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RESEARCH ARTICLE

Behavior of motor units during submaximal isometric contractions in chronically strength-trained individuals

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Abstract

Neural and morphological adaptations combine to underpin the enhanced muscle strength following prolonged exposure to strength training, although their relative importance remains unclear. We investigated the contribution of motor unit (MU) behavior and muscle size to submaximal force production in chronically strength-trained athletes (ST) versus untrained controls (UT). Sixteen ST (age: 22.9 ± 3.5 yr; training experience: 5.9 ± 3.5 yr) and 14 UT (age: 20.4 ± 2.3 yr) performed maximal voluntary isometric force (MViF) and ramp contractions (at 15%, 35%, 50%, and 70% MViF) with elbow flexors, whilst high-density surface electromyography (HDsEMG) was recorded from the biceps brachii (BB). Recruitment thresholds (RTs) and discharge rates (DRs) of MUs identified from the submaximal contractions were assessed. The neural drive-to-muscle gain was estimated from the relation between changes in force (ΔFORCE, i.e. muscle output) relative to changes in MU DR (ΔDR, i.e. neural input). BB maximum anatomical cross-sectional area ($ACSA_{MAX}$) was also assessed by MRI. MViF ($+64.8\%$ vs. UT, $P < 0.001$) and BB $ACSA_{MAX}$ ($+71.9\%$, $P < 0.001$) were higher in ST. Absolute MU RT was higher in ST ($+62.6\%$, $P < 0.001$), but occurred at similar normalized forces. MU DR did not differ between groups at the same normalized forces. The absolute slope of the ΔFORCE $-$ ΔDR relationship was higher in ST ($+66.9\%$, $P = 0.002$), whereas it did not differ for normalized values. We observed similar MU behavior between ST athletes and UT controls. The greater absolute force-generating capacity of ST for the same neural input demonstrates that morphological, rather than neural, factors are the predominant mechanism for their enhanced force generation during submaximal efforts.

NEW & NOTEWORTHY In this study, we observed that recruitment strategies and discharge characteristics of large populations of motor units identified from biceps brachii of strength-trained athletes were similar to those observed in untrained individuals during submaximal force tasks. We also found that for the same neural input, strength-trained athletes are able to produce greater absolute muscle forces (i.e., neural drive-to-muscle gain). This demonstrates that morphological factors are the predominant mechanism for the enhanced force generation during submaximal efforts.

high-density surface electromyography; motor unit behavior; neural adaptations; neural drive; resistance training

INTRODUCTION

Chronic exposure to strength training, a type of exercise characterized by repetitive movements against high loads, on a regular basis for months/years substantially increases the maximal volitional force-generating capacity of skeletal muscle (1). The increase in maximal strength is attributed to the interplay of neural and morphological alterations that occur in a temporally distinct manner, resulting in a well-known mismatch between the time course of muscle strength increase versus muscle growth or hypertrophy (2, 3).

The consensus evidence suggests that the early and rapid muscle-force gains (< 4 wk) are primarily underpinned by neural adaptations at multiple spinal and supraspinal levels of the motor pathway, which ultimately increase the neural drive to agonist muscles (4–6). Previous research has demonstrated a wide range of potential neural mechanisms, such as decreased intracortical inhibition (7), increased corticospinal and motoneuronal excitability (8), resulting in increased

discharge rates (DR) and decreased motor unit (MU) recruitment thresholds of agonist muscles (9–13), increased MU synchronization (14, 15), and decreased antagonist coactivation (16–18). These mechanisms have been observed in the early stages of strength training. Since the muscle contractile apparatus does not substantially adapt at the beginning of the training (8, 10, 19–22), it is commonly assumed (2, 3, 6, 23), and there is some recent evidence (24), that the greater proportion of the initial strength increments are attributable to neural factors. For instance, we recently observed that the neural drive to muscles during submaximal tasks was augmented after just 4 wk of training (9). Furthermore, we also demonstrated that the association between the change in force (ΔFORCE) relative to the change in MU DR (ΔDR), which is considered an indirect estimate of the input-output gain of the motoneuron pool, did not change after 1 mo of strength training (9). This indicates that the force generated by the muscle in response to a given level of neural drive is not influenced by short-term training, which confirms that the early adaptations to training are mainly neural. Conversely, long-term exposure to strength training (>4 wk to years of practice) is associated with substantial morphological changes (e.g., size and architecture) in human skeletal muscles, as extensively reported (2). These changes primarily include increases in muscle fiber cross-sectional area [CSA; (25)], the percentage of type IIA fibers (26), whole muscle size [assessed as CSA (25, 27), or volume (28)], and muscle fiber pennation angle (25, 29).

After long-term strength training, it is suggested that these temporal adaptations are additive and that both neural and morphological adaptations combine to underpin the large enhancement in muscle force generation following prolonged training (2, 18), although their relative importance remains unclear. This is, in part, due to previous comparisons relying on global interference EMG analysis (18, 30–32), which does not reflect the effective neural drive to the muscle, since it is only crudely associated with the underlying MU activity (33–36). The limitations of interference EMG measurements and analyses can be overcome with the adoption of advanced EMG recording (e.g., intramuscular or superficial high-density EMG) and decomposition techniques, which provide a direct estimate of the neural drive to skeletal muscle through the accurate identification of discharge timings of individual MUs (37, 38).

Despite recent reports, advancing our understanding of the adaptations in central and peripheral properties of motor units (i.e., increased firing rates and conduction velocity, decreased recruitment thresholds of MUs) underlying the early muscle force gains induced by strength training (9, 11, 12), it is still unknown whether prolonged involvement in strength training (e.g., months to years of practice) elicits continued and thus more pronounced adaptations in MU behavior. On the other hand, our recent cross-sectional study (1), observed that the larger muscle force (+60%) of long-term (> 4 yr) resistance-trained individuals compared with untrained controls was primarily attributable to their much larger quadriceps muscle volume (+56%), potentially leaving little scope for a significant neural contribution. After almost 3 decades of research in this field, however, the contribution of neural factors at the MU level to enhanced muscle force following chronic exposure to strength training is currently unknown.

The purpose of this study was to determine the neural contribution to muscle force production following long-term exposure to strength training. We investigated MU activity during submaximal voluntary isometric elbow flexion contractions in chronically strength-trained male athletes, compared with untrained male controls. Based on limited existing evidence, we tested the hypothesis that prolonged exposure to strength training causes pronounced adaptations in the neural drive to muscle, likely contributing to the enhanced muscular strength along with morphological changes. To test this hypothesis, here we estimated the neural drive-to-muscle gain as the relation between the relative changes in MU DR (ΔDR), i.e., the neural input to the muscle, and the changes in voluntary muscle force (ΔFORCE), i.e., the muscle output. This relation indicates the response of the muscle to a given level of neural drive and therefore identifies the relative contribution of neural and morphological factors to muscle force production.

METHODS

Participants

Forty-five healthy young males volunteered to participate and provided written informed consent before their involvement in this study, which was approved by the Loughborough University Ethics Approvals (Human Participants) Sub-Committee (R17-P174) and complied with the standards set by the Declaration of Helsinki. General inclusion criteria were age >18 and <40 yr and the absence of underlying health issues, previous traumatic upper-body injury and/or surgery, and no self-reported history of anabolic or androgenic steroid supplementation. The volunteers were recruited to a strength-trained group (ST) or an untrained control group (UT). Specific inclusion criteria for the ST group were as follows: 1) extensive history of upper arm resistance training (RT) with $\geq$ 2 sessions·wk^{-1} for $\geq$ 10 mo·yr^{-1} for at least $\geq$ 3 yr, 2) elbow flexion isometric maximum voluntary torque (iMVT) of $\geq$ 90 Nm. ST group participants had performed both single-joint and multiple-joint resistance training exercises for both the elbow flexors (e.g., dumbbell biceps curl, bent over barbell row, bent over single-arm dumbbell row, and lat pull down) and extensors (e.g., triceps extension, barbell bench press, and shoulder press). Participants reported that 38.1 ± 26.8%, 49.3 ± 24.9%, and 12.6 ± 10.2% of their resistance training over the last year involved near maximum loads [1–5 repetition maximum (RM)], heavy loads (6–14 RM), or moderate loads ($\geq$15 RM), respectively. The ST group had received variable coaching (technique and programming) support. Many of the ST group participants reported regular current or previous use of nutritional supplements (e.g., whey protein and creatine). Specific inclusion criteria for the UT group were no history of systematic upper body resistance exercise and no systematic physical training in the last 18 mo prior to the beginning of the study. Eleven volunteers were deemed ineligible based upon inclusion criteria. Four participants withdrew from the study (noncompliance), which resulted in 30 subjects (ST, n = 16; UT, n = 14) completing the study (Table 1).

