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PHYSIOLOGICAL STATUS AND MOTOR FUNCTION OF SPORTS TRAINEES

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Abstract: The purpose of this brief review is to examine the neural adaptations associated with training, by focusing on the behavior of single motor units. The review synthesizes current understanding on motor unit recruitment and rate coding during voluntary contractions, briefly describes the techniques used to record motor unit activity, and then evaluates the adaptations that have been observed in motor unit activity during maximal and submaximal contractions. Relatively few studies have directly compared motor unit behavior before and after training. Although some studies suggest that the voluntary activation of muscle can increase slightly with strength training, it is not known how the discharge of motor units changes to produce this increase in activation. The evidence indicates that the increase is not attributable to changes in motor unit synchronization. It has been demonstrated, however, that training can increase both the rate of torque development and the discharge rate of motor units. Furthermore, both strength training and practice of a force-matching task can evoke adaptations in the discharge characteristics of motor units. Because the variability in discharge rate has a significant influence on the fluctuations in force during submaximal contractions, the changes produced with training can influence motor performance during activities of daily living. Little is known, however, about the relative contributions of the descending drive, afferent feedback, spinal circuitry, and motor neuron properties to the observed adaptations in motor unit activity.

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Introduction:

The motor unit is the common final pathway of the motor system and comprises a motor neuron in the ventral horn of the spinal cord, its axon, and the muscle fibers that the axon innervates. The average number of fibers innervated by a motor neuron is ~ 300 , but the range extends from tens to thousands (37). The basic function of a motor unit is to transform synaptic input received by the motor neuron into mechanical output by the muscle (57).

The group of motor neurons in the spinal cord innervating a single muscle is referred to as a motor unit pool (15). The motor unit population that forms a motor pool is heterogeneous with respect to the properties of both the motor neurons and the muscle fibers that they innervate (13). A motor neuron can be characterized by its morphology, excitability, and distribution of input (12, 13, 69), whereas muscle fibers vary in contraction speed, force-generating capacity, and resistance to fatigue (14, 70).

Although the distribution of synaptic inputs can influence the order in which motor units are recruited, the most important determinant is the size of the motor neuron. As initially reported by Henneman (59), there is a strong relation between the size of a

motor neuron and the order in which it is activated. This association has become known as the size principle. The influence of size on recruitment order is attributable to its effect on input resistance. According to Ohm's law, the change in membrane potential in response to a synaptic current is proportional to the input resistance of the motor neuron. Because small motor neurons have a high input resistance, they are the first to be recruited in response to an increase in depolarizing synaptic currents. As a consequence of this relation, smaller motor units tend to be activated before larger units. Due to the properties of the muscle fibers innervated by the different motor neurons, this recruitment sequence results in slow-contracting and fatigue-resistant motor units being recruited before fast-contracting and fatigable motor units. Although there is some variability in the recruitment order of motor units with similar thresholds (44, 135), the recruitment order of motor units is essentially the same for isometric and dynamic contractions, including lengthening contractions shortening and (122, 126, 131), and during rapid (ballistic) isometric (33, 34)and shortening (60)contractions. Furthermore, recruitment order during the stretch reflex follows the size principle (17).

MOTOR UNIT RECRUITMENT AND RATE **CODING**

The force that a muscle exerts depends on the amount of motor unit activity (3), changing with the number of motor units that are active (motor unit recruitment) and the rates at which motor neurons discharge action potentials (rate coding). The relative contributions of recruitment and rate coding to the force exerted by a muscle vary with the level of muscle force and the muscle performing the contraction. Due to the exponential distribution of recruitment thresholds within a motor unit pool, most motor units have low recruitment thresholds, and, therefore, low forces are mainly produced by the recruitment of motor units. In most muscles, the upper limit of motor unit recruitment is ~85% of the maximal force (32, 75, 141). In some hand muscles, however, the upper limit of motor unit recruitment is ~60% of maximum (32, 36, 89, 92). The increase in muscle force beyond the upper limit of motor unit recruitment is accomplished entirely by rate coding.

