Concentric versus eccentric training: effect on muscle strength, regional morphology and architecture

Jack Benford[1], Jonathan Hughes[1], Mark Waldron[2,3], Nicola Theis[1*]

[1] School of Sport and Exercise, University of Gloucestershire, Cheltenham, United Kingdom
[2] College of Engineering, Swansea University, Swansea, United Kingdom
[3]School of Science and Technology, University of New England, Armidale, New South Wales, Australia

***Corresponding Author**
Dr Nicola Theis
School of Sport and Exercise,
University of Gloucestershire,
Longlevens, Gloucester, UK
GL2 9HW

Orcid ID
Nicola Theis: https://orcid.org/0000-0002-0775-1355
Mark Waldron: https://orcid.org/0000-0002-2720-4615
Jonathan Hughes: https://orcid.org/0000-0002-9905-8055

Summary

The different architectural adaptations and the regional changes that occur with eccentric (ECC) vs. concentric (CON) muscle actions are not fully understood. The purpose was to investigate regional changes in vastus lateralis muscle (VL) after ECC and CON training. Sixteen males (23 ± 3 y) performed ECC or CON twice weekly over 5 weeks, using a single-leg design. Both training modalities caused similar increases in knee extensor strength (measured with dynamometry) (10-13%) and muscle volume (8%) (measured with 3D ultrasound) after 5-weeks of training. Anatomical cross-sectional area at the mid-point of the muscle was greater after CON training (9%), but greater at the distal end after ECC training (8%). CON training increased fascicle angle at the mid-point (8%), with little change at the distal end (2%). There was a small increase in fascicle length at the mid-point after CON training (3%). Conversely, ECC training caused a greater variation in regional and architectural adaptations. Fascicle length increased at both the mid-point (6%) and distal ends (8%) after ECC training, and similar changes in fascicle angle were also observed in both regions (3-4%). Different region-specific changes are evident after CON and ECC training, with implications for performance and injury risk.

Keywords Muscle · Strength · Concentric · Eccentric · Architecture

Abbreviations

CON – Concentric training
ECC – Eccentric training

Declarations

Funding None

Conflicts of interest/Competing interests There were no conflicts of interest

Introduction

Skeletal muscles produce force by shortening (concentric, CON), lengthening (eccentric, ECC) or contracting isometrically, but the two actions differ in the mechanisms by which force is generated (Franchi et al., 2017). Eccentric actions during maximal voluntary isokinetic exercise usually results in lower muscle activity than CON actions (Fang et al., 2001), but the maximal attainable forces are considerably higher (Franchi et al., 2017). During ECC actions, titin, a protein spanning half the sarcomere, contributes to active stress when the muscle lengthens, acting as a molecular spring and increasing force output compared to CON actions (Herzog, 2014). This notion that ECC actions produce greater force than CON actions suggests that greater hypertrophic responses could be achieved with ECC, compared to CON training (Roig et al. 2009). However, the influence of muscle action mode on strength improvements and muscle hypertrophy is contentious (Wernbom et al. 2007; LaStayo et al. 2014), with some reports of ECC training producing superior adaptations (Hortobagyi et al. 1996; Seger et al. 1998; Vikne et al. 2006) and others showing similar strength and hypertrophic adaptations (Blazevich et al. 2007; Moore et al. 2012; Franchi et al. 2014).

Recent observations suggest that these strength and hypertrophic responses to ECC and CON training might be achieved by differing regional growth and architectural adaptations (Franchi et., 2014; Seger et al., 1998). For example, Franchi et al. (2014) showed different regional patterns of muscle growth in the quadriceps after 10 weeks of CON and ECC training, measuring anatomical cross-sectional area. They found that distal hypertrophy (ECC 8% *vs*. 2% CON) evident after ECC training and larger mid-belly increases after CON training (ECC 7 *vs*. CON 11%). These regional differences might also be accompanied by different architectural characteristics, caused by mechanisms of structural remodelling that are specific to CON and ECC training stimuli. Recent findings have shown that ECC exercise results in a markedly greater increase in fascicle length (Seynnes et al. 2007; Potier et al. 2009) of up to 7% (Franchi, 2014), likely reflecting an increase in the number of sarcomeres in series (Williams & Goldspink 1971; Williams 1990; Lynn & Morgan 1994). In contrast, CON training has been shown to promote greater changes in fascicle angle of up to 30%, compared to a 5% increase after ECC training

(Franchi et al., 2014). These changes might demonstrate a differential mechanism to increase muscle size and strength by the addition of sarcomeres in parallel following CON training (Kawakami et al. 1993; Narici & Maganaris 2007). However, fascicle length in many previous studies has been estimated using a trigonometric extrapolation technique from 2D ultrasound images (Franchi et al., 2014, 2015), which has been shown to underestimate vastus lateralis fascicle length by as much as 12.6-20.3% compared to extended field of view ultrasound (Noorkoiv et al., 2010; Oranchuk et al., 2020). Trigonometric estimation relies on the assumption that the non-imaged fascicles and superficial aponeuroses are linear, which is rarely true in skeletal muscle (Blazevich et al., 2006), particularly in the vastus lateralis, where Noorkoiv and colleagues (2010) noted that curvature existed in almost every visible fascicle, especially at the distal ends, close to the superficial and deep aponeuroses. Consequently, measuring fascicles that are curved, or those that are in muscle regions where the aponeuroses are curved, by means of trigonometric extrapolation can lead to erroneous results in measures of both fascicle length and fascicle angle. In addition, measures of fascicle length and angle in response to CON and ECC training to date, have been limited to imaging only fascicles that lie at the muscle belly (Franchi et al., 2015), with the assumption that changes in architecture observed in this region would be representative of changes along the whole muscle. However, given the regional changes that have been reported in anatomical cross-sectional area with CON and ECC training, this assumption might not be correct. In fact, the greatest change in fascicle length and fascicle angle after ECC training may actually be observed at the distal ends of the muscle, where the stretch stimulus is greatest (Dix & Eisenberg, 1990).

Since changes in architecture can influence the functional properties of muscles (Narici, 1999; Lieber & Fridén, 2000; Narici et al., 2016), a thorough understanding of skeletal muscle remodelling in response to different training modalities is fundamental. For example, a change in fascicle length can shift the optimum length-tension relationship and maximum shortening velocity of the muscle, with notable effects on performance and injury prevention (Brughelli & Cronin, 2007). Variability in architectural characteristics at different regions of the muscle is also of particular importance when trying to model and predict the behaviour of a specific muscle, as large intra-muscular differences can have a considerable effect on estimated force-velocity properties of muscles (Blazevich, 2006) and whole muscle force (Lieber & Friden, 2000). Although, some research has been focused on architectural responses to ECC training, fewer studies have compared isolated CON *vs.* isolated ECC exercise in terms of both architectural and regional changes in the muscle. Thus, the aim of this study was to assess differences in knee extensor muscle strength, and regional changes in the morphological and architectural properties of the vastus lateralis muscle after 5 weeks of CON or ECC exercise. We hypothesised that regional muscle growth would be different between training modalities, with greater muscle growth in the mid-belly after CON training, and greater distal growth after ECC training. We also hypothesised that ECC training would cause significantly greater changes in whole fascicle length, whilst CON training would result in significantly greater fascicle angles but that these changes would also be region-specific.

