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Adaptations in biceps femoris long-head muscle-tendon mechanics during the Nordic hamstring exercise in response to 9 weeks of training

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Abstract

Background: Prolonged Nordic hamstring exercise (NHE) training reduces hamstring injury risk, but the underlying mechanisms remain unclear. This study examined how NHE training alters biceps femoris long-head (BFlh) muscle−tendon unit (MTU) mechanics during the exercise, focusing on how muscle adaptations influence fascicle and sarcomere lengths during the NHE after training.

Methods: Twelve recreationally active participants completed 9 weeks of supervised NHE training and 3 weeks of detraining. Knee flexor torque was measured using ankle-mounted load cells and estimated from the knee joint moment arm. BFlh fascicle lengths were assessed during the NHE using dual-transducer ultrasound, and MTU length was estimated from joint angles using markerless motion capture. Sarcomere lengths during the NHE were estimated using instantaneous BFlh fascicle length and previously calculated serial sarcomere numbers. Linear mixed-effects models analyzed changes between pre-training, post-training, and post-detraining.

Results: Nine weeks of NHE training increased peak knee flexor torque by 40% (previously reported), enabling 37% greater knee extension ($p = 0.012$) and 4% longer MTU lengths at peak torque during the NHE ($p = 0.001$). BFlh fascicles reached 25% longer lengths during the NHE at peak torque after training ($p < 0.001$), while estimated active sarcomere lengths at peak torque were unchanged ($p = 0.266$). Following 3 weeks of detraining, knee flexor torque decreased by 6% (previously reported) and fascicle lengths at peak torque decreased by 14% ($p < 0.001$), while MTU length ($p = 0.578$) and estimated active sarcomere length ($p = 0.753$) at peak torque during the NHE did not significantly change compared to post-training.

Conclusion: Despite the longer fascicle lengths during the NHE after training, estimated active sarcomere length during the NHE relative to optimal sarcomere length remained similar, consistent with the addition of sarcomeres in series, which may contribute to the protective effects of NHE training.

Keywords: Eccentric exercise; Force−length relationship; Muscle−tendon unit dynamics; Sarcomerogenesis

1. Introduction

Prolonged Nordic hamstring exercise (NHE) training has been demonstrated to reduce the risk of hamstring injuries, with meta-analyses reporting an average effect of a 51% decrease in injury rates when the NHE is incorporated into training programs.[1,2] Hamstring strain injuries predominantly affect the biceps femoris long-head (BFlh) muscle, particularly during the late swing phase of high-speed running when the muscle experiences elevated fiber stress at extended lengths while lengthening.[3−6] The NHE similarly requires the BFlh to generate force while lengthening eccentrically,[7−9] though at slower velocities than during sprinting.[10,11] However, the

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mechanics of the BFlh muscle−tendon unit (MTU) during the NHE are complex and cannot be predicted based solely on the movement.[7–9] Determining the dynamic muscle−tendon interactions in the BFlh, particularly active fascicle strain, is crucial for understanding the potential mechanical stimuli that drive hamstring adaptations to eccentric training.[12] Recent findings indicate that BFlh fascicles undergo less lengthening than the MTU during the NHE.[7–9] This decoupling between fascicle and MTU lengthening suggests that tendon lengthening may contribute substantially to overall MTU lengthening.[13]

During the NHE, fascicle and MTU length changes are decoupled for the first 80%−90% of the movement, with tendon lengthening accounting for most of the increase in MTU length during knee extension.[7,9] This decoupling likely reflects the tendon lengthening within the "toe region" of its stress−strain curve,[14] allowing the MTU to lengthen with minimal fascicle lengthening as force in the tendon increases. However, in the last 10%−20% of the NHE, when individuals reach the point where they can no longer generate sufficient knee flexion torque to counteract gravity, fascicles act eccentrically at long lengths, coinciding with increasing force and decreasing muscle activation.[7–9]

Long-term NHE training leads to several neuromuscular adaptations that may alter MTU interactions during exercise. Increases in strength, through hypertrophy[15–19] or greater activation[20,21] allow the MTU to generate force and sustain the NHE movement over a larger range (i.e., greater knee extension). The simultaneous requirement to produce greater forces with greater MTU lengths requires either muscle fascicles to lengthen further or for the tendinous tissue to undergo more lengthening under the greater tension. However, structural adaptations within these tissues, such as longer fascicle lengths or changes in tendon compliance, might also change MTU interactions.

