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RESEARCH ARTICLE

Neural adaptations to long-term resistance training: evidence for the confounding effect of muscle size on the interpretation of surface electromyography

Jakob Škarabot,[1] Thomas G. Balshaw,[1,6] Sumiaki Maeo,[1,2] Garry J. Massey,[1,3] Marcel B. Lanza,[4] Thomas M. Maden-Wilkinson,[1,5] and Jonathan P. Folland[1,6]

[1]*School of Sport, Exercise and Health Sciences, Loughborough University, Leicestershire, United Kingdom;* [2]*Faculty of Sport and Health Science, Ritsumeikan University, Shiga, Japan;* [3]*School of Sport and Health Sciences, University of Exeter, Exeter, United Kingdom;* [4]*Department of Physical Therapy and Rehabilitation, University of Maryland, Baltimore, Maryland;* [5]*Academy of Sport and Physical Activity, Faculty of Health and Wellbeing, Sheffield Hallam University, Sheffield, United Kingdom; and* [6]*Versus Arthritis Centre for Sport, Exercise and Osteoarthritis Research, Loughborough University, Leicestershire, United Kingdom*

Abstract

This study compared elbow flexor (EF; *experiment 1*) and knee extensor (KE; *experiment 2*) maximal compound action potential (M_{max}) amplitude between long-term resistance trained (LTRT; n = 15 and n = 14, 6 ± 3 and 4 ± 1 yr of training) and untrained (UT; n = 14 and n = 49) men, and examined the effect of normalizing electromyography (EMG) during maximal voluntary torque (MVT) production to M_{max} amplitude on differences between LTRT and UT. EMG was recorded from multiple sites and muscles of EF and KE, M_{max} was evoked with percutaneous nerve stimulation, and muscle size was assessed with ultrasonography (thickness, EF) and magnetic resonance imaging (cross-sectional area, KE). Muscle-electrode distance (MED) was measured to account for the effect of adipose tissue on EMG and M_{max}. LTRT displayed greater MVT (+66%–71%, $P < 0.001$), muscle size (+54%–56%, $P < 0.001$), and M_{max} amplitudes (+29%–60%, $P \leq 0.010$) even when corrected for MED ($P \leq 0.045$). M_{max} was associated with the size of both muscle groups ($r \geq 0.466$, $P \leq 0.011$). Compared with UT, LTRT had higher absolute voluntary EMG amplitude for the KE ($P < 0.001$), but not the EF ($P = 0.195$), and these differences/similarities were maintained after correction for MED; however, M_{max} normalization resulted in no differences between LTRT and UT for any muscle and/or muscle group ($P \geq 0.652$). The positive association between M_{max} and muscle size, and no differences when accounting for peripheral electrophysiological properties (EMG/M_{max}), indicates the greater absolute voluntary EMG amplitude of LTRT might be confounded by muscle morphology, rather than providing a discrete measure of central neural activity. This study therefore suggests limited agonist neural adaptation after LTRT.

NEW & NOTEWORTHY In a large sample of long-term resistance-trained individuals, we showed greater maximal M-wave amplitude of the elbow flexors and knee extensors compared with untrained individuals, which appears to be at least partially mediated by differences in muscle size. The lack of group differences in voluntary EMG amplitude when normalized to maximal M-wave suggests that differences in muscle morphology might impair interpretation of voluntary EMG as an index of central neural activity.

M-wave; muscle excitability; sarcolemmal excitability; strength training; surface electromyography

INTRODUCTION

Resistance training is known to increase maximal force-generating capacity of muscle when performed regularly (1). The initial (<2–4 wk) increases in muscle force production following resistance training are thought to be primarily underpinned by neural factors (2), followed by adaptation in muscle morphology (>5–8 wk; 1). It is largely unclear, however, whether neural factors contribute to the substantial increases in force production with long-term resistance training (LTRT; > several months or years).

Owing to logistical issues associated with long-term resistance training research, only limited data concerning neural changes exist from medium-term longitudinal studies. Studies employing surface electromyography (EMG) recordings during maximal voluntary isometric contractions have shown either no change (3) or an increase in signal

Correspondence: J. P. Folland (j.p.folland@lboro.ac.uk).
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amplitude (4). Cross-sectional studies have demonstrated greater EMG activity of LTRT individuals during a maximal voluntary isometric contraction compared with untrained (UT) controls (5, 6). However, greater absolute EMG amplitude with LTRT does not necessarily represent modifications of neural properties (7–10). Indeed, absolute surface EMG amplitude is subject to alterations by various peripheral electrophysiological properties distinct from neural drive. These include muscle propagation of action potentials from the neuromuscular junction to the sarcolemma (e.g., muscle membrane properties, fiber size; 8) and volume conduction of signals from the sarcolemma through the intermediate tissues to the electrode on the skin surface (e.g., subcutaneous adipose tissue, 11). To account for the influence of subcutaneous adipose tissue, which may differ between LTRT and UT individuals, the EMG signal amplitude can be corrected for the muscle-electrode distance (MED; primarily adipose tissue, 12). Such an approach has also revealed greater maximal EMG activity between LTRT and UT individuals (5). However, correction for MED does not account for differences in muscle propagation, specifically muscle morphology (13), and muscle membrane properties (14) that would be expected to influence the size of single fiber action potentials (15, 16). To account for the aforementioned factors, normalization to maximal compound action potential is required (maximal M-wave, M_{max}; 18, 63), particularly in the case of maximal voluntary contractions, where other possible reference values (e.g., EMG during maximal voluntary torque, MVT; 19) are invalid. Comparing voluntary EMG amplitude corrected for MED to normalization to maximal M-wave could therefore allow the distinction between the influence of adipose tissue and other peripheral properties on the amplitude of the signal, both of which could differ between LTRT and UT individuals.

Given the M_{max} may be useful for normalizing voluntary EMG activity during maximal contractions, it is important to consider the potential impact of long-term resistance training on maximal M-wave amplitude. The maximal M-wave represents the summated electrical activity of motor units within the recording volume following depolarization of their axons by a supramaximal electrical stimulus (20) and facilitates the assessment of peripheral electrophysiological properties of the neuromuscular system (20). For example, the maximal M-wave is influenced by, among other factors, changes in muscle morphology and muscle membrane properties (e.g., motor unit conduction velocity and the amplitude of transmembrane action potentials; 21). These factors are known to change with resistance training; for example, the greater muscle size of LTRT individuals (13) that is primarily due to enhanced muscle fiber size (22) may increase the size of single fiber action potentials (16) and thus also the amplitude of M_{max}. Indeed, a strong relationship between muscle size and M_{max} amplitude has been shown in clinical populations (23); however, this relationship remains unexplored in the context of resistance training. A clear relationship between M_{max} and muscle size could indicate a confounding effect of muscle size on the amplitude of absolute EMG and support the necessity for M_{max} normalization of voluntary EMG, especially when comparing individuals and/or groups with distinct muscle sizes. Furthermore, LTRT individuals demonstrate increased motor unit conduction velocity (14, 24). The greater motor unit conduction velocity would theoretically lead to greater synchronization of the constituent motor unit action potentials of an M-wave (21, 25), thereby increasing its amplitude, particularly in the propagating phase of the potential (20).

Data concerning M_{max} amplitude in LTRT individuals are equivocal, with reports of either greater amplitude (6) or no difference (26, 27) in biceps brachii M_{max} compared with controls. However, differences in joint configurations (28), and EMG recordings from single unspecified sites (29), may have contributed to these divergent findings. Furthermore, we are not aware of any data regarding M_{max} amplitude of LTRT individuals in lower limb muscles (e.g., knee extensors). For example, the knee extensors compared with elbow flexors have a significantly different geometry and spread of the innervation zones, which might lead to differences in the amplitude of maximal M-wave between muscle groups (20) and affect the comparison between LTRT and UT individuals.

The purpose of the current investigation was to *1*) compare M_{max} amplitudes between LTRT (i.e., multiple years of resistance training exposure) and UT individuals for both upper (i.e., elbow flexors; *experiment 1*) and lower (i.e., knee extensors; *experiment 2*) body muscles; *2*) assess the relationship between M_{max} and muscle size; and *3*) contrast the absolute voluntary EMG amplitude with that normalized to both MED and M_{max} between LTRT and UT individuals. It was hypothesized that, due to expected larger muscle mass, M_{max} amplitude will be greater in LTRT compared with UT individuals. Furthermore, it was hypothesized that normalization to M_{max} will eliminate any between-group difference in voluntary EMG amplitude.

