Common drive of motor units in regulation of muscle force

Carlo J. De Luca and Zeynep Erim

The neuromuscular system is responsible for all our interactions with our environment. Although recent decades have witnessed numerous discoveries that have shed light into various properties of this system, the basic principles underlying its overall operation still remain poorly understood. In this article, Carlo J. De Luca and Zeynep Erim discuss the concept of common drive of motor units that provides a possible scheme for the control of motor units, unifying various seemingly isolated findings that have been reported. According to this concept, a pool of motor units that makes up a muscle is controlled collectively during a contraction of that muscle. The unique firing patterns of individual motor units are effected, not by separate command signals sent to these units, but by one common drive to which motor units respond differently. The specific architecture of the system and the orderly gradation in the inherent properties of individual elements enable a single source to control the activities of all the motor units in a given pool. Such an arrangement relieves the CNS from the burden of monitoring and regulating each motor unit separately.

Force production in a muscle is regulated by recruitment of motor units and by modulation of the firing rates of recruited motor units. Recent research in motor control has provided insight into the recruitment order of motor units[1,2], the interaction between recruitment and firing rates[3-6] and the interaction between the force output of the muscle and the firing rate of motor units[3,4,6-9]. However, a framework in which the available knowledge is combined to develop an understanding of the operation of the system is lacking. In this article, recent findings related to the control of motor units will be reviewed, and a model will be constructed that brings all this information together in an attempt to explain how the nervous system might function to effect regulation of motor-unit behavior within a muscle.

Firing patterns of motor units

It is generally accepted that command information from higher centers to the motoneurons is coded in the firing times at which the motoneurons are made to fire. In other words, information transmission in the nervous system is accomplished through frequency modulation. The estimation of a mean firing-rate signal indicative of the command input to the unit is, therefore, a natural step in the analysis of the control properties of motor units.

To obtain a reliable estimate of the mean firing rate of a motor unit, access to the precise moments in time when that motor unit fired is needed. This usually entails the correct identification of the complete activation pattern, that is, all the action potentials, of a motor unit in a recording containing the activation of other units also. This is an extremely difficult technical task, especially in higher force levels, where the number of active motor units is higher, increasing the probability of detecting motor-unit action potentials that are similar in appearance and that might superimpose. To break down the EMG signal into the firing activities of constituent motor units, we have developed a decomposition technique[10-13] that uses specially designed quadrifilar needle electrodes and specific data acquisition procedures.

An example of the firing times of four motor units active concurrently during an isometric contraction of the tibialis anterior muscle can be seen in Fig. 1A. The subject attempted to maintain a constant force after reaching the desired level. Figure 1B displays mean firing-rate signals for these motor units. A mean firing-rate signal is calculated as a weighted average of the number of firings in a time window sliding along the time axis. Determined using this method, a mean firing rate is a continuous time signal that provides an estimate of the average firing intensity of the motor unit at any given time during the contraction. This information, in turn, signifies the increase or decrease in the drive to the motoneuron.

Common drive of motor units

In our efforts to gain a deeper understanding of the mechanisms involved in the generation and regulation of muscle force, we have investigated the concurrent activity of motor units active in the same contraction. The joint analysis of the firing-rate signals of such motor units revealed that motor units active in a contraction modulate their firing rates in a highly interdependent fashion. An example of this phenomenon is displayed in Fig. 1B. The firing rates of all motor units vary simultaneously, with an increase (or decrease) in the firing rate of one unit being accompanied by similar changes in the firing rates of

