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# Biceps femoris long-head motor unit discharge rates and recruitment thresholds vary across 9 weeks of eccentric training

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**Abstract**

*Background*: Neural adaptations play a key role in early strength gains from Nordic hamstring exercise (NHE) training, while architectural adaptations also contribute over time. The specific neural adaptations in biceps femoris long-head (BFlh) motor unit firing properties remain unexplored. This study aimed to determine changes in BFlh motor unit discharge rates, recruitment, and de-recruitment thresholds during submaximal isometric contractions after 3 and 9 weeks of NHE training.

*Methods*: Nineteen recreationally active male participants completed a 9-week NHE training program with assessments at pre-training, 3 weeks, and post-training. Motor units were decomposed from high-density surface electromyography signals recorded during submaximal isometric knee flexion contractions. Motor units were tracked between time points by matching action potential waveforms. Changes in discharge rate, recruitment threshold, and de-recruitment threshold of matched units were compared across sessions using linear mixed-effects models.

*Results*: NHE training significantly increased knee flexor strength by 6% at Week 3 ($p = 0.015$) and 17% at post-training ($p < 0.001$). Motor unit discharge rate was increased by 6% after 3 weeks ($p = 0.015$), but this was no longer elevated after 9 weeks of training ($p = 0.365$). The knee flexion torque at which motor units were recruited increased by 12% after 3 weeks ($p < 0.001$) and by 16% at post-training ($p < 0.001$). The torque at which motor units were de-recruited showed no significant change after 3 weeks ($p = 0.515$) but increased by 12% at post-training ($p = 0.006$).

*Conclusion*: NHE training increased motor unit discharge rate and recruitment threshold after 3 weeks, indicating early neural adaptations. After 9 weeks of training, discharge rate adaptations plateaued, while motor units were both recruited and de-recruited at higher torque levels. These findings are consistent with a shift toward structural adaptations contributing to continued strength improvement.

**Keywords:** Hamstrings; Neural adaptations; Nordic hamstring exercise; High-density electromyography

## 1. Introduction

Nordic hamstring exercise (NHE) training is one of the most effective strategies for reducing the risk of hamstring strain injury, with meta-analyses reporting up to 51% reductions in injury incidence when adherence is high.[1,2] Much of this protective effect has been attributed to increases in strength through structural adaptations in the biceps femoris long-head (BFlh), including increases in fascicle length and muscle hypertrophy.[3–12] Despite these well-established architectural adaptations to NHE training, neural adaptations in the hamstrings have not been directly examined. While cross-sectional studies have investigated activation patterns[13–16] and motor unit recruitment strategies in the hamstrings,[17,18] the effects of training on motor unit firing behavior in the hamstrings remain unknown. This represents a significant knowledge gap because motor unit mechanisms appear to predominate during the initial phases of strength increases.[19,20]

A recent meta-analysis identified motor unit discharge rate and recruitment threshold as firing properties that are likely to adapt with resistance training, although reported changes are

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inconsistent.[21] Several studies have observed increases in motor unit discharge rate within the 1st weeks of training,[22–26] with further increases reported after longer training durations.[27] However, other investigations have found no change in discharge rate following short-term[28] and long-term interventions.[29–32] Collectively, these findings suggest that while early increases in discharge rate are possible, they may not be sustained as training progresses.

In contrast, recruitment threshold responses are less predictable. Some studies report both decreases[25,33] and increases,[26] while others report no significant change.[32] This variability likely reflects differences in training protocols, muscles studied, and participant characteristics. De-recruitment thresholds, which tend to exhibit a positive association with recruitment thresholds,[34,35] would be expected to adapt similarly to recruitment thresholds with training. Taken together, these findings suggest that motor unit discharge rate shows early but often transient changes, while recruitment and de-recruitment thresholds exhibit more variable and inconsistent responses.[21,36] With prolonged training, these neural adaptations may diminish as structural changes, such as hypertrophy, become the dominant contributors to increased force capacity.[19,20] Whether such a temporal shift from neural to structural mechanisms occurs in the hamstrings following eccentric training has not been investigated.[37]

Recent advances in high-density surface electromyography (HD-EMG) and signal decomposition algorithms enable reliable identification and tracking of individual motor units during submaximal isometric contractions.[38,39] This technological progress now enables detailed quantification of motor unit recruitment thresholds and discharge rates on the same motor units before and after interventions.[21]

This study aimed to determine the effects of NHE training on BFlh motor unit discharge rate, recruitment threshold, and decruitment threshold during submaximal isometric contractions after 3 and 9 weeks of training. We hypothesized that the recruitment threshold and discharge rate would increase after 3 weeks, reflecting increased motor unit excitability and neural drive in response to early training demands. By 9 weeks, we expected motor unit discharge rates to return toward baseline, consistent with a shift from neural to structural mechanisms as the primary contributors to strength gains, with muscle fiber adaptations becoming more dominant.[19,20] We further hypothesized that both recruitment and de-recruitment thresholds would increase by 9 weeks, reflecting enhanced motor unit force capacity that would reduce the duration of motor unit activation required at given force levels.

## 2. Methods

### 2.1. Study design

A longitudinal within-subject design was used to assess the effects of a 9-week NHE training program[3] on BFlh motor unit discharge rate, recruitment threshold, and de-recruitment threshold. *Prior to* the intervention, baseline HD-EMG recordings were collected during maximal and submaximal isometric knee flexion contractions. These measures were repeated after 3 weeks of training and at the end of the 9-week training program.

