Athletic training affects the uniformity of muscle and tendon adaptation during adolescence

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Mersmann F, Bohm S, Schroll A, Marzilger R, Arampatzis A. Athletic training affects the uniformity of muscle and tendon adaptation during adolescence. J Appl Physiol 121: 893–899, 2016. First published September 1, 2016; doi:10.1152/japplphysiol.00493.2016.—With the double stimulus of mechanical loading and maturation acting on the muscle-tendon unit, adolescent athletes might be at increased risk of developing imbalances of muscle strength and tendon mechanical properties. This longitudinal study aims to provide detailed information on how athletic training affects the time course of muscle-tendon adaptation during adolescence. In 12 adolescent elite athletes (A) and 8 similar-aged controls (C), knee extensor muscle strength and patellar tendon mechanical properties were measured over 1 yr in 3-mo intervals. A linear mixed-effects model was used to analyze time-dependent changes and the residuals of the model to quantify fluctuations over time. The cosine similarity (CS) served as a measure of uniformity of the relative changes of tendon force and stiffness. Muscle strength and tendon stiffness increased significantly in both groups (P < 0.01). However, the fluctuations of muscle strength were greater [A, 17 ± 7 (SD) N·m; C, 6 ± 2 N·m; P < 0.05] and the uniformity of changes of tendon force and stiffness was lower in athletes (CS A, −0.02 ± 0.5; C, 0.5 ± 0.4; P < 0.05). Further, athletes demonstrated greater maximum tendon strain (A, 7.6 ± 1.7%; C, 5.5 ± 0.9%; P < 0.05) and strain fluctuations (A, 0.9 ± 0.4; C, 0.3 ± 0.1; P < 0.05). We conclude that athletic training in adolescence affects the uniformity of muscle and tendon adaptation, which increases the demand on the tendon with potential implications for tendon injury.

Knee; tendinopathy; plasticity; adolescence; biomechanics; time course

NEW & NOTEWORTHY

This study demonstrates for the first time that athletic training during adolescence can disrupt the uniformity of muscle and tendon adaptation. The resultant imbalance of muscle strength and tendon stiffness increases the demand on the tendon. This could have potential implications for the risk of overuse injury, which is a major problem in specific sport disciplines.

TENDONS HAVE THE CRUCIAL ROLE of transmitting the forces generated by the muscles to the skeleton. However, as the ultimate strain of tendons cannot be significantly altered (26), tendons need to adapt in their mechanical properties when the force-generating potential of muscles increases (e.g., because of physical training), to maintain physiological levels of strain during maximum muscle contractions (24). Therefore it is frequently observed in healthy adults that both muscle strength and tendon stiffness increase in response to chronic mechanical loading [see Bohm et al. (7) and Wiesinger et al. (41) for reviews]. Yet there seems to be only a poor association of strength gains and changes in tendons’ structural and mechanical properties (38), and the time course of loading-induced adaptation of muscle and tendon can differ as well (22, 23), potentially because of the lower responsiveness to loading on the transversal level of growth factors (15) or differences between muscle and tendon in the mechanical stimuli that effectively elicit adaptational processes (1, 3, 8, 25). In conclusion, during a training process imbalances might develop between the adaptation of muscle and tendon.

In adolescent athletes, the effects of mechanical loading interact with the stimulus of maturation, which also triggers changes in both muscles and tendons (34, 35). This twofold stimulus might expose young athletes to an increased risk of developing imbalances within the muscle-tendon unit. Recently, we provided evidence of an imbalance in the adaptation of muscle and tendon in junior volleyball athletes (31, 33), which resulted in high levels of tendon stress and tendon strain (31). While stress is a measure of external load (normalized to tendon cross-sectional area) and the ultimate stress of a tendon can be increased or decreased via a modulation of the tendon material properties, ultimate tendon strain is more or less constant (26). Therefore tendon strain is an adequate indicator of the internal mechanical demand placed on the tendon (i.e., how the integrity of the tissue is challenged) during muscle contractions and has been associated previously with tendon overuse (5, 10).