Carlo J. De Luca is at the NeuroMuscular Research Center, and Depts of Biomedical Engineering and Neurology, Boston University, 44 Cummington Street, Boston, MA 02215, USA, and Zeynep Erim is at the NeuroMuscular Research Center, Boston University, 44 Cummington Street, Boston, MA 02215, USA.
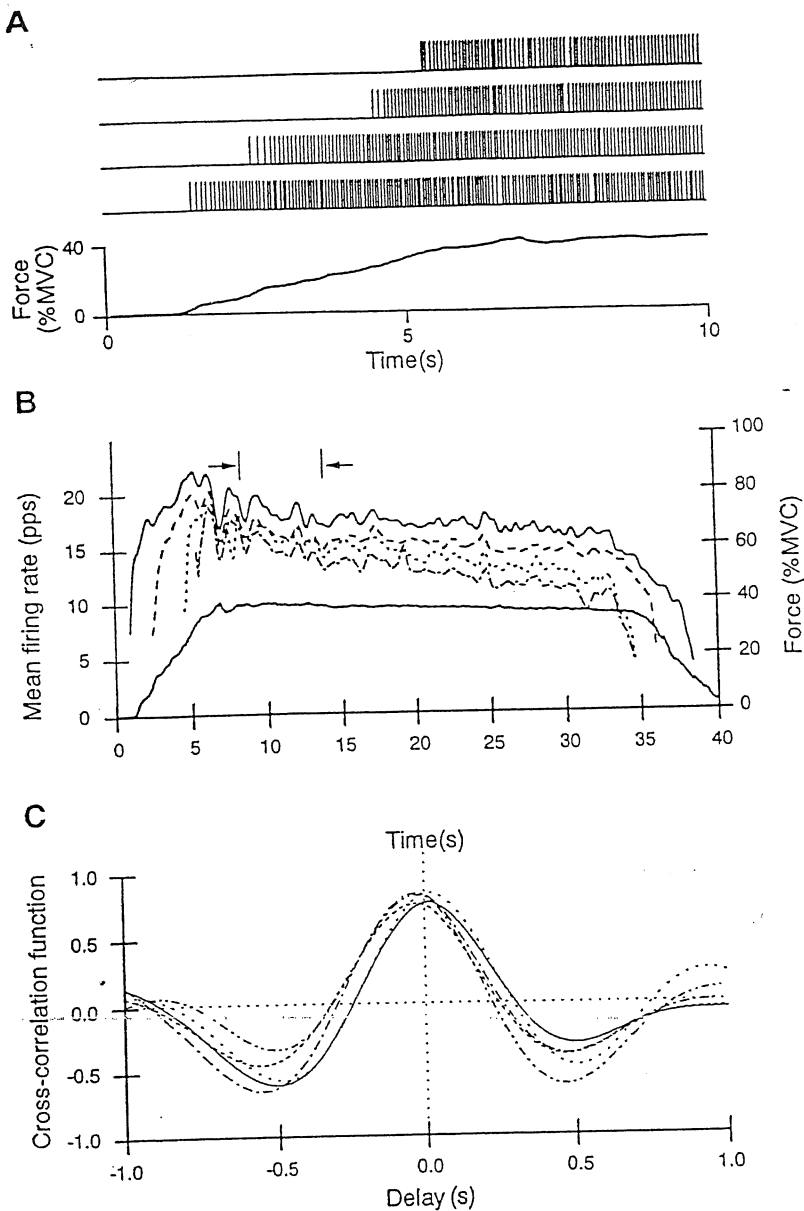
Fig. 1. *Concurrent firing activity of four motor units of the tibialis anterior muscle during the initial ramp of an isometric contraction. (A) Bar plot representing the firing times of the motor units with the force output of the muscle, measured in the same time window, displayed at the bottom. (To enhance visibility, only the first 10s of the contraction is presented.) (B) Firing rates calculated for the motor units in A (broken lines), with the force record superimposed (dark solid line). The firing rates were calculated by passing a 0.95s Hanning window over the motor-unit action-potential impulse trains depicted above. The force is represented as a percentage of the subject's maximal voluntary contraction (MVC). The arrows mark the interval that was used in the cross-correlation analysis. (C) The cross-correlation functions between the firing rates of all the possible pairs of motor units in A and B. The cross-correlation functions were calculated for the 6s window marked in B, where the force output and the firing rates were relatively stable. The average value of the firing-rate signals were removed before cross-correlation in order to analyze exclusively the behavior of the short-term fluctuations.*

firing rates simultaneously, with essentially no time delay. Choosing a different interval or increasing the length of the analysis window changes the resultant cross-correlation function, but not to a significant degree. (For example, if the analysis window is taken as 10–30s of the signals in Fig. 1B, the peak values range from 0.54 to 0.74.) It is important to note that motor units display the highly correlated behavior in this interval also.

We have observed this phenomenon in over 300 contractions and in all muscles we have studied[14], including those in the upper and lower limbs, small and large muscles[15], and those with and without spindles[16]. This phenomenon, which suggests that the activation of motor units is controlled by the same source, has led to the advancement of the concept of common drive. According to this concept, in effecting the desired force output, the CNS regulates the net sum of excitatory and inhibitory inputs to the motoneuron pool. All the motoneurons belonging to the pool receive this same net drive at any given time. Any differences that are displayed among the firing patterns of individual motor units are due to the organization of the pool architecture with respect to the central and peripheral inputs, along with differences in intrinsic characteristics (such as drive–firing rate relationships) of motor units. Any inputs received by an individual motor unit and not shared by other units can be considered as uncorrelated 'noise' in the context of this discussion, and are the reason that the cross-correlation functions in Fig. 1C have values of less than one. The term 'noise', used strictly in the engineering sense, is not meant to dismiss the possible physiological significance of these signals, but instead is meant to distinguish them from the common drive.

