

Inhomogeneous Quadriceps Femoris Hypertrophy in Response to Strength and Power Training

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ABSTRACT

EARP, J. E., R. U. NEWTON, P. CORMIE, and A. J. BLAZEVICH. Inhomogeneous Quadriceps Femoris Hypertrophy in Response to Strength and Power Training. *Med. Sci. Sports Exerc.*, Vol. 47, No. 11, pp. 2389–2397, 2015. **Introduction:** Previous studies have reported inhomogeneous changes in quadriceps femoris (QF) cross-sectional area (CSA) in response to strength training. It is assumed that these differential changes in muscle shape influence the muscle's functional capacity during high-force and high-power movements. The purpose of the current study was to compare intermuscular and intramuscular QF adaptations to high-load strength training and fast-speed power training. **Methods:** Thirty-six non-strength-trained men were randomly assigned to four groups and completed 8 wk of parallel-depth heavy squat-lift training (HS-P), parallel-depth jump squat training (JS-P), volitional-depth jump squat training (JS-V), or no training (C). Quadriceps femoris, vastus lateralis (VL), intermedius (VI), medialis (VM), and rectus femoris (RF) CSA were measured in distal-, mid-, and proximal-thigh regions using extended field-of-view ultrasonography and compared using a 3 × 2 mixed-model MANOVA with Bonferroni *post hoc* tests ($P < 0.05$). **Results:** Parallel-depth heavy squat-lift training and JS-P elicited similar changes in mid-CSA_{QF} as well as summed CSA of the QF, VL, VI, and VM. Cross-sectional area of the VL (CSA_{VL}) and CSA_{VI} increased in both HS-P and JS-P at mid-thigh, but only JS-P significantly increased CSA proximally, and only HS-P significantly increased CSA distally. Cross-sectional area of the VM (CSA_{VM}) increased in HS-P and JS-P distally, but only HS-P increased at mid-thigh. No hypertrophy was observed in RF at any location and no significant differences were observed between JS-P and JS-V. Parallel-depth heavy squat-lift training elicited greater proximal hypertrophy in each of the vasti muscles, whereas only JS-P elicited distal VL and VI hypertrophy. **Conclusions:** These observed inhomogeneous changes in CSA may alter the thigh's moment of inertia and moment arms of muscle "compartments," and the influence of elastic component force transmission on the muscular force expression. Such selective hypertrophy is speculated to be biomechanically beneficial to high-force or high-power movements used in training. **Key Words:** REGION-SPECIFIC HYPERTROPHY, CROSS-SECTIONAL AREA, MUSCLE VOLUME, JUMP SQUAT, BACK SQUAT

The physical structure of a muscle is the primary determinant of its functional capacity (7,16,17). Most significantly, the muscle's cross-sectional area (CSA) is positively associated with its maximal force generating capacity (7). However, even within a muscle that shares a common distal insertion point, like the quadriceps femoris (QF), significant intramuscular (i.e., proximodistally) and intermuscular (between constituent muscles) structural variability exists (9,10). These variations are speculated to allow for different regions of the muscle to serve different functional roles, with some regions ideally suited to high-force production but others potentially suited for faster-speed muscle

shortening or the rapid transfer of force to the tendon (9,23,38). In support of this, selective muscle recruitment has been observed using electromyography, near-infrared spectrometry, and functional MRI when the knee extensors are activated at different joint positions (15), force levels (38,40), and movement speeds (3,38); and inhomogeneous QF hypertrophy has been observed in response to various training interventions (8,22,36,37).

Inhomogeneous structure of the QF can directly affect biomechanical performance. For instance, the proximodistal distribution of mass affects the moment of inertia about both the proximal pivot point (local inertia) and its center of mass (remote inertia) (11). By orienting the mass of the muscle closer to the joint's axis of rotation, the moment of inertia about the joint will be reduced, in turn decreasing the joint angular velocity for a given joint moment or muscular force (1,27). Thus, during tasks when the segment is rapidly accelerated such as jumping or sprinting, having muscle mass distributed close to the axis of rotation of the movement may have a direct benefit to performance in that task (1).

Inhomogeneous muscle structure will also alter the distance that forces developed within muscle fibers must travel

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through the parallel (fiber to fiber and intramuscular) and series (aponeurosis and distal tendon) elastic components to be expressed in joint motion. Since the length of the elastic medium differs between muscle fibers distributed proximodistally, the stiffness and hysteresis properties of, and thus the forces developed by, these fibers will also differ. Specifically, as the loss of stored elastic energy via hysteresis increases with tissue length, the loss of energy during muscular contraction should theoretically be greater for muscle fibers located further from the joint. Furthermore, contractile tissue located closer to the joint will act through a stiffer medium and be better suited for movements during which force must be rapidly developed; in contrast, contractile tissue further from the joint would encounter a more elastic medium and be better suited for relatively slow speed movements during which forces are developed over time (28).

The muscle's shape during contraction has also been shown to influence output velocity and the muscle's force capacity by altering the muscle's architectural gearing ratio (4). Brainerd and Azizi (12) found that muscles experience a relatively large increase in CSA (i.e., bulging) during high-speed movements, which increases longitudinal output velocity relative to muscle fibre velocity at the expense of force capacity, demonstrating a high gear ratio. In contrast, the muscle's architectural gearing ratio will decrease and less bulging will occur for a given amount of muscle fibre shortening during high-force contractions (4). However, while it has been observed that speed and force demands of an exercise can acutely alter muscle shape, it remains unclear if these differences will be expressed over time by differing structural adaptations.