MATERIALS AND METHODS

Participants

Two separate cohorts were tested in this study as part of a series of investigations assessing elbow flexor (*experiment 1*; see Ref. 18) and knee extensor (*experiment 2*; see Ref. 13) neuromuscular function of LTRT individuals. The experimental procedures were approved by the Loughborough University Ethical Advisory committee in accordance with Declaration of Helsinki and participants gave written informed consent before their participation. Physical activity levels were also assessed at the start of the study using the International Physical Activity Questionnaire (IPAQ; 30). In *experiment 1*, a total of 29 participants were recruited for elbow flexor measurements, 15 LTRT (means ± SD, age: 22 ± 4 yr; stature: 1.79 ± 0.07 m; mass: 89 ± 11 kg; IPAQ: 6,518 ± 1,748 metabolic equivalent min/wk), and 14 UT men (22 ± 3 yr, 1.76 ± 0.11 m, 68 ± 10 kg, 1,042 ± 464 metabolic equivalent min/wk). Untrained individuals were of similar height (independent samples *t* test, $P = 0.440$) and age ($P = 0.917$), but were lighter compared with LTRT ($P < 0.001$) and had lower levels of physical activity ($P < 0.001$). In *experiment 2*, 63 men were recruited for knee extensor measurements, of which 14 were LTRT (22 ± 2 yr, 1.84 ± 0.06 m, 92 ± 10 kg, 5,568 ± 1,457 metabolic equivalent min/wk), whereas 49 were UT (25 ± 2 yr, 1.76 ± 0.07 m, 73 ± 9 kg, 2,326 ± 1,337 metabolic equivalent min/wk). Untrained participants in the knee extensor cohort

were older, shorter, lighter, and had lower levels of physical activity (independent samples t test, $P < 0.001$ for all). All participants were asymptomatic at the time of testing and reported no major injuries within the past 3 mo. Untrained participants were not engaged in any systematic training and had not performed lower or upper body resistance training for >18 mo. The LTRT groups reported (via a detailed questionnaire and follow-up oral discussion) regular, systematic, progressive heavy resistance training for ≥3 yr either of the elbow flexors [≥2 × per wk; 6 ± 3 (range 3–16) yr] or knee extensors [≥ 2 × per wk; 4 ± 1 (range of 3–5) yr] with the primary aim of developing maximal strength. Individuals were excluded from participation if they reported the use of androgenic-anabolic steroids. Long-term resistance-trained individuals commonly reported the use of nutritional supplements (e.g., whey protein and creatine).

Experimental Overview

The procedures for the two experiments were similar with participants visiting the laboratory four times in total, with each visit 7 to 10 days apart. All measures were conducted on the dominant limb. The first session involved habituation with the procedures (including stimulations) and practice performing isometric maximal voluntary contractions. Participants then completed two duplicate neuromuscular assessments at a consistent time of day to avoid diurnal variation in neuromuscular function. These sessions involved isometric dynamometry for recording contractile forces and surface EMG during evoked contractions and maximal voluntary isometric contractions of the elbow flexors or knee extensors. The last visit involved assessment of muscle size using B-mode ultrasonography (*experiment 1*) or 1.5-T magnetic resonance imaging (MRI) scans (*experiment 2*). In addition, B-mode ultrasonography was performed in both experiments to measure MED.

Experimental Procedures

Neuromuscular assessment.

Neuromuscular assessment procedures were similar between elbow flexion (*experiment 1*) and knee extensor (*experiment 2*) cohorts. Following skin preparation and EMG electrode placement, the participants performed a standardized warm-up consisting of 5-s isometric contractions at 50 (×3), 75 (×3), and 90% (×1) of perceived MVT with 15–30 s of rest given between efforts. Following warm-up, three supramaximal twitches were evoked with percutaneous nerve stimulation (see *Percutaneous nerve stimulation* for details). After that, the participants performed three to four maximal voluntary isometric contractions and were instructed to "pull/push as hard as possible" for 3–5 s with ≥30 s of rest between efforts. Visual feedback of the force production was provided along with verbal encouragement, and the greatest force obtained during that session was displayed to facilitate maximal effort.

Torque and EMG recording.

Neuromuscular assessments were performed with participants seated in rigid custom-made isometric dynamometers. In *experiment 1*, the participants were seated in an elbow flexion dynamometer (31) with the shoulder and elbow at 90° and 80° of flexion, respectively, the shoulder in slight horizontal abduction (~10°), and the forearm in half-supinated (~45°) position (0° = anatomical position). The wrist was tightly strapped to a brace in series with a calibrated S-beam strain gauge (Force Logic, Swallowfield, UK). In addition, participants were tightly fastened across the pelvis and chest to prevent extraneous movement. In *experiment 2*, the participants were seated in a knee extension dynamometer (32) with knee and hip flexed at 115° and 126° (180° = full extension). To prevent extraneous movements, straps were tightly fastened across the participant's pelvis and shoulders. An ankle strap (35-mm-width reinforced canvas webbing) was positioned at ~15% of tibial length (lateral malleolus to the knee joint center), above the malleoli, and in series with a calibrated S-beam strain gauge (Force Logic, Swallowfield, UK). We have previously shown that the aforementioned positions minimize joint angle changes during maximal isometric efforts (≤4° compared with 10–20° changes commonly observed with commercial dynamometers; 33) and maximize torque production and therefore reduce any confounding influence of the torque-angle relationship (34).

The analog force signal was amplified (×370) and sampled at 2 kHz (Micro 1401; Cambridge Electronics Design Ltd., Cambridge, UK). During the off-line analysis, force data were low-pass filtered (500 Hz, zero-lag fourth-order Butterworth; 32), gravity corrected (subtraction of baseline force), and converted to torque (multiplied by lever length; the distance between the knee/elbow joint and the center of the restraining strap). The greatest instantaneous torque achieved during maximal voluntary isometric contractions was taken as MVT.

Surface EMG (Trigno System; Delsys, Boston, MA) was recorded from superficial elbow flexor (biceps brachii long head, BBL; and biceps brachii short head, BBS) and knee extensor (vastus medialis, VM; vastus lateralis, VL; and rectus femoris, RF) muscles, after skin preparation (shaving, abrading, and cleansing with 70% ethanol), using wireless sensors (fixed 1-cm interelectrode distance; Trigno Standard EMG sensors, Delsys, Boston, MA). Specifically, two sensors were placed over the biceps brachii at set percentages of the length between medial acromion and cubital fossa (BBL: 67%, BBS: 67%). For the knee extensors, six discrete sensors (two per superficial quadriceps muscle) were placed at set percentages of thigh length above the superior border of patella (VM: 35% and 30%, VL: 60% and 55%, RF: 65% and 55%), in parallel with presumed fiber orientation. Multiple rather than single-site recordings were performed to minimize the error in amplitude estimation, which is higher in single-site recordings due to implicit assumption that the amplitude of the signal scales proportionally with excitation across the whole motor pool (35). Averaging from multiple sites therefore likely provides a more comprehensive assessment of motor unit responsiveness to voluntary and evoked stimulation. Furthermore, we have previously shown that multiple site and/or muscle recordings and subsequent averaging of data significantly improve the reliability of voluntary and evoked EMG activity and are thus favorable when assessing larger muscle groups (29).

The EMG signals were initially amplified and band-pass filtered at source (×300; 20–450 Hz) before further amplification (total of ×909) and sampled at 2 (knee extensors) and 4 (elbow flexors) kHz using the same analog-to-digital converter and software as for the force signal, thus allowing

synchronization. Due to the inherent delay in the EMG system (48 ms; Trigno EMG system), EMG signals were first temporally corrected during off-line analysis before additional band-pass filtering (6–500 Hz, zero-lag fourth-order Butterworth). EMG activity was quantified as root mean square (RMS) of the 500 ms epoch around MVT (250 ms either side of MVT). For individual knee extensor muscles, RMS EMG was first averaged across the two independent recording sites (e.g., for VM, activity was averaged between the sensors placed at 35 and 30% of thigh length). After that, averaging across muscles was performed to quantify whole elbow flexor (BBL and BBS) or knee extensor (VM, VL, and RF) EMG activity. Data were expressed in absolute EMG values, normalized to M_{max}, and as absolute values corrected for muscle-electrode distance (see *MED and MED-corrected voluntary EMG amplitude*). Normalization to M_{max} was first performed for each corresponding measurement site before averaging within constituent muscles, and then for the whole muscle group.

