TITLE

Cross-education effects of isokinetic eccentric plantarflexor training on flexibility, strength, and muscle-tendon mechanics

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RUNNING HEAD

Cross-education effects of eccentric training.

ABSTRACT

Introduction: Large increases in joint range of motion (ROM) have been reported after eccentric resistance training, however limited data exist describing the associated mechanisms or potential cross-education effects in the contralateral limb. Therefore, the effects of a 6-week isokinetic eccentric plantarflexor training program were examined in 26 participants. **Methods:** Before and after the training program, dorsiflexion ROM, plantarflexor strength, and muscle-tendon unit (MTU) morphology and mechanics were measured in control (*n*=13) and experimental (*n*=13) young adult groups. Training consisted of 5 sets of 12 maximal isokinetic eccentric plantarflexor contractions twice weekly on the right limb. **Results:** Significant ($P < 0.05$) increases in dorsiflexion ROM (4.0-9.5°), stretch tolerance (40.3-95.9%), passive elastic energy storage (47.5-161.3%), and isometric (38.1-40.6%) and eccentric (46.7-67.0%) peak plantarflexor torques were detected in both trained and contralateral limbs in the experimental group. Significant increases in gastrocnemius medialis (GM) and soleus thickness (5.4-6.1%), GM fascicle length (7.6±8.5%), passive plantarflexor MTU stiffness (30.1±35.5%) and Achilles tendon stiffness (5.3±4.9%) were observed in the trained limb only. Significant correlations were detected between the changes in trained and contralateral limbs for dorsiflexion ROM (*r*=0.59) and both isometric (*r*=0.79) and eccentric (*r*=0.73) peak torques. No significant changes in any metric were detected in the control group. **Conclusion:** Large ROM increases in the trained limb were associated with neurological, mechanical, and structural adaptations, with evidence of a cross-education effect in the contralateral limb being primarily driven by neurological adaptation (stretch tolerance). The large improvements in ROM, muscle size, and strength confirm that isokinetic eccentric training is a highly effective training tool, with potential for use in athletic and clinical populations where MTU function is impaired and current therapies are ineffective.

Keywords: Crossover effects, contralateral, eccentric resistance training, range of motion.

INTRODUCTION

Maximum joint range of motion (ROM) may be influenced by neural (e.g., stretch tolerance/pain perception), mechanical (e.g., tissue stiffness), and structural (e.g., muscle architecture [fascicle length/angle]) factors (1, 2), with the efficacy of muscle stretching training for increasing ROM in healthy populations confirmed in several recent reviews (3–5). However, muscle stretching exercises often fail to provide clinically meaningful improvements in ROM in some neurological conditions (6–9), which is of particular concern as restricted ROM is prevalent in many clinical populations (10–14) as well as in aging (15, 16), with compromised mobility and functional independence (10, 17) limiting the capacity to perform activities of daily living (18, 19). Importantly, ROM changes following muscle stretching programs are more commonly associated with changes in stretch tolerance than any meaningful mechanical or structural muscle-tendon unit (MTU) adaptations (20–22). The limited MTU adaptations are of particular concern for clinical populations where abnormal neurological activity (e.g., spasticity) can result in contractures that compromise mechanical properties (increased tissue stiffness) and structural characteristics (fascicle shortening), and where muscle stretching programs fail to increase ROM (6–9). Thus, identifying other interventions that impart substantial and broad-ranging mechanical and architectural MTU adaptations is an important step towards improving both the magnitude and clinical benefit of ROM increases.

One exercise mode that imposes substantial tissue loads and thus provides a large adaptive stimulus is eccentric-only exercise (23, 24), which promotes greater gains in strength and muscle size (25) than concentric exercise and yet substantially and simultaneously improves ROM (26–29). Indeed, a recent meta-analysis (29) reported a large effect (g = 0.86) of eccentric exercise on passive ROM across joints in the lower limb that was substantially greater than the effects previously reported (g = 0.29-0.49) after traditional resistance training or muscle stretching programs (30). Furthermore, isokinetic forms of eccentric training showed particular promise with an even greater effect being observed (*g* = 1.09) despite the training dose being only half of that imposed in other studies, indicating it to be a more efficient yet more potent driver of ROM adaptation (29). Like muscle stretching training, eccentric training can also result in increased stretch tolerance (31, 32), however additional adaptations are also commonly observed after eccentric training including increased fascicle length (26), a rightward shift in the force-length curve indicative of sarcomerogenesis (33), and the remodeling of both collagenous and non-collagenous extra cellular matrix components (34). These adaptations may have clinical relevance for populations (e.g., cerebral palsy, stroke, spinal cord injury) in which neurological impairment (e.g., spasticity) and abnormal extra-cellular matrix deposition (35, 36) can result in the formation of contractures that result in high tissue stiffness, pain, and permanent muscle shortening that compromise ROM and muscle function. Whilst promising, the potential mechanisms underpinning the large increases in ROM after eccentric training remain unclear, with the relationships between changes in ROM and many mechanical or physiological variables rarely explored (29). This lack of mechanistic understanding is problematic as it limits our ability to intelligently modify these interventions to potentially improve efficacy or determine their suitability for clinical populations where these characteristics are often compromised.

Despite eccentric exercise being a potent driver of ROM, strength, and muscle size increases, injured athletes or clinical populations may have difficulty training the affected limb because of an inability to withstand the substantial tissue loading imposed (e.g., muscle strain injury) or to contract the musculature of the affected limb (e.g., hemiparesis). Thus, a strategy to minimize regression and promote improvements in the affected limb without inflicting pain or increasing (re-)injury risk need to be explored. The beneficial effects of single-limb resistance training on the homologous muscles of the contralateral limb are well documented (37, 38), with strength in contralateral muscles achieving approximately one-third of the gain of the trained limb (38). This phenomenon whereby following unilateral resistance training, strength in an untrained contralateral limb can increase is termed the cross-education effect (37, 38). Whilst cross-education effects have been reported in several muscle groups and following a range of resistance training programs (37–40), larger cross-education strength effects (39, 40) with greater changes in corticospinal inhibition and excitability (40) have been reported after eccentric training than training with other contraction modes. Without detectible peripheral (muscular) adaptations being evident, central changes, including altered corticospinal excitability and/or inhibition influencing activation of the α-motoneuron pool, have been suspected as primary underlying mechanisms (41). Nonetheless, no studies have examined the cross-education effect of eccentric training on ROM, despite substantial central adaptations (increased stretch tolerance and decreased pain perception) (1, 2) and cross-education effects (42) being observed after muscle stretching training. One might suspect, then, that eccentric training could trigger meaningful increases in ROM in both the untrained and trained limbs and become an important tool for augmenting strength and flexibility improvements in both trained and untrained limbs in a range of clinical populations. However, given the lack of current data, a proof-of-concept trial is needed in a healthy population to determine efficacy, identify concomitant adaptations, and reveal potential contraindicated results, before assessments commence in clinical populations.

