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Principles of Motor Unit Physiology Evolve With Advances in Technology

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Movements are generated by the coordinated activation of motor units. Recent technological advances have made it possible to identify the concurrent activity of several tens of motor units, in contrast with much smaller samples available in classic studies. We discuss how these advances in technology have enabled the development of a population perspective of how the central nervous system controls motor unit activity and thereby the forces exerted by muscles.

Movements are controlled by the coordinated activation of neuromuscular units that produce force: the motor units (28, 48). Each motor unit comprises a motoneuron and a muscle unit, where the latter refers to the muscle fibers innervated by the motoneuron. The nervous system produces movements by delivering synaptic inputs to motoneurons that innervate at least several muscles. Once activated, the motoneurons engage the muscle units in the involved muscles to produce both synergistic and antagonistic muscle forces.

To perform movements accurately, the neural drive to muscles (the ensemble output of motoneurons) transmitted by motoneurons from supraspinal centers and sensory receptors must be reliable. As a first approximation, motoneurons process synaptic inputs by functioning as integrate-and-fire systems (66), which means that motoneurons are activated when the time integral of the synaptic inputs causes a change in membrane potential that exceeds the voltage threshold of the motoneuron. The muscle force at which this occurs is known as the recruitment threshold of the motor unit. The rate at which motoneurons discharge action potentials is positively associated with the difference between the synaptic input received by the motoneuron and its voltage threshold. Modulation of discharge rate is known as rate coding (48).

Motor units transduce the neural activation signal into muscle forces, which means that the discharge characteristics of motor units contain information about the neural control signal. It is for this reason that methods were developed to record and decode the discharge characteristics of motor units with intramuscular electrodes (1, 28). One feature of such methods is the high selectivity of the recording, which ensures signal detection but limits the number of motor units that can be discriminated concurrently. Recent developments in electrode technology and biological signal processing have greatly reduced this limitation by making it possible to monitor the concurrent activity of many motor units (85). The concurrent recordings and computational modeling have enabled the development of a population perspective of how the nervous system controls movement. Several key findings indicate that classic concepts of motor unit function derived from recording the activity of only a few motor units need to be revised.

The aim of the current review is to describe the influence of recent advances in technology on our current understanding of how the nervous system controls motor unit activity and thereby the forces exerted by muscles.

Motor Unit Investigation in Humans

Advances in three main areas (electrode fabrication, signal processing, and modeling) have greatly expanded the opportunities to study motor unit activity.

Electrode Fabrication

Motor unit action potentials are recorded by placing electrodes within (1) or above a target muscle. One classic approach is to insert highly selective needle/wire electrodes into the muscle so that it is possible to identify the action potentials of individual motor units (74, 75, 77). However, only a few motor units can be unambiguously discriminated from such recordings.

To overcome the limited sample of motor unit action potentials, advances in electrode design have increased the number of recording sites on each electrode. This has been achieved by microfabricated intramuscular wire electrodes with multiple recording sites (40, 85) and by high-density grids of surface electrodes (52, 61, 72, 73, 81, 108, 119). FIGURE 1 shows examples of these systems and the electric potentials associated with muscle activity recorded at multiple locations inside the

muscle (FIGURE 1A) or on the skin overlaying the muscle (FIGURE 1B).

Multi-channel electrode systems have made it possible to increase the number of motor unit action potentials identified from intramuscular recordings and to introduce accurate methodologies that can identify several motor units from surface recordings. For example, blind source separation methods require several observations (channels) of the same sources to discriminate the activity of single motor units, which has been made possible with the extension of electrode design to multi-channel high-density systems.

Signal Processing

The study of motor unit activity requires the separation of the action potentials for individual motor units from multi-unit recordings. This task, which allows the identification of the times at which motoneurons discharge action potentials, is referred to as EMG decomposition (74). The classic approach to decompose intramuscular EMG signals into single motor unit activities is based on semi-automatic methods to first extract the action potentials that do not overlap in time with those of other motor units (isolated potentials) and then disentangle the action potentials that do overlap with one another (41, 62, 74, 75, 79, 80, 118). This methodology enables each detected action potential to be associated, with appropriate clustering methods, to a specific motor unit. A requirement for this approach is that the number of overlapping action potentials must be substantially less than the number of isolated action potentials. This

