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Research article

The Relationship Between Lower Limb Passive Muscle and Tendon Compression Stiffness and Oxygen Cost During Running

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Abstract

Studies have reported that a stiff triceps surae muscle and tendon-aponeurosis and also a more compliant quadriceps muscle and tendon-aponeurosis, are related to lower oxygen cost during running. However, to date, no study has investigated in a single experiment how oxygen cost during running is related to the stiffness of the free tendons (Achilles tendon, patellar tendon) and all the superficial muscles of two major muscle groups for running (i.e., quadriceps, triceps surae). Thus, 17 male trained runners/triathletes participated in this study and visited the laboratory on three occasions. On the first day, the participants were familiarized with the tests. On the second day, the passive compression stiffness of the triceps surae muscle (i.e., gastrocnemii), Achilles tendon, quadriceps muscle (i.e., vastii, rectus femoris), and patellar tendon was non-invasively measured using a digital palpation device (MyotonPRO). In addition, an incremental test was applied to test the VO_2max of the participants. Thereafter, in the third visit, after at least 48-h of rest, participants performed a 15-min run on the treadmill with a speed reflecting a velocity of 70% VO_2max, to assess oxygen costs during running. The Spearman correlation showed a significant negative correlation between passive Achilles tendon compression stiffness and running oxygen consumption, with a large effect size ($r\rho$ = -0.52; CI (95%) -0.81 to -0.33; P = 0.03). Moreover, no further significant relationship between oxygen cost during running and the passive compression stiffness of the quadriceps muscle and patellar tendon, as well as the triceps surae muscle, was detected. The significant correlation indicates that a stiffer passive Achilles tendon can lead to a lower oxygen cost during running. Future studies will have to test the causality of this relationship with training methods such as strength training that are able to increase the Achilles tendon stiffness.

Key words: Stiffness, knee extensors, plantar flexors.

Introduction

Running economy is a major determinant of endurance performance (Jones, 2016), and can be quantified as energy utilization at a given submaximal exercise intensity (Barnes and Kilding, 2015). While active mechanical work during running is mainly produced by muscles to lift and accelerate the body (Kram and Taylor, 1990), additional passive, positive work is also performed by tendons, recoiling the stored elastic energy of the eccentric phase during the muscle tendon units shortening phase (Alexander and Bennet-Clark, 1977; Roberts, 2016).

Two important muscle groups involved in running are the triceps surae and the quadriceps femoris. With respect to the triceps surae complex, a greater tendon-aponeurosis stiffness was associated with the most economical runners (Arampatzis et al., 2006; Rogers et al., 2017). A possible explanation for these results is that e.g. Lichtwark et al. (2007) and Bohm et al. (2021) showed for the gastrocnemius and soleus muscle a constant shortening of the muscle throughout the stance phase while running. In addition, Bohm et al. (2021) showed that the soleus is operating at the steep rising part of the force-velocity relationship. Hence, a more compliant tendon (for a given joint angular configuration) would result in a decreased muscle force potential and consequently would require an upregulation of the muscle activity (i.e. higher energy demand) to maintain the needed force for supporting and accelerating the body. Moreover, a further study reported a correlation between triceps surae muscle stiffness and running economy (Dumke et al., 2010), indicating that a stiffer muscle favors a better running economy. However, neither of these studies assessed the stiffness of exclusively the free tendon (i.e., Achilles tendon), or measured both tendon and muscle stiffness, to obtain the full picture of the potential relationship between the triceps surae muscle and tendon properties and running economy.