Given the above, the aim of the present study was to examine the effects of a 6-week isokinetic eccentric plantarflexor training program on muscle strength and flexibility in both training and non-training limbs in a healthy adult population. We tested the specific hypotheses that the training would result in broad ranging adaptations, including increases in (i) dorsiflexion ROM,

(ii) plantarflexor stretch tolerance, (iii) peak elastic energy storage, (iv) passive joint (i.e., MTU) stiffness, (v) passive soleus, gastrocnemius medialis, and Achilles stiffness, tone, and elasticity, (vi) maximal active isometric and eccentric plantarflexor torques, (vii) soleus and gastrocnemius medialis thickness, and (viii) gastrocnemius medialis fascicle length in the trained limb, but improvements in only (ix) dorsiflexion ROM, (x) plantarflexor stretch tolerance, (xi) peak elastic energy storage, and (xii) maximal isometric and eccentric plantarflexor torques in the contralateral limb. We therefore hypothesized that peripheral (mechanical or architectural) changes would be absent in the untrained limb and that central (neurological) adaptations would explain the cross-education effects on both ROM and muscle strength.

MATERIALS & METHODS

Participants

Twenty-six recreationally active participants volunteered for the study after completing a pre-test medical questionnaire and providing written informed consent. The participants were randomly assigned to either the experimental (n = 13, 5 males, 8 females, age = 22.5 ± 1.6 y, height = 1.7 ± 0.1 m, mass = 68.7 ± 16.9 kg) or control (n = 13, 5 males, 8 females, age = 22.7 ± 4.6 y, height = 1.7 ± 0.1 m, mass = 72.4 ± 15.7 kg) group. Ethical approval was granted by The University of Northampton's Ethics Committee with the study completed in accordance with the Declaration of Helsinki.

Protocol overview

Participants were familiarized with the experimental testing and training protocols one week before a pre-training experimental data collection session. During experimental trials, the participants laid prone on a physiotherapy bench with the soles of the feet resting flat against a wall and the ankles in the anatomical position. Passive mechanical properties (stiffness, tone, elasticity) of the Achilles tendon and both gastrocnemius medialis (GM) and soleus (Sol) were assessed using myotonometry, and GM and Sol morphology were recorded using ultrasound imaging (described below). Participants then performed a 5-min walking warm-up on a treadmill at a self-selected pace (2.0 ± 0.3 $m \cdot s^{-1}$) before being seated on an isokinetic dynamometer (Biodex System 4 Pro, IPRS, Suffolk, UK) with the hips flexed to 70° and right knee fully extended (0°). The foot was positioned in the footplate with the lateral malleolus aligned with the center of rotation of the dynamometer and the sole of the foot perpendicular to the shank to ensure the ankle was in the anatomical position (0°). To ensure valid and reliable ROM assessments, non-elastic strapping with a rachet mechanism across the ankle was used to minimize heel displacement from the dynamometer footplate. The leg lock-out method was also employed with the dynamometer chair positioned so that the participants' knee was slightly flexed before locking out the knee with non-elastic strapping placed across the thigh to maintain knee extension, which presses the pelvis into the backrest of the seat to further minimize lateral movement and heel displacement (43); one experienced analyst conducted all trials to prevent inter-tester variability.

In the experimental group, three passive ROM trials (described in detail below) were performed on the right (trained) and left (contralateral) limbs to quantify dorsiflexion ROM, peak passive torque (stretch tolerance), the slope of the passive torque-time curve (MTU stiffness), and the area under the passive torque-time curve (peak potential elastic energy storage). Active trials (described below) were performed on the right and then left limbs with three ramped maximal isometric contractions followed by five maximal eccentric contractions to test isometric and eccentric torques, respectively. At least 48 h later, the participants commenced the training program, which consisted of two training sessions per week for 6 weeks (described in detail below). Participants in the control group completed identical testing protocols on the left limb only and then continued with their normal activities for the duration of the training program. Upon program completion, all participants repeated the passive and active experimental trials with 5-7 days between the final training session and testing of the experimental group to minimize potential residual training effects from influencing the data.

Eccentric training program

Before each training session, a standardized 5-min warm-up was performed on a treadmill and participants were then seated in the dynamometer chair in identical positioning to that described above (see Protocol overview). Training was performed on the right limb twice-weekly (at least 48 h between sessions) for 6 weeks and consisted of five sets of 10 repetitions of eccentric plantarflexor contractions. Dorsiflexion ROM was determined using dynamometry at the beginning of the first training session each week, with the dynamometer dorsiflexing the foot from 20° plantarflexion until the point of discomfort. Weekly ROM assessments allowed the training range of motion to increase as the participants adapted to the training to ensure participants trained through a full range of motion. The dynamometer was programmed to dorsiflex the foot through a 30° range to full dorsiflexion at 0.175 $rad \cdot s^{-1}$ ($10° \cdot s^{-1}$; 3-s eccentric contraction) with participants instructed to contract at ~50% of perceived maximal voluntary contraction (MVC) during the first set, followed by four sets at maximal effort (i.e., maximal voluntary isokinetic eccentric contractions). After each contraction, the participant relaxed as the footplate plantarflexed the foot to the starting position at 0.524 $rad \cdot s^{-1}$ ($30° \cdot s^{-1}$), providing a 1-s rest between contractions; 60 s of rest was provided between sets.