Table 1. *Anthropometric, physical activity, muscle strength, and size characteristics for the ST and UT groups*

Variables	Group		
	ST	UT	P Value
Age, yr	22.9 ± 3.5	20.4 ± 2.3	0.002
Height, m	1.82 ± 0.08	1.77 ± 0.07	0.138
Body mass, kg	88.2 ± 12.9	75.0 ± 11.1	0.006
IPAQ score, MET min·wk^{-1}	5150 ± 2655	2618 ± 1420	0.004
RT history, yr	5.9 ± 3.5		
MViF, N	454.7 ± 52.2	275.9 ± 60.3	<0.001
iMVT, Nm	119.3 ± 22.0	67.4 ± 15.2	<0.001
ACSA$_{MAX}$, cm^2	18.4 ± 2.7	10.7 ± 2.1	<0.001

Data are presented as means ± SD; *n* = 16 subjects for the ST group and 14 subjects for the UT group. Between-group comparisons were performed with multiple-independent Student's *t* tests. ACSAMAX, maximum anatomical cross-sectional area; iMVT, isometric maximal voluntary torque; IPAQ, International Physical Activity Questionnaire; MET, metabolic equivalent of task; MViF, maximal voluntary isometric force; RT, resistance training; ST, strength-trained; UT, untrained.

Study Overview

In this cross-sectional study, the participants visited the laboratory on three occasions for measurements of the nondominant arm (defined as the nonwriting hand). The first session involved a thorough explanation of the experimental procedures and a familiarization with the experimental setup. In particular, this session involved the completion/practice of voluntary maximum as well as force-matching submaximal isometric contractions of the elbow flexors. Physical activity was assessed with the International Physical Activity Questionnaire [IPAQ, short version (39)], supplemented with some questions about the participant's resistance training experience. Participants' strength and physical activity were used to evaluate their eligibility for the study. The second visit (7–10 days after the first laboratory visit) comprised the main measurement session, which involved a standardized warm-up, the concomitant recordings of isometric elbow flexor force, and HDsEMG recordings from the biceps brachii (BB) muscle (see *Experimental Protocol*) during maximum voluntary contractions (MVCs) and submaximal ramp contractions. The third visit (2–3 days after the second laboratory visit) involved the acquisition of magnetic resonance T1-weighted axial images (MRI) to measure BB anatomical cross-sectional area (ACSA). Participants were asked to refrain from strenuous physical exercise (48 h) and to avoid caffeine consumption (24 h) before the two main measurement sessions.

Experimental Protocol

After a brief progressive warm-up involving a total of seven isometric contractions of the elbow flexors at different intensities of self-perceived maximal voluntary force (3 × 50, 3 × 75, and 1 × 90%, 5 s duration, 15–30 s rest in between), measurements were completed in the following order.

Maximum voluntary isometric contractions.

Participants performed three to four MVCs separated by 30 s of rest between contractions. Verbal instruction to "pull as hard as possible" for 3–5 s was provided before all MVCs. Moreover, a force-time curve was displayed on a monitor in front of the participant for biofeedback with a horizontal cursor indicating the peak force achieved in the preceding MVCs. Strong verbal encouragement to achieve the maximum within each contraction and to overcome the peak force of the previous MVCs was provided by an investigator. Maximum voluntary isometric force (MViF) was denoted as the greatest instantaneous force recorded out of the three to four MVCs and was used as a reference to determine the target forces for the submaximal contractions.

Submaximal ramp isometric contractions.

Five minutes after the completion of MVCs, the participants completed eight submaximal ramp contractions (2 contractions up to each force of 15%, 35%, 50%, and 70% of MViF). The ramp contractions were separated by 3 to 5 min of recovery and were performed in a randomized order to minimize any potential effects of fatigue on MU activity. As practiced in the familiarization session, the participants were instructed to match as precisely as possible a visual ramp contraction template displayed on a monitor for 5 s before and throughout each contraction. The ramp contraction templates were characterized by a linear increase in force from rest to the specified target force level at a fixed rate of force development of 10% MViF·s^{-1}, followed by 10 s (for 15%–35% of MViF trials) or 5 s (for 50%–70% of MViF trials) of constant force production (plateau) at the target force level. A real-time force recording was overlaid on the template for feedback.

Force Signal Recording

The familiarization and main measurement sessions were completed with the same custom-built isometric elbow flexion dynamometer, consisting of a rigid strength-testing chair adjustable according to the participants' height and upper limb length (Fig. 1A). The specific experimental configuration of the dynamometer was defined for each participant during the familiarization session and subsequently replicated in the main measurement session.

The participants were seated on the dynamometer with a hip joint angle of ~90° and their trunks in an upright position firmly strapped to the seat back (around the waist, chest, and shoulder) to minimize extraneous movement. Their nondominant shoulder joint angle was set at ~90° of flexion (i.e., perpendicular to the trunk) and with slight horizontal abduction at ~10° with the posterior of the upper arm resting on a rigid horizontal board. The elbow joint angle was fixed at ~70° of flexion (~90° = perpendicular to the upper arm) and the forearm in half-supination at ~45° (~0° = anatomical position). This specific elbow joint angle was adopted in line with previous experiments from our research group, which provided reference force data for the definition of the two groups (40, 41). The nondominant wrist was securely fastened with a strap to an adjustable wrist brace, which was connected in series with a calibrated S-beam tension-compression strain gauge (Force Logic, Swallowfield, UK) fixed perpendicular to the forearm. The contralateral upper limb rested on the thigh.

The analog force signal recorded from the strain gauge was amplified (×200), sampled at 2,048 Hz with an external 16-bit analog-to-digital (A/D) converter (EMG-Quattrocento,

A   Experimental setup

B   Monopolar HDsEMG Signals

C   MU Discharge Timings
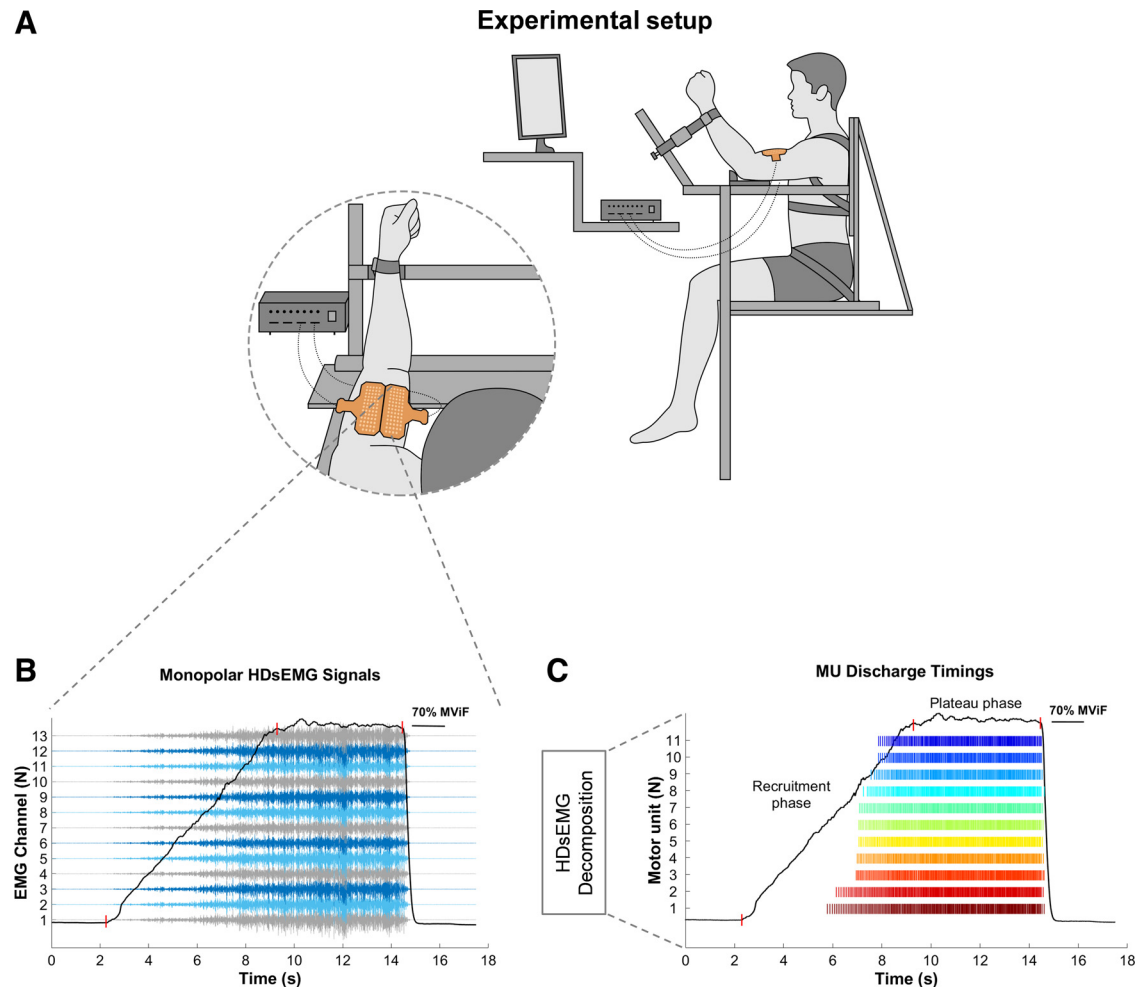
Figure 1. Experimental setup overview. *A*: participants were seated on a rigid isometric strength-testing chair with their nondominant wrist firmly strapped to an adjustable wrist brace connected in series with a calibrated strain gauge, which recorded elbow-flexion voluntary force. Two HDsEMG grids were placed close to each other over the biceps brachii muscle (64 electrodes in each grid) to cover most of the muscle area. *B*: representative example of a linearly increasing ramp contraction (force signal in black) at 70% MViF for an ST subject, with concomitant recording of HDsEMG in monopolar configuration (13 electrodes from one column of the grid are shown in different colors). Three red vertical lines delimitate the two different phases of the isometric ramp contraction adopted for MU activity characterization (i.e. recruitment phase, plateau phase). An increase in biceps brachii muscle myoelectrical activity can be clearly observed as the voluntary force generated is gradually increased (rate of increase, 10% MViF·s^{-1}). As a result of the alignment of the electrode grid to the anatomical direction of muscle fibers, the propagation of several overlapping MUAPs along the electrode column (from electrode 13 to electrode 1) can be observed. *C*: representative example of the HDsEMG decomposition by blind-source separation adopted to extract the MU discharge timings. In this representative subject, 11 MUs (shown in different colors) were identified from biceps brachii muscle during the isometric ramp contraction at 70% MViF. HDsEMG, high-density surface electromyography; MU, motor unit; MUAPs, MU action potentials; MViF, maximal voluntary isometric force; ST, strength-trained.

