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ORIGINAL ARTICLE

Neural adaptations underlying cross-education after unilateral strength training

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Abstract The purpose of this study was to investigate the effects of 4-week (16 sessions) unilateral, maximal isometric strength training on contralateral neural adaptations. Subjects were randomised to a strength training group (TG, $n = 15$) or to a control group (CG, $n = 11$). Both legs of both groups were tested for plantar flexion maximum voluntary isometric contractions (MVCs), surface electromyogram (EMG), H-reflexes and V-waves in the soleus (SOL) and gastrocnemius medialis (GM) superimposed during MVC and normalised by the M-wave (EMG/M_{SUP}, H_{SUP}/M_{SUP}, V/M_{SUP}, respectively), before and after the training period. For the untrained leg, the TG increased compared to the CG for MVC torque (33%, $P < 0.01$), SOL EMG/M_{SUP} (32%, $P < 0.05$) and SOL V/M_{SUP} (24%, $P < 0.05$). For the trained leg, the TG increased compared to the CG for MVC torque (40%, $P < 0.01$), EMG/M_{SUP} (SOL: 38%, $P < 0.05$; GM: 60%, $P < 0.05$) and SOL V/M_{SUP} (72%, $P < 0.01$). H_{SUP}/M_{SUP} remained unchanged for both limbs. No changes occurred in the CG. These results reinforce the concept that enhanced neural drive to the contralateral agonist muscles contributes to cross-education of strength.

Keywords H-reflex · V-wave · Cross-education · Unilateral · Neural adaptation · Strength training

Introduction

It is extensively documented that unilateral strength training enhances strength performance in the contralateral untrained limb (Adamson et al. 2008; Lee and Carroll 2007; Munn et al. 2004, 2005). A meta-analysis (Munn et al. 2004) which was recently updated (Carroll et al. 2006) estimated that the magnitude of this phenomenon termed "cross-education", "cross-transfer" or "contralateral strength training effect" was ~8%, which corresponded well with a large randomised-controlled trial (Munn et al. 2005).

Strength training adaptations are broadly divided into morphological and neural contributions (Behm and Sale 1993; Folland and Williams 2007). Neural mechanisms are likely responsible for contralateral strength gains after unilateral strength training as cross-education occurs with negligible muscle activation in the contralateral untrained limb (Evetovich et al. 2001; Hortobagyi et al. 1997) and is unaccompanied by muscle hypertrophy (Farthing and Chilibeck 2003; Farthing et al. 2005). A study by Shima et al. (2002) provided more direct evidence of an increase in efferent neural drive (i.e. increased motor output from spinal motoneurons) to the untrained contralateral muscles as these authors reported enhanced surface electromyogram (EMG) activity and increased voluntary activation assessed by a

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interpolated twitch technique (Allen et al. 1995), in the untrained limb.

Subsequent studies have attempted to more specifically investigate the sites within the central nervous system that could be responsible for the cross-education effect. The Hoffmann (H)-reflex is a measure of reflex transmission between Ia afferents and homonymous α-motoneurons. H-reflex responsiveness is dependent on a range of factors including spinal motoneuron excitability, presynaptic inhibition, disynaptic inhibition and axonal excitability of efferent and afferent axons (Enoka and Gandevia 2006; Pierrot-Deseilligny and Burke 2005). Lagerquist et al. (2006) examined the effects of 5-week unilateral, isometric strength training of the plantar flexors on the H-reflex amplitudes of both the trained and untrained soleus (SOL) muscle. These investigators reported increased H-reflex excitability of the trained but not the untrained SOL muscle, obtained during a tonic, low-level contraction (10% background EMG). Therefore, it was suggested that supraspinal mechanisms were primarily responsible for the cross-education of strength. However, these authors did not assess whether any supraspinal adaptations occurred, or any measure of neural drive was included.

A cortical contribution to cross-education of strength was recently demonstrated in a study by Lee et al. (2009). Twitch interpolation with transcranial magnetic stimulation to assess changes in the neural drive to the contralateral limb from the motor cortex was employed before and after 4 weeks of unilateral strength training for the left wrist extensors. These authors did not assess changes in the neural drive of the trained limb. It is thus unclear whether similar neural mechanisms are the underlying effects for the trained limb. Adaptations at the level of the spinal cord were not evaluated by Lee et al. (2009).