Methodology

Participants

Sixteen physically active (training for >60 mins per day, minimum 3 days per week), healthy males (mean ± SD: age: 23 ± 3 years; stature: 181.7 ± 7.3 cm; body mass: 76.5 ± 11.3 kg) and with no history of lower-limb injury in the past 12 months, were recruited to participate in this study. Sample size was based on an alpha level of 0.05, power of 0.8 and effect size of 0.72 (Seager et al., 1998; Franchi et al., 2014) 0.72-3.6) (G*Power), giving an estimated sample size of fourteen. All participants provided written informed consent prior to testing. This study was performed in line with the principles of the Declaration of Helsinki. Approval was granted by the Ethics Committee of University of Gloucestershire.

Study Design

Participants underwent 5 weeks of unilateral resistance training. A simple randomisation was conducted, whereby one leg was randomly assigned to a CON training condition and the other to an ECC training condition (Maeo et al., 2018), which was counterbalanced between dominant and nondominant legs (dominant leg assigned to concentric, *n* = 8; dominant leg assigned to eccentric, *n* = 8). Pre- and post-measures of knee extensor strength and vastus lateralis morphology and architecture were assessed at baseline (week 0) and in week 6, respectively. Particpants were asked to maintain a consistent nutritional intake over the course of the training period.

Procedures

Muscle strength

Isometric (30° and 70°) and isokinetic (concentric and eccentric) strength measures were performed on an isokinetic dynamometer (Biodex System 3 Isokinetic Dynamometer, New York) across two separate days to minimise fatigue. In the first session, participants performed one isometric knee extension manoeuvre (30° or 70°) on each leg, followed by one isokinetic knee extension manoeuvre (concentric or eccentric) on each leg. In the second session the remaining measures were completed. The order of measures was randomised between the two sessions and before and after the intervention.

Participants were familiarised with the testing procedures within three days of baseline testing. For each session, participants were secured in a seated position on the dyanmometer, with the lateral epicondyle of the knee joint aligned with the centre of rotation of the dynamometer arm. To reduce the risk of leg or upper body movement during contractions, stabilisation straps were applied tightly over the ankle, thigh and torso, and participants were instructed to cross their arms over their chest. Anatomical zero was set with the dynamometer arm in a vertical position (measured with a spirit level). In order to set each participant's full range of motion they were instructed to move the leg comfortably into full extension and then full flexion whilst the range of motion limits were set. This range was replicated between visits. Following a warm-up of submaximal contractions, participants performed five isometric maximal knee extension actions (120 s rest between each maximal contraction) with a 5 s hold, at 30° or 70°, with a 5-min rest period between sets. Visual feedback was provided on the screen in front of participants to encourage them to maintain maximal torque for the full 5 s. After a further mandatory 5-min rest period, participants performed two sets of five maximal eccentric or concentric actions through a full range of motion at an angular velocity of 30°·s^{-1}. Verbal encouragement was provided throughout, using the same phrases and by the same researcher across all participants and visits. Peak torque from each isometric test, and the concentric and eccentric trials were averaged across the five repetitions to give a final torque value.

Morphological and architectural measures

All morphological (muscle volume and anatomical cross-sectional area) and architectural measures (fascicle length and fascicle angle) were taken on the vastus lateralis muscle and measured using a 3D ultrasound method (Noorkoiv et al., 2018; Macgillivray et a., 2009. For this method, a rigid body of four markers is secured to the handle of an ultrasound probe. As the probe is moved over the object of interest, its position and orientation in space are recorded along with the 2D US images (B-scans) to form a 3D dataset, which describes the scan volume. Slices through this scan volume can be imaged, and from these images and their positions, a 3D lattice volume can be reconstructed (Macgillivray et a., 2009). Postprocessing algorithms are then used to determine the object's parameters such as length, area, perimeter and volume.

A standard two-dimensional ultrasound system (USmart 3300, Ultrasound system: Terason, Burlington, MA, USA) with a 50 mm, 12.5 MHz, linear array probe set to a depth of 8 cm and an optical tracking system (Optitrack V120:Trio (NaturalPoint, Inc., Oregon, USA) constituted the 3D US system. The optical tracking system was mounted on a tripod and used to track the position and orientation of the four markers on the ultrasound probe. 2D B-scan images from the ultrasound machine were combined with positional information from the optical tracking system using dedicated software (Stradwin v5.1 software (Mechanical Engineering, Cambridge University, Cambridge, UK; http://mi.eng.cam.ac.uk/~rwp/stradwin (Treece, 2003) on an additional PC (Pentium 4 3.60 GHz PC running Microsoft Windows XP; Microsoft Corporation, Redmond, WA, USA) to compute 3D US images in near real-time.

Muscle volume and anatomical cross-sectional area

Prior to assessments, participants were asked to lie prone on an examination table for 10-min to allow fluid shifts in the muscle to stabilise. After this point, the knee was angled to 25° and secured in position with foam inserts under the knee. This offered the best view of the markers on the ultrasound probe to the position sensor. Participants were asked to relax the muscles of the thigh during the scanning procedure. To identify the vastus lateralis, the line connecting the most prominent portion of the greater trochanter and the lateral femoral epicondyle (found by palpation) was marked on the skin. Sweeps of the muscle were obtained by moving the probe across the thigh starting at the most prominent portion of the greater trochanter (proximal end) and scanning to the lateral femoral epicondyle (distal end). The same start and end points of the sweeps were used to guide the standardisation of vastus lateralis muscle length and anatomical cross-sectional area analyses. For the estimation of vastus lateralis anatomical cross-sectional area and muscle volume, the probe was orientated in a transverse plane, perpendicular to the muscle. In all cases, the VL muscle was wider than the ultrasound probe and therefore multiple sweeps were taken. The first sweep was performed along the lateral side of the VL, so that the lateral border of the muscle could be visualised. Starting at the proximal end of the muscle, the ultrasound probe was moved over the muscle from the proximal to distal end using a continuous sweeping movement. The probe was then returned to the start position (prominent portion of greater trochanter) and moved approx. 4 cm medially so the mid-section of the muscle was visible. A second sweep from proximal to distal was then performed in this position to capture the mid-section of the muscle. A third and final sweep was then performed which incorporated the medial border of the VL muscle. To ensure the slices can be reconstructed into a 3D volume, the pressure and speed of each sweep must be consistent, with a small degree (approximately 1 cm) of overap between scans. A 2-cm thick echogenic ultrasound gel pad (Aquaflex, Parker Laboratories, NJ, USA) was positioned between the transducer and the skin to conform to the shape of the thigh when light pressure was applied and to avoid gaps at the lateral edges of the image. Echogenic gel was also applied over the skin to improve acoustic coupling and reduce friction as the probe was moving over the skin.

