

Motor Unit Synchronization and Neuromuscular Performance

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SEMMLER, J.G. Motor unit synchronization and neuromuscular performance. *Exerc. Sport Sci. Rev.*, Vol. 30, No. 1, pp 8–14, 2002. *The acute and chronic plasticity of motor unit synchronization suggests that it must represent a deliberate strategy for neuromuscular activation. The most likely functional role of motor unit synchronization is to increase the rate of force development during rapid contractions or as a mechanism to coordinate the activity of multiple muscles in synergy.* **Keywords:** synchrony, motor unit discharge, cross-correlation, coherence, motor control

INTRODUCTION

The excitability of motor neurons within a single motor neuron pool has been studied extensively in humans through the recording of single motor unit activity. Recording single motor unit activity is performed by inserting a fine-wire electrode into the muscle and recording the action potentials of the muscle fibers associated with one motor unit. The impetus for recording from single motor units is that the firing properties of the motor neuron can be inferred from the discharge of the motor unit. This is possible because of the high safety factor for transmission at the neuromuscular junction, where an action potential in a motor neuron will always produce an action potential in its associated muscle fibers. This relation between the motor neuron and the muscle fiber provides the investigator with a relatively simple means of gaining information about the discharge characteristics of motor neurons whose cell bodies lie within the spinal cord.

Common synaptic input delivered by branched neurons at the level of the spinal cord produces correlated discharges of action potentials by motor neurons. The effect on motor unit activity is quantified as motor unit synchronization and is measured by time- and frequency-domain analyses of the discharge times of pairs of motor units. Although technically challenging and tedious, the measurement of motor unit synchronization represents one of only a few techniques that

allows a functional examination of the intact central nervous system during voluntary contractions. Aside from branched common inputs, one alternative mechanism responsible for motor unit synchronization is that it is a consequence of oscillators within the cerebral cortex or brain stem, and the presence of this rhythmicity in the descending drive onto motor neurons may increase force fluctuations or physiological tremor. This line of evidence will not be the focus of the present review, but represents an emerging concept that warrants further consideration. The purpose of this review is to examine the evidence that indicates motor unit synchronization represents a deliberate strategy for neuromuscular activation, rather than an incidental consequence of the activation of divergent connections within the central nervous system. This is achieved by focusing on evidence related to the functional significance and consequences of motor unit synchronization in humans.

QUANTIFICATION AND MECHANISMS OF MOTOR UNIT SYNCHRONIZATION

The most reliable technique to assess the level of motor unit synchronization in human muscles is the cross-correlation of the discharge times of two concurrently active motor units. This technique uses the times of occurrence of discharges from two motor units to construct a histogram in which the discharge times of the reference motor unit, defined as time zero, are correlated with those of the other discharge train, termed the correlated motor unit (Fig. 1, A and B). The appearance of peaks and troughs in the histogram indicate a raising or lowering of the probability of motor unit discharge brought about by a common physical connection between the two neurons. If a tendency toward synchro-