In addition, Gleim et al. (1990) investigated all the lower leg muscles and concluded that overall "tighter" (less flexible in several muscles) athletes showed a better running economy than normal or highly flexible (= "loose") athletes. Interestingly, the authors found a significant difference in oxygen cost between the "loose" and the "tight" participants for every single muscle, except for the quadriceps and hip flexor muscles. This was underlined by Hunter et al. (2011), who found a significant association between running economy and the flexibility of the plantar flexors, but not the quadriceps muscles. Moreover, Arampatzis et al. (2006) concluded that a more compliant quadriceps tendon and aponeurosis is advantageous during submaximal running. They argued that this allows muscles to work closer toward the plateau region of their force-length relationship, and hence increase their muscle force production. In addition, a further study reported that lower vastus lateralis muscle stiffness was associated with a better running economy/performance in endurance athletes (Miyamoto et al., 2019).

It has to be noted that all the aforementioned studies which have assessed tissue stiffness in the longitudinal direction e.g., through the whole muscle-tendon unit over

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force elongation curves (Arampatzis et al., 2006) or shear wave elastography (Miyamoto et al., 2019). In the last years hand-held and low-cost devices such as MyotonPRO came on the market which can also assess tissue stiffness however, with compression instead (Ditroilo et al., 2012). Though, various studies reported a moderate to large correlation between the assessed stiffness of e.g., shear wave elastography and and MyotonPRO mainly in the lower leg muscles in a passive (i.e., resting) position (Kelly et al., 2018; Lee et al., 2021; Khowailed et al., 2022). To date no study related the passive compression stiffness of the lower leg muscle assessed with MyotonPRO to oxygen costs during running. Additionally, these aforementioned studies (Arampatzis et al., 2006; Miyamoto et al., 2019) neither assessed the free tendon of the quadriceps (i.e., the patellar tendon) nor all the superficial muscles (i.e., rectus femoris, vastus medialis/lateralis) of the quadriceps to obtain an overall picture.

Therefore, the purpose of this study was to investigate the relationship between the passive muscle and tendon (i.e., free tendons) compression stiffness of two muscle groups involved in running (i.e., quadriceps, triceps surae) via MyotonPRO and the oxygen costs during submaximal running.

Methods

Study design

This study was undertaken as part of a larger project (Konrad et al., 2022b). For the research question addressed in this work, only the data collected during the "control condition" of the initial project were relevant. During the larger project, participants had to visit the laboratory five times, although only three visits were relevant to this study. On the first day in the laboratory, participants were familiarized with the laboratory equipment and the test procedures. Consequently, the participants were asked to run on the treadmill for at least ten minutes with a self-selected pace to get used to it and the compression stiffness assessment was explained by the investigator. Following the familiarization session, participants visited the laboratory a further two times within a 14-day period, with at least 48-h rest between each test session. Participants were asked to be in a rested state (no hard workout in the 36 h before a measurement), to be fully hydrated, to have their last meal at least 3 h before the test session (Hayes and Walker, 2007; Allison et al., 2008), to keep their nutrition constant during the 14 days, and to wear the same shoes at each test (Allison et al., 2008). The temperature and humidity in the laboratory were kept constant (21°C, 40% humidity) (Allison et al., 2008). On the second visit, the compression stiffness assessments for the triceps surae and quadriceps muscle-tendon units were performed, plus an incremental test, to estimate the maximal oxygen consumption (VO_2max) of the participants. On the third, fourth, and fifth visits, the participants were randomly assigned to one of two interventions (for details, see (Konrad et al., 2022b)) or to no intervention (control condition, relevant for this study). Participants performed a standardized warm-up of 10-min treadmill running at 8 $km.h^{-1}$ (Damasceno et al., 2014), followed by 5 min of rest in a standing position and then a running-specific warm-up with three different exercises (i.e., high knee run, skipping, butt kick run) over a 20-m distance with a high intensity (i.e., 7/10 on the visual analog scale) (Samson et al., 2012; Konrad et al., 2022b). Subsequently, after preparing the participants for the metabolic assessment (i.e., placing the mask), the oxygen cost during running test (15-min run on the treadmill at a velocity of 70% VO_2max) was conducted.

