



ISSN: 0264-0414 (Print) 1466-447X (Online) Journal homepage: http://www.tandfonline.com/loi/rjsp20

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To cite this article: Marika Noorkõiv, Kazunori Nosaka & Anthony J. Blazevich (2015) Effects of isometric quadriceps strength training at different muscle lengths on dynamic torque production, Journal of Sports Sciences, 33:18, 1952-1961, DOI: <u>10.1080/02640414.2015.1020843</u>

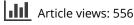
To link to this article: http://dx.doi.org/10.1080/02640414.2015.1020843



Published online: 02 Apr 2015.



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Effects of isometric quadriceps strength training at different muscle lengths on dynamic torque production

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(Accepted 16 February 2015)

Abstract

This study aims to (1) determine whether isometric training at a short vs. long quadriceps muscle length affects concentric torque production; (2) examine the relationship between muscle hypertrophy and concentric torque; and (3) determine whether changes in fascicle length are associated with changes in concentric torque.

Sixteen men performed isometric training at a short (SL, n = 8) or a long muscle length (LL, n = 8). Changes in maximal concentric torque were measured at 30, 60, 90, 120, 180, 240 and 300 rad \cdot s⁻¹. The relationships between the changes in concentric torque, cross-sectional area, volume and fascicle length were tested.

Concentric torque increased significantly after training only in LL and at angular velocities of 30 and 120 rad \cdot s⁻¹ by 12–13% (P < 0.05). Muscle size increased in LL only, the changes were correlated (r = 0.73-0.93, P < 0.05) with the changes in concentric torque. Vastus lateralis (VL) fascicle length increased in both groups (5.4 ± 4.9%, P = 0.001) but the change was not correlated with changes in concentric torque in either group.

Isometric training-induced increases in muscle size and concentric torque were best elicited by training at long muscle lengths. These results highlight a clear muscle length dependence of isometric training on dynamic torque production.

Keywords: dynamic torque, length-specificity, angular velocity

Introduction

After isometric strength training at a specific joint angle, muscle force production tends to improve most at or around the joint angles adopted during the training (Bandy & Hanten, 1993; Del Balso & Cafarelli, 2007; Kitai & Sale, 1989; Noorkõiv, Nosaka, & Blazevich, 2014), although increases in force are purported to occur across a broader range of motion after training at longer muscle lengths (Del Balso & Cafarelli, 2007; Noorkõiv et al., 2014; Weir, Housh, Weir, & Johnson, 1995). Nonetheless, many activities of daily living, including walking, sit-to-stand transitions and stair ascent, require forces to be produced dynamically and with the highest forces being required within a small, well-defined joint range (i.e. at specific muscle lengths). For example, during level walking in young healthy adults, the maximum torque (i.e. joint moment) occurs at knee flexion at about 20°, but during stair climbing the largest joint moment is generated when the knee is flexed to about 60° (Costigan, Deluzio, & Wyss, 2002; Taylor, Heller, Bergmann, & Duda, 2004). In elderly individuals,

completion of a chair rise movement requires knee moment production at about 65° to 90° of knee flexion, depending on the chair height (Burdett, Habasevich, Pisciotta, & Simon, 1985).Thus, it is of great interest to determine whether isometric training, which may be used in clinical populations for rehabilitation purposes, elicits angle-specific dynamic force production increases at or near the joint angles adopted during the isometric training.

Our recent study found that 6 weeks of isometric training elicited knee extension significant $(5.2 \pm 1.0\%, P < 0.01)$ muscular hypertrophy in participants who trained at long quadriceps muscle lengths (LL; i.e. flexed knee angles) but not in participants who trained at shorter muscle lengths (SL; i.e. extended knee angles) (Noorkõiv et al., 2014). Furthermore, changes in hypertrophy in LL were associated with muscle length-specific changes in muscular force production. These differential adaptations might also be expected to influence other force production parameters, such as the force-velocity relationship of the muscle. The force-velocity relationship is one of the most important

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determinants of a muscle's function, so understanding how it is affected by training is of interest to clinicians and researchers. Such changes might be underpinned by changes in absolute muscle size (i.e. cross-sectional area, CSA), and given that isometric training has been shown to increase muscle size (Alegre, Ferri-Morales, Rodriguez-Casares, & Aguado, 2014; Noorkõiv et al., 2014), differential adaptations in the force-velocity (torque-angular velocity) relationship could also be expected after isometric training. The relationship between muscle size and force (i.e. torque) production especially at slow velocity has been demonstrated previously (Alegre et al., 2014; Blazevich, Coleman, et al. 2009; Blazevich & Sharp, 2005). Given this, one could speculate that increases in slow-velocity torque production should be more prominent in LL compared to SL.