### 2.2. Sample size calculation

Sample size estimates were based on a previously observed $3.3 \pm 2.5$ (mean ± SD) pulses per second (pps) increase in tibialis anterior discharge rate after resistance training ($\eta_p^2 = 0.402$; $d \approx 1.32$).[25] This indicated that 10 participants would provide 95% power to detect an effect of $d = 1.32$ across 2 repeated measures at $\alpha = 0.05$. To account for variability in motor unit yield and tracking, we aimed to recruit double the minimum sample size.

### 2.3. Participants

Nineteen recreationally active male participants (age = $23.8 \pm 5.1$ years, height = $1.82 \pm 0.07$ m, mass = $79.9 \pm 9.5$ kg) were recruited. Female participants were not included due to the potential confounding effects of hormonal fluctuations across the menstrual cycle on motor unit properties,[40] which would have been difficult to control across the repeated testing sessions of this intervention. The participants were free from lower limb injuries within the past 18 months and had not performed NHE training within the past 6 months. Throughout the study period, participants were able to maintain their regular physical activity and training programs, provided they did not include eccentrically focused hamstring exercises beyond the study intervention. Each participant provided written informed consent before participation. The protocol was approved by The University of Queensland Ethics Committee (approval No. 2023/HE001835).

### 2.4. NHE training intervention

Participants completed a 9-week NHE training program consisting of 3 sessions per week, with 4–5 sets of 6–8 repetitions per session. This protocol provided a total weekly volume of 72–120 repetitions, which has been shown to increase strength within 3 weeks, with continued improvements across the full 9-week period, at which point hypertrophy of the BFlh was also observed.[3,10]

During the initial laboratory session, participants were familiarized with proper NHE technique using the NordBord device (Version 2.0.0; Vald Performance, Brisbane, QLD, Australia). Participants knelt on the device with their ankles secured by hooks at a self-selected ankle angle. The exercise began from a kneeling position with arms close to the chest, from which participants gradually leaned forward while attempting to maintain a consistent hip angle and controlled knee extension. Each repetition was performed at a controlled average knee extension angular velocity of approximately 18°/s, guided by a metronome set at 60 beats per minute. This cadence allowed for approximately 5 s of time under tension per repetition, which was dependent on their active range of motion.[41] The researcher (MHA) visually monitored

movement speed throughout each repetition to ensure adherence to the prescribed NHE technique. Repetitions where participants deviated substantially from the prescribed technique were repeated. Participants continued lowering until they could no longer control the descent or their hands touched the floor, then they used their arms to assist the return to the starting position, minimizing concentric loading of the knee flexors.

Each session began with a warm-up consisting of dynamic stretching and submaximal NHE repetitions. Participants self-selected recovery periods between repetitions (typically ~5 s), while 2-min rest periods between sets were standardized and monitored. All training sessions were supervised by the researcher (MHA), whether conducted in the laboratory using the NordBord device or remotely, where participants used alternative ankle stabilization methods (e.g., barbell or partner assistance).

### 2.5. Experimental procedures

HD-EMG testing was conducted at 3 time points: pre-training, 3 weeks, and 9 weeks. To account for training-induced changes in muscle architecture and strength, optimal joint angles and maximal voluntary contraction (MVC) values were re-determined at the start of each session, as detailed below.

#### 2.5.1. HD-EMG

Monopolar HD-EMG signals were recorded from the BFlh of the right leg using a 64-channel (16 × 4) adhesive grid (1 mm electrode diameter, 10 mm inter-electrode distance; GR10MM1604; OT Bioelettronica, Torino, Italy), amplified 256 times, and sampled at 2000 Hz (Fig. 1). To guide electrode placement, anatomical landmarks were first identified by palpating the origin at the ischial tuberosity and the insertion at the fibular head of the BFlh muscle. The distance between these landmarks was measured and the midpoint was marked on the skin to identify the approximate location of the middle row of the electrode grid.[3] B-mode ultrasound (ArtUS EXT-1H beamformer and LF11-5H60-A3 transducer; 60 mm; Telemed, Vilnius, Lithuania) was then used to visualize the BFlh muscle in the transverse plane. The medial and lateral borders of the muscle were identified and marked on the skin to determine the medial-lateral center of the muscle. A 3D-printed template matching the dimensions of the electrode grid was then placed over the skin, centered both longitudinally and medio-laterally using the previously marked landmarks. The perimeter of the template was traced onto the skin to create a precise guide for the placement of the electrode grid. This marked area was recorded for each participant with respect to the anatomical landmarks and used to replicate the electrode grid positioning across all testing sessions. The skin was prepared by shaving, abrading, and cleansing with alcohol wipes. Electrodes were applied with double-sided adhesive foam layers (FOA10MM3425; OT Bioelettronica) and filled with conductive paste (AC—CREAM; SPES Medica, Genova, Italy). Four reference electrodes were placed on the medial and lateral malleoli of both legs. Signal quality was verified during brief isometric contractions by assessing raw EMG traces for noise. Once confirmed, the grid was secured with a self-adhesive elastic bandage.

#### 2.5.2. Torque

Knee flexion torque and knee joint angle were recorded using an isokinetic dynamometer (Humac Norm, CSMi Computer Sports Medicine, Stoughton, MA, USA) at 2000 Hz and digitized using an analogue-to-digital converter (Power1401; Cambridge Electronic Design, Cambridge, UK) in and acquisition software (Spike2; Cambridge Electronic Design). These torque and joint position data were synchronized with the wireless HD-EMG data acquisition system (Sessantaquattro; OT Bioelettronica).