Participants

As in a previous study (Damasceno et al., 2014), the inclusion criteria were recreational runners or triathletes participating in endurance competitions, a weekly running volume of more than 30 km, and training for at least two years without any interruptions. The exclusion criteria were pharmacological treatment, any type of neuromuscular disorder, dysfunction in the cardiovascular, respiratory, or circulatory system, and elite runner.

Out of the 18 participants in the overall project (see Konrad et al., 2022b), 17 male trained runners/triathletes (age: 29.6 ± 6.0 years; weight: 74.4 ± 6.7 kg, height: 181.8 ± 3.7 cm) underwent passive tissue compression stiffness measurements relevant for this study. The average VO_2max was 55.9 ± 6.8 $ml{\cdot}kg^{-1}{\cdot}min^{-1}$, and the participants reported an average running distance of 44.1 ± 12.8 km per week. Each participant signed a written informed consent form, and ethical approval was obtained from the local ethical committee of the University of Munich (762/20 S-KH), in accordance with the Declaration of Helsinki.

Procedures

Incremental testing

To determine VO_2max, an incremental test, similar to the test performed in a previous study (Damasceno et al., 2014), was performed on a motorized treadmill (Saturn 300/125, h/p/cosmos, Germany). The test started with a warm-up for 5 min running at 8 $km.h^{-1}$, followed by an increase of 0.5 $km.h^{-1}$ every minute until full exhaustion. The stopping criterion was when the participant was not able to maintain the velocity of the treadmill. Post-hoc, two out of the following three criteria were considered to confirm exhaustion and to determine VO_2max: (a) an increase in VO_2 between the consecutive stages of less than 2.1 ml/kg *min; (b) a respiratory quotient exceeding 1.1; and (c) exceeding the age-predicted (220 bpm minus age) maximum heart rate (Howely et al., 1995; Damasceno et al., 2014). A Cortex MetaLyzer 3B system (CORTEX Biophysik, Germany) was used to measure gas exchange and flow volume, and hence to determine VO_2 and VCO_2 (carbon dioxide output). VO_2 and VCO_2 were averaged at 30-s intervals throughout the tests. Prior to all the running tests (and also the oxygen cost during running tests), the automated gas analysis system was calibrated using both ambient air and calibration gas (5% for CO_2 and 15% for O_2). A 3-L syringe was used for the calibration of the volume sensor. A heart rate transmitter and heart rate monitor (Polar H10, Polar Electro, Kempele, Finland) were used to monitor heart rate.

Oxygen cost during running

To test oxygen cost during running, subjects performed a

15-min run on the treadmill, reflecting a velocity of 70% VO_2max, as determined during the second test day. A time of 15 min was selected since this is considered to be an appropriate duration to achieve a physiological steady state (Barnes and Kilding, 2015). A running velocity of 70% VO_2max is related to moderate intensity, i.e., below the respiratory compensation threshold (Esteve-lanao et al., 2005). The individual velocity of each subject was calculated from the relationship between the VO_2 and the running velocity assessed during the incremental test (Yamaguchi et al., 2015). To calculate the oxygen cost during running at this speed, the VO2 was considered as an average value from the 5 min of running at the steady state in the last phase of the 15-min run (i.e., from 10 to 15 min).

Compression stiffness assessment

A digital palpation device (MyotonPRO, Myoton Ltd., Estonia) was used to assess the passive muscle and tendon compression stiffness of the calf and anterior thigh. All the assessments were performed by an investigator experienced in human anatomy, plus six months of training on especially the MyotonPRO device. The reliability of this device in combination with the investigator has previously been confirmed for the assessment of the addressed muscles (Chen et al., 2019; Schneebeli et al., 2020; Konrad et al., 2022a). For the tissue compression stiffness measurements of the triceps surae (i.e., Achilles tendon, gastrocnemius medialis, and gastrocnemius lateralis), the participant was asked to remain in a resting position, lying prone, with their foot hanging freely off a physiotherapy bed (Chang et al., 2020). Moreover, for the anterior thigh muscles (vastus lateralis, vastus medialis, rectus femoris), the participant was asked to move into a supine position, with their hips and knees fully extended (Klich et al., 2020). For the patellar tendon, the participant was asked to remain in a sitting position, with both hip and knee joints at 90° (Klich et al., 2020).