NHE training has been shown to increase passive fascicle lengths,[22–26] with serial sarcomere addition observed alongside fascicle lengthening following long-term training.[22] However, some studies have not observed these adaptations,[18,27] with the lack of strength gains suggesting that training intensity may have been insufficient to elicit serial sarcomere addition. In theory, serial sarcomerogenesis allows the muscle fascicles to reach longer lengths without excessive sarcomere lengths, as the optimal fascicle length increases.[28–31] By maintaining actin-myosin overlap at longer muscle fascicle lengths, sarcomerogenesis would theoretically preserve the force-generating capacity of the BFlh during the NHE.[28–31] Understanding whether peak torque after NHE training occurs at longer sarcomere lengths or whether the BFlh muscle maintains similar sarcomere lengths despite reaching longer fascicle lengths at peak torque during the NHE could provide insight into adaptations affecting contractile and tendinous tissue adaptations.[32,33]

This study aimed to examine changes in muscle−tendon interaction during the NHE after 9 weeks of training and 3 weeks of detraining. Based on previous findings of increased passive fascicle length following NHE training,[22] we hypothesized that after training, fascicles would reach longer lengths during the NHE, rather than additional lengthening being absorbed by the tendinous tissue. Furthermore, we expected that despite these longer fascicle lengths, estimated sarcomere lengths at peak torque would remain similar post-training due to the addition of sarcomeres in series.[22] After 3 weeks of detraining, we hypothesized that fascicle length at peak torque during the NHE would decrease, but MTU length would remain unchanged, as strength would be maintained with a brief detraining period.

2. Methods

2.1. Study design and sample size calculation

In a longitudinal follow-up intervention design with the same participant cohort as our previous study,[22] we examined the effect of a 9-week NHE training program, followed by a 3-week detraining period, on BFlh MTU mechanics. Participants attended pre-training, post-training, and post-detraining sessions where BFlh MTU length, fascicle length, and force were measured during the NHE. Data collection occurred concurrently with our prior study, allowing the estimation of sarcomere length during the NHE *in vivo* using previously obtained passive sarcomere and passive fascicle length measures. Participants completed the NHE training program described in our prior work.[22] The sample size for the present study was estimated based on the calculations from the prior study, which included the power requirements needed here. A minimum sample size of 10 participants was determined to achieve a statistical power of 95% in detecting an effect size of 0.7 for MTU and fascicle length at peak torque during the NHE, using 3 repeated measures and a significance level of $\alpha = 0.01$.

2.2. Participants

We recruited 12 recreationally active participants as described for the previous study,[22] including 5 males (age = 27.6 ± 4.1 years, height = 1.87 ± 0.07 m, mass = 82.4 ± 7.5 kg, mean ± SD) and 7 females (age = 26.5 ± 3.6 years, height = 1.70 ± 0.04 m, mass = 64.9 ± 9.6 kg). We excluded participants if they had any lower limb injuries within the past 18 months or if they had engaged in NHE training in the previous 6 months. Written informed consent was obtained from each participant before participating. The research protocol received approval from the Stanford University Institutional Review Board (approval No. SQL 97942) and was ratified by The University of Queensland Ethics Committee (approval No. 2022/HE001616).

2.3. NHE

For the NHE, participants kneeled on a padded board with their ankles secured and arms raised (Fig. 1). Participants gradually leaned forward while attempting to maintain a consistent hip angle and controlled knee extension at approximately 18° per second, guided by a metronome set at 60 beats per minute. Upon reaching the floor, participants used their upper body to



Fig. 1. Experimental setup for measuring BFlh fascicle length changes during the NHE using a dual ultrasound probe configuration. Two ultrasound probes were placed inside a 3D-printed ultrasound mold, with elastic bandages used to secure the mold and maintain probe position throughout the exercise. Participants kneeled on a padded platform with the ankles secured via straps connected to load cells. The NHE involves the participant gradually lowering their upper body towards the ground from kneeling while resisting the descent with the hamstrings and other knee flexors. BFlh = biceps femoris long-head; NHE = Nordic hamstring exercise.

return to the initial position. The NHE protocol was evaluated using the Assessing Nordic Hamstring Exercise Quality tool (ANHEQ)[34] and achieved a score of 8/13, classified as "good" quality.

Knee flexor strength was measured at pre-training, post-training, and post-detraining as previously described.[22] Before strength testing, participants performed 2 warm-up sets of 4 repetitions at 50% and 75% of their maximum perceived effort, respectively. After a 3-min rest period, participants completed 4 maximal single NHE repetitions, each separated by a 2-min rest interval. For the maximal repetitions, participants were instructed to descend as low as possible with controlled knee extension at approximately 18° per second, controlled by a metronome. This speed ensured a time under tension of about 5 s per repetition, which was dependent on their active range of motion. Participants were instructed to maintain a constant hip configuration throughout the movement. Eccentric knee flexor strength during the NHE was measured using 2 uni-axial load cells (10 Hz sampling frequency; HT Sensor Technology, Xi'an, China) attached to the ankles via straps. Knee flexor torque was calculated by multiplying the peak force measured by the load cells by the perpendicular distance from the line of action of force (at the center of the ankle strap) to the axis of rotation at the knee, which was approximated by the lateral femoral condyle located via palpation.

