Positive work contribution shifts from distal to proximal joints during a prolonged run

Maximilian Sanno\textsuperscript{1,2}, Steffen Willwacher\textsuperscript{1,3}, Gaspar Epro\textsuperscript{1,4} and Gert-Peter Brüggemann\textsuperscript{1,2,3}

\textsuperscript{1}Institute of Biomechanics and Orthopedics, German Sport University Cologne, Cologne, Germany
\textsuperscript{2}German Research Center of Elite Sport, German Sport University Cologne, Cologne, Germany
\textsuperscript{3}Institute of Functional Diagnostics, Cologne, Germany
\textsuperscript{4}Sport and Exercise Science Research Center, School of Applied Sciences, London South Bank University, United Kingdom

Address for correspondence:
Maximilian Sanno
Institute of Biomechanics and Orthopedics
German Sport University Cologne
Am Sportpark Müngersdorf 6
50933 Cologne, Germany
Tel.: +49-221-49827630
Fax: +49-221-4971598
Email: m.sanno@dshs-koeln.de
ABSTRACT

Purpose: To investigate the joint-specific contributions to the total lower extremity joint work during a prolonged fatiguing run. Methods: Recreational long-distance runners (RR; n = 13) and competitive long-distance runners (CR; n = 12) performed a 10-km treadmill run with near-maximal effort. A three-dimensional motion capture system synchronized with a force-instrumented treadmill was used to calculate joint kinetics and kinematics of the lower extremity in the sagittal plane during the stance phase at 13 distance points over the 10-km run.

Results: A significant ($P < 0.05$) decrease of positive ankle joint work as well as an increase of positive knee and hip joint work was found. These findings were associated with a redistribution of the individual contributions to total lower extremity work away from the ankle towards the knee and hip joint which was more distinctive in the RR group than in the CR group. This redistribution was accomplished by significant ($P < 0.05$) reductions of the external ground-reaction force (GRF) lever arm and joint torque at the ankle and by the significant ($P < 0.05$) increase of the external GRF lever arm and joint torque at the knee and hip.

Conclusion: The redistribution of joint work from the ankle to more proximal joints might be a biomechanical mechanism that could partly explain the decreased running economy in a prolonged fatiguing run. This might be because muscle-tendon units crossing proximal joints are less equipped for energy storage and return compared to ankle plantar flexors and require greater muscle volume activation for a given force. In order to improve running performance, long-distance runners may benefit from an exercise-induced enhancement of ankle plantar flexor muscle-tendon unit capacities.

Key Words: LOCOMOTION, RUNNING MECHANICS, JOINT TORQUE, ANKLE JOINT, LEVER ARM, RUNNING ECONOMY
INTRODUCTION

Long-distance running is one of the most popular recreational activities in the world and is often performed with competitive effort. High-performance runners differ from less successful ones mainly in terms of the energy demand for a given submaximal running velocity, with lower steady-state oxygen uptake indicating better running economy (1). Running economy is a useful predictor of endurance running performance, which depends on a complex interplay of factors such as the runner’s training level, environment, anthropometric parameters, physiology, and biomechanics (1). From a biomechanical perspective, running economy can be related to spatio-temporal running characteristics (2), kinetics of the center of mass (CoM), joint kinematics, and the tendons’ capacity to store and return elastic energy (1,3,4). However, no biomechanical parameter alone can explain the complexity of human running economy (2,5).

Severe modifications of the running style, such as exaggerated knee flexion during the stance phase (i.e., Groucho running), substantially reduce running economy by increasing oxygen uptake (6). Reduction of running economy also occurs during sustained long-distance runs performed until exhaustion (7,8). Fatigue, defined as exercise-induced reduction in the ability to generate muscle force or power due to changes in the neural drive or exhaustion of contractile function (9), can cause a decline in running velocity and changes in spatio-temporal running characteristics and spring-mass behavior (10). However, whether these changes occur when the running velocity is kept constant (as for instance during running on a treadmill) is currently not clear (11–14). Furthermore, despite one study indicating that knee flexion angle at foot contact and mid-stance may be more flexed due to exhaustion on a treadmill (15), most reports show relatively constant hip, knee, and ankle joint kinematics during prolonged fatiguing treadmill runs (13,16). This appears to be independent of the performance level of
runners performing a 10-km treadmill run to volitional exhaustion at a velocity approximating their 10-km race pace (17).

Only a few studies have examined the effects of exhaustion on running kinetics during constant-velocity runs. In general, vertical ground-reaction force (GRF) and leg stiffness decrease during exhausting running, whereas vertical stiffness tends to be rather constant (11,14,18,19). However, considerable inter-individual differences seem to exist in the fatigue-induced changes in running kinetics (18,19). It is surprising that most reports investigating exhausting running have focused on CoM kinetics, although it is known that CoM work is the result of a complex interaction of the joint work done by individual muscles, especially at the lower extremity (20,21). A joint-specific view allows to describe the individual contributions of different muscle groups to the total work of the lower extremity (22–24).