For all of these passive compression stiffness assessments, the probe of the MyotonPRO device was applied perpendicular to the relaxed tissue. The measurement sites of the respective muscles were selected in accordance with SENIAM guidelines (Hermens et al., 1999) for electrode placement during surface electromyography measurements (see Figure 1A and 1 B). For the Achilles tendon, the assessment was performed at the level of the medial malleolus (see Figure 1A) (Schneebeli et al., 2020), and for the patellar tendon, it was performed at the midway point between the distal patellar rim and the tuberosity of the tibia (see Figure 1B and 1C) (Klich et al., 2020).

In total, three consecutive mechanical impacts at an impulse time of 15 ms and a force of 0.3 to 0.4 N were applied using the MyotonPRO device. This was performed three times, which resulted in nine impacts per muscle and tendon. The muscle and tendon compression stiffness of every single mechanical impact was estimated as the force applied relative to the deformation of the tissue. The average value out of the three × three mechanical impacts for each muscle and tendon was taken for the statistical analysis (Ditroilo et al., 2012).

Statistical analyses

SPSS (version 27.0, SPSS Inc., Chicago, Illinois) was used for all the statistical analyses. A Shapiro-Wilk test showed non-normally distributed data for oxygen cost during running, and hence a Spearman rank ($r\rho$) correlation analysis was used to calculate the relationship between the variables. Besides that, the 95% confidence interval (CI) was calculated for the respective correlation analyses. The alpha level was set to 0.05. The $r\rho$ value was taken as the effect size of the Spearman rank correlation, following the suggestion of Hopkins (2002). Effect sizes of 0 - 0.1, 0.1 - 0.3, 0.3 - 0.5, 0.5 - 0.7, 0.7 - 0.9, and 0.9 - 1.0 were defined as trivial, small, moderate, large, very large, nearly perfect, and perfect, respectively.

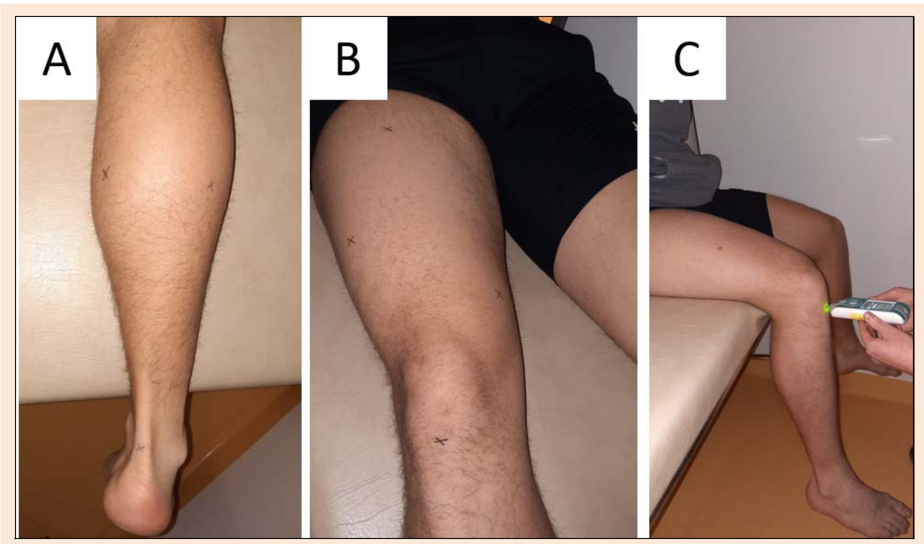

Figure 1. Locations (black marks) of the tissue compression stiffness measurements of the triceps surae (i.e., Achilles tendon, gastrocnemius medialis, and gastrocnemius lateralis) are presented in A, whilst the spots for the anterior thigh muscles (vastus lateralis, vastus medialis, rectus femoris) and patellar tendon are presented in B. C presents an exemplarily assessment of the patellar tendon.