2.4. MTU length

BFlh MTU length during the NHE was estimated using the angle of the hip, knee, and ankle as inputs into the regression equations of Hawkins and Hull.[35] NHE 2D motion capture was recorded using an iOS device (iPod Touch; Apple Inc., Cupertino, CA, USA) mounted on a tripod, positioned perpendicular to the subject at a 60 Hz sampling frequency. Pose estimation was performed using the MediaPipe Pose framework (Version 0.10.14; Google LLC, Mountain View, CA, USA), which uses algorithms to automatically detect 2D body landmarks in each image frame. MediaPipe has been validated against marker-based motion capture systems for joint angle measurements with good accuracy.[36] The landmarks from MediaPipe's pose model that were tracked included the right shoulder, hip, knee, ankle, and foot index. Joint angles were calculated from vectors formed between consecutive landmarks: the hip angle was computed from the angle between vectors connecting the shoulder to hip and hip to knee; the knee angle from vectors connecting the hip to knee and knee to ankle; and the ankle angle from vectors connecting the knee to ankle and ankle to foot index. These joint angles were input into the Hawkins and Hull regression equations[35] to calculate normalized BFlh MTU lengths. Absolute BFlh MTU lengths were then derived by multiplying these normalized lengths by thigh length, which was measured via palpation from the greater trochanter to the lateral femoral epicondyle for each participant.

2.5. Active fascicle length

BFlh fascicle lengths during the NHE were recorded using two 6-cm B-mode ultrasound probes (80 Hz sampling frequency; ArtUS EXT-1H beamformers and LV8-5 N60-A2 transducers; Telemed, Vilnius, Lithuania).[7,37] The 2 ultrasound probes were rigidly connected using a custom-made holder with a 2.2-cm gap between them. This configuration extended the total field of view to 14.2 cm, allowing imaging

of the proximal and distal attachments of the BFlh muscle fascicles (Fig. 2).[7] Probe placement was guided by reference landmarks from 3D ultrasound imaging conducted in the same session. These landmarks were positioned along the BFlh muscle, covering 20%−80% of the distance between the fibular head and the ischial tuberosity.[22] Using these reference marks, the ultrasound probes were positioned where fascicles were most clearly visible throughout their trajectory. The ultrasound probes were oriented to ensure clear visualization of both the superficial and deep aponeuroses to ensure the fascicle of interest was in plane. The exact location of each probe was documented by measuring the distance from both the top and bottom of the probe holder to the most proximal and distal ultrasound reference landmarks. This improved the replication of probe placement in subsequent sessions. Although imaging the identical fascicle plane across sessions cannot be guaranteed, consistent probe placement and orientation to visualize both aponeuroses minimized off-plane imaging errors. Once an optimal image was achieved, self-adhesive elastic bandages securely fastened the probes throughout the exercise.

To synchronize recordings across data streams, we used a custom-made device, built with an Arduino Uno board (Arduino LLC, Monza, Italy). An external trigger generated synchronization pulses to start and stop ultrasound and force recordings while simultaneously activating a light emitting diode (LED) on the side of the NHE device that enabled synchronization with motion capture. During post-processing, the motion capture recordings were aligned to the first frame in which the LED turned on and the last frame before it turned off. This approach enabled the synchronization of all collected signals, including ultrasound, force, and motion capture data.

BFlh fascicle length during the NHE was analyzed using UltraTrack software.[38] Ultrasound images were merged (Fig. 2), accounting for the 2.2-cm gap between the probes. Then, the semi-automated algorithm that facilitated the tracking of muscle fascicle trajectories, identified by the connective tissue that binds the muscle fascicles (i.e., perimysium), and aponeurosis positions was used to calculate instantaneous fascicle lengths. Manual corrections were applied for instances where fascicle drift or excessive muscle movement hindered accurate tracking.[38]

2.6. Active sarcomere length

In our previous study with the same participants, passive sarcomere lengths were measured *in vivo* using 2nd harmonic generation microendoscopy and combined with ultrasound-derived fascicle lengths to calculate serial sarcomere number for the central and distal regions of the BFlh.[22] Specifically, the fascicle lengths and estimated sarcomere lengths reported in this manuscript are active lengths during the NHE. In contrast, our previous measurements of sarcomere and fascicle length were passive lengths measured at rest.[22] In the present study, we combined the mean serial sarcomere number obtained from our previous work with the same participants[22] with the instantaneous fascicle length (see Section 2.5). We then estimated active sarcomere length during the NHE using the equation: $SL = \frac{FL}{SSN}$, where SL represents the active sarcomere length during the NHE, FL is the instantaneous fascicle length obtained from ultrasound, and SSN is the mean serial sarcomere number, derived from our previous research using the same participants.[22] Although passive sarcomere length was measured directly using microendoscopy in our previous study,[22] serial sarcomere number was calculated using fascicle lengths measured by ultrasound, which may have been overestimated[39,40] and could therefore influence the estimates of active fascicle and sarcomere length in the present study.

2.7. Data processing and analysis

From the 4 recorded trials, the NHE trial with the highest recorded peak force was used for analysis. Subsequently, knee flexor torque, fascicle length, and MTU length during the NHE were computed from this trial following up-sampling of all signals to the ultrasound sampling rate. The start of the NHE was identified by the initial increase in torque 2% above resting levels. The end of the NHE occurred at peak torque, which was measured at the end of the eccentric phase, before participants reset for the next repetition. The end of the NHE was further evaluated to account for loss of control during the final portion of the exercise, which occurs in untrained individuals.[41] Given that approximately 50% of the eccentric phase during the NHE is performed in a controlled manner (∼until 45° knee flexion), after which hamstring activation typically decreases and angular velocity increases,[7–9,41,42] a threshold was established to identify this transition. The mean and standard deviation (SD) of knee angular velocity from the start of the NHE until 45° knee flexion were calculated. If the knee angular velocity after 45° was more than 1 SD below this mean value, indicating excessive negative acceleration and