#### 2.5.3. Testing protocol

Each testing session began with the determination of the optimal joint angle for submaximal contractions. To



Fig. 1. Experimental setup for HD-EMG recordings of the BFlh. The participant lay prone on an isokinetic dynamometer bench and performed isometric knee flexion contractions with feedback of the torque signal provided on a screen in front of them. A 64-channel HD-EMG grid was placed over the BFlh to record motor unit activity during the contractions. BFlh = biceps femoris long-head; HD-EMG = high-density electromyography.

standardize testing conditions across sessions, participants laid prone on an isokinetic dynamometer (Humac Norm), with the knee joint axis visually aligned to the dynamometer axis, and performed 2 maximal voluntary isokinetic eccentric knee flexion contractions, moving from 80° (knee flexed) to 10° (knee extended) at 10°/s, with 1-min rest between trials (Fig. 1). Trials were repeated if compensatory movements were observed. The knee joint angle corresponding to peak torque was identified for each trial, with a 3rd trial conducted if these angles differed by more than 10°. The average peak torque angle in that session was then used to set the joint position for all subsequent contractions in the same session. This protocol was necessary because muscle activation and torque capacity depend on muscle length,[17,42,43] and the angle of peak torque may shift across the intervention period due to architectural adaptations from NHE training, such as increases in passive fascicle length.[3–10]

After determining the optimal joint angle, MVCs were performed to determine the intensity for subsequent submaximal testing, with maximal voluntary torque identified as the greatest torque recorded and used to assess strength adaptations. Following a 2-min rest, participants performed two 3-s isometric MVCs at the identified joint angle with 1-min rest between trials. A 3rd trial was conducted if torque values differed by more than 10%, and the average torque value was used to calculate the submaximal target torque. After a 5-min rest and familiarization period, participants completed three submaximal isometric knee flexion contractions at 40% MVC with simultaneous HD-EMG recording for subsequent motor unit decomposition. This torque level was selected because pilot testing showed it was the highest intensity that could be used without compromising motor unit yield. Each contraction consisted of 3-s ascending and descending torque ramps with a 10-s hold at the target intensity, guided by visual feedback on a screen. Two minutes of rest were provided between trials.

### 2.6. Motor unit decomposition and tracking

HD-EMG signals recorded during the three 40% MVC isometric knee flexion contractions were assessed for signal quality on a channel-by-channel basis. For each recording, the variance of each channel was calculated and compared with the median variance across all non-empty, non-zero channels within that recording. Channels were classified as dead if their variance was <1% of the median value, if the signal consisted entirely of zeros, or if channel data were missing. Channels meeting these criteria were replaced with zero-valued signals and effectively excluded from subsequent analyses. Across all recordings, $1.5 \pm 4.3$ channels per participant were excluded. At pre-training, Week 3, and post-training, the number of excluded channels was $3.6 \pm 7.0$, $0.5 \pm 0.9$, and $0.5 \pm 0.8$ channels, respectively. The remaining signals were then band-pass filtered at 10–900 Hz to remove low-frequency artefact while preserving the spiking nature of motor unit action potentials.[44] A wider bandwidth was selected because narrower filters increase the similarity of action potentials across motor units,[45] whereas retaining higher-frequency components preserves waveform distinctiveness and strengthens the sparsity assumptions underlying motor unit decomposition.[44,46]

The filtered signals were then decomposed into individual motor unit action potentials using a validated blind-source separation algorithm.[44] Blind-source separation uses the spatial information from the multi-channel electrode grid to identify individual motor unit discharge patterns by separating overlapping action potentials based on their distinct spatial signatures.[44] This approach enables accurate identification of motor unit firings, with decomposition quality quantified using the silhouette metric.

Of the 3 recordings, the trial with the greatest motor unit yield was selected for further analysis. From this recording, only motor units with a decomposition silhouette metric ≥0.85 were retained for further analysis.[47] A trained researcher (MHA) then manually reviewed the output to remove inaccurate motor units and correct discharge errors, such as missed firings.[38]

The final, corrected spike trains were used to quantify motor unit firing characteristics.[48] Mean discharge rate was calculated during the steady plateau phase of the torque signal. Absolute recruitment threshold was defined as the knee flexion torque (Nm) at motor unit firing onset during the ascending phase of the torque ramp, whereas normalized recruitment threshold was this torque expressed as a percentage of MVC (%MVC). Absolute de-recruitment threshold was defined as the knee flexion torque at motor unit firing cessation during the descending phase of the torque ramp, while normalized de-recruitment threshold represented this torque relative to MVC torque.

Motor units were tracked longitudinally across the intervention (pre-training, Week 3, and post-training) by comparing action potential waveforms across sessions.[46] Tracking motor units longitudinally allows for direct assessment of training-induced adaptations within the same individual motor units. This approach differs from conventional analyses that pool all motor units from each session independently, which does not account for the heterogeneity of different motor units. However, training-induced architectural changes in the BFlh may alter the spatial distribution of action potentials, potentially limiting the number of motor units that can be reliably tracked across all time points.[46] To ensure that the findings from tracked motor units are representative of the broader motor unit population, a complementary pooled analysis of all identified motor units (matched and unmatched) across time points was conducted. Although the representative pool may not consist of the same motor units across time, this analysis provides insight into population-level adaptations. This analysis is provided in the supplementary material.