Percutaneous nerve stimulation.

Percutaneous stimulation (single 200-μs square-wave pulse; DS7AH, Digitimer Ltd., Welwyn Garden City, UK) of the brachial plexus (elbow flexors) or femoral nerve (knee extensors) was delivered to evoke M_{max}. The brachial plexus was stimulated with a securely taped cathode probe (1-cm diameter, Electro-Medical Supplies, Wantage, UK) and a gel-coated anode electrode placed over the deltoid (7 × 10 cm rubber electrode; Electro-Medical Supplies, Wantage, UK). The femoral nerve was stimulated with an identical, securely taped, cathode placed in the femoral triangle and the same anode placed over the greater trochanter. The optimal cathode position was determined in the beginning of the trial as the spot corresponding to the greatest M_{max} peak-to-peak amplitude at a constant submaximal current intensity. The current intensity was then progressively increased until there was a plateau in M_{max} peak-to-peak amplitude, after which it was increased by 30% to ensure supramaximal stimulus intensity. Three supramaximal stimuli were then delivered separated by 15 s. From those trials, peak-to-peak amplitude of M_{max} was calculated and averaged. Example traces from one participant of each group in the knee extensors and elbow flexors are depicted in Fig. 1. In some cases of elbow flexion measurements, negative and/or positive peak values of M_{max} exceeded the maximum range of the recordings. This was the case for 21.8% (LTRT: 30.0%, UT: 13.1%) and 28.7% (LTRT: 38.9%, UT: 17.9%) of all trials, and occurred in 31.0% (LTRT: 40.0%, UT: 21.4%) and 34.5% (LTRT: 46.7%, UT: 21.4%) of the sample population in BBL and BBS, respectively. In such cases, clipped parts of M-waves were interpolated by fitting the M-wave response of the unclipped parts to the sixth-order polynomial curves (R^2 = 0.98–1.00) to obtain the peak values. To test the validity of this approach, a random sample (n = 23) of unclipped trials was retrospectively clipped (i.e., a 10 ms epoch of data around the positive and negative peak was

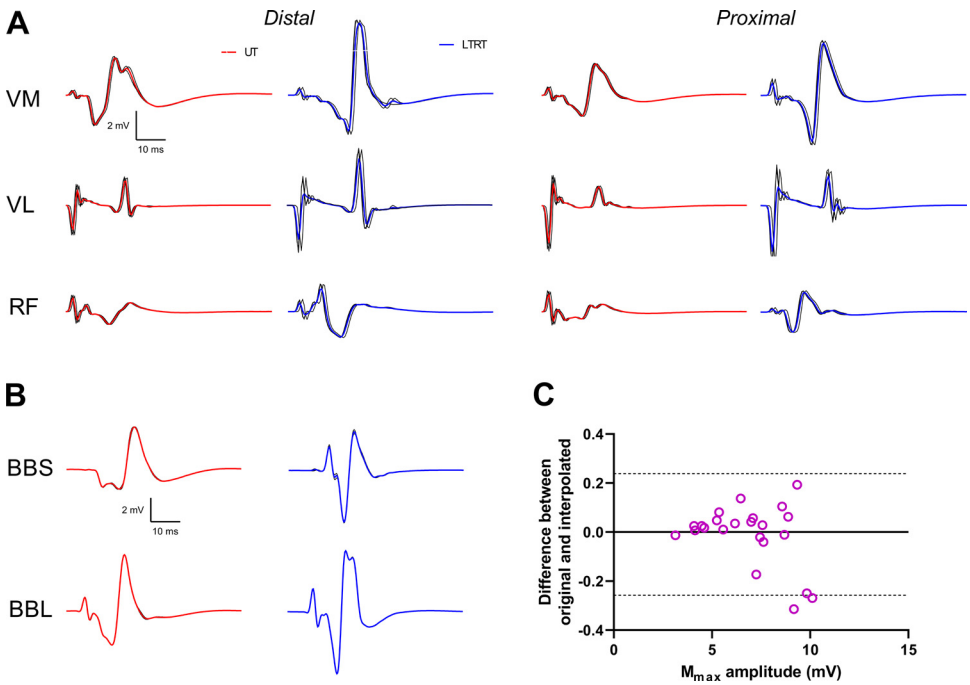

Figure 1. Typical evoked responses to percutaneous nerve stimulation in the knee extensor (*A*) and elbow flexor (*B*) muscles in a long-term resistance trained (LTRT; blue) and an untrained (UT; red) individual. In knee extensors, recordings were made from two sites per muscle. Traces show the three evoked maximal M-waves overlaid in black with the mean response displayed in color. In some cases of elbow flexion measurements, negative and/or positive peak values of maximal M-wave exceeded the maximum input range of EMG sensors. In such cases, clipped parts of M-waves were interpolated with sixth-order polynomials curves. To test the validity of this approach, a random sample (n = 23) of unclipped trials was retrospectively clipped (i.e., a 10 ms epoch of data around the positive and negative peak was deleted) to compare the actual/original measured M_{max} amplitude (i.e., from the unclipped recording to M_{max} estimated from the clipped version with interpolation of the missing data). The comparison (original vs. interpolated maximal M-wave; n = 23) showed excellent agreement as displayed in the Bland–Altman plot (*C*). BBL, biceps brachii long head; BBS, biceps brachii short head; EMG, electromyography; M_{max}, maximal compound action potential; RF, rectus femoris; VL, vastus lateralis; VM, vastus medialis.

deleted) to compare the actual/original measured M_{max} amplitude (i.e., from unclipped recording) to M_{max} estimated from the clipped version with interpolation of the missing data by the sixth-order polynomial fit. Comparison of M_{max} amplitude between the original, unclipped, and the clipped, interpolated measurements revealed excellent agreement [$ICC_{3,1}$: 0.998 (0.996–0.999), Fig. 1*C*], confirming the robustness of the approach.

Muscle size.

Biceps brachii muscle thickness was assessed using B-mode ultrasonography (EUB-8500; Hitachi Medical Systems UK Ltd., Northamptonshire, UK) with participants positioned in the isometric elbow flexion dynamometer. Longitudinal images of the biceps brachii were recorded with the ultrasound probe (9.2 cm linear-array transducer, EUP-L53L; sampling rate 32 Hz, coated with water soluble transmission gel) placed perpendicular to the skin surface with the center of the probe at positions corresponding to EMG electrodes location over the long and short head of the biceps brachii. Muscle thickness of the elbow flexors was quantified as the distance between the subcutaneous adipose tissue-muscle interface and muscle-bone interface at the center of images using a public domain image analysis software (https://physlets.org/tracker/: Tracker v. 4.97). Values from the two images (of the long and short head of biceps brachii) were averaged to provide a mean elbow flexor value.

Quadriceps anatomical cross-sectional area (ACSA) was assessed with a 1.5-T MRI scan of the dominant thigh. A receiver eight-channel whole body coil (Signa HDxt; GE) was used to acquire T1-weighted axial slices (5 mm thick, 0 mm gap) between anterior superior iliac spine and the knee joint space in two overlapping blocks while participants laid supine with the knee joint angle of ~163°. The alignment of the blocks of slices was facilitated by oil-filled capsules placed on the lateral side of each participants' thigh. The quadriceps muscles (VM, VL, RF, and vastus intermedius) were manually outlined in every third image (every 15 mm) starting from the most proximal image in which the muscle appeared (OsiriX software v. 6.0; Pixmeo, Geneva, Switzerland). For each constituent quadriceps muscle, the image with the largest ACSA was taken as its maximum ACSA, and the values from all four constituents were summed for quadriceps ACSA (QACSA).

Due to resource limitations, measures of muscle size were performed with different methodologies in the two experiments. Although muscle thickness is reportedly an acceptable proxy of ACSA (36), we wanted to ensure this was the case in our experiment. For this purpose, muscle thickness of the quadriceps was also assessed by recording longitudinal images of quadriceps muscle in the UT group of *experiment 2* only. Images were recorded at set percentages of thigh length above the superior border of patella that approximated the maximal ACSA for each constituent muscle (VM = 20%, VL and vastus intermedius = 50%, RF = 75%). Muscle thickness was quantified as the mean of the distance between deep and superficial aponeurosis at each end, and the middle of each image. Muscle thickness for each constituent muscle was then summed to quantify quadriceps muscle thickness. This analysis resulted in mean quadriceps muscle thickness of 92.7 ± 10.8 cm, and significant associations with QACSA (Pearson's $r = 0.519$, $P < 0.001$).