Changes in fascicle length within a muscle have also been speculated to be an important factor influencing dynamic force production, with changes in higher velocity force assumed to be positively influenced by increases in fascicle length (Blazevich, Cannavan, et al. 2009; Blazevich & Sharp, 2005). This is because muscle length change is distributed across more sarcomeres so each sarcomere can shorten less, and therefore more slowly, for a given muscle shortening length (Blazevich, Cannavan, et al. 2009; Blazevich & Sharp, 2005; Lichtwark, Wilson 2008). Also, if all sarcomeres shorten simultaneously the cumulative shortening distance, and thus velocity, will be greater. Interestingly, changes in fascicle length in the VL muscle mid-region were found to be similar between the groups $(5.4 \pm 4.9\%)$, P = 0.001) in our previous study, but the response varied between the participants in response to training and also appeared to be greater in distal regions in LL (5.8 ± 6.4%, P = 0.01) (Noorkõiv et al., 2014). These small between-group differences in fascicle length and the highly individual fascicle length responses found in our previous study provide a unique opportunity to examine the effect of fascicle length change on muscle force-velocity characteristics in vivo, especially given that neither group performed high-velocity training and, hence, other (e.g. neural) adaptations to high-velocity training could not influence the training response.

Given the above, the aims of the present study were to: (1) determine whether isometric training at different quadriceps muscle lengths (i.e. joint angles) influences angle-specific torque production measured in concentric contractions; (2) examine the relationship between changes in muscle size and changes in concentric torque production; and (3) determine whether changes in fascicle length after training are associated with higher velocity concentric torque production.

Methods

Participants

Sixteen non-strength trained healthy men with no recent (>12 months) history of lower limb injury or musculoskeletal disorder volunteered for the study. The sample size was calculated based on a study by Kubo et al. (2006) that gave effect size of 80% and 95% power at an alpha level of 0.05 (two-tailed). The participants were randomly assigned to one of two study groups: SL, who performed isometric training at a short quadriceps muscle length (i.e. extended knee joint position; n = 8), or LL, who performed isometric training at a long muscle length (flexed joint position; n = 8). Age was 24.6 \pm 4.9 years in SL and 22.8 \pm 2.5 years in LL (P = 0.38). Body height was 1.80 ± 0.10 m in both SL and LL (P = 0.73); and body weight was 77.5 ± 13.7 kg in SL and 78.2 \pm 10.8 kg in LL (P = 0.89). The participants in both groups were university students with no strength training history or musculoskeletal disorder. The Edith Cowan University Human Research Ethics Committee approved the study. The study was done in accordance with the Declaration of Helsinki. Some data from this study have been previously published elsewhere (Noorkõiv et al., 2014).

Training protocol

The muscle force applied during training was identical between the groups (i.e. 80% of the MVC produced at the optimal knee angle). This was ensured by determining isometric torque-angle relationships for each participant prior to study commencement, which were then resolved to muscle force-angle relations by normalising to the patellar tendon moment arm, as described in detail in a previous study (Noorkõiv et al., 2014). In brief, the patellar tendon moment arms were measured from X-ray images taken at 8 knee joint angles as the perpendicular distance between the instantaneous centre of rotation and the patellar tendon action line (Noorkõiv et al., 2014). Training was performed at a knee angle at which 80% of the maximum quadriceps muscle force, measured at the optimum joint angle, was elicited; that is, the angle at which the force-angle curve fitted to the third-order polynomial crossed the 80% value on y-axis either on the left (i.e. short muscle length) or right (i.e. long muscle length) side of the optimal angle (Noorkõiv et al., 2014). Adjustments were made after 3 weeks of training by retesting the isometric torque-angle relationship and re-calculating the joint angle at which a measured isometric contraction produced a force of 80% of MVC force at the optimal angle (Noorkõiv et al., 2014). Training was performed at a hip angle of 80° (0° = full extension). The participants trained for 6 weeks, three times a week, for five sets of five 5-s maximal voluntary isometric contractions (MVCs) per session on a Biodex isokinetic dynamometer (Biodex Medical Systems, Shirley, New York, USA). A 5-s passive inter-repetition rest and a 1-min inter-set rest were provided. The participants were instructed to exert their maximum force (i.e. 100% MVC) as fast and hard as possible watching the knee extension torque trace on a computer screen. The participants were seated on a Biodex dynamometer as for the isometric testing described below.

Isometric and isokinetic knee extension torque

Knee extension torque was measured on a Biodex System 3 isokinetic dynamometer (Biodex Medical Systems, Shirley, New York, USA) before (week 0) and after the 6 weeks (week 6) of training. The participants were seated with their hip joint angle at 80°, the shoulders and hips were tightly strapped to the dynamometer and the lever arm of the dynamometer was attached to the participants' lower limbs just above the ankle joint, hands were held with crossed forearms just above the shoulder straps on the chest during the MVCs. The knee axis was aligned with the axis of rotation of the dynamometer arm. The deformation of the Biodex system and soft tissues of the lower limb resulted in a small joint rotation during maximal contractions, so the participants performed a maximum knee extension contraction during the measurement of the reference angle to provide more accurate measurements. The effect of antagonist co-contraction was accounted for in all isometric MVCs as described in detail in a previous study (Noorkõiv et al., 2014).