Measures

Passive mechanical properties

Myotonometry (MyotonPRO, Myoton AS, Tallinn, Estonia) was used to measure passive GM, Sol, and Achilles mechanical properties in the right and left limbs in the experimental group and left limb of the control group. These properties included dynamic stiffness ($N \cdot m^{-1}$) characterized as the resistance of the tissue to the force of deformation, natural oscillating frequency (i.e., tone [Hz]) characterized as the intrinsic tension of a tissue at a cellular level, and logarithmic decrement (i.e., inverse of elasticity [arb, relative arbitrary unit]) characterized as the dampening of tissue oscillation. Ultrasound imaging was used to locate the thickest region of GM, the thickest available (i.e., superficial) region of the medial aspect of Sol, and the midpoint of the free Achilles tendon. These positions were recorded to enable repeat measurements at the same sites following training. The myotonometer probe was placed perpendicular on the skin over GM, Sol, and the Achilles tendon with a pre-test pressure of 0.18 N applied by the probe prior to a mechanical pulse of 0.40 N for 15 ms with the myotonometer accelerometer set at 3,200 Hz and data recorded for 200 ms. A multi-scan (five measurements) protocol taken in quick succession was employed with the average of the five measurements used for analysis. The reliability of these measures and methods have been confirmed previously (34).

Muscle thickness and architecture

Ultrasound imaging (Vivid I, General Electric, Bedford, UK) was used to record GM and Sol during tests at the same locations used during the myotonometry tests with a wide-band linear probe (8L-RS, General Electric) with 39 mm field of view and coupling gel (Dahlhausen, Cologne, Germany) between the probe and skin. The probe was orientated to enable longitudinal imaging of each muscle and then manipulated until the superficial and deep aponeuroses were visualized with a single image then captured. The probe was then removed from the skin and repositioned before a second image was captured to allow within-session reliability assessment. Muscle thickness was measured at the image centers as the distance between superficial and deep aponeuroses, with the average of the two images used for analysis. GM fascicle angle was calculated as the average of three fascicles that inserted onto the deep aponeurosis, with the average of the two images used for analysis. As the probe width (39 mm) did not enable the full GM fascicle length to be visualized, fascicle length (FL) was estimated trigonometrically using fascicle angle (FA) and muscle thickness (MT) measurements in the equation: FL = MT/sin(FA).

Range of motion, stretch tolerance, muscle-tendon unit stiffness, and potential elastic energy storage

Three passive dorsiflexion trials were initiated from 20° plantarflexion through to full dorsiflexion at 0.087 $\text{rad}\cdot\text{s}^{-1}$ ($5°\cdot\text{s}^{-1}$) with 30 s rest between trials. During the passive ROM trials, the participants terminated the movement with a hand-held release button at the point of discomfort, a stretch intensity commonly used in ROM studies (44). The movement velocity was too slow to evoke a significant myotatic stretch reflex response (45), which enabled full volitional ROM to be reached and the torque data being reflective of the passive plantarflexor properties. Passive torque data were recorded from the third trial to minimize the influence of thixotropic properties of the skeletal muscles (46). The passive trials enabled dorsiflexion ROM (°), peak passive torque (stretch tolerance), the slope of the passive torque-time curve (MTU stiffness), and the area under the passive torque-time curve (potential elastic energy storage) to be calculated. Using previously established methods (47), stretch tolerance (N·m) was calculated as the peak passive torque measured within a 250-ms epoch at peak dorsiflexion, while energy storage (J) was calculated as the area under the passive torque-time curve from the anatomical position to peak dorsiflexion, multiplied by the rotation velocity (0.087 $\text{rad}\cdot\text{s}^{-1}$). The slope of the passive torque-time curve ($\text{N}\cdot\text{m}\cdot{}^{\circ-1}$) was calculated as the change in plantarflexor torque through the final 10° of dorsiflexion in the pre-stretching trials, with identical joint angles used in post-training analysis (44).

Isometric and eccentric torques

Two minutes later, the participants performed two sets of three submaximal ramped isometric contractions at 50 and 75% of perceived maximum, respectively, followed by three ramped maximal voluntary isometric contractions performed with participants instructed to push "as hard as possible" over a 5-s epoch, separated by a 1-min rest between contractions. The highest value of isometric torque (N·m) from the three maximal trials was used for analysis. Two minutes later the participants performed five maximal eccentric contractions at $10°\cdot s^{-1}$ through a 30º range of motion through to full dorsiflexion with the participants instructed to contract maximally throughout the rotation. As large increases in ROM have been achieved using similar training programs (31), eccentric torque was recorded at 5° below the pre-training ROM, with identical joint angles used in post-training analyses.

Joint torque data during the passive and active trials were directed from the dynamometer to a high-level transducer (HLT100C, Biopac, CA, USA) before analog-to-digital conversion at a 2000-Hz sampling rate (MP150 Data Acquisition, Biopac, CA, USA). The data were then directed to a personal computer (Elitebook, HP Inc., CA, USA) running AcqKnowledge software (v.5.0, Biopac). Data during the passive and active trials were filtered with a zero lag, 6-Hz Butterworth low-pass filter prior to ROM and joint torques being determined.

Data analysis

All data were analyzed using SPSS statistical software (version 28; IBM, Chicago, IL). Three participants' data were missing for Achilles, GM, and Sol mechanical properties at post-training, so multiple imputation was conducted (48) using the automatic method on SPSS to prevent the participants' data being removed from the analyses via listwise deletion. Five imputations were conducted following the calculation of the fraction of missing information (49), with the average of the five imputations included for analyses. Normal distribution for all data sets was assessed using Shapiro-Wilk tests with Levene's test used to determine homogeneity of variance. Where normal distribution was violated, successful log transformations ($\log_{10}$) were performed for Achilles and Sol stiffness and elasticity. However, neither log nor square-root transformations were successful for GM stiffness, or GM, Achilles, or Sol tone, with nonparametric Wilcoxon tests performed for these variables.