High-load, relatively slow-speed (strength) training and high-speed, relatively light-load (power) training are both commonly utilized training programs for athletes as well as young/healthy individuals (5,21,35), and have been shown to increase strength (21,34), power (2,25), and CSA of the QF (CSA_{QF}) (35). However, the extent to which changes in CSA occur intramuscularly and intermuscularly is not known. Despite this, it can be hypothesized that structural adaptations would differ between the two forms of training because differences in muscular and regional activation as well as inhomogeneous intramuscular pressure, stress and strain have been previously reported (18,20,33,37,40). This is supported by the observation that regions of muscle that encounter the greatest muscle activation may also experience the largest increase in CSA (37).

No previous research has investigated the effects of strength versus power training on region- and muscle-specific hypertrophy or whether these adaptations are dependent on the range of motion used in training. Thus, the purpose of the present study was to compare intramuscular and intermuscular changes in CSA_{QF} attributed to strength versus power training. For this study we chose to use matched-depth squatting movements, i.e. back squat and jump squat, because they are both commonly performed and considered to be core exercises in many training programs (5,21). A secondary purpose was

to determine whether these adaptations are dependent on the knee joint range of motion utilized in training. We hypothesized that both forms of training would result in an increase in CSA_{QF}; however, the magnitude and location of these changes would differ based on the training intervention. More specifically we hypothesized that power training would increase CSA to a greater extent in the distal region of the thigh, close to the axis of rotation, which would lead to a decrease the moment of inertia and ability to transfer forces through a short, stiff elastic medium. In contrast, in response to slow-speed, high-load, strength training, CSA would increase to a greater extent in the middle and proximal regions of the thigh, where the potential for hypertrophy is greater because of the larger CSA (7,26). Furthermore, because the movement is performed at submaximal speeds with high external loads, the local moment of inertia will be a smaller contributor to the resistance moment (39) and a longer, more compliant elastic medium may be of some benefit (19).

METHODS

Subjects. Thirty-six healthy men age 18–35 yr volunteered for the study. The subjects were physically active but had not been involved in a structured lower-body resistance training program in the previous 6 months. Subjects were excluded if they had any history of lower body muscle, tendon, or joint injury that would interfere with the training or testing. Before enrolment, subjects were familiarized to all testing and training protocols and required to show proficient squat lift and jump squat technique. This study was reviewed and approved by the University's Human Research Ethics Committee, and all subjects gave their written consent before participation.

Experimental design. At least 48 h after familiarization, knee extensor CSA was measured using extended field-of-view (EFOV) ultrasonography, and one-repetition maximum (1RM) was determined for the parallel back squat exercise. Subjects were then assigned to one of four groups: heavy-load (relatively slow-speed) parallel squat training (HS-P; $n = 9$; height, 178 ± 5 cm; body mass, 88 ± 18 kg; 1RM:BM, 1.00 ± 0.18), jump squat training with jumps performed to parallel thigh depth (JS-P; $n = 9$; height, 175 ± 5 cm; body mass, 69 ± 9 kg; 1RM:BM, 1.20 ± 0.28), jump squat training with jumps performed to volitional depth (JS-V; $n = 9$; height, 177 ± 6 cm; body mass, 69 ± 10 kg; 1RM:BM, 1.04 ± 0.22) and a control group (C; $n = 9$; height, 178 ± 7 cm; body mass, 81 ± 15 kg; 1RM:BM, 1.05 ± 0.21). Training group allocation was done by stratifying subjects based on their 1RM-to-body mass ratio (1RM:BM) and then randomly assigning stratified subjects into their respective group. After the 1RM testing, all subjects undertook a 2-wk washout period to allow possible residual effects from the 1RM testing to subside, after which they commenced training (HS-P, JS-P, or JS-V) three times a week for 8 weeks or were monitored through the control period (C). Control (C) subjects were required to maintain their normal physical

activities but avoid any form of resistance training for the duration of the study. The subjects then repeated their preintervention testing 48–72 h after the final training session. Comparisons were then made to determine training effects and quantify differences between groups. Before all testing, subjects refrained from any exercise for at least 48 h and were instructed to maintain their normal diet and remain euhydrated and avoid alcohol for at least 24 h.

Cross-sectional area and volume. To assess intramuscular (i.e., proximodistally) and muscle-specific CSA, subjects laid supine with their knees extended, muscles relaxed, and their feet supported. In this position, CSA of the VL, VM, VI, RF, and the QF (sum of all four quadriceps components) of their right thigh was measured using transverse EFOV ultrasonography (Alpha 10, Aloka, Co, Ltd, Tokyo, Japan). Images were taken at 33% (proximal), 50% (mid) and 67% (distal) of the length between the greater trochanter and lateral epicondyle of the femur, using a 6-cm linear array probe (UST 5713, Aloka, Co, Ltd, Tokyo Japan) (31). This technique has been shown to provide valid CSA measurements (31). To account for possible fluid shifts, the subjects were asked to lay supine for 20 min before the first images being taken (6).

Transverse EFOV images were deemed acceptable if the femur and aponeurosis of each quadriceps component were visible, solid, and continuous (Fig. 1). Reference markers were placed in a crossing pattern along the muscle and used to anchor the image to ensure equal linear spacing as well as to guide probe path and ensure a constant speed of probe movement during scanning (31). Each scan was repeated until three images were deemed acceptable. Analysis of EFOV images was performed using image analysis software (OsiriX, Pixmeo, Geneva, Switzerland). These procedures resulted in reliable QF, VL, VI, VM, and RF CSA measurements at the proximal (intraclass correlation coefficient [ICC], 0.982–0.996; CV, 3.5%–7.7%; SEM, 0.41–2.68 cm²) mid (ICC, 0.976–0.999; CV, 3.2%–5.0%; SEM, 0.24–1.77 cm²) and distal (ICC, 0.976–0.998; CV, 3.3%–10.7%; SEM, 0.13–1.90 cm²) regions. In addition to regional CSA of each muscle, the sum of the distal, mid, and proximal CSA of the QF and each individual muscle was calculated.