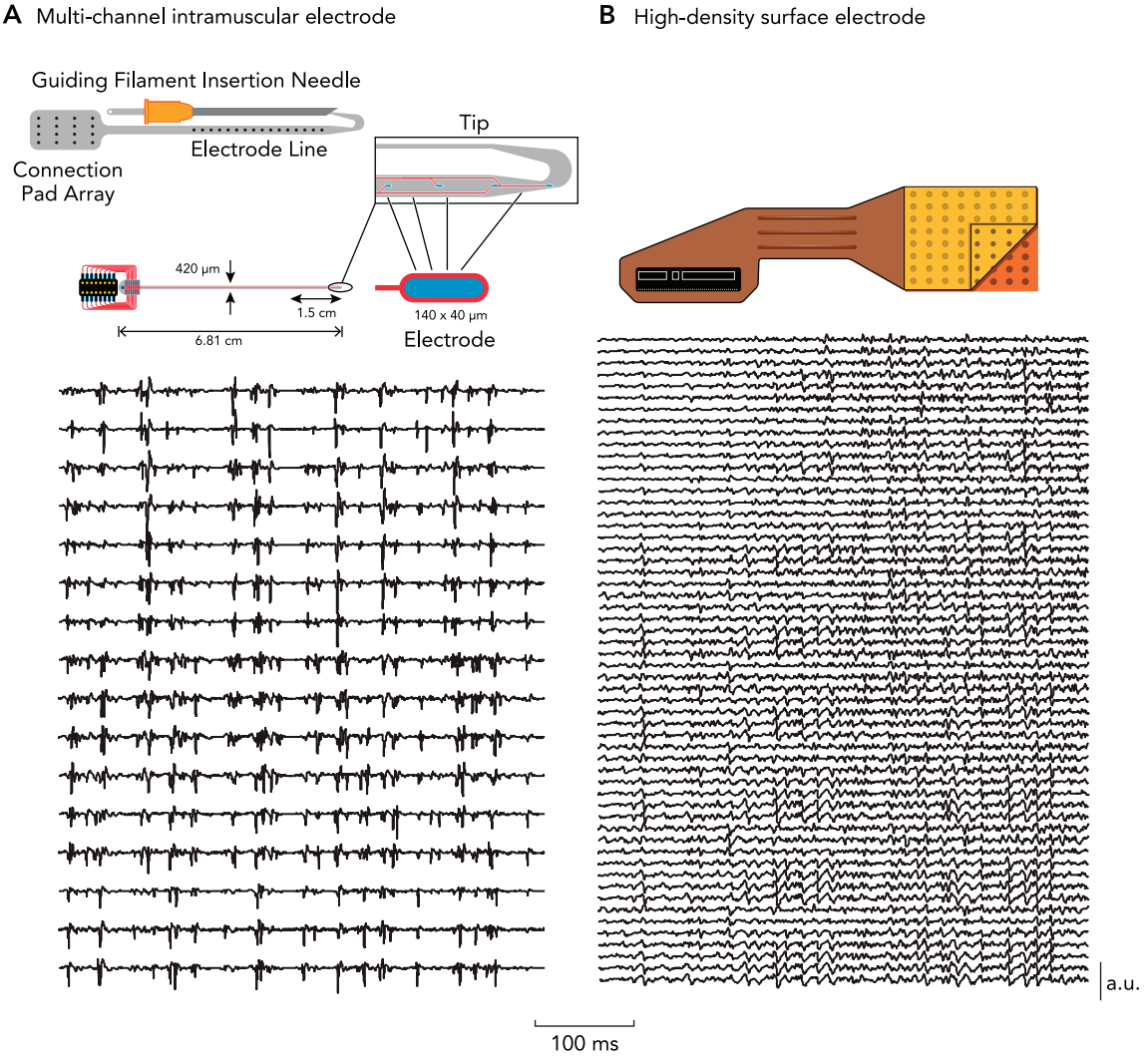

FIGURE 1. **Examples of technology used to obtain multi-channel EMG recordings**
Examples of technology used to obtain multi-channel EMG recordings with an intramuscular electrode (*A*) and high-density surface grids (*B*). *A*: schematic representation of a thin-film wire electrode with 16 recording sites. The wire is inserted into the muscle with a needle that is removed after the insertion, leaving the wire electrode inside the muscle during a contraction. The 16 traces show monopolar signals recorded from the tibialis anterior muscle during a contraction at 10% of the maximal force (85). *B*: the surface electrode grid comprises 8 × 8 electrodes that are equally spaced in the two directions. The 56 traces shown correspond to bipolar signals derived from adjacent recording sites during a low-force dynamic contraction with the wrist flexors.

criterion can be achieved with selective intramuscular recordings at low contraction forces but not with surface EMG signals that mainly comprise overlapping action potentials with similar shapes (31, 35, 37) (see opposing views in Refs. 14, 19, 20, 87). Decomposition of surface EMG signals has not been possible until the last decade (33).

The development of systems with multiple recording sites has changed the approach used to decompose EMG signals. With the availability of several observations (recording sites), the discharge times of many motor units can be identified with blind separation methods (32, 53). These methods are not impeded by the amount of overlap in the recorded action potentials (53-59) and have been proven to identify the discharge times of motor units with high accuracy in both multi-channel intramuscular (93) and surface EMG recordings (58).

The availability of multi-channel electrode technology and advanced decomposition algorithms has made it possible to discriminate the concurrent activity of many motor units. FIGURE 2, for example, shows the activity of 96 motor units in the tibialis anterior muscle during a contraction at 30% of the maximal force (for validation of the accuracy of this approach, see Refs. 32, 34, 57). This motor unit sample is an order of magnitude greater than is possible with classic motor unit recordings. Given that tibialis anterior comprises ~445 motor units (30) and the relatively low muscle force in this example, the identified motor units likely represent a large proportion of those that were active during the contraction. This result was achieved by using two multi-channel intramuscular wires (FIGURE 1A) and one surface grid of electrodes (FIGURE 1B) (85); the surface EMG signals were decomposed with a fully automatic blind source separation method (58, 93), whereas the intramuscular signals were decomposed manually (see Ref. 85 for details).