For motor unit tracking, action potential waveforms were extracted from the decomposed HD-EMG signals using discharge times provided by the decomposition algorithm. Motor units were then matched between sessions based on waveform cross-correlation, with values >0.7 considered for visual confirmation.[25] The large number of HD-EMG channels (64 channels) and consistent electrode grid placement across sessions (Section 0) improved the likelihood that action

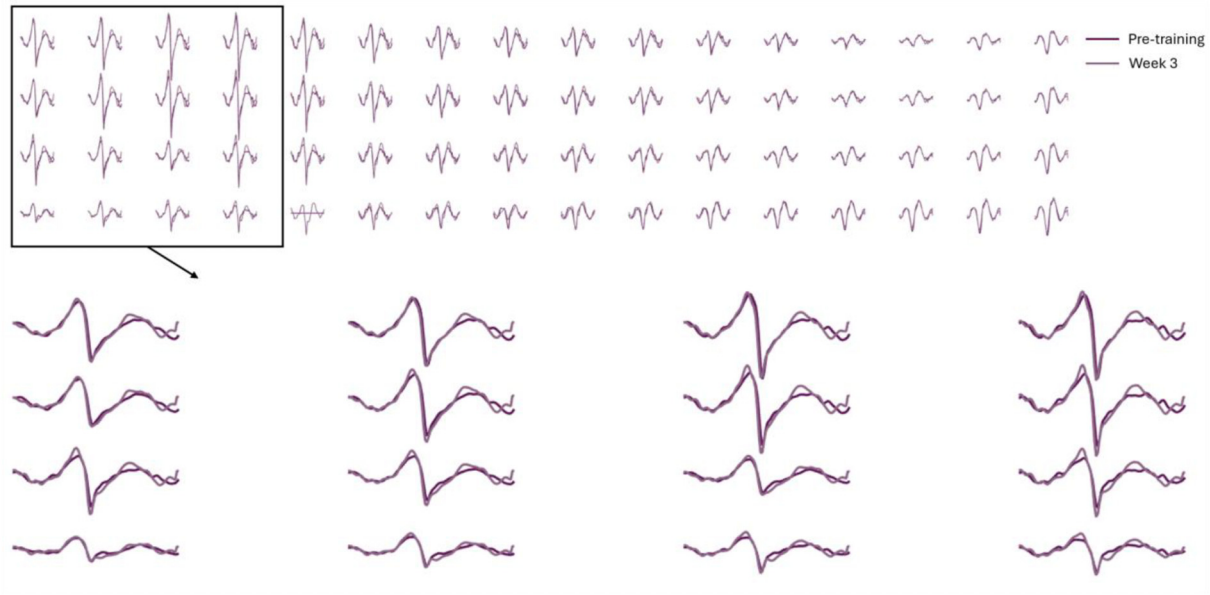



Fig. 2. Example of motor unit tracking across a 9-week NHE training intervention. Motor unit action potentials from the BFlh, recorded using HD-EMG, are shown at pre-training and at Week 3. Sixteen channels (inset) are zoomed to highlight waveform similarity. The cross-correlation coefficient of this motor unit was 0.93, indicating reliable tracking. BFlh = biceps femoris long-head; HD-EMG = high-density electromyography; NHE = Nordic hamstring exercise.

potentials with high cross-correlation corresponded to the same motor unit. Matched motor units were verified by overlaying action potentials from different sessions to confirm waveform consistency (Fig. 2).[46] Motor units were matched in a pairwise fashion between pre-training and Week 3, and between pre-training and post-training. Only the data from matched motor units were included in the statistical analysis.

### 2.7. Statistical analysis

Linear mixed-effects models (LMMs) were used to assess the effects of NHE training on motor unit discharge rate, recruitment threshold, de-recruitment threshold, and isometric knee flexor torque. LMMs account for repeated measures and inter-individual variability, providing a robust framework for longitudinal analysis.[49,50]

For motor unit discharge rate, recruitment threshold and de-recruitment threshold, analyses were restricted to matched motor units. Separate LMMs were employed for 2 distinct comparisons: pre-training to Week 3, and pre-training to post-training. This approach was necessary because motor units were matched between specific time point pairs (pre-training to Week 3, and pre-training to post-training) rather than tracked continuously across all 3 sessions. Continuous tracking could amplify minor variations in motor unit action potential waveforms across multiple pairwise comparisons, limiting the reliability of motor unit tracking.[46] Consequently, the datasets for these comparisons contained different sets of matched motor units and could not be pooled into a single analysis. Time (pre-training to Week 3, or pre-training to post-training) was included as a fixed effect, with participant and individual matched motor units as random effects. An additional pooled analysis of unmatched motor units (full population of identified units) across all time points is provided in the supplementary material.

Models were fit using restricted maximum likelihood estimation. Normality of residuals was assessed with the Shapiro−Wilk test, and outliers were identified and removed using Cook's distance (threshold = 2.5 SD), $p$ values for fixed effects were derived using Satterthwaite's method[51] and reported from Type III analysis of variance tables. Effect sizes were calculated as partial eta squared ($\eta_p^2$), interpreted as small (0.01), medium (0.06), or large (0.14).[52] All analyses were conducted in RStudio (Version 2023.6.1.524; Posit Software, PBC, Boston, MA, USA) using the packages lme4 (v1.1.34), lmerTest (v3.1.3), emmeans (v1.8.7), and sjstats (v0.18.2), with significance set at $\alpha < 0.05$.