For isometric torque, the participants were required to initiate the maximal knee extension contractions as fast and hard as possible and maintain them for 3 s. Real-time gravity-corrected torque was displayed on a computer screen and the participants were strongly verbally encouraged. Each MVC test was performed twice at the same angle before moving to the next angle, for the eight different angles $(30^{\circ}, 40^{\circ}, 50^{\circ}, 60^{\circ}, 70^{\circ}, 80^{\circ}, 90^{\circ} \text{ and } 100^{\circ}; 0^{\circ} = \text{full}$ knee extension). A 1-min passive rest was imposed between tests at the same angle and a 2-min rest was imposed between tests at different knee angles. Finally, the MVC contractions were repeated at the first (30°) joint angle to determine whether the protocol had been completed without significant neuromuscular fatigue, where >5% torque decline was set as the criterion level (coefficient of variation [CV] of two MVC trials of the same participant at the same knee angle at week 0 ranged 0.7-5.0%) (Noorkõiv et al., 2014).

For concentric measurements, the participants were required to initiate the maximal knee extension contractions as fast and hard as possible with the joint rotating from 100° to 0° of knee flexion $(0^{\circ} = \text{full knee extension})$. Torque data were displayed in real time on a computer screen and the participants were strongly verbally encouraged. Each MVC test was performed four times at 30, 60 and 90 rad \cdot s⁻¹ with 30 s rests between them and 2 min before testing at the higher velocity, five times at 120 and 180 rad \cdot s⁻¹ and seven times at 240 and 300 rad \cdot s⁻¹ with the same rest intervals: 30 s between repetitions and 2 min between velocities (Brown & Weir, 2001), and the average of these repeated trials were later used for statistical analysis. The greater number of trials at higher velocities was allowed because pilot testing had revealed a lesser reliability, yet also a lesser influence of fatigue, at the faster movement velocities. The testing always progressed from slow to fast velocities. Testing was repeated at 30 rad \cdot s⁻¹ in order to determine whether significant fatigue was induced by the protocol; the peak torque in all participants was within ± 5% of that obtained in the initial test at 30 rad \cdot s⁻¹. Data were also checked to ensure that the load range that matched the required (i.e. set) angular velocity was reached at all velocities (Brown, 2001).

Torque and velocity signals were collected using LabChart v.6.1.3 software (PowerLab System, ADInstruments, NSW, Australia) at a 1 kHz analogue-digital conversion rate and saved to computer disk. Isometric peak torque was taken as the maximum voluntary torque produced at each joint angle. Peak concentric torque was taken as the maximum concentric value achieved at any joint angle in each repetition at each velocity, and the values were averaged across all trials at each movement velocity. The angle of peak torque was taken at the maximum torque value obtained in the contraction with the highest torque at each velocity.

Quadriceps muscle CSA and volume

These methods have been described in detail previously (Noorkõiv et al., 2014). In brief, the participants sat quietly for 20 min before quadriceps muscle CSA and volume was measured from magnetic resonance imaging (MRI) scans (Siemens 1.5 T Magnetom Espree Open Bore MRI scanner, Siemens, Sweden) taken contiguously at 5-mm intervals from the proximal end of the greater trochanter to the medial femoral condyle. A T₁weighted spin echo acquisition sequence (resolution 512×192 , 400 × 300 mm FoV, slice width = 5 mm, TE = 12 ms, TR = 450 ms, flip angle = 70°, Bandwidth 130 Hz·Px⁻¹) was used. The participants rested in a relaxed supine position with their knees strapped together to avoid lateral hip rotation. Two phased array body surface coils were placed anteriorly along the thigh and a phased array spine coil was used posteriorly. The participants were required to avoid physical activity for 48 h prior to scanning. Muscle CSA and volume were calculated after five scans were digitised using image-processing software (OsiriXv.4.0, Pixmeo, Switzerland). CSAs were selected for analysis at 10% intervals along the muscle length (i.e. CSA of the 5-mm slice) (Noorkõiv et al., 2014).

Fascicle length

B-mode axial-plane ultrasound images (AlokaSSDa10, software number 6.1.0, Aloka, Tokyo, Japan) were taken of VL at 33%, 50% and 66% of the distance from the greater trochanter to the lateral epicondyle (i.e. proximal, mid- and distal regions). A 10 MHz linear-array probe (60 mm width) in extended field-of-view mode was used as described in (Noorkoiv, Stavnsbo, Aagaard, & Blazevich, 2010) (sampling frequency = 90 frames s⁻¹). The participants rested in a supine position with fully extended knee and hip joints. Two scans were obtained during each session, and the CV of the repeated measures was 3.8 ± 3.2% (Noorkõiv et al., 2014).

