Improvements in dynamic plantar flexor strength after resistance training are associated with increased voluntary activation and V-to-M ratio

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Nordlund Ekblom MM. Improvements in dynamic plantar flexor strength after resistance training are associated with increased voluntary activation and V-to-M ratio. J Appl Physiol 109: 19–26, 2010. First published May 6, 2010; doi:10.1152/japplphysiol.01307.2009.—The aim of this study was to investigate if, and via what mechanisms, resistance training of the plantar flexor muscles affects voluntary activation during maximal voluntary eccentric and concentric muscle actions. Twenty healthy subjects were randomized into a resistance training group (n = 9) or a passive control group (n = 11). Training consisted of 15 sessions of unilateral mainly eccentric plantar flexor exercise over a 5-wk period. During pre- and posttraining testing, dynamic plantar flexor strength was measured and voluntary activation was calculated using the twitch interpolation technique. The soleus Hoffman reflex (H-reflex) was used to assess motoneurone excitability and presynaptic inhibition of Ia afferents, whereas the soleus V-wave was used to test for changes in both presynaptic inhibition of Ia afferents and supraspinal inputs to the motoneurone pool. H-reflexes, V-waves, supramaximal M-waves, and twitches were evoked as the foot was moved at 5°/s through an angle of 90° during passive ankle rotations (passive H-reflexes and M-waves) and during maximal voluntary concentric and eccentric plantar flexions [maximal voluntary contraction (MVC) H-reflexes, M-waves, and V-waves]. Training induced significant improvements in plantar flexor strength and voluntary activation during both concentric and eccentric maximal voluntary actions. Soleus passive and MVC H-to-M ratios remained unchanged after training, whereas the soleus V-to-M ratio was increased during both concentric and eccentric contractions after training. No changes were found in the control group for any of the parameters. The enhanced voluntary strength could be attributed partly to an increase in voluntary activation induced by eccentric training. Since the passive and MVC H-to-M ratios remained unchanged, the increase in activation is probably not due to decreased presynaptic inhibition. The increased V-to-M ratio for both action types indicates that increased voluntary drive from supraspinal centers and/or modulation in afferents other than Ia afferents may have contributed to such an increase in voluntary activation. 

The ability of an individual to voluntarily activate a muscle group to its full force-generating capacity is often limited in certain muscle groups, such as the plantar flexors and quadriceps (8, 38, 45). This implies that when attempting to maximally activate these muscle groups the central nervous system does not control muscle activation in the most optimal manner. Physical and/or behavioral adaptations in the nervous system are believed to contribute to increased muscle strength, especially in the initial phase of strength training in novice subjects (19). While several attempts have been made to clarify the mechanisms of these neural adaptations, differences in both methodological paradigms and the tasks tested have hampered the interpretation of the findings of previous studies. Measuring changes in voluntary activation together with changes in the Hoffman reflex (H-reflex) and V-wave may be one way of gaining better understanding of the link between training-induced changes in the nervous system and improvements in voluntary activation. A commonly used method to assess voluntary activation in a maximal muscle action is the twitch interpolation technique (43). The soleus H-reflex, induced by submaximal stimulation of the tibial nerve, and the soleus V-wave, induced by supramaximal stimulation of the tibial nerve, are two spinal reflexes that involve partly but not entirely the same neural circuitry (44). The size of the H-reflex reflects the level of intrinsic motoneurone excitability, magnitude of presynaptic inhibition, and magnitude of postsynaptic inhibition of spinal motor units (46). The V-wave, while being affected by the same factors, is also sensitive to the ongoing neural output from the motoneurones, which can be said to indicate the net excitation of the motoneurone pool (1, 37, 44).