Negative work is facilitated by forcefully stretching activated muscle fascicles or passive elastic structures within the muscle-tendon unit. Positive work originates from active shortening of muscle fascicles or the return of potential strain energy previously stored within passive elastic structures (25,26). Among the different muscle groups of the lower extremity, the ankle plantar flexors are one of the main contributors to total joint work of the lower extremity during running (20–22). It is notable that the relative contribution of ankle plantar flexors does not seem to alter, even when the running velocity is changed (20–22). However, other observations have identified an age-related proximal shift of the individual joint contributions in walking and running in older adults. This is represented foremost by a reduced ankle joint contribution which seems to be due to a reduced ankle plantar flexor muscle strength compared to other more proximal muscle groups (27–30). This indicates that changes in the contractile properties of the lower extremity muscles may lead to modifications in the joint-specific contribution during human locomotion, including running. The literature provides indications towards an altered joint-specific contribution in response to running-induced
fatigue. For example, the maximal muscle strength of hip and knee extensors, and ankle plantar flexors have been demonstrated to decrease after long-distance running, especially following ultra-marathons (31–33). Specifically, running a half marathon, intensive treadmill running over 2 hours or a 5-km run have shown to decrease the isometric ankle plantar flexor muscle strength (34–36).

The triceps surae muscle (TS) is the main plantar flexor of the foot and consists of the soleus and the biarticular gastrocnemius. The relatively short muscle fascicles and pennate architecture of the TS (37,38) allow it to generate force at a lower metabolic cost than longer fibered muscles such as the knee extensors (25). This facilitates an efficient energy storage and return within the long Achilles tendon (26). Theoretically, greater energy storage and return would reduce the work needed to be done by the muscle fascicles during the propulsion phase in running and therefore improve running economy (39). This effect has been confirmed in a study that demonstrated that an increase of the ankle plantar flexor muscle strength by resistance training could reduce oxygen uptake and thus increase running economy (3). Furthermore, well-trained distance runners with a good running economy show greater ankle plantar flexor muscle strength and greater tendon-aponeurosis stiffness than runners with lower running economy (4).

Although it is known that there are differences in individual joint contributions during running, no studies have investigated if and how joint-specific work is altered over the course of a prolonged fatiguing run (especially when performed at constant velocity) and whether there are differences between recreational and competitive runners. The current study therefore aimed to investigate the joint-specific contributions to the total lower extremity joint work during a prolonged fatiguing run in recreational and competitive long-distance runners. The primary hypothesis was that a long-distance run with near-maximal effort would change the work contributions of the lower extremity joints, characterized by a reduction of work at the
ankle joint. A secondary hypothesis was that recreational runners would experience greater running-induced reduction of ankle joint work than competitive long-distance runners. The results of the present study might improve our understanding of fatigue-related alterations in running mechanics and reductions in running economy in prolonged fatiguing runs.

METHODS

Participants

A total of 25 male runners were recruited and separated into two groups based on their individual long-distance running performance level. The recreational runners (RR) group included physically active students (n = 13; age 24.3 ± 3.4 years; height 1.84 ± 0.05 m; mass 81.3 ± 7.4 kg) with individual season best times >47:30 min in a 10-km run. The competitive runners (CR) group included competitive long-distance runners (n = 12; age 24.7 ± 3.8 years; height 1.82 ± 0.06 m; mass 73.0 ± 7.9 kg) with individual season best times <37:30 min in a 10-km run. Runners with self-reported history of musculoskeletal injury of the lower extremity in the preceding 12 months were excluded. Each participant signed a written informed consent prior to the study. The Research Ethics Committee of the German Sport University Cologne approved this study (No. 102/2017). All procedures were in accordance with the Declaration of Helsinki.

Experimental protocol

All participants performed a 10-km treadmill run with near-maximal effort (105% of their individual season best time over the 10-km distance). The near-maximal effort was selected for safety reasons and to ensure that all participants could complete the task. The average calculated 105% time was 52:49 ± 2:21 min (approximate running velocity of 3.2 m·s⁻¹) for the RR group and 37:32 ± 1:17 min (approximate running velocity of 4.4 m·s⁻¹) for the CR group. The treadmill’s inclination was set at 0% to avoid the effects of gradient on running kinematics or kinetics. All participants wore light-weight (~0.170 kg) racing flat shoes.
A practice run was performed 7 days before the actual run to allow participants to familiarize with the racing flat shoe and the treadmill. All participants stated that they regularly used different kinds of running shoes, including racing flat shoes. No further footwear adaptation was conducted. Prior to the treadmill run, the participants performed warm-up exercises with self-determined duration. During the actual treadmill run the participants were continuously encouraged and kept informed of the covered distance.

