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HIGHLIGHTED TOPIC | Neural Changes Associated with Training

Training adaptations in the behavior of human motor units

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> Duchateau, Jacques, John G. Semmler, and Roger M. Enoka. Training adaptations in the behavior of human motor units. J Appl Physiol 101: 1766-1775, 2006. doi:10.1152/japplphysiol.00543.2006.—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.

> electromyogram; discharge rate; recruitment; motor unit synchronization; steadiness

AS DEFINED BY SHERRINGTON (124), 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 shortening and lengthening contractions (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).

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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 $\sim 85\%$ of the maximal force (32, 75, 141). In some hand muscles, however, the upper limit of motor unit recruitment is $\sim 60\%$ 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 slowcontracting 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

120 120 ŝ 80 Recruitment threshold (N) Torque 100 60 MU 3 80 å 6 8 10 12 60 MU 2 Time (s) 40 20 n ò 200 400 600 800 Mean rate of torque development (N/s)

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).]

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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).

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 slow-contracting 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 historydependent 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.

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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 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).

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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), training-induced 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 ~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



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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



Fig. 2. Changes in strength (MVC force) of the quadriceps femoris muscles (*A*) and the discharge rate of MUs in vastus lateralis (*B*) for young (\bigcirc) and old (\bullet) adults during a 6-wk training program. The measurements at *days 1* and 8 represent baseline measurements. The discharge rates were recorded during submaximal (10 and 50%) and maximal (100%) isometric contractions. pps, Pulses per second. [Adapted from Kamen and Knight (63).]

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

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.

Motor Unit Synchronization

Since the classic observation of Milner-Brown et al. (88) that the synchronization of motor unit discharge is greater in a strength-trained hand muscle, it has frequently been assumed that strength gains can involve an increase in motor unit synchronization. However, this study was based on an indirect assessment of synchronization obtained from the surface EMG, which is now known to contain several limitations (146). Nonetheless, the cross-correlation of discharge times from pairs of motor units, which represents the gold standard to quantify motor unit synchronization during voluntary contractions in humans, has indicated that the amount of motor unit synchronization can vary with contraction type (122) and the type of habitual physical activity performed by an individual (118, 121, 122). However, a recent study found that significant strength gains after 4 wk of training were not accompanied by increases in synchronization between pairs of concurrently active motor units in the first dorsal interosseus muscle (120). These experimental data are consistent with a simulation study that suggested motor unit synchronization does not influence the maximal force that can be produced by a muscle (145). The central mechanisms that influence the correlated discharge of motor units and its expression as short-term synchronization appear to be unrelated to the activation characteristics that influence the force capacity of a muscle.

Coordination Between Muscles

Another possible adaptation in the activation of the motor unit pool with training is the distribution of activation among the muscles involved in the task (8, 123). A frequently examined example of this effect is coactivation of agonist and antagonist muscles (7, 31, 80, 104). Coactivation increases joint stability and stiffness and varies with factors such as the intensity and type of the contraction, movement speed, the amount of fatigue, and the level of training (for review, see Ref. 66). Alterations in coactivation with training may be related to a change in the ability to focus the motor command to the appropriate muscles involved in the task, through the differential modulation of intracortical inhibition (148). Because coactivation reduces the net force produced by the agonist muscles, the level of coactivation has to be adjusted by the nervous system when it impedes the performance of the agonist muscles. For example, elite athletes exhibit reduced coactivation of the semitendinosus muscle compared with

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Fig. 3. A: comparison of the torque (a) and rectified electromyography (EMG) of the tibialis anterior (b) recorded in one subject during a fast (ballistic) isometric ankle dorsiflexion, before and after dynamic training. Although a similar relative torque (41 vs. 44% MVC) was reached during the contractions, before and after training, the rate of torque development was increased after training, and this was accompanied by an earlier and intensified EMG activity at the onset of the contraction. *B*: schematic representation of the effects of dynamic training on the torque (*a*) and behavior of single MU from the tibialis anterior (*b* and *c*) during fast isometric contractions with the ankle dorsiflexor muscles. Before training (*left* trace), the classic behavior of MUs during a fast contraction comprised a short time lapse between the first two action potentials followed by longer interspike intervals. After training (*left* trace), the typical MU behavior involved a high instantaneous discharge rate that was maintained during the subsequent interspike intervals. Training (*B*, *c*) also increased the incidence of double discharges (interspike intervals < 5 ms) among the activated units (33% of units after training compared with 5% before training). [Adapted from Van Cutsem et al. (140).]