MED and MED-corrected voluntary EMG amplitude.

Using a B-mode ultrasound probe placed perpendicular to the surface of the muscle, images of the distance between the skin surface and peripheral surface of the muscle were obtained at each of the sites where EMG electrodes were placed over the elbow flexor and knee extensor muscles. MED was measured by one trained investigator (Tracker v. 4.92). Using the quadratic relationship between EMG and M_{max} amplitude and MED at the specific measurement site, EMG and M_{max} amplitude was corrected for MED as described previously (12). Briefly, an individual's residual EMG and M_{max} amplitude (i.e., measured vs. expected/predicted according to the cohort relationship of EMG and M_{max} amplitude with MED) were summated with the pooled group mean of absolute EMG and M_{max} amplitude. Whole corrected EMG and M_{max} amplitude for each muscle group were then calculated by averaging corrected EMG and M_{max} amplitudes across the recording sites.

Data Analysis and Statistics

The data from duplicate sessions were averaged before further statistical analyses. All analyses were performed in SPSS v. 24 (IBM, Armonk, NY). All data are presented as means ± SD (with individual participant data also plotted). Significance was set at an α level of 0.05. Normality of data was assessed with the Shapiro–Wilk test. Data were distributed normally; thus, independent samples *t* tests were performed to assess the differences in evoked and voluntary force and EMG variables between LTRT and UT individuals. Effect sizes (Cohen's *d*) were estimated for absolute difference and were classified as trivial, small, moderate, and large when <0.20, 0.20–0.50, 0.50–0.80, and >0.80, respectively (37). To assess the possible relationship between muscle size and M_{max}, bivariate correlation and linear regression were performed between muscle thickness and M_{max}, and QACSA and M_{max} for elbow flexors and knee extensors, respectively.

Using values obtained during the two duplicate neuromuscular assessments, variability and reliability were assessed using within-participant coefficient variation (CV; SD/mean × 100) and intraclass correlation coefficient ($ICC_{3,1}$; 38), respectively. A paired-samples *t* test was used to calculate bias. The ICC values were defined as poor, moderate, good, and excellent when <0.50, 0.50–0.75, 0.75–0.90, and >0.90, respectively (17). The CV values were considered acceptable, intermediate, and unacceptable when <12%, 12%–20%, and >20%, respectively (5).

RESULTS

Between-Test Session Reliability and Variability

Reliability data are presented in Supplemental Table S1 (all Supplemental material is available at https://doi.org/10.6084/m9.figshare.13797674). Maximal voluntary torque demonstrated excellent reliability and acceptable variability. Whole muscle group (knee extensor and elbow flexor) EMG variables had higher reliability and lower variability than for

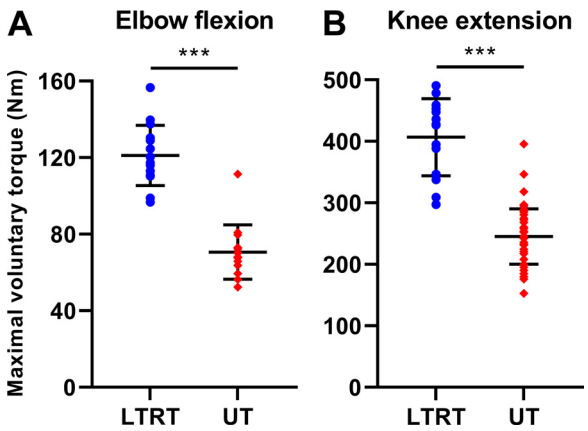

Figure 2. Elbow flexor (*A*) and knee extensor (*B*) maximal voluntary torque of long-term resistance-trained (LTRT; elbow flexors; $n = 15$; knee extensors, $n = 14$) individuals compared with untrained controls (UTs; elbow flexors, $n = 14$; knee extensors, $n = 49$). ***$P < 0.001$ between groups determined from independent samples *t* tests.

individual constituent muscles. Specifically, M_{max} and absolute voluntary EMG activity exhibited good and moderate (elbow flexors), and excellent and good (knee extensors) reliability, respectively, and variability was intermediate to acceptable for both muscle groups. When M_{max} was corrected for MED, reliability was good (elbow flexors) and excellent (knee extensors), and variability was acceptable. Voluntary EMG activity normalized to M_{max} exhibited poor and good reliability, and variability intermediate and acceptable for the elbow flexors and knee extensors, respectively. Voluntary EMG corrected for MED displayed intermediate-to-acceptable variability and good reliability.

Experiment 1: Elbow Flexors

Long-term resistance-trained individuals produced 71% greater elbow flexor MVT ($t_{27} = -9.045$, $P < 0.001$; Fig. 2*A*), and this was accompanied by 56% greater muscle thickness ($t_{27} = -7.588$, $P < 0.001$; Table 1) compared with UT.

Elbow flexor M_{max} was 29% greater in LTRT compared with UT individuals ($t_{27} = -2.412$, $P = 0.010$; Fig. 3*A*). This reflected a greater M_{max} in LTRT compared with UT for the short head of biceps brachii (35%; $t_{27} = -2.477$, $P = 0.020$), but not for the long head ($t_{27} = -1.789$, $P = 0.085$). When corrected for MED, elbow flexor M_{max} was still greater in LTRT compared with UT (22%; $t_{27} = -2.10$, $P = 0.045$; Fig. 3*C*), and this was also the case for the short (31%; $t_{27} = -2.432$, $P = 0.022$), but not the long head of the biceps brachii ($t_{27} = -1.092$, $P = 0.285$). Elbow flexor M_{max} was associated with biceps brachii thickness ($r = 0.466$, $P = 0.011$; Fig. 4), and this was also the case for the short ($r = 0.489$, $P = 0.007$), but not the long head of biceps brachii ($r = 0.249$, $P = 0.193$).

No differences were demonstrated between groups for elbow flexor voluntary EMG activity ($t_{18.0} = -1.346$, $P = 0.195$), and this was also the case for the long head of the biceps brachii ($t_{15.9} = -0.336$, $P = 0.741$). However, voluntary EMG activity of the short head of biceps brachii was 26% greater in LTRT compared with UT individuals ($t_{27} = -2.149$, $P = 0.041$; Fig. 5*A*). There were no differences between LTRT and UT when elbow flexor EMG activity was normalized to M_{max} (whole elbow flexor: $t_{27} = 0.456$, $P = 0.652$; BBL: $t_{27} = 0.507$, $P = 0.616$, BBS: $t_{27} = 0.333$, $P = 0.742$; Fig. 5*B*). When corrected for MED, EMG activity of the elbow flexors ($t_{19.5} = -0.997$, $P = 0.331$) and the long head of biceps brachii ($t_{15.3-0}.268$, $P = 0.793$) were similar between LTRT and

Table 1. *Maximum voluntary torque, muscle size, evoked and voluntary EMG, in absolute terms and normalized to M_{max} and muscle-electrode distance, of the elbow flexors in long-term resistance-trained and untrained individuals*

	LTRT ($n = 14$)	UT ($n = 49$)	*P* (*t* test)	Effect Size	% Difference
		Torque, Nm			
MVT	121 ± 16	71 ± 14	<0.001***	3.36 "Large"	71
		Muscle size			
BB thickness, cm	3.65 ± 0.54	2.34 ± 0.36	<0.001***	2.81 "Large"	56
		M_{max} amplitude, mV			
Elbow flexor	9.2 ± 2.5	7.1 ± 2.2	0.023*	0.90 "Large"	29
BBL	8.8 ± 2.7	7.2 ± 2.3	0.085	0.67 "Moderate"	23
BBS	9.6 ± 2.8	7.1 ± 2.6	0.020*	0.92 "Large"	35
		M_{max} corrected for muscle electrode distance, mV			
Elbow flexor	9.0 ± 2.3	7.4 ± 1.7	0.045*	0.78 "Moderate"	22
BBL	8.5 ± 2.6	7.5 ± 1.9	0.285	0.41 "Small"	13
BBS	9.5 ± 2.6	7.2 ± 2.3	0.022*	0.90 "Large"	31
		Absolute voluntary EMG, mV			
Elbow flexor	0.904 ± 0.151	0.774 ± 0.330	0.195	0.51 "Moderate"	17
BBL	0.723 ± 0.134	0.695 ± 0.388	0.741	0.13 "Trivial"	5
BBS	1.077 ± 0.242	0.854 ± 0.315	0.041*	0.80 "Moderate"	26
		Voluntary EMG/M_{max}, %			
Elbow flexor	10.7 ± 3.7	11.4 ± 4.4	0.652	0.17 "Trivial"	−6
BBL	8.9 ± 2.6	9.5 ± 3.5	0.616	0.19 "Trivial"	−6
BBS	12.5 ± 6.2	13.3 ± 6.6	0.742	0.12 "Trivial"	−6
		Voluntary EMG corrected for muscle electrode distance, mV			
Elbow flexor	0.879 ± 0.137	0.801 ± 0.259	0.331	0.38 "Small"	−4
BBL	0.700 ± 0.112	0.729 ± 0.364	0.793	0.11 "Trivial"	10
BBS	1.059 ± 0.230	0.873 ± 0.213	0.033*	0.84 "Large"	21

BBL, biceps brachii long head; BBS, biceps brachii short head; EMG, electromyography; LTRT, long-term resistance-trained; M_{max}, maximal compound action potential; MVT, maximal voluntary torque; UT, untrained. Symbols denote significant difference between LTRT and UT: ***$P < 0.001$, *$P < 0.05$.