Computational Modeling

The augmented quality and quantity of information made available by experimental multi-channel recordings have also made it possible to develop more realistic mathematical descriptions of motor unit function with computational approaches (67). Models of motoneuron pools have been developed (10) and used to complement experimental findings (11, 36, 89, 91, 115). Moreover, sensitivity analyses of model parameters provide insight on key experimental findings under different conditions (16, 24, 25, 29).

In addition to the mathematical description of motor unit function with computational models, analytical approaches based on the theoretical modeling of motor unit function have suggested alternative methods for information extraction with respect to classic signal analysis methodologies. For example, the coherence analysis of motor unit discharge times has been refined using analytical derivations based on emerging knowledge on motoneuron function (91, 94).

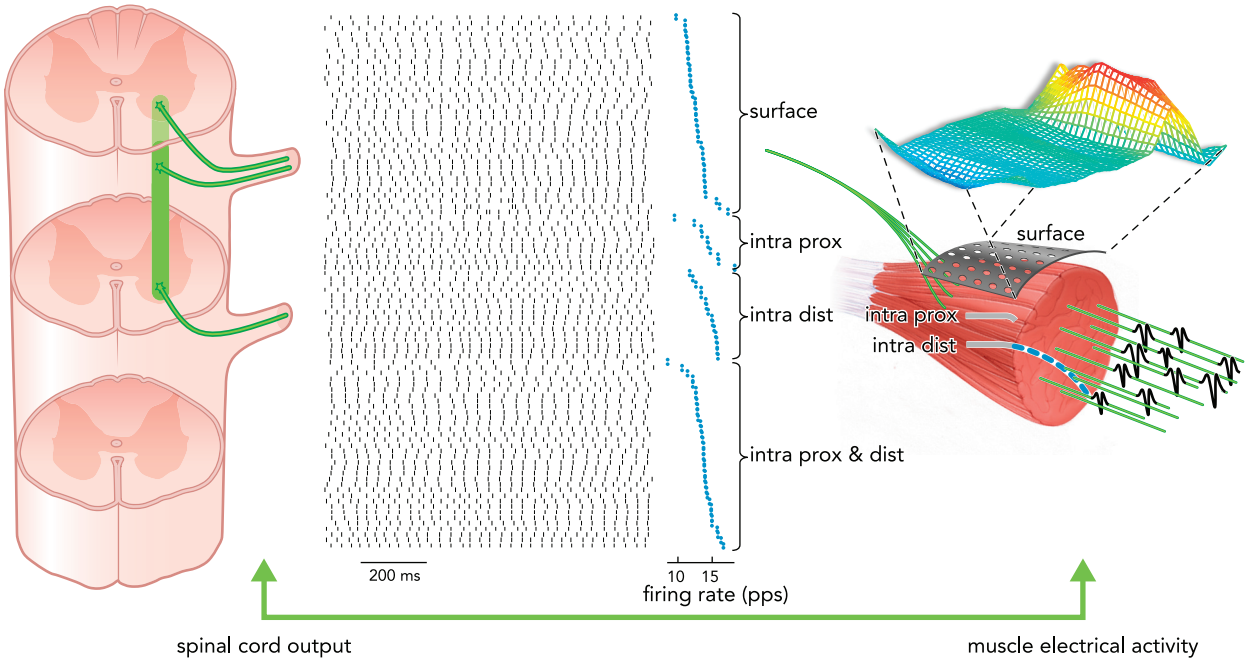

FIGURE 2. **Decomposition of multi-channel surface and intramuscular EMG recordings into the discharge times of 96 motor units**
The recording systems are the same as shown in FIGURE 1. The EMG signals were recorded during isometric contractions of the tibialis anterior muscle at 30% of the maximal force (85). The discharge rate of each identified motor unit is also reported. pps, Pulses per second.

Population View of Motor Unit Activity

The technological advances that have made it possible to study the concurrent activity of many motor units have shifted our understanding of motor unit function to a population view. This shift has produced significant findings on the linearity in the transformation of synaptic input into an output signal by motoneurons, the influence of independent input on the activation signal sent from motoneurons to muscle, and the characteristics of the synaptic input that determines the force exerted by muscle.

Input-Output Linearity

Individual motoneurons process synaptic input nonlinearly, mainly due to the presence of a voltage threshold and the relatively low rates at which they discharge action potentials. One consequence of this nonlinearity is that the same synaptic input received by motoneurons with different intrinsic properties will result in output signals that may comprise different nonlinear terms, i.e., frequency components (39, 65, 90). Due to this nonlinearity, the strength of the common synaptic input received by two motoneurons will not be translated into a proportional degree of correlation between the discharge times of the two trains of action potentials (13, 91). Rather, the amount of correlation in the output signals will depend on the characteristics of the synaptic input and on the intrinsic properties of the two motoneurons (13, 94, 110). It is for this reason that the variability in correlation between the discharge times of action potentials by pairs of motoneurons that receive the same strength of common input can be quite large (18, 105).