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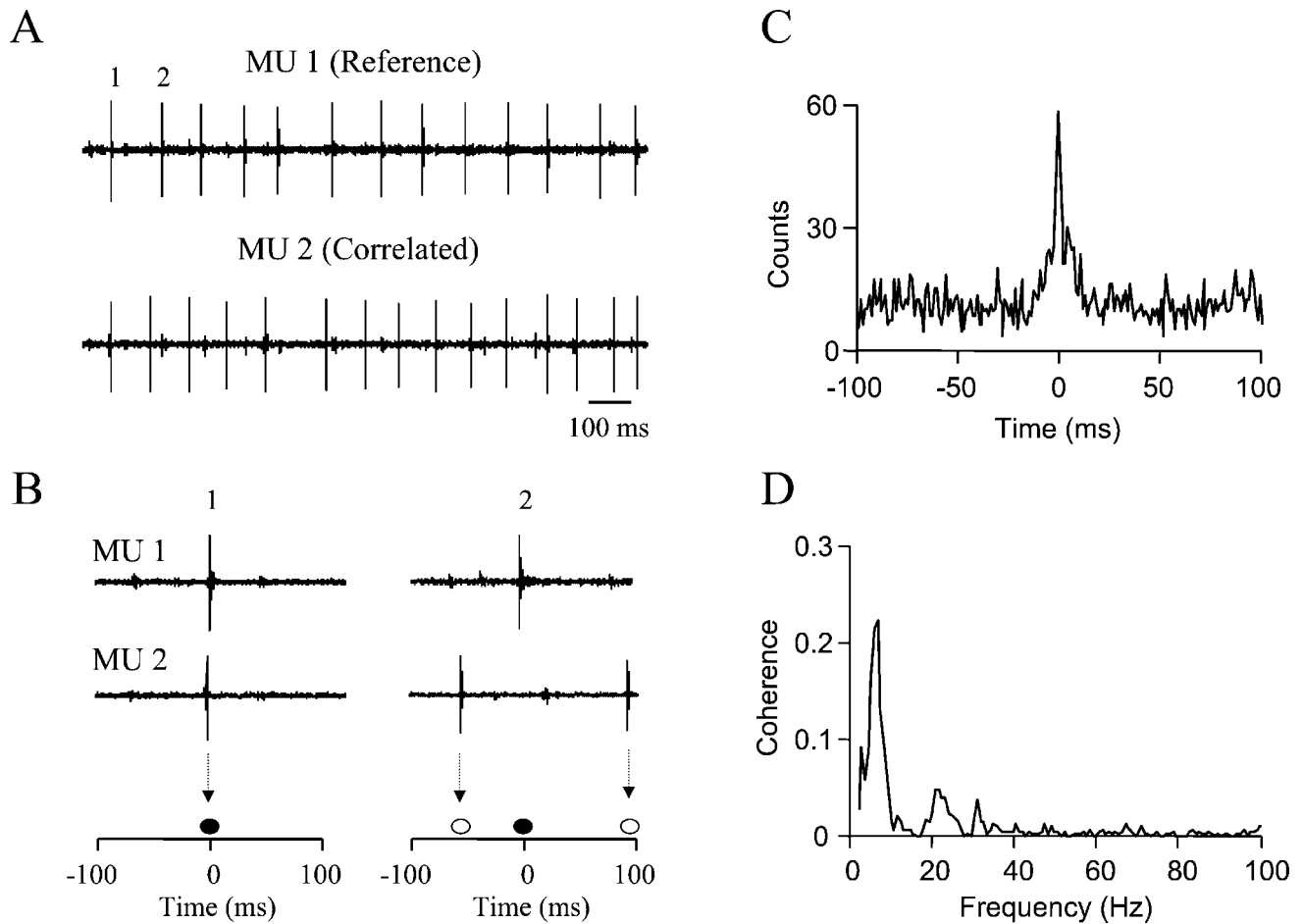


Figure 1. Quantification of motor unit synchronization. A. A train of single motor unit action potentials from two motor units. B. Construction of the cross-correlation histogram for the first two discharges from the reference motor unit (MU 1) in panel A. The discharge times from the reference motor unit (MU 1) are placed at time zero in the histogram, and the relative discharges of the correlated motor unit (MU 2) are plotted at the appropriate time with respect to motor unit 1. The *closed circles* represent the time of discharge of motor unit 2 with respect to the first discharge of motor unit 1. The *open circles* represent the time of discharge of motor unit 2 with respect to the second discharge of motor unit 1. This process continues for each discharge of the reference motor unit. C. An example of a cross-correlation histogram constructed from a 2-min recording of the motor units in panel A. D. An example of coherence analysis from the motor units recorded in panel A.

nization exists, there will be a peak in the cross-correlation histogram around the time of discharge of the reference motor unit (Fig. 1C). The size of the cross-correlation histogram peak is an indication of the relative strength of inputs to the two motor neurons that are derived from common and noncommon sources. A greater proportion of shared input between the neurons will be revealed as an increase in the size of the central peak in the cross-correlation histogram. Although population measures of motor unit synchronization have been established (8,16), the cross-correlation procedure has become the most widely used method of determining the interdependence of human motor unit discharges.