OT Bioelettronica, Turin, Italy), and, in turn, synchronized with the HDsEMG signals at source. The force signal was recorded with the software OT BioLab Ver. 2.0.6352.0 (OT Bioelettronica, Turin, Italy). Immediate biofeedback of the force expressed during each contraction performed as well as the target force templates were provided through the Spike 2 computer software (CED, Cambridge, UK) and displayed on a monitor placed at a distance of 1 m from participants' eyes.

HDsEMG Signal Recording

HDsEMG signals were detected from the surface of the BB muscle of the nondominant arm with two semidisposal bidimensional grids of 64 equally spaced electrodes each [13 rows (10.9 cm) × 5 (3.7 cm) columns; gold-coated; diameter 1 mm; interelectrode distance (IED) 8 mm; OT Bioelettronica, Turin, Italy]. This electrode configuration characterized by two grids placed close to each other to form a unique array of 128 electrodes was chosen to cover both BB short and long heads (31). In particular, the array was centered on the middle (proximal-distal) of the muscle belly (average distance of the distal edge of the array from the antecubital fossa, 5.9 ± 1.3 cm), aligned to the anatomical direction of muscle fibers (Fig. 1*A*). The array of electrodes was positioned after the experimental configuration of the dynamometer was completed and participants were seated with elbow joint angle fixed at ∼70° of flexion (see *Force Signal Recording*). Prior to electrode placement, an experienced investigator identified the muscle belly of the short and long heads of the BB through palpation while the arm was in the

dynamometer configuration, and outlined its profile with a surgical marker. After that, the skin surface was shaved, lightly abraded, and cleansed with 70% ethanol. To optimize the skin-to-electrode contact, the two electrode grids were attached to the skin overlying the BB muscle with disposable biadhesive foam layers whose holes, in correspondence with the electrodes, were filled with conductive paste (SpesMedica, Battipaglia, Italy).

The main ground electrode (strap electrode, dampened with water) was placed in proximity of the ulna styloid process of the tested arm, whereas the reference electrode for the two grids was placed over the radial styloid process.

The HDsEMG signals were recorded in monopolar derivation, amplified ($\times$150), sampled at 2,048 Hz, band-pass filtered (10–500 Hz) at source, and converted to digital data through a 16-bit A/D converter (EMG-Quattrocento, OT Bioelettronica, Turin, Italy). Similar to the force signal, HDsEMG signals were recorded with the software OT BioLab v. 2.0.6352.0 (OT Bioelettronica, Turin, Italy) and stored on an external hard disk for offline analyses (MATLAB R2016a, MathWorks, Natick, MA).

Muscle Size

T1-weighted axial MRI of the nondominant arm was obtained with a 3 T scanner (Discovery MR750w, GE Healthcare, Chicago, IL) and a receiver 16-channel flex coil. Axial images (perpendicular to the humerus) were obtained from the humeral head to below the elbow joint in three overlapping blocks, aligned with the humerus, using the following parameters: time of repetition $\sim$600 ms, time of echo $\sim$12.8 ms, the field of view $\sim$180 $\times$ 180 mm, image matrix $\sim$260 $\times$ 260, pixel size $\sim$0.69 $\times$ 0.69 mm, slice thickness $\sim$5 mm, interslice gap $\sim$5 mm, with the PROPELLER mode. Participants were scanned while in the supine position, with the elbow joint fully extended and relaxed. Oil-filled capsules were placed on the skin along the humerus to facilitate alignment between the blocks during analysis. The anatomical cross-sectional area (ACSA) of the BB muscle was segmented (as one mass for the long and short heads) along the humerus using a public domain DICOM software (Horos, v. 3.3.6; https://horosproject.org). The maximum ACSA ($ACSA_{MAX}$) of the BB muscle of each participant was used for further analysis.

◼ DATA ANALYSIS

Force Signal Analysis

In offline analysis, the analog force signal was converted to newtons (N) and the offset was removed by subtracting baseline force values (i.e., gravity compensation). The signal was low-pass filtered with a fourth-order, zero-lag Butterworth filter with a cut-off frequency of 15 Hz. For clarity, the force values (N) have been used when computing MU variables (i.e., MU RT), whereas torque values (Nm), derived by multiplying the force signal by the respective lever arm length (distance from the elbow joint center to the center of the wrist brace), were only adopted as specific inclusion criteria for the ST group. Only one of the two isometric ramp contractions at each force intensity (15%, 35%, 50%, and 70% MViF) was analyzed for each participant.

Specifically, the ramp contractions yielding the lowest deviation from the given template (force trajectory) at each force target and without any pretension or countermovement ($\leq$ 0.5 N from the force baseline in the 150 ms before the force onset) were included in the analyses (34, 42). The actual absolute (N) and normalized (% MViF) force values performed by participants during the submaximal ramp contractions were assessed by averaging the force values over the whole constant force phase (plateau) of the ramp contractions at any of the specified target force level (15%, 35%, 50%, and 70% MViF).

HDsEMG Signal Analysis

Monopolar HDsEMG recordings were digitally band-pass filtered between 20 and 500 Hz with a second-order zero-lag Butterworth filter, before being decomposed (Fig. 1, *B* and *C*). The filtered HDsEMG signals were decomposed with a convolutive blind source separation algorithm, into the activity of individual MUs (43, 44). The adopted decomposition algorithm has been extensively validated and provides accurate and reliable identification of individual MU discharge timings in a broad range (0%–70% MViF) of voluntary force levels (35, 43, 45). The accuracy of the decomposition was indirectly verified by calculating the pulse-to-noise ratio (PNR) for each MU. The PNR is a signal-based metric, which correlates with both sensitivity and false alarm rate in the identification of MU discharges (43). After the discharge timings were identified, they were converted to binary spike trains and manually inspected by an experienced operator who only retained those MUs characterized by PNR > 30 dB (sensitivity > 90%, false alarm rates < 2%) and/or a reliable discharge pattern (interspike interval < 2 s) (9, 43, 44, 46). In addition, only the MUs extracted from the grid of electrodes, which showed the highest number of identified MUs, were included in the analysis. For all participants (30/30), this was the grid located on the short head of the BB muscle.

From the series of MU discharge timings, the recruitment threshold (MU RT), the average discharge rate (DR) (average MU DR), as well as the MU DR in the recruitment phase (recruitment MU DR) and the plateau phase (plateau MU DR) of the submaximal ramp contractions were computed for each identified MU. The MU RT corresponded to the force value in absolute terms (absolute MU RT, N) or normalized terms (normalized MU RT, % MViF) at which the first MU action potential (MUAP) was discharged. The average MU DR was calculated as the mean DR during the entire isometric ramp contraction (from force onset to offset). The recruitment MU DR was calculated as the average of the first four MUAPs in the ascending phase of the ramp contraction, whereas plateau MU DR was calculated as the average DR over the constant force phase (plateau) of the ramp contraction at the relative force target. Based on their normalized MU RT, the identified MUs were also classified into low-threshold (LT MUs) if their MU RT ranged between 0% and 30% MViF, or into high-threshold (HT MUs) if their MU RT ranged between 50% and 70% MViF (11, 34). Average MU DR, recruitment MU DR, and plateau MU DR were also assessed for these subpopulations of MUs.

The neural drive-to-muscle gain was estimated by computing the change in force from MU RT to the plateau phase

of the submaximal ramp contractions (ΔFORCE), as a function of the change in MU DR from the recruitment (recruitment MU DR) to the plateau phase (plateau MU DR) (ΔDR). In this model, the ΔDR provides an indirect estimate of the increase in neural drive to the muscle (i.e., neural input), whereas the ΔFORCE provides a measure of the corresponding increase in generated force (i.e., muscle output) (9). Differences in the ΔFORCE versus ΔDR relationship between the ST athletes and UT controls would imply a distinct contribution of neural and morphological factors to voluntary force generation between the two populations. For clarity, in our previous publication (9) we adopted a similar analysis to estimate the input-output gain of the motor neuron, which was estimated by computing the change in MU DR at the plateau relative to that at the recruitment (ΔDR), as a function of the change in force from the recruitment to the plateau phase (ΔFORCE). Conversely, in the current study, we adapted this model to estimate the neural drive-to-muscle gain, which can be interpreted as a more direct assessment of the relation between the input to a muscle (ΔDR) and its output (ΔFORCE).