The absolute force at which a motor unit is recruited is not fixed and varies with the speed and

type of muscle contraction. For example, the recruitment thresholds of motor units in the tibialis anterior decrease progressively with an increase in the rate of force development (Fig. 1; Ref. 33). As a consequence of this adjustment, motor units are activated earlier during rapid contractions, and approximately three times as many motor units are recruited to produce a given peak force during a rapid contraction compared with a slow-ramp contraction (33). Due to this effect, most motor units are likely to be recruited when performing a rapid contraction with a load equivalent to 33% of maximum. The extent of the reduction in recruitment threshold, however, is greater for units in slow-contracting muscles (e.g., soleus) compared with fast-contracting muscles (e.g., masseter) (34). The greater reduction in recruitment thresholds for slow muscle likely facilitates their ability to perform fast contractions. Furthermore, recruitment thresholds can be lower during dynamic contractions compared with isometric contractions (133) and at short muscle lengths compared with long lengths during isometric contractions (98).

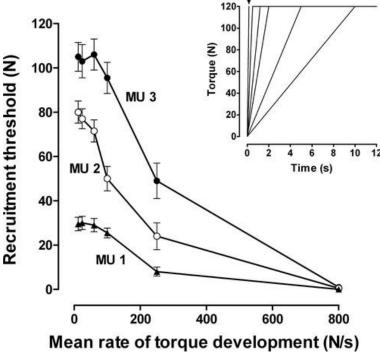


Fig. 1. The reduction in recruitment threshold (means \pm SD for 10 trials) for three motor units (MU) in tibialis anterior with an increase in the mean rate of torque development by the dorsiflexor muscles. Inset: six different rates of increase in torque to the target force of 120 N [~50% maximal voluntary contraction (MVC)], with the most rapid contraction (0.15 s to peak force) indicated by the arrow. The thresholds decreased for rates >60 N/s and become zero for the most rapid contraction. Note that the decrease in recruitment threshold was greatest for unit with the highest recruitment threshold, but there was no change in recruitment order predicted by the size principle. [Adapted from Desmedt and Godaux (33).1

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Although the rate at which a motor neuron discharges action potentials increases linearly with the depolarizing current it receives (68, 114), there is a sigmoidal relation between discharge rate and muscle force (40, 83, 90, 92). The minimal rate at which most motor neurons discharge action potentials repetitively during voluntary contractions is 5-8 pulses per second (pps) (126, 141), but the maximal discharge rates vary across muscles. Average rates of 30-50 pps have been recorded for most muscles during isometric contractions (for a review, see Ref. 37), whereas rates of ~10 pps have been recorded for the slowcontracting soleus muscle (11). Instantaneous discharge frequencies during rapid contractions, however, can reach values of 100–200 pps (33, 139, 140).

The maximal discharge rate usually matches the fiber-type composition of the muscle with muscles that contain a high percentage of slow fibers displaying lower maximal rates (6). The general slope of the relation between discharge rate and muscle force has been reported to vary as a function of recruitment threshold of the motor unit in some studies (45, 90), but not in others (89). There is also no consensus on the relative distributions of minimal and maximal discharge rates across the motor unit population. Some studies found that the minimal rate was constant (90) or decreased with recruitment threshold (132), whereas others suggested that the minimal rate increased with recruitment threshold (40, 52, 92). Similarly, some studies found a negative correlation between peak discharge rate and recruitment threshold during ramp isometric contractions (32, 36), whereas a recent study reported that peak discharge rate increased with recruitment threshold when subjects performed discrete isometric contractions at various target forces (92). One potential explanation for the difference in the association between recruitment threshold and peak discharge rate between studies might be that a continuous ramp contraction and a series of brief contractions evoke different history-dependent effects, such as those that involve persistent inward currents (50, 58).

In addition to depending on mean discharge rate, muscle force is influenced by the variability and modulation of motor unit discharge. The coefficient of variation for discharge rate, which is a measure of relative discharge rate variability and a factor that has a significant effect on the force fluctuations during steady contractions (39, 74, 134), appears to decline exponentially with an increase in muscle force above the recruitment threshold of each motor unit in a hand muscle (92). Additionally, the trains of action

potentials discharged by each motor neuron can also be modulated in distinct frequency bands (30, 42, 138), and the amount of modulation appears to vary across subjects and tasks (62, 118, 119, 121).