**Monitoring of heart rate and rating of perceived exertion**

A heart rate monitor (M51; Polar Electro, Kempele, Finland) kept track of the heart rate during the run to quantify the cardiovascular load. Immediately after the run, the Borg scale was used for rating perceived exertion (on a scale of 6–20).

**Kinematics and kinetics**

The kinematics and kinetics were captured with 13 infrared cameras using a three-dimensional motion capture system (250 Hz, MX-F40; Vicon Motion Systems, Oxford, UK) synchronized with four multi-axis force transducers (1000 Hz, MC3A-3-500-4876; AMTI Inc., Watertown, USA) embedded in a single-belt treadmill (Treadmetrix, Park City, USA). Prior to motion capturing, spherical retroreflective markers (diameter: 13 mm; ILUMARK GmbH, Feldkirchen/Munich, Germany) were attached to 78 bony landmarks (40). The markers for the foot were attached at the corresponding positions on the shoe. All marker trajectories and the GRF data were smoothed using a recursive, fourth-order digital Butterworth filter with a cutoff frequency of 20 Hz.

A three-dimensional inverse dynamics model of the total body, consisting of 15 rigid body segments (40, 41), was implemented to calculate the kinematic and kinetic parameters of the CoM and lower extremity, using custom MATLAB routines (MathWorks Inc., Natick, USA). Body height and body mass were imported to the model to obtain the inertial properties
for each segment (40,42). Joint torques were expressed in the anatomical coordinate system of
the proximal segment. External GRF lever arms were determined within the sagittal plane and
expressed in the coordinate system of the proximal segment. Lever arms were obtained by
dividing the GRF term of Hof’s explicit joint torque equation (41) by the amplitude of the GRF
vector. A reference trial was recorded in an upright position to determine the neutral position
of all joints (0° joint angle) prior to the beginning of the run. The hip joint center was
determined using the regression equations provided by Bell and co-workers (43). The negative
and positive work at the hip, knee, and ankle joint was calculated over the entire stance phase
by numerical integration of the power-time curve. Positive work was determined by summing
up all positive integrals and negative work by summing up all negative integrals during the
entire stance phase (21).

Parameters

Step length, step frequency, and contact time were assessed for spatio-temporal
characterization of the running. Additionally, various kinematic and kinetic parameters were
determined during the stance phase of the right leg from the sagittal plane for further analysis
over the course of the run. To improve reliability, the data were averaged over 20 stance phases
at each of the 13 distance points (0 km, 0.2 km, 0.5 km, 1 km, 2 km, 3 km, 4 km, 5 km, 6 km,
7 km, 8 km, 9 km, and 10 km). Positive and negative work were calculated for the hip, knee,
and ankle joint. Subsequently, the relative joint-specific contributions to the total lower
extremity joint work were determined. Further, joint kinetic (maximal power and maximal
external torque) and joint kinematic (maximal angular velocity and angle) parameters were also
assessed. External GRF lever arms of all three joints were determined at the instant of maximal
vertical GRF. All kinetic parameters were normalized to total body mass. To describe the
vertical displacement of the total body, the CoM height at touch-down of the foot (CoMTD),
and at the minimal height (CoMmin) during the stance phase were calculated.
Statistical analysis

Two-way repeated-measure analysis of variance (ANOVA) with performance level (RR vs. CR) as between subject factor was used to analyze the effects of running distance at all 13 distance points. If a significant running distance main effect or interaction effect between performance level and running distance was detected by two-way ANOVA, a univariate repeated-measures ANOVA with 78 pairwise post-hoc comparisons using Bonferroni correction (resulting in an adjusted alpha level of 0.000641) was applied for each group to determine any significant differences between the various distance points. The values obtained at the different distance points were compared with the values at the beginning of the run (0 km). All parameters were presented as group means (and standard deviations). Cohen’s $d$ effect sizes were calculated to explain the strength of an observed effect, using the equation

$$d = \frac{\bar{x}_j - \bar{x}_i}{\sqrt{s_j^2 + s_i^2 / 2}}$$

with $\bar{x}_{i,j}$ as the average and $s_{i,j}^2$ as the sample variance of different distance points. The subscript $i$ represented the 0 km distance point. The subscript $j$ represented the different distance points after the 0 km distance point (0.2 km to 10 km). Effect sizes of $\geq 0.2$ were considered as small, $\geq 0.5$ as medium, and $\geq 0.8$ as large (44). The partial eta squared ($\eta^2_p$) value was determined to explain the proportion of the total variance between both groups, the running distance main effect, and the interaction effect between performance level and running distance, respectively. Cohen (44) suggested norms for $\eta^2_p$ as small (0.01), medium (0.06), and large (0.14). Significance for all statistical procedures was tested at a level of $\alpha = 5\%$ ($P < 0.05$) using SPSS Statistics 23 (IBM Corp., Armonk, NY, USA).