Statistics

The Shapiro–Wilk test was used to check the normality of the distribution of data for all the variables considered. The corresponding nonparametric tests were adopted where non-normally distributed data were observed. However, the majority of the variables analyzed in this study exhibited a normal distribution.

Between-group differences in anthropometrical characteristics (i.e., age, body mass, and height), physical activity habits (IPAQ score), elbow flexors maximal isometric strength measurements (i.e., MViF, iMVT), and muscle size (i.e., $ACSA_{MAX}$) were investigated with multiple-independent Student's t test.

Similarly, between-group differences in actual absolute (N) and normalized (% MViF) force values achieved during the submaximal ramp contractions (15%, 35%, 50%, and 70% MViF) were assessed with multiple-independent Student's t test (e.g., 15% MViF of ST vs. UT).

Between-group differences in the average number of identified MUs per subject, when considering data from the submaximal ramp contractions (15%, 35%, 50%, and 70% MViF), were investigated with independent Student's t test. Similarly, between-group differences in the average number of identified MUs per subject at the four different target forces were investigated with multiple-independent Student's t test. Average between-group differences in absolute and normalized MU RT, average MU DR, recruitment MU DR, and plateau MU DR assessed during the submaximal contractions were assessed with multiple-independent Student's t test. In addition, data across the four different target forces (e.g., 15%, 35%, 50%, and 70% MViF) for each participant were collapsed to produce overall MU properties, irrespective of contraction level. Between-group differences in the extracted MU properties across the four different force targets were assessed with one-way ANOVAs and Bonferroni corrected. Between-group differences in discharge characteristics (i.e., average MU DR, recruitment MU DR, and plateau MU DR) of LT

MUs and HT MUs were assessed with one-way ANOVAs and Bonferroni corrected.

To estimate the neural drive-to-muscle gain, the association between ΔFORCE (i.e., muscle output) and ΔDR (i.e., neural input) was assessed with Pearson's product-moment correlation coefficient (r) and associated significance for each individual participant, from data collapsed over the four target force levels, for both absolute and normalized values. The coefficient of determination (R^2) was adopted as an index of predictive power for each individual participant. Between-group differences in R^2 values from the individual linear regressions were investigated with independent Student's t test, for both absolute and normalized values. Similarly, the slopes of the individual regression lines, i.e., rate of change of force as a function of MU DR were extracted and statistically compared between the two groups, in both absolute (N) and normalized (% MViF) values, with independent Student's t test.

All statistical analyses were performed with the software SPSS, v. 23.0 (SPSS Inc., Chicago, IL). Statistical significance was set at $\alpha < 0.05$ for all tests. Results are expressed as means ± SD for each group.

RESULTS

Descriptive Characteristics, Muscle Strength, and Size

Between-group differences for anthropometrical characteristics, physical activity habits, and elbow flexor maximal voluntary isometric force are summarized in Table 1. The ST group showed significantly higher body mass ($P = 0.006$) and habitual physical activity (IPAQ score, $P = 0.004$) compared with the UT group. As expected, participants of the ST group with an average resistance training history of almost 6 yr, showed significantly higher elbow flexor MViF compared with the UT group ($+64.8\%$, $P < 0.001$, Table 1). MViF within the ST group ranged from 376.8 to 566.6 N, whereas it ranged from 195.2 to 378.7 within the UT group. This force gap between ST and UT groups was even higher for elbow flexor iMVT, derived by multiplying the force signal by the respective lever arm (forearm) length ($+76.9\%$, $P < 0.001$, Table 1). Similarly, biceps brachii $ACSA_{MAX}$ was significantly greater in ST compared with the UT group ($+71.9\%$, $P < 0.001$, Table 1). $ACSA_{MAX}$ within the ST group ranged from 14.1 to 24.3 cm², whereas it ranged from 7.1 to 14.8 cm² within the UT group.

As expected, the ST group generated significantly higher absolute forces during each of the four isometric submaximal ramp contractions to specified target force levels ($P < 0.05$, in all cases). Conversely, no between-group differences were observed for normalized (% MViF) force generated during submaximal contractions at any of the specified target force levels ($P > 0.05$, in all cases), which confirmed that both groups performed equivalent normalized submaximal contractions. The actual absolute and normalized force values achieved during the ramp contractions for both groups are summarized in Table 2.

HDsEMG Decomposition

The total number of identified MUs from the BB muscle, across all participants and contractions, was 827 (ST, $n = 505$;

Table 2. *Actual absolute (N) and normalized (% MViF) force values achieved during submaximal isometric ramp contractions at 15%, 35%, 50%, and 70% MViF for the ST and UT group*

Target Force	Absolute Force, N			Normalized Force, %MViF		
	ST	UT	P Value	ST	UT	P Value
15% MViF	68.1 ± 1.2*	41.6 ± 0.9	0.014	15.0 ± 0.3	15.1 ± 0.3	0.294
35% MViF	157.9 ± 3.0*	96.4 ± 2.3	< 0.001	34.7 ± 0.7	35.0 ± 0.8	0.163
50% MViF	227.6 ± 4.1*	137.8 ± 3.6	< 0.001	50.0 ± 0.9	49.9 ± 1.3	0.450
70% MViF	314.7 ± 6.5*	184.5 ± 3.8	< 0.001	69.3 ± 1.4	69.8 ± 1.4	0.400

Data are presented as means ± SD; n = 16 subjects for the ST group and 14 subjects for the UT group. *Significantly higher force values in ST than UT. MViF, maximal voluntary isometric force; ST, strength-trained; UT, untrained.

UT, n = 322). This number considers the MUs detected from all participants (n = 30) during the ramp contractions at all four force levels (15%, 35%, 50%, and 70% MViF). Figure 2 depicts the distribution and number of the identified MUs as a function of their recruitment threshold (y-axis) and the four ramp contractions to specific forces (x-axis) for each group. As a result of the increase in the number of superimposed MU action potentials in the interference EMG signal (9), fewer MUs were identified at the highest force levels (i.e., 70% MViF) in both groups.

When considering all contractions (15%, 35%, 50%, and 70% MViF), there were no significant between-group differences in the average number of identified MUs per subject (ST, 31.6 ± 13.4; UT, 23.0 ± 10.5; P = 0.064). Specifically, the average number of identified MUs per subject during contraction to each force level was 9.4 ± 3.6 and 6.9 ± 2.3 at 15% MViF, 8.4 ± 4.0 and 7.3 ± 3.0 at 35% MViF, 8.0 ± 4.4 and 6.1 ± 3.5 at 50% MViF, 5.8 ± 3.4 and 3.8 ± 2.7 at 70% MViF, for the ST and UT group, respectively. No significant between-group differences in the average number of MUs per subject were observed to any of the four force levels analyzed (P > 0.05 in all cases).

When we clustered the identified MUs according to their normalized MU RT (LT MUs: 0%–30% MViF; HT MUs: 50%–70% MViF), we identified a total of 351 LT MUs (ST, n = 223; UT, n = 128) and 63 HT MUs (ST, n = 36; UT, n = 27).
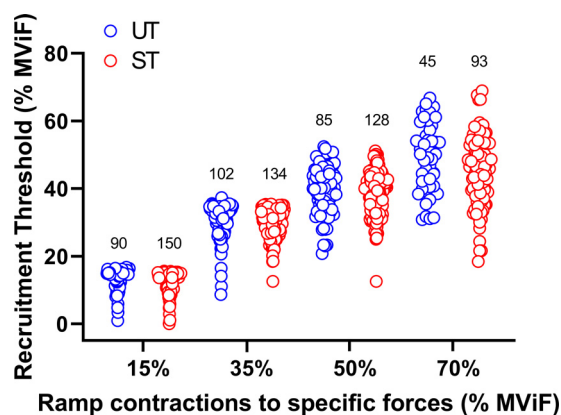
MU Recruitment Threshold

The absolute force value (N) at which the first MUAP was discharged, i.e., absolute MU RT, was greater for ST than for the UT group for any of the four force levels analyzed (P < 0.001 in all cases, Fig. 3A). Similarly, when MU RT data were collapsed across the four contractions for each participant, it was significantly greater in ST (142.3 ± 22.0 N) compared with UT (87.5 ± 20.2 N) group (+ 62.6%, P < 0.001, Fig. 3C). Conversely, no between-group differences were observed for normalized MU RT, i.e., force value relative to maximum (% MViF) at which the first MUAP was discharged, both when considering individual force levels (P > 0.05 in all cases, Fig. 3B) or when collapsing data across contractions (ST, 31.4 ± 3.9% MViF; UT, 31.9 ± 5.1% MViF; P = 0.752; Fig. 3D).