In contrast to individual motoneurons, groups of motoneurons exhibit a more linear transformation of common synaptic input into a cumulative train of action potentials that provides the activation signal for muscle (90). The contrasting transformations achieved by individual motoneurons (nonlinear) and groups of motoneurons (approximately linear) have a profound impact on the methods that can be used to analyze neural connectivity and correlation indexes between trains of motor unit action potentials.

Independent Inputs

In addition to common synaptic input, motoneurons also receive synaptic inputs that are independent for each neuron. The origin of common and independent synaptic inputs is not yet known. For example, common synaptic input could arise from the branching of last-order axons onto motoneurons or from a common source that projects to multiple neurons via anatomically separate pathways. It is difficult to distinguish between these two potential origins of common synaptic input due to the similar influence of the two sources on the output of the motoneuron pool.

At the level of individual motoneurons, independent and common synaptic inputs have similar effects on the trains of action potentials they discharge. In contrast, the relative influence of independent and common synaptic inputs received by groups of motoneurons on the force generated by muscle differs substantially. The activation signal sent to muscle (the neural drive to the muscle) corresponds to the sum of the discharge events of the activated motor units. The sum, which is similar to an average, attenuates the influence of components that differ from those that are common. Therefore, the independent synaptic inputs received by each motoneuron are effectively suppressed in the neural drive to the muscle and have small influence on the force generated by the muscle (36). The reduced influence of independent synaptic inputs on muscle force provides new insights on such movement attributes as the accuracy of force control.

Synaptic Inputs Responsible for Force Generation

Based on the preceding discussion, the concept emerges that it is the common synaptic input received by a population of motoneurons that mainly determines the force exerted by muscle. This common input is transformed into the neural drive to the muscle with a gain that is varied by neuromodulation (49). Moreover, the time course of the mechanical response (twitch) elicited in muscle by each action potential reduces the effective neural drive to a relatively small low-frequency bandwidth of the common synaptic input to motoneurons (≤10 Hz) (2). From this perspective, muscle force can be controlled by delivering common synaptic input in the low-frequency bandwidth to a large number of motoneurons whose gain is regulated by neuromodulatory pathways (116). For this reason, the neural signal resulting from this low-frequency common input has been termed the effective neural drive to the muscle, the drive that generates muscle force (88).

Computational studies have recently suggested that common input resulting from a low-frequency modulation of a higher carrier frequency (e.g., 20 Hz) may also contribute to the effective neural drive to the muscle (115). This finding is consistent with our prior suggestion that amplitude demodulation of high-frequency carriers might explain the role of high-frequency components in the neural drive to the muscle (39, 92). Components that

modulate high-frequency carriers might contribute to the average force (115), although the relative significance of demodulated high-frequency common input with respect to low-frequency common input in the resultant neural drive to the muscle is unclear. Nonetheless, there is no doubt that muscle force depends on the effective neural drive to the muscle (the drive within the low-frequency bandwidth of force) and that force control can be obtained only from input common to many motoneurons.

The above conclusion on the role of common synaptic input in generating muscle force is obvious when considering the function of a population of motor units rather than individual units separately. Indeed, a population of motor units can modulate force only if all the units generate common force trajectories. If each motor unit produced independent and random force trajectories, the net output would be constant, and force control would be greatly compromised. The population view, as opposed to the single-unit view, provides a simple way of interpreting force generation as directly determined by the low-frequency components of the neural drive to muscle (36), generated by common synaptic input to motoneurons. Such a perspective has implications for some of the classic methods used to study motor unit function, such as short-term synchronization (39).

From the preceding perspective, differentiation of motoneurons by size is needed to linearize the transmission of common synaptic input (88). Accordingly, a computational study indicated that a population of motoneurons with a broad range of innervation numbers was needed to optimize several criteria for motor performance (26). Significantly, the same study also showed that activation of the motoneurons did not require an order based strictly on motoneuron size (26). Despite the general acceptance of the size principle as a requisite mechanism to ensure adequate force control (5, 8, 12, 22, 23, 50, 114), the activation order of motor units can be more variable than that prescribed solely by differences in motoneuron size, as suggested by the computational study (26) and also evident in experimental data (e.g., Ref. 46). Changes in recruitment order due to differences in intrinsic biophysical properties (e.g., specific membrane conductance) and the strength of synaptic currents (6, 44, 48) likely have a relatively minor influence on force control.

The delivery of common input to motoneurons determines the discharge characteristics of the pool, which also depend on the intrinsic properties of motoneurons and the neuromodulatory input that each motoneuron receives (49). Due to the interaction between motoneuron properties and the different types of inputs received by motoneurons, some observations on the modulation of discharge rate remain unexplained. For example, there is not yet an adequate explanation for why the initial discharge rate of motor units with different recruitment thresholds depends on the force trajectory during a prescribed task (48). Gradual increases and then decreases in muscle force (i.e., ramp contractions) are characterized by the first recruited motor units exhibiting greater initial and peak discharge rates than later recruited motor units (15, 17, 99) but not in all muscles (97). In contrast, the discharge rates of low-threshold motor units when matching relative target forces (% recruitment threshold) are less than those for higher-threshold motor units (3, 84). Also, peak discharge rates during submaximal ballistic contractions are least for low-threshold motor units (21, 113). These differences in rate modulation across conditions likely depend on the relative time courses of the changes in ionotropic and neuromodulatory synaptic inputs, and adjustments in the intrinsic properties of the motoneurons (48).