The concept of common drive finds support in Henneman's well-known size principle[1], which states that a relationship exists between the susceptibility of a motoneuron to discharge and its size: the smaller the motoneuron, the higher the susceptibility to discharge. Hence, a common driving source can effect different activation patterns in different motor units. Even though motor units of a given motoneuron pool might receive a common drive, their individual thresholds will cause them to begin their firing at different instances. Furthermore, the differences in their susceptibility to excitation will also cause the motor units to fire at different rates during a voluntary contraction, even if they are driven by the same source. As discussed by Henneman and Mendell[17] who assumed implicitly an arrangement with a common driving source, the rank-ordered arrangement of the susceptibilities of motoneurons relieves the CNS from the task of deciding which motor units to activate, and simplifies the circuitry that would have been necessary were the motor units to be activated selectively.

De Luca and colleagues[9] postulated that the source of common drive can be central as well as peripheral. A possible peripheral mechanism has been described by Henneman and Mendell, who have emphasized the importance of the arrangement of afferent fibers in providing the cohesive behavior of the motoneuron pool[17]. We maintain that further investigations are necessary to determine the relative weights of central and peripheral sources. However, experiments on the

others. To further investigate this common behavior displayed by motor units, we used cross-correlation analysis. Figure 1C represents the cross-correlation function calculated between pairs formed among the motor units displayed in the top panel. The high peak values reached by the cross-correlation functions attest to a high level of correlation between the firing activities of motor units, while the near-zero location of the peaks demonstrates that they modulate their

orbicularis oris inferior muscle of the lip, which is accepted as containing no muscle spindles, that is, feedback elements, revealed cross-correlation levels that were comparable to other muscles[16]. This finding rules out the possibility that common fluctuations in motor-unit firing rates could result solely from peripheral feedback. Furthermore, it is believed that spindle activity in isometric contractions is minimal. All the contractions we report on here were isometric, hence decreasing the probability that the observed common drive behavior stemmed from peripheral inputs mainly.

Since, the concept of common drive of motor units was first introduced by De Luca and colleagues[9], it has been supported by others[18-21]. Corroborative data for this concept can also be found in earlier studies[3,22,23]. During the past decade of research, we have not encountered any findings, in our own work or in the reports of others, that contradict the hypothesis of common drive. On the contrary, further observations have been valuable in defining specifics of a model of motor-unit control based on common drive.

'Onion-skin' phenomenon and common drive

A less commonly observed phenomenon of motor unit behavior is that during isometric contractions, the firing rates of earlier recruited motor units are greater than those of later recruited motor units[3,4,6,23-25]. This recruitment-ordered firing behavior is exemplified in Fig. 1B where the firing rates of motor units are plotted as a function of contraction time. At each moment in time, earlier recruited motor units (or motor units with lower recruitment thresholds) maintain higher firing rates than later recruited ones (or ones with higher recruitment thresholds), resulting in an orderly nesting of firing-rate curves under one another – hence, the term 'onion skin'. Occasionally, we have observed deviations from this behavior where the firing rate of a later recruited motor unit will 'cross over' and reach higher levels than earlier recruited ones. However, these deviations can be accounted for by the stochastic nature of the firing activities and the excitation characteristics of individual motor units.

The onion-skin phenomenon represents an apparent paradox in conventional teachings of motor control. It is well known that the later recruited, higher-threshold motor units have shorter-duration, higher-amplitude force twitches compared with their earlier recruited, lower-threshold counterparts[26,27]. Therefore, the higher-threshold motor units require greater firing rates to tetanize (and produce their maximal force) than the lower-threshold motor units.
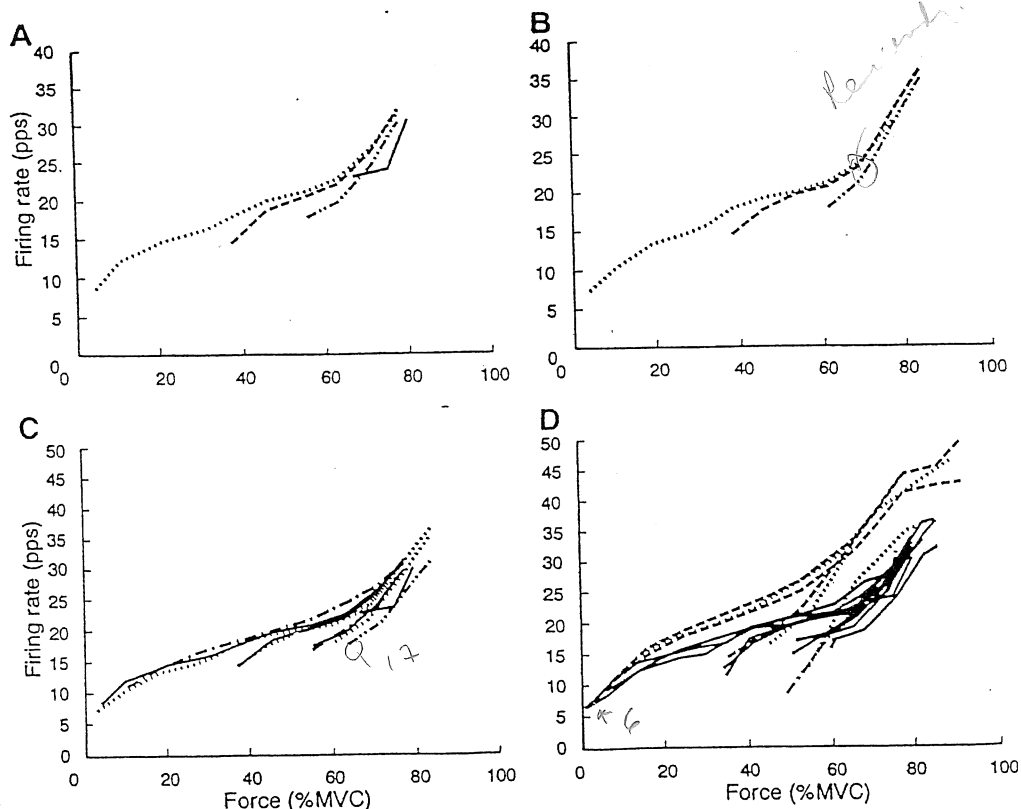