One-repetition maximum. After completing a warm-up consisting of 5 min of low-intensity cycling (Monark 915E, Monark Exercise AB, Sweden; 1.5 kp, 60 rpm) and a series of bodyweight and submaximal load (50%, 75%, and 90% of estimated 1RM) parallel-depth squats, the subjects had their free-weight parallel-depth squat lift 1RM determined using the protocols outlined by Bachele et al. (5). The subjects were permitted up to six attempts to find their 1RM with a 3-min passive recovery between each attempt. The 1RM was defined as the greatest load that could be successfully lowered to and raised from parallel-depth while maintaining correct technique. Parallel-depth was defined at the position at which the greater trochanter and lateral epicondyle of the femur were parallel with the floor.

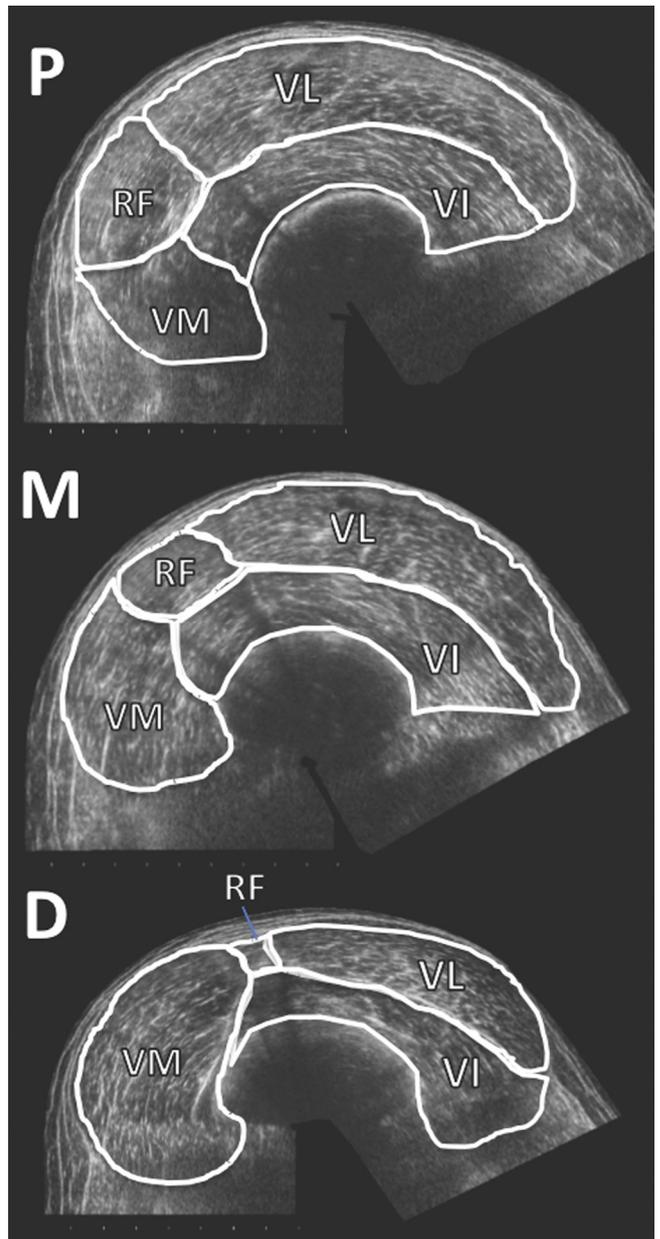


FIGURE 1—Example of extended-field-of-view images of the knee extensors taken in the proximal (P), mid (M), and distal (D) regions of the thigh. The VL, VI, VM, and RF in each region are outlined.

To ensure consistency during testing and training, before 1RM testing, the subjects performed a parallel-depth squat during which knee angle was measured using an electronic goniometer (MLTS700, AD Instruments USA) and bar depth was recorded using a ceiling-mounted linear position transducer (PT5A-150, Celesco Transducer Products, Chatsworth, CA) sampling at 1000 Hz. These values were then used as the criteria for performing an acceptable parallel-depth squat. The knee was required to flex to within 2.5° and bar depth to be within 1.25 cm of the criterion values for the repetition to be accepted subsequent analysis or considered appropriate during training. Depth testing was also randomly performed throughout the training program to ensure consistent training depth.

