Walking and Running Require Greater Effort from the Ankle than the Knee Extensor Muscles

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ABSTRACT

KULMALA, J.-P., M. T. KORHONEN, L. RUGGIERO, S. KUITUNEN, H. SUOMINEN, A. HEINONEN, A. MIKKOLA, and J. AVELA. Walking and Running Require Greater Effort from the Ankle than the Knee Extensor Muscles. *Med. Sci. Sports Exerc.*, Vol. 48, No. 11, pp. 2181–2189, 2016. **Introduction**: The knee and ankle extensors as human primary antigravity muscle groups are of utmost importance in a wide range of locomotor activities. Yet, we know surprisingly little about how these muscle groups work, and specifically, how close to their maximal capacities they function across different modes and intensity of locomotion. Therefore, to advance our understanding of locomotor constraints, we determined and compared relative operating efforts of the knee and ankle extensors during walking, running, and sprinting. **Methods**: Using an inverse dynamics biomechanical analysis, the muscle forces of the knee and ankle extensors during walking (1.6 $m \cdot s^{-1}$), running (4.1 $m \cdot s^{-1}$), and sprinting (9.3 $m \cdot s^{-1}$) were quantified and then related to maximum forces of the same muscle groups obtained from a reference hopping test that permitted natural elastic limb behavior. **Results**: During walking, the relative effort of the ankle extensors was almost two times greater compared with the knee extensors (35% ± 6% vs 19% ± 5%, $P < 0.001$). Changing walking to running decreased the difference in the relative effort between the extensor muscle groups, but still, the ankle extensors operated at a 25% greater level than the knee extensors (84% ± 12% vs 63% ± 17%, $P < 0.05$). At top speed sprinting, the ankle extensors reached their maximum operating level, whereas the knee extensors still worked well below their limits, showing a 25% lower relative effort compared with the ankle extensors (96% ± 11% vs 72% ± 19%, $P < 0.01$). **Conclusions**: Regardless of the mode of locomotion, humans operate at a much greater relative effort at the ankle than knee extensor muscles. As a consequence, the great demand on ankle extensors may be a key biomechanical factor limiting our locomotor ability and influencing the way we locomote and adapt to accommodate compromised neuromuscular system function. **Key Words:** WALKING, RUNNING, SPRINTING, RELATIVE EFFORT, MUSCLE FORCE, LOCOMOTOR PERFORMANCE

Within each human step, muscles must produce force on the ground to support and propel the body forward. The majority of this force during walking and running is produced by extensor muscles of the knee and ankle (40). However, although the force production requirements of these muscles are known to greatly depend on speed and mode of locomotion (5), it is still not clear to what extent of their individual maximal capacities do our primary locomotor muscles actually work during walking or running. Knowing the operating efforts of these muscles would be important not only for better understanding of the biomechanical constraints on walking and running ability, but also for gaining insights into the mechanisms that determine the way we locomote and adapt to accommodate compromised neuromuscular system function. This information, in turn, would be relevant in the broad context of human locomotion from sports performance enhancement to prevention and rehabilitation of locomotor impairments.

Historically, most experimental assessments of muscle efforts in locomotion have relied on the normalization procedure, originally introduced by Dubo et al. (11), where either the muscle EMG or less frequently the joint moments (20) produced in a given task are related to the reference level obtained from maximal isometric or isokinetic contraction of the same muscle. However, although both EMG and mechanical approaches consistently suggest greater operating

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effort for the ankle than knee extensors in locomotion (4,7,11,26), the relative values in these studies have often exceeded the 100% maximum level, indicating the difficulty in defining the precise operating effort. The major disadvantage associated with the EMG approach lies in the complex EMG–force relation of the muscle (31), which becomes particularly evident in dynamic movements such as running (26). The mechanical approach, on the other hand, suffers from the mismatch problem due to disparity in joint moment definition between locomotion (inverse dynamics) and the maximum force reference test (isokinetic dynamometer) (1). Furthermore, the mismatch likely occurs in muscle functional characteristics—during walking and running, the knee and ankle extensors are known to undergo stretching (eccentric) before their shortening (concentric) action, which can substantially enhance their force production through use of muscle–tendon unit (MTU) elasticity and stretch reflex potentiation when compared with pure isolated muscular contractions in an isokinetic dynamometer (21).