## 3. Results

### 3.1. Motor unit decomposition and longitudinal tracking

Decomposition of the HD-EMG signals resulted in 611 motor units across all participants and testing sessions, with an average of $7.8 \pm 5.5$ motor units identified per participant at pre-training, $6.6 \pm 4.3$ after 3 weeks, and $8.0 \pm 5.4$ after 9 weeks. Longitudinal tracking was successful for an average of $2.8 \pm 1.7$ motor units per participant from pre-training to post-training and $2.8 \pm 1.8$ from pre-training to Week 3. This resulted in 71 matched motor unit pairs for the full training period and 61 pairs for the 3-week interval. Tracking reliability was high, with average motor unit action potential waveform cross-correlations of $0.79 \pm 0.05$ and $0.79 \pm 0.06$ for the 9-week and 3-week comparisons, respectively (Fig. 2).

### *3.2. Effects of NHE training on motor unit properties and strength*

NHE training produced significant and time-dependent changes in both isometric knee flexion strength and BFlh motor unit properties during submaximal ramp isometric contractions in longitudinally tracked motor units (Fig. 3). The training intervention was effective in increasing knee flexor strength from the isometric MVCs (Fig. 3A), with significant improvements of 5.58 ± 1.98 Nm at 3 weeks ($p = 0.015$) and 13.96 ± 0.59 Nm at 9 weeks compared to pre-training values ($\eta_p^2 = 0.67$, $p < 0.001$).

Mean discharge rate (Fig. 3B) increased significantly by 0.97 ± 0.47 pps after 3 weeks of training ($\eta_p^2 = 0.11$, $p = 0.015$). However, this adaptation was not maintained by 9 weeks ($\Delta = 0.16 \pm 0.16$ pps; $\eta_p^2 = 0.01$, $p = 0.365$).

Absolute recruitment threshold (Fig. 3C) increased significantly by 2.80 ± 0.61 Nm after 3 weeks of training ($\eta_p^2 = 0.26$, $p < 0.001$) and further increased by 3.78 ± 0.95 Nm after 9 weeks compared to pre-training ($\eta_p^2 = 0.23$, $p < 0.001$). Normalized recruitment threshold (Fig. 3D) also increased after 3 weeks by 1.70 ± 1.76%MVC ($\eta_p^2 = 0.13$, $p = 0.007$), but did not differ from pre-training after 9 weeks ($\Delta = 0.11 \pm 0.90$%MVC; $\eta_p^2 = 0.00$, $p = 0.712$). While statistically significant at 3 weeks, the magnitude of change in normalized recruitment threshold was moderate and may have fallen within the bounds of measurement error.

Absolute de-recruitment threshold (Fig. 3E) showed no significant change after 3 weeks (−0.49 ± 2.19 Nm; $\eta_p^2 = 0.00$, $p = 0.515$) but increased significantly by 3.26 ± 1.83 Nm after 9 weeks ($\eta_p^2 = 0.07$, $p = 0.006$). Normalized de-recruitment threshold (Fig. 3F) decreased after 3 weeks by 2.61 ± 0.79%MVC ($\eta_p^2 = 0.10$, $p = 0.003$), with no difference between pre-training and post-training (−0.87 ± 0.63%MVC; $\eta_p^2 = 0.00$, $p = 0.953$).

## 4. Discussion

This study demonstrates that NHE training alters BFlh motor unit firing properties during submaximal isometric contractions (Fig. 4). After 3 weeks of training, discharge rates and normalized recruitment threshold increased, but by the end of the 9-week training program, they had returned to baseline. In contrast, the absolute recruitment threshold progressively increased across the training period, while the de-recruitment threshold increased significantly by 9 weeks. These results, combined with studies using the same training protocol demonstrating architectural adaptations,[3,10] are consistent with a gradual shift from neural to structural adaptations as an important contributor to strength gains after NHE training.

### *4.1. Motor unit firing adaptations to training*

The significant increase in BFlh motor unit discharge rate and both absolute and normalized recruitment threshold during submaximal isometric contractions after 3 weeks of NHE training highlights an early neural adaptation that likely underpins short-term strength gains. Elevated discharge rates reflect greater motoneuron excitability and central drive.[25,27] Increased absolute recruitment thresholds of tracked motor units indicate that individual motor units were activated at higher force levels, which may reflect an enhanced capacity to convert neural input into force. The increase in normalized recruitment thresholds suggests that, assuming orderly recruitment according to the size principle, tracked motor units were recruited later relative to the available pool during the isometric contraction. Additionally, the population-level increase in absolute recruitment threshold suggests that fewer motor units were required to achieve a given submaximal torque as absolute force capacity increased (Supplementary Fig. 1; Section 2 of Supplementary analysis). These findings align with classic observations suggesting that strength training enhances neural efficiency such that greater force can be produced without increased motor unit recruitment at submaximal levels.[53] In contrast, reductions in recruitment thresholds following strength training have been reported, indicating that motor units are activated at lower force levels.[25] However, recruitment threshold estimates must be interpreted cautiously because only a subset of the active motor unit pool can be detected during a contraction, limiting inferences about true recruitment strategies. Accordingly, the inconsistency across studies remains difficult to resolve, although differences in experimental design and training protocol may account for the divergent outcomes.