Emerging Principles of Motor Unit Function

The three concepts described in the preceding section have a major impact on several aspects of motor unit function as established with classic methods. The following three examples indicate how some traditional concepts need to be revised based on the findings obtained with population recordings of motor unit activity.

Accuracy in Force Control

When requiring an individual to exert a constant force during a brief contraction, small oscillations in force around the target value are observed and indicate that the control of force is not perfectly accurate. The determinants of accuracy in force control, also referred to as force steadiness, have been of interest for decades (27, 45, 69, 70, 109, 111). Moreover, force steadiness has been used as a paradigm to compare fine motor control by different groups of individuals, such as young and elderly adults (3, 42, 60, 68, 69, 98, 112).

One of the factors suggested as a potential determinant of steadiness is the variability in the interspike interval of the active motor units, where variability is often quantified as the standard deviation of the interspike interval normalized relative to the mean (45, 69, 84). However, for each motoneuron, this variability is determined by both independent (synaptic noise) and common synaptic inputs as well as by the nonlinearity of the motoneuron behavior (27, 78, 100). Conversely, independent inputs and nonlinear components have a small influence on the activation signal transmitted by the

activated motor units and thus on force (see preceding section). It is therefore not surprising that some experimental studies have failed to find an association between the coefficient of variation for interspike interval in individual motoneurons and force steadiness (3, 104). Accordingly, Negro et al. (88) demonstrated that, except at low forces, the variability in interspike interval was poorly correlated with the coefficient of variation for force during steady submaximal contractions (≤20% of maximal force) performed by hand and leg muscles.

Given the bandwidth of the force exerted by muscles and the filtering effect of the pool of motoneurons, force oscillations during steady contractions are almost exclusively determined by the low-frequency component of the neural drive to the muscle, i.e., the effective neural drive (17, 39, 88). The amplitude of this component is strongly associated (negatively) with force steadiness (38), and its time series is highly correlated with the fluctuations in muscle force (88). Muscle force can indeed be predicted accurately by the effective neural drive to the muscle. To demonstrate this principle, FIGURE 3 shows experimental recordings of 11 concurrently active motor units of the abductor digiti minimi muscle during a low-force contraction (10% of the maximal force). The low-pass-filtered cumulative discharge times of these motor units provides a reasonable estimate of the effective neural drive to muscle. This estimate explains most of the variance in the low-pass-filtered individual spike trains (72% in this example, in agreement with more extensive results presented in Ref. 88), indicating a strong common input to this set of motoneurons. Moreover, the filtered cumulative discharge times also explain most of the variance in the force exerted by the muscle (R^2 = 0.70). The fluctuations in force during steady submaximal contractions are, therefore, mainly explained by these *common* oscillations at low frequency in the discharge times of the activated motor units. These oscillations likely correspond to the variability in the common input to the motoneurons in the same bandwidth (36), although higher frequency components of the common input may be demodulated by the residual non-linear behavior in the motoneuron pool and may add