Training program. The subjects assigned to one of the three training groups (HS-P, JS-V, and JS-P) trained three times a week for 8 wk. The subjects in the HS-P group performed squats to a parallel-depth during which their form was strictly monitored. For the duration of the training, HS-P performed a repeating nonlinear microcycle in which set, repetition and loading schemes varied daily to incorporate training targeted for both hypertrophy and strength in each microcycle (5,14). This program allowed for similar repetition ranges and relative loads (% 1RM load) to be used in each microcycle; however, absolute load (kilogram lifted) and amount of work performed did increase throughout the program as subject strength increased. Parallel-depth heavy squat-lift was performed with loads between 75% and 90% of 1RM load (day 1, three sets \times three repetitions at 90%; day 2, three sets of eight repetitions at 75%; day 3, three sets of six repetitions at 80%). Loads were progressed throughout the training program as the subject increased their strength. Subjects in the JS-V and JS-P groups performed jump squats with loads between 0% and 30% of their 1RM load (day 1, seven sets of six repetitions at 0%; day 2, five sets of five repetitions at 30%; day 3, seven sets of six repetitions at 0%). The JS-V subjects performed jumps with a countermovement to volitional depth (approximately $\frac{1}{2}$ to $\frac{1}{4}$ parallel squat depth), whereas the JS-P subjects performed jumps with a countermovement to parallel depth. After 4 wk of training, the subjects in all training groups were reassessed for 1RM, and revised loading intensities were prescribed for JS-V and JS-P. Previous literature has shown significant improvements in neuromuscular performance after training with similar programming parameters [14]. However, as a limitation of the current investigation, it must be noted that the simultaneous presentation of high volumes of training with high-intensity training may not have provided the optimal stimulus to maximize adaptations. Furthermore, given the inherent differences in high-load strength training and fast-speed power training, the total work performed by the groups was not equalized and therefore may influence the subsequent adaptations.

Statistical analysis. A 3×2 mixed factorial MANOVA and Bonferroni *post hoc* tests were used to examine differences in strength and CSA in HS-P, JS-P, and C between the groups and over time, as well as to examine possible interaction effects. Cohen *d* was used to determine the effect size (ES) of change scores in HS-P and JS-P compared to C. In addition, Student's *t*-tests were used to compare differences in adaptation to JS-P and JS-V to determine whether the range of motion used in power training influenced adaptations. Means, standard deviations, and percentage changes from baseline are reported. To determine reliability of measures, ICC, coefficient of variation (CV), and SEM were reported. Intraclass correlation coefficient was calculated using a two-way mixed-model test of absolute agreement, whereas CV and SEM were calculated using the following equations: $CV = (SD/\bar{x}) \times 100$ and $SEM = SD\sqrt{1-0.7}$. All statistical analyses were conducted using PASW version 18.0.1 (IBM, New York, USA), and statistical significance was accepted at α level of $P < 0.05$.

RESULTS

Preintervention and postintervention values (cm^2), as well as effect sizes and average percent changes from baseline of muscle-specific and regional-specific CSA are reported in Tables 1 and 2. Changes in region-specific and summed CSA of QF are depicted in Figures 2 and 3. Summed CSA_{QF} increased similarly in HS-P ($14.7\% \pm 6.7\%$; ES, 3.70; $P = 0.000$) and JS-P ($14.3\% \pm 7.8\%$; ES, 3.24; $P = 0.000$) versus C ($-0.6\% \pm 1.9\%$); however, no significant differences between the two training groups were observed ($P = 0.925$). Similarly, both HS-P and JS-P increased CSA_{QF} compared to the control group in the proximal (HS-P, $15.4\% \pm 7.7\%$; ES, 2.43; JS-P, $11.5\% \pm 8.5\%$; ES, 1.74; C, $0.7\% \pm 4.0\%$), mid (HS-P, $13.3\% \pm 9.7\%$; ES, 2.46; JS-P, $13.6\% \pm 9.6\%$; ES, 2.22; C, $-1.4\% \pm 4.0\%$), and distal (HS-P, $15.4\% \pm 7.4\%$; ES, 3.18; JS-P, $19.5\% \pm 13.1\%$; ES, 2.64, C, $-1.7\% \pm 5.3\%$) regions.

TABLE 1. Changes in regional and muscle-specific CSA of the QF, VL, VI, VM, and RF taken at 33% (proximal-), 50% (mid-), and 67% (distal-) thigh length in response to 8 wk of parallel-depth squat (HS-P) or jump squat (JS-P) training or no training (C).