Reconstruction of volume, anatomical cross-sectional area and length measurements were performed using Stradwin software, which integrates the stack of 2D US images with positional information from the probe to form a 3D volume data set. Although minimal probe pressure during the scanning procedure was assured, the position and pressure correction functions were applied to the data prior to digitisation to increase the clarity of slices and precision of the data, as suggested by Treece et al. (2002). For the digitisation process, the visible VL muscle in each 2D cross-sectional slice was traced. As there were multiple sweeps, Stradwin divided the space into a number of partitions, with each partition associated with a particular sweep. Once all partitions and all slices were digitised, the sweeps were integrated and adjusted to be perpendicular to the longitudinal axis of the VL muscle. The segmented data was exported as voxels (resolution = 1 pixel width). The 3DUS image acquisition and analysis was practiced by the researcher on 10 participants prior to undertaking this study (approximately 35 hours of training and practicing).

Anatomical cross-sectional area was measured by averaging five axial scans at the mid-point of the muscle (50% muscle length), assumed to represent the muscle belly; and an average of five axial scans at the distal end of the muscle (70% muscle length). Axial plane scans along the entire length of the VL were also calculated and combined to give muscle volume. On average, the number of axial scans obtained in each participant was the same for the baseline and post-training periods. Volume was calculated as:

$$\text{Volume (cm}^3) = \Sigma \text{ anatomical cross-sectional area (slice thickness + gap between slices)}$$

The absolute difference between the same series of images digitised twice was 2.4 ± 1.9% for volume and 1.8 and 1.4% for ACSA.

Fascicle length and angle

To measure whole fascicle length and angle, the ultrasound probe was orientated in the sagittal plane to the muscle, to give the largest, continuous vastus lateralis fascicle visualisation. In accordance with the method of Noorkoiv et al. (2010), fascicle path was drawn on the skin according to the path seen from the real-time ultrasound image by moving the probe along the muscle. To record whole fascicle length, a single sweep of the muscle was taken starting from the proximal end of the muscle and moving to probe along the muscle to the distal end, maintaining a consistent speed and pressure and following the curvature of the line drawn on the skin. This was repeated three times. Vastus lateralis fascicle length was measured in ImageJ (National Institutes of Health, USA) using the curved line tool, from the insertion on the superficial aponeurosis to the deep aponeurosis. Three visible fascicles from approximately the mid-point of the muscle (50% muscle length) and the distal point of the muscle (70% muscle length) were measured and averaged (coefficient of variation = 1.7%). The angle of each visible fascicle at the mid-point and distal end was measured as the angle between the fascicle and the deep aponeurosis using ImageJ (National Institutes of Health, USA) (coefficient of variation = 1.3%).

Resistance Training Protocol

Resistance training on the isokinetic dynamometer was performed twice weekly for 5 weeks with a minimum of 48 h between sessions (Maeo et al., 2018; Zatsiorsky & Kraemer. 2006). Before each training session, all participants completed a warm-up of eight submaximal efforts at $30°\cdot s^{-1}$. To train the concentric limb, participants performed eight continuous maximal knee extension manoeuvres at $30°\cdot s^{-1}$. Each maximal knee extension was followed by passive knee flexion to return to the starting point. To train the eccentric leg, participants again performed eight continuous maximal knee extension manoeuvres at $30°\cdot s^{-1}$ but this time, against the resistance of the dynamometer moving in the opposite direction. Once full flexion was reached, the dynamometer was passively returned to the extended position. For both legs, participants completed four sets of eight maximal voluntary contractions (Blazevich et al., 2007) with 1-min rest between sets. Both concentric and eccentric actions were performed through each participant's full range of motion, which was matched at each visit. Participants were instructed to perform maximally during all four sets, and verbal encouragement was provided throughout. During the training period, participants were instructed to refrain from any form of intensive resistance training and to record any activities they took part in each week.

Data Analysis

All dependent variables were assessed for differences in training condition (CON *vs.* ECC) and time (pre *vs.* post) and were analysed using a series of two-way repeated measures ANOVA's (α level of 0.05) (IBM SPSS Statistics, Version 24.0, Armonk, NY: IBM Corp). In case of a significant condition × time interaction, *post hoc* paired *t*-tests with Bonferroni correction were conducted. Training data were presented as absolute values and all other variables were presented as percentage change from baseline.

Results

Training data, expressed as group means across the 5 weeks, is presented in table 1. Training attrition was 100% with all participants completing all training sessions. There was a significant condition × time interaction for peak torque measured in week 1 and week 5, in CON and ECC conditions ($F_{(1,15)} = 18.736$, $P < 0.001$). *Post hoc* tests demonstrated increases in peak training torque between week 1 and 5, in both CON ($t_{(31)} = -6.076$, $P < 0.001$) and ECC conditions ($t_{(31)} = -7.537$, $P < 0.001$), with peak torque greater in the ECC condition compared to the CON condition at week 1 ($t_{(31)} = -6.111$, $P < 0.001$) and week 5 ($t_{(31)} = -6.329$, $P < 0.001$).

Table 1

Muscle strength

Pre and post values for each condition are presented in Table 2. For knee extensor strength variables, there were no significant condition × time interactions (isometric strength 30°: $F_{(1,15)} = 0.084$, $P = 0.776$; isometric strength 70°: $F_{(1,15)} = 0.011$, $P = 0.918$; concentric strength: $F_{(1,15)} = 0.211$, $P = 0.652$; eccentric strength: $F_{(1,15)} = 0.011$, $P = 0.916$) and no differences between CON or ECC conditions (isometric strength 30°: $F_{(1,15)} = 2.941$, $P = 0.107$; isometric strength 70°: $F_{(1,15)} = 0.025$, $P = 0.904$; concentric strength: $F_{(1,15)} = 0.001$, $P = 0.972$; eccentric strength: $F_{(1,15)} = 1.405$, $P = 0.254$). There were significant main effects of time for all knee extensor strength variables, (isometric strength 30°: $F_{(1,15)} = 26.211$, $P < 0.001$; isometric strength 70° $F_{(1,15)} = 11.247$, $P = 0.004$; concentric strength: $F_{(1,15)} = 27.780$, $P < 0.001$; eccentric strength: $F_{(1,15)} = 11.828$, $P = 0.004$), with *post hoc* tests showing increases in isometric strength at 30° ($t_{(31)} = -5.556$, $P < 0.001$) and 70° ($t_{(31)} = -4.162$, $P < 0.001$) and concentric ($t_{(31)} = -6.514$, $P < 0.001$) and eccentric strength ($t_{(31)} = -3.197$, $P < 0001$) after 5 weeks of training (Figure 1).