RESULTS

Perceived exertion after the run was comparable between the two groups (RR: 16.9 ± 1.3; CR: 17.1 ± 1.2), although maximal heart rates were significantly different (RR: 171 ± 14 BPM; CR:
186 ± 10 BPM; $P = 0.023$, $\eta^2_p = 0.206$) after the 10-km distance. There were significant ($P < 0.05$) differences between the groups in each of the analyzed spatio-temporal parameters, which could be related to the different running velocity. However, none of the spatio-temporal parameters changed significantly over the course of the run in either group. For additional details, (see Appendix, supplemental digital content 1 (SDC 1), Tab. 1 -- Group means and standard deviations of heart rate and spatio-temporal parameters; SDC 1, and Fig. 1 left top -- Changes in heart rate; SDC 1, Fig. 1 left center -- Changes in step length; SDC 1, Fig. 1 right center -- Changes in step frequency; SDC 1, Fig. 1 central bottom -- Changes in contact time).

**Joint work**

There was a significant ($P < 0.05$) running distance main effect for all positive and negative joint works other than the negative ankle joint work. For the joint work, a significant ($P < 0.05$) intergroup effect was found only for the negative ankle joint work, with the RR group showing relatively lower negative hip, knee, and ankle joint work. For additional details, (see Appendix, SDC 1, Tab. 1 -- Group means and standard deviations of joint work).

The positive joint work of the ankle decreased significantly ($P = 0.002$, $d = 0.88$) and the positive joint work of the knee increased significantly ($P = 0.046$, $d = 0.69$) from the beginning to the end of the run in the RR group (Fig. 1). In the RR group, the positive work of the ankle joint decreased significantly for the first time at 5 km ($P = 0.017$) which continued to decrease up to the end of the run whereas, in the CR group, positive work of the ankle joint showed a steady modest decrease over the course of the run (Fig. 2). In the RR group, there was a slight increase in the positive joint work at the knee and hip joint, with statistically significant ($P < 0.05$) increase at the knee joint at 2 km, 8 km, and 10 km. The further distance points between 2 km and 8 km as well as the 9 km were slightly above the level of significance ($P > 0.05$). In the CR group, the positive work showed a minor increase at the knee joint, but
did not change at the hip joint (Fig. 2). A significant \((P < 0.05)\) intergroup difference but no running distance main effect was seen for the total positive work of all three joints (Tab. 1). Therefore, it is not surprising that the relative joint-specific contributions to the total positive lower extremity joint work showed changes from the beginning of the run (hip 19%, knee 29%, ankle 52%) to the end of the run (23%, 33%, 44%) in the RR group but not in the CR group (beginning of the run: hip 22%, knee 28%, ankle 50% vs. end of the run: 22%, 31%, 47%).

In the RR group, negative joint work was slightly increased at the hip, knee, and ankle over the course of the run. In contrast, the negative knee joint work of the CR group was only slightly increased and at the ankle slightly decreased (Fig. 2). There was no running distance main effect but a significant \((P < 0.001)\) intergroup difference and a significant \((P = 0.015)\) interaction effect between performance level and running distance for the total negative work of all three joints. The RR group showed a distinctly higher increase in total negative work of the lower extremity than the CR group \(+9\% \text{ vs. } -1\%\); Tab. 1). However, the relative joint-specific contributions to the total negative lower extremity joint work remained unchanged in both groups over the course of the run (RR group: hip 7%, knee 45%, ankle 48% at 0 km vs. 8%, 45%, 47% at 10 km; CR group: 7%, 34%, 59% at 0 km vs. 8%, 36%, 56% at 10 km).

Joint torque and external GRF lever arm

A significant \((P < 0.05)\) running distance main effect was identified for all joint torques, with significant \((P < 0.05)\) intergroup differences in the knee and ankle joint torques (Tab. 1). In the RR group, hip joint torque showed a significant \((P < 0.05)\) increase for the first time at 6 km which continued to increase until the end of the run; in the CR group, hip joint torque showed a slight nonsignificant increase over the course of the run. In both groups, knee torque increased slightly and ankle torque decreased slightly over the course of the run (Tab. 1). Significant \((P \)
< 0.05) running distance main effects were seen for the external GRF lever arm of all three joints (Tab. 1). The external GRF lever arm of the ankle was slightly decreased, while the GRF lever arm of the knee and hip joint was slightly increased (Fig. 3).

*** insert Table 1 about here ***

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Joint angle and angular velocity

We found a significant \( P < 0.05 \) running distance main effect for the maximal knee flexion angle and for the knee flexion angle at touch-down of the foot. The knee flexion angle at touch-down of the foot increased significantly \( P < 0.05 \) over the course of the run in both groups (Tab. 2). Additionally, the RR group showed a significant \( P < 0.05 \) increase in the maximal knee flexion angle and a significant decrease in plantar flexion angle at toe-off over the course of the run (Tab. 2). A significant \( P < 0.05 \) intergroup difference in the ankle plantar flexion angle at touch-down of the foot was observed which can explain the difference in foot positioning at touch-down of the foot (Tab. 2). Maximal ankle dorsiflexion did not change.