		HS-P			JS-P			C		
		Before (cm^2)	After (cm^2)	Δ (%)	Before (cm^2)	After (cm^2)	Δ (%)	Before (cm^2)	After (cm^2)	Δ (%)
D	QF	60.8 \pm 13.2	70.2 \pm 15.4	15.4*	52.2 \pm 11.2	62.0 \pm 14.8	18.8*	60.4 \pm 13.3	59.4 \pm 13.8	-1.7
	VL	15.3 \pm 4.4	17.6 \pm 4.6	15.0	12.8 \pm 3.0	16.1 \pm 4.5	25.8*	16.2 \pm 4.1	15.5 \pm 4.2	-4.3
	VI	18.3 \pm 4.1	21.0 \pm 5.1	14.8	15.4 \pm 2.9	18.5 \pm 4.9	20.1*	17.3 \pm 3.4	17.2 \pm 3.1	-0.5
	VM	25.3 \pm 5.2	29.8 \pm 5.2	17.8*	22.2 \pm 6.7	25.2 \pm 5.7	13.5*	25.2 \pm 6.7	25.0 \pm 7.7	-0.7
	RF	1.9 \pm 1.2	1.9 \pm 1.2	0.0	1.9 \pm 0.7	2.4 \pm 1.0	26.3	1.7 \pm 0.6	1.7 \pm 0.8	0.0
M	QF	80.3 \pm 13.0	91.0 \pm 12.1	13.3*	66.4 \pm 15.5	75.4 \pm 16.0	13.6*	78.8 \pm 13.3	77.7 \pm 13.9	-1.4
	VL	28.0 \pm 4.4	30.9 \pm 4.2	10.4*	21.6 \pm 5.5	25.5 \pm 6.5	18.1*	27.2 \pm 5.0	26.6 \pm 5.1	-2.2
	VI	27.0 \pm 5.8	31.6 \pm 5.7	17.0*	23.7 \pm 5.7	26.2 \pm 5.2	10.5*	26.5 \pm 3.3	25.5 \pm 4.0	-3.8
	VM	18.3 \pm 5.0	22.0 \pm 3.8	20.2*	15.0 \pm 4.7	17.1 \pm 4.7	14.0	18.5 \pm 5.3	18.6 \pm 5.1	0.5
	RF	7.0 \pm 2.7	6.8 \pm 2.6	-2.9	6.1 \pm 1.8	6.6 \pm 1.3	8.2	6.7 \pm 1.5	6.3 \pm 1.4	-6.0
P	QF	79.0 \pm 8.4	91.2 \pm 11.8	15.4*	67.9 \pm 15.6	75.7 \pm 15.6	11.5*	74.3 \pm 11.9	74.8 \pm 5.3	0.7
	VL	29.3 \pm 4.6	34.3 \pm 5.5	17.1*	23.5 \pm 7.5	26.5 \pm 7.0	12.8	27.1 \pm 4.7	17.8 \pm 5.3	2.6
	VI	27.4 \pm 3.9	33.3 \pm 6.1	21.5***	23.5 \pm 7.3	26.0 \pm 4.7	10.6	26.1 \pm 4.9	26.1 \pm 4.7	0.0
	VM	10.2 \pm 2.2	11.2 \pm 2.9	9.8	10.0 \pm 1.9	11.4 \pm 1.4	14.0	8.6 \pm 2.4	8.9 \pm 1.8	3.5
	RF	12.0 \pm 3.2	12.4 \pm 2.9	3.3	10.9 \pm 2.8	11.8 \pm 2.2	8.3	12.5 \pm 2.2	11.9 \pm 2.1	4.8

Values are mean \pm SD.

*Significantly different from C ($P < 0.05$).

**Significantly different from JS-P ($P < 0.05$).

P, proximal; M, mid; D, distal.

TABLE 2. Changes in summed CSA (SUM) along the length of the thigh of the QF, VL, VI, VM, and RF in response to 8 wk of HS-P or JS-P training or C.

	HS-P			JS-P			C		
	Before (cm ²)	After (cm ²)	Δ (%)	Before (cm ²)	After (cm ²)	Δ (%)	Before (cm ²)	After (cm ²)	Δ (%)
QF	220.0 ± 31.3	252.4 ± 33.2	14.7*	186.4 ± 41.3	213.1 ± 4.53	14.3*	213.6 ± 37.3	211.9 ± 38.8	-0.6
VL	72.6 ± 10.5	82.4 ± 10.5	13.5*	57.9 ± 14.4	68.1 ± 17.5	17.6*	70.5 ± 13.1	69.9 ± 13.2	-0.9
VI	72.7 ± 12.3	85.8 ± 15.5	18.0*	62.6 ± 5.2	70.7 ± 17.3	12.9*	69.9 ± 10.1	68.8 ± 10.7	-1.6
VM	53.7 ± 9.0	62.9 ± 8.2	17.1*	47.2 ± 11.1	53.7 ± 10.2	13.8*	52.3 ± 12.9	53.1 ± 13.7	1.5
RF	21.0 ± 6.7	21.2 ± 6.5	1.0	18.9 ± 4.8	20.9 ± 3.2	10.6	20.9 ± 3.9	20.1 ± 3.6	-3.8

Values are mean ± SD.

*Significantly different from C ($P < 0.05$).

Furthermore, when HS-P was compared to JS-P, mean differences were not statistically significant in any region of interest. However, the mean difference in HS-P was 34% greater than that in JS-P in the proximal region ($P = 0.258$), which, whereas not statistically significant, may be of clinical relevance as HS-P demonstrated a greater treatment effect size than JS-P (effect size of HS-P, 2.43; effect size of JS-P, 1.74).

In the proximal region of the thigh, the increase in CSA_{VL} was significantly greater in HS-P than C (ES, 1.73; $P = 0.006$), but the increase in JS-P was not different from that in C (ES, 1.01; $P = 0.173$). Mean proximal CSA_{VI} was significantly greater in HS-P than in JS-P and C (ES, 2.23; $P = 0.023$ and $P = 0.000$) but not different between JS-P and C ($P = 0.124$). Proximal CSA of VM and RF did not significantly increase in HS-P ($P = 0.859$ and $P = 0.905$) or JS-P ($P = 0.353$ and $P = 0.254$).

In the mid-region of the thigh, the increases in CSA_{VL} and CSA_{VI} were significantly greater in HS-P (ES, 1.78 and 1.89; $P = 0.008$ and $P = 0.000$) and JS-P (ES, 2.23 and 1.95;

$P = 0.001$ and $P = 0.012$) than C. However, no significant differences were found between the two training groups in mid-CSA_{VL} or mid-CSA_{VI} ($P = 0.792$ and $P = 0.200$). Mean mid-CSA_{VM} significantly increased in HS-P ($20.2\% \pm 11.8\%$; ES, 2.13; $P = 0.001$) but not in JS-P ($14.0\% \pm 14.0\%$; ES, 1.19; $P = 0.107$) compared to C. Mid-CSA_{RF} did not significantly increase in HS-P or JS-P ($P = 0.866$ and $P = 0.150$).