MEASURING MOTOR UNIT ACTIVITY

Surface electromyography (EMG) records the action potentials generated by active motor units as detected by electrodes placed on the skin over the muscle (41). EMG is often used, therefore, to estimate the motor output from the spinal cord during various types of contractions. However, the surface EMG is insensitive to modest changes in motor unit activity. For example, Mottram et al. (94) showed that, although the surface EMG of the biceps brachii increased at a comparable rate during two types of fatiguing contractions, there were significant differences between the two tasks in the decrease in discharge rate and increase in recruitment of single motor units.

The limitations of surface EMG recordings have been recognized for several decades. The magnitude of the difficulty in interpreting surface EMG records has recently been underscored with results on the extent to which the signal underestimates the amount of motor unit activity due to signal cancellation from the overlap of the positive and negative phases of motor unit potentials (29, 65). Although amplitude cancellation does not increase linearly across excitation levels (65), the increase is monotonic, and normalization of the surface EMG amplitude to the value obtained with maximal activation provides a reasonable estimate of the amount of muscle activation. Importantly, these results underscore the need to normalize EMG recordings across muscles, between subjects, and between days.

The preferred method to study motor unit behavior, however, is to use an electrode that can record the discharge of identifiable single motor units, because this provides information on the discharge characteristics of motor neurons in the spinal cord due to the faithful transmission of each neuronal action potential to the muscle fibers. Several electrodes have been developed for this purpose: fine-wire electrode (89), concentric needle electrode (129), subcutaneous electrode (38), arrays of electrodes distributed over the surface of the muscle (85), and macro-EMG (128). Each technique has its advantages and limitations (for review, see Ref. 84). The most common method is to use a fine-wire electrode. The procedure consists of inserting wires (diameter: 10-50 µm), which are insulated except for the ends, into the muscle with a hypodermic needle. The ends of the wires serve as the detection surface to record the action potentials of

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single motor units. Because it is often difficult to discriminate the action potentials of single motor units at high forces, an alternative approach is to use a concentric needle electrode to record the activity of several motor units and then use a signal-processing algorithm to decompose the composite signal into the constituent single motor unit potentials (78, 84).

MAXIMAL CONTRACTIONS

The strength of a muscle is often estimated as the peak force achieved during a maximal voluntary contraction (MVC). Changes in MVC force are attributable to adaptations in the force capacity of the muscle fibers and the activation characteristics of the involved motor units. A common approach used to identify the neural mechanisms that contribute to changes in MVC force is to assess the maximality of a contraction. When an individual is unable to activate a muscle or a group of muscles maximally (4), traininginduced increases in MVC force could involve improvements in motor unit activation. Different methods have been used to estimate the maximal activation of the motor unit pool: surface EMG (2, 54, 91), interpolated twitch (5, 72), and the ratio of evoked tetanic force to MVC force (28, 35). The results obtained with these different methods provide mixed information on the potential contributions of changes in motor unit activity to gains in MVC force. At the whole muscle level, the classic approach is to record changes in average EMG activity during a maximal contraction. For example, it has been found that the EMG during an MVC often increases after a program of strength training (2, 54, 91). This result has not been consistent, however, as some studies have not found that EMG increases with MVC force (18), even when the EMG was normalized to the maximal M wave (64). These mixed results are not particularly surprising, given what is known about the influence of amplitude cancellation on estimates of EMG amplitude.

An alternative approach is to compare the force exerted during an MVC with the force that can be elicited artificially with electrical stimulation (10, 86). The stimulus can be either applied during an MVC to determine whether the voluntary force can be increased or delivered to a resting muscle so that the evoked tetanic force can be compared with the voluntary force. Most individuals are able to achieve full activation of the biceps brachii muscle in about one out of four attempts when a few stimuli are superimposed during static and concentric MVCs (4, 48). This conclusion has been confirmed with the application of transcranial magnetic stimulation (TMS) during an MVC (136). In contrast, many individuals exhibit submaximal activation during an MVC when the superimposed stimulus involves a brief train of shocks (67, 130). Furthermore, muscle activation appears to be markedly less than maximal during eccentric contractions (5, 102, 142).