For data that satisfied parametric assumptions, separate two-way mixed-model analysis of variance (ANOVA) revealed significant differences at baseline between the control group and both limbs of the experimental group in the primary outcome measures (ROM and strength). As performing an ANCOVA with baseline data as the covariate would violate one of the ANCOVA assumptions (i.e., each dataset must be from different groups), separate two-way repeated measures ANOVAs were used to test for the within-subjects effects of time (×2 [pre- and post-training]) and limb (×2 [trained and contralateral limbs]) in the experimental group for i) ROM, ii) stretch tolerance, iii) elastic energy, iv) MTU stiffness, v) passive mechanical properties (stiffness, tone, elasticity) of the Achilles, GM and Sol, and vi) maximal isometric and vii) eccentric plantarflexor torques. Paired *t*-tests or Wilcoxon tests were used to separately determine the influence of time and differences between limbs in the control group. Standardized effect sizes were calculated for ANOVA (partial eta squared [η_p^2]), *t*-test (Cohen's d [*d*]), and Wilcoxon (r) tests. Pearson's (*r*) or Spearman's (*rs*) correlation tests were conducted to quantify the relationship between changes in all variables within, and between, the trained and contralateral limbs. Group data that meet normal distribution assumptions are reported as mean ± SD, data that failed these assumptions are reported as median (*Ms*) and interquartile range (IQR). Absolute or percentage change (time) or difference (limb) data are reported as mean ± SD. Statistical significance for all tests was accepted at $P < 0.05$.

Reliability

To determine within-session reliability, paired *t*-tests were performed on data sets from two trials during the pre-training testing session with intraclass correlation coefficients (ICC) and coefficients of variation (CV) calculated. Passive mechanical properties (stiffness, tone, elasticity) of the Achilles, GM and Sol were determined using the first two trials of the MyotonPRO multi-scan. GM and Sol muscle thickness and GM fascicle angle were determined from two ultrasound images. ROM, stretch tolerance, MTU stiffness, and elastic energy were measured using the second and third passive ROM trials on the dynamometer, with maximal isometric and eccentric torques calculated using the greatest two MVC trials. No significant difference was detected between trials for any measure with high ICCs and low CVs calculated (passive mechanical properties of the Achilles [ICC = 0.99-1.00; CV = 1.06-6.52%], GM [0.99-1.00; 0.65-2.91%], Sol [0.99-1.00; 0.92-2.26%], and for Sol thickness [1.00; 1.8%], GM thickness [1.00; 1.4%], fascicle angle [0.95; 3.3%], and fascicle length [0.92; 3.5%], dorsiflexion ROM [0.99; 2.8%], plantarflexor stretch tolerance [0.99; 4.0%], MTU stiffness [0.99; 5.9%], elastic energy [0.98; 4.1%], maximal isometric [0.98; 4.5%] and eccentric [0.98; 5.9%] torques), demonstrating excellent within-session reliability for all measures.

Sample size

Effect sizes (Cohen's *d*) were calculated from mean ± SD changes in the primary variables (strength, ROM, fascicle length, stretch tolerance, energy storage) from previous studies employing similar methods (50–52). To ensure adequate statistical power for all variables, power analysis was conducted on the variable with the smallest effect size (fascicle length) using the following parameters: $\beta = 0.20$, $\alpha = 0.05$, $d = 1.17$. The analysis revealed that 26 participants were required for statistical power and to account for possible attrition (31), 29 participants were recruited. Two withdrew from the study with non-related injuries and one was diagnosed with a musculoskeletal condition during baseline testing, with statistical analyses conducted on complete datasets for 26 participants (13 control, 13 experimental).

RESULTS

In the control group, no significant change was detected after 6 weeks in dorsiflexion ROM (-0.28 ± 3.93°, $d = -0.07$), plantarflexor MTU stiffness (-4.4 ± 17.4%, $d = -0.47$), stretch tolerance, (-2.5 ± 13.6%, $d = -0.26$), elastic energy (-0.6 ± 19.1%, $d = -0.04$), Achilles stiffness (2.3 ± 11.2%, $d = 0.18$), tone (2.4 ± 10.3%, r = 0.17), or elasticity (2.5 ± 9.9%, $d = 0.29$), Sol stiffness (2.3 ± 13.1%, $d = 0.15$), tone (2.0 ± 10.5%, r = 0.05), elasticity (-1.5 ± 8.7%, $d = -0.13$) or muscle thickness (1.2 ± 8.2%, $d = 0.12$), GM stiffness (8.3 ± 13.7%, $d = 0.57$), tone (1.3 ± 7.2%, r = 0.10), elasticity (-0.7 ± 8.3%, $d = -0.04$), muscle thickness (1.3 ± 6.7%, $d = 0.16$), fascicle length (2.9 ± 9.9%, $d = 0.29$) or angle (-2.1 ± 6.9%, $d = 0.48$), or maximum isometric (3.6 ± 9.7%, $d = 0.42$) or eccentric (-4.0 ± 8.9%, $d = -0.45$) plantarflexor torques.

Range of motion

In the experimental group, a significant interaction effect for ROM was detected ($F_{1,\,12} = 20.051$, $P < 0.001$, $\eta_p^2 = 0.626$), with significant increases in ROM (Figure 1A) in both the trained (9.5 ± 5.4°, $P < 0.001$, $d = 1.75$) and contralateral (4.0 ± 4.1°, $P = 0.004$, $d = 0.98$) limbs. No significant difference was detected between limbs at pre-training (0.5 ± 4.4°, $P =$

0.689, $d = 0.11$), however ROM was significantly greater in the trained limb after training (6.0 ± 5.7°, $P = 0.002$, $d = 1.07$).

Muscle-tendon unit stiffness (slope of the passive torque curve)

A significant interaction effect for MTU stiffness was detected ($F_{1,\,12} = 4.799$, $P = 0.049$, $\eta_p^2 = 0.286$), with a significant training-related increase in MTU stiffness (Figure 1B) in the trained limb (30.1 ± 35.5% [0.18 ± 0.22 N·m·$^{\circ-1}$], $P = 0.012$, $d = 0.82$) but not in the contralateral limb (7.2 ± 21.1% [0.03 ± 0.12 N·m·$^{\circ-1}$], $P = 0.422$, $d = 0.23$). No significant difference was detected between limbs at pre-training (5.8 ± 19.8% [0.05 ± 0.16 N·m·$^{\circ-1}$], $P = 0.306$, $d = 0.30$), however MTU stiffness was significantly greater in the trained limb after training (28.3 ± 34.7% [0.20 ± 0.25 N·m·$^{\circ-1}$], $P = 0.013$, $d = 0.81$).