In the distal region of the thigh, the increases in CSA_{VM} and CSA_{QF} were significantly greater in HS-P (ES, 3.24 and 3.18; $P = 0.000$ and $P = 0.001$) and JS-P (ES, 1.66 and 2.06; $P = 0.006$ and $P = 0.000$) than C. However, no significant differences were found between the two training groups in either muscle ($P = 0.277$ and $P = 0.987$). The increase in mean distal CSA_{VL} and CSA_{VI} were greater in JS-P than C (ES, 1.58 and 1.45; $P = 0.009$ and $P = 0.036$); however, changes in HS-P were not significantly different from C (ES, 1.38 and 1.62; $P = 0.058$ and $P = 0.079$). Distal CSA_{RF} did not significantly increase in HS-P or JS-P ($P = 1.000$ and $P = 0.298$).

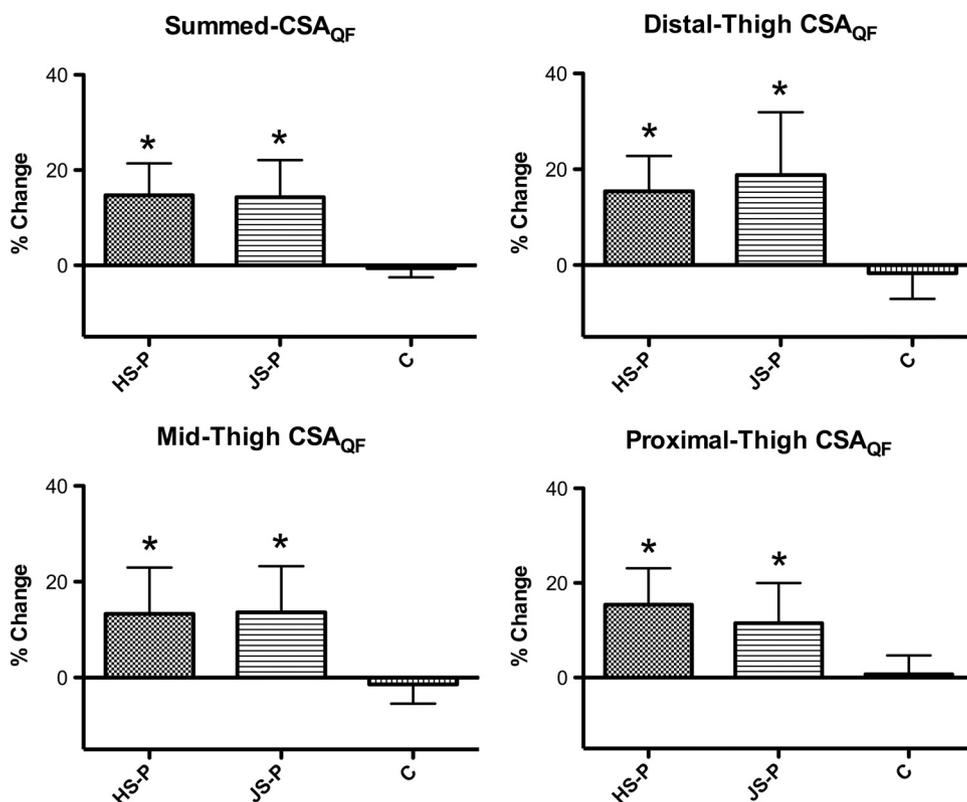


FIGURE 2—Training-specific adaptations (% change) in QF muscle and CSA at the distal, mid, and proximal thigh and the sum of the three regions (SUM) in response to 8 wk of HS-P or JS-P training performed to parallel depth, or no training (C). *Significantly greater increase than C.

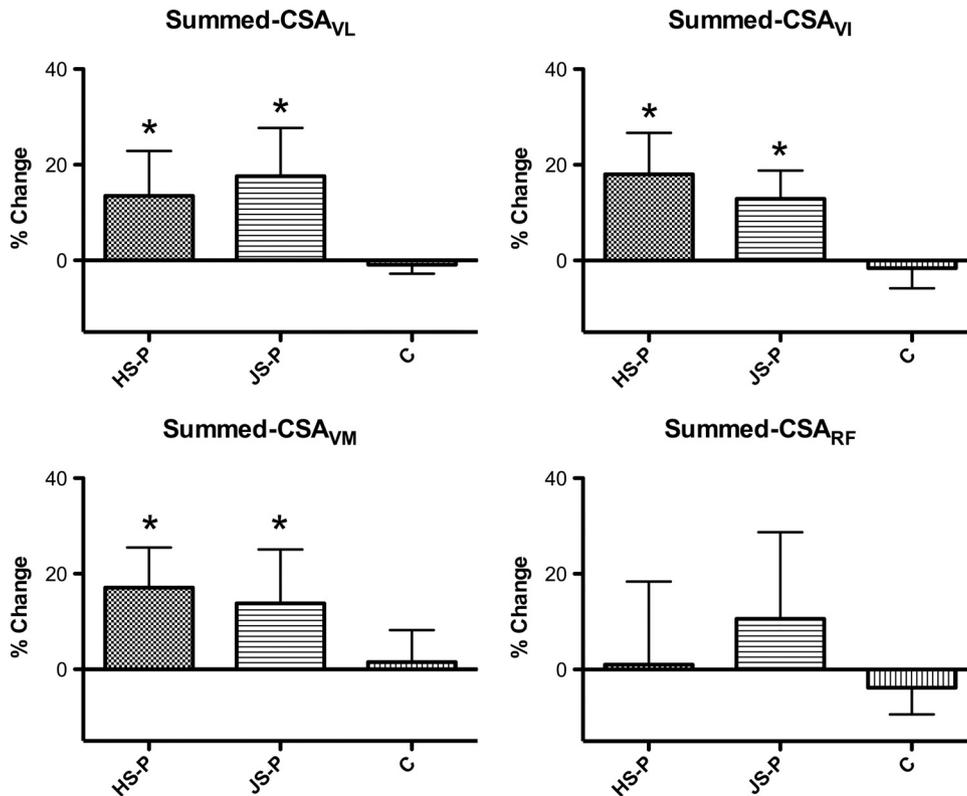


FIGURE 3—Training-specific adaptations (% change) in VL, VI, VM, and RF SUM in response to 8 wk of HS-P or JS-P training performed to parallel depth, or no training (C) *Significantly greater increase than C.