The V-wave has been increasingly used in studies investigating neural adaptations in response to strength training (Aagaard et al. 2002; Del Balso and Cafarelli 2007; Duclay et al. 2008; Fimland et al. 2009; Gondin et al. 2006). The V-wave is an electrophysiological variant of the H-reflex that is evoked by supramaximal nerve stimulation during maximal voluntary contraction. The peak-to-peak amplitude of the V-wave is considered to reflect motoneuron rate coding and reflex excitability (Aagaard et al. 2002; Upton et al. 1971). It has been suggested that combined H-reflex and V-wave measurements can improve our understanding of adaptations within the central nervous system (Aagaard et al. 2002; Gondin et al. 2006). A recent review recommended the inclusion of V-wave measurements to elucidate the mechanisms of cross-education (Hortobagyi 2005).

The approach used in the present study was to examine effects of unilateral, isometric plantar flexion strength training on voluntary strength and neural adaptations of the ipsilateral and contralateral limb using combined H-reflex, V-wave and conventional EMG measurements. It was hypothesised that contralateral strength increases would be accompanied by increased efferent neural drive.

Methods

Subjects

26 healthy, recreationally active subjects were randomly assigned to a unilateral strength training group (TG; $n = 15$, 4 males, 11 females; age 24 ± 2; height 175 ± 6; body mass 70 ± 10; means ± standard deviation, SD) or to a control group (CG; $n = 11$, 5 males, 6 females; age 24 ± 1; height 24 ± 1; body mass 70 ± 9) using a 3:2 ratio. All subjects provided informed written consent prior to the measurements. The investigation was approved by the regional ethics committee and conformed to the standards set by the latest revision of the Declaration of Helsinki.

Muscle strength and EMG activity

The measurement of plantar flexion maximum voluntary isometric contraction (MVC) force from both limbs was recorded by a force transducer (Model 363-D3-50-20P1, Revere Transducers, Tustin, CA, USA) that responds linearly within a load range of 0–250 kg with a reproducibility error of 0.1% attached to the custom-made dynamometer. The force signal was recorded at 1 kHz and digitally low-pass filtered (10 Hz). The distance between the heel block and the centre of the force transducer (0.15 m) was employed to calculate torque.

EMG activity was recorded from the SOL, gastrocnemius medialis (GM) and tibialis anterior muscles using pairs of self-adhesive electrodes with an interelectrode distance of 25 mm (Ambu M-00-S, Ballerup, Denmark). For the SOL muscle, electrodes were placed along the mid-dorsal line of the leg ~5 cm distal to the gastrocnemius. For the GM and tibialis anterior muscles, electrodes were placed according to the recommendations by SENIAM (Hermens et al. 2000). Electrodes were placed in the presumed underlying direction of the muscle fibres. The shape of M-waves and H-reflexes of the SOL and GM obtained at rest and during submaximal contractions was carefully observed before testing; if it was suspected that the electrodes were overlying the innervation zone, they were placed more distally on the muscle. EMG was sampled (ME6000 Biomonitor, Mega Electronics LTD, Kuopio, Finland) at 2 kHz, common mode rejection ratio: 110 dB, amplified and band-pass filtered (8–500 Hz).

Stimulation

H-reflexes, V-waves and M-waves were evoked in the posterior tibial nerve by a constant-current stimulator (DS7AH, Digitimer, Welvyn Garden City, UK). Square wave stimuli (1 ms) were delivered with gel-coated bipolar felt pad electrodes (8 mm diameter, 25 mm between tips; Digitimer). The cathode was medial to the anode to avoid anodal block (Pierrot-Deseilligny and Burke 2005). After careful search for the optimal site of placement as determined by clear SOL H-reflexes and M-waves with a minimal EMG response for the tibialis anterior muscle, rigid taping and straps secured a constant pressure and location during the experimental session. Gradually increasing current (2 mA increments) was delivered until the maximal M-wave (M_{MAX}) was reached for the SOL muscle. During MVCs, superimposed V-waves and M-waves (M_{SUP}) were evoked by employing 200% of the current needed to evoke SOL M_{MAX}. SOL H-reflexes were superimposed on MVCs (H_{SUP}) with a stimulation intensity that produced concomitant SOL M-waves 12.5–17.5% of SOL M_{SUP}. V-waves and H_{SUP}s were manually elicited ~3 s after the onset of contraction.