A few studies (1, 7, 17, 18, 29, 40) have investigated the effects of strength training on H-reflex modulations in the isometric plantar flexion. Most of these studies (1, 7, 28, 39) have studied reflex regulation in a passive or submaximally activated muscle, despite the fact that this may not be applicable to maximum voluntary actions. To further increase the understanding of what mechanisms contribute to increased voluntary activation, the effects of training on combined measures of H-reflexes and V-waves during maximal voluntary muscle actions have been presented (1, 11, 17, 18, 21). After dynamic resistance training, such as typically used in fitness centers, Aagaard et al. (1) observed increases in both V-waves and H-reflexes in high-intensity isometric plantar flexions but unaltered H-reflexes when the muscle was passive. This was also supported by two later studies (17, 18). The mechanisms of neural activation are believed to differ between action types (14). Therefore, the effects from strength training may be different for concentric and eccentric actions as opposed to isometric actions. Duclay et al. (11) reported that pure eccentric training induced increased H-reflexes and V-waves also during dynamic, mainly eccentric, maximum voluntary contraction (MVCs), suggesting that decreased presynaptic inhibition may have occurred as a result of training. While the above studies agree that dynamic training of the plantar flexors induced plastic changes in H-reflexes and V-waves, in isometric and dynamic MVCs, none of them reported whether these adaptations were associated with increased voluntary activation as assessed by twitch interpolation analysis. Increases in spinal reflexes have been shown to sometimes occur without

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associated improvements in voluntary activation, as measured via twitch interpolation (39). Assuming that changes in spinal reflexes are associated with changes in voluntary activation without assessing the latter may therefore lead to erroneous conclusions. Also, the only study investigating how resistance training affects dynamic MVC (11) investigated pure eccentric training, a training form not typically used in fitness and strength conditioning settings. The aims of this study were therefore to investigate whether resistance training induces parallel changes in strength, voluntary activation (as measured with a twitch interpolation technique), H-reflexes, and V-waves in maximal voluntary concentric and eccentric plantar flexor actions and, if so, whether there are associations between the changes in maximal muscle strength, voluntary activation, and evoked spinal motoneurone responses.

METHODS

Subjects. Twenty healthy subjects (12 men and 8 women) participated in this study. None of the participants exercised >3 times/wk or pursued resistance training on a regular basis. Subjects were first matched in pairs based on age, sex, and level of activity. Subsequently, from each pair, one subject was randomly allocated to the training group and one subject to the control group. Mean ± SD values for height, weight, and age were 1.80 ± 0.09 m, 73.8 ± 14.8 kg, and 27 ± 4.8 yr for the training group (n = 9) and 1.77 ± 0.10 m, 70.6 ± 10 kg, and 27 ± 6 yr for the control group (n = 11). All subjects provided written informed consent before inclusion in the study. This study was approved by the local ethics committee and adhered to the Declaration of Helsinki. After the initial measurement session, all subjects were instructed not to change their activity level and participants in the training group initiated the mainly eccentric strength training program. The first measurement session was performed between 2 and 5 days before the training period, and the second measurement session was performed between 5 and 7 days after the end of the 5-wk training period.

Training. Dynamic plantar flexor exercise was performed with the subject standing upright in a Smith machine with both feet placed on a 15-cm-high step. The bar carrying the weights was applied on the subject’s shoulders, and the design of the Smith machine ensures that it only translates vertically. Subjects performed bilateral calf raises (concentric plantar flexion) and unilateral (right leg) lowering (eccentric plantar flexion) exercises. The plantar flexors therefore trained at higher loads in the eccentric phase compared with the concentric phase. A metronome was used to guide the subjects to keep the same pace (1 s raising up on toes and 3 s lowering down on heels, resulting in angular velocities of 10–30°/s) through all exercise sessions. Each subject trained 3 times/wk for 5 wk, resulting in a total of 15 training sessions, which were surveyed and supervised by the same experimenter. Each session consisted of a 10-min warm-up on a stationary bike and the plantar flexor training, which progressed from five to six sets of five repetitions. At least once per week, the weight load was adjusted to be just above the maximum load achievable in a unilateral concentric calf raise in the Smith machine. The subject was then asked to perform five repetitions. If the subject was able to continue after five repetitions, the load applied in the subsequent set was increased until the load could be performed more than five times. Sets were separated by 2 min of rest, and a training session required ~15 min to complete. The mean ± SD increase in load applied over the training period was 81 ± 33% (61 ± 18 kg).