Tendinopathy not only has an exceptionally high prevalence in volleyball athletes (29) but also is the most frequent overuse injury in adolescent elite athletes (28). This supports the assumption that an imbalance in the adaptation of muscle and tendon in adolescent athletes might be of clinical relevance and demonstrates the necessity of deepening our understanding of the development of muscle and tendon during adolescence and the effect of mechanical loading. To date, however, the time course of muscle-tendon unit adaptation during adolescence and the effect of athletic training are largely unknown. Consequently, the present longitudinal study investigates for the first time the development of muscle and tendon properties in 3-mo intervals during 1 yr in adolescent athletes and nonathletes in vivo. Because of the seasonal variations in mechanical loading in athletes, we hypothesized that there will be greater fluctuations in the development of muscle and tendon functional, morphological, and mechanical properties and indications of an increased mechanical demand for the tendon due to a lower uniformity of muscle and tendon adaptation (i.e., imbalance) in adolescent athletes compared with similar-aged controls.
METHODS

Participants and experimental design. As an a priori power analysis to determine a target sample size was not possible because of a lack of appropriate longitudinal data on the development of muscle and tendon in adolescence, we tried to recruit as many participants as possible. Twenty-six adolescent volleyball athletes from the extended pool of the German junior national team and a group of 13 similarly aged habitually active controls agreed to participate in the present longitudinal study, and measurements were scheduled every 3 mo for 1 yr. Nineteen participants dropped out of the study because of the time-consuming procedures, and thus 12 adolescent athletes (5 female, 7 male; age 16 ± 1 (SD) yr) and 8 controls (5 female, 3 male; ±4 h of recreational training per week; age 16 ± 1 yr) completed the investigation period. All measurements were conducted on the dominant leg (i.e., leading leg in the spike jump or leg used for kicking a ball, respectively). The study has been approved by the university ethics committee, and all participants (and respective legal guardians) signed informed consent to the experimental procedures.

Measurement of maximum knee joint moment. Knee extensor muscle strength was measured combining dynamometry, kinematic, and electromyographic (EMG) recordings. Effects of gravitational forces and the misalignment of rotation axes of knee joint and dynamometer were accounted for on the basis of the inverse dynamics approach suggested by Arampatzis et al. (2). For this purpose, six reflective markers were fixed to the following anatomical landmarks: anterior epicondyles, and malleoli. Kinematic data were recorded using a Vicon motion capture system (version 1.7.1; Vicon Motion Systems, Oxford, UK) integrating eight cameras operating at 250 Hz. For estimating the contribution of the antagonistic muscles to the resultant joint moment (6, 30), the EMG activity of the lateral head of the biceps femoris was recorded (Myon m320RX; Myon, Baar, Switzerland).

Following a standardized warm-up, the participants performed three trials of isometric maximum voluntary knee extension contractions on a dynamometer (Biodex Medical, Shirley, NY) at 85° trunk flexion (supine = 0°) and resting knee joint angles of 65-75° (0° = full extension) in 5° intervals to measure the maximum knee extension moment (MVC). Additionally, a passive knee extension trial (driven by the dynamometer at 5°/s) and two trials of knee flexion contractions were recorded to account for moments of gravity (2) and to establish an activation-flexion moment relationship that was used to estimate the knee flexion moment generated during maximum effort knee extension due to antagonistic coactivation (for more information on the procedure, see Mademli et al. (30)).

Measurement of tendon mechanical properties. For the assessment of the patellar tendon mechanical properties, the participants completed five trials of isometric ramp contractions (i.e., steadily increasing effort from rest to maximum effort in ~5 s) in the knee joint angle where the highest individual joint moments were accomplished during the MVC assessment. The tendon elongation during the contractions was captured at 25 Hz by a 10 cm ultrasound probe (7.5 MHz; My Lab60; Esaote Canada, Georgetown, ON, Canada) overlaying the patellar tendon in the sagittal plane fixed by a modified knee brace. The knee extension moments were calculated using the same considerations as for the MVC calculation (i.e., correction for angles misalignments, gravitational forces, and antagonistic coactivation), and the ultrasound images were synchronized off-line with the data captured in the Vicon system by an externally induced voltage peak, which could be identified in both the ultrasound images and the analog data stream.