Fig. 2. Firing rates of motor units as a function of muscle force during isometric contractions. Each curve represents the behavior of the firing rate of a given motor unit in a given contraction as muscle force is increased. Firing rates and force averages were computed over 0.5 s windows at 1 s intervals during the linearly increasing parts of force trajectories attempting to reach 100% maximal voluntary contraction (MVC). The resultant curves were smoothed to emphasize the main trends. (A) Four motor units detected in an isometric contraction of the tibialis anterior muscle. (B) Three motor units detected in another contraction of the same muscle in the same subject as in A. (C) All the motor units detected in four separate contractions performed by the same subject. Curves with the same line type represent motor units detected during the same contraction. (D) All the motor units detected in a total of nine contractions performed by three different subjects. Curves with the same line type represent data obtained from the same subject (but not necessarily the same contraction).

Thus, if the neuromuscular system was designed to maximize the force output of a muscle under voluntary control, the higher-threshold motor units would be driven to fire at higher rates. This is not so. One possible explanation for the higher-threshold motor units being driven at lower firing rates is that they are fatigued more quickly than the lower-threshold motor units[26], and would be more quickly exhausted, and thereby would not be able to contribute to a sustained contraction. It appears that the neuromuscular system is designed to optimize some combination of force and duration over which the force is sustained.

The onion-skin phenomenon implies that, under voluntary control, the neuromuscular system might have a reserve capacity for generating unusual levels of force for brief periods of time. In extraordinary circumstances, it is conceivable that the higher-threshold motor units might be activated briefly with dramatically greater firing rates that tetanize and contribute even more to the muscle-force capability. The potential of motoneurons to fire at unusually high rates under increased excitation has been reported by Kernell[28], and explained by Baldissera and colleagues[29]. However, we hasten to add that we have only seen such extraordinary performance in two motor units during one contraction in one subject[4]
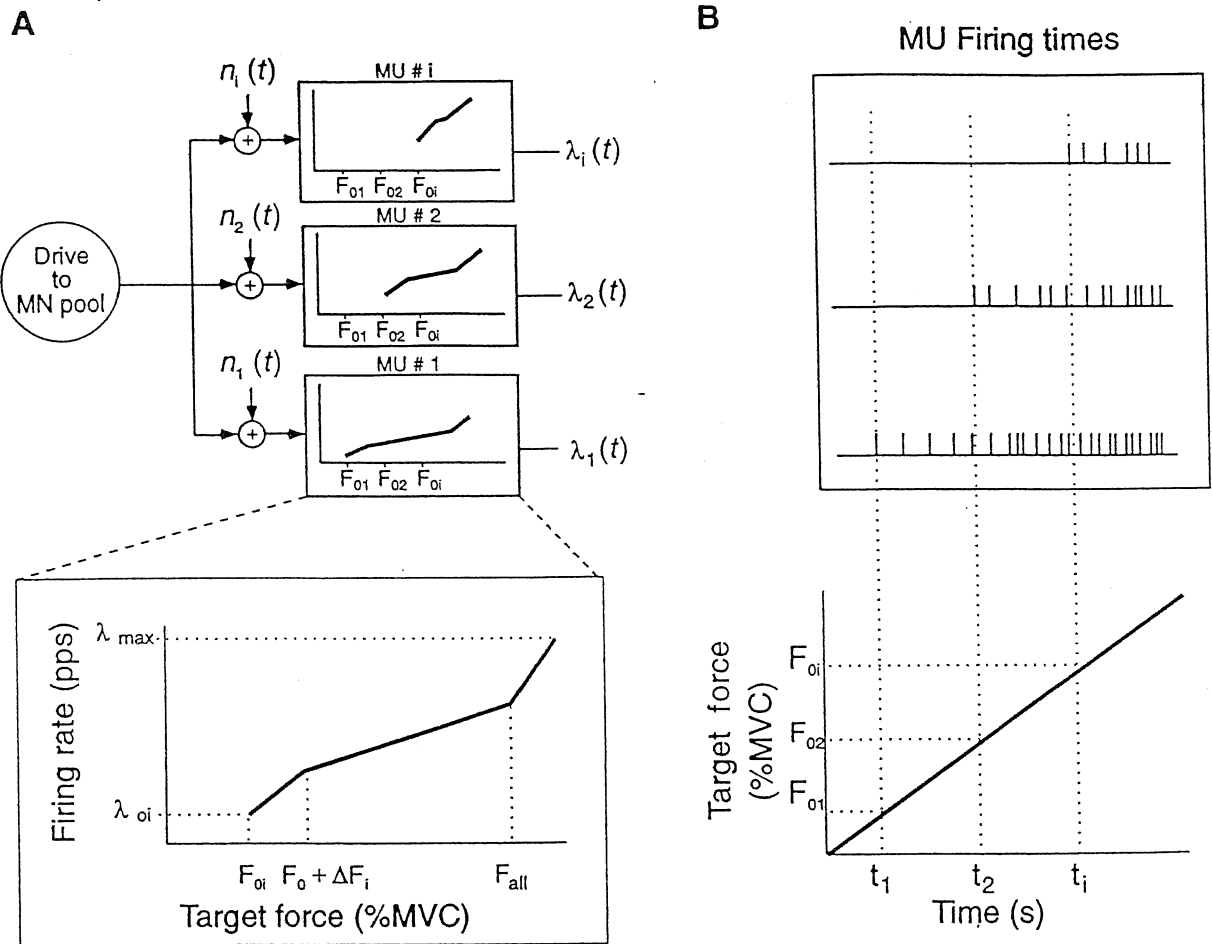
A