Figure 2

Morphological and architectural measures

Muscle volume and anatomical cross-sectional area

For vastus lateralis muscle volume, there was no significant condition × time interaction ($F_{(1,15)} = 0.150$, $P = 0.704$) and no difference between CON and ECC conditions ($F_{(1,15)} = 0.568$, $P = 0.963$). There was a significant main effect of time ($F_{(1,15)} = 100.323$, $P < 0.001$), with follow-up tests demonstrating an increase in muscle volume after 5 weeks of training ($t_{(31)} = -11.811$, $P < 0.001$) (Figure 2A). For anatomical cross-sectional area, there were significant condition × time interactions at both the mid-point ($F_{(1,15)} = 9.947$, $P = 0.007$) and distal end of the muscle ($F_{(1,15)} = 49.925$, $P < 0.001$). *Post hoc* tests demonstrated no differences between conditions at baseline (mid-point: $t_{(31)} = -1.094$, $P = 0.291$) (distal end: $t_{(31)} = -1.263$, $P = 0.226$), but both CON and ECC training resulted in significant increases in vastus lateralis anatomical cross-sectional area at the mid-point (CON: $t_{(31)} = -32.245$, $P < 0.001$; ECC: $t_{(31)} = 4.456$, $P < 0.001$) and at the distal end of the muscle (CON: $t_{(31)} = -4.184$, $P < 0.001$; ECC: $t_{(31)} = -9.266$, $P < 0.001$). At the mid-point, there were significantly greater increases in anatomical cross-sectional area with CON training ($t_{(31)} = 2.277$, $P = 0.045$), whilst at the distal end, greater changes were observed after ECC training ($t_{(31)} = -2.255$, $P = 0.048$) (Figure 2B).

Figure 2

Fascicle length and angle

Fascicle length measured at the mid-point of the muscle had a significant condition × time interaction ($F_{(1,15)} = 17.141$, $P = 0.001$). *Post hoc* tests showed no differences at baseline ($t_{(31)} = -0.276$, $P = 0.768$) but there was a significant increase in fascicle length at the mid-point of the muscle after 5 weeks of both CON ($t_{(31)} = -6.036$, $P < 0.001$) and ECC training ($t_{(31)} = -8.474$, $P < 0.001$), with greater increases in the ECC condition ($t_{(31)} = -3.973$, $P = 0.001$). At the distal end of the muscle, there was also a significant condition × time interaction ($F_{(1,15)} = 97.569$, $P < 0.001$), with no evidence of baseline differences ($t_{(31)} = -0.975$, $P = 0.345$). Fascicle length increased significantly at the distal end of the muscle after 5 weeks of ECC training ($t_{(31)} = -11.120$, $P < 0.001$), but not with CON training ($t_{(31)} = -0.187$, $P = 0.855$) (Figure 3A).

For fascicle angle, there were significant condition × time interactions at both the mid-point ($F_{(1,15)} = 33.108$, $P < 0.001$) and distal end of the muscle ($F_{(1,15)} = 23.658$, $P < 0.001$). *Post hoc* tests demonstrated no differences at baseline between CON and ECC conditions (mid-point: $t_{(31)} = -1.403$, $P = 0.181$) (distal end: $t_{(31)} = 0.293$, $P = 0.774$). At the mid-point of the muscle, fascicle angle increased from pre to post (CON: $t_{(31)} = -13.402$, $P < 0.001$) (ECC: $t_{(31)} = -5.565$, $P < 0.001$), but was significantly higher after 5 weeks of CON compared to ECC training ($t_{(31)} = 2.384$, $P = 0.031$). Fascicle angle in the distal part of the muscle also increased after 5 weeks of CON ($t_{(31)} = -9.141$, $P < 0.001$) and ECC training ($t_{(31)} = -8.466$, $P < 0.001$), but the increase was significantly greater after ECC training ($t_{(31)} = -2.933$, $P = 0.010$) (Figure 3B).

Figure 3

Table 2

Discussion

The present study investigated the effects of 5 weeks CON *vs*. ECC training on knee extensor strength, vastus lateralis muscle volume and regional changes in anatomical cross-sectional area, fascicle length and angle. We hypothesised that both modalities would result in similar increases in knee extensor strength and muscle volume, but that the different training modalities would cause regional differences in anatomical cross-sectional area and muscle architecture. In line with our hypothesis, we found regional differences in anatomical cross-sectional area, which differed between training modalities. ECC training caused greater increases in the distal part of the muscle compared to CON training, where cross-sectional area was greater in the mid-point of the muscle. We also found that ECC training caused significantly greater changes in whole fascicle length at both the mid-point and the distal end, whilst CON training resulted in significantly greater fascicle angles, with greatest changes at the mid-point of the muscle. To the best of our knowledge, no study has measured the region-specific changes in fascicle length and fascicle angle, as well as regional changes in anatomical cross-sectional area that might result from isolated CON *vs*. ECC training. The use of 3D ultrasound in this current study was also implemented, to overcome the measurement errors arising from 2D ultrasound and provide clearer conclusions on the adaptions, which might occur from these different training modalities.

The hypothesis that knee extensor strength and vastus lateralis muscle volume would increase with both training conditions was supported. Despite the fact that ECC training resulted in significantly higher peak training torques than CON training over 5 weeks (Table 1), similar increases in muscle strength (10-13%) and muscle volume (8%) were observed between conditions. Although this may seem unexpected, given the higher training load in the ECC condition, these findings are in line with several studies, even when CON and ECC training was matched for load or neural drive (Blazevich et al., 2007; Franchi et al., 2014; Franchi et al., 2015; Gonzalez-Izal et al., 2014; Maeo et al., 2018; Timmins et al., 2016; Wernbom, 2007). One explanation is that ECC actions do not elicit a higher mechanical load, but they generate higher forces through the stretch and recoil of passive structures, such as titin, which might act as a molecular spring, increasing force output during lengthening actions (Herzog, 2014), consistent with our training data. Conversely, Franchi et al. (2015) argued that perhaps ECC actions do indeed produce a greater mechanical stimulus, but the hypertrophic response to ECC training is blunted by inflammatory responses and muscle damage, which is higher in ECC compared to CON actions (Franchi et al., 2015). Whilst this is also a plausible explanation, the repeated bout effect with continued ECC exercise, such as in the present study, is also well documented (Margaritelis et al., 2015). The greater muscle fiber microdamage experienced during ECC actions has been shown to diminish after just eight sessions of ECC exercise (Nikolaidis et al.2008), potentially negating any differences in muscle damage between training modalities after this point. Thus, the exact mechanics behind these similar strength and volume adaptations with CON and ECC training still remains unknown.