Tendon force was calculated by dividing the knee extension moment (measured as in MVC assessment) by the tendon moment arm. In 10 athletes the tendon moment arm at the first measurement session could be assessed by magnetic resonance imaging (MRI) using the procedure described earlier (31). For all other participants the moment arm (MA) was predicted using an equation derived from a regression analysis of 77 MRI-based data sets from earlier studies with stepwise inclusion of anthropometric data. The final model included mass in kilograms (m), sex (s; coded as 0 for male and 1 for female), and height in centimeters (h) as prediction variables, while age and knee width were excluded. The regression equation was

\[ MA = 25.88 + 0.078 \cdot m - 2.242 \cdot s + 0.128 \cdot h \]  

with an \( R^2 \) of 0.55 (\( P < 0.001 \)) and SE of 2.25 mm. The tendon moment arm for the subsequent sessions was scaled considering the relative changes predicted by the regression equation. For each session the moment arm was adjusted to the knee joint angle position on the basis of the regression equation suggested by Herzog and Read (19).

The patellar tendon elongation was determined by a manual frame-by-frame tracing of its deep insertion at the patella apex and tibial tuberosity using a custom-written MATLAB interface (version R2015a; MathWorks, Natick, MA). The force-elongation relationship of the five trials of each participant was averaged to achieve an excellent reliability (37), using the highest common force value as peak force. The resultant function was fitted by a second-order polynomial, and tendon stiffness was calculated between 50 and 100% of the peak tendon force.

Architecture of vastus lateralis muscle. Vastus lateralis (VL) architecture was assessed at a knee joint angle of 60° with the ultrasound probe positioned over the muscle belly at ~60% of thigh length (32). The upper and deeper aponeuroses were marked in custom-written MATLAB interface by setting reference points along the aponeuroses that were approximated by a linear least squares fitting. Subsequently, we digitized the visible features of multiple fascicles and calculated pennation angle and muscle thickness with respect to the average inclination of the fascicle portions and the distance of the aponeuroses, respectively (31).

Statistics. Normality and homoscedasticity of the data were tested in SPSS (version 20.0; IBM, Armonk, NY) using the Kolmogorov-Smirnov and Levene’s tests, respectively, using an adjusted (more conservative) significance level of \( \alpha = 0.02 \) considering the small sample sizes. Normality was present in all target parameters, and homoscedasticity was present in most, but not all parameters.

A linear mixed-effects model (LMM) was formulated and processed in MATLAB to analyze the time- and group-dependent development. Further, we were able to use the residuals to the model as a measure of fluctuations of muscle and tendon properties, as, in contrast to general linear models, the inclusion of random effects accounts for individual differences in the development over time. The model equation was

\[ y_{ij} = \beta_0 + \beta_1 g_i + \beta_2 f_{ij} + \beta_3 t_{ij} g_i + b_{0i} + b_{1i} f_{ij} + e_{ij} \]  

where \( i \) is index for participant (1, ..., 20); \( j \) is index for session (0, ..., 4); \( g_i \) is athletes = 0, control = 1; \( f_{ij} \) is measurement session (0, ..., 4); \( \beta_0 \) is y-intercept constant for athletes; \( \beta_1 \) is y-intercept constant for difference between controls and athletes; \( \beta_2 \) is slope constant for athletes; \( \beta_3 \) is slope constant for difference between controls and athletes; \( b_{0i} \) is subject-specific y-intercept (random effect); \( b_{1i} \) is subject-specific slope (random effect); and \( e_{ij} \) is residual.
presence of heteroscedasticity (40). Considering the unbalanced design with regard to sex, differences between groups were tested for selected parameters (i.e., MVC normalized to body mass, pennation angle, and maximum strain). The absolute residuals to the LMM fit of the contextually most relevant parameters (i.e., MVC, tendon stiffness and strain, and VL thickness and pennation angle) were compared between groups using Welch’s *t*-test.

The association of muscle and tendon properties was modeled in the LMM as well (by exchanging the measurement session variable with the respective prediction variable), predicting muscle strength by muscle thickness or pennation angle and tendon stiffness by tendon force. The absolute residuals to the model fit of tendon stiffness predicted by tendon force were compared between groups to analyze respective prediction uncertainties.