Significant \( P < 0.05 \) running distance main effects were seen for maximal knee extension velocity and for maximal ankle plantar flexion velocity (Tab. 2). In the CR group, the maximal ankle plantar flexion velocity showed a significant \( P < 0.05 \) increase for the first time at 2 km which continued to increase until the end of the run (Tab. 2).

CoM kinematics and GRF

Significant \( P < 0.05 \) running distance main effects were found for \( \text{CoM}_{TD} \) and \( \text{CoM}_{\text{min}} \). Both parameters decreased significantly \( P < 0.05 \) over the course of the run, especially in the RR group (Tab. 2). Further results can be found in the Appendix. For additional results of joint kinetics, joint kinematics, CoM kinematics, and maximal vertical GRF, please refer to SDC 1, Tab. 1 -- Group means and standard deviations of joint kinetics, joint kinematics, CoM kinematics, and the maximal vertical GRF; SDC 1, Fig. 1 right top -- Changes in vertical GRF; SDC 1, Fig.
DISCUSSION

The purpose of this study was to investigate the joint-specific contributions to the total lower extremity joint work during a prolonged fatiguing run in recreational and competitive long-distance runners. The primary hypothesis of this study was that a long-distance run with near-maximal effort would change the work contributions of the lower extremity joints, characterized by a reduction of work at the ankle joint. The joint work magnitudes in the current study are comparable with the findings of Roy et al. (24). We found a running distance main effect on the positive and negative work at all three joints, except for negative work at the ankle joint. The decrease in positive ankle joint work was counteracted by increases in positive knee and hip joint work. Over the course of the 10-km treadmill run with near-maximal effort, joint-specific contributions to positive work displayed a clear redistribution away from the ankle towards the knee and hip joints. Therefore, our primary hypothesis can be accepted.

When trying to reveal the potential underlying mechanisms, we found that knee and hip joint flexion angles slightly increased over the course of the 10-km treadmill run, but the ankle dorsiflexion angle did not change. Thus, a lower CoM height during the stance phase was observed, which could be explained by the changes in knee and hip flexion angles. Due to the lower and more backward positioning of the CoM, the point of force application under the foot was shifted slightly posteriorly, decreasing the external GRF lever arm of the ankle, but extending the GRF lever arms of the knee and hip joint (Fig. 4). These alterations in GRF lever arms could explain the increases in knee and hip joint torques, as well as the decreases in the ankle joint torque (Fig. 3).
In this study, we found maximal torque magnitudes to be higher at the ankle joint compared to the more proximal joints during running. In contrast, it has been reported that the maximal voluntary joint torque of the ankle plantar flexors during isolated strength testing is smaller than that of the knee or hip extensors (45). Therefore, our findings could suggest that the ankle plantar flexors might have suffered more from fatigue than proximal muscle groups, probably because the ankle plantar flexors worked closer to their maximal voluntary joint torque capacity compared to knee and hip. Several studies have described decreases in maximal voluntary ankle plantar flexor muscle strength after a 5-km run (36), a half marathon (34), and intensive treadmill running over 2 hours (35). Furthermore, in ultra-marathons, additional fatigue effects in knee and hip extensors have been reported (31–33). Nonetheless, the contraction velocity and joint ankle configuration are different between isometric strength testing and running. Future studies should integrate more sophisticated, non-isometric strength tests utilizing running-specific contraction conditions in order to resolve joint-specific reductions in force generation capacities after fatiguing runs.

The finding that maximal ankle torque and positive work decline during a 10-km treadmill run with near-maximal effort seems counterintuitive given the positive characteristics of ankle plantar flexor muscle-tendon unit work for running economy. Our results show that the reduced ankle joint work output was compensated by more positive work at the knee and hip joints, especially for the RR group. This redistribution of positive work towards more proximal muscle groups might lead to a greater metabolic cost. This is because these proximal joint work requirements might be satisfied to a greater extent by work performed by muscle fascicles as compared to tendon energy storage and return. It can be assumed that, in contrast to the knee and hip extensor muscle-tendon units, the TS muscle-tendon unit is better equipped for energy storage and return during running (25,26). Furthermore, shorter muscle fibers reduce
the cost of force generation due to a reduction in muscle volume to cross-sectional area ratio (46), which therefore is also assumed to be beneficial for running economy (39). The TS has relatively short fascicles and high pennation angles compared to the knee and hip extensor muscles (37,38). Consequently, force production of the TS might be metabolically less costly compared to long-fibred muscles (25). Accordingly, running economy might be reduced when the TS muscle-tendon unit is less involved in the lower extremity energy exchange, either due to less work performed by tendon energy storage and return or due to higher muscle volume activation at the hip and knee joint. Recent results of Holt and co-workers (47) support the latter explanation. They found that replacing muscle stretch-shortening work with tendon elastic energy storage and return did not significantly reduce the cost of force production. However, due to the limitations of the chosen methodology in the current study, these interpretations are rather speculative and need to be further verified by in vivo assessments of the behavior of lower extremity muscle-tendon units during prolonged fatiguing running.