Although both training conditions showed similar changes in vastus lateralis muscle volume, regional morphological patterns of hypertrophy differed significantly. Whilst ECC training promoted greater hypertrophy in the distal portion of the muscle compared to CON training (ECC: 8% *vs*. CON: 2%), increases in anatomical cross-sectional area at the mid-point of the muscle were greater with CON training (CON: 9% *vs*. ECC: 5%). A novel finding of the study was that these regional changes in anatomical cross-sectional area coincided with differential changes in fascicle length and fascicle angle at the mid-point and distal end of the muscle. Fascicle length at the mid-point of the muscle, increased significantly after both CON (3%) and ECC training (6%), but the changes were considerably greater after ECC training. Conversely, at the distal end of the muscle, CON training did not induce any change in fascicle length compared to baseline (0.2%), whilst in the ECC condition fascicle length increases were greater than at the mid-point (8%). Studies which have investigated fascicle length changes at the mid-point of the muscle over the same training duration show similar changes. Franchi et al. (2015) identified a 5% increase in fascicle length after 4 weeks of ECC training and a 12% increase over 10 weeks (Franchi et al., 2014), reflecting the higher training duration. Regional differences in fascicle angle were also observed in this study. In agreement with previous studies, CON training caused a greater change in fascicle angle at the mid-point of the muscle (8%) compared to ECC training (3%), with similar values previously reported after 4 weeks of CON training (Franchi et al., 2015; 8%). However, at the distal end of the muscle, CON training caused much lower increases in fascicle angle (2%), whilst in the ECC training condition, increases in fascicle angle were similar to those found at the mid-point of the muscle (4%). Collectively, our findings support the notion that adoption of a resistance training programme using only one mode of contraction is unlikely to elicit complete muscle adaptation (growth). If the basic aim of a training programme is to maximise muscle hypertrophy, then both forms of contraction should be considered. The capacity to target growth in specific regions of the muscle using CON or ECC contractions could also be important in a musculo-skeletal rehabilitation setting, where under- or over-development of selected muscle regions could impair muscle function, delay recovery or increase the risk of subsequent injury.

Taken together, these results suggest that CON training induces adaptations predominantly in the mid-point of the muscle and results in greater anatomical cross-sectional area due to predominant increases in fascicle angle. These findings of increased fascicle angle may reflect an increase in the number of in-parallel sarcomeres. In previous studies, this increase has been shown to occur mainly in the central region of the vastus lateralis muscle with CON training (Reeves et al., 2009), which is consistent with the results shown here. Conversely, ECC training caused a wider variation of regional changes along the length of the muscle from the mid-point to the distal end. The greatest changes were at the distal end of the muscle, where anatomical cross-sectional area was higher after ECC training, although reasonably large changes were also observed at the mid-point. Increases in fascicle length contributed most to the increased anatomical cross-sectional area after ECC training, and this was evident at both the mid-point and more so in the distal region. The increase in fascicle length may represent in-series sarcomere addition, which is greater in response to lengthening actions, such as ECC exercise in animal studies (Holly et al., 1980; Butterfield, Leonard, Herzog, 2005) and greater at the distal end of the muscle, where the stretch stimulus is likely to be highest. However, results demonstrate that these adaptions also occurred, to a lesser extent in the mid-belly. The finding that fascicle angle increased at the mid-belly and distal end with ECC training as well as CON training, suggests that adaptations are not limited to the mid-belly of the muscle or to CON training. In fact, the results demonstrate that ECC training appear to cause an adaptation at the mid-point and distal end of the muscle, which may be reflective of an increase in both in-parallel and in-series sarcomeres.

This is the first study to report regional changes in fascicle length and angle after CON and ECC training after just 5 weeks of training. The finding that ECC training causes greater adaptations in the distal region of the muscle, suggests that measurements taken only at the mid-belly of the vastus lateralis in previous studies may not have been representative of whole muscle adaptations; consistent with a recent anatomical study where irregularity of fascicles within the vastus lateralis muscle were reported (Oranchuk 2020). Our findings also highlight that previous studies, which extrapolate from scans at the mid-belly of the muscle are likely to underestimate the true change in fascicle length and fascicle angle. For example, trigonometric methods result in large differences compared to an extended field of view and fail to account for curvature in the fascicles, which is significant at the distal end of the vastus lateralis muscle (Oranchuk, 2020) and at the distal ends of the fascicles, where sarcomere addition is thought to occur (Williams & Goldspink. 1971). Thus, studies using 2D ultrasound and measuring only at the mid-belly need to be interpreted with caution depending on what training stimulus has been used.

It should be acknowledged that the use of an isokinetic dynamometer will give a different resistive stimulus to typical concentric and eccentric training modalities, which compromises ecological validitity. In addition, this study investigates just one of the four main knee extensor muscles, whose contributions will change particularly during CON and ECC exercise. Thus, differential adaptations may occur in different muscle.

Conclusion

Differences in morphological and architectural characteristics might be important for both rehabilitation and performance. Region-specific changes in muscle architecture can influence the function of muscles (Narici, 1999; Lieber and Fridén, 2000; Narici et al., 2016), such as longer fascicles increasing maximum shortening velocity or a greater number of parallel fibres increasing force output. These factors may serve to reduce the risk of injury, facilitate recovery from injury or enhance performance in sport or in an ageing or disabled population. Distinct architectural remodelling through a loss of sarcomeres in series and in parallel, occurs in ageing and a number of neurodevelopmental conditions, such as cerebral pasly (Matthiasdottir, Hahn, Yaraskavitch & Herzog, 2014). An understanding as to how contraction mode affects the muscle and what could be the best intervention with different populations could be important, alongside the importance of tracking changes in different regions of the muscle, where some adaptions might be more pronounced than at the mid-belly of the muscle. This study is the first to highlight regional changes in architectural, as well as morphological characteristics, in the vastus lateralis muscle in response to CON and ECC training. Future research into the effects that increased fascicle length, angle and cross-sectional area have in different regions of the muscle is needed to close the gap between these findings and its application in an applied setting.

References

Blazevich AJ., Cannavan D, Coleman DR, Horne S. Influence of concentric and eccentric resistance training on architectural adaptation in human quadriceps muscles. J Appl Physiol (2007); **103**: 1565-1575.

Blazevich AJ, Gill ND, Zhou S. Intra-and intermuscular variation in human quadriceps femoris architecture assessed in vivo. J Anat (2006); **209**: 289-310.

Brughelli M, Cronin J. Altering the length-tension relationship with eccentric exercise. Sports Med (2007); **37**: 807-826.