Although early structural adaptations, such as fascicle and sarcomere lengthening, have been documented in the hamstrings within the first few weeks of eccentric training,[4] these changes alone are unlikely to explain the substantial reduction in injury risk (conferred by NHE) observed during this early phase.[1,2] While adaptations in non-contractile tissues, including connective tissue remodeling and changes in tendon properties, may also contribute to injury protection,[54–56] the higher discharge rates at Week 3 likely enhanced force generation at the motor unit level.[57,58] The increased discharge rates observed at 3 weeks would be expected to enhance temporal summation of motor unit action potentials, thereby increasing tetanic force and overall muscle contractile output.[57,58] Given that substantial architectural changes are unlikely at this early stage,[59] these increases in neural drive represent a potential mechanism underlying the observed gains in maximal force output. This indicates that short-term strength improvements are closely linked to motor unit firing property adaptations occurring alongside initial architectural modifications.[19,20]

While these motor unit adaptations capture the final connection between the nervous system and the muscle fibers it controls, the upstream neural mechanisms driving these changes remain less well understood. Elevated discharge rates after 3 weeks of NHE training may reflect reduced motor cortical and intracortical inhibition, allowing greater central drive to motoneurons.[60,61] Subcortical contributions are also possible, with evidence from primates indicating that the reticulospinal tract can strengthen its influence on motoneurons following resistance training.[62] At the spinal level, a shorter