The counter effect of a fatigue induced reduction in TS involvement has been confirmed in a study that demonstrated that an increase in the contractile force of the TS muscle-tendon unit induced by resistance training could improve running economy (3). Furthermore, well-trained distance runners with high running economy typically show greater TS muscle strength and greater tendon-aponeurosis stiffness than runners with lower running economy (4). Previous findings show that running economy substantially reduces when running is performed with an excessively flexed knee joint, also called Groucho running style (6). The observed more flexed knee joint angles (maximal and during touch-down of the foot) in the present study could be a strategy to minimize vertical GRF when running into exhaustion (11). Our findings are furthermore consistent with the work of Peltonen et al. (48) who postulated that changes in running technique result from muscle fatigue. Additionally, Derrick and co-workers (15) assumed that altered kinematics result in increased metabolic costs during the latter stages of
an exhausting run. Based on the current findings, the frequently reported increase in oxygen
uptake during long-distance running (7,8) may partly be caused by the additional metabolic
cost due to the redistribution of work towards more proximal muscle groups potentially because
of TS fatigue. For most parameters in the present study we observed a nearly linear change as
a function of running distance. Future studies should explore whether this behavior can also be
observed for longer running distances or runs with maximal effort or if a rapid alteration in
running mechanics occurs at greater levels of fatigue compared to our 10-km treadmill run with
near-maximal effort.

Due to methodological reasons the present study was performed on a treadmill whereas
distance running is most often performed overground. Previous studies have found that
differences in lower extremity kinematics between overground and treadmill running are rather
small and show inconsistent trends for individual participants, depending on shoe or treadmill
condition (49). However, it can be generalized that running on a treadmill leads to a flatter foot
strike pattern in comparison to overground running (49,50). This could be partly a protective
behavior due to a higher stiffness of force-instrumented treadmills and the associated higher
joint loading (51). Furthermore, treadmill running has shown to increase the maximal knee
flexion angle and decrease knee extension power with no modifications in ankle plantar flexion
power (52). If and to what extent the hard surface of the present treadmill may influence the
redistribution in joint kinetics in comparison to overground running, the effect of different
cushioning shoes or surfaces like bitumen, Tartan, or forest floor should be investigated in
future studies of prolonged fatiguing running. Additionally, an early study suggested that the
energy requirements of the runners could be reduced by running on a treadmill because the
backward motion of the belt assists the runner by moving the supporting leg back during the
stance phase (53). Nonetheless, Riley and co-workers (52) concluded that a treadmill-based
analysis of running mechanics can be generalized to overground running mechanics if the belt
speed is adequately regulated.

When considering our second hypothesis, it is generally accepted that high-
performance runners differ from less successful ones mainly in terms of the running economy
and fatigability. Therefore, the second hypothesis of the current study was that the RR group
would experience a greater running-induced reduction of positive ankle joint work than the CR
group. We found a significant ($P < 0.05$) decrease of the positive ankle joint work of the RR
group for the first time at 5 km ($P = 0.017$) which continued to decrease up to the end of the
run. However, no change of the positive ankle joint work was found for the CR group. Both
findings allow us to accept our second hypothesis. The tendency ($p = 0.126$) towards an
interaction between performance level and running distance for positive ankle joint work is an
additional indication. When trying to explain the greater reduction in the positive ankle joint
work of the RR group, we speculate that the RR group suffered more from an ankle plantar
flexor muscle fatigue than the CR group. Thus, the CR group showed a tendency towards a
lower rate of decrease in positive ankle plantar flexor work. This suggests that the CR group
had a higher muscular capacity and attempted to maintain the ankle plantar flexor work as long
as possible. Future studies should directly assess the relationship between the redistribution of
lower extremity joint work and localized ankle plantar flexor muscle fatigue after prolonged
fatiguing runs. Referring to the plantar flexor muscle capacity, an earlier study has shown that
well-trained distance runners have greater ankle plantar flexor muscle strength than less trained
runners (4) which might indicate a specific adaptation to maintain high positive ankle joint
work output in prolonged fatiguing runs. Our results also confirm a significant ($P < 0.001$)
group difference for ankle joint torque during running and could be due to the different ankle
plantar flexor muscle strength, as well as the dissimilar running velocity. Nevertheless, the
running distance main effect for ankle joint torque in our study was significant ($P < 0.001$) and
accordingly we found a decrease in ankle joint torque for each group by approximately 5% by the end of the run compared to the beginning. It is noteworthy, however, that the ankle joint torque of both groups was similarly decreased even though there are distinct decreases in the positive ankle joint work.