Experimental setup and procedures. For all measurements, subjects lay prone with their knees straight and their right foot firmly attached to a metal plate mounted to an isokinetic dynamometer (IsoMed 2000, D. & R. Ferstl, Hemau, Germany). Foot placement was adjusted so that the ankle joint was aligned with the axis of the torque motor. Shoulder pads and a broad velcro strap over the right thigh of the subject were applied to prevent extraneous movements. In the dynamic trials, the isokinetic dynamometer moved the ankle at an angular velocity of 5°/s through a range of movement of 75–105° starting at an ankle angle of 75° in shortening (concentric) trials and 105° in lengthening (eccentric) trials. The order of all measures within each measurement session is shown in Fig. 1. The total duration of each measurement session was ~2 h.

Initially, electric stimulation was applied to the tibial nerve to induce a passive isometric M-wave and H-reflex recruitment curve in the soleus electromyographic (EMG) signal. The intensity needed to achieve an H-reflex with a direct M-wave constituting 20% of the supramaximal M-wave was noted, and a supramaximal stimulation was defined as 150% of the intensity causing a leveling off in the M-wave recruitment curve. Adjustments to the stimulus intensity were made for passive muscle shortening and lengthening, respectively. Subsequently, four passive rotations of the foot were performed with supramaximal electrical stimulation applied as the foot moved through 90°. The stimulation evoking the passive supramaximal M-wave in the soleus EMG also evoked a resting twitch in the torque curve. Between each ankle rotation, the foot was stationary for 45 s before being rotated in the opposite direction. At least 15 s before the next ankle rotation was initiated, subjects were instructed to perform a submaximal 3-s plantar flexion to ensure that the thixotropic state of the muscle was similar between trials (39). After the passive rotations with supramaximal stimulation, the stimulus intensity was adjusted, and passive ankle rotations were performed with submaximal electrical stimulation applied as the foot moved through 90°. Passive rotations were performed until 10 trials in each direction had been recorded with a direct M-wave peak-to-peak amplitude at 20% of the passive supramaximal M-wave. The stimulation evoked a direct M-wave and a subsequent passive H-reflex in the soleus EMG.

After the passive ankle rotations, eight MVC concentric and eccentric plantar flexor actions were performed in which a supramaximal electrical stimulation was delivered as the foot passed 90°. The stimulation evoked an MVC supramaximal M-wave and a subsequent V-wave in the soleus EMG. It also evoked a superimposed twitch in the torque curve. As for passive ankle rotations, a concentric trial was always followed by an eccentric trial, with a 45-s rest between trials. After these maximal muscle actions, subjects rested for 10 min before performing a last set of eight MVC concentric and eccentric actions. In these MVCs, the stimulus intensity was adjusted to achieve direct M-wave amplitudes at 20% of the supramaximal M-wave measured during the MVC. Electrical stimulation was delivered at 90° during maximal voluntary shortening and lengthening trials until four trials in each direction had been attempted. Only trials with direct M-wave amplitudes at 20 ± 5% of the supramaximal M-wave were included for further analysis. The stimulation evoked a direct M-wave and a subsequent MVC H-reflex in the soleus EMG.

Stimulation procedures. Transcutaneous electrical stimulation was applied to the tibial nerve through a cathode (Ag-AgCl, Blue M-00-A, electrode sensor area: 13.2 mm², Ambu, Ølstycke, Denmark) placed in the popliteal fossa and an anode (carbon rubber electrode, 100 × 50 mm, CEFAR Medical, Malmö, Sweden) positioned on the anterior aspect of the thigh, just proximal to the patella. The stimulation consisted of a square 1-ms pulse delivered by a constant-current stimulator (Digitimer D87A, Digitimer, Hertfordshire, UK) to induce H-reflexes, M-waves, and V-waves in the EMG signal from the soleus muscle and resting or interpolated twitches in the torque signal.

Plantar flexor strength and voluntary activation. Torque signals were analog to digital converted at 5 kHz using a CED 1401 data-acquisition system and Signal software (Cambridge Electronic Design, Cambridge, UK).