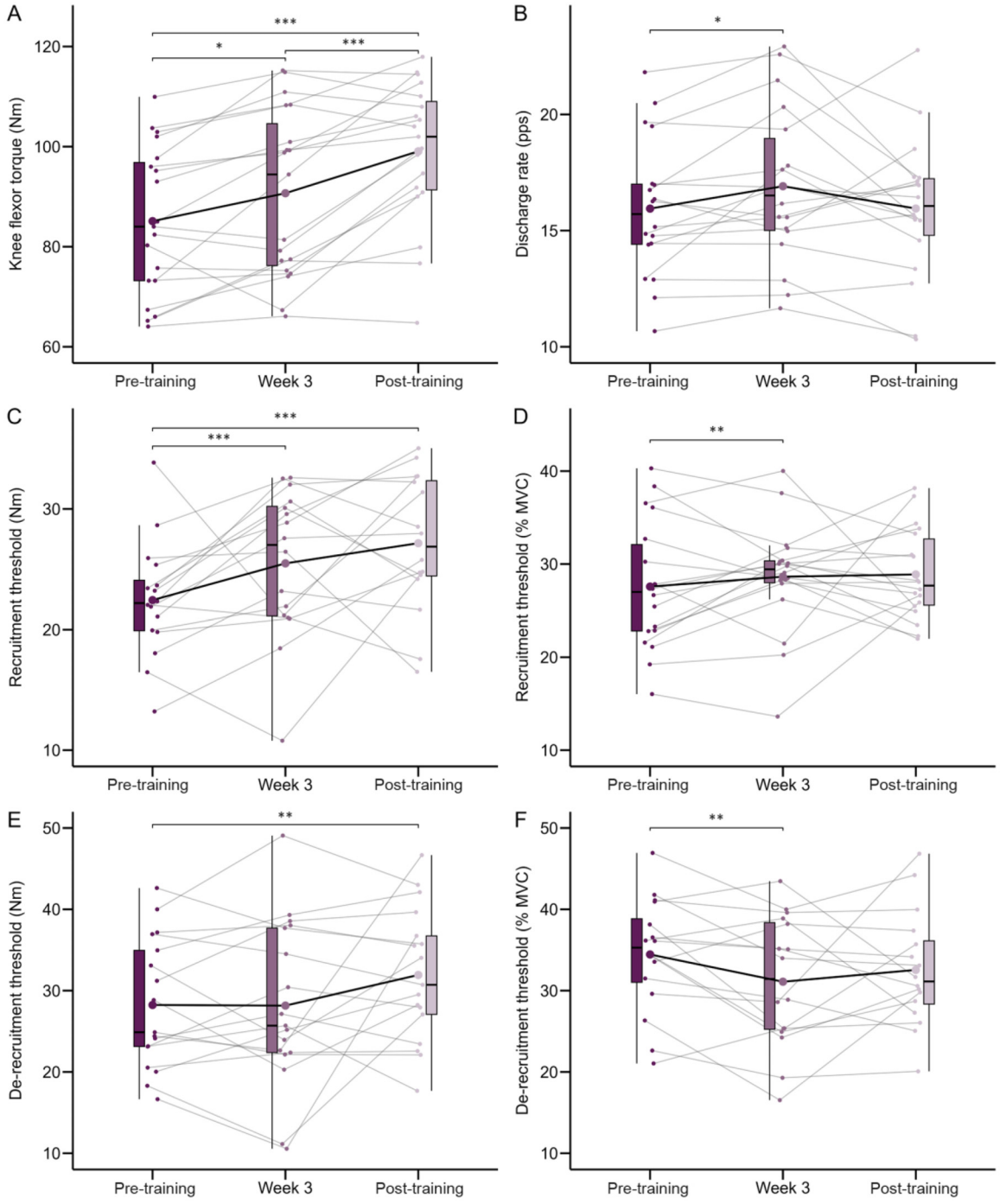



Fig. 3. Adaptations in matched BFlh motor unit properties following NHE training. (A) Isometric knee flexor torque increased progressively across the intervention, with significant increases from pre-training to Week 3 ($p = 0.015$) and post-training ($F_{2,31} = 32$, $\eta_p^2 = 0.67$, $p < 0.001$). (B) Motor unit discharge rate significantly increased after 3 weeks of NHE training ($F_{1,50} = 6$, $\eta_p^2 = 0.11$, $p = 0.015$). No significant difference in motor unit discharge rate between pre- and post-training ($F_{1,61} = 1$, $\eta_p^2 = 0.01$, $p = 0.365$). (C) Absolute motor unit recruitment threshold increased after 3 weeks ($F_{1,55} = 19$, $\eta_p^2 = 0.26$, $p < 0.001$) and remained elevated post-training ($F_{1,64} = 19$, $\eta_p^2 = 0.23$, $p < 0.001$). (D) Normalized motor unit recruitment threshold increased after 3 weeks ($F_{1,52} = 8$, $\eta_p^2 = 0.13$, $p = 0.007$), but was not significantly different at post-training compared to pre-training ($F_{1,106} = 0$, $\eta_p^2 = 0.00$, $p = 0.712$). (E) Absolute motor unit de-recruitment threshold showed no significant change after 3 weeks ($F_{1,87} = 0$, $\eta_p^2 = 0.00$, $p = 0.515$) but increased significantly post-training ($F_{1,112} = 8$, $\eta_p^2 = 0.07$, $p = 0.006$). (F) Normalized motor unit de-recruitment threshold significantly decreased after 3 weeks of training ($F_{1,90} = 10$, $\eta_p^2 = 0.10$, $p = 0.003$), but no significant difference between pre- and post-training ($F_{1,66} = 0$, $\eta_p^2 = 0.00$, $p = 0.953$). Normalized recruitment and de-recruitment thresholds have been expressed relative to a percentage of MVC. Each panel shows comparisons of values between time points, with individual participant data (dots), paired trajectories (lines), and box plots (median and interquartile range). The main effects summarized in brackets include F-statistic values, degrees of freedom, $p$ values, and effect size ($\eta_p^2$) categorized as small (0.01), medium (0.06), and large (0.14). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ indicate significant differences between time points. BFlh, biceps femoris long head; MVC, maximal voluntary contraction; NHE = Nordic hamstring exercise; pps = pulses per second.

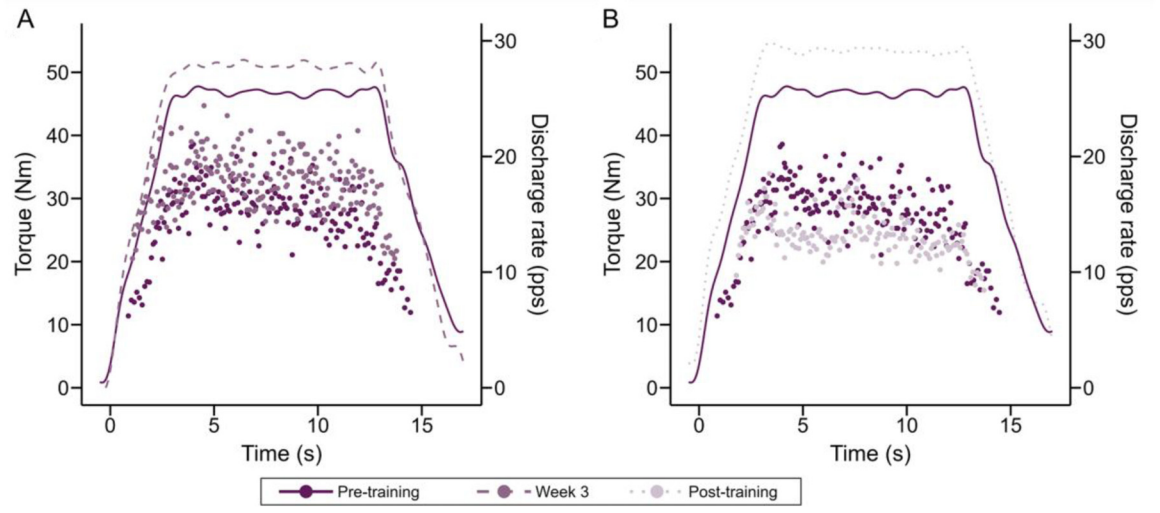



Fig. 4. Motor unit discharge and recruitment adaptations during submaximal ramp contractions. Representative examples of torque and instantaneous motor unit discharge times across training for a representative motor unit. (A) From pre-training to Week 3, torque production increased alongside increases in both recruitment threshold and discharge rate. (B) From pre-training to post-training, torque production and recruitment threshold increased, but discharge rate returned to pre-training levels. Knee flexor torque (primary y-axis, lines) and instantaneous discharge rate (secondary y-axis, dots) of a representative motor unit tracked across training timepoints. The solid line shows torque at pre-training, the dashed line shows torque after 3 weeks of training, and the dotted line shows torque post-training. Individual dots represent instantaneous firing rates of a single motor unit, with colors corresponding to timepoints shown in the legend. pps = pulses per second.

afterhyperpolarization period may make motoneurons more responsive to signals coming from the brain.[63] Spinal reflex pathways may also adapt, enhancing excitatory drive to motoneurons.[64,65] Although the precise contribution of each pathway remains unclear, the convergence of these mechanisms provides a plausible basis for the elevated motor unit discharge rates observed in the early stages of NHE training.