Considering angular velocity could provide a possible explanation for the different reduction of positive ankle joint work between the two groups of runners. We found a significant ($P < 0.016$) interaction between performance level and running distance for ankle plantar flexion velocity. From the beginning to the end of the run, increased ankle plantar flexion velocity (+4%) and knee extension velocity (+7%) were observed in the CR group which might be a compensation strategy to counteract the reduced ankle torque and to maintain the positive ankle joint work generation as long as possible (see Appendix, SDC 1, Fig. 4 -- Changes in angular velocities). In contrast to the CR group, we did not find this compensational strategy for the RR group because the ankle plantar flexion velocity did not change when comparing the beginning with the end of the run. Although, during the first 2 km of the run an increase of the ankle plantar flexion velocity (+2%) in the RR group was observed, which could not be maintained until the end of the run (SDC Fig. 4) (see Appendix, SDC 1, Fig. 4 -- Changes in angular velocities). Similar to the CR group, the knee extension velocity was also increased (+6%) over the course of the run in the RR group. Such divergent alteration of angular velocities between the knee extensors and the ankle plantar flexors may be due to fatigued biarticular gastrocnemius muscle-tendon units which usually ensure the mechanical energy transfer between the knee and ankle joint (54,55). Further investigations should examine if the energy transfer between the knee extensors and the foot changes during prolonged fatiguing runs and if this change is due to a reduced capacity of biarticular muscle-tendon units. Based on the data in this study, a discussion of increasing the ankle plantar flexion or knee extension velocity as compensational strategy to maintain positive ankle joint work
and the efficiency of energy transfer between knee and ankle remains highly speculative without a detailed analysis of muscles and tendon fascicle behavior through e.g. ultrasound measurements.

Despite dissimilar reductions in positive ankle joint work, the ankle joint torque in both groups decreased by approximately 5% by the end of the run compared to the beginning. When considering the minimal changes observed in ankle joint kinematics (< 2° for all parameters) and therefore internal Achilles tendon lever arm, this suggests that less force was acting on the Achilles tendon, leading to a lower strain and hence decreasing energy storage in the tendon. Accordingly, the increase in angular velocity in the CR group must originate from higher muscle fascicle contraction velocity and not by a faster tendon recoil. We did not find a running distance main effect for negative ankle joint work, which suggests that the runners were able to keep the sum of negative muscle fascicle and tendon work relatively constant over the course of the run. It is known that in unfatigued running, both soleus and gastrocnemius medialis muscle fascicles undergo nearly constant shortening during the stance phase by operating from the plateau region towards the ascending limb of muscle force-length relationship (56,57). Therefore, one could speculate that when Achilles tendon strain and therefore energy storage is reduced over the course of the run, the TS muscle fascicles stretch-shortening behavior might have changed as well. More detailed studies should focus on direct measurements of the lengthening and shortening amplitudes of muscle fascicles and tendinous structures when running into exhaustion, potentially with the aid of ultrasonography. These experiments could also consider potential creep effects of tendinous structures, which may attenuate the above described mechanism. Nonetheless, literature reports are contradictory regarding to the possible fatigue-related changes in the material properties through a repeated cyclic loading of the Achilles tendon, e.g. in long-distance running (34,48).

LIMITATIONS
This study has several limitations. First, the individual season best times were self-reported, and it is possible that the participants did not disclose their actual best times. Second, the running economy was not directly quantified. Running economy has consistently been reported to decrease during long-distance runs performed until exhaustion (7,8) and therefore it is very likely that the participants of the present study also suffered from a reduced running economy. In addition, we did not use spirometry because we speculated that wearing the spirometer would affect running mechanics. Third, we did not determine the isometric or isokinetic force capacities of the leg extensors to quantify the possible alteration of muscular capacity before-after the course of the run. And, fourth, we did not directly quantify the viscoelastic behavior of tendinous tissues and the contraction patterns of muscle fascicles of the main leg extensor muscle-tendon units before-after or over the course of the run.

CONCLUSION

Our findings demonstrate that a 10-km treadmill run with near-maximal effort leads to a clear redistribution of joint work from the ankle to the knee and hip joint in recreational runners. The reduction in positive ankle joint work and ankle joint torque may be due to fatigued ankle plantar flexors. This could partly explain the decreased running economy in a prolonged fatiguing run, because the muscle-tendon units crossing proximal joints are less equipped for energy storage and return compared to ankle plantar flexors. Furthermore, due to the activation of the longer muscle fascicles and greater muscle volumes of the more proximal muscle groups can possibly incur a greater metabolic cost. Therefore, in order to improve running performance, long-distance runners may benefit from an exercise-induced enhancement of ankle plantar flexor muscle-tendon unit capacities (TS muscle strength and Achilles tendon stiffness) to postpone the redistribution of work from distal to proximal joints.