Plantar flexor strength (torque) was measured from the four maximal voluntary trials (MVCs) per action type (concentric and eccentric) performed with supramaximal stimulation as the foot moved through 90° (Fig. 1). Plantar flexor strength was taken as the mean torque over the 50 ms just before the electric stimulation. For each...
action type, the mean plantar flexor strength from the four trials was used for further analysis. Voluntary activation was assessed by means of the twitch interpolation technique in the same maximal voluntary concentric and eccentric actions as used for strength measures. Voluntary activation during each of the four maximal attempts per action type was calculated as follows: voluntary activation (in %) = \( \frac{1}{\text{IT}/\text{RT}} \), where IT is the interpolated twitch and RT is the resting twitch (2). To achieve the interpolated twitch during maximal voluntary plantar flexion, the mean torque measured during the 50 ms preceding the electrical stimulation was subtracted from the peak torque detected within 200 ms from when the electrical stimulation was applied. Resting twitch was measured as the peak torque occurring within 200 ms from when the electrical stimulation was applied during passive shortening (concentric) or lengthening (eccentric). Two passive trials per movement direction were performed. The higher of the two resting twitches was used for the calculation of voluntary activation in the maximal concentric and eccentric trials, respectively. For each action type, the mean voluntary activation from the four trials was used for further analysis.

EMG. EMG activity was recorded from the soleus using a pair of surface electrodes (Ag-AgCl, Blue M-00-A, electrode sensor area: 13.2 mm\(^2\), Ambu) with one electrode placed over the soleus muscle and one electrode over the Achilles tendon in a belly-tendon configuration for the registration of H-reflexes, M-waves, and V-waves. Signals were bandpass filtered between 20 and 2,000 Hz, amplified 100 times, and analog to digital converted at 5 kHz (1401, Cambridge Electronic Design). Peak-to-peak amplitudes of H-reflexes, M-waves, and V-waves were measured. The passive H-to-M ratio (H:M ratio) for each action type was calculated as the mean of 10 H-reflexes divided by the largest of the supramaximal M-waves. The MVC H:M ratio for each action type was calculated as the mean of four MVC H-reflexes divided by the largest of the supramaximal MVC M-waves. The V-to-M ratio (V:M ratio) for each action type was calculated as the mean of four V-waves divided by the largest of the supramaximal MVC M-waves.

Additionally, to measure the eccentric-to-concentric ratio for the EMG, pairs of electrodes were placed centrally over the central bulk of the soleus, medial gastrocnemius, and tibialis anterior muscles. Signals were bandpass filtered between 10 and 1,000 Hz, amplified 1,000 times, and analog to digital converted at 5 kHz (1401, Cambridge Electronic Design). The root mean square for each muscle was measured over the same 50-ms period as for strength. The root mean square EMG (EMG_{rms}) for each muscle and action type was calculated as the mean of the same four MVCs as used for calculating strength. From these means, the ratio of the eccentric to concentric EMG_{rms} for each muscle (soleus, medial gastrocnemius, and tibialis anterior muscles) and time (before and after) was calculated.

Statistics. Normality of the data was first checked using the Shapiro-Wilk W-test. Subsequently, repeated-measures multivariate ANOVA was performed for strength and voluntary activation, with the within-subject factors of time (before and after) and action type (shortening and lengthening) and the between-subject factor of group (training or control). Repeated-measures multivariate ANOVA was performed for eccentric-to-concentric EMG_{rms} ratios with the within-subject factors of time (before or after) and the between-subject factor of group (training or control). Repeated-measures ANOVA was performed for the H:M ratio with the within-subject factors of time (before or after), action type (shortening and lengthening), and muscle activation (passive or MVC) and the between-subjects factor of group (training or control). Finally, repeated-measures ANOVA was performed for the V:M ratio with the within-subject factors of time (before and after) and action type (concentric or eccentric) and the between-subject factors of time and action type.
factor of group (training or control). Whenever significant interactions or main effects were found, a Tukey’s honestly significant-difference test was performed. To search for relations between variables affected by training, a multiple regression was performed with changes in strength as the dependent variable and changes in voluntary activation and changes in the V:M ratio as the independent variables. Significance was accepted at $P < 0.05$. All statistical procedures were performed using the Statistica software package (version 8.0, Statsoft).

