

Resistance Training: Cortical, Spinal, and Motor Unit Adaptations

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Abstract/Résumé

During the first few weeks of isometric resistance training there is an increase in maximal muscle force output that cannot be accounted for by muscle hypertrophy. Early on, researchers postulated the existence of neural adaptations to training primarily through the use of surface electromyographic recordings. More recent evidence also suggests that increased excitation may occur at the cortical levels following short-term resistance training. Alterations in synergistic activation and reductions in antagonist activation are neural factors that have been identified as changing during the early stages of resistance training which could contribute to maximal force generation. Neural adaptations that occur during the ramp-up phase of isometric contraction include decreases in motor unit recruitment thresholds, increased motor unit discharge rates, and increases in double discharges. An increase in the maximal rate of force development also occurs during the early stages of resistance training, but whether the neural mechanisms associated with the increase in the rate of rise are also associated with the increase in maximal force has not been elucidated. More work is needed to examine the integration of changes in cortical and spinal excitability with single motor unit firing patterns during this simple form of exercise before we can extend our understanding to different types of training.

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Au cours des premières semaines d'un entraînement à la force statique, on observe une amélioration de la force maximale non attribuable à l'hypertrophie des muscles. C'est principalement par l'électromyographie de surface que les chercheurs avaient postulé les adaptations nerveuses en réponse à l'entraînement à la force. De récentes observations suggèrent une augmentation de l'excitation au niveau cortical à la suite d'un programme à court terme d'entraînement à la force. Parmi les facteurs nerveux qui présentaient un potentiel de changement au début d'un programme d'entraînement à la force et qui pouvaient expliquer une amélioration de la force musculaire, notons les modifications de l'activation des muscles synergistes et la réduction de l'activité des antagonistes. Les adaptations nerveuses qui se manifestent au cours de la phase de gradation de la tension isométrique sont la réduction du seuil d'activation des unités motrices, une augmentation de leur fréquence de décharge, et de leur double décharge. Au début d'un programme d'entraînement à la force, on observe également une amélioration du taux maximal d'augmentation de la force, mais on ne sait pas si cette amélioration est en lien avec l'augmentation de la force maximale. Il faut mener d'autres études pour bien analyser l'influence des modifications de l'excitabilité médullaire et corticale sur les modalités de la décharge d'unités motrices isolées au cours d'une forme simple d'exercice avant de faire des applications à diverses formes d'entraînement.

Introduction

In this brief review we focus primarily on adaptations in the activation of human skeletal muscle during the early stages of adaptation to isometric resistance training. We have chosen isometric contractions because they represent the simplest form of muscular activity and are the easiest to control experimentally. Potential contributions to the increase in isometric force production may occur in the extent of contractile protein accumulation, firing patterns of motor units, whole-muscle synergistic activation, and corticospinal plasticity. While early evidence suggests that changes do occur in some of these elements, the definitive adaptation that leads to increased force production has not been clearly identified. It may well be that small adaptations at multiple locations along the path of activation act together to produce a change in muscle performance.

The question of whether there are changes in the control strategies of the central nervous system that enhance muscle force during the early stages of isometric resistance training has been of interest since the early work of DeLorme and Watkins (1951). Moritani and DeVries (1979) were among the first to attempt to quantify the so-called neural adaptations to training. They observed an increase in the biceps brachii muscle surface EMG during maximal voluntary isometric contraction (MVC) following 8 weeks of resistance training, with no apparent change in upper limb girth. They therefore proposed that the disproportionate increase in muscle force relative to limb girth must be attributable to some unspecified neural factors. Increases of 15 to 18% in MVC force have been found during the first 4 weeks of resistance training (Cannon and Cafarelli 1987, Griffin and Cafarelli, 2003) and up to 36% by 8 weeks (Moritani and DeVries 1979, Rich and Cafarelli 2000).

More recently, techniques for observing hypertrophy with greater precision such as ultrasound (Young and Bilby, 1993), magnetic resonance imaging (MRI)

(Conley et al., 1997; Housh et al., 1992; Narici et al., 1989; 1996), and computerized tomography (Garfinkel and Cafarelli, 1992) have all shown that there are small but significant increases in muscle cross-sectional area during the first 8 to 12 weeks of training (cf. Phillips, 2000). In contrast, after only 2 weeks of training Akima et al. (1999) found no increase in the cross-sectional area of quadriceps femoris using MRI scans. These data all suggest that somewhere between the 2nd and 8th weeks of isometric resistance training, muscle tissue is capable of a limited degree of hypertrophy.