Training-induced changes in JS-V and JS-P were compared using a series of independent *t*-tests. These results revealed no significant differences in changes in strength or summed or regional CSA of the QF or any of its constituent muscles, suggesting that the observed differences in hypertrophy were related to the training modality used (i.e., strength vs power) rather than the range of motion used in training.

No treatment effect was found in any CSA measurement over time in C. Before the training intervention, no significant differences were observed between the groups in any CSA measurements with the exception of mid-CSA_{VL}, which was significantly greater in the HS-P group than the JS-P group, and no significant differences were found between the groups in relative strength (1RM:BM). In response to training, relative strength (1RM:BM) significantly increased in all training groups (HS-P, 45.3% ± 17.4%; JS-V, 22.0% ± 11.4%; JS-P, 21.8% ± 13.0%), but no significant change was found in C (1.6% ± 4.8%; Fig. 4). In addition, a significant interaction effect was observed between HS-P and JS-P ($P = 0.001$) and JS-P and C ($P = 0.011$), showing that whereas both forms of training were effective at increasing relative strength, HS-P was more effective than JS-P.

DISCUSSION

The primary finding of the present study was that altering movement velocity by manipulating the training load elicited

differential region-specific hypertrophy after heavy-squat lift (strength) and jump squat (power) training. Whereas similar increases in muscle mid CSA_{QF} and summed CSA of the entire QF were observed, hypertrophy was not uniform between the QF components along the length of the muscle. Furthermore, these changes were observed despite both forms of training movements using similar joint ranges of motion;

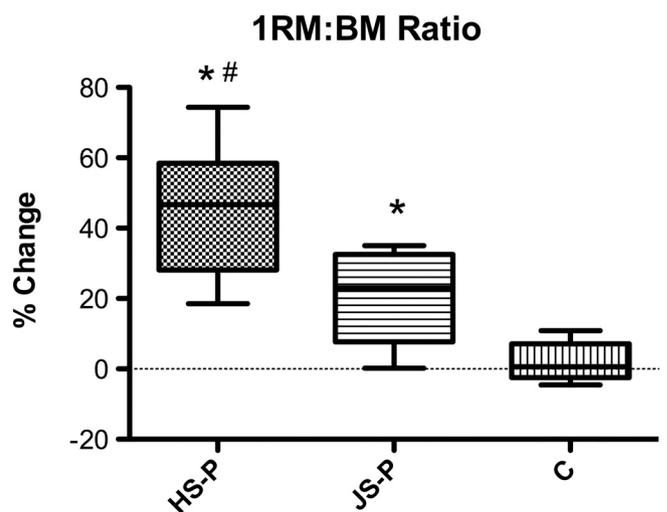


FIGURE 4—One-repetition maximum-to-body mass ratio (1RM:BM) adaptations (% change) in response to 8 wk of HS-P or JS-P training performed to parallel depth, or no training (C). *Significantly greater increase than C. #Significantly greater increase than JS-P.

responses between JS-P and JS-V were similar and indicate a lack of effect of squat depth (i.e., knee joint range of motion).

Heavy-load (relatively slow-speed) strength training and lighter-load (relatively fast-speed) power training are both effective training modalities for increasing strength capacity, muscular power, maximal speed, and athletic performance (14,35). Whereas both forms of training are physiologically and mechanically demanding, as they require substantial muscle activation to generate large forces, the specific stresses that they place upon the body have been shown to differ (13,14,35). Strength training such as that performed in HS-P is generally characterized by very high muscle forces and relatively slow joint angular velocities during which the muscles experience a long time under tension (5,13,14). In contrast, power training such as JS-P requires maximal acceleration of the load and body so that the fastest possible velocity is reached prior take-off (30). During these exercises, fast joint angular velocities and rapid force development are realized. Furthermore, while the muscles are maximally voluntarily activated, the maximum force developed is greater during the heavy squat, in part due to the force-velocity relationship (13). The aforementioned differences in the demands of strength and power training are likely to not only influence training adaptations but may also be benefitted by different structural adaptations.

In the present study, we hypothesized that region-specific changes in hypertrophy would be present between strength and power training. Indeed, we found that whereas both forms of training were effective at increasing CSA_{QF} along the length of the muscle as well as SUM of the QF, VL, VI, and VM, HS-P training was a more potent stimulus for muscle growth in the proximal regions of the thigh in VI (proximal region: HS-P, 21.5%; ES, 2.23 vs JS-P, 10.6%; ES, 1.38), VL (proximal region: HS-P, 17.1%; ES, 1.73 vs JS-P, 12.8%; ES, 1.01), and VM (mid region: HS-P, 20.2%; ES, 2.13 vs JS-P, 14.0%; ES, 1.91). In contrast, only JS-P elicited significant hypertrophy of VL and VI in the distal region.