To the best of our knowledge, the study by Hortobágyi et al. (18) quantifying the relative knee extensor muscle efforts in stair walking and rising from a chair is the only one, to date, in which the joint moments produced across measured activities and during the maximal isometric reference force test were defined using the identical inverse dynamics method. Even though the investigators were not able to fully match the type of muscle contraction in the dynamic activities with the isometric reference test, their procedure provided a very reasonable approximation of relative knee extensor muscle effort across the studied activities for young and old adults (42%–54% vs 78%–88% of maximal capacity). An obvious strength of this procedure is the fact that it eliminates all inaccuracies due to methodological differences between movement and reference test measurements. Surprisingly, however, there have been no studies attempting to quantify the relative muscle efforts during level walking and running using this "matched method approach."

Therefore, the purpose of this research was to pursue a better understanding of how our key locomotor muscles work and, specifically, how close to their individual maximal capacities they function during level walking and running. We determined the relative efforts of the knee and ankle extensors across different modes and intensity of locomotion by using the inverse dynamics approach and a maximal force reference test that permitted natural springlike behavior of the limb. Of the several stretch-shortening type of movements described in the literature, we selected maximal two-leg hopping exercise as a reference test, because it has been shown to enable humans to produce the greatest muscle moments from their knee and ankle extensors (49). Based on the existing literature (4,7), we hypothesized that the relative efforts of the extensor muscles would be greater at the ankle than knee during walking, but virtually equal during running, where deeper knee flexion excursion has been shown to increase muscular demand more at the knee than the ankle extensor level (5). Nonetheless, because greater speed-related increase in the muscular outputs in running has been shown to occur in the extensor muscles of the ankle compared with the knee (43), we hypothesized that the maximum speed sprinting would therefore require greater relative effort from the ankle than knee extensors.

METHODS

Participants. Twelve healthy subjects participated in this study (age, 27 ± 6 yr; height, 181 ± 5 cm; and mass, 73 ± 8 kg). Each subject came from a background of competition (sprinters and long jumpers) and several years of training. The subjects provided informed consent and confirmed that they did not have a previous history of any musculoskeletal problems, such as a recent injury or surgery, which could have an effect on the locomotor patterns. The study was approved by the local ethics committee, which was performed in accordance with the Declaration of Helsinki.

Biomechanical analysis. Biomechanical measurements were conducted in an indoor sports hall. First, after a thorough warm-up period, the subjects performed three walking trials at a self-selected speed and three running trials at 4.0 ± 0.2 $m \cdot s^{-1}$. Next, each subject sprinted 60 m at maximum effort twice. The locomotor speeds were monitored using photocells positioned 30 and 40 m along the track. The same part of the track was used as a motion capture area. Finally, to precisely determine the maximum forces each athlete could develop from their knee and ankle extensors during natural movement, measurements of a series of maximal two-legged hops were taken from each subject. Beginning with each foot standing on one of two force plates, each subject jumped repeatedly as high as possible over a period of 10 s, rested for 3 min, and then repeated the 10-s jumping cycle. Of the several plyometric exercises described in the literature, this movement has been shown to enable athletes to produce the greatest joint moments from their knee and ankle extensor muscles (49). Subjects used their own running shoes during walking and hopping and their own track shoes during running and sprinting.

An eight-camera system (Vicon T40, Oxford, UK) and five force platforms (total length, 5.7 m; AMTI, Watertown, MA) were used to record marker positions and ground reaction force (GRF) data synchronously at 300 and 1500 Hz, respectively. Anthropometric measurements (height, mass, leg length, and knee and ankle diameters) and bilateral placement of 22 retroreflective markers (on the shoe over the second metatarsal head and over the posterior calcaneus, lateral malleolus, lateral shank, lateral knee, lateral thigh, anterior superior iliac spine, posterior superior iliac spine, clavicula, sternum, seventh cervical vertebra, and 10th thoracic vertebra) were performed according to the Vicon Plug In Gait full body model. To avoid impact artifacts, marker trajectories and GRF data were low-pass filtered using a fourth-order Butterworth filter with a cut-off frequency of 18 Hz (6). Foot contact and toe-off events were determined based on the 20-N vertical GRF threshold level.