The return of discharge rates and normalized recruitment thresholds to baseline levels by 9 weeks, despite continued increases in strength and absolute recruitment thresholds, aligns with evidence suggesting a transition from neural to structural mechanisms underlying force production capacity.[21] By this stage, hypertrophy reported in studies with similar timelines[8–12] may have contributed to the increased force capacity of individual motor units, as indicated by the elevated absolute recruitment thresholds of tracked units. As muscle fibers increase in size, leading to greater twitch forces, each motor unit can contribute more force without requiring higher firing rates, which may explain the normalization of discharge rates. Indeed, improvements in contractile properties, such as increased twitch force, reduce the neural drive necessary to achieve a given force level.[66–68] By Week 9, concurrent increases in absolute recruitment and de-recruitment thresholds may reflect twitch potentiation, which has been shown to reduce the discharge rates required per motor unit.[68]

Despite increased absolute recruitment thresholds, the absence of changes in normalized thresholds at 9 weeks suggests that adaptations at this stage are predominantly contractile in nature, reflecting increased force capacity of motor units.[21] The continued increase in absolute recruitment threshold at the population level (Supplementary Fig. 1B) further reflects that fewer motor units were recruited as force capacity increased. Additionally, adaptations in muscle–tendon interaction[69] and material properties, including increased tendon stiffness,[54,70] may further contribute by improving the efficiency of force transmission and reducing electromechanical delay.[71] Because hypertrophy differs among the hamstring muscles after similar training protocols[8–10] the observed BFlh firing adaptations may reflect a shift in the relative contribution of each hamstring muscle to overall force production. These adaptations suggest that structural and mechanical changes may explain why discharge rates and normalized recruitment thresholds return to baseline while absolute recruitment thresholds remain elevated in the later stages of training. However, these interpretations should be considered within the context of the present experimental design, which assessed superficial motor units at a single submaximal force level in the BFlh muscle.

Collectively, these results from BFlh motor units during submaximal contractions suggest that NHE training may induce protective adaptations through a complex interplay of structural and neural mechanisms. Early protection (3 weeks) is driven by increased motor unit discharge rates, which enable greater force per motor unit. Non-contractile adaptations in extracellular matrix[72] and tendon properties[54] may further contribute to this early protective phase. Longer-term protection (9 weeks) may reflect a transition to structural mechanisms, where muscle hypertrophy increases motor unit force capacity, sustaining elevated recruitment thresholds while fascicle lengthening enhances force production capacity at extended muscle lengths.

### 4.2. Limitations

Several methodological considerations limit the interpretation and generalizability of these findings. The absence of a

control group precludes definitive attribution of the observed motor unit adaptations to the NHE intervention. However, the reliability of motor unit decomposition techniques in the absence of training has been established previously,[39,46] providing confidence that the adaptations reported here reflect training effects rather than measurement error or individual variability.

A limitation of this study is the exclusion of female participants. This decision was made to avoid the confounding effects of menstrual cycle hormonal fluctuations on neuromuscular function,[40] which would have been difficult to control across repeated testing sessions spanning several months. Future studies could address this by recruiting females and standardizing testing to a consistent menstrual cycle phase (e.g., early or late follicular phase) across time points. In addition, motor unit decomposition from HD-EMG is more challenging in females, often resulting in a lower motor unit yield compared with males.[73]

While HD-EMG provides a non-invasive assessment of motor unit properties, this technique is limited to superficial muscle regions (~1 cm depth) and may not capture neural adaptations occurring in deeper BFlh motor units. Longitudinal tracking of identical motor units across training to ensure that the analysis is conducted on the same population of motor units is also technically challenging, particularly in the presence of training-induced architectural changes, resulting in a relatively small number of matched units.[46] Nonetheless, this approach has been validated and shown to provide reliable tracking of motor units across experimental sessions.[25,46] To account for the reduced sample inherent to longitudinal tracking, we also performed a complementary pooled analysis of all identified motor units, which demonstrated the same temporal and directional adaptations as the tracked motor units, supporting the representativeness of the results across the entire pool of identified motor units.

HD-EMG was recorded during submaximal isometric contractions due to the technical requirements for reliable motor unit decomposition, which necessitate relatively stable, low-force conditions for accurate motor unit identification. However, these isometric assessments may not reflect what happens during dynamic tasks. A further limitation is that motor unit properties were assessed at a single submaximal force level. Although this torque was chosen based on pilot testing as the highest intensity that maintained reliable motor unit yield, adaptations in higher-threshold units may not have been fully captured. Additionally, while the knee joint axis was visually aligned with the dynamometer and procedures were standardized across sessions, some axis misalignment may have occurred during maximal or ramp contractions, which could introduce systematic errors in absolute torque estimates.[74,75] However, the magnitude of these systematic errors is likely minimal relative to the training-induced changes in torque and is therefore unlikely to affect the interpretation of the results.

Our findings are limited to BFlh and cannot determine whether synergists demonstrated similar neural adaptations. Given that hypertrophy varies across hamstring muscles following similar training protocols,[8–10] neural adaptations may likewise be nonuniform across the hamstrings. Addressing these limitations in future research may offer a more complete understanding of hamstring motor unit adaptations and how they contribute to injury prevention.

## 5. Conclusion

NHE training induces distinct adaptations in BFlh motor unit firing properties, with a temporal pattern in line with a shift from neural to structural mechanisms across time. After 3 weeks, increased discharge rates enhance force production per motor unit, which is reflected in the increased absolute and normalized recruitment thresholds. By 9 weeks, absolute recruitment and de-recruitment thresholds had increased even as discharge rates and normalized recruitment thresholds returned to baseline. Together with studies showing BFlh hypertrophy after 9 weeks of the same eccentric training protocol, these findings are consistent with the mechanisms underlying strength increases shifting from primarily neural to predominantly muscular adaptations over the course of NHE training.

## Authors' contributions

MHA was responsible for data collection and performed the data analysis. 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.

## 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.

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## Supplementary materials

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