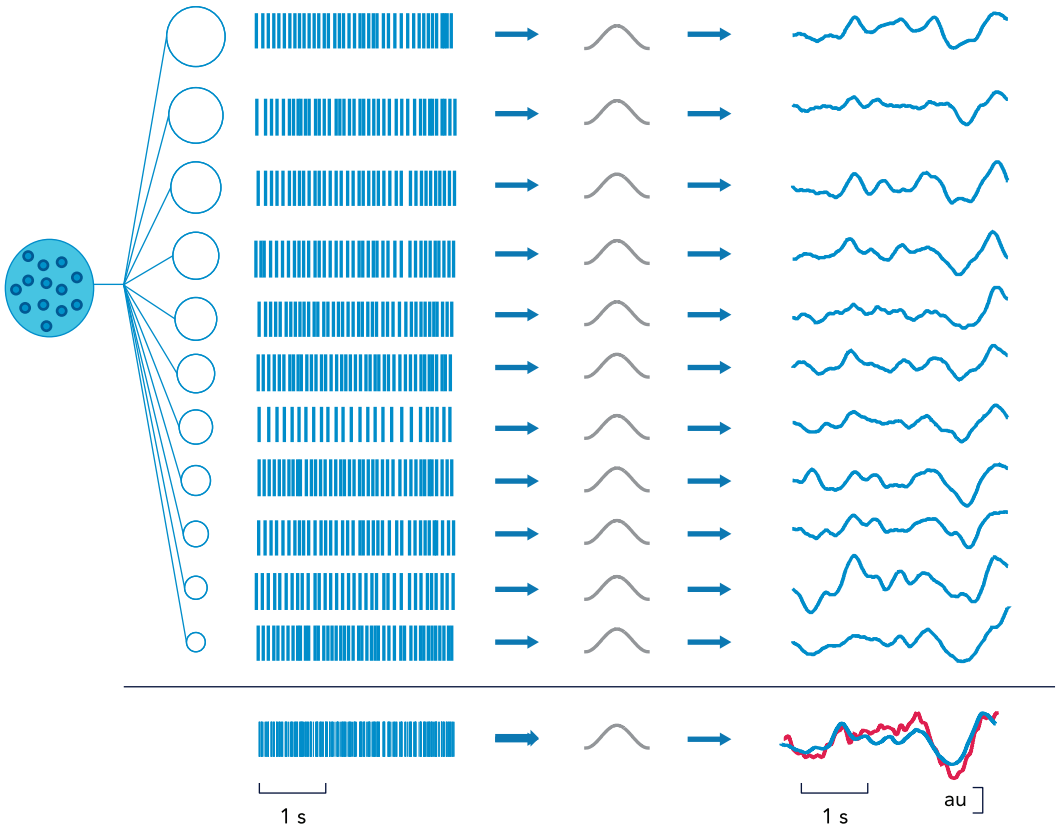

FIGURE 3. **Low-frequency oscillations of the neural drive to muscle predict the force it exerts**
The activity of 11 motoneurons has been decoded from intramuscular EMG signals obtained from the abductor digiti minimi muscle during a contraction at 10% of the maximal force. The series of discharge times (column of spikes) were low-pass filtered with a 400-ms-duration Hanning window (*middle* column) to extract only the low-frequency oscillations (*right* column) (88). The cumulative series of discharge times (*bottom* trace), which corresponds to the sum of the motor unit discharge times, were also low-pass filtered to resemble the force exerted by the muscle (red trace). The sizes of the circles representing the motoneurons are for graphical purposes only and are not intended to indicate the actual sizes of the motoneurons.

some components as well to the effective neural drive to the muscle (115).

Short-Term Synchronization and Other Correlation Indexes

Because the recruitment of one motor unit adds relatively little to the force being exerted by a muscle (43), even weak contractions require the concurrent activation of many motor units. This is accomplished by the delivery of common synaptic input to several large groups of motor units (within and across muscles). Such common synaptic input to a population of motor units invariably elicits some degree of correlation in the timing of the action potentials discharged by the involved motoneurons, as has been reported in classic experimental studies for several decades (64, 101, 103). One measure of the correlation between motor unit discharge times is short-term synchronization (107), which is quantified as the peak of the cross-histogram between pairs of motor unit discharge times. Several approaches have been developed to quantify and normalize this peak (9, 101, 102), with claims on specific properties for each index, including the independence on discharge rate (96). Short-term synchronization has been interpreted as the presence of shared input to pairs of motoneurons and has been associated with specific functional effects (7, 51, 76, 82, 83, 102, 107), including force steadiness (63, 106, 117).

The cross-correlation histogram used to quantify short-term synchronization is the time representation of the coherence function; the two functions are associated by the Fourier transform. Due to the properties of the Fourier transform, the peak of the cross-correlation histogram is the area of the coherence function in its entire bandwidth, whereas the peak of the cross-correlation histogram filtered by a certain bandwidth corresponds to the area of the coherence function in that bandwidth. Such an effect is also produced by filtering the discharge times of motor unit action potentials due to the linearity of the involved operators. The coherence function, therefore, quantifies the correlation associated with different frequency bandwidths. The area of the entire frequency bandwidth corresponds to the classic concept of short-term synchronization, whereas the low-frequency portion of this function represents the concept of common drive (17). Other bandwidths of the coherence function can be associated with different common features of the neural drive to muscle.

Due to the input-output nonlinearity of individual motoneurons, the relative strength of common synaptic input to a pool is not proportional to the amount of correlation between the discharge times for pairs of motoneurons. Therefore, it is not possible to infer details about the structure of synaptic input to motoneurons based on the strength of the correlation between trains of action potentials for two motoneurons. Such an approach can produce misleading results (18, 102). For example, De Luca and Kline (18) concluded that the synaptic input to the motoneurons innervating a single muscle is not distributed to the entire population due to the absence of significant correlations between the trains of action potentials discharged by most pairs of motor units. The low levels of correlation in the output signals for pairs of motor units, however, may be attributable to the nonlinearity of the transformation of synaptic input by the individual motoneurons. By extension, it is not appropriate to compare correlation levels in the discharge times for pairs of motor units between muscles, subject groups, or conditions (91).

The coherence (correlation) values between cumulative discharges for the same muscle in the low-frequency bandwidth of force generation increase monotonically with the number of motor units used to derive the estimate and reaches the maximal value of 1 if the common synaptic input is uniformly distributed to the entire pool of motoneurons (FIGURE 4A). This is due to the observation that the cumulative discharge times of any group of motor units approximates the common synaptic input (see previous discussion on the reduction of independent input in the cumulative discharge times) (39). The slope of the increase in the coherence values as a function of the number of motor units used in the calculation depends on the proportion of common synaptic input relative to the amount of independent synaptic input. Indeed, the averaging process to compute the cumulative discharge times tends toward the common component more quickly when the proportion of this component is greater. This property can be verified with an analytical function that describes the coherence peak as a function of the number of motor units used in the estimate when the common input to the pool is assumed to be uniform (94). When the analytical function was fitted to the experimental data in FIGURE 4A by optimizing the unknown parameters, it was possible to estimate the proportion of common synaptic input relative to independent synaptic input received by a motoneuron pool in the force bandwidth in experimental conditions. The result was that most (>60%) of the synaptic input delivered to motoneurons in the effective bandwidth was common to the entire pool (94). The relative influence of sources of common input at higher frequencies demodulated in the effective bandwidth (115) is still unknown but does not influence the above conclusions.