Experimental procedures

Subjects came to the laboratory at a consistent time of day at the pre- and post-test. The skin was prepared, EMG electrodes were positioned on the muscles and interelectrode resistance was checked (<5 kΩ). The subjects were placed in a slightly reclined chair mounted on a solid wooden platform with one foot (random order) placed in a custom-made ankle dynamometer. Rigid straps secured the heel and forefoot to the foot-plate with the ankle at 90°. The thigh, hip and back were secured with broad velcro straps, and helped maintain the subject in the same position (knee flexed at 80° from full extension, hip at 90°) throughout the session. The opposite limb was resting on a chair. One of the test leaders ensured that the subject did not perform unwanted muscle activity. After positioning the subject, the stimulating electrode was placed in the popliteal fossa. Next, the testing procedure was performed and consisted of

1. Increasing electrical stimulation (2 mA increments) until SOL M_{MAX} was reached.
2. 7 plantar flexion MVCs with V-waves were performed with 1 min intervals between repetitions.
3. 8–12 MVCs with SOL H-reflexes were performed with 1 min intervals between repetitions, so that at least 3 recordings met the inclusion criteria of a concomitant M-wave 12.5–17.5% of SOL M_{SUP}.
4. The procedure was repeated for the opposite leg.

To optimise performance during every MVC attempt, the criteria proposed by Gandevia (2001) related to practice, instruction, visual feedback and standardised verbal encouragement were followed.

In a separate session preceding the pre-test, subjects were thoroughly familiarised with the testing procedures including percutaneous electrical pulses delivered to the posterior tibial nerve and practiced MVCs of both limbs.

Training intervention

Training group subjects performed 16 sessions (4 weeks) of unilateral plantar flexion MVC training of the dominant limb on the same apparatus as used for the testing sessions. Each training session started with some warm-up repetitions (40–70% of MVC) followed by six series of six MVCs. Each repetition lasted 4 s and was separated by a rest interval of 10 s. Two-minute rest was given between series. During every repetition, subjects could visually observe the contraction force on a computer screen and were vigorously encouraged by the test leader.

Data analysis

Maximum voluntary isometric contraction torque was calculated as the average of the two best attempts (highest peak force) of the seven MVCs used also to record V-waves. The raw EMG values of the same two MVCs were converted to the root mean square (RMS) of the 500 ms epoch coinciding with peak force before the superimposed stimulus, subsequently normalised by M_{SUP}, and averaged.

Peak-to-peak amplitudes of H-reflexes, M-waves and V-waves were calculated. Only V-waves with a concomitant $M_{SUP} > 90\%$ of the highest M_{SUP} was included (to ensure stable stimuli conditions) and normalised by the concomitant M_{SUP}, and averaged. The H_{SUP}s with a concomitant M-wave 12.5–17.5% were normalised by the average M_{SUP} from the V-wave measurements, and averaged.

Statistics

To assess between-group differences, the Mann–Whitney *U* test was used to compare the change scores of the non-dominant limbs from CG subjects with the change scores of untrained (non-dominant) limbs from TG subjects. Similarly, the change scores of the dominant limbs from CG subjects were compared with the trained (dominant) limb of TG subjects. Pre- to post-test differences within each group were analysed using the Wilcoxon-signed rank test. Significance was set at $P \leq 0.05$ (two-tailed).

Results

No differences were observed between the TG and CG at pre-test (Table 1). The subjects completed all strength training sessions within 4–5 weeks. No significant changes occurred for the set of dependent variables from pre- to post-test in the CG (Table 1). Mean percentage changes from