B MU Firing times

Fig. 3. (A) *Model for the regulation of recruitment and firing rates of motor units. The common input received by all the motor units in the motoneuron pool is combined with the individual 'noise' signal before it is entered into the individual blocks representing the input–output characteristics of the motor unit. The input–output curves for each motor unit determine the point of recruitment and the firing rate of that motor unit at any force level during the ramp. A blow-up of the input–output curve is presented in the bottom panel, detailing the behavior of the firing rate of motor unit i as a function of the targeted force level. It is assumed that there is a proportional relationship between the targeted force level and the drive to the motoneuron pool. (B) The response of three motor units when driven by an input that linearly increases with time. The driving signal is plotted at the bottom as a function of time. The recruitment order and the firing times of the motor units as the drive increases is given at the top panel. As the drive increases, new motor units are recruited and already active ones increase their firing rates, as dictated by their input–output curves. Abbreviations: MU, motor unit; and MN, motoneuron.*

among more than 300 contractions and 1000 motor units studied.

Firing rates during ramp contractions

To detail more specifically the behavior of motor-unit firing rates, the firing-rate–force relationship in the tibialis anterior muscle at force levels reaching the subject's maximal voluntary contraction (MVC) level was studied. The subjects were asked to trace a force trajectory that increased linearly from 0 to the target force level at 10% $MVC\,s^{-1}$. The firing-rate–force relationship was investigated by plotting the average firing-rate values (obtained by averaging over a 0.5 s window) against average force values (obtained by averaging force values over the same interval) (Fig. 2). The results obtained showed that the firing-rate–force relationship for each motor unit can be characterized into three contiguous regions. The first is the region where the motor unit is newly recruited. In this region, in which a force increase of 10 to 20% of MVC level occurs, the firing rate increases rapidly with force. The second region that follows is one in which

the motor unit increases its firing rate more slowly as force increases. The boundary between the second and the third region coincides with the force level after which recruitment of new motor units is not observed. In this last region, motor units increase their firing rates much faster than in the previous region, possibly to compensate for the fact that the other means of force production, that is, motor-unit recruitment, is no longer available. The behavior of this latter region might differ among muscles depending on the tetanization force characteristics and the architectural arrangement of the muscle fibers and the visco-elastic properties of the muscle and tendon tissues. Another significant observation is that, as the force increases, the firing-rate curves tend to converge to similar firing-rate values at the highest force levels (Fig. 2). This behavior is not seen in Fig. 2D because the curves represent a collection from different subjects and contractions with slightly different force profiles. This collection of curves is presented to demonstrate the general group behavior of motor-unit firing rates. Furthermore, it is also

evident in Fig. 2 that at a given value of force, higher-threshold motor units display higher slopes in their firing-rate–force curves; higher-threshold units are more sensitive to changes in the drive to generate force.

Figure 2 also shows that the initial firing rates of motor units increase with the recruitment threshold. This relationship is not robust, it is not even evident in Fig. 1 where the order in initial firing rates is disturbed by the first motor unit. Nonetheless, the generality of the relationship has been reported previously[4]. Again, as in the case of the less than complete cross correlations of the firing rates, in addition to the common drive, individual motor units receive uncorrelated noise inputs that preclude the system from displaying totally predictable characteristics.