Results

The average speed during the 15-min runs was 11.3 ± 1.2 km.h[-1], corresponding to individual running speeds at 70% VO_2max. The values of the passive muscle and tendon compression stiffness are presented in Table 1. There is a significant negative correlation between Achilles tendon compression stiffness and oxygen consumption during submaximal running, with a large effect size (rρ = -0.52; CI (95%) -0.81 to -0.33; P = 0.03). This means that Achilles tendon compression stiffness is positively related to oxygen cost during running. No further significant correlation is apparent between the other tested parameters and oxygen cost during running (see Figure 2).

Table 1. Values (mean ± standard deviation) of the passive stiffness measurements

	Mean		Standard deviation
Achilles tendon stiffness (N/m)	798.57	±	64.42
Gastrocnemius medialis stiffness (N/m)	297.28	±	40.14
Gastrocnemius lateralis stiffness (N/m)	327.93	±	48.17
Patellar tendon stiffness (N/m)	799.05	±	84.97
Vastus lateralis stiffness (N/m)	306.46	±	41.54
Vastus medialis stiffness (N/m)	256.74	±	34.12
Rectus femoris stiffness (N/m)	248.04	±	19.74

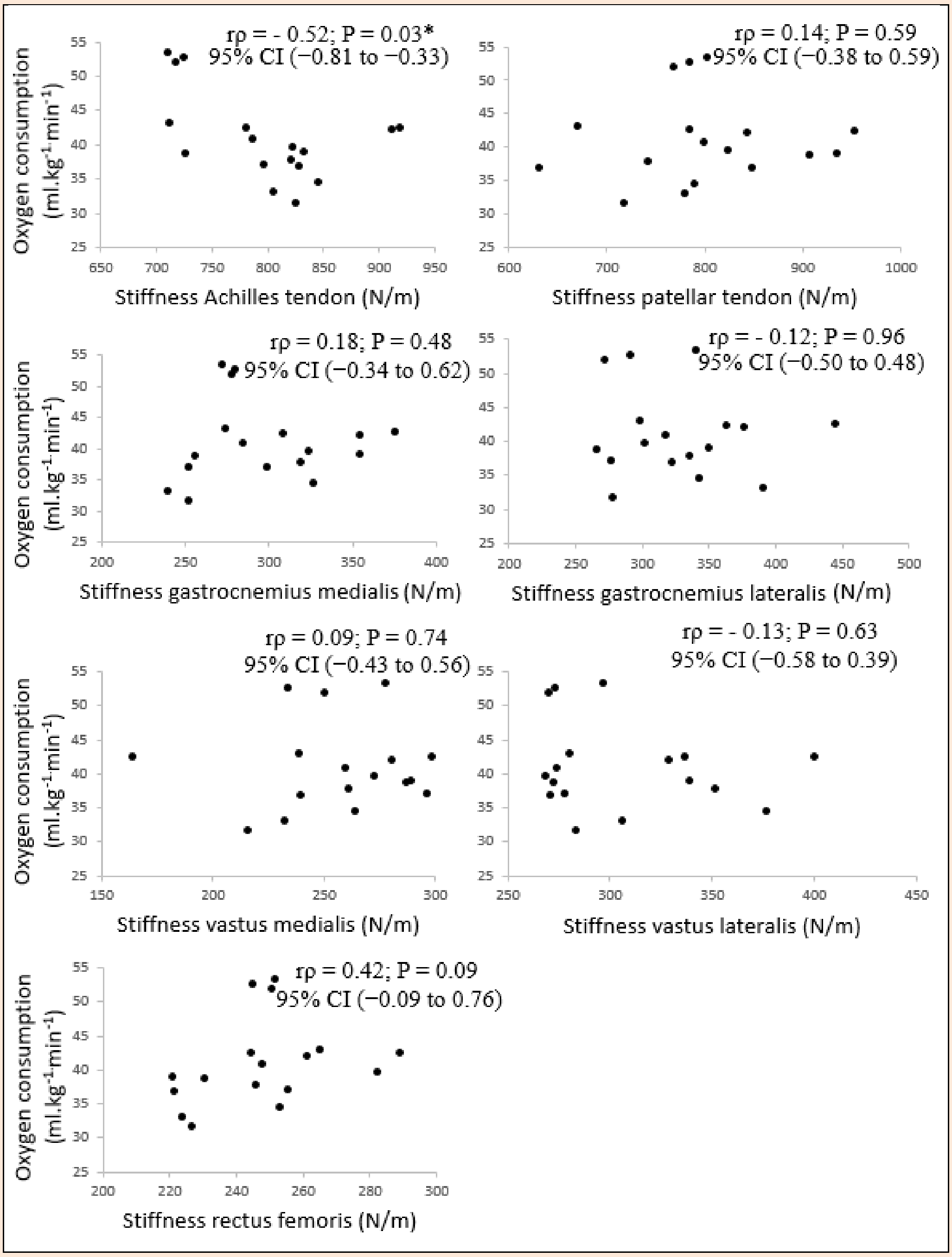

Figure 2. Correlation between oxygen consumption (low values = lower oxygen cost during running) and passive stiffness of the Achilles tendon, patellar tendon, gastrocnemius medialis, gastrocnemius lateralis, vastus medialis, vastus lateralis, and rectus femoris. * indicates a significant correlation.

Discussion

This study was the first to investigate the relationship between passive muscle and tendon compression stiffness (i.e., free tendons) of two major muscles involved in running (i.e., quadriceps, triceps surae) and oxygen cost during running. While a significant relationship between oxygen cost during running and passive Achilles tendon compression stiffness was detected, no other significant relationships with the passive compression stiffness of the quadriceps muscle and patellar tendon were observed, as well as the passive compression stiffness of the triceps surae muscle.

