Neural Issues in the Control of Muscular Strength

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During the earliest stages of resistance exercise training, initial muscular strength gains occur too rapidly to be explained solely by muscle-based mechanisms. However, increases in surface-based EMG amplitude as well as motor unit discharge rate provide some insight into the existence of neural mechanisms in the earliest phases of resistance exercise training. Moreover, other phenomena such as the cross transfer of strength following unilateral exercise and neural changes following limb immobilization also support a role for neural control in muscular strength. While studies to date have focused on the phenomenon of neural change, future studies will need to focus on the many motoneuron influences as well as intrinsic motoneuronal properties that may be responsible for these neural adaptations.

Key words: disuse, EMG, exercise, training

The anecdotal and scientific literature is replete with references to the relationship between muscular strength and various muscle characteristics, such as muscle size, myosin adenosine triphosphatase enzymatic concentrations, contractile characteristics, and other muscular factors. Even mythical stories involving Milo and his pet bull provide insight to the centuries-long thinking about large muscles. We now realize that a variety of neural factors are also involved in the expression of large muscular forces. Until recently, relatively little research has been concerned with neural issues controlling muscular strength. However, there is ample evidence that neural control is a critical element for producing large levels of muscular force. While not a comprehensive review, this research note will provide an introduction to some of the evidence for the existence of neural factors in high muscle force activities and detail some of the mechanisms through which these could be operative.

Evidence for the Existence of “Neural Factors”

Temporal Issues in the Gains of Muscular Strength

Perhaps the most frequently cited evidence for such “neural factors” is the observation that muscular strength increases quite rapidly, following even one exercise training session. Indeed, several investigators have reported that maximal force increases of as much as 15% are possible just a few days following an exercise training session (Kamen, 1983; Kroll, 1965; Schenck & Forward, 1965). Such “quick jumps in strength” are unlikely to be attributable to alterations in either muscle hypertrophy or other muscle characteristics (see Figure 1).

Advances in medical imaging suggest that muscle size alone does not determine muscular force capability. While the linear relationship between muscle cross-sectional area (CSA) and maximal force is generally between $r = .5 - .8$, the available evidence suggests that muscle cross-sectional area may account for as little as 10% of the variance in muscular force production. Sipila & Strommen (1994), for example, reported correlations between quadriceps CSA and knee extensor force of $r = .44$. Lower correlations of $r = .15$ (Young, Stokes, & Crowe, 1985) have also been reported, suggesting that muscle size can be a poor predictor of muscular force production (see Figure 2). One might expect to observe higher
associations, because muscle protein synthesis increases following a single exercise session (MacDougall et al., 1995), which might suggest that some increase in muscle mass should follow each exercise session. However, even though maximal muscular force begins to increase shortly after resistance training onset, significant increases in gross muscle size or muscle fiber cross-sectional area are not observed until about the 8th week of exercise training (Hickson, Hidaka, Foster, Falduto, & Chatterton, 1994; Kamen, 1983; Moritani & deVries, 1979; Narici, Roi, Landoni, Minetti, & Cerretelli, 1989; Ploutz, Tesch, Biro, & Dudley, 1994; Staron et al., 1994).

**Limb Disuse**

During a period of limb immobilization, such as when a limb is casted, the rate of muscle strength loss greatly exceeds the loss of muscle size (Desplanches, 1997). Moreover, in immobilized muscle the loss of mechanical tension recorded during voluntary contractions is greater than that obtained with electrically evoked contractions (Duchateau & Hainaut, 1987). Just as the early gains in muscular force during training are attributable to neural mechanisms, so, too, the early losses in muscular force during detraining or limb disuse are attributable to neural mechanisms.

**Cross-Transfer of Muscular Strength**

Since the late 1800s, we have known that resistance training performed in one limb can produce increases in muscular force in the contralateral musculature. Scripture, Smith, and Brown (1894) were likely the first to demonstrate this phenomenon, and this cross-transfer effect (also called cross-education) has been demonstrated in numerous laboratories (Hortobágyi, Lamberti, & Hill, 1997; Houston, Froese, Valeriote, Green, & Ranney, 1983; Kannus et al., 1992). Indeed, the magnitude of the cross-training effect can be as great as 77% following unilateral eccentric exercise training of the knee extensors (Hortobágyi et al., 1997). Moreover, improvements in muscle blood flow accompany these contralateral limb strength increases (Yasuda & Miyamura, 1983), resulting in increased muscular endurance on the contralateral side (Kannus et al., 1992).

There is ample evidence that the mechanism for this cross-transfer of strength concept has a neural basis. First, little or no change in the size of the contralateral musculature accompanies the increase in muscular strength contralaterally, as might be expected if muscle mass gains were a significant contributor (Hortobágyi et al., 1996; Housh, Housh, Johnson, & Chu, 1992; Hous-

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**Figure 1.** The mere assessment of maximal isometric force frequently elicits an increase in maximal force (Kamen, 1993). Here, maximal planter flexion isometric force was assessed in 12 men on each of 6 days over a 14-day interval. During this interval, planter flexion MVC increased by 21%.