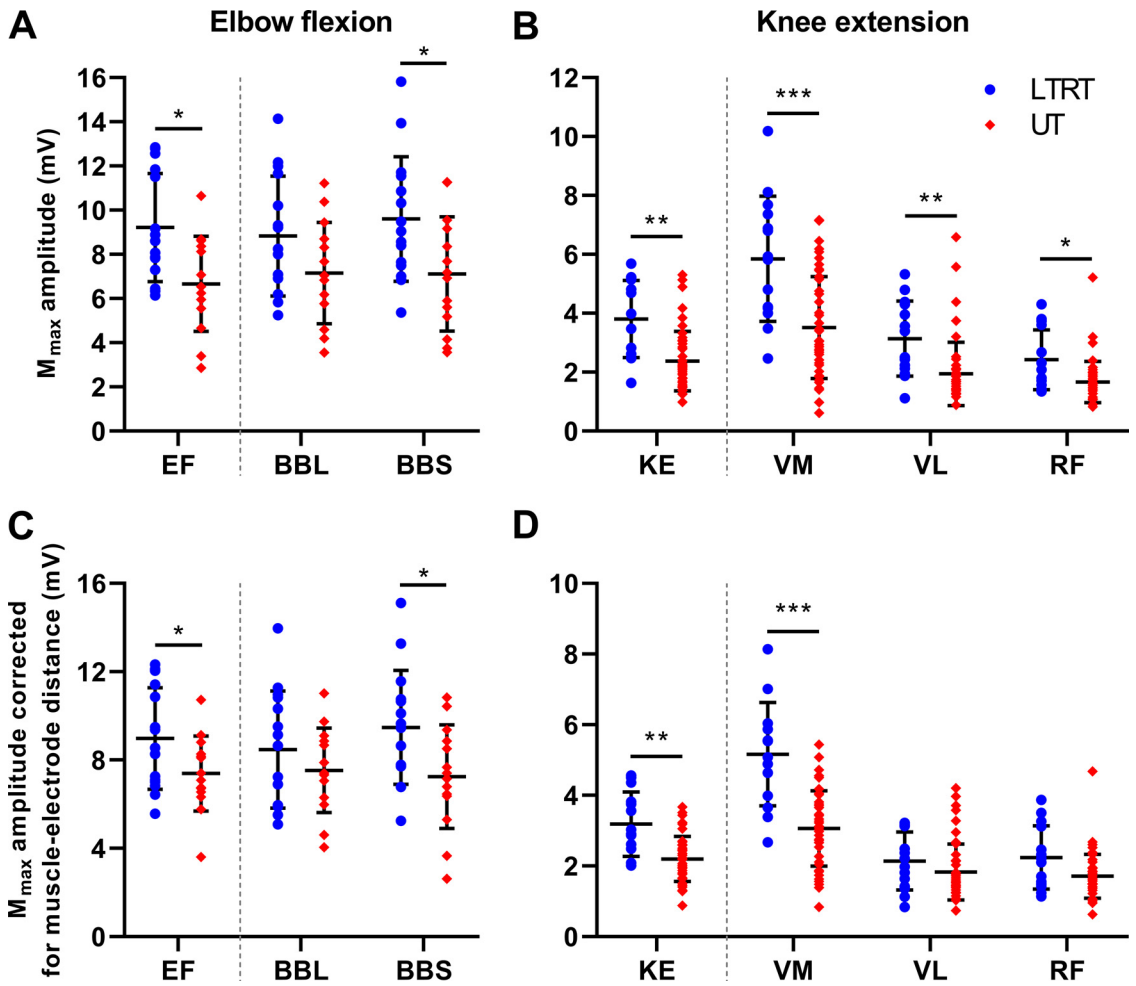

Figure 3. Absolute (*A* and *B*) and muscle-electrode distance corrected (*C* and *D*) M_{max} peak-to-peak amplitude of elbow flexors (*A* and *C*) and knee extensors (*B* and *D*) of long-term resistance-trained individuals (LTRTs; elbow flexors; $n = 15$; knee extensors, $n = 14$) compared with untrained controls (UTs; elbow flexors, $n = 14$; knee extensors, $n = 49$). Symbols denote a significant difference between groups determined from independent samples *t* tests as follows: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$. BBL, biceps brachii long head; BBS, biceps brachii short head; EF, whole elbow flexor measurement, mean of the individual elbow flexor muscles; KE, whole knee extensor measurement mean of individual knee extensor muscles; M_{max}, maximal compound action potential; RF, rectus femoris; VL, vastus lateralis; VM, vastus medialis.

UT. However, the EMG activity of the short head of biceps brachii when corrected for MED was still greater by 21% in LTRT compared with UT controls ($t_{27} = -2.252$, $P = 0.033$, Fig. 5*C*).

Experiment 2: Knee Extensors

Compared with UT, LTRT individuals produced 66% greater knee extension MVT ($t_{17.0} = -9.007$, $P < 0.001$; Fig. 2*B*). Muscle size, specifically QACSA, was 54% greater for LTRT than UT ($t_{61} = -12.953$, $P < 0.001$; Table 2).

Knee extensor M_{max}, averaged across six recording sites, was 60% greater in LTRT compared with UT individuals ($t_{17.6} = -3.774$, $P = 0.001$), with similar differences noted in VM (+67%; $t_{61} = -4.227$, $P < 0.001$), VL (+62%; $t_{61} = -3.527$, $P = 0.001$), and RF (+45%; $t_{16.7} = -2.612$, $P = 0.018$; Fig. 3*B*). Correction for MED maintained the difference between LTRT and UT in the knee extensor M_{max} (45%; $t_{16.768} = -3.781$, $P = 0.002$; Fig. 3*D*), as well as for VM (69%; $t_{61} = -5.985$, $P < 0.001$), with a tendency for a difference in RF ($t_{16.782} = -2.090$, $P = 0.052$), but not VL ($t_{61} = -1.293$, $P = 0.201$). Knee extensor M_{max} was associated with QACSA ($r = 0.501$, $P < 0.001$; Fig. 4), and a significant relationship was also observed for each of the constituent muscles (VM: $r = 0.430$, $P < 0.001$; VL: $r = 0.369$, $P = 0.003$; RF: $r = 0.419$, $P = 0.001$).

Voluntary EMG activity of the knee extensors during MVT production was 64% greater in LTRT compared with UT ($t_{61} = -4.853$, $P < 0.001$) with differences observed across all muscles; VM (+66%; $t_{61} = -4.853$, $P < 0.001$), VL (+67%; $t_{61} = -4.140$, $P < 0.001$), and RF (+58%; $t_{61} = -3.726$, $P < 0.001$; Fig. 5*D*). When normalized to M_{max}, no differences were observed between LTRT and UT individuals in whole knee extensor EMG activity ($t_{61} = 0.444$, $P = 0.659$; Fig. 5*E*), or for the individual muscles investigated (VM: $t_{61} = -1.664$, $P = 0.601$; VL: $t_{61} = -1.049$, $P = 0.298$; RF: $t_{61} = -1.025$, $P = 0.310$).