The finding of a stiffer Achilles tendon assessed with MyotonPRO via compression in the current study being related to lower oxygen cost during running was expected due to findings from similar previous studies (Arampatzis et al., 2006; Rogers et al., 2017). However, it has to be noted that these studies have used force-elongation curves to assess Achilles tendon stiffness. Bringing those findings together it can be assumed, that runners with stiffer Achilles tendons might benefit from a higher return of elastic energy during the stretch-shortening phase in submaximal running. This is underlined by studies which have reported that the gastrocnemius fascicles mainly work on the ascending limb of their force-length curve during the stance phase of running (Monte et al., 2020). Hence, it can be assumed that a stiffer serial elastic structure would lengthen less, allowing the fascicles to elongate and therefore work at muscle lengths closer to their optimum. The causality of this relationship has been investigated in training studies, with conflicting results. While Albracht and Arampatzis (2013) and Bohm et al. (2021a) reported an increase in Achilles tendon stiffness and an improvement in running economy following 14 weeks of isometric strength training, Fletcher et al. (2010) reported no such changes after 8 weeks of Achilles tendon stiffness training. However, the stiffness changes in the study by Fletcher et al. (2010) were not significant probably due to the shorter intervention time compared to the other studies (Albracht and Arampatzis, 2013; Bohm et al., 2021). Furthermore, Fletcher et al. (2010) reported a significant correlation between the changes in tendon stiffness and the changes in running economy, in both the intervention group and the control group. This indicates, at least, the existing relationship between running economy and Achilles tendon stiffness. In addition to the isometric strength training performed in these studies, other training regimes, such as hypertrophy weight training (e.g., 10 repetitions with 80% maximum strength; (Kubo et al., 2007)) or plyometric training (Fouré et al., 2010) of the calves, can increase Achilles tendon stiffness. Consequently, it is recommended that endurance athletes perform isometric strength training, hypertrophy weight training, or plyometric training of the calf muscles to increase their Achilles tendon stiffness, and hence likely improve their running economy.