Statistical analysis

Data distribution was tested with the Shapiro–Wilks test. Intra- and inter-group differences were tested with two-way repeated measures ANOVA by comparing the changes in dependent variable over time (i.e. pre and post training) at eight angles. Tukey's post-hoc comparisons of significant between group × time interactions of SL and LL were made with a one-way ANOVA. Paired *t*-tests were used to examine further significant within-group × time interactions. Pearson's correlation coefficients were computed to examine relationships between the training-induced changes in the measured variables. The α -level was set at 0.05 during all statistical tests, except for confidence interval (i.e. α -level = 0.1). Effect sizes of the changes were calculated as the difference in the mean change of the group divided by the pooled mean standard deviation; an effect size of 0.2 was considered as small, 0.5 as medium and 0.8 as large. All statistical analyses were computed using SPSS Statistics software version 20.0.0 (IBM Corp., New York, USA).

Results

Isometric training angle and isometric torque changes

The average $(\pm s)$ isometric training angles were 43.1 ± 4.6° at week 0 and 38.1 ± 3.7° at week 6 in SL (angles ranging from 30° to 50°), and 86.9 ± 6.5° at week 0 and 87.5 ± 6.0° at week 6 in LL (ranging from 75° to 100°). Although adjustments were made after retesting at week 3, there were no statistically significant changes in the training angles over the 6-week period. The optimum angle for isometric torque production before training was 64 ± 5° in both SL and LL, and after 6 weeks of training it was 62 ± 7° and 63 ± 9° in SL and LL, respectively.

Concentric torque, CSA and muscle volume changes

The peak concentric torque produced at each angular velocity was not different before the training between SL and LL (Figure 1), but after 6 weeks of training there were significant between-group differences, as shown by a significant time × velocity \times group interaction effect (P = 0.000). Peak concentric torque did not change with training in SL, but increased from weeks 0 to 6 at 30 rad \cdot s⁻¹ $(13.0 \pm 4.0\%; 90\% \text{ CI} = 6.5 \text{ to } 20.0; P = 0.02;$ ES = 0.7) and 120 rad $\cdot s^{-1}$ (12.1 ± 5.8%; 90%) CI = 2.5 to 21.6; P = 0.05; ES = 0.6) as well as at 60 rad \cdot s⁻¹ (10.7 ± 4.6%; 90% CI = 3.2 to 18.3; P = 0.06; ES = 0.55) and 90 rad $\cdot s^{-1}$ $(10.1 \pm 4.2\%; 90\% \text{ CI} = 3.2 \text{ to } 17.0; P = 0.06;$ ES = 0.54) indicated by a large effect size in LL (Figure 1). There were no differences in the angle

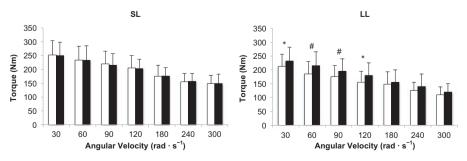


Figure 1. Torque–velocity relationships for SL and LL measured before (white columns) and after (black columns) 6 weeks of training. * = P < 0.05 for torque change from week 0 to week 6. Effect size (ES) values have been reported.

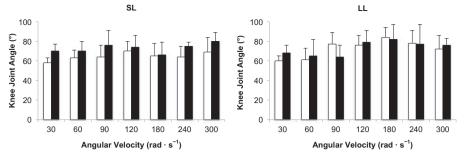


Figure 2. Mean angle of maximum concentric torque production during isokinetic (30, 60, 90, 120, 180, 240 and 300 rad \cdot s⁻¹) knee extensions in the SL and LL training groups before (white columns) and after (black columns) 6 weeks of training. No statistically significant changes over the training period were evident.

of peak concentric knee extension torque between the LL and SL (Figure 2) groups before training, and the two-way repeated measures ANOVA revealed no significant changes in the angle of peak torque at any velocity after training (Figure 2).

Quadriceps muscle CSA increased after training only in LL (Table I). The baseline values of muscle volume for VL were 680.7 <u>+</u> 144.4 and $634.7 \pm 142.5 \text{ cm}^3$, vastus medialis (VM) 502.2 ± 89.6 and 468.5 ± 160.2 cm³, vastus intermedius 570.4 \pm 134.1 and 532.1 \pm 197.9 cm³, and femoris (RF) 294.8 rectus ± 67.4 and $267.2 \pm 64.4 \text{ cm}^3$, for SL and LL, respectively. Muscle volume increased after training in VL by $6.3 \pm 1.4\%$ (90% CI = 3.7 to 8.3; P < 0.01; ES = 0.3), VM by $4.8 \pm 0.9\%$ (90% CI = 3.3 to 6.3; P < 0.01; ES = 0.1) and RF by 8.2 ± 1.5% (90%) CI = 5.7 to 10.7; P < 0.01; ES = 0.4), but no significant change was observed in vastus intermedius (90% CI = 0.1 to 6.1; n.s.; ES = 0.1). Muscle volume did not change in SL.