The population view of motor unit activity also has direct consequences for the functional meaning of

the correlation indexes derived from the discharge times of motor unit action potentials. These indexes express the strength of shared (common) synaptic input to motoneurons relative to independent noise. This approach has limited functional significance, not because the synaptic input is not common, as recently claimed (18), but rather because force control depends on only the common synaptic input. Quantifying its relative strength with respect to an input that has a negligible impact on force generation (independent input) does not provide functional information about force control. In contrast, the absolute power or amplitude of the actual common component (not its relative strength with respect to independent input) has a direct functional significance (38, 88) (see also FIGURE 3).

Neural Connectivity

Coherence between the discharge times for pairs of motor units in different muscles has been used to characterize the connectivity between motoneuron pools (e.g., Refs. 47, 95). Due to the nonlinearity in the transformation of synaptic input by motoneurons, however, coherence analyses typically exhibit considerable variability as intramuscular coherence. Because individual motoneurons discharge action potentials at relatively low rates, the output only represents the low-frequency components of the synaptic input. To determine neural connectivity with coherence measures, it is necessary to use the cumulative discharge times from several motoneurons so that the synaptic input can be represented over a broader frequency range.

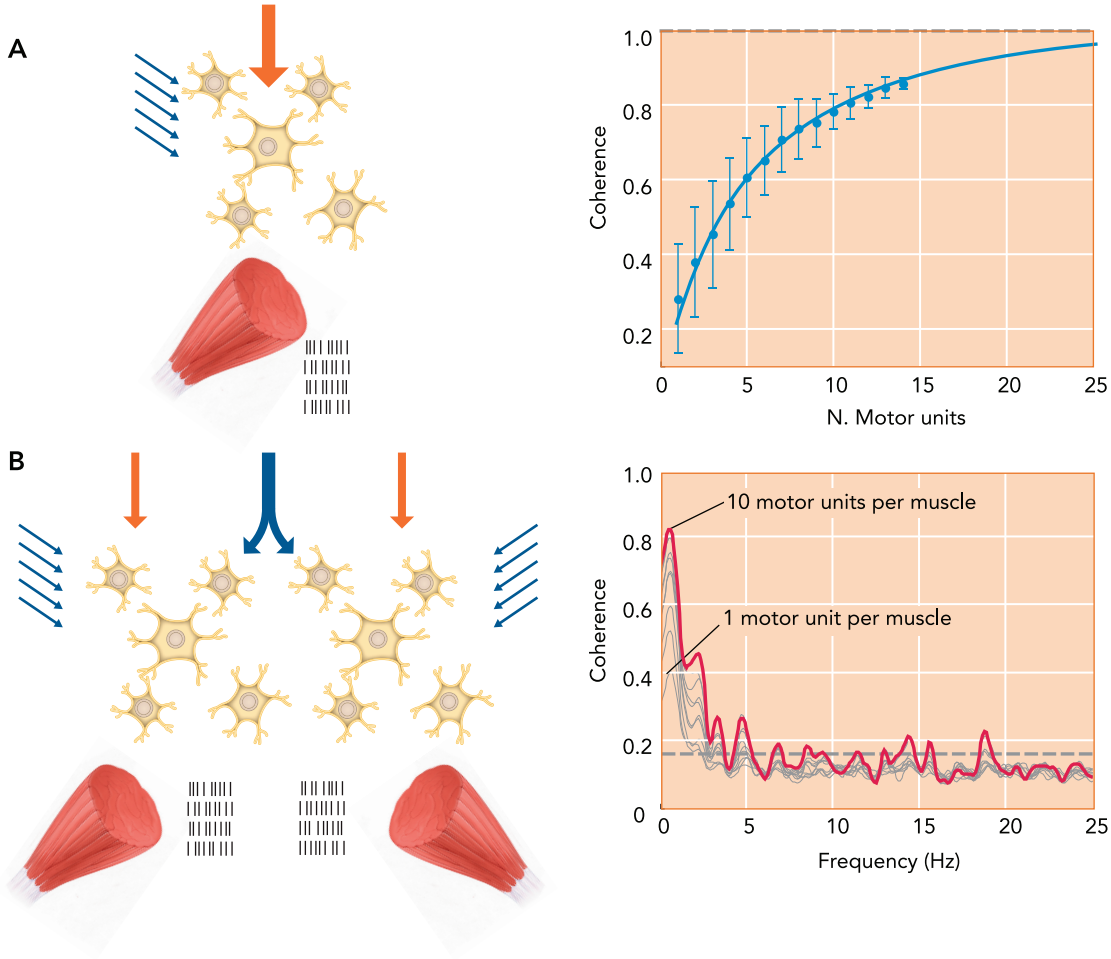

FIGURE 4. **Common and independent inputs to motoneurons within the same motoneuron pool**
A: common (orange arrow) and independent (thin blue arrows) inputs to motoneurons within the same motoneuron pool (one muscle). Coherence was computed from cumulative discharge times for sets of motor units (two separate groups) from the same muscle. The coherence peak, shown in the plot on the right, increases monotonically with the number of motor units used for the estimate. The experimental relation between coherence peak and number of motor units (open symbols) was fit by a function (dashed orange line) that was derived theoretically and approached a value of 1 (94). *B*: schematic representation of two pools of motoneurons innervating separate muscles. Each motoneuron receives independent inputs (thin blue arrows), input common to the motoneurons of the same pool (orange arrows), and input shared between the two pools (thick blue arrows). The coherence functions estimated from recorded discharge times of motor units belonging to each muscle are shown. Coherence was computed for pairs of motor units (1 motor unit per muscle) and for cumulative series of discharge times with an increasing number of motor units (≤10) from each muscle.

This approach has the advantage that several motoneurons transmit the synaptic input in the cumulative output almost linearly for a large frequency bandwidth, which means it is appropriate to analyze the signals with linear techniques, such as coherence analysis.

To illustrate these concepts, FIGURE 4B shows coherence functions computed between the discharge times of motor units in the vastus medialis and lateralis muscles during brief contractions with the knee extensor muscles at 30% of the maximal force. The peak intermuscular coherence value for a pair of motor units was ~0.4, and the coherence values exceeded the confidence level only for frequencies below ~2 Hz. However, when the coherence analysis was extended to include a greater number of motor units, both the level of coherence and its bandwidth increased (FIGURE 4B), as for the case of intramuscular coherence (FIGURE 4A). An analysis with 10 motor units from each muscle resulted in coherence values that exceeded the confidence level for low frequencies up to ~4 Hz, with a peak value of >0.8 and for higher frequencies with significant peaks of ~0.2. The multi-unit result indicates that most of the input to the two muscles is shared (coherence of >0.8) (71), mainly at frequencies <4 Hz but with some higher-frequency components. This example indicates that valid estimates of the neural connectivity between two muscles require a sufficient number of motor units. A practical criterion is to add motor units until the coherence estimates remain stable, i.e., until the coherence values change negligibly when further motor units are added. With a similar approach, it has been shown that much of the synaptic input received by motoneurons innervating synergistic muscles is shared (common) (71).

