Physiology and Mathematics of Myoelectric Signals

CARLO J. DE LUCA, SENIOR MEMBER, IEEE

Abstract—The myoelectric (ME) signal is the electrical manifestation of the neuromuscular activation associated with a contracting muscle. It is an exceedingly complicated signal which is affected by the anatomical and physiological properties of muscles, the control scheme of the peripheral nervous system, as well as the characteristics of the instrumentation that is used to detect and observe it. Most of the relationships between the ME signal and the properties of a contracting muscle which are presently employed have evolved serendipitously. The lack of a proper description of the ME signal is probably the greatest single factor which has hampered the development of electromyography (EMG) into a precise discipline.

In this article, a structured approach for interpreting the informational content of the ME signal is presented. The mathematical model which is developed is based on current knowledge of the properties of contracting normal muscles. These properties are discussed with particular emphasis on those aspects which are sufficiently understood to allow formulation. Most of the information presented pertains to human muscles, with occasional reference to mammalian muscles for supportive data. The extent to which the model contributes to the understanding of the ME signal is restricted by the limited amount of physiological knowledge currently available. However, even in its present form, the modeling approach supplies an enlightening insight into the composition of the ME signal.

THE MOTOR UNIT ACTION POTENTIAL

NDER normal conditions, an action potential propagating down a motoneuron activates all the branches of the motoneuron; these in turn activate all the muscle fibers of a motor unit [49], [73]. When the postsynaptic membrane of a muscle fiber is depolarized, the depolarization propagates in both directions along the fiber. The membrane depolarization, accompanied by a movement of ions, generates an electromagnetic field in the vicinity of the muscle fibers. A recording electrode located in this field will detect the potential or voltage (with respect to ground) whose time excursion is known as an action potential. A schematic representation of this situation is presented in Fig. 1. In the diagram, the integer n represents the total number of muscle fibers of one motor unit that are sufficiently near the recording electrode for their action potentials to be detected by the electrode. For indwelling needle electrodes, the muscle fibers of the motor unit must be

Manuscript received September 11, 1978; revised March 2, 1979. This research was supported in part by the R.S.A. under Grant 23-P-55854, the National Institutes of Health (NIAMDD) under Grant AM 19665, United C.P. Research and Educational Foundation, Incorporated under Grant R723-76, the Charles A. Dana Foundation, Incorporated, and the Hearst Foundation, Incorporated.

The author is with the Department of Orthopaedic Surgery, Children's Hospital Medical Center, Harvard Medical School, Boston, MA 02115 and with the Massachusetts Institute of Technology, Cambridge, MA 02139.

less than 1.5 mm from the electrode [11]. For the sake of simplicity, only the muscle fibers from one motor unit are depicted. The action potentials associated with each muscle fiber are presented on the right side of Fig. 1. The individual muscle fiber action potentials represent the contribution that each active muscle fiber makes to the signal detected at the electrode site.

For technical reasons, the recording electrode is typically bipolar and the signal is amplified differentially. The shape of the observed action potential will depend on the orientation of the recording electrode contacts with respect to the active fibers. For simplicity, in Fig. 1 the recording electrode contacts are aligned parallel to the muscle fibers. With this arrangement, the observed action potentials of the muscle fibers will have a biphasic shape and the sign of the phases will depend upon the direction from which the muscle membrane depolarization approaches the recording site [33]. To clarify the relative position of the neuromuscular junction of each muscle fiber and the recording site in Fig. 1, lines have been drawn between the nearest point on each muscle fiber and the contacts at the recording site. In the diagram, a depolarization approaching from the right side is reflected as a negative phase in the action potential and vice versa. Note that when the depolarization of the muscle fiber membranes reaches the point marked by the two lines, the corresponding muscle fiber action potential will have a zero interphasic value.

The amplitude of the action potentials is dependent on the diameter of the muscle fiber, the distance between the active muscle fiber and the recording site, and the filtering properties of the electrode. In human muscle tissue, the amplitude increases as $V = ka^{1.7}$, where a is the radius of the muscle fiber and k is a constant [78], and decreases approximately inversely proportional to the distance between the active fiber and the recording site [11]. The filtering properties of a bipolar electrode are a function of the size of the recording contacts [33], the distance between the contacts [56], and the chemical properties of the metal-electrolyte interface [23].