Table 1 Torque and surface electromyogram recordings

	Strength training group				Control group			
	Trained leg (dominant)		Untrained leg (non-dominant)		Dominant leg		Non-dominant leg	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
MVC (N m)	132 ± 27	183 ± 30**	128 ± 34	163 ± 39**	147 ± 38	146 ± 50	142 ± 29	133 ± 40
Soleus								
EMG (μV)	289 ± 115	354 ± 146*	222 ± 83	274 ± 89*	311 ± 132	328 ± 128	294 ± 129	308 ± 102
M_{SUP} (μV)	9,839 ± 2,215	9,226 ± 2,244	8,728 ± 2,222	8,082 ± 2,688	9,321 ± 2,154	9,476 ± 1,141	9,249 ± 2,013	9,367 ± 2,035
H_{SUP} (μV)	5,565 ± 2,272	5,743 ± 2,488	5,039 ± 2,678	4,927 ± 2,565	6,213 ± 2,506	5,827 ± 1,944	4,644 ± 1,872	5,075 ± 1,594
V-wave (μV)	2,265 ± 1,542	3,484 ± 1,779**	2,122 ± 1,688	2,370 ± 1,745	3,187 ± 1,607	3,029 ± 1,647	2,784 ± 1,214	2,700 ± 1,135
EMG/M_{SUP}	0.029 ± 0.009	0.040 ± 0.016*	0.026 ± 0.009	0.035 ± 0.008**	0.034 ± 0.031	0.034 ± 0.035	0.032 ± 0.011	0.033 ± 0.008
V/M_{SUP}	0.223 ± 0.132	0.379 ± 0.146**	0.239 ± 0.150	0.279 ± 0.150	0.337 ± 0.134	0.330 ± 0.165	0.304 ± 0.112	0.283 ± 0.106
H_{SUP}/M_{SUP}	0.571 ± 0.182	0.612 ± 0.172	0.567 ± 0.181	0.584 ± 0.145	0.676 ± 0.214	0.602 ± 0.165	0.520 ± 0.220	0.567 ± 0.187
MatH_{SUP}/M_{SUP}	0.15 ± 0.01	0.15 ± 0.01	0.16 ± 0.01	0.15 ± 0.02	0.15 ± 0.01	0.15 ± 0.01	0.15 ± 0.01	0.15 ± 0.01
Gastrocnemius medialis								
EMG (μV)	174 ± 75	239 ± 64**	183 ± 80	202 ± 69	191 ± 84	210 ± 112	179 ± 66	196 ± 79
M_{SUP} (μV)	7,231 ± 2,460	6,633 ± 1,831	8,130 ± 2,774	8,237 ± 2,190	7,351 ± 2,623	7,469 ± 1,882	7,373 ± 2,540	8,116 ± 2,097
V-wave (μV)	1,298 ± 888	1,689 ± 822	1,353 ± 621	1,552 ± 949	1492 ± 781	1,686 ± 708	1,253 ± 529	1,389 ± 390
EMG/M_{SUP}	0.025 ± 0.008	0.041 ± 0.021**	0.025 ± 0.012	0.025 ± 0.008	0.027 ± 0.008	0.028 ± 0.012	0.027 ± 0.013	0.024 ± 0.007
V/M_{SUP}	0.187 ± 0.085	0.307 ± 0.233*	0.181 ± 0.073	0.187 ± 0.088	0.198 ± 0.081	0.221 ± 0.067	0.194 ± 0.095	0.182 ± 0.052
Tibialis anterior								
Co-activation (μV)	76 ± 46	99 ± 47	70 ± 44	75 ± 32	68 ± 22	70 ± 30	86 ± 43	70 ± 36

Data are means ± SD

MVC maximum voluntary isometric contraction, *EMG* electromyogram root mean square activity, M_{SUP} maximal M-wave superimposed on MVC, H_{SUP} H-reflex superimposed on MVC, *V* V-wave