Correction for MED resulted in 42% greater EMG activity of the knee extensors in LTRT compared with UT ($t_{61} = -5.959$, $P < 0.001$; Fig. 5*F*). The corrected EMG activity was 63% greater in LTRT compared with untrained in VM ($t_{17.0} =$

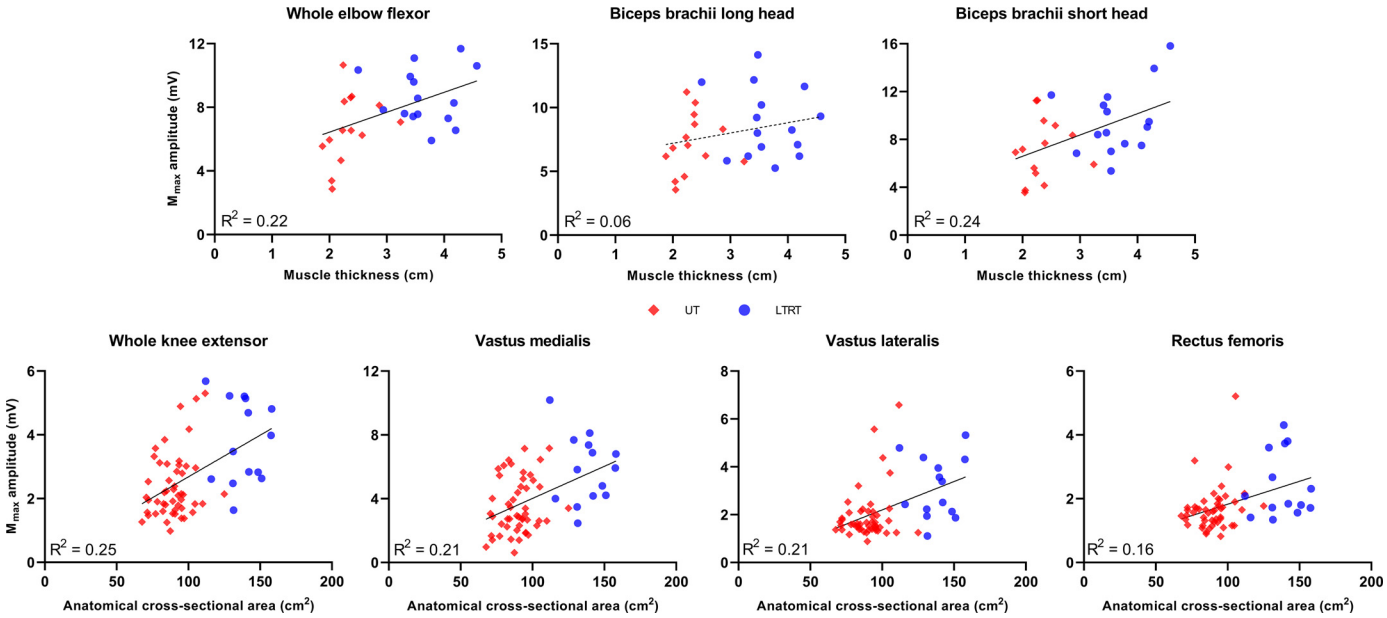

Figure 4. Maximal M-wave plotted as a function of muscle size (muscle thickness for elbow flexors and anatomical cross-sectional area for knee extensors) in long-term resistance-trained (LTRT, blue circles; elbow flexors; $n = 15$; knee extensors, $n = 14$) and untrained controls (UTs, red diamonds; elbow flexors, $n = 14$; knee extensors, $n = 49$). The dashed trend line denotes a nonsignificant relationship ($P = 0.193$). M_{max}, maximal compound action potential.

-5.973, $P < 0.001$), but not in VL ($t_{16.2} = -1.755$, $P = 0.098$) and RF ($t_{14.9} = -2.035$, $P = 0.060$).

DISCUSSION

This study examined the differences in M_{max} and surface EMG activity during maximal isometric voluntary contractions between LTRT and UT individuals in upper and lower limb muscles. As expected, LTRT individuals were stronger and had a greater muscle size compared with UT (5, 13, 26, 27). This superior muscle strength and size were accompanied by greater M_{max} amplitude of both muscle groups in LTRT individuals, even when corrected for the confounding influence of muscle-electrode distance. Furthermore, M_{max} was found to be associated with muscle size of both muscle groups, confirming findings of a previous investigation in clinical populations (23), but presenting a novel finding in the context of LTRT and UT individuals. Absolute voluntary EMG activity at MVT was greater only in the knee extensors of LTRT, but not the elbow flexors, and these between-group differences/similarities were maintained for voluntary EMG corrected for muscle-electrode distance. However, normalization of voluntary EMG to M_{max} amplitude removed any differences between the groups for both muscles. The dependence of differences in EMG activity between LTRT and UT individuals according to the normalizing procedure, the physiological inferences that stem from these observations, as well as differences in M_{max} amplitude are discussed below.

Long-Term Resistance-Trained Individuals Exhibit Greater Maximal Compound Action Potential Amplitude

In agreement with our hypothesis, LTRT individuals exhibited greater M_{max} amplitudes compared with untrained individuals for both the elbow flexor and knee extensor muscle groups. Previous studies of the elbow flexors found either greater (6) or similar (26, 27) M_{max} amplitude in LTRT individuals compared with controls, and no studies had examined the knee extensors. Compared with previous studies reporting no difference in M_{max}, this investigation tested responses on a significantly larger sample population and measured surface EMG signals from multiple constituent muscles of each muscle group (and, in the case of knee extensors, from multiple sites per muscle), which could have contributed to the differences between the studies. Indeed, multisite recordings and averaging of EMG amplitudes across multiple sites and, where possible, muscles have been shown to be more reliable both for M_{max} and voluntary EMG amplitudes (29; see also Supplemental Table S1), and likely provide a more comprehensive assessment of motor unit responsiveness to voluntary and evoked stimulation.

The observation that M_{max} was greater in LTRT individuals was consistent for both muscle groups investigated and across individual muscles, suggesting the findings are robust. There are many possible mechanisms underpinning the observed differences including differences in the major processes of muscle propagation, from the neuromuscular junction to the sarcolemma, and volume conduction from the sarcolemma through the intermediate tissues to the electrode on the skin surface (25). Since many factors within these processes change concurrently with long-term resistance training, the current experiment was not able to discern a specific mechanism. Differences in adipose tissue, which may impact volume conduction, were unlikely responsible for a large between-group difference in M_{max} amplitude as the differences were maintained when responses were corrected for muscle-electrode distance. As expected (13), LTRT individuals had greater muscle size (biceps brachii thickness both elbow flexors and knee extensors, we showed the size of the muscle was positively associated with M_{max} amplitude, a novel finding in