MU Discharge Rate

The average MU DR assessed across the entire isometric ramp contraction to any of the four force levels, did not differ significantly between the ST and UT group (P > 0.05 in all cases, Fig. 4A). Similarly, no between-group differences were observed for recruitment MU DR (i.e., average of the first 4 MUAPs) or plateau MU DR (i.e., average of all MUAPs during the plateau phase) during the submaximal isometric contractions (P > 0.05 in all cases, Fig. 4, B and C). When data were collapsed across the four contraction levels for each subject, there were also no between-group differences for average MU DR assessed across the whole contraction [ST, 20.7 ± 3.3 pulses per second (pps); UT, 20.9 ± 3.6 pps; P = 0.775; Fig. 4D], or recruitment MU DR (ST, 14.6 ± 3.0 pps; UT, 14.5 ± 2.2 pps; P = 0.870; Fig. 4E), or plateau MU DR (ST, 21.1 ± 3.2 pps; UT, 21.3 ± 3.6 pps; P = 0.889; Fig. 4F). Similarly, when the identified MUs were clustered according to their normalized MU RT (i.e., LT MUs, HT MUs), there were no between-group differences for average MU DR assessed across the whole contraction (LT MUs: ST, 17.5 ± 4.9 pps; UT, 17.5 ± 5.2 pps; P = 0.999; HT MUs: ST, 25.3 ± 5.9 pps; UT, 23.7 ± 6.0 pps; P = 0.648; Fig. 4G), or recruitment MU DR (LT MUs: ST, 12.6 ± 4.4 pps; UT, 12.5 ± 5.0 pps; P = 0.991; HT MUs: ST, 15.9 ± 5.8 pps; UT, 13.8 ± 2.8 pps; P = 0.253; Fig. 4H), or plateau MU DR (LT MUs: ST, 17.9 ± 5.3 pps; UT, 17.9 ± 4.7 pps; P = 0.999; HT MUs: ST, 25.8 ± 6.0 pps; UT, 24.2 ± 6.5 pps; P = 0.644; Fig. 4I).

Neural Drive-to-Muscle Gain

The neural drive-to-muscle gain was estimated by assessing the relation between ΔFORCE (i.e., muscle output) and

Figure 2. Number and distribution of identified MUs from biceps brachii muscle. Swarm plot of the total number and distribution of identified MUs (n = 827) as a function of their normalized recruitment threshold force values (y-axis) at each of the four contractions to target forces (15%, 35%, 50%, and 70% MViF) in UT (blue empty circles) and ST (red empty circles) group. A decrease in the overall number of identified MUs is clearly observable in both groups at the highest force levels, as a consequence of the higher superimposition of MUAPs in the interference HDsEMG signal. HDsEMG, high-density surface electromyography; MU, motor unit; MUAPs, MU action potentials; MViF, maximal voluntary isometric force; ST, strength-trained; UT, untrained.
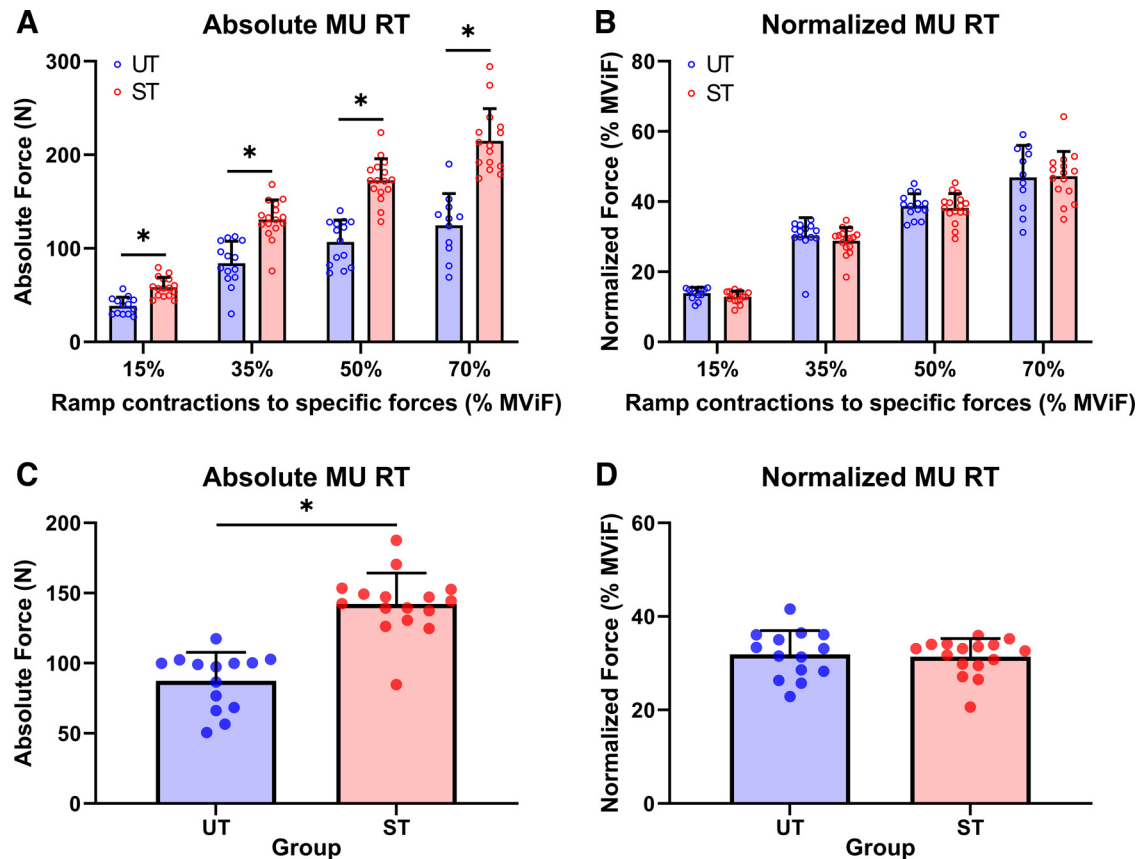
Figure 3. MU recruitment thresholds. Bar plots representing absolute (*A*) and normalized (*B*) MU RT at each of the four contractions to target forces (15%, 35%, 50%, and 70% MViF) in UT (blue bars) and ST (red bars) group (*x*-axis). Bar plots in *C* and *D* display group means ± SD values for absolute and normalized MU RT force values (*y*-axis). In all the graphs, individual average values from collapsed data across all four submaximal contractions are also displayed, and each subject is indicated with an unfilled (*A*, *B*) or filled (*C*, *D*) circular marker (in blue, UT; in red, ST). *$P < 0.001$. MU, motor unit; MViF, maximal voluntary isometric force; RT, resistance training; ST, strength-trained; UT, untrained.

ΔDR (i.e., neural input). A significant association was observed between ΔFORCE (i.e., change in force from MU RT to the plateau) and ΔDR (i.e., change from recruitment MU DR to plateau MU DR) in all participants, in both absolute (N) and normalized values (% MViF). For the whole cohort the average R^2 values of this relation were 0.50 ± 0.16 (range: 0.16–0.80), for absolute values, and 0.50 ± 0.16 (range: 0.16–0.80), for normalized values ($P < 0.05$ in all cases), with no between-group differences in average R^2 values (absolute, $P = 0.436$; normalized values, $P = 0.523$).

The linear regressions between ΔFORCE and ΔDR, when considering all identified MUs, are depicted as scatter plots in Fig. 5 for both absolute (*A*) and normalized (*B*) values for both groups. Then, the comparison of individual data within each group revealed that the slopes of the regression lines, representing the absolute change in voluntary force (i.e., force at MU RT to plateau) relative to the change in MU DR (i.e., recruitment MU DR to plateau MU DR), were significantly higher in ST than UT group (ST, 5.69 ± 2.43 N·pps^{-1}; UT, 3.41 ± 1.33 N·pps^{-1}; $+66.9\%$, $P = 0.004$; Fig. 5*C*). This indicates that for similar changes in neural drive (ΔDR) the ST group produced greater changes in absolute force (ΔFORCE) than the UT group.

Conversely, no between-group differences were observed in normalized values (ST, $1.24 \pm 0.45\%$ MViF·pps^{-1}; UT,

$1.23 \pm 0.41\%$ MViF·pps^{-1}; $P = 0.948$, Fig. 5*D*). Participant-specific values for linear regressions between ΔFORCE and ΔDR, both in absolute and relative values, are summarized in Table 3.