* $P < 0.05$, ** $P < 0.01$ from pre-test

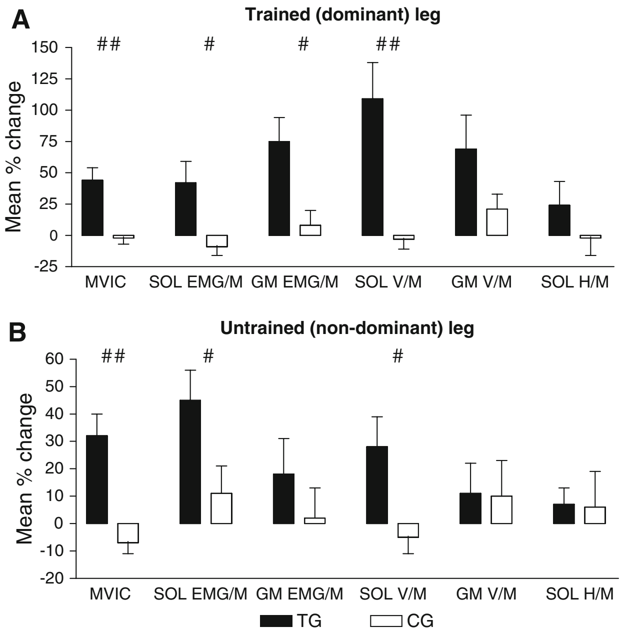

Fig. 1 Mean percentage changes of the trained (dominant) leg (**a**) and untrained (non-dominant) leg (**b**) from pre- to post-test in the training group (TG) and the control group (CG). $^{\#}P < 0.05$, $^{\#\#}P < 0.01$, different from Δ control leg value. *MVC* maximum voluntary isometric contraction, *SOL* soleus, *GM* gastrocnemius medialis, *EMG* electromyogram root mean square activity, *V* V-wave, *M* M_{SUP} (superimposed M-wave), *H* H_{SUP} (superimposed H-reflex). Note different scaling of the *y*-axes. Mean values ± SE

pre- to post-test and between-group differences are shown for the dominant (trained) and non-dominant (untrained) limbs in Fig. 1a and b, respectively. Absolute strength, EMG data and calculated ratios are presented in Table 1.

MVC torque

For the trained and untrained leg in the TG, MVC torque increased by 44 ± 37% and 32 ± 30%, respectively ($P < 0.01$; Table 1). These improvements were also significantly different from the changes of the analogous limbs in the CG (40 and 33%, respectively, $P < 0.01$; Fig. 1a, b).

EMG activity

In the TG, SOL EMG/M_{SUP} increased by 42 ± 17% ($P < 0.05$) in the trained limb and by 45 ± 43% ($P < 0.01$) in the contralateral untrained limb (Table 1). These changes were also significantly different compared to the CG (38 and 33%, respectively, $P < 0.05$; Fig. 1a, b). The GM EMG/M_{SUP} increased by 62 ± 16% from pre- to post-test for the trained leg ($P < 0.01$) but not in the untrained leg for the TG (Table 1). Moreover, there was a between-group difference in the changes of the trained (dominant) limb (60%, $P < 0.05$; Fig. 1a). No changes could be observed for absolute (μV) tibialis anterior co-activation during MVC (Table 1).

H-reflex and V-wave responses

On average, 3.2 ± 0.5 SOL H_{SUP} recordings met the inclusion criterion of a concomitant M-wave 12.5–17.5% of SOL M_{SUP}. The amplitudes of the small M-waves accompanying H_{SUP} stimulation relative to M_{SUP} are presented in Table 1. For the stimulation of V-waves, on average, 5.4 ± 1.4 and 4.6 ± 1.4 recordings for the SOL and GM muscles, respectively, met the inclusion criterion of a concomitant $M_{SUP} > 90\%$ of the highest M_{SUP} evoked in the V-wave protocol.

There were no within- or between-group changes for either leg in the H_{SUP}/M_{SUP} ratio for either SOL or GM (Table 1; Fig. 1a, b). On the other hand, unilateral training increased the SOL V/M_{SUP} ratio of the trained limb by 109 ± 28% ($P < 0.01$; Table 1), and this was also significantly different from the change in the CG ($P < 0.01$; Fig. 1a). The 29 ± 11% increase of the SOL V/M_{SUP} ratio of the untrained limb in the TG was not significantly different from pre- to post-training ($P = 0.105$), but changed significantly compared to the CG (24%, $P < 0.05$; Fig. 1b). In the TG, the GM V/M_{SUP} ratio was increased by 69 ± 27% ($P < 0.05$; Table 1) in the trained leg, although this was not significant compared to CG changes (Fig. 1a). No changes could be observed in the GM V/M_{SUP} ratios for the non-dominant (untrained) leg within or between groups (Table 1; Fig. 1b). Examples of SOL V-wave, H_{SUP} and M-wave recordings are demonstrated in Fig. 2 for one subject.