Because activation seems to be near maximal when assessed with the twitch superimposition technique, there are minimal changes after strength training when the activation of the motor unit pool is estimated with this technique (55, 72). In contrast, Duchateau and Hainaut (35) observed an increase in the ratio of MVC force to tetanic force for the adductor pollicis muscle before and after 6 wk of strength training. The training involved voluntary contractions and loads that were $\sim 65\%$ of maximum. The greater increase in MVC force (22%) compared with tetanic force (15%) suggests that the training produced an adaptation that resulted in a 7% increase in the activation of the motor unit pool for the hand muscle.

Although a decrease in the deficit detected with the interpolated twitch and an increase in the ratio of tetanic and MVC forces indicate that muscle activation is enhanced after strength training, the source of the improvement could be anywhere from the motor command to the processes involved in neuromuscular propagation. Identifying the locus of the adaptation is difficult. For example, a change in the ratio between tetanic force and MVC force could be produced by a change in the contribution of synergist muscles, such as those required for postural stabilization (77), which are activated during voluntary contractions but not evoked contractions. Furthermore, these techniques cannot distinguish between contributions from recruitment and rate coding to increases in MVC force. For example, what does an increase in voluntary activation from 90 to 98% of maximum indicate about the activation of the motor unit pool? Because the upper limit of motor unit recruitment is ~85% MVC (32, 75, 141), increases in force above this level can only be achieved with adaptations in discharge rate and not by an increase in recruitment. However, Pucci et al. (105) reported that strength training increased voluntary activation from 96 to 98%, but there was no change in discharge rate as measured with multiunit recordings.

Single Motor Unit Recording

Although it is a relatively trivial matter to record the activity of a single motor unit during a voluntary contraction, assessing the effect of a chronic intervention is much more challenging. In addition to the technical difficulties of identifying the activity of single motor units, the comparison of motor unit function before and after an intervention requires a sufficient sample size to represent the population of motor units and an adequate number of measurements to characterize the behavior. As a consequence, few

studies have compared motor unit behavior before and after strength training.

Kamen and Knight (63) reported that a 33% increase in the MVC force for the knee extensor muscles after 6 wk of strength training was accompanied by increases in the maximal discharge rates of motor units in the vastus lateralis of young (15% increase) and old (49% increase) adults (Fig. 2). Similarly, Van Cutsem et al. (140) compared the average instantaneous discharge rate of motor units at the beginning of a rapid contraction in the tibialis anterior before and after 12 wk of dynamic training. The training consisted of rapid contractions with the dorsiflexor muscles against a load that represented 30-40% of maximum (Fig. 3). Both the rate of increase in torque and the associated EMG during submaximal dynamic contractions increased with training. To assess the contribution of motor unit discharge rate to the faster rate of increase in torque for the submaximal dynamic contractions, the instantaneous rate for the first four action potentials was determined in single motor units before and after training. Although no change was observed in the recruitment order of motor units, the average instantaneous discharge rate increased from 69 to 96 pps with training. Furthermore, training caused a significant increase in the number of motor units (from 5 to 33%) that discharged with brief interspike intervals (<5 ms). Thus the increase in the rate of force development during rapid contractions appears to have been achieved by an adaptation in motor unit discharge rate. conclusion, the neural adaptations that accompany changes in physical training are diverse. This brief review has examined the influence of these adaptations on the motor output from the spinal cord as it is expressed in the recruitment and rate coding of single motor units. There is some evidence that adaptations in motor unit activity can contribute to improvements in motor performance. For example, the increase in maximal rate of torque development is accompanied by a greater motor unit discharge rate, whereas the reduction in discharge variability appears to improve steadiness during submaximal contractions after a training program. Because the data are limited by technical constraints, however, it has been difficult to demonstrate a clear association between neural adaptations and changes in motor unit activity. Nonetheless, recent work on rapid contractions, steady contractions, and force-tracking tasks appear to represent promising strategies for identifying the relations between central adaptations, motor unit activity, and muscle function.

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