Stretch tolerance (peak passive torque)

A significant interaction effect was detected for stretch tolerance ($F_{1,\,12} = 14.356$, $P = 0.003$, $\eta_p^2 = 0.545$), with significant increases in stretch tolerance (Figure 2A) observed in the trained (95.9 ± 40.7% [22.7 ± 15.3 N·m], $P < 0.001$, $d = 1.48$) and contralateral (40.3 ± 26.9% [8.7 ± 6.9 N·m], $P < 0.001$, $d = 1.25$) limbs. No significant difference was detected between limbs at pre-training (3.1 ± 25.9% [0.61 ± 5.11 N·m], $P = 0.676$, $d = 0.12$), however stretch tolerance was significantly greater in the trained limb after training (42.6 ± 32.9% [14.6 ± 12.9 N·m], $P = 0.002$, $d = 1.13$).

Potential elastic energy storage (area under the passive torque curve)

A significant interaction effect was detected for elastic energy ($F_{1,\,12} = 21.136$, $P < 0.001$, $\eta_p^2 = 0.638$), with significant increases in elastic energy (Figure 2B) in the trained (161.3 ± 49.6% [6.93 ± 4.07 J], $P < 0.001$, $d = 1.70$) and contralateral (47.5 ± 36.0% [1.76 ± 0.96 J], $P < 0.001$,

$d = 1.90$) limbs. No significant difference was detected between limbs at pre-training (3.8 ± 33.0% [0.20 ± 1.27 J], $P = 0.580$, $d = 0.16$), however elastic energy was significantly greater in the trained limb after training (93.2 ± 89.3% [5.37 ± 4.83 J], $P = 0.002$, $d = 1.13$).

Achilles mechanical properties

A significant interaction effect was detected for Achilles stiffness ($F_{1,\,12} = 6.433$, $P = 0.026$, $\eta_p^2 = 0.349$), with a significant increase in stiffness (Table 1) in the trained limb (5.3 ± 4.9% [53.6 ± 52.0 $\text{N}\cdot\text{m}^{-1}$], $P = 0.003$, $d = 1.03$) but not in the contralateral limb (1.7 ± 4.6% [18.7 ± 47.4 $\text{N}\cdot\text{m}^{-1}$], $P = 0.180$, $d = 0.40$). Stiffness was significantly greater at pre-training in the contralateral limb (4.1 ± 6.3% [43.4 ± 65.3 $\text{N}\cdot\text{m}^{-1}$], $P = 0.034$, $d = 0.66$), however no difference was detected between limbs after training (0.8 ± 4.3% [8.5 ± 44.7 $\text{N}\cdot\text{m}^{-1}$], $P = 0.507$, $d = 0.19$).

A significant interaction effect was detected for Achilles elasticity ($F_{1,\,12} = 74.949$, $P < 0.001$, $\eta_p^2 = 0.862$), with a significant decrease in elasticity in the trained limb (-131.6 ± 66.0% [-0.572 ± 0.200 arb], $P < 0.001$, $d = -2.86$) but not the contralateral limb (0.17 ± 17.38% [0.002 ± 0.082 arb], $P = 0.926$, $d = 0.03$). No significant difference was detected between limbs at pre-training (13.5 ± 24.2% [0.048 ± 0.097 arb], $P = 0.096$, $d = 0.50$), however elasticity was significantly lower in the trained limb after training (-168.3 ± 113.4% [-0.622 ± 0.199 arb], $P < 0.001$, $d = -3.13$).

Wilcoxon tests revealed a significant increase in Achilles tone after training in the trained limb (6.4 ± 7.6% [2.2 ± 2.7 Hz], $P = 0.019$, $z = 2.341$, $r = 0.46$) but not in the contralateral limb (2.1 ± 5.9% [0.8 ± 2.2 Hz], $P = 0.116$, $z = 1.572$, $r = 0.31$). Significantly greater tone was detected in the contralateral limb at pre-training (6.8 ± 7.3% [2.7 ± 2.7 Hz], $P = 0.011$, $z = 2.551$, $r =$

0.50), however no difference was detected between limbs after training (3.2 ± 5.5% [1.3 ± 2.1 Hz], $P = 0.075$, z = 1.782 , r = 0.35).

Gastrocnemius medialis mechanical properties

Wilcoxon tests revealed a significant increase in GM stiffness after training (Table 1) in the trained limb (7.5 ± 7.9% [22.1 ± 23.4 $N \cdot m^{-1}$], $P = 0.010$, z = 2.588, r = 0.51) but not in the contralateral limb (5.8 ± 13.5% [13.2 ± 45.6 $N \cdot m^{-1}$], $P = 0.311$, z = 1.013, r = 0.20). No significant differences were detected in stiffness between limbs at pre- (1.5 ± 8.9% [8.4 ± 36.0 $N \cdot m^{-1}$], $P = 0.650$, z = 0.454, r = 0.09) or post-training (0.3 ± 5.0% [0.5 ± 14.4 $N \cdot m^{-1}$], $P = 0.576$, z = r = 0.11).

No significant interaction effect was revealed for GM elasticity ($F_{1,\,12} = 0.120$, $P = 0.735$, $\eta_p^2 = 0.010$). Main effect analyses revealed no significant effect of limb ($F_{1,\,12} = 1.960$, $P = 0.187$, $\eta_p^2 = 0.140$) but a significant effect of time ($F_{1,\,12} = 8.607$, $P = 0.013$, $\eta_p^2 = 0.418$) with lower elasticity post-training (collapsed limb data = -13.6 ± 19.3% [-0.133 ± 0.190 arb], $d = -0.70$; trained limb = -12.2 ± 17.1% [-0.117 ± 0.164 arb], $d = -0.72$; contralateral limb = -10.8 ± 18.9% [-0.098 ± 0.171 arb], $d = -0.57$).