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CONFLICTS OF INTEREST

The manufacturer of the shoes (Adidas AG; Herzogenaurach, Germany) was not involved in the study design or the collection, analysis, or interpretation of data. None of the authors have any financial interests in or affiliations with any organization or entity mentioned in this study. The authors did not receive funding from any organization or company for performing this study. There are no conflicts of interest to declare. The results of the present study are presented clearly, honestly, and without fabrication, falsification, or inappropriate data manipulation. The results of this study do not constitute endorsement by the American College of Sports Medicine.

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FIGURE LEGENDS

FIGURE 1: The individual negative and positive joint work of recreational runners (RR; n = 13) and competitive runners (CR; n = 12) at the beginning (0 km) and at the end (10 km) of the 10-km treadmill run with near-maximal effort. Significant differences are represented by *\( P < 0.05 \) and **\( P < 0.01 \). The values in parentheses show the Cohen’s \( d \) effect sizes.

FIGURE 2: Changes in joint work (means ± standard deviation) over the course of the 10-km treadmill run with near-maximal effort of recreational runners (RR; n = 13) and competitive runners (CR; n = 12). The gray area represents the standard deviation of the hip joint work. All significant differences from the values at the beginning of the run are represented by *\( P < 0.05 \) and **\( P < 0.01 \). The values in parentheses show the Cohen’s \( d \) effect sizes.

FIGURE 3: Changes in external ground-reaction force lever arm of the hip, knee, and ankle joint (means ± standard deviation) over the course of the 10-km treadmill run with near-maximal effort of recreational runners (RR; n = 13) and competitive runners (CR; n = 12). The gray area represents the standard deviation of the external ground-reaction force lever arm of the knee joint. All significant differences from the values at the beginning of the run are represented by *\( P < 0.05 \). The values in parentheses show the Cohen’s \( d \) effect sizes.

FIGURE 4: Schematic illustration of the stance phase during maximal vertical ground-reaction force (GRF\(_{vert}\)) at the beginning (0 km, unfilled lines) and the end (10 km, black lines) of the 10-km treadmill run with near-maximal effort. GRF\(_{vert}\), joint angles and segment lengths are not to scale, as also the dashed lines representing external ground-reaction force lever arm of the hip, knee, and ankle joint. The percentage rates at each joint represent the relative changes of positive joint work after the 10-km treadmill run of recreational (RR; top value) and
competitive (CR; bottom value) runners. Note: The 10-km treadmill run with near-maximal effort led to increased knee and hip joint torques as well as a decreased ankle joint torque, probably due to fatigue of the ankle plantar flexors. The flexion angle of knee and hip joints increased slightly, but there were no alterations in the ankle joint angle. Hence, the center of mass (CoM_{\text{min}}) shifted slightly deeper and posteriorly, causing the point of force application under the foot to shift, thereby modifying the external ground-reaction force lever arms (decrease at ankle joint and increase at knee and hip joints). The positive joint work contribution shifted from the ankle joint to proximal joints.

**TABLE 1:** Positive (pos) and negative (neg) total joint works, maximal (max) external joint torques, and external lever arms at maximal vertical ground-reaction force (GRF_{\text{max}}) of lower extremity joints (mean ± standard deviation) for recreational runners (RR; n = 13) and competitive runners (CR; n = 12) at the beginning (0 km) and at the end (10 km) of the 10-km treadmill run with near-maximal effort. Note: Significant differences between 0 km and 10 km are represented by **P < 0.01. The values in parentheses show the Cohen’s d effect sizes. To explain the group difference between RR and CR, the partial eta squared (\eta^2_p) values are presented, as well as the running distance main effect and interaction effect between performance level and running distance.

**TABLE 2:** Kinematic parameters of lower extremity joints (mean ± standard deviation) for recreational runners (RR; n = 13) and competitive runners (CR; n = 12) at the beginning (0 km) and the end (10 km) of the 10-km treadmill run with near-maximal effort during foot touch-down (TD), maximal values (max), maximal vertical ground-reaction force (GRF_{\text{max}}), and toe-off (TO). The center of mass (CoM) height at foot touch-down (CoM_{\text{TD}}), and the minimal height (CoM_{\text{min}}) during the stance phase. Note: Significant differences between 0 km and 10 km.
km are represented by *$P < 0.05$ and **$P < 0.01$.* The values in parentheses show the Cohen’s $d$ effect sizes. To explain the group difference between RR and CR, the partial eta squared ($\eta_p^2$) values are presented, as well as the running distance main effect and interaction effect between performance level and running distance.

**SUPPLEMENTAL DIGITAL CONTENT**

SANNO_SDC_Positive_work_contribution_R2.pdf