Besides Achilles tendon compression stiffness, we also measured the compression stiffness of both gastrocnemii. In contrast to a previous study (Dumke et al., 2010), we did not find a significant relationship between triceps surae muscle compression stiffness and oxygen cost during running.

A potential explanation for the differences between our findings and the results of Dumke et al. (2010) likely lies in the methods used to estimate muscle stiffness. Dumke et al. (2010) used a free oscillation technique, where the stiffness of the triceps surae muscle was estimated using various maximum isometric voluntary contractions and by assuming the muscle-tendon unit to be a dampened spring model (Walshe, 1996). In contrast, we directly measured passive muscle compression stiffness on the muscle belly with a digital palpation device (MyotonPRO). In general, the reliability (Chen et al., 2019; Schneebeli et al., 2020; Lee et al., 2021; Konrad et al., 2022a), as well as the construct validity (Schneebeli et al., 2020), of the MyotonPRO device has been confirmed in previous studies. However, in the current study, we measured only passive compression stiffness of both muscle and tendon tissues, but not active stiffness. We decided to do so, since reliability values for passive compression stiffness (i.e., rested muscle) obtained with the MyotonPRO device were slightly higher than those for active compression stiffness (i.e., contracted muscle) in a previous study (Lee et al., 2021), as well as in our pilot experiments. While a lower passive muscle stiffness is an indicator of higher flexibility (Magnusson et al., 1997), lower active muscle stiffness is associated with lower force production since fewer cross-bridges are activated (Morgan, 1977). To the best of the authors' knowledge, the relationship between active and passive muscle and tendon stiffness in respect to oxygen cost during running and running biomechanics has not been well elaborated, which makes it difficult to compare the respective literature. Thus, we recommend that future studies should also relate active muscle stiffness, as well as active tendon stiffness, estimated by force-elongation curves of the various lower limb muscles, to oxygen cost during running.

With regard to the quadriceps, we did not find any relationship between the patellar tendon or the quadriceps muscle and oxygen cost during running. Based on previous studies that have reported that a better running economy is related to lower tendon-aponeurosis stiffness (Arampatzis et al., 2006) and lower muscle stiffness (Miyamoto et al., 2019), we would have expected a negative relationship with oxygen cost during running. Contrary to the triceps surae muscle, the quadriceps fascicles (e.g., from the vastus lateralis) work on the descending limb of their force-length curve during the stance phase of running, and hence a more compliant serial elastic structure could therefore take up more of the muscle-tendon unit lengthening, thus allowing the fascicles to work at shorter lengths closer to their optimum (Monte et al., 2020). We have not found any significant relation between oxygen cost during running and the compression stiffness of the vastii or rectus femoris. However, rectus femoris muscle compression stiffness showed a tendency for a positive relationship ($r\rho = 0.42$; $P = 0.09$) with oxygen consumption. Such a potential relation would indicate that a more compliant muscle tissue is related to lower oxygen cost during submaximal running. Besides the rectus femoris muscle, the iliopsoas muscle is the main contributor to hip flexion (Byrne et al., 2010), and contributes significantly during running (Montgomery et al.,

1994) which makes this muscle another main candidate for affecting oxygen cost during running. Unfortunately, in the current study, it was not possible to measure the iliopsoas muscle compression stiffness with the MyotonPRO device as it is a deep-lying muscle. Hence, we recommend that future studies should explore the relationship between hip flexor extensibility (i.e., with a modified Thomas test (Harvey, 1998)) or stiffness of the iliopsoas muscle (i.e., with shear wave elastography (Nojiri et al., 2021)) and oxygen cost during running.