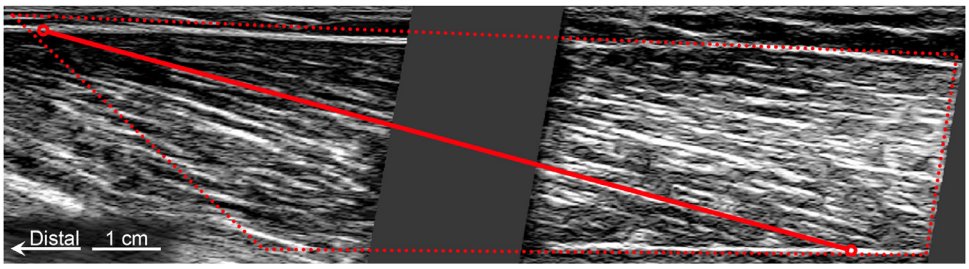


Fig. 2. Representative merged ultrasound image from the dual probe setup, with the tracked fascicle highlighted in red and the region of interest outlined with a red dotted line. The ultrasound probes were positioned with a 2.2-cm gap between them to provide a field of view of 14.2 cm.

loss of eccentric control, the endpoint of the NHE was adjusted to the point where this threshold was first exceeded.

To investigate the effect of NHE training and detraining on BFlh MTU mechanics, discrete metrics were extracted from the time-series data. These discrete measurements included MTU length, fascicle length, estimated sarcomere length, and knee flexor torque at the point of peak torque during the NHE before training, post-training, and after detraining. These discrete measures reflect corresponding changes in the MTU mechanics of the BFlh muscle, including adaptations in the force−length relationship and passive properties like tendon stiffness, and how these training-induced adaptations are induced and regress over time.

To differentiate the contributions of the contractile and tendinous components within the BFlh, we examined how fascicle length changed at given MTU lengths across time. Specifically, we compared fascicle lengths and MTU lengths at 50%, 75%, and 100% of the pre-training MTU lengths across time points. The pre-training MTU length was defined as the change in MTU length from the start to the end of the NHE, with corresponding values at 50%, 75%, and 100% used as reference points for comparison across time points. At post-training and detraining, fascicle lengths were assessed at the same absolute MTU lengths as pre-training to determine whether training led to longer fascicles at equivalent MTU lengths. These specific lengths were chosen because they occur after the initial shortening of the fascicles at the onset of the NHE,[7–9] allowing an evaluation of adaptations in the lengthening phase.

Additionally, we calculated the relationship between MTU length and fascicle length by calculating the slope (m) using the equation: $m = \frac{FL_{100\%} - FL_{50\%}}{MTU_{100\%} - MTU_{50\%}}$, where $FL_{50\%}$ is fascicle length at 50% of pre-training MTU length, and $FL_{100\%}$ is fascicle length at the MTU length at peak torque for each time point (pre-training, post-training, or detraining). $MTU_{50\%}$ is 50% of pre-training MTU length, and $MTU_{100\%}$ is the MTU length at peak torque for each time point. This slope shows how changes in MTU length relate to fascicle length, providing insight into the relative contributions of contractile versus elastic elements.

The mean and SD of time series data displaying the changes in BFlh fascicle length, MTU length, and knee flexor torque throughout the NHE were calculated for visual representation.

2.8. Statistical analysis

Linear mixed effects models (LMMs) were used to assess the effects of NHE training and detraining on MTU length, fascicle length, estimated sarcomere length, and eccentric knee flexor torque at peak torque. LMMs were also used to analyze the effect of training and detraining on fascicle length at specific MTU lengths, as well as the slope of the relationship between MTU length and fascicle length. By accommodating repeated measures and individual variability, LMMs provide a robust method for understanding these effects.[43,44] In all models, participants were included as a random effect, while "Time" was treated as a fixed effect.

In the LMMs, the restricted maximum likelihood estimation was used for model fitting. Satterthwaite's method was used to determine p values for fixed effects,[45] presented in Type III Analysis of Variance tables. Effect sizes were reported as partial *eta* squared (η_p^2), with interpretations of 0.01, 0.06, and 0.14 for small, medium, and large effects, respectively.[46] *Post hoc* pairwise comparisons were conducted to identify significant main effects, with adjustments made using Tukey's correction. Residual normality was assessed using the Shapiro−Wilk test, with outliers identified and removed through Cook's distance method (threshold: 2.5 times the SD). Analysis was performed using RStudio (Version 2023.6.1.524; Posit Software, PBC, Boston, MA, USA), with significance at $\alpha < 0.05$. The following R packages were used: lme4 (Version 1.1.34), lmerTest (Version 3.1.3), emmeans (Version 1.8.7), and sjstats (Version 0.18.2).