DISCUSSION

This study aimed to determine the neural contribution to muscle force production following long-term exposure to strength training. Despite the substantially higher maximal force-generating capacity (i.e., MViF) and ACSA$_{MAX}$ of ST athletes ($+64.8\%$ and $+71.9\%$, respectively), recruitment strategies and discharge rate characteristics of MUs identified from BB of ST athletes were similar to those observed in the UT controls during equivalent (normalized) submaximal force tasks. In contrast with our initial hypothesis, these similarities suggest that the recruitment and discharge properties of the identified MUs were not responsible for the observed between-group differences in absolute forces generated during submaximal ramp contractions. Moreover, by estimating the neural drive-to-muscle gain, as the relation between the ΔDR (i.e., the input to the muscle) and the ΔFORCE (i.e., the muscle output), we investigated the contribution of neural and morphological factors to muscle force production after long-term exposure to strength training.
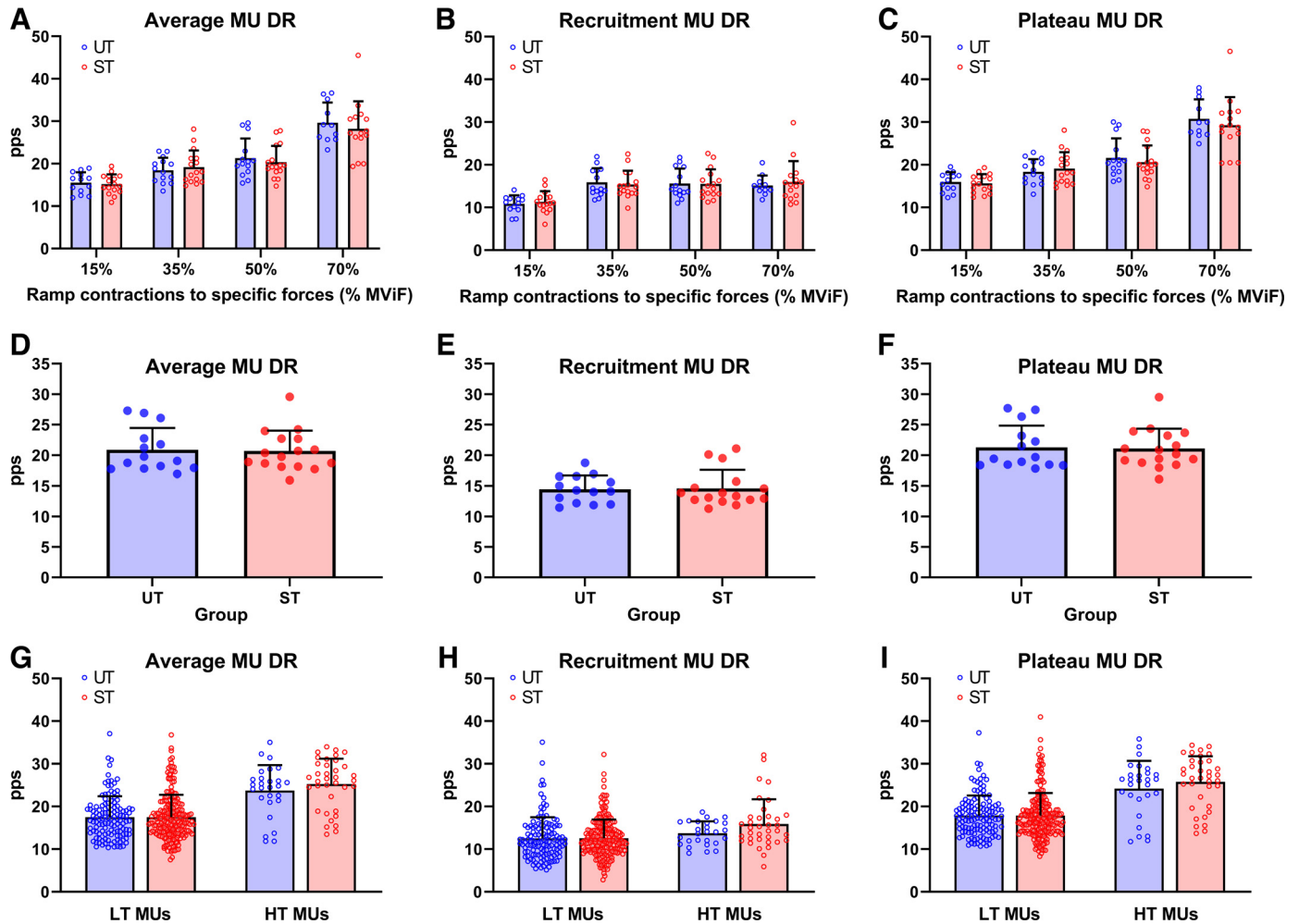
Figure 4. MU discharge rate. Bar plots representing average MU DR (*A*) assessed across the whole isometric ramp contraction, recruitment MU DR (*B*), and plateau MU DR (*C*) at each of the four contractions to target forces (15%, 35%, 50%, and 70% MViF) in UT (blue bars) and ST (red bars) group (*x*-axis). Bar plots in *D*, *E*, *F* display group means ± SD values for average MU DR, recruitment MU DR, and plateau MU DR (*y*-axis). In all the graphs (*A*–*F*), individual average values from collapsed data across all four submaximal contractions are also displayed, and each subject is indicated with a filled (*A*, *B*, *C*) or unfilled (*D*, *E*, *F*) circular marker (in blue, UT; in red, ST). Bar plots in *G*, *H*, *I* show group means ± SD values for average MU DR, recruitment MU DR, and plateau MU DR for the identified populations of LT MUs (0%–30% MViF) and HT MUs (50%–70% MViF). Each unfilled circular marker (in blue, UT; in red, ST) indicates a single MU. DR, discharge rates; HT, high-threshold; LT, low-threshold; MU, motor unit; MViF, maximal voluntary isometric force; ST, strength-trained; UT, untrained.

The higher absolute slope of the regression line (+66.9%), representing the change of the muscle output (i.e., force) relative to the change of the neural input (i.e., MU DR), observed in the ST athletes compared with the UT controls indicated that for the same ΔDR, ST athletes are able to generate higher muscular forces. These results suggest a greater contractile response to the same net neural input during submaximal voluntary force tasks. In addition, the absence of between-group differences in the normalized slope of the regression lines further indicates that MU discharge properties may play only a limited role in volitional force generation during equivalent (normalized) submaximal force tasks after years of strength training practice. Thus, the greater absolute forces of ST athletes appeared to be largely due to morphological differences rather than agonist neural drive per se.

It has to be considered that much of the direct evidence of MU adaptations have been typically provided following relatively short-duration strength training interventions (from 2 to 12 wk) since this time window is suggested to be predominantly dominated by neural alterations, whereas currently, it is still unknown if long-term exposure to strength training (e.g., from months to years of practice) elicits continued and thus more pronounced adaptations in MU behavior. As a consequence of this lack of knowledge, there is still uncertainty on the relative contribution of MU recruitment and discharge rate properties to the enhanced muscular strength typically observed in chronically strength-trained individuals. For this purpose, by applying state-of-the-art techniques for the noninvasive recording of MU behavior (i.e., HDsEMG), we compared MU activity during equivalent (normalized) submaximal isometric force tasks (at 15%, 35%, 50%, and 70% MViF) in chronically strength-trained male athletes with untrained male controls. To ensure that all participants performed equivalent (normalized) submaximal isometric force modulating tasks, we
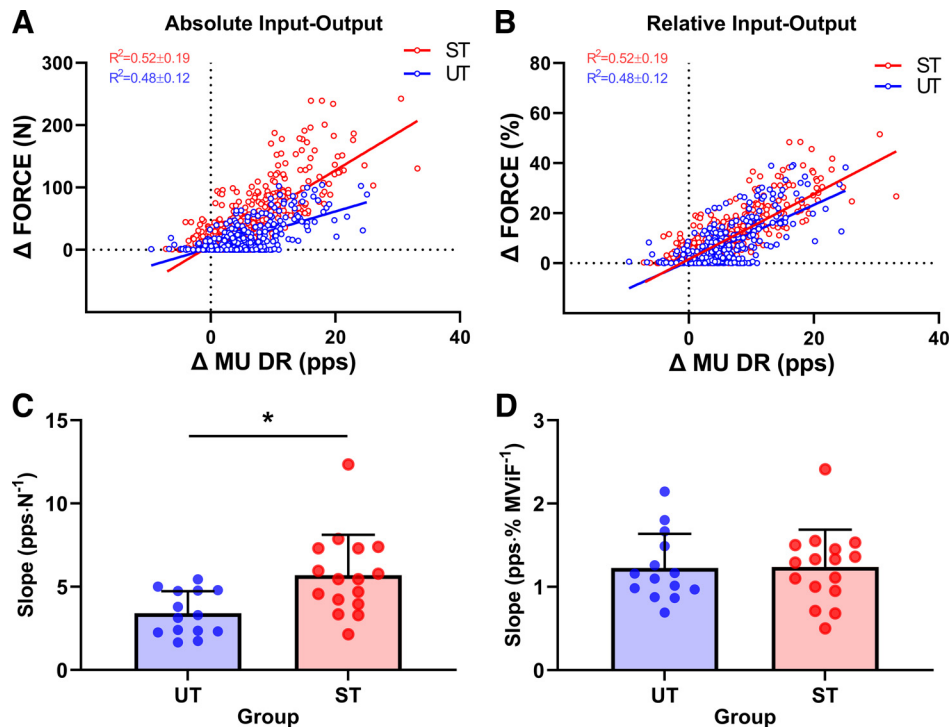
Figure 5. Estimated neural drive-to-muscle gain. Scatter plots (*A*, *B*) representing the association between the change in voluntary force (*y*-axis, ΔFORCE) from MU RT to the plateau phase of the isometric ramp contractions, relative to the change in MU DR (*x*-axis, ΔDR), from the recruitment (recruitment MU DR) to the plateau (plateau MU DR), when considering all identified MUs data pooled by group irrespective of individuals. Absolute values are shown in *A* (N), whereas normalized (% MViF) values are shown in *B*. Each empty circle represents one MU (in blue, UT; in red, ST). Bar plots (*C*, *D*) representing group means ± SD and individual values (circular-filled markers) for the rate of change (slope) of ΔFORCE relative to ΔDR in absolute (pps·N^{-1}, *C*) and normalized (pps·% $MViF^{-1}$, *D*) values when data were collapsed across all four contractions, respectively. The average slope of the regression line representing the absolute change in ΔFORCE (i.e. the muscle output) relative to the change in ΔDR (i.e. the neural input) was significantly higher in the ST group than in the UT group (*C*). *$P = 0.004$. The group means ± SD of the coefficient of determination (R^2) of individual linear regressions is reported in the upper left corner of graphs *A* and *B* (in blue, UT; in red, ST). DR, discharge rates; MU, motor unit; MViF, maximal voluntary isometric force; RT, resistance training; ST, strength-trained; UT, untrained.

statistically compared the normalized force values achieved during the ramp contractions with elbow flexors between the two groups (Table 2). The comparison confirmed that both groups performed at equivalent force levels. Moreover, the accuracy and reliability of the decomposition technique for MU identification used in this study have been tested in a number of previous reports (43, 46). The identification of a similar average number of MUs per subject in both groups (ST, 31.6 ± 13.4; UT, 23.0 ± 10.5), allowed a robust and reliable between-group comparison of MU activity during the submaximal modulating tasks at equivalent force levels.