Analysis of knee and ankle extensor muscle moment productions for each measured task was performed using the standard inverse dynamics approach (Vicon Plug In Gait model, Nexus v. 1.7). Assuming that all limb muscles cross only a single joint and that no muscle co-contractions occur, the muscle forces were calculated following previously published models for the knee (15) and ankle (47) extensors. Input variables for both models included joint angle and net extensor moment (M). First, the knee extensor muscle effective moment arm (L_{knee}) was calculated as a function of knee flexion angle using the nonlinear equation as follows:

$$L_{\text{knee}} = 8.0\text{E}^{-5}x^3 - 0.013x^2 + 0.28x + 0.046 \qquad [1]$$

where x indicates knee angle.

Second, knee extensor force (F_{knee}) was calculated as follows:

$$F_{\text{knee}} = M_{\text{knee}}/L_{\text{knee}} \qquad [2]$$

Finally, ankle extensor force (F_{ankle}) was determined by dividing the net ankle extensor moment by the estimated ankle extensor muscle lever arm (L_{ankle}) as described by Self and Paine (47):

$$F_{\text{ankle}} = M_{\text{ankle}}/L_{\text{ankle}} \qquad [3]$$

$$L_{\text{ankle}} = -0.5910 + 0.08297a - 0.0002606a^2 \qquad [4]$$

where a indicates ankle angle.

Kinematic and kinetic data during ground contact were time normalized (0%–100%) and averaged across several ground contacts. To avoid muscle fatigue, only two maximal sprinting trials were collected per subject. Therefore, the leg that demonstrated a greater number of successful force plate contacts on any of the five force plates during two sprinting trials was selected for the analysis. The total number of analyzed contacts per subject was five during walking and running, and two to four during sprinting. During hopping, the three best trials were selected for the analysis based on the magnitude of the peak vertical GRF.

Finally, the relative efforts of the knee and ankle extensors were determined as a ratio of peak muscle forces developed during locomotion modes to maximum muscle force produced by the same muscle group during the two-leg hopping task (Fig. 1). In addition to maximum force-based analysis, we also determined relative efforts for each locomotion mode using the joint angular velocity matched force value from the hopping test as a reference.

Statistical analysis. To examine whether relative efforts differed between the knee and the ankle extensors, we used a two-tailed dependent sample t-test. In addition, to test whether ground contact times, peak vertical GRF, joint angles, and angular velocities differed between locomotor and