Some small changes in the muscle during the early stages of training may be attributed to phenotypic changes in muscle tissue. For example, in weight lifters the rate of protein synthesis, but not degradation in the biceps brachii muscles, increases by 50% within 4 hours of a training session (Chesley et al., 1992), and by 109% within 24 hours (MacDougall et al., 1992). By comparison, increases in type II fiber area occur within 5 weeks (Krotkiewski et al., 1979) and 8 weeks (Ishida et al., 1990) of resistance training. A preferential type II fiber hypertrophy could account for some of the increase in force output per cross-sectional area of the muscle, since type II fibers have greater specific force than type I fibers (Trappe et al., 2003).

Muscle force is modulated by motor unit recruitment and the rate coding of their discharge, both of which are controlled by the central nervous system. Thus the observation that there may be some degree of muscle hypertrophy early in the adaptive process does not negate the possibility that there are neural contributions to increased maximal force output. Over the years many researchers have used maximal surface EMG to quantify changes in neural activity (Hakkinen et al., 1985; Moritani and DeVries, 1979; Narici et al., 1989; Yue and Cole, 1992). However, it is possible that activation could increase and not be reflected in the surface signal (Farina et al., in press). It has also been shown that increases in MVC force frequently occur without a change in the amplitude of surface EMG (Cannon and Cafarelli, 1987; Garfinkel and Cafarelli, 1992; Hakkinen and Komi, 1983; Keen et al., 1994; Komi and Buskirk, 1972; Narici et al., 1996; Rich and Cafarelli, 2000).

Several factors could potentially influence EMG activity in a training (pre/post) experimental design. Among them are subtle shifts in electrode placement, altered extracellular volume and/or osmolarity, reductions in subcutaneous fat, changes in skin temperature, and differences in phase cancellation following weeks of training. To control for these potential confounding factors, some researchers measured maximal M-waves before and after training. While there does not appear to be any training-induced increase in M-wave amplitude in young adults (Duchateau and Hainut, 1984; Keen et al., 1994; Sale et al., 1983), significant increases in M-wave amplitude have been reported in older men and women (Hicks et al., 1992).

In young adults it has been observed that an increase in maximal surface EMG is not necessarily accompanied by a change in the amplitude of the M-wave (Van Cutsem et al., 1998). In comparison, Pucci and Cafarelli (1998) found that when surface EMG increased after resistance training, there was an approximately proportional increase in amplitude of the M-wave. Despite these potential confounds, the recording of the surface electromyogram continues to be used as a method for assessing neural activation of muscle. Table 1 summarizes the findings

Table 1 Studies of Changes in Maximal Force and Surface EMG Before and After Resistance Training