The model

A simple model for the activation of motor units, based on all the issues outlined above is presented in Fig. 3. The purpose of this model is to conceptualize the mechanisms, based on observed phenomena, underlying the control of motor units, not to model individual physiological entities that are at work here. In this model, the net drive to the motoneuron pool is regulated by the CNS. Each motor unit, characterized by its particular input–output curve which determines its response to the common drive, receives the same net drive along with an additive noise, n_i (t), which represents the unique inputs that are received by that motor unit and that are not shared by other units. The response of each motor unit is represented by its firing rate, λ_i (t). This model, whereby all motor units receive a common input, is suggested by the highly correlated, in-phase common fluctuations of firing rates displayed in Fig. 1B and C, while the inclusion of additive noise inputs is based on the less-than-complete cross correlations displayed in Fig. 1C. An input–output curve describes the output of a given system in response to any input in the range of all the possible inputs. In the present context, the importance of the input–output curves lies in specifying a unique response for each motor unit, given a commonly received input. The input–output curves described here are those that define the drive–firing-rate relationship for a monotonically increasing input. Assuming a direct proportionality between the targeted force level and the drive to the motoneuron pool, the results presented in Fig. 2 can be used to make inferences about the drive–firing-rate relationships of motor units. Based on this information, Fig. 3A uses the approximation of representing the drive–firing-rate curve, for a given motor unit, with three linear regions.

Figure 3B uses a linearly increasing drive to the motoneuron pool to demonstrate the operation of the model presented in A. As the net drive to the pool is increased, smaller motor units with low recruitment thresholds are the first to surpass their thresholds and begin firing. With increasing drive, the next unit in the hierarchy becomes recruited and begins firing. However, its firing rate, as governed by its drive–firing-rate curve, is lower than those of the earlier recruited ones that are also receiving higher inputs than they did initially. Further increases in drive level will recruit other motor units and cause increases in the
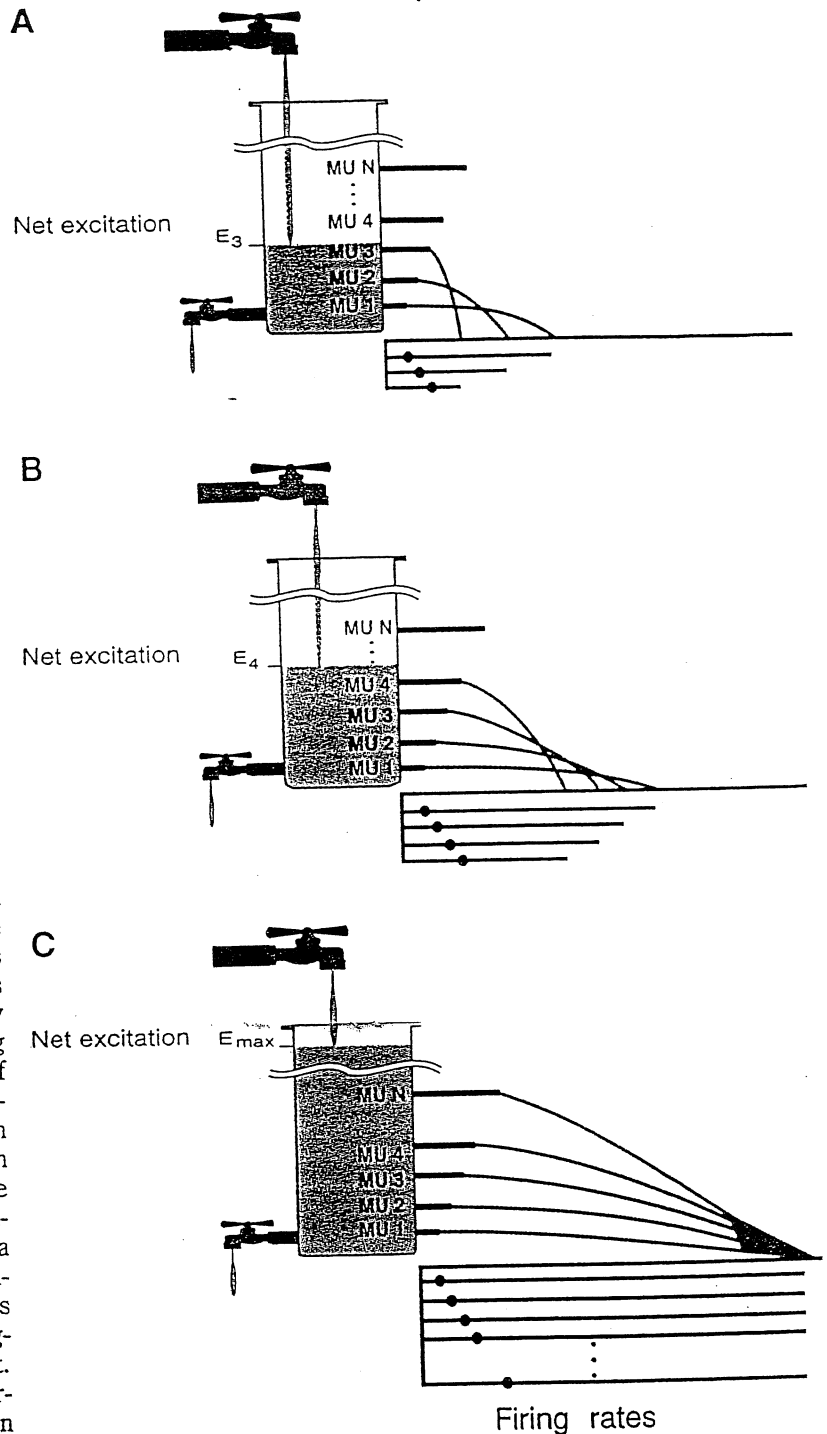

