05*§	0.01	<0.01	0.02
		Stance	0.23 ± 0.02	0.21 ± 0.02*	0.26 ± 0.02§	0.23 ± 0.02*§	<0.01	<0.01	<0.01
Duty factor [%]			34 ± 3	32 ± 3*	38 ± 3§	35 ± 3*§	0.03	<0.01	<0.01
Work [J]	**positive**	**Ankle**	55 ± 13	62 ± 15*	62 ± 18§	69 ± 20*§	0.95	<0.01	<0.01
		Knee	14 ± 8	16 ± 10	17 ± 9§	19 ± 10§	0.61	0.14	<0.01
	negative	**Ankle**	32 ± 14	36 ± 16*	37 ± 18§	43 ± 20*§	0.25	<0.01	<0.01
		Knee	27 ± 11	29 ± 12	31 ± 11§	31 ± 11	0.13	0.14	<0.01
	net	**Ankle**	23 ± 6	26 ± 7	25 ± 10	26 ± 11	0.27	0.08	0.60
		Knee	-13 ± 7	-13 ± 5	-14 ± 9	-12 ± 6	0.39	0.57	0.82
Peak shortening velocity [mms^{-1}]		**GM MTU**	0.45 ± 0.27	0.43 ± 0.26*	0.53 ± 0.30§	0.50 ± 0.38*	0.06	<0.01	0.01
		SOL MTU	0.40 ± 0.34	0.34 ± 0.31*	0.48 ± 0.41§	0.45 ± 0.49*	0.09	<0.01	<0.01
		GM fasc.	1.68 ± 1.06	1.82 ± 1.22	1.87 ± 1.41	2.00 ± 1.23	0.76	0.68	0.15
		SOL fasc.	1.96 ± 1.55	1.99 ± 1.74	1.89 ± 1.12	2.53 ± 1.84	0.47	0.10	0.47
Mean shortening velocity [mms^{-1}]		**GM fasc.**	1.03 ± 0.66	1.34 ± 0.91	0.99 ± 0.85§	1.18 ± 0.75	0.29	0.05	0.03
		SOL fasc.	0.78 ± 0.86	0.98 ± 1.21	0.64 ± 0.81	1.02 ± 1.41	0.97	0.24	0.26
AGR during stance		**GM**	1.16 ± 0.06	1.16 ± 0.08	1.17 ± 0.10	1.17 ± 0.10	0.61	0.92	0.27
Force [N]		**AT**	4336 ± 931	4644 ± 1037*	4501 ± 1029§	4896 ± 1059*§	0.21	<0.01	<0.01
Impulse [Ns]			469 ± 59	452 ± 61*	560 ± 76^{5}	529 ± 75*§	<0.01	<0.01	<0.01

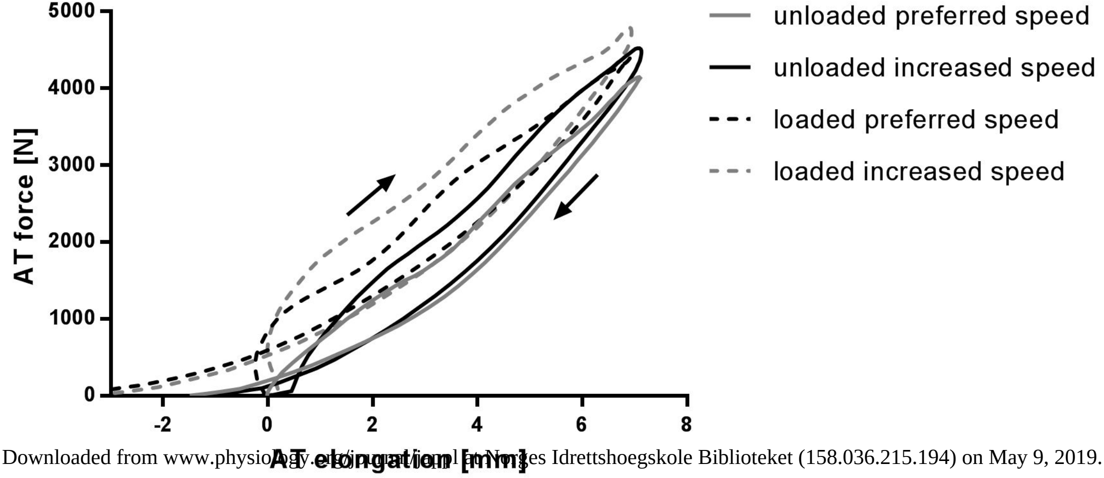
Data for work, shortening velocities of gastrocnemius (GM) and soleus (SOL) muscle-tendon units (MTU) and fascicles, and force were obtained during the stance phase. Values are mean ± SD. * Significantly different from the preferred speed condition with the same load; § Significantly different from the unloaded condition at the same speed.