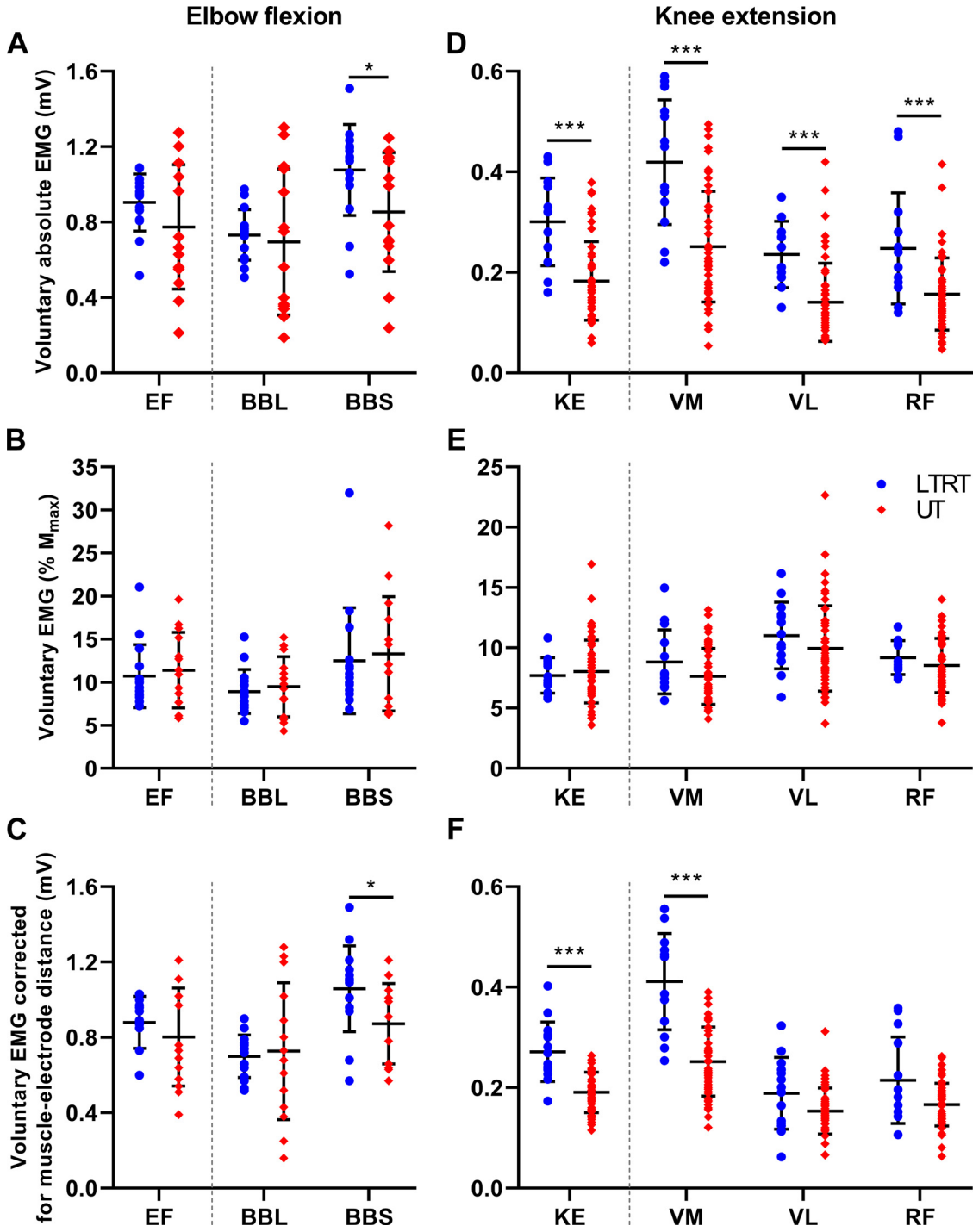

Figure 5. Voluntary absolute EMG during maximal voluntary torque (MVT) production (*A* and *D*), voluntary EMG during MVT normalized to M_{max} (*B* and *E*), and voluntary EMG during MVT corrected for the confounding influence of muscle-electrode distance (*C* and *F*) of long-term resistance-trained individuals (LTRTs; elbow flexors; $n = 15$; knee extensors, $n = 14$) compared with untrained controls (UTs; elbow flexors, $n = 14$; knee extensors, $n = 49$). Symbols denote a significant difference between groups determined from independent samples *t* tests as follows: $^{***}P < 0.001$, $^{*}P < 0.05$. BBL, biceps brachii long head; BBS, biceps brachii short head; EF, whole elbow flexor measurement, mean of individual elbow flexor muscles; EMG, electromyography; KE, whole knee extensor measurement, mean of individual knee extensor muscles; M_{max}, maximal compound action potential; RF, rectus femoris; VL, vastus lateralis; VM, vastus medialis.

the context of resistance training. Therefore, it seems likely that differences in muscle size contribute to the greater M_{max} amplitude of LTRT individuals compared with UT. The positive relationship between muscle size and M_{max} amplitude is likely the result of greater single fiber action potentials of larger muscle fibers (16, 39), leading to greater M_{max} amplitude in LTRT compared with UT individuals.

Table 2. *Maximum voluntary torque, muscle size, evoked and voluntary EMG (in absolute terms and normalized to M_{max} and muscle-electrode distance) of the knee extensors in long-term resistance-trained and untrained individuals*

	LTRT (n = 14)	UT (n = 49)	P (t test)	Effect Size	% Difference
		Torque, Nm			
MVT	407 ± 63	245 ± 45	<0.001***	3.27 "Large"	66
		Muscle size			
QACSA, cm^2	138 ± 14	90 ± 12	<0.001***	3.92 "Large"	54
		M_{max} amplitude, mV			
Knee extensor	3.8 ± 1.3	2.4 ± 1.0	0.001**	1.33 "Large"	60
VM	5.8 ± 2.1	3.5 ± 1.7	<0.001***	1.28 "Large"	67
VL	3.1 ± 1.3	1.9 ± 1.1	0.001**	1.07 "Large"	62
RF	2.4 ± 1.0	1.7 ± 0.7	0.018*	0.97 "Large"	45
		M_{max} corrected for muscle-electrode distance, mV			
Knee extensor	3.2 ± 0.9	2.2 ± 0.6	0.002	1.25 "Large"	45
VM	5.2 ± 1.5	3.1 ± 1.1	<0.001***	1.81 "Large"	69
VL	2.1 ± 0.8	1.8 ± 0.8	0.201	0.39 "Small"	17
RF	2.2 ± 0.9	1.7 ± 0.6	0.052	0.69 "Moderate"	31
		Absolute voluntary EMG, mV			
Knee extensor	0.301 ± 0.087	0.183 ± 0.078	<0.001***	1.47 "Large"	64
VM	0.418 ± 0.125	0.251 ± 0.110	<0.001***	1.47 "Large"	66
VL	0.235 ± 0.066	0.141 ± 0.078	<0.001***	1.25 "Large"	67
RF	0.249 ± 0.110	0.157 ± 0.072	<0.001***	1.13 "Large"	58
		Voluntary EMG/M_{max}, %			
Knee extensor	9.2 ± 1.4	8.5 ± 2.3	0.310	0.31 "Small"	8
VM	7.7 ± 1.5	8.0 ± 2.6	0.659	0.13 "Trivial"	−4
VL	8.8 ± 2.6	7.6 ± 2.3	0.101	0.50 "Moderate"	16
RF	11.0 ± 2.8	9.9 ± 3.5	0.298	0.32 "Small"	11
		Voluntary EMG corrected for muscle-electrode distance, mV			
Knee extensor	0.271 ± 0.059	0.191 ± 0.040	<0.001***	1.81 "Large"	42
VM	0.411 ± 0.096	0.252 ± 0.069	<0.001***	2.11 "Large"	63
VL	0.189 ± 0.071	0.153 ± 0.046	0.098	0.68 "Moderate"	23
RF	0.215 ± 0.086	0.166 ± 0.043	0.060	0.88 "Large"	29

EMG, electromyography; LTRT, long-term resistance-trained; M_{max}, maximal compound action potential; MVT, maximal voluntary torque; QACSA, quadriceps anatomical cross-sectional area; RF, rectus femoris; UT, untrained; VL, vastus lateralis; VM, vastus medialis. Symbols denote significant difference between LTRT and UT: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

Increased conduction velocity of motor units and/or muscle fibers would theoretically increase synchronization of the individual motor unit action potentials that constitute M_{max}, thus increasing its amplitude (21, 25), and could potentially also contribute to the greater M_{max} of LTRT individuals we have found. Indeed, motor unit conduction velocity has been shown to be greater in LTRT individuals (14, 24). However, M_{max} has also been shown to remain unchanged following short-term resistance training (≤7 wk; 40–43), despite a study of similar duration showing increases in conduction velocity (44), suggesting that increased conduction velocity of motor units might not necessarily be related to increased M_{max} amplitude in the context of resistance training.

M_{max} amplitude may also increase through Na^+/K^+ pump-induced hyperpolarization of the sarcolemmal membrane (45) leading to increased single-fiber action potential amplitude. Changes in Na^+/K^+ pump activity have been shown with resistance training (46, 47), and thus the association between M_{max} and muscle size could merely be an artifact of other peripheral changes (e.g., augmented transmembrane potentials) following resistance training. However, it seems unlikely that the greater muscle size of LTRT individuals is not the result of greater fiber size (22, 48), which leads to greater single-fiber action potentials (16, 39). Therefore, the greater M_{max} amplitudes of LTRT individuals compared with UT are likely the result of greater single-fiber action potential amplitudes, which would be expected to also affect the voluntary EMG amplitude (25).

Comparison of Voluntary EMG Amplitude between Long-Term Resistance-Trained and Untrained Individuals and the Effect of Signal Normalization

Absolute voluntary EMG activity was greater for all the knee extensor muscles in LTRT individuals compared with UT. These findings are in agreement with a study that recorded absolute voluntary EMG activity of the knee extensors muscles of LTRT individuals and interpreted it as greater agonist activation compared with untrained (5). In contrast to the knee extensors, absolute voluntary EMG of the whole elbow flexors did not differ between LTRT and UT individuals, though differences between groups were noted for the short head of the biceps brachii. The similarity of whole elbow flexor amplitude in the current study was in contrast to a previous experiment (6), although that involved measurements from only one unspecified head of the biceps brachii and maximal voluntary contractions while restrained by a hand rather than by a dynamometer that precluded measurement of functional differences between their groups.