**Figure 2.** Imperfect correlations between muscle size and maximal voluntary force are frequently obtained, as can be appreciated in these data (Sipila & Suominen, 1994).
ton et al., 1983). Second, activating both the contralateral and the ipsilateral motor cortex produces unilateral muscle activation (Kristeva, Cheyne, & Deecke, 1991; Stinear, Walker, & Byblow, 2001). Consequently, it is not unlikely that high force single limb activities result in sufficient activation of the ipsilateral motor cortex to result in an enhancement of contralateral muscle group activity. Finally, a period of resistance exercise training involving the fifth finger abductor produces increases in motor unit discharge rates in the contralateral musculature (Patten, Kamen, & Rowland, 2001), suggesting that contralateral limb motoneurons receiving frequent subthreshold excitation demonstrate a discharge adaptation. Thus, there is little doubt that neural mechanisms are responsible for the cross-transfer of strength phenomenon.

Possible Neural Mechanisms Mediating High Force Activities

Motor Unit Recruitment.

One question frequently raised concerning maximal strength production is: which motor units are activated during high levels of muscular force. The anecdotal literature is replete with references to the selective recruitment of fast-twitch fibers during high-force activities. However, it has long been recognized that motor units are recruited into action in an orderly fashion, according to size (Henneman, Somjen, & Carpenter, 1965). Small motor units, consisting of slow-twitch muscle fibers and slower-conducting motor neurons, are activated at low force levels; larger motor units, consisting of muscle fibers with more fast-twitch characteristics, are recruited at higher force levels.

While the original work documenting this size recruitment principle was developed in a feline model, we now know that this recruitment scheme also exists in human muscles (Masakado, Kamen, & DeLuca, 1991). Ordinarily recruitment seems to be maintained even during the most rapid movements (Desmedt & Godaux, 1977), and there is virtually no scientific evidence that fast-twitch fibers are the only muscle fibers recruited during the highest force activities. Under a few conditions involving eccentric contractions (Nardone, Romano, & Schieppati, 1989), or cutaneous receptor activation (Masakado et al., 1991), fast-twitch fibers might be recruited at lower force levels, albeit with earlier activation of smaller, slow-twitch motor units.

Are all motor units recruited during maximal force production? One technique used to answer this question involves applying a maximal electrical stimulus to the muscle while an individual attempts a maximal isometric contraction. The thinking is that if some motor units are "held in abeyance" (i.e., not normally activated during maximal voluntary effort) greater force would be observed immediately after the superimposed electrical stimulus than immediately prior to the stimulus. However, in most studies virtually full activation is present in these "superimposed twitch" contractions, suggesting that virtually all motor units are maximally activated. The size of the superimposed twitch decreases with strength training (see Figure 3), and this could be interpreted as evidence of increased ability to activate more motor units with strength training (Knight & Kamen, 2001). However, the size of the force response obtained immediately after a superimposed electrical stimulus to the muscle appears to bear a greater relationship to motor unit discharge rate than the number of active motor units (Knight, Kamen, & Burke, 1998).

Motor Unit Discharge Rate

When motor units are recruited into action, they begin to discharge at a threshold rate of about 8–12 impulses/s (imp/s). As the demand for more force increases, the firing rate increases. During maximal isometric contractions, motor unit firing rate can exceed 50 imp/s in small hand muscles, like the first dorsal interosseous (FDI; Kamen, Sison, Du, & Patten, 1995) and abductor digiti minimi (ADM; Patten & Kamen, 2000). Maximal discharge rate is considerably lower in larger muscles like the quadriceps, where maximal firing rate may be less than 100.

Figure 3. The central activation ratio (CAR) is a measure of the magnitude of additional force produced by delivering a supramaximal electrical stimulus to the muscle group during maximal voluntary effort. Higher CAR values indicate more complete neural activation. The figure indicates that CAR scores obtained by stimulating vastus lateralis increase during exercise training provide additional evidence that strength training improves neural activation (Knight et al., 2001).
30 imp/s (Kamen, Knight, Larocche, & Asermely, 1998; Leong, Kamen, Patten, & Burke, 1999).

Benefits to the larger discharge rates are observed in smaller muscles, and these benefits concern the role small muscles play in motor control. Small muscles of the hand, for example, are involved in fine motor activity and precision motor control. Force production during these tasks is best controlled by subtle changes in discharge rate rather than de novo recruitment or deactivation of an entire motor unit. Altering discharge rate from, say, 42 imp/s to 44 imp/s produces a more subtle force change than activating an additional motoneuron and all the muscle fibers innervated by that motoneuron.