Recently, the frequency domain equivalent of cross-correlation analysis has been applied to human motor unit studies in an attempt to detect periodic firing of common inputs to motor neurons (5). These studies have revealed that coherence can be detected between pairs of motor units in a hand muscle at frequencies of 1–12 Hz and 16–32 Hz during voluntary isometric abduction of the index finger (Fig. 1D). The finding of significant coherence between motor unit pairs at these frequencies implies some common periodicity

of the presynaptic input. While cross-correlation analysis estimates the strength of the common input to two motor neurons, coherence analysis contributes details of the frequency of the common input. Therefore, coherence analysis between two motor units provides additional information about the properties of the inputs responsible for motor unit synchronization that cannot be obtained solely from cross-correlation analysis.

Most motor units that are activated during a voluntary contraction produce a narrow central peak in the cross-correlation histogram. A peak duration of a few milliseconds in the cross-correlation histogram is commonly referred to as motor unit “short-term” synchronization (10). The most widely accepted mechanism responsible for the short-term synchronization of motor units is that it arises through branched inputs from single presynaptic neurons that increase the probability of simultaneous discharge in the motor neurons sharing these inputs (Fig. 2A). This hypothesis has been confirmed by matching the time course of short-term synchronization with equations based on a model of the branched-axon input (7). However, from these equations,

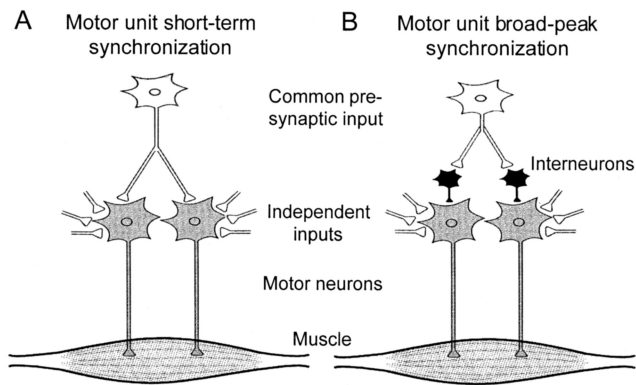


Figure 2. Mechanisms of motor unit synchronization. A. Short-term synchronization is revealed as a narrow peak in the cross-correlation histogram and is produced by a common presynaptic input. B. Broad-peak synchronization is caused by inputs (interneurons) that are themselves synchronized by a common presynaptic input.

only the narrowest central peaks of synchronization can be caused exclusively by a branched presynaptic input that is common to the motor neurons. For peaks with broader durations, synchronization of separate presynaptic inputs to the motor neurons (broad-peak synchronization) must be considered (Fig. 2B). The majority of studies examining motor unit synchronization in healthy human muscles show cross-correlation peak widths from 10–20 ms, which probably reflect a combination of these two forms of input.

Several observations in humans clearly favor the branched input from supraspinal centers in the synchronization of motor unit discharges during voluntary contractions. Two studies involving patients with conditions that affect the corticospinal pathway underscore this view. First, motor unit discharge has been examined in 11 patients with sporadic amyotrophic lateral sclerosis, which is a progressive degenerative disease principally affecting the motor system, which includes the loss of large diameter corticospinal neurons, altered corticospinal excitability, and a slower conduction velocity of the corticospinal pathway. In such patients, almost no motor unit synchronization could be detected in the dominant extensor carpi radialis muscle compared with strong motor unit synchronization in the same muscle of 12 age-matched controls (Fig. 3A). Second, Farmer *et al.* (4) had the unique experience of performing a series of neurophysiological tests on a patient with Klippel-Feil syndrome who had abnormally branched, fast-conducting corticospinal tract fibers that projected to motor neuron pools on both sides of the spinal cord. When using cross-correlation analysis of individual motor unit discharges from both hands (one motor unit in each hand), the cross-correlation histogram revealed a central synchronous peak similar to that observed when two motor units are cross-correlated from the same hand (Fig. 3B, upper panel). This is never seen in normal subjects (Fig. 3B, lower panel). In contrast to corticospinal input, vigorous vibration of an intrinsic hand muscle, which activates muscle spindle afferents, has no effect on the strength of motor unit synchronization (see (3)) indicating that peripheral afferents are unlikely to be an important contributor to the generation of motor unit synchronization. These three observations strongly implicate branched corti-