Reference	Muscle	#Subjects/ #Control	Training Mode/Duration	MVC (% Δ)	EMGmax (% Δ)
Komi et al. (1978)	Quadriceps	3/3	Isometric, 12 wks	20	38
Moritani and De Vries (1979)	Elbow flexors	15/15*	Dynamic, 8 wks	36	12
Hakkinen and Komi. (1983)	Quadriceps	14/10*	Dynamic, 16 wks	25	11
Hakkinen and Komi (1983)	Quadriceps	11/9	Dynamic, 16 wks	26	0
Hakkinen et al. (1985a)	Quadriceps	11/8	Dynamic, 24 wks	27	0
Hakkinen et al. (1985b)	Quadriceps	11/8	Dynamic, 24 wks	12	0
Hakkinen and Komi (1986)	Quadriceps	11/8	Dynamic, 24 wks	14	0
Cannon and Cafarelli (1987)	Adduc poll.	9/7	Isometric, 5 wks	16	0
Cannon and Cafarelli (1987)	Adduc poll.	7/7	Isom. Stim., 5 wks	15	0
Narici et al. (1989)	Quadriceps	4/0	Dynamic, 8 wks	21	42
Hakkinen et al. (1992)	Quadriceps	10/0	Dynamic, 3 wks	9	21
Yue and Cole (1992)	Abd. digiti minimi	8/9	Isometric, 4 wks	30	44
Yue and Cole (1992)	Abd. digiti minimi	10/9	Imagined, 4 wks	22	0
Garfinkel and Cafarelli (1992)	Quadriceps	8/7	Isometric, 8 wks	28	0
Carolan and Cafarelli (1992)	Quadriceps	10/10	Isometric, 8 wks	33	0
Weir et al. (1994)	Quadriceps	7/6	Isometric, 6 wks	23	0
Keen et al. (1994)	First dorsal inter.	10/0	Dynamic, 12 wks	39	0
Hakkinen and Kallinen (1994)	Quadriceps	10/0	Dynamic, 6 wks	16	0
Weir et al. (1995)	Quadriceps	9/7	Isometric, 6 wks	27	0
Narici et al. (1996)	Quadriceps	7/0	Dynamic, 24 wks	30	0
Van Cutsem et al. (1998)	Ankle dorsiflexors	5/0	Dynamic, 12 wks	30	20
Hakkinen et al. (1998)	Quadriceps (males)	21/0	Dynamic, 24 wks	14	21
Hakkinen et al. (1998)	Quadriceps (females)	21/0	Dynamic, 24 wks	22	43
Rich and Cafarelli (2000)	Vastus lateralis	10/10	Isometric, 8 wks	36	0
Rabita et al. (2000)	Rectus femoris	9/7	Dynamic, 4 wks	39	37
Rabita et al. (2000)	Vastus lateralis	9/7	Dynamic, 4 wks	39	0
Rabita et al. (2000)	Vastus medialis	9/7	Dynamic, 4 wks	39	0
Aagard et al. (2002)	Quadriceps	15/0	Dynamic, 14 wks	14	0
Griffin and Cafarelli (2003)	Tibialis anterior	10/10	Isometric, 4 wks	18	30

*Significant change of MVC or EMG max in control group.

of 25 fairly recent studies that recorded surface EMG during isometric MVCs before and after resistance training.

Motor Unit Recruitment and Firing Rate

An increase in maximal muscle force could occur if there was a training-induced activation of previously inactive motor units or a higher rate of discharge, particularly in large motor units. Currently the interpolated twitch technique is the best method available for measuring activation level in whole human muscle, although the technique itself has some limitations (Belanger and McComas, 1981; Dowling et al., 1994). Voluntary activation assessed in this way has been found not to change (Herbert et al., 1998) nor to increase (Huber et al., 1998; Knight and Kamen, 2001; Pensini et al., 2002) with resistance training. However, the changes in activation can only account for a small fraction of the increase in maximal force. Increases in force and EMG amplitude may also be caused by changes in motor unit firing patterns. But little evidence is available to give a clear picture of what happens to motor unit firing rates in a longitudinal training study.

In some instances, average motor unit firing rates do not change during isometric submaximal (50% MVC) (Rich and Cafarelli, 2000) or maximal (Pucci and Cafarelli, 1998) contractions of the quadriceps muscle following 8 weeks of resistance training. However, cross-sectional studies in older weight trainers suggest that years of training may be associated with increased maximal firing rates. It is also possible that increases in maximal EMG could be attributed to potentiation of the M-wave rather than an increase in activation (Pucci and Cafarelli, 1998). This would not necessarily add to force production. Motor unit synchronization following isometric resistance training would also lead to an increase in surface EMG amplitude. Motor unit firing rate synchronization is higher in weight lifters than in control subjects (Semmler and Nordstrom, 1998).

Ramp-Up to Maximum

Changes in motor unit recruitment and discharge rates occur during ramp contractions following resistance training. For example, motor unit recruitment thresholds of the first dorsal interosseous (Keen et al., 1994; see Figure 1) and the tibialis anterior (Van Cutsem et al., 1998) muscles decreased following training. This earlier recruitment of motor units which occurs during ramp contractions may also occur during the performance of MVCs, since the initial rate at which MVC torque increased was faster after resistance training of the quadriceps muscle (Aagaard et al., 2002; see Figure 2; Rich and Cafarelli, 2000).