RESULTS

Plantar flexor strength and voluntary activation. Repeated-measures multivariate ANOVA revealed a statistically significant interaction between intervention (training vs. control) and time (before vs. after) for the dependent variables of strength and voluntary activation ($F_{2,17} = 10.1$). In the training group, pooled concentric and eccentric plantar flexor strength increased significantly by 19.3% from 134.2 ± 48.0 to 160.1 ± 41.0 Nm, whereas it remained unaltered in the control group (Fig. 2). Training induced a significant increase in voluntary activation by 9.8% from 83.2 ± 13.5% before training to 91.2 ± 4.8% after training, whereas the control group showed no change in voluntary activation (Fig. 3). There was no three-way interaction among time, action type, and group, i.e., changes in strength and voluntary activation over time within each group were the same for concentric and eccentric muscle actions.

Ratio of eccentric to concentric $EMG_{rms}$. Multiple repeated-measures ANOVA revealed no interactions of time and group on the ratio of eccentric to concentric $EMG_{rms}$ ($F_{3.6} = 1.82$). Thus, training showed no action type-specific changes in neural activation in soleus, medial gastrocnemius, or tibialis anterior muscles.

Evoked spinal reflex responses. Neither passive nor MVC H:M ratios were affected by training. A significant interaction was found for the H:M ratios between action type (concentric or eccentric) and muscle activation (passive or MVC) ($F_{1.18} = 74.27$). The passive H:M ratio was significantly and considerably larger during passive muscle shortening (concentric) compared with passive muscle lengthening (eccentric). For the MVC H:M ratio, there were no differences between action types. The difference between action types found for the passive H:M ratio was not affected by training, since no significant main or interactive effects of time and group were found for either passive or MVC H:M ratios. Table 1 shows the amplitude of the direct M-waves induced during H-reflex stimulation normalized to the supramaximal M-wave from the same action type and same activation level. There were no significant changes over time or between groups in direct M-to-supramaximal M ratio. Table 1 also shows supramaximal M-waves. There was a significant decrease in passive ($F_{1.18} = 8.12$) and MVC supramaximal ($F_{1.18} = 5.95$) M-waves from before to after the training period, but this change was not different for groups or action types.

For the V:M ratio, there was a significant interaction between intervention and time ($F_{1.18} = 9.09$). In the training group, the pooled concentric and eccentric V:M ratio increased significantly by 77% from 0.19 ± 0.07 before training to 0.33 ± 0.13 after training, whereas in the control group it remained unchanged (Fig. 4, A and B). Since no three-way interactions between intervention, time, and action type were found, changes in the V:M ratio within each group were the same for concentric and eccentric muscle actions.

Associations among changes in strength, voluntary activation, and the V:M ratio. To assess whether the increase in strength after dynamic resistance training was associated with the increased voluntary activation and increased V:M ratio, a multiple linear regression was performed separately for each group. In the training group, there was a significant association between the increase in strength, on the one hand, and the increases in voluntary activation ($\beta = 0.71$) and the V:M ratio ($\beta = 0.52$), on the other hand ($F_{2,6} = 8.8$, adjusted $r^2 = 0.66$; Fig. 5). In the control group, no such association was found. A correlation between voluntary activation and the V:M ratio showed no association in either the training group or control group.

DISCUSSION

Main findings. The main findings of this study were that 5 wk of resistance training in a Smith machine induced improvements in plantar flexor strength, increased voluntary activation...
Table 1. Peak-to-peak amplitudes of supramaximal and direct M-waves

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<th>Before the Training Period</th>
<th>After the Training Period</th>
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<td>Direct M-wave/supramaximal M-wave, %</td>
<td>Training group</td>
<td>20 ± 1.0</td>
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<tr>
<td></td>
<td>Control group</td>
<td>20 ± 0.6</td>
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<tr>
<td>Supramaximal M-wave, mV</td>
<td>Training group</td>
<td>9.8 ± 2.1</td>
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<td></td>
<td>Control group</td>
<td>9.4 ± 2.1</td>
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Values are means ± SD. Shown are peak-to-peak amplitudes of supramaximal and direct M-waves, expressed as a percentage of the peak-to-peak amplitude of supramaximal M-waves from the same condition (direct M-wave/supramaximal M-wave). Direct M-waves were induced by the stimulus used for eliciting Hoffman reflexes in passive concentric, passive eccentric, maximum voluntary contraction (MVC) concentric, and MVC eccentric exercises before and after the training period in the training group and control group. There was a significant decrease in supramaximal M-waves over time (*P < 0.05). This decrease was not different between action types or groups.