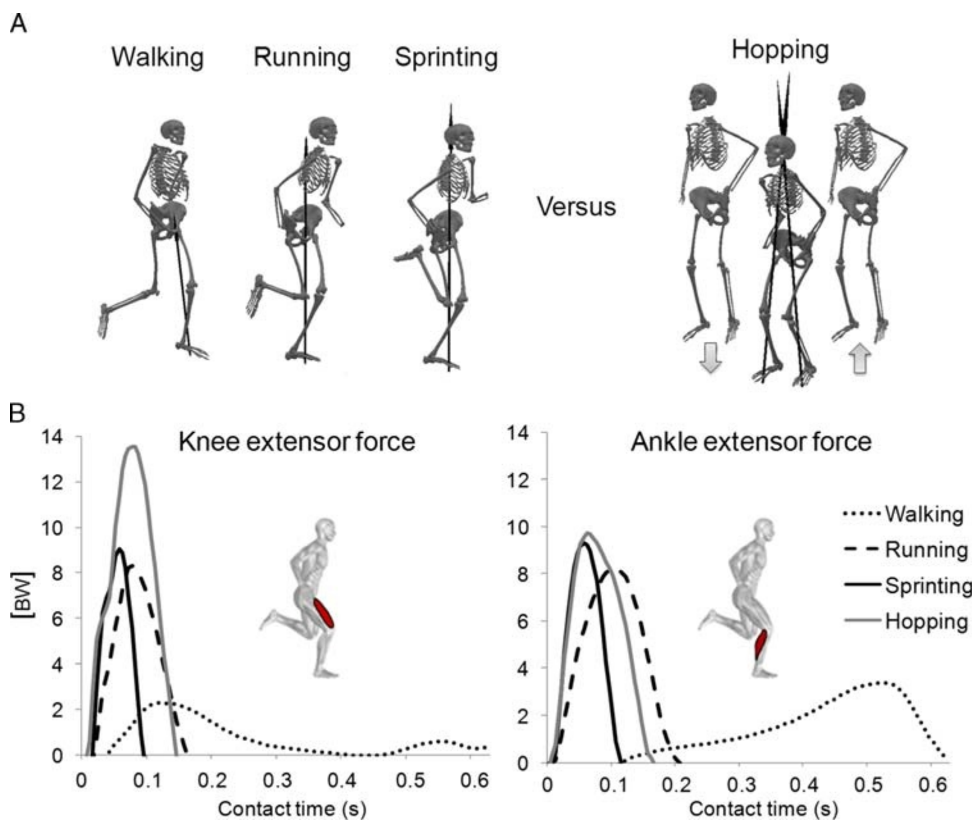

FIGURE 1—A, Locomotion and hopping tasks performed in the experiments. B, Ensemble average curves of knee and ankle extensor muscle forces during the stance phase of walking, running, sprinting, and hopping. The relative extensor muscle efforts were determined as a ratio of peak muscle forces developed during locomotion modes to maximum muscle force produced by the same muscle group during the two-leg hopping task.

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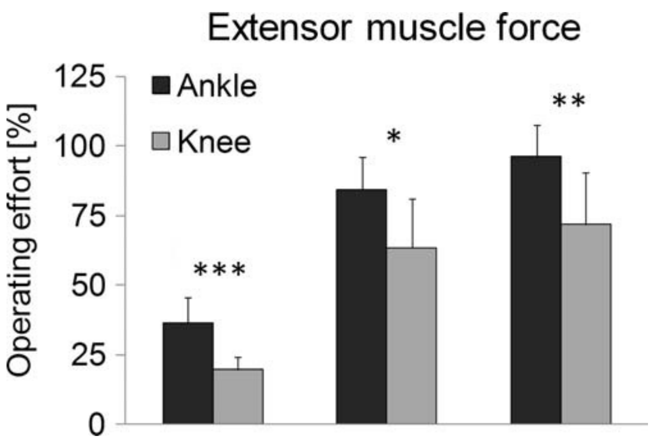

FIGURE 2—Relative knee and ankle extensor muscle forces during walking, running, and sprinting.

hopping tasks, we used a repeated-measures ANOVA followed by Bonferroni *post hoc* testing for pairwise comparisons. All tests were performed with SPSS software (version 22; SPSS, Chicago, IL). P values less than 0.05 were considered significant.

RESULTS

Analysis of relative muscular effort showed that regardless of the mode of locomotion, the ankle extensors operated at a greater proportion of their maximal capacity compared with the knee extensors (Fig. 2 and Table 1). During walking (average speed of all subjects, $1.6 \pm 0.1\ \mathrm{m{\cdot}s^{-1}}$), the operating muscle force was 46% greater at the knee than ankle extensors ($P < 0.001$). During running ($4.1 \pm 0.2\ \mathrm{m{\cdot}s^{-1}}$), a difference in the relative efforts decreased between muscle groups; however, ankle extensors showed 25% greater operating force when compared with the knee extensors ($P < 0.05$). Finally, analysis of maximal speed sprinting ($9.3 \pm 0.4\ \mathrm{m{\cdot}s^{-1}}$) showed 96% operating force for the ankle extensors suggesting maximum effort, which was 25% greater than what was produced by the knee extensors ($P < 0.01$).

The total limb force production, determined as a peak vertical GRF, reached 3.82 ± 0.51 body weight (BW) during hopping (Table 2). In walking, running, and sprinting, peak vertical GRF values were 2.58, 0.68, and 0.47 BW greater, respectively, compared with hopping ($P < 0.001$, $P < 0.001$, and $P < 0.01$). Ground contact time was 0.17 ± 0.02 s for hopping, which was significantly shorter than that for walking (0.63 ± 0.02 s, $P < 0.001$) and running (0.21 ± 0.02 s, $P < 0.001$), but longer than that for sprinting (0.12 ± 0.01, $P < 0.001$).

TABLE 2. Ground contact time and peak vertical GRF during walking, running, sprinting, and a reference hopping task.

	Walking	Running	Sprinting	Hopping
Contact time (s)	0.63 ± 0.02***	0.21 ± 0.02**	0.12 ± 0.01***	0.17 ± 0.02
Peak vertical GRF (BW)	1.24 ± 0.07***	3.14 ± 0.31***	3.34 ± 0.33**	3.82 ± 0.51

Data are shown as mean ± SD.
** $P < 0.01$ and *** $P < 0.001$, statistically significant difference compared with the hopping.