The uniformity of the development of tendon force and stiffness was calculated as cosine similarity (CS) of the relative changes between groups (i.e., intercept) were not tested.

Table 1. One-year development of anthropometric data for adolescent volleyball athletes and controls measured in 3-mo intervals

<table>
<thead>
<tr>
<th></th>
<th>Baseline</th>
<th>3 mo</th>
<th>6 mo</th>
<th>9 mo</th>
<th>12 mo</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body height, cm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Athletes</td>
<td>187.4 ± 6.8</td>
<td>187.8 ± 7.2</td>
<td>188.0 ± 7.3</td>
<td>188.2 ± 7.1</td>
<td>188.5 ± 7.6</td>
</tr>
<tr>
<td>Controls</td>
<td>169.4 ± 8.5</td>
<td>169.8 ± 8.6</td>
<td>170.3 ± 9.0</td>
<td>170.4 ± 9.1</td>
<td>170.4 ± 9.1</td>
</tr>
<tr>
<td>Body mass, kg</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Athletes</td>
<td>73.0 ± 9.5</td>
<td>73.3 ± 9.8</td>
<td>73.9 ± 10.4</td>
<td>74.3 ± 10.3</td>
<td>74.8 ± 10.6</td>
</tr>
<tr>
<td>Controls</td>
<td>56.8 ± 8.8</td>
<td>57.4 ± 9.5</td>
<td>58.0 ± 9.8</td>
<td>59.1 ± 9.2</td>
<td>59.4 ± 9.6</td>
</tr>
</tbody>
</table>

Values are means ± SD. *Significant change over time (i.e., slope; *P* < 0.05). There were no group differences of change over time (i.e., slope; *P* > 0.05). Note that differences between groups (i.e., intercept) were not tested.

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between the five measurement sessions in a four-dimensional vector space:

\[ CS = \cos(\theta) = \frac{A \cdot B}{\|A\| \cdot \|B\|} = \frac{\sum_{i=1}^{2} A_i B_i}{\sqrt{\sum_{i=1}^{2} A_i^2} \sqrt{\sum_{i=1}^{2} B_i^2}} \] (3)

A and B represent the vectors of the relative intersession changes (i = 1, . . . , 4). CS can take values from 1 (indicating equal orientation of the vectors, i.e., high similarity) to −1 (opposing orientation, i.e., low similarity).

The significance level for the LMM hypothesis testing and the Welch’s t-test for the residuals and the CS was set to \( \alpha = 0.05 \).

RESULTS

Anthropometric data are shown in Table 1. There was a marginal but statistically significant increase of body height and mass (−0.6%, \( P = 0.001 \); −2.8%, \( P = 0.003 \)), without group differences of change over time (\( P = 0.76 \) and 0.33, respectively).

Muscle strength and tendon properties. Both absolute and normalized muscle strength increased significantly over time (\( P < 0.001 \) and \( P = 0.003 \), respectively; Fig. 1 and Table 2). The increase was independent of group, as there was no difference between groups with regard to the change over time (\( P = 0.54 \) and 0.58, respectively). There were greater fluctuations of muscle strength over time in athletes compared with controls (i.e., greater residuals, \( P < 0.001 \); Fig. 2), and normalized muscle strength was significantly greater in athletes (\( P = 0.016 \); Table 2). Tendon stiffness increased significantly (\( P = 0.003 \); Fig. 1), again independent of group (\( P = 0.2 \)), however, without differences in the fluctuations between groups (\( P = 0.33 \), Fig. 2). Maximum tendon strain did not change significantly over time (\( P = 0.56 \); Fig. 1) in both groups (\( P = 0.8 \)). However, maximum strain was greater in athletes (\( P < 0.001 \)) and demonstrated greater fluctuations (\( P = 0.001 \), Fig. 2). A post hoc stepwise regression analysis identified the fluctuations of MVC as a significant predictor of the fluctuations of strain (\( P = 0.006 \), \( R^2 = 0.346 \)), while the fluctuations of tendon stiffness did not contribute significantly (\( P = 0.42 \)). Independent of group (\( P = 0.63 \)), tendon force increased significantly over time (\( P = 0.014 \); Table 2) and was a significant predictor of tendon stiffness in the LMM (\( R^2 = 0.82 \); \( P = 0.036 \)).