Discussion

The present study investigated the contralateral neural adaptations after unilateral strength training. The main finding was that efferent neural drive as suggested by increased SOL EMG/M_{SUP} and V/M_{SUP} accompanied contralateral strength gains, whereas no change was observed for the H_{SUP}/M_{SUP} ratio. These changes were comparable with the adaptations of the trained limb, with the exception that the GM EMG/M_{SUP} and V/M_{SUP} ratios also increased for the trained limb. A novel finding in the present study was increased SOL V/M_{SUP} in the untrained limb of the TG compared to the CG. The implications of these findings are discussed below.

Effects of unilateral strength training on MVC torque

The present unilateral strength training regime resulted in an increase in both the trained (44%) and contralateral untrained (32%) plantar flexors. This is a considerably greater cross-education effect than the ~8% effect

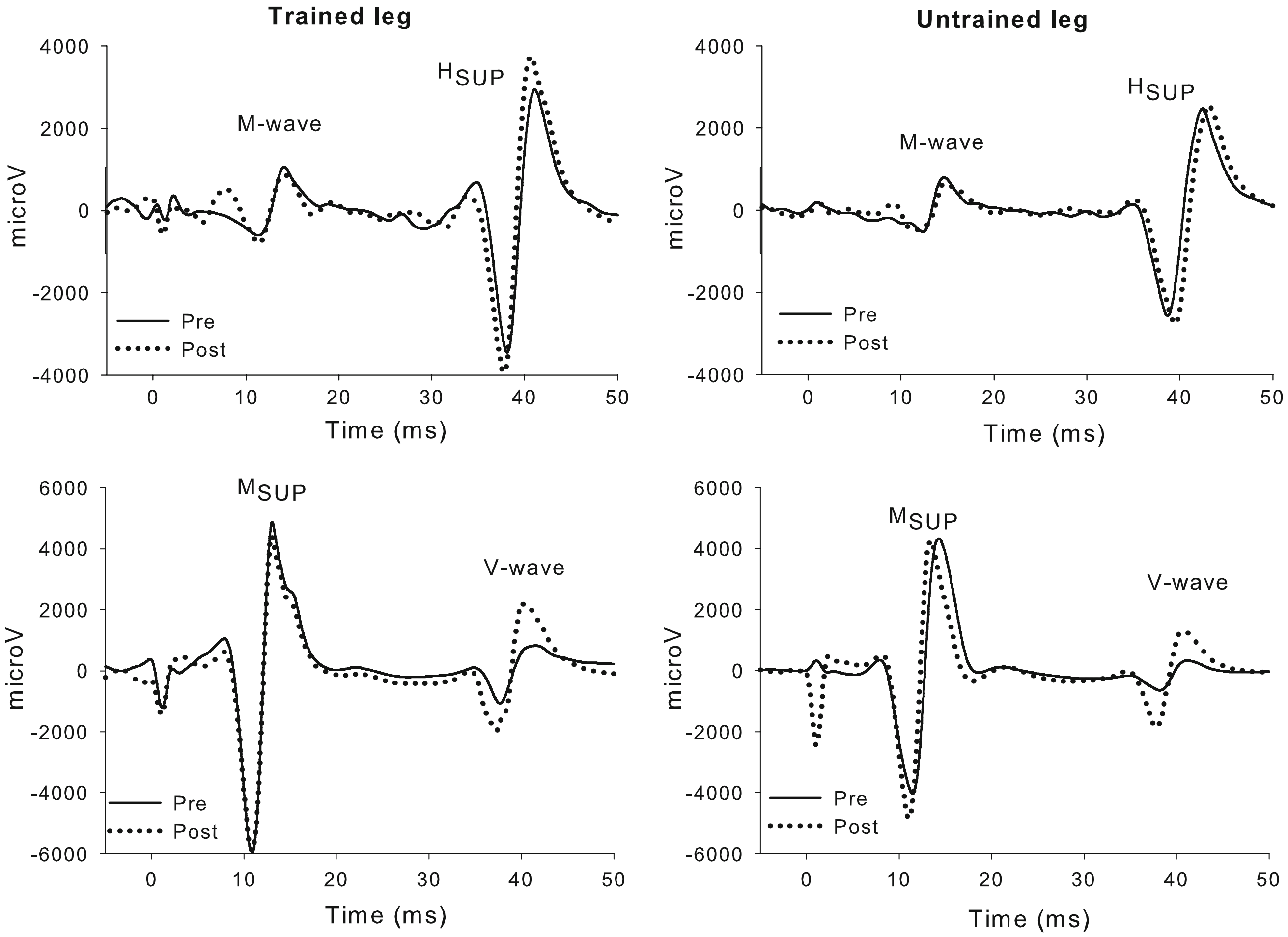

Fig. 2 Soleus V-wave, superimposed H-reflex (H_{SUP}), and M-wave (M_{SUP}) recordings (means of at least three trials) of the trained and untrained leg before and after 4 weeks of unilateral strength training from one subject of the training group

reported in recent meta-analyses (Carroll et al. 2006; Munn et al. 2004). In the meta-analyses, an inclusion criterion for eligibility was that resistance employed in training was >50% of maximum voluntary strength. Several studies that employed unilateral training with higher intensity (>85% of maximum voluntary strength) have demonstrated cross-education effects in the order of 18–77% (Adamson et al. 2008; Farthing et al. 2007; Hortobagyi et al. 1997; Komi et al. 1978; Lagerquist et al. 2006). The results from these studies and the present study indicate that employing high contraction intensity during training induces greater cross-education of strength than moderate intensity training.

In the current study, the magnitude of the change in the untrained contralateral leg was ~69% of the trained leg. This exceeds the 52% magnitude of the trained limb reported in a recently updated meta-analysis (Carroll et al. 2006) but is considerably less than the 105 and ~95% magnitude of the trained limbs recently reported by Farthing et al. (2007) and Adamson et al. (2008), respectively.