Correlations between changes in isokinetic torque, CSA and muscle volume

Correlations between the changes in concentric peak torque (i.e. torque at 30 and 120 rad \cdot s⁻¹ in LL) and the changes in CSA and volume were tested. The changes in torque at 30 rad \cdot s⁻¹ were positively correlated with the changes in VL CSA at 20% and 30% region (r = 0.79; P = 0.02 and r = 0.93; P = 0.001, respectively) and negatively correlated at the proximal 80% region (r = -0.70, P = 0.05) (Figure 3). The change in torque at 30 rad \cdot s⁻¹ was positively correlated with the changes in CSA of RF at the 30% region (r = 0.76; P = 0.03), CSA of VM at 30% the region (r = 0.73; P = 0.04) and RF volume (r = 0.74; P = 0.04) (Figure 3) in LL. No significant correlations were found with the changes in peak concentric torque at 120 rad \cdot s⁻¹, CSA and muscle volume in LL. No significant correlations were found between these variables in SL (Figure 3).

Correlations between changes in peak concentric torque and fascicle length

Detailed data describing the absolute fascicle length values are presented previously (Noorkõiv et al., 2014). The fascicle length increase in the VL midregion from the baseline (82.8 \pm 7.6 and 83.0 ± 10.8 mm, in SL and LL, respectively) was identical between the groups, having a mean of $5.4 \pm 4.9\%$ (4.8 ± 4.4 mm, 90% CI = 3.4 to 7.4; P = 0.001; ES = 0.5) increase. One-way ANOVA (weeks 0 and 6) showed a significant group \times time (SL and LL before and after training) effect for distal VL fascicle length (P = 0.01). Distal and proximal VL fascicle length did not change in SL, but fascicle length increased 5.8 \pm 6.4% (0.5 \pm 0.5 mm; 90% CI = 2.1 to 10.0; P = 0.02; ES = 0.3) at the distal region of VL in LL but did not change in the proximal region. RF fascicle length did not change in either group. Changes in fascicle length of any muscles were not correlated with the changes in peak concentric torque at any velocities in either group.

Discussion

Peak concentric torque

An important finding of the present study was that peak concentric torque production increased after training only in LL (at 30 and 120 rad \cdot s⁻¹, with trends (ES = 0.5, P = 0.06) towards increases at 60 and 90 rad \cdot s⁻¹). This has important practical implications, because isometric training can elicit improvements in dynamic torque production in the quadriceps muscle when performed at a long but not short muscle length, although these changes appear limited to slower and moderate-velocity movements. These results are congruent with Alegre et al., (2014) who found a significant increase in concentric knee extension strength after isometric training at 90° of knee flexion but not after training at a short quadriceps muscle length (i.e. 50° of knee flexion), and highlight a clear muscle length