Wilcoxon tests revealed a significant increase in GM tone after training in the trained limb (4.6 ± 5.9% [0.75 ± 0.98 Hz], $P = 0.036$, z = 2.097, r = 0.41) but not in the contralateral limb (3.4 ± 7.0% [0.49 ± 1.11 Hz], $P = 0.152$, z = 1.433, r = 0.28). No significant differences were detected in tone between limbs at pre- (0.8 ± 5.6% [0.11 ± 0.92 Hz], $P = 0.625$, z = 0.489, r = 0.10) or post-training (2.0 ± 3.8% [0.37 ± 0.69 Hz], $P = 0.075$, z = 1.782, r = 0.35).

Soleus mechanical properties

No significant interaction effect was revealed for Sol stiffness ($F_{1, 12} = 0.135$, $P = 0.720$, $\eta_p^2 = 0.011$). Main effect analyses revealed no significant effect of group ($F_{1, 12} = 0.187$, $P = 0.673$, $\eta_p^2 = 0.015$) but a significant effect of time ($F_{1, 12} = 5.634$, $P = 0.035$, $\eta_p^2 = 0.320$) with greater stiffness (Table 1) after training (collapsed limb data = 3.1 ± 6.7% [15.8 ± 38.5 $N \cdot m^{-1}$], $d = 0.41$; trained = 3.7 ± 7.8% [17.7 ± 41.6 $N \cdot m^{-1}$], $d = 0.43$; contralateral = 2.5 ± 5.6% [13.9 ± 36.6 $N \cdot m^{-1}$], $d = 0.38$).

No significant interaction ($F_{1, 12} = 2.304$, $P = 0.965$, $\eta_p^2 = 0.000$) or main effects of time ($F_{1, 12} = 0.002$, $P = 0.343$, $\eta_p^2 = 0.075$) or limb ($F_{1, 12} = 0.975$, $P = 0.343$, $\eta_p^2 = 0.075$) were detected for Sol elasticity.

Wilcoxon tests revealed significant increases in Sol tone after training in the trained (4.3 ± 7.1% [0.93 ± 1.53 Hz], $P = 0.046$, z = 1.992, r = 0.39) and contralateral (2.3 ± 3.2% [0.51 ± 0.79 Hz], $P = 0.046$, z = 1.992, r = 0.39) limbs. No significant differences in tone were detected between limbs at pre- (0.2 ± 10.8% [0.16 ± 2.50 Hz], $P = 0.861$, z = 0.175, r = 0.03) or post-training (1.2 ± 4.5% [0.26 ± 1.15 Hz], $P = 0.249$, z = 1.153, r = 0.23).

Soleus muscle thickness

A significant interaction effect was detected for Sol thickness ($F_{1, 12} = 5.586$, $P = 0.036$, $\eta_p^2 = 0.318$), with a significant increase in thickness (Figure 3A) observed in the trained limb (5.4 ± 7.5% [0.8 ± 1.0 mm], $P = 0.018$, $d = 0.76$) but not in the contralateral limb (0.8 ± 5.1% [0.1 ± 0.7 mm], $P = 0.799$, $d = 0.07$). No significant differences in thickness were detected between limbs at pre- (-2.0 ± 9.1% [-0.3 ± 1.3 mm], $P = 0.395$, $d = -0.25$) or post-training (2.6 ± 11.6% [0.4 ± 1.6 mm], $P = 0.396$, $d = 0.24$).

Gastrocnemius medialis muscle thickness, fascicle length, and fascicle angle

A significant interaction effect was detected for GM thickness ($F_{1,12} = 6.885$, $P = 0.022$, $\eta_p^2 = 0.365$), with a significant increase in thickness (Figure 3B) observed in the trained (6.1 ± 8.1% [1.1 ± 1.3 mm], $P = 0.015$, $d = 0.79$) but not the contralateral limb (0.6 ± 5.6% [0.1 ± 1.0 mm], $P = 0.699$, $d = 0.11$). No significant difference was detected between limbs at pre-training (0.2 ± 8.0% [0.0 ± 1.5 mm], $P = 1.000$, $d = 0.00$), however thickness was significantly greater in the trained limb after training (5.6 ± 7.6% [0.9 ± 1.3 mm], $P = 0.023$, $d = 0.73$).

A significant interaction effect was detected for GM fascicle length ($F_{1,12} = 13.833$, $P = 0.003$, $\eta_p^2 = 0.535$), with a significant increase in fascicle length observed in the trained (7.6 ± 8.5% [3.7 ± 3.9 mm], $P = 0.005$, $d = 0.94$) but not the contralateral limb (-0.3 ± 5.8% [-0.2 ± 2.9 mm], $P = 0.826$, $d = -0.06$). No significant differences in fascicle length were detected between limbs at pre- (-2.0 ± 7.7% [-1.1 ± 4.1 mm] $P = 0.335$, $d = -0.28$) or post-training (5.8 ± 9.2% [2.7 ± 4.6 mm], $P = 0.053$, $d = 0.59$).

No significant interaction ($F_{1,12} = 1.667$, $P = 0.221$, $\eta_p^2 = 0.122$) or main effects of time ($F = 0.051$, $P = 0.826$, $\eta_p^2 = 0.004$) or limb ($F = 0.886$, $P = 0.365$, $\eta_p^2 = 0.069$) were detected for GM fascicle angle.

Isometric plantarflexor strength

No significant interaction effect was revealed for isometric torque ($F_{1,12} = 3.170$, $P = 0.100$, $\eta_p^2 = 0.209$). Main effect analyses revealed a significant effect of time ($F_{1,12} = 46.132$, $P < 0.001$, $\eta_p^2 = 0.794$), with greater isometric torque (Figure 4A) after training (collapsed limb data = 39.3 ± 31.0% [33.7 ± 18.8 N·m], $d = 1.80$; trained limb = 40.6 ± 28.0% [36.7 ± 18.9 N·m], $d = 1.94$; contralateral limb = 38.1 ± 34.9% [30.7 ± 18.9 N·m], $d = 1.63$). Main effect analyses also revealed a significant effect of limb ($F_{1,\,12} = 9.177$, $P = 0.010$, $\eta_p^2 = 0.433$) with greater isometric torque in the trained limb (collapsed time data = 6.9 ± 10.6% [6.6 ± 10.2 N·m], $d = 0.65$; pre-training = 5.6 ± 11.0% [3.6 ± 8.6 N·m], $d = 0.42$; post-training = 8.3 ± 10.5% [9.6 ± 11.2 N·m], $d = 0.86$).