3. Results

3.1. Effects of training on muscle−tendon interaction

Before training, BFlh fascicles during the NHE initially shortened, then were isometric for approximately 1 cm of MTU lengthening, and then lengthened as torque neared its peak in the final portion of the movement (Figs. 3E and 4). This pattern of fascicle length during the NHE was similar after 9 weeks of training, but fascicles were at longer average lengths throughout the movement ($\eta_p^2 = 0.63$, $p < 0.001$) and reached significantly greater lengths at peak torque (pre-training: 6.99 ± 1.44 cm; post-training: 8.74 ± 1.08 cm; $\eta_p^2 = 0.71$, $p < 0.001$). With increased torque capacity (pre-training: 1.35 ± 0.47 Nm/kg; post-training: 2.13 ± 0.40 Nm/kg; previously reported;[22] Fig. 3A), participants reached greater knee extension (pre-training: $37.04^\circ \pm 13.24^\circ$; post-training: $23.27^\circ \pm 13.45^\circ$; $\eta_p^2 = 0.33$, $p = 0.012$; Fig. 3B), resulting in longer MTU lengths at peak torque (pre-training: 37.71 ± 3.12 cm; post-training: $39.16^\circ \pm 2.85$ cm; $\eta_p^2 = 0.45$, $p = 0.001$; Fig. 3C). Despite the increased fascicle length during the NHE, estimated sarcomere lengths at peak torque did not change significantly (pre-training: 2.48 ± 0.66 μm; post-training: 2.41 ± 0.52 μm; $\eta_p^2 = 0.24$, $p = 0.266$; Fig. 3F). Following detraining, knee flexor torque (detraining: 1.94 ± 0.52 Nm/kg; previously reported[22]) and fascicle length at peak torque during the NHE decreased significantly (detraining: 7.52 ± 1.21 cm; $p < 0.001$), while MTU length (detraining: 38.81 ± 3.02 cm; $p = 0.578$) and estimated sarcomere length (detraining: 2.36 ± 0.52 μm; $p = 0.753$) remained unchanged compared to post-training.

3.2. Effect of training on the contribution of contractile and elastic elements

Fascicle length was significantly longer after NHE training for a given MTU length. This was evident when comparing fascicle lengths before and after training at the same MTU lengths, with significant increases at 50% ($p = 0.002$), 75% ($p < 0.001$), and 100% ($p < 0.001$) of the pre-training MTU length. The slope of the MTU−fascicle length did not change significantly