Van Cutsem et al. (1998) observed an increase in the number of motor units that fired doublets (2- to 5-ms interspike intervals) during ballistic dynamic contractions of the tibialis anterior muscle following 12 weeks of dynamic resistance training. Doublets are typically defined as two pulses that occur within 20 ms or less (Simpson, 1969); they are commonly observed during voluntary and reflex contraction (cf. Garland and Griffin, 1999) and increase in frequency during dynamic muscle fatigue (Griffin et al., 1998). Thus, firing doublets may be a strategy on the part of the central nervous system to increase force during resistance train-

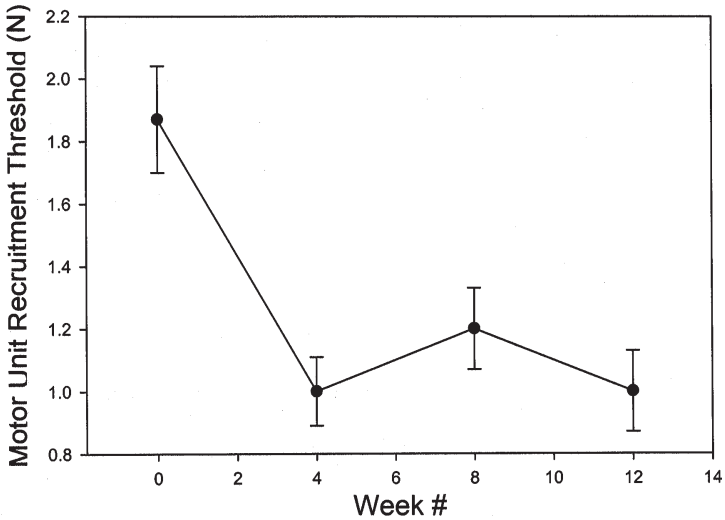


Figure 1. Single motor unit recruitment thresholds are plotted against weeks of resistance training. Motor unit recruitment thresholds were lower following 4 weeks of resistance training of the flexor dorsal interosseous muscle. Data from Keen et al. (1994).

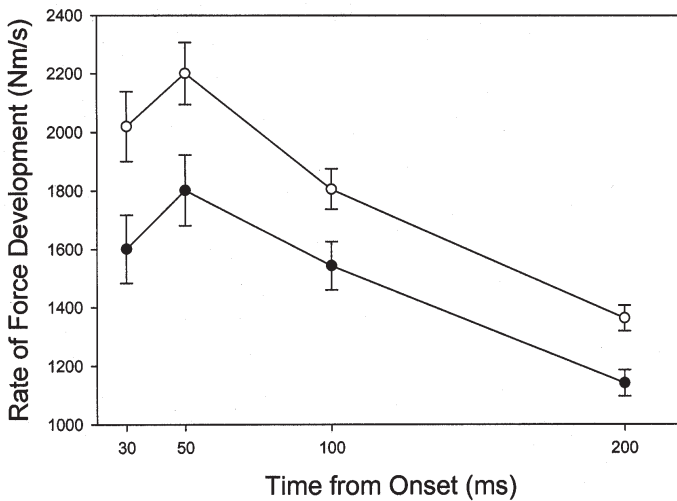


Figure 2. Rate of force development at 30, 50, 100, and 200 ms during the rising phase of an isometric maximal voluntary contraction of the quadriceps muscle before (at pretraining, closed circles) and after (open circles) 14 weeks of resistance training. Increases were significant for all 4 times. Data from Aagaard et al. (2002).

ing and fatigue. Human subjects can also learn to increase the number of doublets fired by single motor units (Bawa and Calancie, 1983; Denslow, 1948). It has been postulated that a doublet positioned at the onset of a stimulus train can increase force generation by enhancing calcium release from the sarcoplasmic reticulum (Duchateau and Hainaut, 1986) and by taking up the slack of the passive elements of the muscle more rapidly with the force generated by the first pulse in the doublet (Stein and Parmigianni, 1981).

Increases in the number of doublets and reductions in motor unit recruitment thresholds are indicative of increases in the excitability of the central nervous system during the early ramp-up phase of contraction. These changes in motor unit firing patterns could increase the rate of rise of force from the onset of contraction. Increases in the rate of rise of muscle contraction during MVCs have been observed following resistance training (Aagaard et al., 2002; Rich and Cafarelli, 2000). However, it is unlikely that this increased rate of rise contributes to increased maximal force output.