A Contemporary View of Force Control

Technological advances in the study of motor units have made it possible to record the activity of a large number of motor units concurrently and to derive a population perspective of how the nervous system controls muscle force. The synaptic inputs delivered to the several hundred, on average, motoneurons innervating muscles comprise both common and independent synaptic inputs. Although the input-output properties of individual motoneurons are nonlinear, the engagement of a large number of motoneurons partly linearizes the transformation and suppresses the influence of synaptic (independent) noise. The motoneuron pool, therefore, corresponds to an averaging system that augments the common (and linear) components of the synaptic inputs it receives relative to the independent components. Due to the low-pass filtering property of muscle, it is the low-frequency components of the common synaptic input that generates the effective neural drive to muscles and controls muscle force, although a role for demodulated high-frequency common input has been also postulated (92) and validated in simulation (115).

Common synaptic input establishes correlations between the discharge times of motor units, although this correlation is usually weak when assessed between pairs of units due to the nonlinearity of the individual motoneurons. Estimates of the shared synaptic input delivered to a population of motoneurons by correlation analysis derived from the discharge times for pairs of motor units underestimate the strength of the common synaptic input and lead to erroneous conclusions about its frequency content. Population measures, which provide accurate measures of the proportion of common synaptic input, indicate that most of the synaptic input received by the motoneuron pool innervating both single (94) and synergistic muscles (71) is common, in contrast to the results achieved for pairs of motor units. Due to the significance of common synaptic input and attenuation of a role for independent synaptic inputs, the classic concepts of synchronization or common drive–indexes of the amounts of shared synaptic input with respect to independent synaptic input in large and small bandwidths, respectively–have limited functional significance. Indeed, the accurate control of muscle force by the nervous system depends solely on the power or amplitude of the low-frequency oscillations (or demodulated to the low frequency) present in the common synaptic input (common, not independent, noise).

Based on this perspective, movements emerge due to a combination of muscle forces that are determined by synaptic inputs shared (common) by groups of motoneurons. The involved motoneurons may belong to the same or multiple muscles or constitute only one part of a muscle. The central nervous system sends common synaptic inputs to the functional groups of motoneurons that produce a specific force vector, likely independently on the anatomical muscle boundaries. This reduces the challenges of movement control to that of generating activation signals for a few groups of motoneurons that can produce the requisite forces. Because the synaptic input is delivered to multiple motoneurons, the activation is approximately linear, and a movement can be controlled by simply changing the relative strength of the common synaptic inputs to each of these groups of motor units. Moreover, the relatively high synaptic noise due to the excitory and inhibitory inputs delivered to the thousands of synaptic connections

of each motoneuron (4) is effectively filtered by the same strategy. This view, made possible by advances in technology for motor unit studies, provides a foundation for the global-level prediction about the modularity of human movement generation (86) and describes the neural mechanisms by which motor modules can be engaged and combined linearly by the central nervous system. ■

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