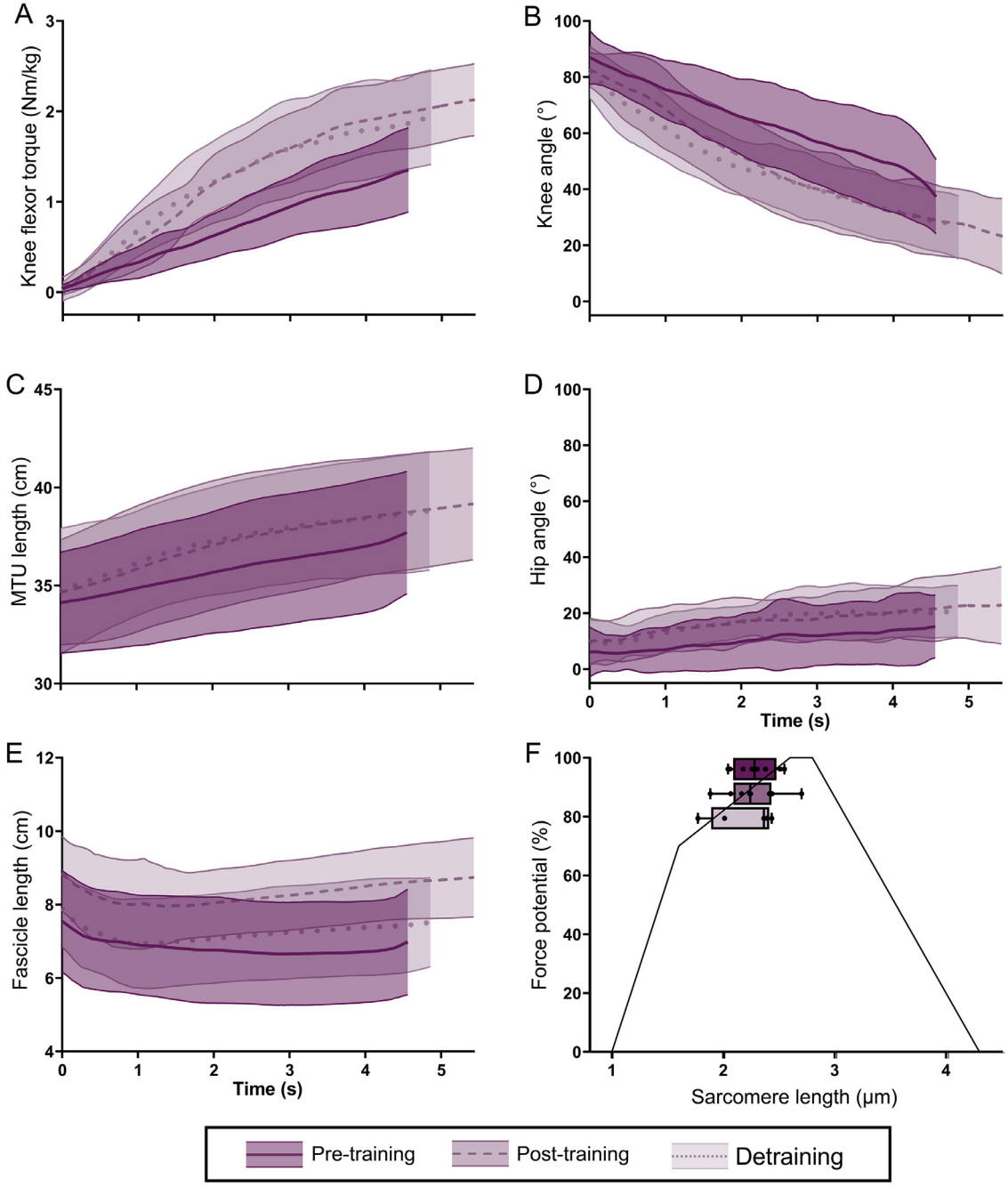


Fig. 3. Adaptations in BFlh mechanics during the NHE across training and detraining phases. Time-series data show measurements from movement onset to peak knee flexion torque for pre-training (solid purple line), post-training (dashed line), and detraining (dotted line). Lines represent mean values; shaded areas indicate ±1SD. (A) Knee flexor torque increased with training and decreased following detraining but remained above pre-training levels (previously reported[22]). (B) Knee angle at peak knee flexion torque during NHE decreased significantly after training ($F_{2,22} = 5$, $p = 0.012$, $\eta_p^2 = 0.33$) and remained unchanged following detraining ($p = 0.769$). (C) MTU length at peak torque increased after training ($F_{2,22} = 9$, $p = 0.001$, $\eta_p^2 = 0.45$) and was maintained during detraining ($p = 0.578$). (D) Hip angle at peak torque showed no significant changes across training or detraining ($F_{2,22} = 2$, $p = 0.207$, $\eta_p^2 = 0.13$). (E) Fascicle length at peak knee flexion torque was significantly longer post-training ($F_{2,22} = 27$, $p < 0.001$, $\eta_p^2 = 0.71$) and decreased after detraining ($p < 0.001$). (F) Estimated sarcomere length at peak torque during the NHE, plotted on the theoretical sarcomere force−length relationship (adapted from Burkholder and Lieber[62]). Estimated sarcomere length at peak torque showed no significant changes post-training or following detraining ($F_{2,10} = 2$, $p = 0.266$, $\eta_p^2 = 0.24$). Box plots depict the interquartile range (boxes), minimum and maximum values (whiskers), and individual participant data (dots). The main effects summarized in brackets include *F*-statistic values, degrees of freedom, *p* values ($p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$), and effect size (η_p^2) categorized as small (0.01), medium (0.06), and large (0.14). BFlh = biceps femoris long-head; MTU = muscle−tendon unit; NHE = Nordic hamstring exercise.

post-training ($p = 0.072$; Fig. 4). Following detraining, fascicle lengths decreased significantly at 50% ($p = 0.015$), 75% ($p = 0.008$), and 100% ($p = 0.009$) of the pre-training MTU length, demonstrating the reversibility of these adaptations. However, the slope of the MTU−fascicle length relationship remained unchanged after detraining ($p = 0.314$; Fig. 4).

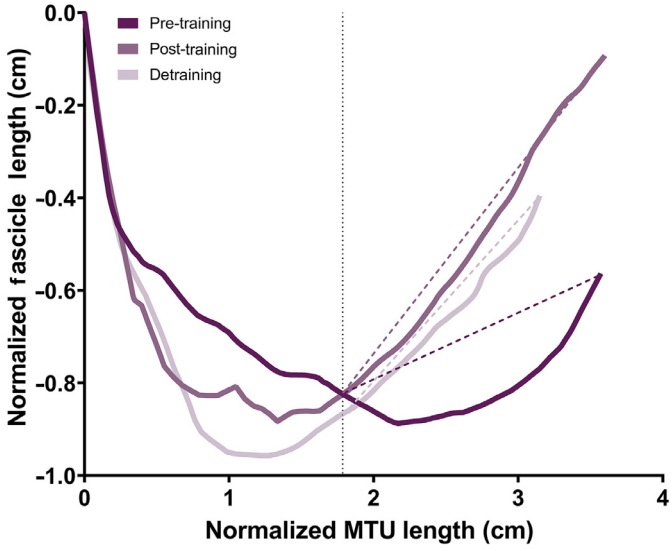


Fig. 4. The relationship between normalized change in MTU length and normalized change in fascicle length during the NHE across pre-training, post-training, and detraining phases. The continuous lines represent the group mean curves for each phase, with the x-axis showing the normalized change in MTU length and the y-axis showing the corresponding normalized change in fascicle length. The vertical dotted line indicates where the beginning of the slope was measured (50% of pre-training MTU length), while the dashed lines represent the average slopes for each training phase. NHE training did not significantly change the average slope of the MTU−fascicle length relationship ($F_{2,22} = 3$, $p = 0.072$, $\eta_p^2 = 0.21$). BFlh = biceps femoris long-head; MTU = muscle−tendon unit; NHE = Nordic hamstring exercise.