Table 2. Measures of neural activation.

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<td></td>
<td>Before the Training Period</td>
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<tr>
<td>V:M ratio</td>
<td>Training group</td>
<td>2.7 ± 2.1</td>
<td>3.5 ± 2.0</td>
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<td></td>
<td>Control group</td>
<td>2.0 ± 2.3</td>
<td>1.4* ± 2.5</td>
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Values are means ± SD. Shown are measures of neural activation. Different procedures for measuring changes in neural activation exist in the literature. Measuring changes in absolute EMG levels can be easily criticized due to the difficult task of achieving identical recording conditions, whereas ratios of EMG levels between eccentric and concentric actions are less problematic (27, 41). Different regimens for electric or magnetic stimulation of the nervous system at various levels also exist. The twitch interpolation technique has been extensively used to estimate vol-
Notably, the MVCs with supramaximal stimulation of the tibial nerve, not only the M-wave but most likely also the V-wave contribute to the superimposed twitch (for similar reasoning regarding mechanical contributions from the H-reflex, see Refs. 6 and 33). The increase in the V-wave after training probably increases the interpolated twitch, but since there is no V-wave in a passive muscle it does not contribute to the resting twitch. If, as in the present study, training increases the V-wave, this increase will mask the increase in voluntary activation as assessed via the twitch interpolation. This is most likely why there was no association between increased voluntary activation and increased V:M max ratio despite the relatively strong association between increased strength, on the one hand, and increased voluntary activation and V:M ratio, on the other hand.

Neural mechanisms of strength improvements. The finding of no increases in the passive H:M ratio after training in the present study is in agreement with most previous studies (1, 11, 17, 40) on both isometric and dynamic muscle actions. Still, cross-sectional studies (5, 13, 32) have tended to find a significantly lower passive H:M ratio in athletes trained for explosive-type movements as opposed to nontrained or endurance-trained athletes. Some of these differences seen in the cross-sectional studies may be due to genetics rather than adaptations to training. In addition, long-term training may have induced dissimilarities between athletes in the mechanical properties of the muscle tendon complex (10), such as its stiffness and the individual position on the force-length curve at a given ankle angle. Measuring reflexes at a relatively longer muscle length will result in lower H:M ratios (20), most likely because stretch of the muscle will induce homosynaptic postactivation depression via increases in muscle spindle firing.

The absence of training-induced modulations in passive H-reflexes does not reduce the number of different possible mechanisms for increased voluntary activation. Lagerquist et al. (29) tried to resolve this by eliciting H-reflexes with muscles active at 10% of MVC, as controlled via concurrent EMG feedback. They found an increased H:M ratio at low stimulation intensities but no change at intensities resulting in maximal H-reflexes. While controlling surface EMG amplitude does not guarantee constant motoneuron output (16, 28), feedback of EMG likely stabilized the motoneuron output, making fluctuations in the H:M ratio more likely to be induced by changes in presynaptic inhibition. The Lagerquist et al. study (29) thus provides some support for decreased presynaptic inhibition of Ia afferents after isometric strength training. However, reduced presynaptic inhibition at 10% MVC does not warrant that reduced presynaptic inhibition contributes to increases in voluntary activation during training. In addition, long-term training may have induced dissimilarities between athletes in the mechanical properties of the muscle tendon complex (10), such as its stiffness and the individual position on the force-length curve at a given ankle angle. Measuring reflexes at a relatively longer muscle length will result in lower H:M ratios (20), most likely because stretch of the muscle will induce homosynaptic postactivation depression via increases in muscle spindle firing.

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thought to be more sensitive to altered presynaptic inhibition than changes in supraspinal input (9, 34, 35), whereas V-waves are more sensitive to changes in suprapinal input to the motoneurone pool (9, 44). The lack of increases in the H:M ratio at MVC in the present study therefore indicates that the increases in the V:M\text{max} ratio mainly came about due to increased motoneuronal excitability from supraspinal inputs or afferents other than Ia afferents. Since the V-wave most likely recruits both large and small motoneurones, whereas the H-reflex mainly activates small motoneurones, it can, however, not be excluded that the increases in the V:M\text{max} ratio occurred partly due to a selective decrease in presynaptic inhibition of Ia afferents synapsing onto large motoneurones or that the increased supraspinal excitation induced selective increases in recruitment or firing frequency of large motoneurones (1, 9, 21).