Dix DJ, Eisenberg BR. Myosin mRNA accumulation and myofibrillogenesis at the myotendinous junction of stretched muscle fibers. J Cell Biol (1990); **111**: 1885-1894.

Fang Y, Siemionow V, Sahgal V, Xiong F, Yue GH. Greater movement-related cortical potential during human eccentric versus concentric muscle contractions. J Neurophysiol (2001); **86**: 1764-1772.

Franchi MV, Atherton PJ, Reeves ND, Flück M, Williams J, Mitchell WK, Selby A, Beltran Valls RM, Narici MV. Architectural, functional and molecular responses to concentric and eccentric loading in human skeletal muscle. Acta Physiol (2014); **210**: 642-654.

Franchi MV, Reeves ND, Narici MV. Skeletal muscle remodeling in response to eccentric vs. concentric loading: morphological, molecular, and metabolic adaptations. Front Physiol (2017); **8**: 447.

Franchi MV, Wilkinson DJ, Quinlan JI, Mitchell WK, Lund JN, Williams JP, Reeves ND, Smith K, Atherton PJ, Narici MV. Early structural remodeling and deuterium oxide-derived protein metabolic responses to eccentric and concentric loading in human skeletal muscle. Physiol Rep (2015); **3**: e12593.

Gonzalez-Izal M, Cadore EL, Izquierdo M. Muscle conduction velocity, surface electromyography variables, and echo intensity during concentric and eccentric fatigue. Muscle Nerve (2014); **49**: 389-397.

Herzog, W. The role of Titin in eccentric muscle contraction. J Exp Biol (2014); **217**: 2825-2833.

Holly RG, Barnett JG, Ashmore CR, Taylor RG, Mole PA. Stretch-induced growth in chicken wing muscles: a new model of stretch hypertrophy. Am J Physiol (1980); **238**: C62-C71.

Hortobagyi T, Hill JP, Houmard JA, Fraser DD, Lambert NJ, Israel RG. Adaptive responses to muscle lengthening and shortening in humans. J Appl Physiol (1996); **80**: 765-772.

Kawakami Y, Abe T, Fukunaga T. Muscle-fiber pennation angles are greater in hypertrophied than in normal muscles. J Appl Physiol (1993); **74**: 2740-2744.

LaStayo P, Marcus R, Dibble L, Frajacomo F, Lindstedt S. Eccentric exercise in rehabilitation: safety, feasibility, and application. J Appl Physiol (2014); **116**: 1426-1434.

Lieber RL, Fridén J. Functional and clinical significance of skeletal muscle architecture. Muscle Nerve (2000); **23**: 1647-1666..

Lynn R, Morgan DL. Decline running produces more sarcomeres in rat vastus intermedius muscle fibers than does incline running. J Appl Physiol (1994); **77**: 1439-1444.

Maeo S, Shan X, Otsuka S, Kanehisa H, Kawakami Y. Neuromuscular Adaptations to Work-matched Maximal Eccentric versus Concentric Training. Med Sci Sports Exerc (2018); **50**: 1629.

Margaritelis NV, Theodorou AA, Baltzopoulos V, Maganaris C N, Paschalis V, Kyparos A, Nikolaidis M G (2015). Muscle damage and inflammation after eccentric exercise: can the repeated bout effect be removed? Physiol Rep (2015); **3**: e12648.

Matthiasdottir S, Hahn M, Yaraskavitch M, Herzog W. Muscle and fascicle excursion in children with cerebral palsy. Clin Bio (2014); **29**: 458-462.

Moore DR, Young M, Phillips SM. Similar increases in muscle size and strength in young men after training with maximal shortening or lengthening contractions when matched for total work. Eur J Appl Physiol (2012); **112**: 1587-1592.

Narici M. Human skeletal muscle architecture studied in vivo by non-invasive imaging techniques: functional significance and applications. J Electromyogr Kines (1999); **9**: 97-103.

Narici M, Franchi M, Maganaris C. Muscle structural assembly and functional consequences. J Exp Biol (2016); **219**: 276-284.

Narici MV, Maganaris CN. Plasticity of the muscle-tendon complex with disuse and aging. Exerc Sport Sci Rev (2007); **35**: 126-134.

Nikolaidis MG, Jamurtas AZ, Paschalis V, Fatouros IG, Koutedakis Y, Kouretas D. The effect of muscle-damaging exercise on blood and skeletal muscle oxidative stress. Sports Med (2008); **38**: 579-606.

Noorkoiv M, Stavnsbo A, Aagaard P, Blazevich AJ In vivo assessment of muscle fascicle length by extended field-of-view ultrasonography. J Appl Physiol (2010); **109**: 1974-1979.

Noorkoiv M, Theis N, Lavelle G A comparison of 3D ultrasound to MRI for the measurement and estimation of gastrocnemius muscle volume in adults and young people with and without cerebral palsy. Clin Anat (2018); **32**: 319-327.

Oranchuk DJ, Nelson AR, Storey AG, Cronin JB. Variability of regional quadriceps architecture in trained men assessed by B-mode and extended-field-of-view ultrasonography. Int J Sport Physiol (2020); **15**: 430-436.

Potier TG, Alexander CM, Seynnes OR. Effects of eccentric strength training on biceps femoris muscle architecture and knee joint range of movement. Eur J Appl Physiol (2009); **105**: 939-944.

Prager RW, Rohling RN, Gee AH, Berman L. Rapid calibration for 3-D freehand ultrasound. Ultrasound Med Biol (1998); **24**: 855-869.

Reeves ND, Maganaris CN, Longo S, Narici MV. Differential adaptations to eccentric versus conventional resistance training in older humans. Exp Physiol (2009); **94**: 825-833.

Roig M, O’Brien K, Kirk G, Murray R, McKinnon P, Shadgan B, Reid WD. The effects of eccentric versus concentric resistance training on muscle strength and mass in healthy adults: a systematic review with meta-analysis. Br J Sports Med (2009); **43**: 556-568.

Seger JY, Arvidsson B, Thorstensson A, Seger JY. Specific effects of eccentric and concentric training on muscle strength and morphology in humans. Eur J Appl Physiol Occupational Physiol (1998); **79**: 49-57.

Seynnes OR, de Boer M, Narici MV. Early skeletal muscle hypertrophy and architectural changes in response to high-intensity resistance training. J Appl Physiol (2007); **102**: 368-373.

Timmins R, Ruddy J, Presland J, Maniar N, Shield A, Williams M, Opar DA. Architectural changes of the biceps femoris after concentric or eccentric training. Med Sci Sport Exerc (2016); **48**: 499-508.

Vikne H, Refsnes PE, Ekmark M, MEDBØ JI, Gundersen V, Gundersen K. Muscular performance after concentric and eccentric exercise in trained men. Med Sci Sport Exerc (2006); **38**: 1770-1781.