cospinal axons as an important source of short-term synchronization in motor units, at least for low force isometric contractions.

FUNCTIONAL SIGNIFICANCE OF MOTOR UNIT SYNCHRONIZATION

There are numerous examples of acute changes in motor unit synchronization between pairs of motor units due to alterations in the task performed. The significance of these findings lies in the interpretation that a change in motor unit synchronization between the same two motor units represents a modification in the descending corticospinal command used by the central nervous system to activate the motor units. Specifically, this interpretation indicates that the common input to motor neurons from corticospinal neurons is influenced by the task-related behavior of the active motor units. The question arises, therefore, as to whether the task-related alterations in motor unit synchronization represent a desired neural strategy to promote a functional outcome or whether they are simply a manifestation of the activation of a complex array of connections within the nervous system.

The preeminent study on the functional role of motor unit synchronization in the control of movement was performed by Milner-Brown *et al.* (8), who examined motor unit synchronization in the first dorsal interosseus muscle using a surface EMG-based population index. They found that motor unit synchronization increased after a 6-wk strength-training program in untrained control subjects (Fig. 4A) and concluded that the increase in motor unit synchronization was due to an enhancement of the descending drive from the motor cortex and the cerebellum. This study has been widely cited in the literature as an example of a neural adaptation to strength training and remains the most influential observation on the functional role of motor unit synchronization in humans. However, it has been shown recently that the indirect method of estimating motor unit synchronization from the surface EMG used by Milner-Brown *et al.* (8) has several limitations (16). For this reason, Semmler and Nordstrom (12) examined the effect of habitual physical activity on motor unit synchronization in the first dorsal interosseus muscle using the more direct method of cross-correlation of motor unit discharge. From a total of 544 motor unit pairs in 5 musicians (piano, violin, and flute), 5 weightlifters, and 6 untrained (right-handed) subjects, they found that the strength of motor unit synchronization (index Common Input Strength) during a simple index finger abduction task was largest for the dominant and nondominant hands in weightlifters who did not specifically train the hand muscles. Furthermore, it was revealed that the strength of motor unit synchronization during index finger abduction was lowest in both hands of musicians and the dominant hand of untrained subjects (Fig. 4B), which are the hands that are used most often for skilled movement. The weak motor unit synchronization in both hands of musicians is probably a consequence of low activity in the rapidly conducting corticospinal pathway during the performance of the simple index finger abduction task in skilled hands (11). The central nervous