The whole muscle group findings were largely unaffected once voluntary EMG was corrected for MED (i.e., greater in LTRT for the knee extensors, but similar for the elbow flexors) although the magnitude of the knee extensor differences was somewhat moderated (+42% for MED-

corrected EMG vs. +64% for absolute EMG, and one rather than three constituent muscles showing differences). Thus, the observed effects were not fundamentally influenced by any differences in adipose tissue between the groups. These contrasting findings for the two muscle groups could be due to the suggestion that neural adaptations following resistance training might be limited in the elbow flexors (49) due to a high baseline activation level (50) that may be higher than that of the knee extensors (51). This possibility is supported by the lack of changes in elbow flexor EMG activity following short-term resistance training (3 wk; 6, 49).

Critically, however, when EMG activity was normalized to M_{max}, a recommended procedure to account for the peripheral electrophysiological properties of the signal (including muscle propagation and volume conduction) and attempt to isolate central neural activation (12), there were no differences between LTRT and UT groups for either the elbow flexors or knee extensors, or any of their constituent muscles. The marked differences in M_{max} between groups and the clear association of muscle size with M_{max} quantitatively demonstrate the confounding influence of peripheral electrophysiological properties on the EMG signal amplitude. Therefore, this study provides original evidence to reinforce the theoretical basis for M_{max} normalization. Based on these findings, voluntary EMG normalized to M_{max}, as opposed to absolute voluntary EMG or voluntary EMG corrected for MED, appears to provide the best index of central neural activation. These findings also indicate that caution is warranted when interpreting absolute EMG amplitude, particularly when comparing individuals and/or groups displaying differences in muscle morphology (e.g., aging, disuse, resistance training, and athletic performance), due to the confounding influence of muscle size.

Despite the chronic strength training exposure (≥3 yr) and markedly greater strength of our LTRT groups, we found no evidence for greater neural activation in two separate experiments with different muscle groups. Although this finding conflicts with a medium-term study (4), it agrees with another (3), and indirectly supports a previous supposition that neural adaptations might be maximized in the early stages of resistance training (5). Overall, the similar EMG activity normalized to M_{max} of LTRT individuals for both muscle groups suggests that the contribution of agonist neural activity to the substantially greater force production capacity of LTRT individuals (+66%–71%) is minor compared with muscle size (+54%–56%).

Specific to the knee extensors, the similarity of voluntary EMG activity when normalized to M_{max} suggests the difference in absolute EMG activity between groups may have been the result of peripheral adaptation to long-term resistance training (e.g., enhanced single-fiber action potential amplitude due to hypertrophy; 15), rather than changes in central neural properties. The knee extensor results of this study contrast with some (52, 53), but not all (54), short-term training studies that found augmented EMG activity when normalized to maximal M-wave. This contrast may reflect the greater sensitivity of repeated-measures longitudinal studies to detect relatively subtle differences compared with the current cross-sectional study.

Study Limitations and Future Considerations

Although this study provides novel insight into neuromuscular adaptations with long-term resistance training in both upper and lower limb muscle groups in a large cohort, it is important to acknowledge the study limitations. The cross-sectional study design precludes control of training variables in the long-term resistance-trained groups, and knowledge of their baseline neuromuscular function (i.e., before engaging in training), which might be innately high. However, in the absence of a longitudinal training intervention of several years, which is logistically very challenging, cross-sectional studies can highlight the unique characteristics of LTRT individuals and deemphasize any similar characteristics that are unlikely to be responsive to adaptation.

The observation that EMG activity, when normalized to M_{max}, was not different between LTRT and UT individuals does not necessarily exclude the influence of neural adaptations on strength increases with long-term resistance training. Indeed, interference EMG is only a crude indicator of neural drive to the agonist muscle(s) (7, 8, 10), largely due to the influence of amplitude cancellation on the signal amplitude (9), which might have prevented detection of modifications in neural strategies of LTRT individuals in this investigation. Future studies using emerging techniques such as advanced EMG decomposition (55, 56) are needed to discern potential changes in motor unit properties with long-term resistance training. The current study also only assessed agonist muscle EMG, although there is extensive evidence for decreased antagonist activity (5, 53) and tentative evidence for increased stabilizer activity (49) after resistance training, both of which may contribute to the greater strength of LTRT individuals. It should also be noted that the recordings of knee extensors involved muscles that exclusively extend the knee (except for RF, which is also a hip flexor, but given the hip position in this study likely acts as primarily a knee extensor). Conversely, the elbow flexors recordings involved the two heads of biceps brachii, which both flex the elbow and supinate the forearm, which might have contributed to differences (or lack of them) between LTRT and UT in elbow flexors compared with knee extensors.

Although the use of multiple site recordings is beneficial in terms of minimizing error when estimating activity across the motor pool and improved reliability, it has the potential to introduce cross talk between sensors. To minimize the potential for cross talk, we used sensors with short interelectrode distance (10 mm; 57) and spatially separated them in proximo-distal and medio-lateral directions. As reported previously (12), the distance between individual sensors was a minimum of 3.5 cm (and typically >4 cm), which is consistent with estimations that cross talk in such an electrode setup would account for only ~4% of the signal (58). Therefore, some small, limited cross talk might still have been present between sensors, although there is currently no accepted analytical approach to assess the extent of cross talk within an inferential EMG signal (8).

A bipolar (single differential) electrode configuration was used in this study to record EMG signals. This configuration type is most commonly used in exercise science studies and clinical fields because of its ability to minimize noise and

cross talk (59) and is thus recommended when quantifying voluntary interference EMG amplitude (60). However, although quantifying the amplitude of a maximal M-wave is valid with bipolar configuration, examining the shape of the signal is problematic due to inherent loses in the signal as a result of amplitude cancellation (61). Analyzing the shape of the signal potentially allows greater mechanistic insight (25) as it may distinguish between factors contributing to the propagating (e.g., sarcolemmal excitability) and nonpropagating phases of the potential (e.g., muscle architecture) which do not necessarily change concurrently in response to interventions (20). Future studies should consider the analytical approach of separating maximal M-wave phases recorded with monopolar configuration, to potentially gain greater insight into the mechanisms augmenting maximal M-wave amplitude with long-term resistance training.

Lastly, the present experiments were conducted on a male-only population; therefore, these data may only be generalized to males. Although presumably the physiological differences between LTRT and UT individuals are likely to be similar regardless of sex (62), further investigation is required to confirm whether similar findings would be obtained in a female population.

Conclusions

This investigation showed that LTRT men exhibit greater maximal compound action potential amplitude in the elbow flexors and knee extensors compared with UT controls, which, based on the positive association between M_{max} and muscle size, appears to be partially mediated by the differences in muscle morphology between groups. This indicates that absolute voluntary EMG signal amplitudes may be confounded by peripheral muscle morphology, rather than providing a discrete measurement of central neural activity. Some differences were observed in absolute voluntary EMG amplitude for the knee extensors, but not elbow flexors between LTRT individuals and UT that were maintained even after correction for MED. Subsequently, however, when voluntary EMG amplitude was normalized to M_{max}, to account for the peripheral electrophysiological properties of the EMG signal (and potential confounders such as muscle size), there were no differences between LTRT and UT individuals for any muscle group or individual muscles. Therefore, this study provides no evidence for a difference in central neural activity between the groups and thus agonist neural adaptation during maximal isometric muscle contractions in LTRT men.

SUPPLEMENTAL DATA

Supplemental Table S1: https://doi.org/10.6084/m9.figshare.13797674.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

J.Š., T.G.B., and J.P.F. conceived and designed research; T.G.B., S.M., G.J.M., M.B.L., and T.M.M-W. performed experiments; J.Š., T.G.B., S.M., and M.B.L. analyzed data; J.Š. and J.P.F. interpreted results of experiments; J.Š. prepared figures; J.Š. drafted manuscript; J.Š., T.G.B., S.M., G.J.M., M.B.L., T.M.M-W., and J.P.F. edited and revised manuscript; J.Š., T.G.B., S.M., G.J.M., M.B.L., T.M.M-W., and J.P.F. approved final version of manuscript.

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