To approximate muscle contractile conditions during measured tasks, we analyzed joint angles and angular velocities at the time of peak extensor muscle forces. At the knee level, flexion angles at the time of peak knee extensor force (F_{Kmax}) were 32.9°, 12.9°, and 12.0° greater during hopping compared with walking, running, and sprinting, respectively ($P < 0.001$, $P < 0.001$, and $P < 0.01$; Table 1). Furthermore, at the time of peak ankle extensor force (F_{Amax}), the ankle plantarflexion angles were 14.5° and 4.3° greater during hopping than during walking and running, respectively ($P < 0.001$ and $P < 0.05$; Table 1). Knee angular velocities at F_{Kmax} were relatively low and showed no significant differences between hopping and locomotor tasks. At the ankle level, angular velocities at F_{Amax} in walking showed positive values and differed significantly ($P < 0.05$) from hopping where negative velocity was present at F_{Amax} (Table 1). An analysis of relative efforts using joint angular velocity matched reference force values had minimal effects on the operating levels of the muscle groups (Table 1).

DISCUSSION

The present article provides the most comprehensive description available to date of operating muscular efforts of human primary locomotor muscles across walking, running, and sprinting. The results highlight that, regardless of the mode of locomotion, humans operate at a clearly greater

TABLE 1. Comparisons of relative muscular efforts of the knee and ankle extensors during walking, running, and sprinting.

	Walking ($1.6 \pm 0.1\ \mathrm{m{\cdot}s^{-1}}$)		Running ($4.1 \pm 0.2\ \mathrm{m{\cdot}s^{-1}}$)		Sprinting ($9.3 \pm 0.4\ \mathrm{m{\cdot}s^{-1}}$)		Hopping Reference Test	
	Knee	Ankle	Knee	Ankle	Knee	Ankle	Knee	Ankle
Extensor muscle force (N)	1866 ± 397	2410 ± 377	6073 ± 1422	5960 ± 1292	6962 ± 2045	6759 ± 1308	9808 ± 1925	7075 ± 1246
Extensor muscle force (BW)	2.6 ± 0.4	3.4 ± 0.3	8.5 ± 1.5	8.3 ± 1.4	9.8 ± 2.8	9.5 ± 1.3	13.9 ± 3.0	9.9 ± 1.4
Operating effort (%)	19 ± 5	35 ± 6***	63 ± 17	84 ± 12*	72 ± 19	96 ± 11**		
Joint angular velocity matched operating effort (%)	20 ± 5	35 ± 7***	63 ± 18	85 ± 12*	73 ± 19	97 ± 12**		
Joint angle at peak force (deg)	25.0 ± 4.9******	14.0 ± 3.4******	44.8 ± 4.7******	26.5 ± 4.6	45.9 ± 7.5*****	24.2 ± 5.2****	57.9 ± 7.3	28.5 ± 4.4
Joint angular velocity at peak force ($\mathrm{deg^{-1}}$)	−15.7 ± 34.6	42.2 ± 27.5****	−4.6 ± 53.8	24.1 ± 44.7	−6.6 ± 76.3	−35.5 ± 60.6	2.0 ± 135.1	−34.3 ± 69.0

Data are shown as mean ± SD.
Operating efforts were determined by normalizing extensor muscle forces across different modes of locomotion to maximum force, as well as to joint angular velocity matched force quantified in two-leg hopping. Positive angular velocities indicate shortening of the MTU at peak force, whereas negative values represent lengthening of the MTU at peak force.
Statistical significance between knee and ankle extensor operating effort: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
Statistical significance between locomotion mode and the force reference test: **** $P < 0.05$, ***** $P < 0.01$, ****** $P < 0.001$.

proportion of capacity at the ankle than knee extensor muscles. This observation offers a new insight into biomechanical constraints of human locomotor ability and provides the basis for better understanding of the mechanisms that influence the way we locomote and adapt to accommodate compromised neuromuscular system function.

Walking. As expected, during walking, the participants operated at a greater proportion of capacity at the ankle than knee extensor muscles. The relative force of the ankle extensors was almost two times greater compared with the knee extensors, which is consistent with previous studies (4,7); however, the relative level at which both muscle groups were operating was remarkably lower in the present study. Our analysis demonstrate 19% and 35% operating force for the knee and ankle extensors, respectively, whereas previous studies (4,7) have reported a relative level approximately two times greater for both muscle groups, when normalization to the maximum isokinetic force reference test was used. Nevertheless, the current and previous observations (4,7) imply that during walking, much lower muscular reserve is available at the ankle than knee extensors to buffer any loss of muscular capacity. Consequently, these findings may explain why muscular weakness, for example, due to aging, typically first challenges the normal function of the ankle extensors during walking, leading to compensatory actions such as shorter steps and shift of the joint kinetics from the ankle toward more proximal joints (4,9,25).