Fig. 4. A simple hydraulic model to summarize the rules governing the regulation of motor units in muscle-force production. The water flow into the tank corresponds to the drive to the motoneuron pool, while the outflow from the individual spouts, and the distance it travels (indicated by a horizontal arrow), corresponds to the recruitment of a given motor unit and its firing rate. The length of each spout is representative of the initial firing rate, while the circle on the arrow representing the firing rate indicates the initial firing rate below which the motor unit cannot fire. The outlet valve on the bottom left represents the inhibition to the pool. The net accumulation of the water in the vat corresponds to the common drive (excitation–inhibition). Broken lines are used to show that vat height is much greater than the distance between individual spouts. (A) The behavior of firing rates when the drive is only enough to recruit three motor units. (B) The recruitment of a new motor unit, and the increase in the firing rates of already active motor units as the drive to the pool is further increased. (C) The convergence of the firing rates to the same value at maximal firing rates for the case of an extreme drive (water height) where the differences between the individual spout heights become negligible compared with the water level.

firing rates of the already-active units, with the reverse proportionality between the firing rates and recruitment thresholds being preserved. This recruitment-ordered firing behavior is exemplified in Fig. 1B and Fig. 2.

In drawing conclusions about the relationship between the net drive level and the firing behavior of the motor unit based on observations on the firing-rate-force relationship, we are associating the force output of the muscle directly to the drive to the motoneuron pool. This simplification overlooks the fact that the actual cause–effect chain has the order drive to firing rate to force, and assumes that the observed force output matched completely the force output desired or intended by the subject. (An alternative to this would be to consider the force trajectory that the subject was asked to trace. However, this would introduce irrelevant factors such as the subject's co-operativeness and concentration, into the analysis.) Since the net excitation to the anterior horn cell is a completely inaccessible signal, drawing parallels between the measured force and the drive level appears to be the preferable solution.

In Fig. 4, we present a metaphorical model to help visualize the basic properties of motor-unit control. As indicated by this simplified hydraulic model, the control of motor-unit firing can be described by a simple system where the structure provides the ordered and co-ordinated response to a common drive (or net excitation). The water flowing in and out of the tank corresponds to the excitation and inhibition impinging on the motoneuron pool; with the water accumulating in the tank corresponding to the net excitation or drive to the motoneuron pool. (Wavy separation lines are used to indicate that the overall height of the tank is much greater than that represented in the Fig.) The height of the spout reflects the recruitment threshold of the motor unit, that is, the excitation level at which it becomes active. The initiation of outflow from an individual spout corresponds to the recruitment of a given motor unit. The distance the outflow travels from the tank signifies the magnitude of the firing rate, with the initial value at recruitment being determined by the length of the spout. The magnitude of the firing rate is indicated by the horizontal arrow, and the circle on the arrow indicates the initial firing rate. As the water level rises (net excitation increases), the distance of the outflow increases as a function of the pressure at the level of the spout.

This model outlines major properties of motor-unit behavior. The phenomenon of common drive is represented by the net accumulation of the water in the tank (excitation–inhibition) which affects all spouts (motor units) below the water level simultaneously. The onion-skin property is denoted by the water from lower spouts reaching longer distances in both submaximal contractions represented in Figs 4A and B. The positive correlation between the recruitment threshold of a motor unit and its initial firing rate at recruitment is represented by increasing spout length (which determines the distance the output water will travel from the tank when the water level first reaches that spout) with increasing spout height. The constant interaction between motor-unit recruitment and firing-rate modulation is evident in the comparison of A, which displays the behavior of firing rates when

the drive is only sufficient to recruit three motor units (E_3), with B, which represents an increase in the drive to the pool (E_4) resulting in the recruitment of a new motor unit as well as in increases in the firing rates of already active motor units.