The prediction uncertainties, however, were significantly greater in athletes (\( P = 0.035 \); Fig. 3), and there was less uniformity (i.e., significantly lower CS) in the development of tendon force and stiffness compared with controls (\( P = 0.045 \); Fig. 3).

Further, significant time-dependent increases were found for the tendon moment arm (\( P < 0.001 \); Table 2), irrespective of group (\( P = 0.72 \)). No significant changes over time or differences in the time-dependent changes were observed in tendon rest length (\( P = 0.45 \) and 0.26, respectively; Table 2).

The mean values of the female subgroups \((n = 5 \text{ each})\) of the crucial fluctuation and uniformity measures (e.g., MVC residuals of 15 and 5 N·m or CS of −0.04 and 0.38 for female athletes and controls, respectively) were representative of the reported total group means, and thus we are confident that our findings were not biased by the unbalanced sample composition with regard to sex.

Vastus lateralis architecture. There was a significant increase in VL thickness in athletes (\( P < 0.001 \); Table 2), but not controls (\( P = 0.59 \)). No significant group differences were found in the fluctuations of VL thickness (\( P = 0.22 \)). Pennation angle was greater in athletes compared with controls (\( P = 0.002 \)) and did not show a systematic change over time (\( P = 0.12 \)). The fluctuations of pennation angle were significantly greater in athletes as well (\( P = 0.036 \)). Both VL thickness and pennation angle were significant predictors of muscle strength in the LMM (\( R^2 = 0.94 \), \( P = 0.017 \); and \( R^2 = 0.96 \), \( P < 0.001 \), respectively).

Table 2. One-year development of normalized knee extensor muscle strength, vastus lateralis architecture, and patellar tendon properties of adolescent volleyball athletes and controls measured in 3-mo intervals

<table>
<thead>
<tr>
<th>Session</th>
<th>Baseline</th>
<th>3 mo</th>
<th>6 mo</th>
<th>9 mo</th>
<th>12 mo</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Normalized MVC,</strong># N·m/kg</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Athletes</td>
<td>4.15 ± 0.53</td>
<td>4.19 ± 0.57</td>
<td>4.21 ± 0.53</td>
<td>4.31 ± 0.55</td>
<td>4.50 ± 0.73</td>
</tr>
<tr>
<td>Controls</td>
<td>3.36 ± 0.81</td>
<td>3.33 ± 0.81</td>
<td>3.58 ± 0.84</td>
<td>3.59 ± 0.92</td>
<td>3.52 ± 0.88</td>
</tr>
<tr>
<td><strong>Muscle thickness,</strong>#†‡ mm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Athletes</td>
<td>21.9 ± 4.1</td>
<td>24.6 ± 3.8</td>
<td>23.9 ± 4.7</td>
<td>26.1 ± 4.0</td>
<td>27.1 ± 3.9</td>
</tr>
<tr>
<td>Controls</td>
<td>18.2 ± 1.6</td>
<td>19.5 ± 1.8</td>
<td>20.5 ± 2.0</td>
<td>19.7 ± 1.6</td>
<td>18.9 ± 2.2</td>
</tr>
<tr>
<td><strong>Pennation angle,</strong># deg</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Athletes</td>
<td>10.1 ± 1.9</td>
<td>10.3 ± 2.1</td>
<td>9.9 ± 2.0</td>
<td>10.2 ± 1.9</td>
<td>10.9 ± 1.9</td>
</tr>
<tr>
<td>Controls</td>
<td>7.6 ± 0.7</td>
<td>8.2 ± 0.4</td>
<td>9.2 ± 0.7</td>
<td>9.1 ± 0.9</td>
<td>9.1 ± 0.7</td>
</tr>
<tr>
<td><strong>Tendon moment arm,</strong># mm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Athletes</td>
<td>55.2 ± 3.7</td>
<td>55.3 ± 3.7</td>
<td>55.4 ± 3.8</td>
<td>55.4 ± 3.8</td>
<td>55.5 ± 3.9</td>
</tr>
<tr>
<td>Controls</td>
<td>50.6 ± 2.5</td>
<td>50.7 ± 2.5</td>
<td>50.8 ± 2.6</td>
<td>50.9 ± 2.6</td>
<td>50.9 ± 2.7</td>
</tr>
<tr>
<td><strong>Rest length, mm</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Athletes</td>
<td>52.7 ± 4.3</td>
<td>52.2 ± 5.3</td>
<td>52.8 ± 4.3</td>
<td>52.6 ± 4.5</td>
<td>53.1 ± 6.1</td>
</tr>
<tr>
<td>Controls</td>
<td>49.4 ± 4.3</td>
<td>50.6 ± 5.2</td>
<td>49.5 ± 4.4</td>
<td>48.9 ± 4.2</td>
<td>49.4 ± 4.2</td>
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<tr>
<td><strong>Tendon force,</strong># N</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Athletes</td>
<td>5,117 ± 981</td>
<td>5,120 ± 944</td>
<td>4,971 ± 1,184</td>
<td>5,229 ± 1,182</td>
<td>5,690 ± 1,292</td>
</tr>
<tr>
<td>Controls</td>
<td>3,351 ± 566</td>
<td>3,672 ± 822</td>
<td>3,739 ± 434</td>
<td>3,669 ± 506</td>
<td>3,788 ± 371</td>
</tr>
</tbody>
</table>