Running. When gait was changed from a walk to a run ($4.1 \pm 0.2\ \mathrm{m{\cdot}s^{-1}}$), the peak extensor muscle forces increased more at the knee (3.2-fold) than the ankle level (2.5-fold). This result was expected because of a considerable decrease in knee extensor effective mechanical advantage that occurs during running due to deeper knee flexion (5). As a result, the difference in the relative effort between muscle groups decreased, but still, the ankle extensors operated at a significantly greater proportion of capacity than the knee extensors (84% vs 63%). Consequently, running gait appears to require clearly greater operating effort from the ankle than knee extensors. This suggests that the ankle extensors may be more prone to running-induced muscular fatigue than the knee extensors, which would possibly make declined ankle propulsion ability a key limiting factor of prolonged running performance. Although no direct evidence for this has yet appeared, previous studies (39,42) have reported a significant reduction in the extensor muscle EMG at the ankle but not at the knee during intensive long-distance running, thus supporting the suggestion of a greater level of fatigue in the ankle extensors.

The above findings may also shed new light on understanding why the majority of both recreational and competitive runners favor using a rearfoot rather than forefoot striking pattern (28), if sufficient cushion, provided by the shoe or surface, is available (30). According to a long-standing hypothesis, natural running patterns are believed to be selected because they coincide with the minimum metabolic cost (19). However, this theory is not well supported in human running because the energy expenditure appears to be essentially similar between rearfoot and forefoot striking (41). An alternative explanation for the preference of using rearfoot striking may be the simple fact that it requires clearly lower force production from the ankle extensors than forefoot striking (24), and although this lower demand is achieved at the cost of greater knee extensor muscle force production with rearfoot striking (35), it may be a more advantageous running pattern for most runners because of larger muscular capacity reserve at the knee than at the ankle extensor level. Accordingly, a lower demand of the ankle extensors when using rearfoot striking can be a potential strategy to prevent fatigue of this muscle group. However, despite different lower limb muscle force production patterns in rearfoot and forefoot striking, the total volume of active muscle, which explains the majority of the energy expenditure of running (23), may remain essentially equal, explaining the similar energy cost of the different running patterns.

Sprinting. Our analysis of top speed sprinting ($9.3 \pm 0.4\ \mathrm{m{\cdot}s^{-1}}$) showed that the ankle extensors operated at significantly greater relative effort than the knee extensors (96% vs 72%), as was the case in walking and running. This remarkable difference in relative effort may be due to very different functional roles of the ankle and knee extensors in locomotion: while both muscle groups are important contributors to vertical GRF, the ankle extensors also provide the majority of the horizontal propulsive GRF (45). Because sprinting speed has been shown to be related more to the magnitude of propulsion than vertical GRF (38), the maximum effort from the ankle rather than from knee extensors may, therefore, be required to achieve top speed. Accordingly, these results may provide a rationale for understanding age-related alterations in lower limb mechanics observed previously in running and sprinting studies, in which older adults were capable of producing similar amounts of joint moments at their knee but not at their ankle extensors during submaximal (8) and even during maximal speed running (25) when compared with the young adults.

Interestingly, the ankle extensors were able to develop virtually equal peak force during sprinting versus hopping despite clearly shorter ground contact time, suggesting that the peak force production ability of the ankle extensors was not diminished during sprinting. This is contrary to common theory that due to increasingly shorter ground contact time with greater locomotor speeds, the force production of the ankle extensors diminishes (as well as in other limb muscles) because of greater muscle fiber shortening velocity requirement (45,50,51), which, according to the well-known force–velocity relationship (17), severely compromises a maximum force a muscle can produce. Most direct evidence supporting this theory comes from a previous experimental study (50), which demonstrated that approximately 0.6 BW greater peak vertical GRF can be applied by limb muscles over a longer period of ground contact during maximal one-leg

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forward hopping than sprinting. Furthermore, by comparing extensor muscle forces expressed as a grand mean value over a broad range of speeds of hopping (2.5–7.5 m·s^{-1}) versus running (2.5–10.5 m·s^{-1}), the investigators (50) found that greater vertical GRF values in hopping were achieved by producing greater extensor muscle forces across the ankle, knee, and hip. Unfortunately, however, no comparative data of the extensor muscle forces were provided for the maximal hopping and sprinting, making comparison of the muscle forces with the present study difficult. Like previous investigators (50), we measured greater peak vertical GRF (approximately 0.5 BW) during maximal hopping than sprinting, but as can be expected from the different running speeds, our muscle force results from maximal sprinting differ from the mean values calculated over a wide range of speeds of the previous work (50), which are only roughly half of the values reported here. However, our magnitudes of the knee and ankle extensor forces agree well with other studies with comparable running and sprinting speeds (35,45,46).