Coactivation and Cross-Education

Other evidence of centrally mediated neural adaptations to strength training includes reductions in agonist/antagonist coactivation (Carolan and Cafarelli, 1992; Hakkinen et al., 1998; 2000), changes in synergistic muscle activation (Rabita et al., 2000), and strength increases in the untrained contralateral leg. Studies have found reductions in hamstring EMG activity during quadriceps strength training (Carolan and Cafarelli, 1992; Hakkinen et al., 1998; 2000). This neural strategy could increase maximal force output. It also appears that specific muscles of task synergies may be preferentially activated during resistance training. For example, Rabita et al. (2000) found that the surface EMG of the rectus femoris muscle increased following dynamic resistance training of the quadriceps muscles whereas the EMG of the vastus lateralis and vastus medialis muscles did not.

Although many studies have observed strength increases in the contralateral limb following resistance training (cf. Zhou, 2000), few have recorded the EMG activity of the untrained limb during the actual training sessions. Hortobagyi et al. (1997) found that the EMG activity of the contralateral quadriceps muscle during a single training session was 8% of the maximal EMG during MVC. They reasoned that such a small amount of activation could not account for the observed increase of 25% MVC force of the untrained limb. However, when subjects were provided with visual feedback of the contralateral quadriceps EMG during single-leg training to ensure no voluntary activation of the contralateral limb, no evidence of the "transfer effect" was found (Garfinkel and Cafarelli, 1992). Thus it appears that the CNS is inclined to recruit both limbs during unilateral training at maximal intensity.

Cortical Plasticity

It has been argued that the increases in muscle force during the early stages of resistance training are greater than can be accounted for by muscle hypertrophy alone. Findings of increases in surface EMG and lower recruitment thresholds suggest adjustments in the CNS strategy for activating muscle. The next question

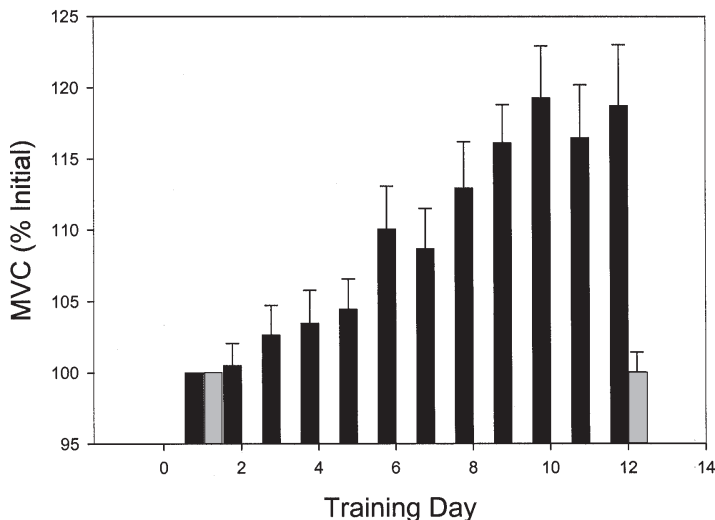


Figure 3. Maximal voluntary contraction (MVC) forces for the tibialis anterior muscle plotted as percent initial (% Day 1) for every training day during 4 weeks of isometric resistance training, 3 times per week (black bars). Control group (grey bars) measures were recorded at beginning and end of the month. Redrawn from Griffin and Cafarelli (2003).

may be, What is the mechanism behind this increase in motoneuronal excitation, and at what level does it originate? There is ample evidence that significant increases in cortical representation and motor-evoked potential (MEP) amplitude during motor learning occur in humans (cf. Sanes and Donoghue, 2000). Additionally, cortical representation of the human tibialis anterior muscle diminishes after the limb has been immobilized, but increases again with muscular contraction (Liepert et al., 1995).

It may be that similar cortical adaptations also occur in response to resistance training, but few studies have measured this directly. Yue and Cole (1992) found significant increases in muscle force with imagined muscle contractions. However, this finding has not been replicated (Herbert et al., 1998). Carroll et al. (2002) used transcranial electric and magnetic stimulation to record MEP amplitudes before and after 14 weeks of resistance training of the first dorsal interosseus (FDI) muscle. They found no change in MEP amplitude when normalized to maximal M-waves. They did not measure changes in maximal surface EMG. Keen et al. (1994) found no change in EMG following 12 weeks of dynamic resistance training of the FDI muscle.