Muscle region (%)	SL				LL			
	Pre	Post	90% CI	ES	Pre	Post	90% CI	ES
Vastus lateralis (cm ²))							
10	3.3 ± 2.0	3.1 ± 1.3	-0.8 to 0.4	-0.1	4.9 ± 4.1	4.3 ± 2.0	0.3 to 1.1	0.4
20	10.8 ± 2.9	10.7 ± 2.8	-0.5 to 0.4	0.0	11.7 ± 5.6	11.6 ± 3.3	0.2 to 1.3	0.3
30	18.9 ± 3.1	18.3 ± 2.8	-1.1 to -0.2	-0.2	18.2 ± 4.6	$19.2 \pm 4.4 \star$	0.5 to 1.5	0.2
40	24.7 ± 3.5	24.6 ± 3.8	-0.6 to 0.4	0.0	23.3 ± 5.2	24.5 ± 5.3*	0.4 to 2.1	0.3
50	29.4 ± 5.5	29.1 ± 5.6	-0.9 to 0.2	-0.1	26.9 ± 5.9	$28.8 \pm 5.6*$	1.1 to 2.8	0.3
60	29.0 ± 4.7	28.8 ± 5.4	-0.9 to 0.6	0.0	27.2 ± 5.2	$29.6 \pm 6.0 \star$	1.3 to 3.6	0.4
70	26.4 ± 6.1	26.2 ± 6.3	-1.0 to 0.5	0.0	26.5 ± 4.4	27.5 ± 4.7	-0.2 to 2.3	0.2
80	23.9 ± 7.7	24.3 ± 7.6	-1.2 to 2.0	0.1	20.4 ± 5.3	22.5 ± 5.9	0.3 to 3.9	0.4
90	14.8 ± 4.3	14.7 ± 3.8	-1.0 to 0.9	0.0	10.3 ± 5.1	13.2 ± 4.8	-0.3 to 6.0	0.6
Vastus medialis (cm ²)							
10	14.1 ± 2.9	14.5 ± 3.5	-0.3 to 1.2	0.1	13.2 ± 6.6	$13.8 \pm 6.6*$	0.1 to 1.0	0.1
20	23.1 ± 3.4	23.2 ± 4.0	-0.4 to 0.6	0.0	21.3 ± 8.9	$22.2 \pm 9.6*$	0.3 to 1.6	0.1
30	25.3 ± 3.7	24.9 ± 4.1	-1.0 to -0.4	-0.1	23.4 ± 8.8	$24.9 \pm 9.1*$	0.8 to 2.2	0.2
40	23.0 ± 3.1	22.9 ± 3.0	-0.6 to 0.3	0.0	21.9 ± 6.7	22.9 ± 6.3*	0.5 to 1.5	0.2
50	19.3 ± 3.8	19.0 ± 3.8	-0.5 to 0.2	-0.1	19.0 ± 4.7	19.5 ± 4.5	-0.1 to 1.1	0.1
60	14.9 ± 2.9	15.0 ± 2.6	-0.8 to 0.2	0.1	16.2 ± 3.4	16. ± 3.7	-0.8 to 0.9	0.0
70	11.3 ± 2.6	11.3 ± 2.4	-0.5 to 0.6	0.0	11.0 ± 2.0	11.8 ± 1.6	-0.3 to 0.5	0.3
80	7.8 ± 2.1	7.8 ± 1.6	-0.5 to 0.7	0.0	8.1 ± 0.8	$8.6 \pm 1.0*$	0.3 to 0.9	0.7
90	4.6 ± 1.4	3.9 ± 1.4	-1.4 to -0.03	-0.5	4.7 ± 0.9	$4.9 \pm 1.0*$	-0.1 to 0.6	0.3
Vastus intermedius (cm ²)							
10	6.0 ± 1.5	5.6 ± 5.6	-1.0 to 0.2	-0.4	4.6 ± 1.5	4.4 ± 1.5	-0.9 to 0.5	0.2
20	13.3 ± 2.1	13.0 ± 13.0	-0.5 to -0.1	-0.1	12.7 ± 3.9	12.4 ± 3.9	-1.1 to 0.4	0.1
30	17.5 ± 3.4	17.8 ± 17.8	0.07 to 0.7	0.1	17.4 ± 5.0	16.8 ± 4.8	-1.3 to 0.2	0.1
40	22.2 ± 5.6	21.9 ± 21.9	-0.9 to 0.5	0.0	21.2 ± 5.8	21.4 ± 5.5	-0.3 to 0.8	0.0
50	25.7 ± 5.7	24.6 ± 24.6	-2.1 to -0.3	-0.2	23.9 ± 6.4	24.6 ± 7.4	-0.3 to 1.7	0.1
60	26.4 ± 5.2	26.8 ± 26.8	-0.9 to 1.6	0.1	24.8 ± 7.5	24.8 ± 7.1	-1.3 to 1.3	0.0
70	22.8 ± 5.8	23.0 ± 23.0	-0.6 to 0.8	0.0	19.8 ± 7.9	21.7 ± 6.6	0.5 to 3.2	0.3
80	14.1 ± 3.8	15.8 ± 15.8	0.01 to 3.4	0.4	13.2 ± 6.6	13.4 ± 6.4	-1.2 to 1.5	0.0
90	7.8 ± 4.0	7.1 ± 7.1	-3.1 to 1.6	-0.2	6.7 ± 4.4	8. 7 ± 4.3	0.9 to 3.1	0.5
Rectus femoris (cm ²)								
10	2.2 ± 0.9	2.4 ± 1.0	-0.2 to 0.4	0.1	2.2 ± 0.8	$2.6 \pm 1.0*$	0.2 to 0.6	0.5
20	5.3 ± 1.5	5.6 ± 1.6	0.04 to 0.6	0.2	5.1 ± 1.3	$5.6 \pm 1.4^{\star}$	0.3 to 0.8	0.4
30	8.3 ± 2.0	8.7 ± 2.3	0.02 to 0.7	0.2	7.8 ± 1.7	$8.3 \pm 1.6^{*}$	0.1 to 1.0	0.3
40	11.2 ± 2.7	11.4 ± 2.8	-0.2 to 0.6	0.1	9.9 ± 2.1	$10.8 \pm 2.0*$	0.5 to 1.3	0.4
50	13.5 ± 3.0	13.7 ± 2.9	0.01 to 0.5	0.1	12.2 ± 2.7	$13.2 \pm 2.8^{\star}$	0.6 to 1.5	0.4
60	14.4 ± 3.1	14.3 ± 2.9	-0.4 to 0.3	0.0	13.2 ± 3.1	$14.4 \pm 3.3^{\star}$	0.7 to 1.7	0.4
70	13.8 ± 3.5	13.7 ± 3.1	-0.9 to 0.6	0.0	12.6 ± 2.7	$13.7 \pm 2.8*$	0.7 to 1.6	0.4
80	12.4 ± 3.2	11.9 ± 2.8	-1.3 to 0.2	-0.2	11.3 ± 2.3	$2.5 \pm 2.5^{*}$	0.7 to 1.2	0.4
90	7.3 ± 2.3	6.3 ± 1.8	-1.9 to 0.2	-0.5	7.3 ± 2.3	$7.7 \pm 2.4*$	0.1 to 0.9	0.2

Table I. Muscle cross-sectional areas (cm^2) assessed before (pre) and after (post) 6 weeks of training at 10% intervals along the single quadriceps muscles proximo-distally (i.e. 9 muscle regions) in groups that trained either at short (SL) or long muscle length (LL).