Effects of unilateral strength training on EMG activity

Ipsilateral strength training resulted in increased SOL EMG/M_{SUP} of the untrained limb in the TG. Increased contralateral EMG activity is in line with the results by Moritani and deVries (1979), Farthing et al. (2007) and Shima et al. (2002), but in contrast to the findings by Cannon and Cafarelli (1987). For example, Shima and co-workers reported increased integrated EMG activity of the contralateral untrained plantar flexors after 6 weeks of dynamic unilateral strength training.

In the current study, no change was observed for the GM EMG/M_{SUP} of the untrained limb in the TG. During plantar flexion training and testing, subjects maintained 80° of knee flexion (0° = full extension). Unchanged EMG activity for this muscle may be explained by the fact that the plantar flexion force contribution from this muscle is considerably reduced when the knee is flexed (Cresswell et al. 1995). However, this is not consistent with the fact that GM EMG/M_{SUP} increased for the trained limb. It is possible that the differences between GM EMG/M_{SUP} of the trained and untrained muscles may be a result of the larger improvements in strength of the trained compared to the untrained limb (44 vs. 32%).

Also in the trained limb, SOL EMG/M_{SUP} was significantly increased. This is in line with other investigations employing plantar flexion training and testing at similar knee angles (Duclay et al. 2008; Gondin et al. 2006).

The EMG signal is a complex outcome of motor unit recruitment and rate coding (Aagaard 2003), affected by several physiological and non-physiological factors (for review, see Farina et al. 2004). Some of these factors can be partly controlled by normalising to the maximal compound muscle action potential (i.e. M_{MAX} or M_{SUP}) (Gandevia 2001). Nevertheless, as the contralateral limb did not undertake any training, it is conceivable that the changes in EMG/M_{SUP} reflect augmented neural drive to the muscle, due to either or both of these mechanisms.