Eccentric plantarflexor strength

A significant interaction effect was detected for eccentric torque ($F_{1,\,12} = 14.437$, $P = 0.003$, $\eta_p^2 = 0.546$) , with significant increases in eccentric strength (Figure 4B) in the trained (67.0 ± 35.3% [61.7 ± 29.0 N·m], $P < 0.001$, $d = 2.13$) and contralateral (46.7 ± 37.1% [40.5 ± 23.7 N·m], $P < 0.001$, $d = 1.71$) limbs observed. No significant difference was detected at pre-training between limbs (-0.8 ± 15.5% [-2.0 ± 13.6 N·m], $P = 0.613$, $d = -0.14$), however eccentric strength was significantly greater in the trained limb after training (13.2 ± 14.7% [19.3 ± 22.1 N·m], $P = 0.009$, $d = 0.87$).

Correlations

Where between-limb changes were examined, significant correlations were detected between the changes in trained and contralateral limb dorsiflexion ROM ($r = 0.59$, $P = 0.033$ [Figure 5A]), isometric ($r = 0.79$, $P = 0.001$) and eccentric ($r = 0.73$, $P = 0.005$) torques (Figure 5B). Where within-limb changes were examined, in the trained limb a significant correlation was detected between the changes in eccentric strength and GM thickness ($rs = 0.56$, $P = 0.049$). In the contralateral limb, significant correlations were detected between the change in dorsiflexion ROM and changes in plantarflexor stretch tolerance ($r = 0.60$, $P = 0.030$) and elastic energy ($r = 0.70$, $P = 0.008$), and between the changes in stretch tolerance and elastic energy ($r = 0.65$, $P = 0.016$). Significant correlations were also detected between the changes in isometric and eccentric strength ($r = 0.78$, $P = 0.002$).

DISCUSSION

The primary aim of the present study was to examine the direct and cross-education effects of isokinetic eccentric training on dorsiflexion ROM in the trained and contralateral limbs, and to identify potential mechanisms associated with the changes in ROM in healthy adults. In agreement with our hypothesis, a large increase in passive dorsiflexion ROM (~10°) was detected in the trained limb, which is consistent with recent meta-analyses summarizing passive ROM changes across several lower-limb joints following eccentric training (26, 29). Simultaneous large increases in stretch tolerance (~96%), elastic energy storage (~161%), muscle fascicle length (~8%), and passive MTU stiffness (30%) were also detected. These findings are consistent with similar studies (31, 32) and recent meta-analyses (26, 29) highlighting the potential for eccentric training to simultaneously influence a broad range of neurological, mechanical, and architectural characteristics associated with ROM. These wide-ranging adaptations likely explain the substantially greater increases in ROM following eccentric training than those reported following muscle stretching programs (53), which are usually associated with a narrower neurological (i.e., stretch tolerance) adaptative profile (2, 54). Furthermore, as twice-weekly eccentric training was performed in the present study, the results are indicative of isokinetic eccentric training being a more efficient intervention than traditional muscle stretching because muscle stretching sessions were performed daily in the studies included in the previous review (53). However, despite these concomitant adaptations, no significant correlations were observed between the changes in ROM and other neurological, mechanical, or architectural measures in the trained limb. Therefore, whilst the present data confirm a substantial ROM increase and a wide-ranging adaptive profile influencing several ROM-associated characteristics, the primary mechanisms underpinning the increase in ROM following eccentric training remain unclear.

The present study is the first to examine and then identify a cross-education (cross-transfer) effect on joint ROM in the contralateral limb following eccentric training, where a 4° increase in dorsiflexion range was observed, equating to ~40% of the increase observed in the trained limb. In agreement with our hypothesis, the increase in ROM in the contralateral limb was associated with large increases in stretch tolerance (~40%) and elastic energy potential (~48%), with strong correlations observed between the change in ROM and changes in both stretch tolerance (r = 0.60) and elastic energy (r = 0.70), indicative of neurological adaptations underpinning the change in ROM in the contralateral limb. Furthermore, significant correlations were detected between the changes in trained and contralateral limb dorsiflexion ROMs (r = 0.59), suggesting a subject-specific adaptive profile in which greater changes in ROM in the trained limb were associated with greater changes in the contralateral limb. These findings are consistent with adaptations recently reported following high- but not low-intensity static muscle stretching training (42), indicative of greater tissue loading being important for promoting the cross-education effect on ROM. The mechanisms underpinning the increased stretch tolerance (i.e., altered pain sensitivity) are unknown, although mechanisms associated with Gate Theory are commonly suggested (55, 56) where type III afferents are thought to inhibit pain perception as pressure receptors associated with larger myelinated neurons connect to the same spinal interneurons as unmyelinated nociceptive fibers (type IV afferents) within the spinal horn (57). Regardless of the mechanisms, the present findings offer a proof-of-concept that isokinetic eccentric training may be a strong driver of mechanical and functional adaptation.

In addition to the wide-ranging structural and functional adaptations reported in the present study, other studies have also confirmed eccentric training-induced increased fascicle length

(26), a rightward shift in the force-length curve indicative of sarcomerogenesis (33), and the remodeling of both collagenous and non-collagenous extra-cellular matrix components (34), likely influence passive tissue stiffness and ROM. These adaptations have clear clinical relevance for populations where abnormal extra-cellular matrix deposition (35, 36) can result in the formation of contractures, shortened fascicle length, and longer sarcomeres, which result in high tissue stiffness and permanent muscle shortening, compromising ROM and muscle function. Collectively, these findings suggest that eccentric exercise may prove to be a useful exercise prescription tool in clinical populations (e.g., traumatic brain injury, spinal cord injury, stroke, cerebral palsy) who demonstrate ongoing pain and ROM (e.g., spasticity and contracture) deficits, particularly when traditional muscle stretching practices are ineffective (6–9). Whilst the increased passive ROM and fascicle length are promising for clinical populations where these factors are compromised, a limitation of the present study was that the intervention was performed in a healthy population. An important next step is to assess both the direct (trained) and cross-education (contralateral) effects of isokinetic eccentric training in these clinical cohorts. Furthermore, the inclusion of a range of functional performance tests to examine the impact on gait (e.g. stride length, toe clearance, knee flexion and hip abduction), strength (e.g. sit-to-stand, stair descent), and dynamic balance (e.g. timed-up-and-go) will determine the ability of this intervention to influence clinical 'field-based' measures of muscle function.