One limitation is that we have assessed oxygen cost during running only at a single submaximal running velocity. It is possible that the stiffness of the various muscles and tendons affects oxygen cost during running at other velocities. Another limitation is that we only assessed relationships and not causality. Therefore, we recommend to relate the changes in stiffness by e.g., stretching (Nakamura et al., 2021) or strength training (Fouré et al., 2010) with oxygen cost during running. Consequently, future studies should assess the oxygen cost during running and lower limb stiffness of endurance athletes either several times throughout a season or in training studies. For training studies, we recommend ≥14 weeks as applied by Albracht and Arampatzis (2013) and Bohm et al. (2021). These authors showed an increase in tendon stiffness with a subsequent decrease in oxygen consumption during running. An additional limitation is that we recruited male participants only in this larger stretching project (Konrad et al., 2022b), since there is evidence that male and female runners respond differently to a single bout of stretching before running (Mojock et al., 2011). A further limitation might be the methods used to assess stiffness in the current study. We have used a non-invasively digital palpation device (MyotonPRO) which assess compression stiffness. Contrary other studies on that topic assessed the stiffness in the longitudinal direction e.g., through the whole muscle-tendon unit over force elongation curves (Arampatzis et al., 2006) or shear wave elastography (Miyamoto et al., 2019). Although these methods are indeed different, various studies reported a moderate to large correlation between the assessed stiffness of e.g., shear wave elastography and and MyotonPRO (Kelly et al., 2018; Lee et al., 2021; Khowailed et al., 2022). Moreover, we used the SENIAM recommendations for the spots to measure muscle compression stiffness with the MyotonPRO. The results of the muscle compression stiffness measurements are likely affected by the locations where they are applied on the muscle. Thus, standardization of points of application is a crucial factor for validity and reliability of the method, and also supports comparability with other studies. SENIAM guidelines provide internationally accepted descriptions for EMG sensor locations on muscles. We adopted these sensor locations in order to have clearly defined and valid spots of muscle tissue for the respective muscle of interest. Moreover, although, the soleus muscle is a crucial muscle in running (Bohm et al., 2021) we decided not to measure soleus stiffness, since MyotonPRO can assess superficial tissue only. Future studies should use other techniques to assess soleus stiffness which allow to measure deep lying muscles (e.g., shear wave elastography) and relate it to oxygen costs during running. Lastly, we analyzed the free tendon and not the individual parts of triceps surae muscle tendon unit. Albracht and Arampatzis (2013) and Bohm et al. (2021a) evaluated changes in tendon stiffness of the gastrocnemius muscle tendon unit and the soleus muscle tendon unit using an identical isometric plantarflexion training. In the respective studied muscle tendon unit, they found an increase in tendon stiffness after the training period. Therefore, one can assume that adaptations with respect to tendon stiffness, do not just occur isolated for one particular muscle tendon unit, e.g. soleus but for all parts including the free tendon. Hence, we do not believe that our results would be different if each muscle tendon unit had been studied separately.

Conclusion

In conclusion, our analyses showed that recreational athletes with a stiffer passive Achilles tendon (assessed with compression via MyotonPRO) had lower oxygen cost during running , while passive patellar tendon compression stiffness, quadriceps muscle compression stiffness, and triceps surae muscle compression stiffness were not related to oxygen consumption during submaximal running. According to our findings, but also in accordance with previous studies (Albracht and Arampatzis, 2013; Bohm et al., 2021), strategies to increase Achilles tendon stiffness should be incorporated into the training regimes of endurance athletes, to increase their oxygen cost during running.

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Key points

- This study was the first to investigate how oxygen cost during running is related to passive muscle and tendon compression stiffness (i.e., free tendons) of two relevant muscle groups for running (i.e., quadriceps, triceps surae).
- A higher passive Achilles tendon compression stiffness was related to lower oxygen cost during running.
- Passive patellar tendon compression stiffness and compression stiffness of the quadriceps muscle, as well as compression stiffness of the triceps surae muscle, were not significantly related oxygen cost during running.

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