4. Discussion

This study demonstrates that the known increases in peak knee flexor torque and passive fascicle lengths after 9 weeks of NHE training[22] corresponded with BFlh fascicles reaching longer lengths at peak torque during the NHE. This shift in fascicle length during the exercise may reflect an increase in optimum fascicle length, potentially via serial sarcomerogenesis, thereby enabling sarcomeres to remain on the ascending limb of the force−length curve and near optimal length during the NHE.

4.1. Muscle−tendon mechanics adaptations during the NHE following training and detraining

Following 9 weeks of NHE training, peak knee flexor torque increased by 40%,[22] allowing individuals to reach 37% greater knee extension during the exercise. Consequently, BFlh MTU lengths were 4% longer at peak torque. Fascicle lengths during the NHE were also 25% longer after training. Throughout the NHE, BFlh fascicles initially shortened, were briefly isometric for about 1 cm of MTU lengthening before lengthening near peak torque. After training, fascicles followed these same mechanics but were consistently longer throughout the movement. These longer fascicle lengths during the NHE likely reflect a combination of increased knee extension and the increase in passive fascicle length observed in our earlier work.[22] Although some studies have not observed passive fascicle lengthening with NHE training,[18,27] and increases in passive fascicle length do not always translate to longer active lengths,[47] the results of the present study are consistent with fascicles reaching longer lengths during the NHE after training.

We provide the 1st estimates of sarcomere lengths in active muscle during the NHE by combining fascicle length measurements during the exercise with serial sarcomere numbers from the same participants. While increased passive sarcomere lengths have been reported after 3 weeks of NHE training,[23] active sarcomere or fascicle length during the exercise itself was not assessed. The sarcomerogenesis hypothesis proposes that muscles adapt to maintain sarcomeres within their optimal operating range when repeatedly exposed to mechanical stimuli at long muscle lengths.[28,29] Given the longer passive sarcomere lengths observed after 3 weeks of NHE training,[23] it is plausible that sarcomeres may transiently reach the descending limb of the force−length curve during active lengthening in the NHE. This transient overstretching could provide the mechanical stimulus for the subsequent addition of sarcomeres in series observed after 9 weeks of training.[22] In the current study, we found that fascicle lengths were consistently longer throughout the NHE after training, yet estimated sarcomere lengths at peak torque remained unchanged. This result is consistent with an increased optimal fascicle length, which could be explained by the previously reported serial sarcomerogenesis.[22] This structural adaptation would be expected to allow sarcomeres to generate force on the ascending limb of the force−length curve across a greater range of motion, reaching near-optimal lengths at peak torque.[28−31] Therefore, BFlh fascicles were able to maintain higher force potential at longer lengths.

The decoupling between MTU and fascicle lengthening during the NHE highlights the potential influence of passive tissue properties on the distribution of lengthening within the MTU. Although changes in tendon stiffness could affect this distribution, tendon adaptations typically occur over a longer time course than muscle adaptations.[48,49] Early changes in passive tissue properties may have occurred, but were insufficient to alter the MTU−fascicle length relationship within the 9-week training period. This is consistent with the limited evidence of tendon or aponeurosis hypertrophy observed following 10 weeks of hamstring training, despite substantial muscle hypertrophy.[16] More prolonged training may be required before tendon adaptations become large enough to measurably influence MTU mechanics during the NHE.

After detraining, strength decreased by 6% and BFlh muscle fascicle lengths at peak torque decreased by 14%, whereas MTU length and estimated sarcomere length at peak torque were maintained. Fascicle lengths were also shorter for a given MTU length following detraining. The reduction in fascicle length at peak torque may reflect a loss of sarcomeres in series, consistent with reductions in passive fascicle lengths observed after detraining.[22,24,50,51] The maintenance of MTU length at peak torque despite shorter fascicles suggests that changes in passive tissue properties may have occurred. These changes, such as altered stiffness or compliance of elastic

tissues,[52–54] may provide the necessary buffering to keep sarcomeres within their optimal range during the NHE after detraining.

4.2. Considerations for hamstring injury prevention strategies

Following 9 weeks of NHE training, a shift in the torque–length relationship during the NHE was observed, with BFlh fascicles reaching longer lengths at peak torque while estimated sarcomere lengths at peak torque remained unchanged. These findings build on our previous passive measurements in the same participants,[22] suggesting that increases in fascicle length through serial sarcomerogenesis underlie adaptations in *in vivo* MTU mechanics during the NHE. These adaptations suggest that fascicles may lengthen further without increasing the lengthening of individual sarcomeres during the NHE, consistent with how the sarcomerogenesis hypothesis influences the sarcomere force–length relationship.[28–31] After training, the increased fascicle length does not alter the lengthening behavior during the NHE. Rather, BFlh fascicles reached longer lengths likely due to the increased passive length.[22] While the NHE is a slow, controlled movement and does not mimic the rapid fascicle and MTU length change seen during high-speed running,[3–6,55] increases in strength, through hypertrophy[15–19] and potentially neural adaptations (e.g., enhanced motor unit recruitment),[20,21] allow the MTU to generate higher forces. This increased strength, combined with increased serial sarcomere number, likely enables BFlh fascicles to reach longer lengths without compromising force production.[56] Although the precise injury etiology during high-speed running remains unclear,[57–61] the adaptations induced by NHE training may enhance protection against injury. By conserving sarcomeres within their optimal length range,[62] despite longer fascicle lengths, the hamstrings may be able to generate high forces when exposed to the greater and faster MTU lengthening experienced during high-speed running.[3–6,55] This mechanism may partly explain the effectiveness of NHE training in reducing hamstring injury risk.[1,2]