Concluding remarks

Viewed through the simplicity of common drive and the size principle, the control of the motor units within a muscle presents a functional elegance that relates the specifics of the hierarchical grading to the local size-related excitation of the motor units. This organization frees the CNS to provide a global input to the motoneuron pool corresponding to the intended output of the muscle. The model has addressed only isometric, constant-force or slowly and monotonically increasing contractions. Time-varying processes such as fatigue and potentiation of motor-unit twitches, which have not been considered here, limit the scope of the model. The applicability of the model to ballistic or non-isometric conditions remains to be investigated. It is also important to emphasize that the suggested model and the rules outlined represent the main relationships underlying control of motor units. It is not our intention to imply a deterministic system whereby the behavior of one motor unit could be predicted precisely in comparison with other motor units based on parameters such as their recruitment threshold or mean firing rate. The firing activity of motor units is a stochastic process and random variations can cause some samples to behave against the model. However, the model represents the basic rules governing force production and is a useful tool for speculating on the general behavior of motor units under different conditions.

Selected references

1 Henneman, E., Somjen, G. and Carpenter, D. O. (1965) J. Neurophysiol. 28, 560–580
2 Milner-Brown, H. S., Stein, R. B. and Yemm, R. (1973) J. Physiol. 230, 359–370
3 Person, R. S. and Kudina, L. P. (1972) Electroencephalogr. Clin. Neurophysiol. 32, 471–483
4 De Luca, C. J., LeFever, R. S., McCue, M. P. and Xenakis, A. P. (1982) J. Physiol. 329, 113–128
5 Broman, H., De Luca, C. J. and Mambrito, B. (1985) Brain Res. 337, 311–319
6 Monster, W. and Chan, H. (1977) J. Neurophysiol. 40, 1432–1443
7 Stein, R. B., French, A. S., Mannard, A. and Yemm, R. (1972) Brain Res. 40, 187
8 Milner-Brown, H. S., Stein, R. B. and Yemm, R. (1973) J. Physiol. 230, 371–390
9 De Luca, C. J., LeFever, R. S., McCue, M. P. and Xenakis, A. P. (1982) J. Physiol. 329, 129–142
10 LeFever, R. S. and De Luca, C. J. (1982) IEEE Trans. Biomed. Eng. 29, 149–157
11 LeFever, R. S. , Xenakis, A. P. and De Luca, C. J. (1982) IEEE Trans. Biomed. Eng. 29, 158–164
12 Mambrito, B. and De Luca, C. J. (1984) Electroencephalogr. Clin. Neurophysiol. 58, 175–188
13 De Luca, C. J. (1993) Methods Clin. Neurophysiol. 4, 1–28
14 Masakado, Y., Noda, Y., Nagata, M., Kimura, A. and Chino, N. (1992) Proc. 9th Int. Congress on Elecromyography Clin. Neurophysiol. Jerusalem, Israel, p. 33
15 De Luca, C. J. (1989) in Computer-Aided Electromyography and Expert Systems, pp. 103–109, Elsevier
16 Kamen, G. and De Luca, C. J. (1992) Int. J. Neurosci. 64, 167–175
17 Henneman, E. and Mendell, L. M. (1981) in Handbook of Physiology (The Nervous System: Motor Control Vol. II, part I), pp. 423–507, American Physiological Society
18 Kamen, G., Greenstein-Solar, S. and De Luca, C. J. (1992) Brain Res. 576, 165–167

19 Nordstrom, M. A., Miles, T. S. and Turker, R. S. (1986) *Proc. XXX Int. Congr. Physiol.* 111

20 Stashuk, D. and De Bruin, H. (1988) *IEEE Trans. Biomed. Eng.* 35, 1–10

21 Guiheneuc, P. (1992) in *EMG: Actualites en Electromyographie* (Cadilhac, J. and Dapres, G., eds), pp. 35–38, Sauramps Medical

22 Monster, A. W. (1979) *Brain Res.* 171, 349–354

23 Hoffer, J. A. *et al.* (1987) *J. Neurophysiol.* 57, 530–553

24 De Luca, C. J. and Forrest, W. J. (1973) *Kybernetik* 12, 160–168

25 Tanji, J. and Kato, M. *Exp. Neurol.* 40, 771–783

26 Burke, R. E. (1981) in *Handbook of Physiology (The Nervous System: Motor Control Vol. II, part I)*, pp. 345–422, American Physiological Society

27 Fleshman, J. W., Munson, J. B., Sypert, G. W. and Friedman, W. A. (1981) *J. Neurophysiol.* 46, 1326–1338

28 Kernell, D. (1965) *Acta Physiol. Scand.* 65, 87–100

29 Baldissera, F., Gustafsson, B. and Parmiggiani, F. (1978) *Brain Res.* 146, 69–82