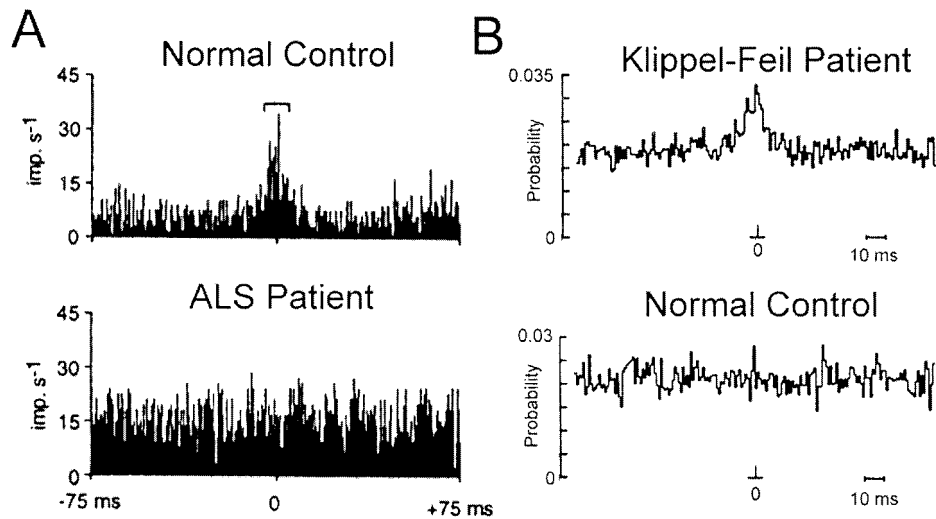


Figure 3. Evidence for the role of the corticospinal pathway for motor unit synchronization. A. Examples of cross-correlation histograms from a pair of motor units in a healthy control subject (upper panel) and from a patient with sporadic amyotrophic lateral sclerosis (ALS). (Reprinted from Schmied, A., J. Pouget, and J-P. Vedel. Electromechanical coupling and synchronous firing of single wrist extensor motor units in sporadic amyotrophic lateral sclerosis. *Clin. Neurophysiol.* 110:960–974, 1999. Copyright © 1999 Elsevier Science. Used with permission.) B. Examples of cross-correlation histograms constructed from one motor unit in each hand of a patient with Klippel-Feil syndrome (upper panel) and one motor unit in each hand of a normal individual (lower panel). (Reprinted from Farmer, S.F., D.A. Ingram, and J.A. Stephens. Mirror movements studied in a patient with Klippel-Feil syndrome. *J. Physiol. (Lond).* 428:467–448, 1990. Copyright © 1990 Cambridge University Press. Used with permission.)

system has the capacity to change the balance of the descending command between direct and indirect pathways, and relegation of the simple task to less-direct pathways may be an adaptation accompanying skilled performance of the hand and a mechanism to alter the strength of common inputs to motor neurons. This neural strategy may free up direct corticospinal neurons to command more complex aspects of a task performed with a skilled hand if the need arises. Nevertheless, the observations of altered motor unit synchronization with exercise and habitual physical activity suggest that motor unit synchronization must represent a deliberate neural strategy for movement control, either directly related to an increase in some aspect of motor output in weightlifters or inversely related to skilled neuromuscular performance in musicians.

Although increased motor unit synchronization does not directly alter the magnitude of force output and hence muscle strength (see 15 and Fig. 6A), it may be beneficial during the performance of contractions where rapid force development is required. Intuitively, it would be expected that increased synchronous motor unit activity at the initiation of a contraction would lead to a greater rate of force development. Van Cutsem *et al.* (14) measured the activity of single motor units in the tibialis anterior muscle from five subjects before and after 12 wk of dynamic muscle training. They found that dynamic training increased the speed of voluntary ballistic contractions, and this seemed to be related to an alteration in motor unit activation (Fig. 5). The altered motor unit activation included earlier motor unit recruitment, an increase in double discharges (doublets), and enhanced maximal discharge rate of motor units. However, it is conceivable that an increase in motor unit synchronization also contributed to the increased rate of force development after dynamic training in this study. Although Van Cutsem *et al.* (14) found that motor unit synchronization (as indicated by the indirect