It is believed that the physiological CSA of a muscle plays a major role in determining its force-generating capacity (7). However, possessing a large CSA along the entire length of a muscle would likely be metabolically inefficient, as this would increase the moment of inertia of the limb and require more active tissue to produce a given joint motion. For this reason, selective regional hypertrophy might be preferential to symmetrical hypertrophy, as it may alter how force is expressed during complex movements when force is developed either at different speeds or muscle lengths (9). While assessing the intrinsic variability within the QF, Blazeovich et al. (9) hypothesized that this variability may be exploited by aggregated muscle actions, which allow specific regions of the muscle to be optimally suited for specialized tasks, such as producing large forces at fast or slow muscular shortening speeds or at different joint positions. Such specialization would allow a muscle to function effectively during tasks with specific force-time and range of motion characteristics while minimizing metabolic costs.

While previous studies have observed differences in region-specific changes in CSA_{QF} in response to strength training (8,22,29,36,37), the present study is the first to examine the influence of external load and speed of movement on these adaptations. In the present study, we observed VL, VI, and VM regional hypertrophy to be greater closer to the joint's axis of rotation (i.e., in the distal thigh) during power training, where peak joint angular velocity is a primary determinant of performance. A likely benefit of orienting muscle mass closer to the joint center of rotation is that thigh moment of inertia (about the knee joint) would be reduced. As joint moment is the product of the limb's moment of inertia and the joint's angular acceleration, manipulation of the moment of inertia will have a greater influence on joint moment during rapid acceleration movements such as those experienced during the squat-based power training compared to slower strength training. Whether other factors, such as changes in the relative contributions of different muscle "compartments" (directly via selective hypertrophy of compartments or indirectly through changing the moment arms of these compartments (11)) might influence performance cannot be determined from the current data.

It should be noted that distributing muscle mass toward the distal thigh would be advantageous for the knee extensors and flexors, as the thigh moves around the knee such as during closed chain movements like squatting or jumping. However, at the same time, the hip extensors and flexors would require significantly more joint torque to accelerate the thigh around the hip, such as during sprint running. Greater distal mass might have a significant impact on JS-P performance, where thigh average velocity is relatively slow (compared to sprint running) slow, and most of the torque generated at the hip acts to accelerate the body rather than the thigh. Thus, the observed distal adaptations to JS-P may be fundamentally relevant for jumping but may not translate to different movements such as sprinting. Whereas no studies have directly examined this question, Wakahara et al. (36,37) observed a similar result in the triceps brachii when comparing open chain to closed chain exercises. Thus, it seems that optimal distribution of muscle mass may differ between open and closed chain movements. However, it should be noted that both the present study and the studies by Wakahara et al. (36,37) were performed in non-strength-trained individuals, and additional research is needed to determine whether these results will carry over to well-trained individuals over longer training durations.

One possible explanation for inhomogeneous changes in CSA could be differences in the distribution of muscle fiber types along the length of the muscle (37). However, variations in fiber type distribution along the length of the QF are not typically observed (23,24), so it is unlikely that this is a major contributing factor. In contrast, several studies have reported that regions of the muscle can be selectively activated during high-intensity or high-velocity contractions (36,37,40). Wakahara et al. (37) observed that the region of the muscle showing the greatest muscle activation also

experienced greatest training-induced increases in CSA_{QF}. Thus, it seems that by selectively activating parts of a muscle, specifically the parts that are best intrinsically suited for a specific movement, parts of a muscle may be trained selectively, resulting in inhomogeneous adaptations along the length of that muscle. Although we hypothesize that muscle possessed this added dimension of plasticity, it is beyond the scope of the current study to definitively describe such a mechanism for adaptation, as region-specific muscle activity was not recorded throughout training.

Another possible explanation for region-specific adaptations would be inhomogeneous stress/strain of the muscle during a contraction. Finni et al. (20) previously observed that strain along the length of, and between, muscles of the QF are inhomogeneous during even simple isometric contractions. Furthermore, as muscle that is located close to the joint passes through a shorter elastic component, it should encounter greater stiffness than muscle distributed further from the joint (32); i.e., tissue stiffness is inversely proportional to tissue length. Thus, such an arrangement would likely be beneficial for movements where a high rate of force development is necessary such as in a JS-P (16). In contrast, when force amplitude is more important than rate of force development, such as during HS-P, muscle mass acting through a more compliant elastic component may be beneficial, as it would increase time for peak muscle activation to occur and may decrease initial movement velocity so that the muscle works at a more beneficial portion of the force-velocity relationship (19).

In summary, the present study is the first to observe inhomogeneous adaptation in the knee extensors to HS-P

(strength) and JS-P (power) training. Whereas both forms of training provided a potent stimulus for hypertrophy at the mid-thigh region (CSA_{QF}) and at several distinct locations, a pattern of adaptation was present in the three largest knee extensor muscles (VL, VI, and VM), where HS-P resulted in greater adaptations in the proximal thigh and JS-P in the distal thigh. These differential adaptations are likely to alter the moment of inertia of the thigh, the amount of elastic tissue through which the muscle's contractile tissue operates, and the relative contribution of different muscular regions (compartments) because of small changes in their moment arms with hypertrophy. Furthermore, as no differences were present between JS-P and JS-V, the observed differences can be attributed to the load and speed of movement used for training rather than the range of motion used in training. Regional muscle hypertrophy represents an added dimension of specificity that requires future examination to determine the exact mechanisms responsible and implications for performance. Lastly, as region- and muscle-specific adaptations differed between the training groups, the potential for selective hypertrophy should be taken into account when selecting a CSA measurement site in exercise training studies and when choosing exercises to use to increase performance in a specific task.

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