sedentary subjects when performing isokinetic contractions with the knee extensor muscles (5), and strength gains can be accompanied by a reduction in coactivation of the antagonist muscles within the first week of training (18). In short-term training, however, the reduction in coactivation is not always evident (54). Possible adaptations in coactivation during maximal contractions, however, have not been examined at the motor unit level.

Even less attention has been afforded to the changes that occur in synergist and postural muscles. These effects are significant, as indicated by the specificity of strength gains (143), the importance of postural requirements (77, 109), the improvement in coordination that occurs after strength training (19), and the transfer effects associated with cross education (95). As with coactivation, however, these adaptations with maximal contractions have not been examined at the level of the motor unit.

SUBMAXIMAL CONTRACTIONS

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The force that a muscle exerts during a voluntary contraction is not constant but fluctuates about an average intended value. The magnitude of the fluctuations is influenced by such factors as the intensity of the contraction, the type of muscle contraction, the muscle group involved in the task, the level of physiological arousal, and the amount of fatigue (21, 22, 47, 93, 108). One functional outcome of these fluctuations is that, when an individual repeats a task several times, the characteristics of the performance vary from trial to trial and influence the accuracy with which the task can be performed (22, 56, 113, 125).

The variability in motor output is attributable to differences in the motor units that are recruited, within and across muscles, and the rates at which the motor neurons discharge action potentials. Because the force that a newly recruited motor unit contributes to the net force declines exponentially with an increase in muscle force (46), tasks that involve low forces are more susceptible to the variable forces produced by the few active motor units (Fig. 4A). Furthermore, the fluctuations in motor unit force are exacerbated at low forces, because the rates at which motor neurons discharge action potentials during voluntary contractions are located on the lower region of the force-frequency relation, which causes each motor unit to contribute an unfused tetanus to the net force (Fig. 4, *B* and *C*; Refs. 40, 83, 90, 92). This effect is most pronounced for the last recruited motor unit, as it likely discharges action potentials at the lowest rate (32, 101).

The adaptations that can occur in motor unit behavior and the effect on motor performance have been examined in two protocols: steady contractions and force-tracking tasks. Steadiness is defined as the ability to produce a constant force or trajectory during a voluntary contraction and is quantified as the fluctuations in force during an isometric contraction or the fluctuations in acceleration during an anisometric contraction (16, 47, 51). The fluctuations in motor output during steady contractions are strongly influenced by the variability in discharge rate (Fig. 4; Ref. 76, 92, 134). Accordingly, a training intervention found that 2 wk of practicing a steadiness task with a light load (10% of maximum) produced modest parallel declines in the fluctuations in index finger acceleration during slow shortening and lengthening contractions and the discharge rate variability of single motor units in a hand muscle (74). Four weeks of subsequent strength training with heavy loads (70% of maximum) did not further improve either steadiness or discharge rate variability. In the old adults studied by Kornatz et al. (74), there was a strong association between the fluctuations in motor output and manual dexterity, as assessed with the Purdue pegboard test.

Another influence of strength training on motor units is the reduction in activity that is necessary to lift the same absolute load after training compared with before training. For example, Ploutz et al. (103) reported a reduction in the amount of contrast shift in magnetic resonance images of the quadriceps femoris muscles when lifting the same absolute loads after 9 wk of strength training. This result suggests that less muscle mass was activated to lift the same load after training. Although the cross-sectional area of quadriceps femoris increased