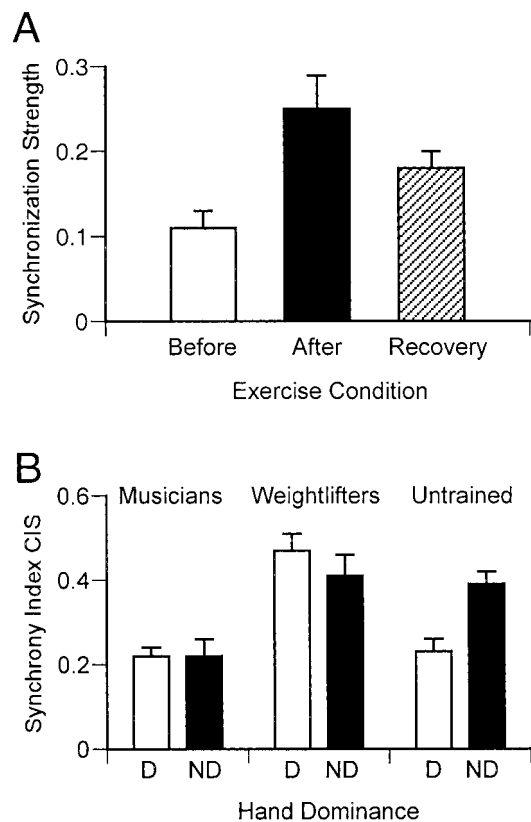


Figure 4. Motor unit synchronization is influenced by exercise and habitual physical activity. A. Strength of motor unit synchronization measured using a surface EMG population index before and after 6 wk of strength training and after 6 wk of recovery in four subjects (8). B. Strength of motor unit synchronization from the cross-correlation histogram obtained in the dominant (D) and nondominant (ND) hands of five musicians, five weightlifters, and six untrained right-handed subjects. [Adapted from Semmler, J.G., and M.A. Nordstrom. Motor unit discharge and force in skill- and strength-trained individuals. *Exp. Brain Res.* 119: 27–38, 1998. Copyright © 1998 Springer-Verlag. Used with permission.]

surface EMG population index) did not seem to change as a result of the dynamic training, the recent finding that motor unit synchronization is enhanced during contractions that require movement (13) suggests that it may play a role in force development during rapid contractions, even under isometric conditions.

Perhaps the greatest benefit of motor unit synchronization to neuromuscular performance is achieved during tasks that involve the simultaneous activation of multiple muscles. Because there is significant branching of inputs between muscles, one point of view is that the branching pattern of last-order synaptic inputs to motor neurons can be a significant determinant of the pattern of muscle synergy in some circumstances. Evidence for this view comes from the cross-correlation analysis of single motor units lying in functionally linked but anatomically distinct muscles (see 1 for a review). For example, motor unit synchronization has been shown to exist between left and right masseter muscles during jaw clenching, and left and right rectus abdominus muscles during trunk curl, but not for the coactivation of homologous muscles of the left and right upper limbs (2). From these data, it has been concluded that at least 25% (and typically between 50 and 70%) of the inputs between functionally linked muscles result from the shared synaptic drive of common presynaptic inputs during muscle coactivation (1). It was further reasoned by Bremner *et al.* (1) that even a relatively small contribution to the total synaptic drive from branched common inputs can be highly influential in determining the pattern of coactivation or muscle synergy between different muscles. Therefore, the functional significance of motor unit synchronization may lie in the selection and activity of common inputs between muscles. By inference, the increased motor unit synchronization observed in a single muscle of weightlifters (Fig. 4B) may also reflect increased common inputs between muscles and be a nervous system adaptation to aid in the coactivation of many muscles to produce force rapidly. Conversely, the lower motor unit synchronization in musicians may reflect minimal common inputs between muscles to promote independent and skilled muscle synergies.

CONSEQUENCES OF MOTOR UNIT SYNCHRONIZATION

Motor unit synchronization has the potential to be a significant factor influencing the amplitude of force fluctuations and tremor exhibited within a muscle. The effect of motor unit synchronization would be large particularly if the motor units that are discharging just below their tonic discharge frequency are synchronized or if synchronous discharges between groups of motor units are correlated in time. However, the extent to which the rather weak motor unit synchronization seen in most muscles influences the precision of force production remains unclear.