The cross-education effects of resistance training on strength are well-described (38). One recent meta-analysis confirmed a significantly greater cross-education effect after eccentric training than other contraction modes (37). In the present study, very large increases in eccentric (~67%) and isometric (41%) plantarflexor strength were observed in the trained limb alongside moderate increases in GM and Sol thickness (~5-6%) and a large increase in Achilles tendon stiffness (5.3 ± 4.9%); such findings are consistent with studies of similar duration in both young (31) and older adults (51). Additional to this, however, strong cross-education effects were detected in eccentric (~47%) and isometric (~38%) plantarflexor strength, also consistent with similar previous studies after eccentric training (39-77%) (58, 59). The increases in isometric and eccentric strength in the contralateral limb equate to ~67-90% of the change in the trained limb, magnitudes consistent with previous results (58) after eccentric-only training (~85%) but substantially greater than those previously reported (~35%) after traditional resistance training (38). The changes in contralateral (untrained limb) strength in the present study occurred without changes in musculotendinous morphology or mechanical properties, indicating a primary role of central rather than peripheral adaptations. Given that a systematic review (60) has confirmed the cross-education benefits (31-46%) of resistance training on muscle strength in hemiparetic stroke survivors, the greater changes detected in the present study may have important implications for exercise prescription in clinical (e.g., hemiplegic stroke, cerebral palsy, multiple sclerosis) and athletic (e.g., unilateral limb injury) populations where both strength and the ability to exercise the affected limb are compromised. Whilst these data are encouraging, a limitation of the present study was the use of an isokinetic dynamometer to perform the eccentric-only contractions. This laboratory-based equipment is expensive, not portable, and is not realistic for scalability to address functional impairments at a population level. As cross-education effects have been reported in other contraction modes (37), the efficacy of, and adherence to, field-based resistance training programs using a range of contraction modes need to be performed to determine their effectiveness.

CONCLUSION

The increases in both passive ROM and strength after eccentric training in the trained limb are substantially greater than those previously reported after traditional muscle stretching or resistance training programs. These changes were associated with a broad range of neurological, mechanical, and architectural adaptations, which may have important implications for athletic and clinical populations in which these characteristics influence athletic performance and activities of daily living. Potentially of greater importance, these are the first data to identify a substantial cross-education effect of eccentric training on maximum passive joint ROM and confirm previously reported large cross-education effects on strength in contralateral homologous muscles. The significant changes in ROM and strength in the untrained limb occurred without peripheral mechanical or architectural changes, so central neurological adaptations likely underpin the ROM (e.g., stretch tolerance) and strength (e.g., changes in corticospinal excitability and/or inhibition) improvements. The capacity for a single intervention to influence multiple mechanical and functional outcomes may have important implications for exercise prescription in populations that demonstrate unilateral ROM (e.g., muscle strain, joint injury, spasticity, contracture) or strength (e.g., hemiparesis) deficits, and the current data provide proof-of-concept support for future studies to assess the impact of isokinetic eccentric exercise training in clinical populations.

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Author Contributions

All authors were involved in conception and design. ADK, JCT and BAB performed the data collection and ADK conducted the data analyses. All authors contributed to the writing and revision of the manuscript.

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Retention rights statement

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Data availability statement

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CONFLICTS OF INTEREST

No conflict of interest exist. The results of the present study do not constitute endorsement by ACSM. The results of the study are presented clearly, honestly, and without fabrication, falsification, or inappropriate data manipulation.

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TABLE AND FIGURE CAPTIONS

Table 1. Mean (± SD) or median (IQR) stiffness, tone, and elasticity of the Achilles tendon, gastrocnemius medialis and soleus muscles in the trained and contralateral limbs during pre- and post-training assessments.

Figure 1. Mean (± SD) dorsiflexion range of motion (ROM [A]) and muscle-tendon unit (MTU) stiffness (B) in the trained and contralateral limbs during pre- and post-training assessments. Significant increases in ROM were detected in the trained and contralateral limbs with a significant difference between limbs also detected at post-training. A significant increase in MTU stiffness was detected in the trained limb with a difference between limbs also detected post-training. *Significance accepted at $P < 0.05$.

Figure 2. Mean (± SD) plantarflexor stretch tolerance (A) and elastic energy potential (B) in the trained and contralateral limbs during pre- and post-training assessments. Significant increases in stretch tolerance and elastic energy were detected in the trained and contralateral limbs after training with a significant difference between limbs also detected post-training. *Significance accepted at $P < 0.05$.

Figure 3. Mean (± SD) soleus (Sol [A]) and gastrocnemius medialis (GM [B]) muscle thickness in the trained and contralateral limbs during pre- and post-training assessments. Significant increases in GM and Sol thickness were detected in the trained and contralateral limbs with a significant difference in GM thickness between limbs also detected post-training. *Significance accepted at $P < 0.05$.

Figure 4. Mean (± SD) isometric (A) and eccentric (B) plantarflexor strength in the trained and contralateral limbs during pre- and post-training assessments. Significant increases in isometric and eccentric strength were detected in the trained and contralateral limbs after training with a difference in eccentric strength between limbs also detected post-training. *Significance accepted at $P < 0.05$.

Figure 5. Correlations between the trained and contralateral limb changes (Δ) in dorsiflexion range of motion (ROM [A]) and plantarflexor torques (B). Significant correlations were detected between the changes in trained and contralateral limb dorsiflexion ROM ($r = 0.59$), isometric ($r = 0.79$) and eccentric ($r = 0.73$) torques. Significance accepted at $P < 0.05$.