Values are means ± SD. Muscle strength (MVC) was normalized to body mass. *Significant difference between groups (i.e., intercept; \( P < 0.05 \)), †significant change over time (i.e., slope; \( P < 0.05 \)), and ‡significant group difference in change over time (i.e., slope; \( P < 0.05 \)). †Significant change over time was present only in athletes. Note that differences between groups were tested only for normalized MVC and pennation angle.
DISCUSSION

The present study investigated in vivo the development of knee extensor muscle and tendon properties in 3-mo intervals during 1 yr in adolescent elite volleyball athletes and nonathletes. As main results we found 1) increased fluctuations of muscle strength (and tendon force) and 2) less uniformity in the changes of tendon force and stiffness over time in athletes compared with nonathletes. In consequence, maximum tendon strain demonstrated considerable fluctuations over time with increased average levels and episodically markedly elevated individual levels of strain compared with controls. Therefore our hypotheses were confirmed.

The current investigation demonstrated for the first time that athletic training might disrupt the uniformity of muscle and tendon adaptation during adolescence. We found evidence that the marked fluctuations of muscle strength in athletes were not accompanied by a matched adaptive response of the tendon, as indicated by the lower association and uniformity measures for tendon force and stiffness. In consequence, the tendon strain during maximum contractions demonstrated considerable fluctuations as well. In contrast to controls, the development over time in athletes was characterized by episodes of very high individual levels of strain in the range of 10–12.5%. With regard to the generally accepted strain dependency of tendon failure (26), this implies an increased mechanical demand on the tendon and, thus, a greater challenge for the integrity of the tissue. Average maximum tendon strain over time was significantly greater in athletes compared with controls as well (*P < 0.05). The high prevalence of tendon overuse in adolescent athletes (28) and volleyball players (29) and the consistent reports of a mechanical weakening of the tendon concomitant with tendinopathy (5, 11, 18) give reason to believe that an imbalance in the adaptation of muscle and tendon might increase the risk of tendon injury.

Our regression analysis suggests that the fluctuations of strain were due to the fluctuations of muscle strength rather than tendon stiffness. Considering the lower metabolic rate (27) and vascularization (39) of tendon compared with muscle, it seems possible that muscle adapts at a higher rate to altered mechanical loading. Moreover, it is known that changes in muscle activation can lead to rapid gains in muscle strength.
(14), while changes of tendon properties require morphological and/or structural changes. In the present study, both VL thickness and pennation angle were associated with muscle strength, yet only pennation angle demonstrated significantly greater fluctuations over time in athletes compared with controls. Changes of pennation angle are thought to be indicative of a modulation of the physiological cross-sectional area of a muscle (20) and, thus, its strength capacity. Therefore the architectural remodeling of the muscle might be associated with the observed fluctuations of strength in the adolescent athletes, which, in turn, might have been induced by variations in training volume and content, as has been described previously in adult athletes [see Koutedakis (21) for reviews].