A recent study has systematically addressed the effect of motor unit synchronization on the surface EMG and isometric force using a computer model of muscle contraction (15). By imposing two physiological levels of motor unit synchronization on the motor neuron pool (moderate and high synchrony), the authors found that motor unit synchronization significantly increased the amplitude of the fluctuations in the simulated force (Fig. 6A), particularly at low and intermediate levels of excitation (Fig. 6B). The increased force fluctuations were the result of changes in the timing, but not the number, of motor unit action potentials, because at each level of excitation, exactly the same number of action potentials were used to simulate the force. This study indicates that the increased force fluctuations were caused solely by alterations in the relative timing of the action potentials, because the level of motor unit synchronization was systematically varied, while keeping all other factors related to motor neuron activation constant.

Most studies that have examined the relation between motor unit synchronization and tremor in humans have used a correlative approach during low force isometric contractions, where the mean values for each muscle are subjected to a linear regression analysis. The general consensus from these studies is that the strength of motor unit synchronization in normal human muscles is a poor reflection of tremor amplitude. For example, Semmler and Nordstrom (12) examined

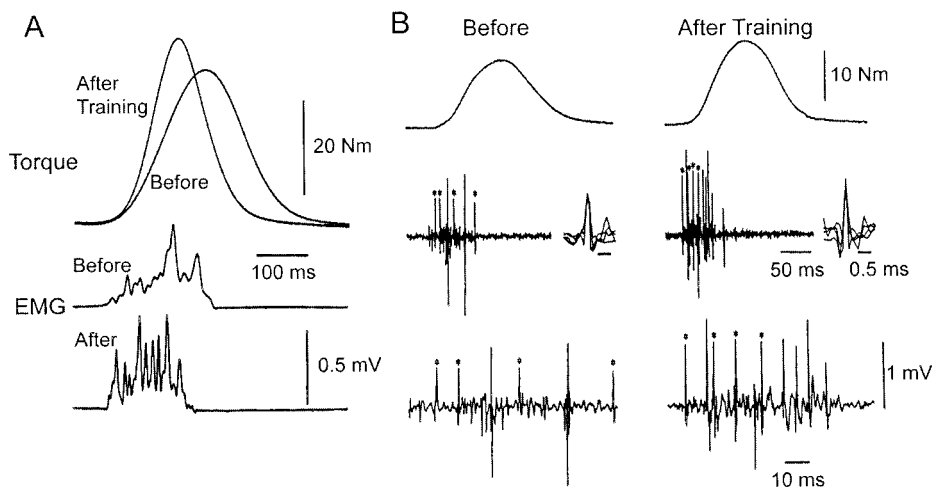


Figure 5. Altered motor unit activation leads to an increased rate of force development after dynamic muscle training. A. Comparison of the torque and rectified EMG recorded in one subject during a rapid isometric contraction before and after dynamic training. B. Torque and single motor unit recordings during a rapid contraction obtained before and after dynamic training. The single motor unit trace at the bottom represents an expanded view of the upper trace. [Adapted from Van Cutsem, M., J. Duchateau, and K. Hainaut. Changes in single motor unit behaviour contribute to the increase in contraction speed after dynamic training in humans. *J. Physiol. (Lond)*. 513:295–305, 1998. Copyright © 1998 Cambridge University Press. Used with permission.]