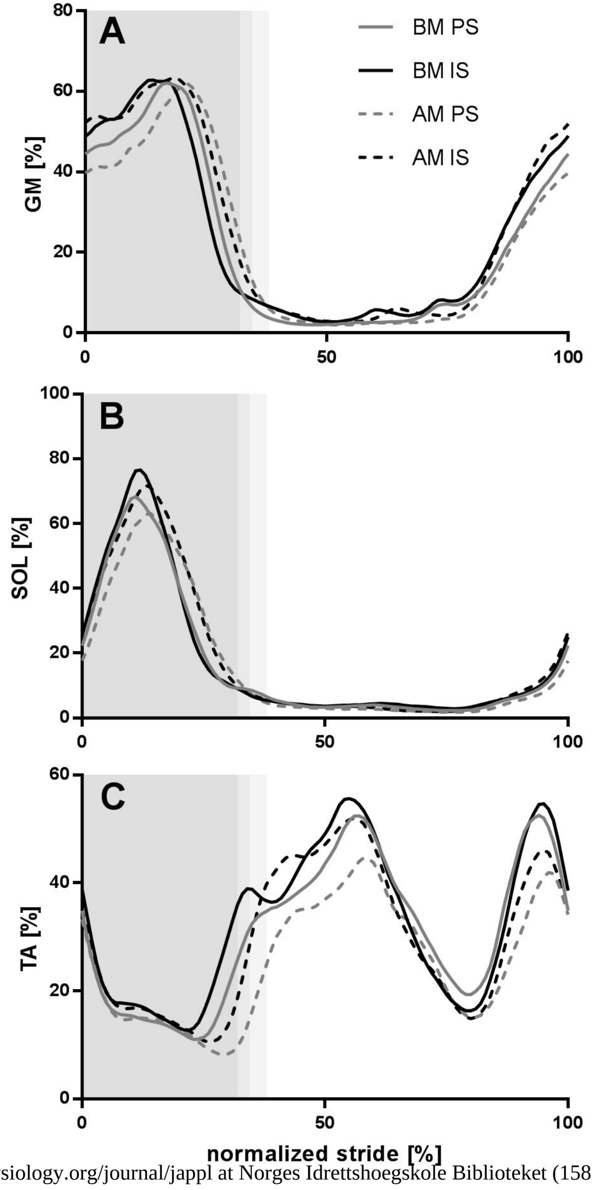
load ↑
speed ↑
Stance phase duration (%)
45
40
35
30
25
* § #
A
PS
IS
GM mean EMG (%)
80
60
40
20
0
§ #
D
unloaded
loaded
PS
IS
Tendon recoil (mm)
0
-5
-10
-15
-20
*
B
PS
IS
SOL mean EMG (%)
80
60
40
20
0
§ #
E
PS
IS
Tendon recoil velocity (mm s-1)
0
-100
-200
-300
-400
* § #
C
PS
IS
MTU GM velocity (mm s-1)
0
-200
-400
-600
-800
-1000
* §
F
PS
IS



Gastrocnemius
Soleus
A
B
C
D
E
MTU length [mm]
fascicle length [mm]
AT length [mm]
normalized stride [%]
unloaded preferred speed
unloaded increased speed
loaded preferred speed
loaded increased speed
500
450
400
350
400
350
300
250
60
50
40
30
50
40
30
20
240
230
220
210
200
0
50
100



unloaded preferred speed
unloaded increased speed
loaded preferred speed
loaded increased speed
AT force [N]
5000
4000
3000
2000
1000
0
-2
0
2
4
6
8
AT elongation [mm]


A
B
C
BM PS
BM IS
AM PS
AM IS
GM [%]
SOL [%]
TA [%]
0
20
40
60
80
100
0
50
100
normalized stride [%]