In contrast, increases in maximal EMG of the tibialis anterior muscle were found with training (Griffin and Cafarelli, 2003; Van Cutsem et al., 1998). Significant increases in MEP amplitude during low force contractions following 4 weeks of resistance training of the tibialis anterior muscle occurred that corresponded to increases in surface EMG with no significant change in the maximal M-wave (Grif-

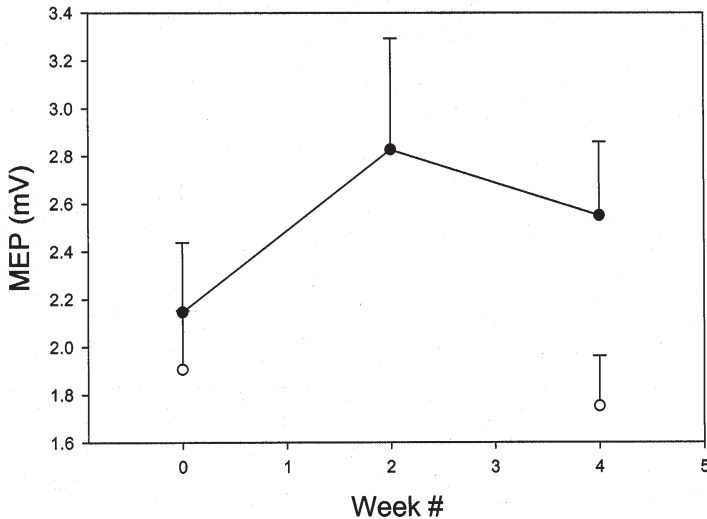


Figure 4. Motor-evoked potential peak-to-peak amplitudes are plotted after 2 and 4 weeks of isometric resistance training of the tibialis anterior muscle. Training group is plotted as closed circles, the control group as open circles. There was a significant increase in MEP amplitude after only 2 weeks of training (6 training days) which remained after 4 weeks. Redrawn from Griffin and Cafarelli (2003).

fin and Cafarelli, 2003). The increase in MEP amplitude was significantly higher after 2 and 4 weeks of resistance training compared to baseline. Figure 3 shows the increase in maximal force output on every training day (3 times per week) for one month. Figure 4 shows the mean tibialis anterior MEP amplitudes after 2 and 4 weeks of resistance training. Notice that maximal force output increases progressively from the onset of training but that MEP amplitudes were no higher in Week 4 than they were in Week 2. Future studies are needed to determine the time frame of increases in cortical excitability in relation to increases in maximal muscle force during resistance training.

Spinal Cord

Increases in central excitation may also be manifested at the level of the spinal cord. V-reflex amplitudes are higher in the triceps surae muscles of weight lifters compared to control subjects and increase with resistance training (Aagard et al., 2002). However, soleus muscle H-reflexes evoked at rest do not change with resistance training (Aagard et al., 2002). Soleus maximal H/M wave ratios are higher in athletes than in untrained subjects (Nielsen et al., 1993), but sprinters and volleyball players (Casabona et al., 1990) and power-trained athletes (Rochconger et al., 1979) had lower maximal H/M ratios than untrained subjects. Cross-sectional studies have found that maximal H/M ratios of the triceps surae muscles are higher in endurance-trained than in strength-trained athletes (Maffiuletti et al., 2001;

Rochcongar et al., 1979). Thus it appears that endurance training increases the amplitude of the H-reflex at rest, but spinal adaptations to resistance training are only evident when the muscle is engaged. It is also possible that endurance-trained athletes have a higher percentage of type I fibers than resistance-trained athletes, and that their motoneurons would thus receive greater input from Ia afferents of muscle spindles. Longitudinal studies of differences between neural adaptations to resistance and endurance training are needed to control for the genetic differences between these two groups of athletes.

In conclusion, the full elucidation of neural adaptations to training is still in the early stages. Few studies have recorded changes in single motor unit firing rates following training. However, it appears there are modulations in motor unit firing patterns in response to training which include reductions in motor unit recruitment thresholds, increased firing rate synchronization, and increased double discharges. There is some indication that the motor cortex displays an increase in cortical excitability with resistance training. However, further studies are needed to determine the relationship between changes in motor neuron excitability at the cortical and spinal levels in relation to changes in motor unit rate coding and recruitment patterns during resistance training. This type of work is necessary for helping us to understand the full range of neuromuscular mechanisms that enhance muscle force output.

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