The present results of increased V-waves after mainly eccentric training support the findings of Duclay et al. (11), although their results also showed an increased H:M ratio at MVC in eccentric plantar flexions. The different results regarding the MVC H:M ratio between the present study and the study of Duclay et al. (11) may be due to Duclay et al. training and testing subjects in the same task, whereas the present study assessed a transfer task. The positioning of the subjects and the angular velocities used during training and testing may also have affected the results. Duclay et al. (11) tested and trained subjects with flexed knees, whereas training of the present study was performed with subjects standing in a Smith machine with extended knees. The angular velocity used by Duclay et al. (11) was higher (20°/s) than that used here (5°/s). At higher angular velocities of plantar flexion, the H:M ratio evoked in an eccentric MVC is depressed compared with that evoked in an concentric MVC (12). This difference is most likely caused by more presynaptic inhibition during eccentric MVC at higher velocities. Consequently, the potential for reduced presynaptic inhibition should be larger in fast eccentric MVCs compared with concentric MVCs. In the slow dynamic plantar flexion MVCs used here, we found no differences between the concentric and eccentric MVC H:M ratio and were therefore less likely to find action type-dependent increases in the MVC H:M ratio. An important difference between the present study and that of Duclay et al. (11) is that Duclay et al. only used EMGs to measure changes in neural activation (see Measures of neural activation for a critique of this method). The findings of the present study show training-induced improvements in voluntary activation, as measured by the twitch interpolation technique, in parallel with the increased V:M\text{max} ratio. While this does not prove that the increased V:M\text{max} ratio and improved voluntary activation are related, it adds evidence to the study of Duclay et al. (11).

Interestingly, whereas the findings of the present study and a few other studies using V-waves in the plantar flexors have shown that resistance training induces improvements in strength, occurring partly due to increased supraspinal activation, other studies using transcranial magnetic stimulation to assess cortical voluntary activation and corticospinal excitability have found varying results regarding strength training induced changes in cortical excitability (3, 4, 26, 30). Lee et al. (30) assessed cortical voluntary activation after 4 wk of unilateral strength training of the right wrist and failed to find a significant increase in voluntary activation or motor-evoked potentials from transcranial magnetic stimulation. Also, Carroll et al. (4) found no indications of altered corticospinal excitability after training involving finger abduction. These studies investigated cortical excitability after strength training in muscles where the ability to achieve full voluntary activation is high even before training, thus having small possibilities of finding increased voluntary activation, let alone the mechanisms for such increases. Beck et al. (3), on the other hand, showed that ballistic strength training of the plantar flexors increased corticospinal excitability more than sensory motor training or compared with the passive control group. Also, Griffin and Cafarelli (23) observed increased corticospinal excitability for the tibialis anterior muscle after 4 wk of isometric resistance training. Considering that mechanisms of neural activation have been suggested to differ between upper and lower limbs (36), it seems both possible and likely that the mechanisms for increases in neural activation with training may still be action type specific. Care should therefore be taken when trying to understand neural effects from strength training based on data from different limbs, action types, and exercises.

Summary. In conclusion, the findings from this study show that 5 wk of resistance training induce increased muscle strength, voluntary activation, and V:M\text{max} ratios to the same extent in concentric and eccentric maximal voluntary plantar flexions. The improvements in strength were associated with improvements in voluntary activation and V:M\text{max} ratios. Training was performed with subjects in a Smith machine, whereas testing was performed in an isokinetic dynamometer, indicating that improvements in strength and voluntary activation could be successfully transferred from one dynamic task to another. While it cannot be ignored that some hypertrophy may have occurred, the data from the present study suggest that dynamic resistance training primarily improves dynamic plantar flexor strength via enhanced supraspinal input to the motoneurone pool, increased motoneurone excitability, and/or increased excitation from afferents other than Ia afferents.

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