Note: * = P < 0.05 for torque change from week 0 to week 6; 90% confidence intervals (90% CI) and the effect sizes (ES) for the average change in CSAs are given; 90% CI = 90% CI for the change in CSA.

dependence of isometric training on dynamic torque production.

It has been shown previously that isometric training with force developed rapidly can result in both an increased rate of force development and movement velocity, especially in untrained participants (Behm, 1995). However, it has also been shown that the effects of isometric training on dynamic explosive force production are relatively minor (Häkkinen, 1994) and that traditional heavy weight training, including isometric training, primarily increases maximum strength measured at slower movement velocities (Häkkinen, 1994; Harris, Stone, O'Bryant, Proulx, & Johnson, 1999; McBride,

Triplett-McBride, Davie, & Newton, 1999). These were also found in the present study, showing that peak concentric torque increased significantly in LL at slower and moderate angular velocities but not at faster velocities. Thus, in addition to the increases in isometric torque production and muscle CSA shown in our previous study (Noorkõiv et al., 2014), it appears that isometric training at a long muscle length is a useful tool for increasing dynamic torque production at specifically slower angular velocities in previously non-strength-trained individuals. These results provide sufficient evidence to explicitly test whether such training is also sufficient to elicit improvements in functional performance (e.g.

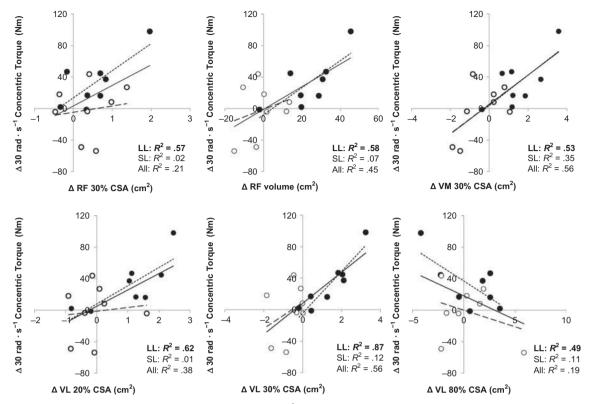


Figure 3. Relationships between the relative changes in 30 rad \cdot s⁻¹ peak concentric torque and relative changes in rectus femoris (RF) muscle cross-sectional area (CSA) and volume, vastus medialis (VM) CSA and vastus lateralis (VL) CSA at different muscle regions. Black circles represent the group that trained at a long muscle length (LL), and white circles are the group that trained at a short muscle length (SL). A line of best fit is given for LL (short-broken line), SL (long-broken line) and all participants (continuous line) with R^2 values.

walking, chair rise, stair walking and running), especially in clinical populations, in future studies.

The lack of change in concentric (isokinetic) torque at the slowest velocities in SL was unexpected, however a similar finding has been reported previously (Alegre et al., 2014). A possible explanation for this may be that the average isometric training angle in the present study was 40° in SL, but the angle at which peak concentric torque occurs at slower movement velocities is 50°-70° (Froese, Houston 1985; Noorkõiv et al., 2014; Taylor, Cotter, Stanley, & Marshall, 1991). Thus, a lack of training specifically at the optimal angle(s) for concentric torque production (i.e. 50°-70°) may have reduced the chance of improvement in concentric torque. Alegre et al., (2014) have recently suggested that a lesser muscle damage and fascicle stress, nonoptimal working range and neural factors are associated with the lack of change in dynamic torque production after training at short muscle length.

Relationships between changes in muscle size and peak concentric torque

Changes in muscle size in LL (in RF, VL and VM) were correlated with the changes in torque at 30 rad \cdot s⁻¹. It has been shown that muscle anatomical

CSA is a strong predictor of isometric and slowvelocity dynamic knee extension torques (Bamman, Newcomer, Larson-Meyer, Weinsier, & Hunter, 2000; Blazevich, Coleman, et al. 2009; Kanehisa, Ikegawa, Tsunoda, & Fukunaga, 1995). Muscle anatomical CSA increased significantly in LL and, importantly, changes in RF, VM and VL muscle CSA were significantly correlated with the increase in concentric torque at the slowest (30 rad \cdot s⁻¹) velocity. Also, it is notable that the positive correlations between the changes in concentric torque and muscle CSAs remained significant when the data from both groups were pooled (i.e. LL + SL). This finding supports the supposition that increase in muscular size is a factor that can influence peak force production when measured at slow muscle shortening velocities (e.g. 30 rad \cdot s⁻¹). The data are also suggestive that increases in isometric and slow-velocity dynamic torque production have some commonality in their underlying mechanisms.