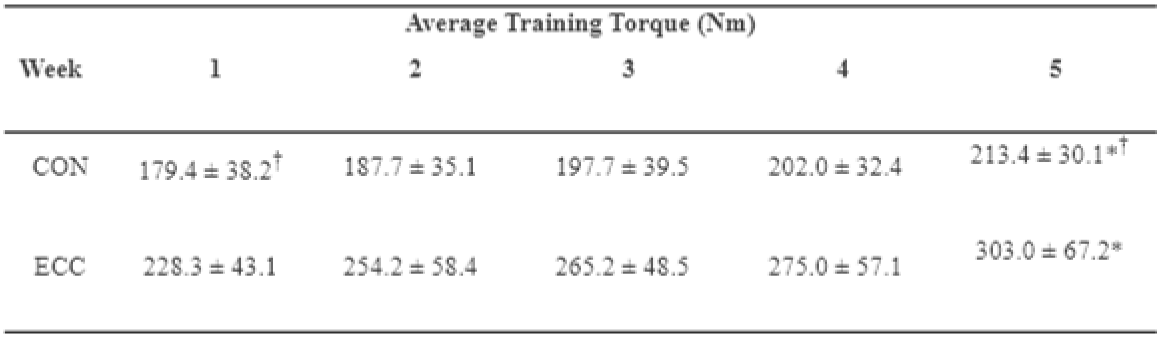
Wernbom M, Augustsson J, Thomeé R. The influence of frequency, intensity, volume and mode of strength training on whole muscle cross-sectional area in humans. Sport Med (2007); **37**: 225-264.

Williams PE. Use of intermittent stretch in the prevention of serial sarcomere loss in immobilised muscle. Ann Rheum Dis (1990); **49**: 316-317.

Williams PE, Goldspink G Longitudinal growth of striated muscle fibres. J Cell Sci (1971); **9**: 751-767.

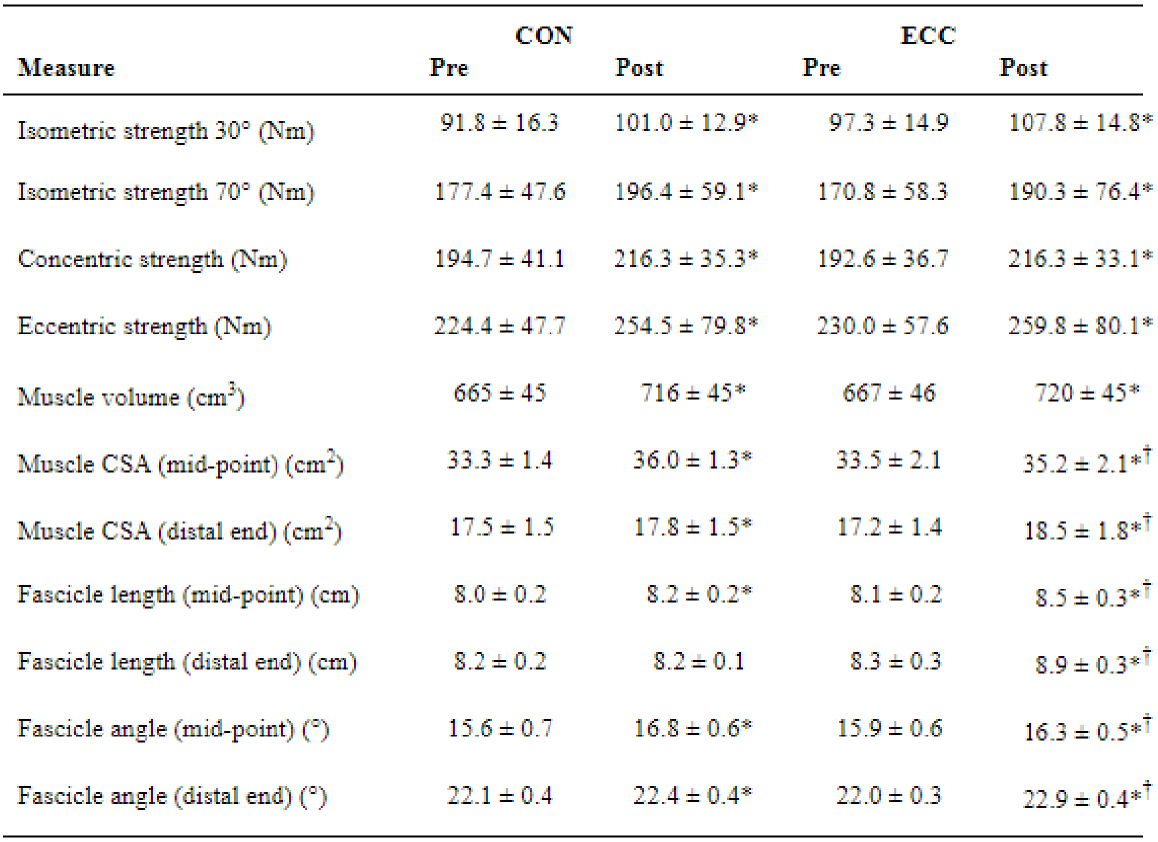
Zatsiorsky V, Kraemer W *Science and practice of strength training* (2nd ed) (2006), Champaign, IL: Human Kinetics.

Table 1.



	Average Training Torque (Nm)				
Week	1	2	3	4	5
CON	179.4 ± 38.2†	187.7 ± 35.1	197.7 ± 39.5	202.0 ± 32.4	213.4 ± 30.1*†
ECC	228.3 ± 43.1	254.2 ± 58.4	265.2 ± 48.5	275.0 ± 57.1	303.0 ± 67.2*

Table 2.



	CON		ECC	
Measure	Pre	Post	Pre	Post
Isometric strength 30° (Nm)	91.8 ± 16.3	101.0 ± 12.9*	97.3 ± 14.9	107.8 ± 14.8*
Isometric strength 70° (Nm)	177.4 ± 47.6	196.4 ± 59.1*	170.8 ± 58.3	190.3 ± 76.4*
Concentric strength (Nm)	194.7 ± 41.1	216.3 ± 35.3*	192.6 ± 36.7	216.3 ± 33.1*
Eccentric strength (Nm)	224.4 ± 47.7	254.5 ± 79.8*	230.0 ± 57.6	259.8 ± 80.1*
Muscle volume (cm^3)	665 ± 45	716 ± 45*	667 ± 46	720 ± 45*
Muscle CSA (mid-point) (cm^2)	33.3 ± 1.4	36.0 ± 1.3*	33.5 ± 2.1	35.2 ± 2.1*†
Muscle CSA (distal end) (cm^2)	17.5 ± 1.5	17.8 ± 1.5*	17.2 ± 1.4	18.5 ± 1.8*†
Fascicle length (mid-point) (cm)	8.0 ± 0.2	8.2 ± 0.2*	8.1 ± 0.2	8.5 ± 0.3*†
Fascicle length (distal end) (cm)	8.2 ± 0.2	8.2 ± 0.1	8.3 ± 0.3	8.9 ± 0.3*†
Fascicle angle (mid-point) (°)	15.6 ± 0.7	16.8 ± 0.6*	15.9 ± 0.6	16.3 ± 0.5*†
Fascicle angle (distal end) (°)	22.1 ± 0.4	22.4 ± 0.4*	22.0 ± 0.3	22.9 ± 0.4*†