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Fig. 4. Simulated forces from a modified version of the Fuglevand model of MU recruitment and rate coding (46). There were 180 MUs in the pool. A: the force added by selected MUs (29, 48, 67, 99, 136, 146, 159, 169, 175, and 180) to the net muscle force up to the upper limit of MU recruitment (59% of the maximal force). The contribution to the net force by a newly recruited unit is greatest at low forces. B: the unfused tetani produced by MU 90 when the net muscle force was 10%, 20%, and 40% of maximum (% max). MU 90 was recruited at 3.9% MVC force. C: the tetani produced by MUs 1, 30, 60, and 180 at forces slightly above the recruitment threshold for each MU. The recruitment thresholds were 0.01, 0.49, 1.52, and 58.3% MVC force, respectively. The mean discharge rate and coefficient of variation for discharge rate for the four MUs were as follows: MU 1 = 6.5 pps and 11.8%; MU 30 = 7.0pps and 7.3%; MU 60 = 7.6 pps and 11.5%; MU 180 = 15.8 pps and 7.5%. au, Arbitrary units. [Generated by M. Jesunathadas].

(6%), muscle biopsies indicated that fiber area did not change with training. Furthermore, there was a reduction in the area of contrast shift in the muscles of the untrained leg (right) after training when lifting the same absolute loads. Presumably, these adaptations involved some changes in motor unit activity, such as greater discharge rates for the active units and higher recruitment thresholds for the nonrecruited units. Alternatively, the ability to lift the same absolute load with less active muscle mass may have been attributable to a more effective transmission of the force from the contractile proteins to the skeleton. In the absence of data, however, the underlying mechanism is not known. Nonetheless, the available data examining the influence of strength training on the discharge rate of motor units during submaximal and maximal contractions show mixed results (26, 79, 100, 106).

The adaptability of motor unit behavior has also been assessed with force-tracking tasks (99). For example, Knight and Kamen (73) examined the modulation of discharge rate during the course of a single experimental session in which subjects performed 15 trials of tracking a sinusoidal force profile. The target force averaged 20% MVC force and comprised the sum of two sine waves: 0.15 and 0.5 Hz. Subjects found it more difficult to match the 0.5-Hz component of the target force, but tracking at both frequencies improved with practice. The improvement in performance was accompanied by a reduction in discharge rate variability and an increase in the modulation of discharge rate at 0.5 Hz. This result is consistent with other findings on the association between fluctuations in motor output and modulation of discharge rate at low frequencies (23, 137). Nonetheless, the improvement in force tracking at 0.15 Hz observed by Knight and Kamen (73) was not accompanied by a corresponding change in discharge rate modulation at that frequency.

MECHANISMS OF ADAPTATION

Despite evidence that suggests a significant role for neural mechanisms in the adaptations associated with strength training, there has been less progress on identifying the specific mechanisms responsible for these adaptations. The potential mechanisms that might explain the increased activation of the agonist muscles after training include subtle changes in the pattern of motor unit recruitment and increases in the neural drive (110, 117).

Although the timing of motor unit activation can be slightly changed with training (26), it has been shown that the population of motor units examined before and after the intervention still followed the size principle during a ramp contraction, after either isometric or dynamic training (53). Furthermore, the order of recruitment during rapid contractions did not change after 12 wk of dynamic contractions with loads of 30-40% of maximum in the tibialis anterior (140). Although the size principle appears to be preserved after training, the absolute force at which a specific unit is recruited depends on the increase in the contractile characteristics (force and contraction time) of low-threshold units after training. Essentially nothing is known, however, about the influence of training on the upper limit of motor unit recruitment. Decreases in the upper limit of recruitment, such as has been observed for old adults (71), results in a greater proportion of the force capacity of the muscle relying on rate coding (25). It is unknown if training can expand the range of motor unit recruitment and thereby modify the relative contributions of recruitment and rate coding to the gradation of muscle force across the operating range of the muscle.

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The discharge rates of motor units during high-force contractions appear to place the motor units on the upper region of the force-frequency relation but not on the plateau (83). Accordingly, the maximal rate of force development during a tetanic contraction is usually obtained at a frequency that is greater than the average discharge rate of motor units observed during fast voluntary contractions (87). These observations suggest that the MVC force and its maximal rate of development are less than the intrinsic capacity of the muscle and can thus be improved by increasing motor unit discharge rate. Consistent with this expectation, changes in discharge rate with training have been observed during MVCs (63, 100) and at the onset of a fast contraction (140).