As maturation alone seems to be associated with a uniform adaptation of muscle and tendon (reflected in our data by the greater cosine similarity and lower prediction uncertainties of tendon stiffness by tendon force) and, thus, quite constant levels of maximum strain, the observed imbalanced adaptation in adolescent athletes can be explained by the different temporal dynamics of muscle and tendon in the adaptation to altered mechanical loading and the dissimilar responsiveness to specific mechanical stimuli. Discrepancies between muscle and tendon in the time course of adaptation in response to loading were reported by Kubo and colleagues for the patellar (23) and the Achilles tendons (22), respectively. The studies provided evidence that muscle functional and morphological changes can precede significant changes of tendon mechanical or morphological properties. Moreover, there is convincing evidence that the mechanical stimuli that effectively elicit tissue adaptation differ between muscle and tendon as well, as both high and low loading magnitudes can facilitate muscle strength but only high-magnitude loading facilitates tendon adaptation (1). It has also been observed on the transcriptional level of growth factors in rats (16, 17) and humans (15) that muscle and tendon tissue show differentially graded responses to specific loading regimen, and it has been hypothesized by the authors that this might induce an imbalanced adaptation of muscle and tendon following certain training modes (16). Interestingly, plyometric loading, which is the predominant type of loading in volleyball and, thus, for the athletic group of the present study, has been demonstrated to be an effective stimulus for muscle but not tendon adaptation (25). It has been hypothesized that short strain durations (as in plyometric jumps) could be less effective in triggering the transmission of the external strain to the tendon cells via the viscoelastic extracellular matrix and thus induce a lower biological response compared with other loading regimens featuring greater strain durations (7). Therefore preventive intervention strategies would need to incorporate mechanical stimuli that more effectively increase the tendon loading capacity (i.e., increasing Young’s modulus and/or cross-sectional area). A series of systematic controlled experimental studies (1, 3, 8) provided evidence that such an intervention should include repetitive loading using high-intensity muscle contractions ($\geq 85\%$ MVC; irrespective of contraction type) and long contraction durations ($\sim 3$ s).

Though the present study investigated a cohort at high risk for the development of tendinopathy and the mechanical strain theory is held as the most probable explanation of the underlying injury mechanism (4, 13), the association of the observed nonuniform muscle and tendon adaptation and the resultant high levels of strain with injury risk or tendinopathy remains an assumption and needs further investigation. Moreover, it was not possible to obtain MRI for all participants and measurement sessions, which is strongly suggested for the assessment of tendon cross-sectional area (12), and thus the time course of the development of tendon morphology, total and regional tendon stress, and the material properties of the tendon during adolescence with and without the influence of mechanical loading is still largely unknown. Additionally, the analysis of regional strain distribution might provide further insight into the complex loading pattern of tendons during contractions, though it should be acknowledged that increased total tendon strain, as found in the present study, is associated with increased regional strains as well (9, 36).

In conclusion, the present study provides evidence that athletic (volleyball) training during adolescence is associated with increased fluctuations of the knee extensor strength capacity. The fluctuations of strength were not compensated accordingly by changes of the patellar tendon mechanical properties and result in an increased demand on the tendon (i.e., maximum strain) in athletes compared with controls. Future studies should address the potential of training interventions facilitating tendon adaptation to restore the balance of muscle and tendon development in adolescent athletes.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

F.M. and A.A. conception and design of research; F.M. performed experiments; F.M., A.S., R.M., and A.A. analyzed data; F.M., S.B., and A.A. interpreted results of experiments; F.M., S.B., and A.A. prepared figures; F.M., S.B., and A.A. drafted manuscript; F.M., S.B., and A.A. edited and revised manuscript; F.M., S.B., A.S., R.M., and A.A. approved final version of manuscript.

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