We attribute the similar peak force of the ankle extensors measured in maximal sprinting versus hopping to a unique structure and function of the triceps surae MTU, which is known to greatly facilitate elastic energy storage and return during locomotion (21,29). Although no studies have yet measured *in vivo* muscle function in human sprinting, previous evidence from submaximal running indicates that the springlike behavior of the Achilles tendon enables muscle fibers of the ankle extensors to operate at low shortening velocities and near the plateau of the force–length relationship, up to a speed of 5 m·s^{-1} (27). Potentially, tendon compliance together with the history-dependent properties of the MTU, such as the stretch-induced force enhancement (16) and viscoelastic resistance to stretching (33), allows the muscle fiber contractile conditions of the ankle extensors to remain favorable at greater running speeds independent of ground contact time, which thus may enable greater force development of the ankle extensors during sprinting than would otherwise be possible.

Although we determined operating efforts of the knee and ankle extensors across different modes of locomotion, our reference test did not allow us to quantify maximal capacity and thus operating efforts of the hip extensors, which also play an important role in locomotion. This leaves open the question of which muscle groups ultimately constrain human locomotor performance. However, some insights into this issue may be sought from the recent modeling study (2), which examined the effects of speed on the limb muscle force production abilities during walking and running, based on the predicted muscle fiber force–length and force–velocity dynamics. Although the walking results supported the previous hypothesis (36) that increased muscle fiber shortening velocity compromises the force production ability of the ankle extensors at greater walking speeds and thus cause the walk-to-run transition, the running results revealed a dramatic decrease in the force production ability at the hip extensors rather than ankle or knee extensors when speed increased from 2 to 5 m·s^{-1}. This phenomenon may be due to disadvantageous function of the hip extensor muscles for producing force because they do not undergo a springlike function during limb support, but rather exhibit active shortening at a substantial rate (14,44). If the same decreasing trend in the hip extensor muscle force production ability continues with greater running speeds, as can be expected because of progressive increases in step frequency and hip movement velocity (45), it is likely that, in addition to ankle extensor capacity, diminished peak force of the hip extensors may constrain sprinting speed.

Practical implications, limitations, and future directions. The muscles operating closest to their functional limits logically produce the weak link for locomotor ability and, therefore, are likely the most efficient therapeutic targets for exercise interventions aimed at improving walking or running performance (4). Consequently, evidence that both walking and running require greater effort from the ankle than knee extensor muscles suggests that exercise interventions designed to enhance locomotor ability should especially focus on improving ankle extensor capacity. This idea is further supported by the previous studies indicating that the loss of ankle extensor strength (48) and a consequent propulsive deficit during gait (4,9,25) are the main contributors to locomotor decline in older age. Future research is warranted to examine the effectiveness of ankle-targeted training interventions on the locomotor ability and movement mechanics across the broad context of human locomotion ranging from sport performance enhancement to prevention and rehabilitation of mobility impairments.

The current approach and findings constitute proof of principle for assessing relative muscle efforts in locomotion, a fundamental issue that deserves further investigation. Specifically, there is a need for future studies to strengthen our understanding of relative muscle efforts during locomotion across different subject groups, as well as to refine the measurement approach used to quantify muscular efforts. For example, given the relatively low angular velocities of both extensor muscle groups at the time of peak force across locomotor modes, it may be worth investigating whether the isometric force test, similar to the study by Hortobágyi et al. (18), can be used to provide a comparable reference force level with the dynamic hopping test. If so, such a reference test may be easier to conduct and, therefore, more suitable when examining relative muscle efforts in older adults and persons with limited functional abilities.