The changes that can be evoked in neural circuits with training are produced, in general, by adaptations at either of two main levels: 1) supraspinal levels: corticospinal neurons, subcortical neurons, and inhibitory and excitatory intracortical interneurons; 2) spinal level: motor neurons, and inhibitory and excitatory interneurons. Some studies involving short-term motor skill training have reported that changes within the primary motor cortex enlarge the cortical representation of the muscles and increase the excitability of corticospinal pathways (24, 97), possibly due to selective alterations in intracortical inhibition (81). Despite the observation that several weeks of skill training can increase corticospinal excitability (61, 97), strength training does not seem to be accompanied by similar adaptations (20, 61). For example, Jensen et al. (61) found that skill training three times per week for 4 wk increased the maximal motor-evoked potential (MEP) induced by TMS and decreased the minimal stimulus intensity required to elicit MEPs at rest and during a contraction. In contrast, the maximal MEP and the slope of the input-output relation both decreased significantly at rest but not during contraction in strengthtrained subjects. Furthermore, Carroll et al. (20) found that the 33% increase in maximal isometric torque of a hand muscle after 4 wk of strength training was accompanied by no change in corticospinal excitability measured at rest and was reduced when tested during contractions. They also observed that the degree of reduction in MEPs evoked by transcranial electrical stimulation and TMS was similar. Because TMS largely excites cortical neurons through interneurons and transcranial electrical stimulation excites the corticospinal fibers at the axon hillock (107), these results suggest that strength training changed the functional properties of spinal cord circuitry, but not the output from the motor cortex.

These divergent effects of skill and strength training on the nervous system are supported by data on motor unit synchronization. Motor unit synchronization is a measure of the correlated discharge of action potentials by motor units and is presumed to provide an index of the strength of common branched input to motor neurons via the corticospinal pathway (27, 43, 115). Motor unit synchronization is largest in weightlifters, intermediate in untrained subjects, and least for highly skilled musicians (118), suggesting that the modification of activity in branched corticospinal inputs to motor neurons is related to some aspect of strength development in weightlifters or to skilled hand function in musicians. However, computer simulations (145) and experimental data (120) indicate a poor association between changes in motor unit synchronization and gains in strength. These findings suggest that alterations in motor unit synchronization may be more closely related to fine motor performance, where long-term skilled use of the digits may reduce the common input to motor neurons to promote skilled neuromuscular performance, rather than contributing to increases in strength with training (116).

Training adaptations within the spinal cord are often assessed in humans by testing electrically evoked reflexes, including the Hoffmann (H) reflex. The H reflex includes a monosynaptic connection between the group Ia afferent and the α -motor neuron. Some studies have shown that strength training increases the amplitude of the H reflex (1, 112). Furthermore, when an electric stimulus sufficient to evoke a maximal M wave is applied to a motor nerve during an MVC, two reflex responses (V1 and V2) can be elicited. The V1-to-M-wave ratio has been used as an index of reflex potentiation, where there is an increase in the amplitude of the reflex (V1) relative to the direct muscle response (M wave) after strength training (1, 111). Observations on the operant conditioning of the spinal stretch reflex and the H reflex suggest that much of the plasticity in these reflexes appears to be located in the spinal cord (144) and appears to be attributable to the role of spinal interneurons in integrating the sensory and motor signals that are transmitted to the motor neurons (96).

Although many investigators have used the H reflex as an index of motor neuron excitability, the connection between the afferent and the motor neuron is modulated by presynaptic mechanisms, and hence the amplitude of the H reflex depends on more than the responsiveness of the motor neuron (147). In this context, given the observation that acute withdrawal of group Ia feedback reduces discharge rate during a maximal contraction (82), it is likely that training-induced changes in afferent feedback can also influence motor unit discharge rate. In addition to a possible role of afferent feedback in mediating training adaptations, other evidence also indicates that the properties of motor neurons can be altered by physical activity (49). For example, Beaumont and Gardiner (9) reported that endurance training in rats changed the biophysical properties of motor neurons, which resulted in a more hyperpolarized resting membrane potential, increased threshold for spike initiation. and faster rise times for antidromic spikes. These adaptations, which likely reflect alterations in ionic conductances of motor neurons, can modify the recruitment thresholds and discharge patterns of the neurons.

In 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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GRANTS

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