Training Influences on Motor Unit Firing Rate

Inasmuch as motor unit firing rate is a key parameter determining the level of muscular force produced, one might wonder whether firing rate is adaptable, subject to exercise training, or other influences. In fact, several investigators have demonstrated that motor unit firing rate can be altered. In the FDI muscle, for example, immobilizing the second finger for 6 weeks reduces maximal firing rate (Seki, Taniguchi, & Narusawa, 2001), which could be one reason why force declines, particularly during the early phase of limb disuse.

Older adults exhibit lower discharge rates than college-age participants (Kamen et al., 1995; Patten et al., 2001), and older individuals who maintain a lifestyle of high force activities exhibit faster motor unit discharge rates than a group of active, elderly participants (Leong et al., 1999). However, these cross-sectional studies can be confounded by genetic, long-term nutritional, or other influences. Some completed longitudinal investigations have provided insight into the role exercise training might have in altering motor unit discharge rate. For example, in one recent study (Kamen et al., 1998) maximal discharge rate was assessed in the vastus lateralis muscle in college-age and elderly individuals. These participants then completed 6 weeks of exercise training involving both maximal isometric and 10-RM dynamic contractions. Results confirmed previous suggestions that the early period of resistance exercise training is marked by adaptations in neural control factors, and one of these neural changes is an increase in motor unit discharge rate. As indicated in Figure 4, when muscular strength was retested 1 week after the initial testing session, increases in discharge rate were observed in both young and older adults. Further increases in discharge rate were observed in the older adults after the 6-week training period.

In another investigation (Patten et al., 2001), both young and older adults followed a resistance exercise training program using a small muscle in the hand, the ADM. After the initial maximal force assessment, both maximal force and maximal motor unit discharge rate increased during a retest, 48 hr later.

Descending Influences on High Force Activities

The information presented above suggests that exercise training can influence motor unit activity. What changes in neural centers are responsible for these adaptations? Unfortunately, our knowledge of descending influences on motor unit activity following exercise training is scant. However, we have some insight into the kinds of brain mechanisms that may underlie early increases in maximal force capacity.

A powerful tool developed recently to explore the role of the supraspinal centers in movement involves transcranial magnetic stimulation (TMS). A painless magnetic stimulus is used to evoke an electrical potential in cortical neurons. When the stimulator is held over a cortical motor area, the resulting EMG activity can be recorded and quantified in the corresponding muscles by measuring the size of the response, termed the motor evoked potential (MEP; Mills, 2000).

One might speculate that cortical excitability changes might occur following a period of exercise training. Other observations support this idea of a long-term adaptation in cortical centers. For example, if the afferent input from myelinated nerve fibers is removed by an ischaemic nerve block, motor cortical inhibition is temporarily removed, resulting in an increased excitability of the corticospinal system (Pascual-Leone et al., 1993). Following limb amputation or spinal cord injury, patients also exhibit long-term changes in cortical activation (Schwenkreis et al., 2000; Shimizu, Hino, Komori, & Hirai, 2000).

![Figure 4](https://example.com/figure4.png)

**Figure 4.** Resistance exercise training with the knee extensors produces increase in motor unit discharge rates in the vastus lateralis in both young and older adults (Kamen et al., 1998).
The mechanisms underlying performance changes following mental practice have also been studied using TMS and some imagery tools. For example, one report found that mental practice training involving imagining a muscle contraction produces significant strength gains using fifth-finger abduction (Yue & Cole, 1992). As well, the mere task of thinking about a physical activity (as might be done during mental practice) increases the size of the MEP response, suggesting that this imagery task activates cortical centers responsible for movement (Kiers, Fernando, & Tomkins, 1997; Yahagi & Kasai, 1999). These studies begin to reveal the mechanisms through which mental practice can aid physical movement.

Summary

A dilemma exists in our scientific knowledge of muscular strength acquisition. An understanding of the early phase of strength acquisition has considerable societal import and practical application. Space flight participants, patients recovering from stroke, long-term bed rest or limb immobilization, and frail elderly individuals achieve considerable benefit from just a short period of resistance training. Yet, our focus has been on the peripheral factors accompanying long-term gains in maximal force production, even though a month or more of exercise training may be required before changes in muscular variables can be observed. Thus, our knowledge of the mechanisms underlying muscular strength production is greatest during the interval when the rate of strength gain is low and scant during the interval when the most rapid gains in maximal force are achieved. To date, we have learned that motor unit discharge behavior can be altered in this early phase of strength training, indicating that influences on the motoneuron comprise part of this neural adaptation. Future research will need to identify what specific neural pathways summate at the motoneuron and identify specific neural sites that demonstrate adaptation. Such “neural factors” research will lead to programs to optimize early muscular force gains for individuals most at need as well as an understanding of the mechanisms that underlie achieving large muscular force capability in elite athletes.

References


**Author's Note**

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