The magnitude of the difference in MViF of chronically ST athletes versus UT controls found in the current study was substantial (+64.8%), and this was in line with previous observations (31, 48). We also observed that the greater MViF of ST versus UT was accompanied by a significantly higher BB $ACSA_{MAX}$ (+71.9%), which similarly was in line with several previous observations (1, 48, 49).

MU Behavior after Long-Term Strength Training

We observed that normalized MU RT and discharge characteristics (average, recruitment, and plateau MU DR) of MUs identified from BB muscle did not differ between chronically ST and UT individuals, during submaximal isometric force-modulating tasks. In particular, despite significantly higher absolute MU RT values in the ST group (+62.6%; Fig. 3, *A*

and *C*), we observed no between-group differences in normalized MU RT values (Fig. 3, *B* and *D*). The higher absolute MU RT found in the ST group indicates a greater contractile (force) response of the MUs of these chronically trained males compared with the control cohort. In turn, this could largely explain the higher maximal force-generating capacity (i.e., MViF, +64.8%) observed in ST athletes. Nevertheless, the absence of differences in normalized MU RT suggests very similar recruitment strategies of MUs to produce an equivalent normalized (relative) force trajectory during submaximal ramp contractions irrespective of ST experience. Our results of unaltered normalized MU RT forces after chronic exposure to strength training are somewhat contrary to previous studies of short-term strength training, although no previous studies, to our knowledge, have investigated long-term strength training effects. Indeed, a marked reduction of MU RT forces assessed through HDsEMG (9) or intramuscular EMG (10), which indicates an earlier and/or compressed MU recruitment to produce a submaximal prescribed force trajectory ($\leq$ 70% MViF), has been previously reported in the initial weeks of an isometric (9) or dynamic (10) strength-training intervention. Similarly, Patten and Kamen (50) found that normalized MU RT assessed via quadrifilar needle electrode during submaximal ankle dorsiflexions ($\leq$ 60% MViF) was reduced after a 6-wk force modulation training. The results of these previous studies imply that alterations of MU recruitment

Table 3. *Participant-specific coefficient of determination, intercept, and slope of the linear regressions between ΔFORCE and ΔDR derived from the isometric submaximal ramp contractions, in absolute and normalized values*

| Participant | Group | Neural Drive-to-Muscle Gain | | | | | |
| | | Absolute, N | | | Normalized, %MViF | | |
		R^2	Intercept	Slope	R^2	Intercept	Slope
S1	ST	0.26#	10.24	3.30	0.26#	2.21	0.71
S2	ST	0.68*	5.53	7.30	0.68*	0.98	1.29
S3	ST	0.53*	13.55	7.87	0.53*	2.63	1.53
S4	ST	0.77*	−22.76	12.34	0.77*	−4.44	2.41
S5	ST	0.58*	2.41	3.96	0.58*	0.58	0.95
S6	ST	0.52*	15.07	7.39	0.52*	3.05	1.50
S7	ST	0.16#	17.43	2.15	0.16#	4.08	0.50
S8	ST	0.36#	9.08	4.69	0.36#	1.94	1.00
S9	ST	0.33#	9.43	4.23	0.33#	2.46	1.10
S10	ST	0.38#	3.40	4.57	0.38#	0.83	1.11
S11	ST	0.45#	2.06	5.78	0.45#	0.49	1.36
S12	ST	0.68*	−1.39	5.95	0.68*	−0.31	1.33
S13	ST	0.80*	−3.15	7.30	0.80*	−0.67	1.55
S14	ST	0.58*	26.31	3.34	0.58*	5.37	0.68
S15	ST	0.78*	3.24	5.45	0.78*	0.86	1.45
S16	ST	0.50#	20.45	5.46	0.50#	4.98	1.33
		0.52 ± 0.19	**6.93 ± 11.33**	**5.69 ± 2.43**	**0.52 ± 0.19**	**1.56 ± 2.38**	**1.24 ± 0.45**
U1	UT	0.41*	0.06	2.32	0.41*	0.03	0.97
U2	UT	0.50*	2.82	4.77	0.50*	0.74	1.26
U3	UT	0.54*	−0.73	3.79	0.54*	−0.23	1.17
U4	UT	0.30#	16.11	3.30	0.30#	4.28	0.88
U5	UT	0.68*	−5.02	5.00	0.68*	−1.67	1.67
U6	UT	0.58*	−14.90	5.44	0.58*	−4.93	1.80
U7	UT	0.47*	−0.37	2.26	0.47*	−0.19	1.16
U8	UT	0.62#	4.53	1.66	0.62#	1.88	0.69
U9	UT	0.50*	5.28	2.35	0.50*	2.28	1.01
U10	UT	0.28#	−1.84	4.79	0.28#	−0.57	1.49
U11	UT	0.36*	4.84	2.41	0.36*	1.97	0.98
U12	UT	0.57*	3.04	4.74	0.57*	1.38	2.14
U13	UT	0.40#	1.94	1.74	0.40#	0.97	0.87
U14	UT	0.45*	0.29	3.13	0.45*	0.10	1.10
		0.48 ± 0.12	**1.15 ± 6.71**	**3.09 ± 1.07**	**0.43 ± 0.12**	**0.43 ± 2.13**	**1.23 ± 0.41**

Group means ± SD are also displayed. *$P < 0.001$, #$P < 0.05$. DR, discharge rate; MViF, maximal voluntary isometric force; R^2, coefficient of determination; ST, strength-trained; UT, untrained.

strategies are determinant changes for the generation of muscle force in the initial weeks of training (4–12 wk), whereas they may have a smaller effect in explaining chronic adaptations to strength training. At present, however, it is unclear if both short-term (adjustments) and long-term (adaptations) alterations of MU recruitment strategies occur during maximal voluntary force production tasks (see *Limitations and Methodological Considerations*).

Similarly, we found no differences in MU discharge properties assessed during the submaximal ramp contractions between chronically ST and UT individuals. This was evident both when MU DR was assessed across the whole ramp contraction (i.e., average MU DR; Fig. 4D), as well as during the recruitment (i.e., recruitment MU DR; Fig. 4E) and the plateau phase (i.e., plateau MU DR; Fig. 4F) of the submaximal contractions. Furthermore, when we clustered the identified MUs according to their MU RT in LT MUs (0%–30% MViF) and HT MUs (50%–70% MViF), we observed similar MU discharge characteristics between ST and UT individuals (Fig. 4, G–I). Our findings suggest that MU discharge properties (i.e., neural input) may not be the main determining factor for the increased absolute force-generating capacity during submaximal ramp contractions following long-term exposure to strength training. There is very limited data on the

MU DR of chronically ST individuals; however, in agreement with our findings, Leong et al. (51) reported similar discharge characteristics of MUs ($n = 109$) identified from rectus femoris muscle assessed at the plateau (50% MViF) of submaximal isometric ramp contractions between well-trained older weight lifters and untrained age-matched controls. Nevertheless, the MU recordings in that study (51) were obtained with a different methodological approach (i.e., four-wire needle electrode), a technique which presents several and well-documented technical limitations (e.g., the high selectivity of recordings, possibility to record only at low contraction forces, invasiveness) (52).

There are a few more previous reports that have assessed longitudinal changes in response to short-term (≤8 wk) ST in humans and these show somewhat divergent findings. Increases in MU DR have been implicated in the rapid gains in muscular force occurring after a few weeks of strength training (4–6 wk) (9, 12). For instance, Del Vecchio et al. (9), recently observed an increase in average MU DR at the plateau of submaximal contractions (from 20.4 to 23.8 pps, approx +3 pps), suggesting that alterations of the discharge characteristics of MUs (e.g., of both low-threshold and high-threshold) may play a key role to the increased muscle force production in the initial weeks (≤ 4 wk) of strength-training

practice. Alternatively, two studies did not report any increase in average MU DR at the plateau of submaximal isometric ramp contractions (at 50% and 70% MViF, respectively) after 6 (13) and 8 (53) wk of dynamic strength training, respectively. However, the methodological approach to the recording and extraction of MU properties [i.e., fine-wire needle electrodes, (13); and 5-pin surface sensor array, (53) vs. HDsEMG, (9)] adopted by these studies may, in part, explain these different findings.