Fig 1

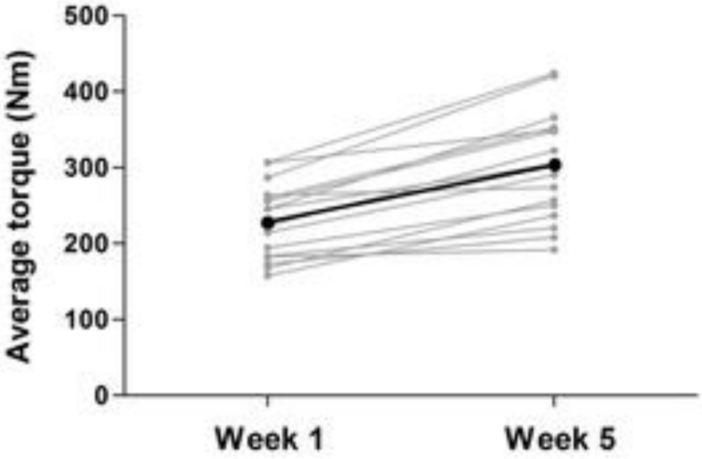


Fig 2.

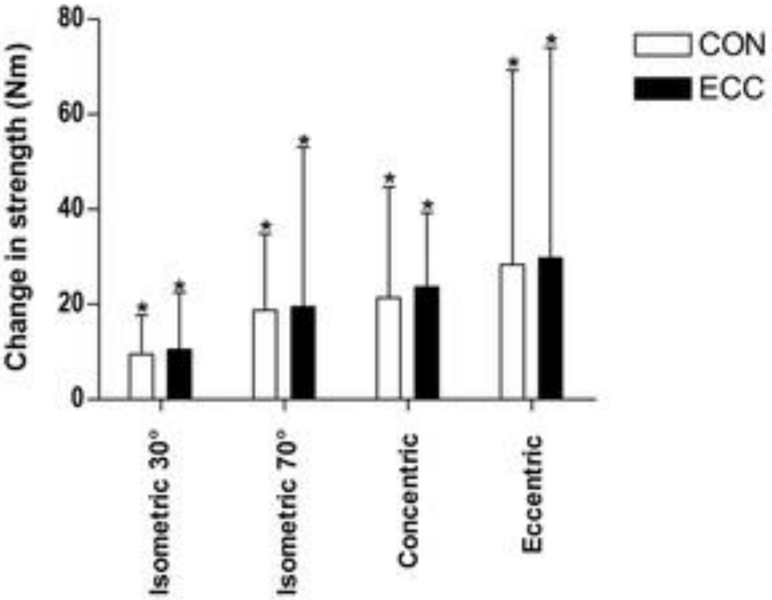


Fig 3.

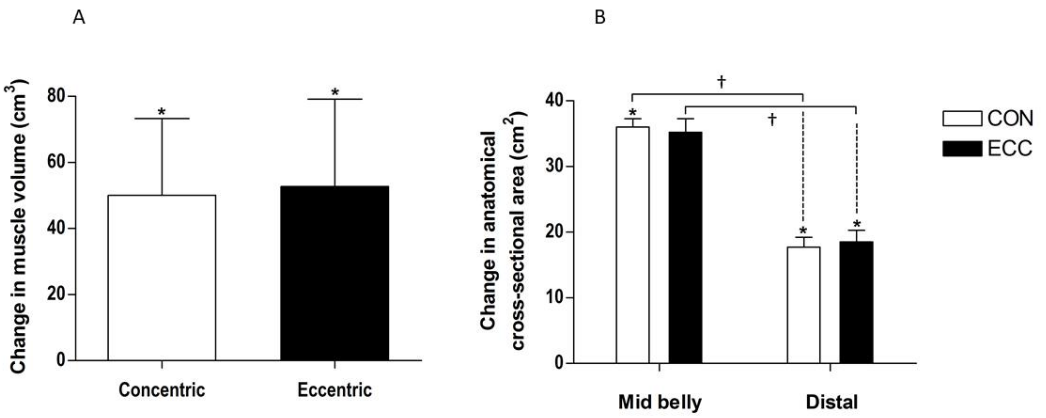
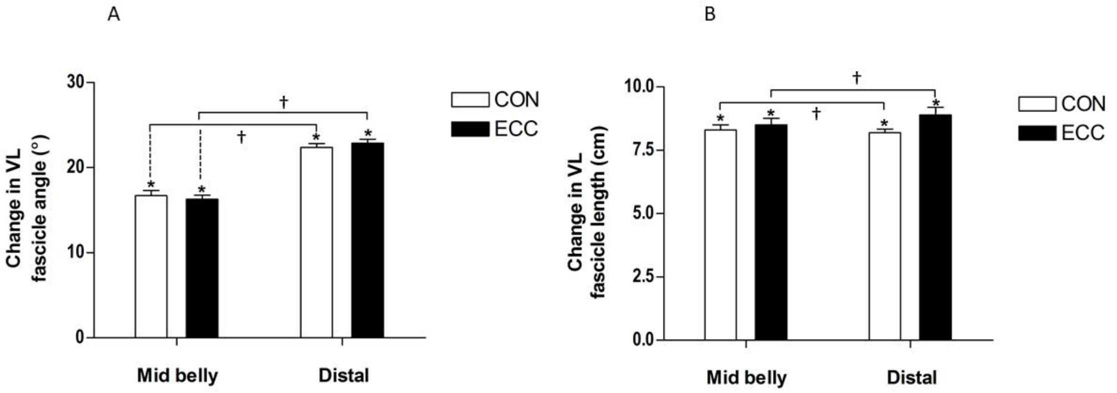

A
B
Change in muscle volume (cm^3)
80
60
40
20
0
*
*
Concentric
Eccentric
Change in anatomical cross-sectional area (cm^2)
40
30
20
10
0
†
†
*
*
*
Mid belly
Distal
CON
ECC

Fig 4.


A
B
Change in VL fascicle angle (°)
30
20
10
0
†
†
*
*
*
*
Mid belly
Distal
CON
ECC
Change in VL fascicle length (cm)
10.0
7.5
5.0
2.5
0.0
†
†
*
*
*
*
Mid belly
Distal
CON
ECC