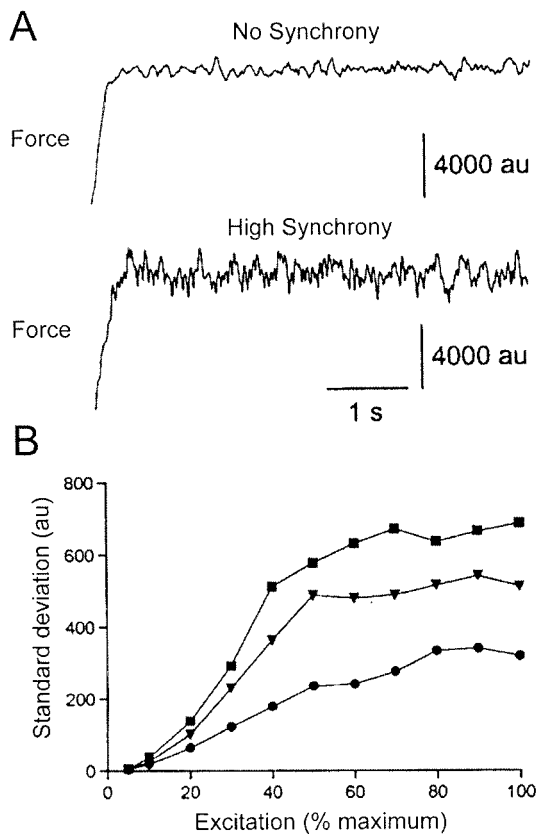


Figure 6. Motor unit synchronization increases force fluctuations in simulated contractions. A. Comparison of the output of the simulated force for the no- and high-synchrony conditions. B. Fluctuations in the simulated force as a function of excitation level for the no-synchrony (circles), moderate-synchrony (triangles), and high-synchrony (squares) conditions. [Adapted from Yao, W., A.J. Fuglevand, and R.M. Enoka. Motor-unit synchronization increases EMG amplitude and decreases force steadiness of simulated contractions. *J. Neurophysiol.* 83:441–452, 2000. Copyright © 2000 American Physiological Society. Used with permission.]

the effect of habitual physical activity on the association between motor unit synchronization and physiological tremor in the first dorsal interosseus muscle. Although the amplitude of motor unit synchronization and tremor was greater in weightlifters compared with musicians, on an individual muscle basis, there was no statistical association between the two dependent variables. These data suggest that motor unit synchronization was not responsible for the differences in tremor exhibited in these subjects, at least under these recording conditions. However, using coherence analysis to quantify motor unit synchronization, it has recently been shown that motor unit synchronization in the frequency ranges 1–12 Hz and 15–30 Hz can account for an average of 20% of the total tremor signal (6). Therefore, a frequency-domain analysis may be more applicable to the characterization of motor unit synchronization and its influence on tremor amplitude.

Despite strong evidence from computer simulation studies, the role of motor unit synchronization on steady force production during voluntary contractions is unresolved. Contradictory findings exist regarding the relation between motor unit synchronization and involuntary force fluctuations in

humans. Although many possibilities exist, one likely explanation for this discrepancy is that the pair-wise comparison of motor unit synchronization through cross-correlation analysis is not sufficient to reflect the synchronization between all active motor units during voluntary contractions. Because the strength of motor unit synchronization is fairly weak (usually between 0.2 and 0.8 extra synchronous discharges per second) and varies considerably between different pairs of motor units in the same subject, a large number of motor unit pairs from one muscle need to be analyzed to obtain a reliable estimate of motor unit synchronization from the cross-correlation histogram. However, it is not always possible to meet these criteria under experimental conditions. Furthermore, cross-correlation analysis between pairs of motor units does not provide information on the extent to which synchronous discharges from other motor units are correlated in time, which is an issue that could substantially influence motor output. Clearly, an alternative measure of synchronization is needed; one that accurately reflects the synchronization and coherence of a population of motor units activated during voluntary contractions.

SUMMARY

Motor unit synchronization is a measure of the correlated discharge of action potentials by motor units and is quantified by both time- and frequency-domain analyses from pairs of motor units. The measurement of motor unit synchronization reveals details about the distribution and plasticity of shared, branched-axon inputs to motor neurons arising from the corticospinal pathway. The acute and chronic plasticity of motor unit synchronization suggests that it must represent a deliberate strategy for neuromuscular activation. Although increased motor unit synchronization contributes to larger force fluctuations, the most likely functional role of motor unit synchronization is to increase the rate of force development during rapid contractions or as a mechanism to coordinate the activity of multiple muscles to promote skilled muscle synergies.

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