No effects of unilateral strength training on H-reflex responses

For the first time, H-reflex responses were obtained during maximum contractions to assess H-reflex excitability of the contralateral limb after unilateral strength training. However, the present study did not observe any changes in the H_{SUP}/M_{SUP} ratio of the trained or untrained limb. Only one study has investigated the H-reflex pathway in both the trained and untrained legs after unilateral strength training (Lagerquist et al. 2006). This study reported a significant increase in H-reflex amplitude for the trained but not untrained SOL muscle at a stimulation intensity corresponding to 5% of M_{MAX} (i.e. on the ascending part of the H-reflex recruitment curve). Conversely, the maximal H-reflex normalised by M_{MAX} was not affected by training in that study. Lagerquist and colleagues obtained H-reflex measurements during a low-level, tonic submaximal contraction (10% of maximal EMG activity). These authors inferred from their results that the increase in strength of the trained limb was at least partly due to spinal mechanisms, whereas the cross-education effect was mediated by supraspinal mechanisms (Lagerquist et al. 2006). However, the lack of a positive H-reflex finding for the untrained limb does not mean that spinal adaptations did not occur. Nevertheless, although theoretically plausible (Carroll et al. 2006; Lee and Carroll 2007), there is presently no solid evidence that spinal mechanisms are underlying the cross-education effect.

The present unchanged H_{SUP}/M_{SUP} ratios indicate that spinal α-motoneuron excitability and presynaptic inhibition remained unchanged after unilateral MVC training, under the testing conditions of the current study. In the present study, H-reflexes were superimposed on MVCs at a stimulation intensity that produced M-waves at 12.5–17.5% of M_{SUP}. In contrast to the present findings, Aagaard et al. (2002) reported a ~20% increase in the SOL H-reflex evoked during MVC at a stimulation intensity corresponding to 17.5–22.5% of M_{SUP}. Although there was a small difference in the proportion of motor axons recruited by stimulation, this seems unlikely to explain the different findings. The discrepant results may be explained by the quite different training interventions employed, i.e. 16 sessions (4 weeks) of unilateral MVC training in the current study versus 38 sessions (14 weeks) of a high-volume, dynamic, multi-exercise, lower-limb, training program employing 4–12 repetitions. The present training intervention probably induced minimal hypertrophy of the plantar flexors, whereas 14 weeks of training likely induced substantial hypertrophy that the central nervous system would have to adapt to. The H-reflex volley relies preferentially on small motoneurons (Pierrot-Deseilligny and Burke 2005; Schieppati 1987). 14 weeks of 4–12 repetition, multi-exercise of the entire lower limb may have affected the recruitment and/or rate coding of the motoneurons activated by the H-reflex to a larger extent than the 4 weeks of MVC training performed in the present study. Unchanged H-reflex excitability of the trained and untrained limbs obtained during MVC in the current study suggests that this pathway was not affected by the present training intervention. However, adaptations of other spinal pathways cannot be excluded, and different testing conditions may have provided different results (i.e. different levels of muscle contraction and/or stimulation intensities).

Effects of unilateral strength training on V-wave responses

A novel finding of this study was that SOL V/M_{SUP} increased in the untrained limb in the TG compared to the control limb in the CG. The amplitude of the V-wave is dependent on the reflex excitability and the collision between evoked antidromic potentials and the efferent motor drive. That is, if the descending motor drive from supraspinal levels increases to the contralateral limb after unilateral training, the volley of evoked antidromic action potentials would be increasingly cancelled due to collision with more efferent impulses in the α-motoneuron axons. This would permit more of the “V-reflex” to pass to the muscle, which would result in a higher peak-to-peak amplitude of the V-wave (Aagaard et al. 2002). In addition, increased spinal motoneuron excitability, reduced presynaptic and postsynaptic inhibition (i.e. reflex excitability) could also have contributed to the increased V-wave amplitude (Aagaard 2003). The increase in efferent neural drive from spinal motoneurons is probably caused by increased descending drive, motoneuron excitability and/or changes in presynaptic inhibition mediating augmented motoneuron recruitment and/or rate coding (Aagaard et al. 2002).

No change was observed for the GM V/M_{SUP} in the untrained leg of the TG, under the testing conditions of the current study. As suggested above, the smaller improvement of the untrained compared to the trained limb in the TG or the smaller contribution of the gastrocnemius to plantar flexion torque at a flexed knee angle may explain this result (Cresswell et al. 1995).

Conclusions

EMG and V-wave, but not H-reflex, responses increased in both the trained and untrained plantar flexor muscles after 4 weeks of unilateral strength training. By reporting increased EMG activity and, for the first time, augmented V-wave responses of the contralateral untrained limb, this study has reinforced the concept that enhanced neural drive to the agonist muscles contributes to cross-education of strength.

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