4.3. Limitations

This study has several limitations that suggest directions for future research. The absence of a control group limits our ability to isolate the effects of training and detraining from other factors, such as measurement error. Additionally, because this study was a planned follow-up using the same participant cohort as our previous work,[22] the sample size was determined by earlier power calculations based on fascicle length. This may have limited our ability to detect statistically significant effects for some variables.

We estimated active sarcomere length during the NHE by combining active fascicle lengths measured with ultrasound and mean serial sarcomere numbers calculated from passive measurements in our previous study.[22] Although active sarcomere length measurements have been achieved in live animals,[63,64] the magnitude of muscle length change during the NHE makes direct *in vivo* imaging of active sarcomere length infeasible in humans. While fascicle length measurement with ultrasound has inherent limitations,[65] using an analogous ultrasound imaging approach for both passive and active measures maintains internal validity. Furthermore, fascicle length changes measured with ultrasound at different joint angles have been correlated to *in vivo* sarcomere length changes measured with microendoscopy.[66] However, because the serial sarcomere number was derived from ultrasound-based fascicle length measurements,[22] there is potential for length overestimation,[39,40] which may influence the values of the estimated active sarcomere lengths. We also recognize that sarcomere lengths are nonuniform within the muscle and that serial sarcomere number varies between regions due to differences in fascicle length.[23,66] Nevertheless, combining passive and active ultrasound measures in the same participants provides the best available estimation of active sarcomere length changes with current technology.

According to the ANHEQ evaluation criteria,[34] our protocol achieved a total score of 8/13, corresponding to a "good" rating. The study was conducted with rigid fixation at the heels, increased kneeling height to enable full knee extension, and real-time feedback on the quality of NHE repetitions, with all sessions supervised by the researcher (MHA) to ensure consistent execution and high compliance. However, the protocol could have been strengthened by including a separate familiarization session, optimizing patellar glide, extending inter-set rest from 2 min to 3 min, and incorporating individualized exercise progression rather than a uniform periodized program. Implementing these modifications to achieve a higher ANHEQ score may result in larger magnitudes of adaptation than observed in this study, which should be considered when interpreting our findings. Additionally, as our protocol was performed with the hips in a neutral position, future studies should investigate muscle–tendon adaptations and the resulting mechanics when the NHE is executed across different hip flexion angles.[7,51,67,68]

We used regression equations to estimate BFlh MTU length,[35] but did not calculate BFlh muscle force, as our experimental setup would have required numerous assumptions for an inverse dynamics analysis based on 2D joint kinematics and external torque estimations.

We did not examine adaptations to the MTU mechanics of the BFlh muscle during the initial weeks of training, only assessing pre-training, post-training, and after detraining. This leaves a gap in understanding early training adaptations, where previous studies have shown significant passive sarcomere and fascicle length changes.[23]

Although our findings offer insights into adaptations in BFlh MTU mechanics from NHE training and detraining, the direct link between these changes and injury risk needs further investigation. Caution should be taken when generalizing these results to high-speed activities, because the NHE is a slow, controlled movement that does not replicate the rapid muscle lengthening seen during high-speed running.[3–6,55] Addressing these limitations could provide a deeper understanding of hamstring adaptations and their effect on injury mitigation.

5. Conclusion

Our results indicate that 9 weeks of NHE training allows the BFlh fascicles to reach longer lengths during the NHE. Together with previous results suggesting that serial sarcomerogenesis accompanies the increase in fascicle length, these adaptations appear to allow fascicles to generate force at greater lengths while maintaining estimated active sarcomere lengths near optimal. By enhancing force production capacity at longer muscle lengths, these mechanical adaptations may contribute to the protective effects of NHE training against hamstring injury.

Authors' contributions

MHA was responsible for data collection and performed the data analysis; APS and RDG were responsible for data collection. All authors participated in the conception and design of the study, the interpretation of results, and manuscript writing. All authors have read and approved the final version of the manuscript, and agree with the order of presentation of the authors.

Declaration of competing interest

The authors declare that they have no competing interests.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used Chat Generative Pre-Trained Transformer (ChatGPT; OpenAI, San Francisco, CA, USA) to enhance readability and language, aiding in formulating and structuring content. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Data availability

The data that support the findings of this study are openly available in the UQ eSpace at Andrews M, Pai S A, Gurchiek R, et al. Adaptations in hamstring muscle-tendon mechanics publication dataset. The University of Queensland; 2026.10.48610/d5d2607.

Supplementary materials

Supplementary materials associated with this article can be found in the online version at doi:10.1016/j.jshs.2026.101134.

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