Although not directly comparable with the results of the current study, animal models also suggest considerable adaptive changes in the intrinsic properties of motor neurons (e.g., higher excitability, decreased intracellular current required to evoke rhythmic firing, increased maximum and average discharge frequencies) occurring after a few weeks (5 wk) of weight-lifting training (54). However, the possibility that changes in the intrinsic properties and excitability of motor neurons may affect their volitional firing and thus MU behavior should be investigated more explicitly in a chronically strength-trained human population.

Taken together, our results demonstrate that non-neural factors, likely play a more determinant role for the increased volitional force-generating capacity during submaximal force-modulating tasks (from 15% to 70% of MViF) after years of strength-training practice. This supports our recent findings that the greater knee extensor strength (+60%) of a chronically ST group versus UT controls was primarily due to differences in muscle volume (+56%) rather than much more modest differences in specific tension [the functional consequence of greater agonist activation +8%; (1)] or antagonist coactivation, which accounted for <3% of the difference in high-level muscular torque (18).

Neural Drive-to-Muscle Gain: The Role of Morphological Factors

To further determine the contribution of neural factors to voluntary force generation in individuals with a history of long-term strength training, we studied the relation between the changes in voluntary muscle force (ΔFORCE) as a function of the changes in MU DR (ΔDR), which we defined as neural drive-to-muscle gain. This relation can be considered as conceptual and computational evolution of the traditional torque-agonist EMG relation, first proposed by Moritani and DeVries in the late 1970s (3), and subsequently adopted by several studies (18, 55–58) to investigate the nature of the underpinning neural and morphological adaptations to strength training. In our adapted model, the ΔDR was calculated as the difference between recruitment MU DR (average of first 4 MUAPs) and plateau MU DR and corresponds to the input received by the muscles (i.e., indirect estimate of the net neural drive to the muscle). In turn, the ΔFORCE was computed as the difference between the target force (plateau) and MU RT in both absolute (N) and normalized values (% MViF) and reflects the output of the muscle (i.e., voluntary force generated).

We observed that the slope of the regression lines, representing the absolute change in voluntary force (ΔFORCE) as a function of the change in MU DR (ΔDR), was significantly higher in the chronically ST athletes compared with the UT controls (Fig. 5C). These results indicate that for a given net

neural drive, chronically ST athletes were able to generate significantly higher absolute forces compared with the UT controls (Table 2), and indirectly suggests that morphological factors (i.e., the muscle gain) likely play a more dominant role over neural factors for volitional force generation during submaximal force-modulating tasks after years of training practice. For instance, this means that for a similar change in net neural drive, i.e., 20 pps, a UT individual was able to generate ~50–70 N change in absolute force, whereas a chronically ST athlete was able to generate a substantially greater change in absolute force, in the order of ~100–120 N. Therefore, considering the similar net neural drive to the muscle of the two very different individuals, it is likely that morphological factors (e.g., muscle size) play a dominant role compared with neural factors (e.g., neural drive) in explaining the higher absolute force production of the ST individual.

In line with this interpretation, no differences in the normalized slopes of the regression lines were found (Fig. 5D), indicating that for the same net neural drive (i.e., input) the normalized (relative) force (i.e., output) is similar (Fig. 5B), whereas greater absolute forces can be achieved because of morphological adaptations in ST individuals (Fig. 5A). The absence of between-group differences in the normalized slopes, which means that similar normalized forces are achieved with similar neural drives, further suggests that there is minimal neural adaptation in ST individuals to perform the same relative submaximal task. On the other hand, it also confirms, as shown in Fig. 5, A and C, that the higher absolute forces performed by ST athletes, can be likely achieved because of the greater contribution of morphological adaptations over neural factors.

As previously suggested (9), neural adaptations occurring in the common final pathway of the motor system (i.e., MU level) in humans, may have a more determining role in the initial stages (≤ 4 wk) of strength training, by primarily mediating the rapid gains in muscle force, which typically occur in the absence of substantial alterations of the contractile apparatus (7, 20–22). In particular, with a similar analysis but interpreted at the motor neuron level (i.e., input-output gain of the motor neuron), the authors observed that the association between the change in force (ΔFORCE) relative to that of MU DR (ΔDR), similarly assessed during submaximal isometric contractions, was unchanged after 4 wk of strength training (9). This indicates that in the initial weeks of training the skeletal muscle is likely, not able to generate higher forces for the same relative net neural drive, hence the increased force-generating capacity of the muscle is the result of an increased net excitatory input to the motor neuron pool or changes in intrinsic motor neuron properties, rather than the result of morphological alterations (9). On the contrary, the absolute force generated by the muscle in response to the same net neural activation was augmented during submaximal force-modulating tasks (Fig. 5A) in a population with a history of long-term strength training, which again suggests a potentially greater role played by morphological over neural factors for the increased volitional force-generating capacity in contractions up to 70% MViF, after years of training practice.

Limitations and Methodological Considerations

There are some limitations within the current study that should be recognized. The cross-sectional nature of the current study provides a weaker level of evidence than longitudinal intervention studies and this may confound the discerning of the contribution of selection (i.e., innate differences) from the influence of prolonged exposure to strength training on both neural and morphological adaptations. Although it may be impractical and challenging to follow the same individuals for several years, this approach would provide a more in-depth overview of the neural and morphological adaptations to prolonged strength training. In this respect, if on one side, the morphological adaptations that occur in response to long-term exposure to strength training have been well described (2), on the other, the precise nature, loci, and timeline of neural adaptations to this prolonged form of exercise are unknown. Nevertheless, considering the impracticality of implementing supervised longitudinal training interventions of several years, the results of the present study provide novel insight into how MU behavior likely adapts with prolonged strength training.

It should also be noted that the results of the present investigation could be specific to the elbow joint and open kinetic chain isometric elbow flexion task that was adopted. More importantly, our findings of similar recruitment strategies and discharge characteristics of ST athletes and UT controls should be considered specific to the submaximal ($<$ 70% MViF) force-modulating task performed. Indeed, current methodological constraints associated with the decomposition of HDsEMG recordings during maximum volitional contractions (e.g., MVC), seem to preclude at present, the accurate and reliable identification of MU discharge timings during maximum force production tasks. In particular, the increase in the number of superimposed and overlapping MUAPs in the interference signal that occur at maximum force levels complicates the separation of the contributions of individual motor units, substantially reducing their number and accuracy (9, 43). This methodological issue was also evident in the current study, where fewer MUs were identified at the highest force levels (i.e., 70% MViF) compared with the lowest (i.e., 15% or 35% MViF; Fig. 2). Thus, whether the neural response is altered (e.g., augmented neural drive) during maximum volitional contractions after years of prolonged exposure to strength training remains to be elucidated. In this respect, although evidence from previous studies, which adopted surface electromyogram recording (59), interpolated twitch technique (60), tetanic stimulation (61), and functional MRI (62), indirectly suggest that healthy untrained individuals have some modest scope for increasing their agonist maximum activation through an increased MU recruitment, MU firing frequency, and/or MU synchronization following short-term strength training, further research is needed to determine whether long-term exposure to ST may elicit adaptations in maximum activation capacity of the involved MU pool and particularly from a MU population perspective.

It is also important to mention that for consistency with a previous study from our research group (9), where changes in motor neuron output after short-term strength training was investigated, here we similarly assessed the neural input to the muscle as the change in discharge rate (ΔDR) between the recruitment and the target force. In this respect, it should be noted that there may be other measures for assessing the neural input, such as the variability/regularity of MU DR (i. e., MU firing patterns), which were not quantified in the current analysis.

Moreover, it should be recognized that changes other than purely neural factors could influence the DR of motor neurons. For example, there is evidence that the intrinsic contractile properties of the muscle may slow down after resistance training (28), or somewhat contradictorily that the force-frequency relationship may be shifted to the right (63) after resistance training. Irrespective of the direction of these changes, alterations in the contractile properties of the muscle might require a different DR to achieve the same force, even in the absence of any neural adaptations.

Finally, it should also be acknowledged that despite the adopted technique for MU recording allowed us to sample and study a larger population of MUs compared with previous more selective intramuscular methods (46, 64, 65), current HDsEMG decomposition techniques mainly allow the identification of the most superficial MUs active in the muscle. A combination of both multichannel surface and intramuscular techniques could provide a better understanding of how MUs are distributed across different regions of the muscle (surface vs. depth), and consequently may allow more in-depth and complete decoding of the neural drive to muscle during a voluntary contraction and of its potential adaptations following a training intervention (66).

Conclusions

We tested the hypothesis that exposure to chronic strength training induces pronounced adaptations in the neural drive to the muscle, which, in turn, may contribute, along with morphological changes to the enhanced muscular strength. Despite the marked differences in strength ($+65\%$) and strength training experience ($\sim$6 yr), we observed that recruitment strategies and discharge characteristics of MUs identified from the BB of ST athletes were similar to those observed in a UT control cohort during equivalent submaximal force-modulating tasks. These findings suggest that there is no modulation of the neural activity during contractions up to 70% of the maximum in males with a long history of strength training. Thus, in disagreement with our hypothesis, the greater absolute force-generating capacity of chronically ST athletes for the same level of neural excitation, i.e., net neural drive, indicates that morphological factors, such as the larger muscle size, i.e., $ACSA_{MAX}$ of ST athletes ($+72\%$), plays a dominant role compared with neural factors in explaining their enhanced volitional force production during submaximal effort.

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

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

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