Nonetheless, an intriguing finding of the present study was that increases in CSA in the proximal VL muscle (i.e. 80% region) were associated with smaller increases in concentric torque production at 30 rad \cdot s⁻¹. This suggests that there is a muscleand location-specific effect of hypertrophy on the change in dynamic torque. The reasons for this negative correlation cannot be determined for the present study, but it might suggest one (or more) of four possibilities. First, there may be a direct negative consequence of proximal hypertrophy in VL as far as slow-velocity dynamic torque capacity is concerned. The results indicate that hypertrophy elsewhere in the muscle (i.e. distally) may be of greater importance, and correlations were observed for these regions (see Figure 3). Second, muscle architecture varies amongst different regions of muscles (Blazevich, Gill, & Zhou, 2006) and these regions would likely produce different force generating effects. Therefore, hypertrophy in a location with an architecture unsuited to contractions with specific force-time-velocity characteristics might not be useful; it is well known that there are "compartments" in large muscles and that these can be uniquely activated (Blemker & Delp, 2005; Finni, Havu, Sinha, Usenius, & Cheng, 2008; Noorkõiv et al., 2014). Third, force produced closer to the knee will be more readily transferred to the joint, because the forces will be transmitted through a length of elastic material (laterally between fibres and muscles) as shown previously (Finni et al., 2008). Shorter connective tissue pathways are theoretically stiffer since stiffness is inversely proportional to length of a spring (Hooke's law, i.e. stiffness = 1/k + 1/k + 1/k ..., where k = stiffness of a serially arranged tissue segment). Therefore, they will stretch less for a given force, store less energy because of this, and thus will lose less energy in the force transmission process. Thus, changes in muscle size or architecture in different regions may have different effects on the magnitude of force transferred to the distal tendon, and thus contribute differently to joint torque. Fourth, fibres (or compartments) within a muscle cross the joint with different moment arms and lines of action (Blemker & Delp, 2005), and hypertrophy in specific regions may influence this. Therefore, selective hypertrophy will differently influence the contribution of fibres (or compartments) within a muscle; some of these fibres or compartments may not be optimal for force production under specific contraction conditions. These four factors might have influenced the correlations between the change in CSA and change in joint torque, including the negative correlation observed for the proximal VL muscle. Further research is required to more clearly understand the effects of region-specific hypertrophy, especially given the indication of the present data that hypertrophy in some regions maybe associated with a lesser increase in torque production. Complex modelling study would be needed to determine the specific effects of selective hypertrophy of the type reported here, and the present data might be of use in a future model validation process.

Correlations between changes in fascicle length and peak concentric torque

Another hypothesis of the present study was that the increase in fascicle length would specifically influence isokinetic torque production at faster velocities. Given the predicted relationship between fibre (or fascicle) length and muscle contraction velocity (Lieber, 2009; Thom, Morse, Birch, & Narici, 2007) it could be predicted that the increase in fascicle length would be associated with increases in force production at faster knee extension velocities. For example, longer fascicles have been found in sprinters as compared to non-sprinters (Abe, Kumagai, & Brechue, 2000; Kumagai et al., 2000) and increases in fascicle length have been observed when slower velocity strength training is replaced by higher velocity sprint/jump training in athletes (Blazevich, Gill, Bronks, & Newton, 2003). However, changes in concentric torque at faster movement velocities (i.e. 180 rad \cdot s⁻¹ or faster) were not found after the training in either group, and no correlation was observed between the changes in torque at any test velocity. Thus, the hypothesis that increases in fascicle length would be associated with improvements in high-velocity torque production was not supported. It is possible that either (1) the increases in fascicle length of the magnitude elicited by the training (5% in a mid-thigh VL muscle regions) were insufficient to elicit measureable changes in torque production, (2) the increase in fast torque production requires task-specific training to elicit optimal neural adaptations before the changes in muscle architecture can have a meaningful functional effect (Blazevich et al., 2003; Blazevich & Sharp, 2005), or (3) changes in fascicle length were not reflective of changes in fibre length (i.e. serial sarcomere number) so there was no change in the mechanical capacity of the fibres. Further research is required to explicitly test these hypotheses.

Conclusion

Increases in slow (i.e. 30 rad \cdot s⁻¹)- and moderatevelocity (120 rad \cdot s⁻¹) concentric isokinetic torque were evident only after isometric training at longer muscle lengths, and the torque changes were correlated with changes in muscle CSA, and changes in dynamic torque production and increases in CSA were not observed for the group that trained at shorter muscle lengths. The angle of peak torque in the concentric contractions was not noticeably modified after the isometric training at either short or long muscle lengths, despite angle-specific changes being detected under isometric contraction as previously reported. The present results provide no evidence that a ~5% increase in fascicle length elicited by the isometric training in some portions of VL influences torque production at any (including fast) velocity, suggesting that training-related changes in fascicle length have little effects on dynamic force production, at least when specific high-velocity training is not performed concurrently. Taken together the present study suggests that, when dynamic training is not recommended or possible, muscle size and dynamic force production improvements might be best elicited by isometric training performed at long muscle lengths.

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