There are several limitations associated with this study. First, because our analysis was limited to males with excellent physical condition, caution must be made in generalizing these results to persons with typical or limited functional capacities. Based on previous studies on relative muscle efforts in older healthy adults (4,18,20) and diabetic patients (7), such persons can be expected to operate clearly closer to their maximal force production capacities during locomotion than the athletic subjects in the current study. Second, our inverse dynamics-based analysis was unable to account the effects of muscle co-contractions and two-joint muscles when calculating forces of the knee and ankle extensors. Consequently, although our magnitudes of peak knee and ankle extensor muscle forces across walking, running, and sprinting are within the range of values reported by others (10,22,45,46), we may underestimate the true muscle forces in the present study. However, because all measured activities are equally affected, it is unlikely that the differences in the operating efforts between the knee and the ankle extensors in this study are due to methodological issues. Third, although the study by Sugisaki et al. (49) suggests that the maximal two-leg hopping task enabled humans to produce the greatest muscle moments from their knee and ankle extensors compared with several other stretch-shortening types of movements, we cannot completely confirm that this movement task enabled both extensor muscle groups to reach their maximum force in our subjects. However, the peak extensor forces of the knee (13.9 BW) and ankle (9.9 BW) in our hopping test are in line with the previously reported peak forces developed by trained athletes during very demanding activities such as squatting, jumping, and sprinting (forces up to 12–13 BW for both muscle groups) (22,37), suggesting that the maximum effort was most likely required from both muscle groups. This postulation is also fairly well supported by reported *in vivo* values of maximal force capacity normalized to physiological muscle cross-sectional area of the knee (25–30 $N \cdot cm^{-2}$) (12,34) and ankle extensors (11–15 $N \cdot cm^{-2}$) (13,32). In the present study, normalized force estimations using magnetic resonance imaging measurements of physiological muscle cross-sectional areas of quadriceps (280 cm^2) (34) and triceps surae (326 cm^2) (13) muscles from similarly sized subjects yield values of 36 and 22 $N \cdot cm^{-2}$ for the knee and ankle extensors, respectively. Even though our values for both muscle groups are slightly larger than those reported earlier, we feel that they are still realistic, because the previous analyses (12,13, 32,34) were confined to the untrained subjects and to isometric contractions. Possibly, the subjects in our study may have been able to reach greater normalized muscle forces because of their training background and usage of a reference force test that allowed a stretch-shortening type of muscle action. Thus, when viewed in the above light, it seems reasonable to assume that both extensor muscle groups reached their maximum capacity limits in our reference hopping test.

The final limitation is that we did not match the joint angles and angular velocities between locomotor tasks and the reference force test. Therefore, although our reference force test allowed natural springlike limb behavior, the muscle contractile conditions at the time of peak muscle force may have differed between the conditions, which thus may influence the maximal muscle force production capacity. This can lead to underestimation of relative efforts particularly during walking, where elastic limb behavior and its advantage on the muscle force production are less pronounced compared with the springlike hopping reference test. Also, angles and angular velocities at the time of F_{Kmax} and F_{Amax} during walking differed the most from hopping. However, running, sprinting, and hopping all demonstrated springlike limb behavior with very similar joint angular velocities at the time of F_{Kmax} and F_{Amax}, suggesting an isometric type of muscle contraction at the peak force production. Furthermore, although knee flexion and ankle plantarflexion angles at the time of F_{Kmax} and F_{Amax} were greater during hopping than running and sprinting (12°–13° and 2°–4°, respectively), such differences appear to have very limited effects on the peak muscle moment production capability (3,18). In addition, an analysis of relative effort using joint angular velocity matched reference force values for each locomotion mode demonstrates essentially similar operating force levels compared with the normalization using the peak muscle forces from hopping (Table 1). This provides us with confidence that our approach is a reliable tool for assessing the relative efforts of the knee and ankle extensors and that our overall conclusions drawn from the data are not significantly influenced by the issues that limit the accuracy with what we can estimate the operating muscle efforts in this study.

CONCLUSION

This study provides the most comprehensive description available to date of operating efforts of the knee and ankle extensor muscles during walking, running, and sprinting. The results demonstrate that, regardless of the mode of locomotion, the ankle extensors operate much closer to their capacity limits compared with the knee extensors. This functional feature likely poses a primary biomechanical constraint on the human locomotor ability and, thus, may also influence the way how we locomote and adapt to accommodate compromised neuromuscular system function. These findings have relevance in the broad context of human locomotion from sport performance enhancement to prevention and rehabilitation of locomotor impairments.

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