The duration of the action potentials will be inversely related to the conduction velocity of the muscle fiber, which ranges from 2 to 6 m/s. The relative time of initiation of each action potential is directly proportional to the difference in the length of the nerve branches and the distance the depolarizations must propagate along the muscle fibers before they approach the detectable range of the electrode. It is inversely proportional to the conduction velocities of the nerve branch and the muscle fiber. The time delay caused by propagation along the muscle fibers is an order of magnitude greater than

MOTOR UNIT ACTION POTENTIAL Recording Site α motoneuron muscle fiber h(t) Superposition Active Fibers Active Fibers

Fig. 1. Schematic representation of the generation of the motor unit action potential.

that caused by the nerve branch because of the much faster nerve conduction velocity (30-75 m/s). Furthermore, according to Lang and Tuomola [51], the duration increases as the recording site is moved away from the neuromuscular junction. This is due likely to the decreasing diameter, and hence the decreasing conduction velocity of the muscle fibers as they approach the tendon.

The shapes and, therefore, the frequency spectrum of the action potentials will be affected by the tissue between the muscle fiber and the recording site. The presence of this tissue creates a low-pass filtering effect whose bandwidth decreases as the distance increases [55]. This tissue filtering effect is much more pronounced for surface electrode recordings than for indwelling electrode recordings because indwelling electrodes are located closer to the active muscle fibers.

Thus far, muscle fiber action potentials have been considered distinguishable individual events. However, since the depolarizations of the muscle fiber of one motor unit overlap in time, the resultant signal present at the recording site will constitute a spatial-temporal superposition of the contributions of the individual action potentials. The resultant signal is called the motor unit action potential (MUAP) and will be designated as h(t). A graphic representation of the superposition is shown on the right side of Fig. 1. This particular example presents a triphasic MUAP. The shape and the amplitude of the MUAP are dependent on the geometric arrangement of the active muscle fibers with respect to the electrode site as well as all the previously mentioned factors which affect the action potentials.

If muscle fibers belonging to other motor units in the detectable vicinity of the recording electrode are excited, their MUAP's will also be detected. However, the shape of each MUAP will generally vary due to the unique geometric arrangement of the fibers of each motor unit with respect to the recording site. MUAP's from different motor units may have similar amplitude and shape when the muscle fibers of each motor unit in the detectable vicinity of the electrode have a similar spatial arrangement. Note that even slight movements of indwelling electrodes will significantly alter the geometric arrangement and, consequently, the amplitude and shape of the MUAP.

Given the various factors which affect the shape of an observed MUAP, it is not surprising to find variations in the amplitude, number of phases, and duration of MUAP's recorded by one electrode, and even larger variations if MUAP's are recorded with different electrodes. In normal muscle, the peakto-peak amplitude of an MUAP recorded with indwelling electrodes (needle or wire) may range from a few microvolts to 10 μ V, with a typical value of 300 μ V. The amplitude has been found to be inversely related to the muscle temperature [77]. According to Buchthal et al. [10], the number of phases of MUAP's recorded with bipolar needle electrodes may range from one to four with the following distribution: 3 percent monophasic, 49 percent biphasic, 37 percent triphasic, and 11 percent quadriphasic. MUAP's having more than four phases are rare in normal muscle tissue, but do appear in abnormal muscle tissue [59]. The time duration of MUAP's may also vary greatly, ranging from less than 1 ms to 13 ms [84], [2].

It should be emphasized that the amplitude and shape of an observed MUAP are a function of the properties of the motor unit, muscle tissue, and recording electrode. The filtering properties of the electrode (and possibly the cable connecting the electrode to the preamplifiers, as well as the preamplifiers themselves) can cause the observed MUAP's to have additional phases and/or longer durations. This is an inevitable behavior of most filter networks.

PROPERTIES OF MOTOR UNIT ACTION POTENTIAL TRAINS

The electrical manifestation of an MUAP is accompanied (with a delay of a few milliseconds) by a twitch of the muscle fibers. In order to sustain a muscle contraction, the motor units must be repeatedly activated. The resulting sequence of MUAP's is called a motor unit action potential train (MUAPT). The shape of the MUAP's within a MUAPT will remain constant if the geometric relationship between the electrode and the active muscle fibers remains constant, if the properties of the recording electrode do not change, and if there are no significant biochemical changes in the muscle tissue. Biochemical changes within the muscle could affect the muscle fiber conduction velocity and muscle tissue filtering properties.

The muscle fibers of a motor unit are randomly distributed throughout a subsection of the normal muscle and are intermingled with fibers belonging to different motor units. Evidence for this anatomical arrangement in the rat and cat has been presented by Edstrom and Kugelberg [29], Doyle and Mayer [28], and Burke and Tsairis [15]. There is also indirect electromyographic evidence suggesting a similar arrangement occurs in human muscles [82], [83]. The cross-sectional area of a motor unit territory ranges from 10 to 30 times the crosssectional area of the muscle fibers of the motor unit [9], [7]. This admixture implies that any portion of the muscle may contain fibers belonging to 20-50 motor units. The distribution of motor units, according to size, appears to differ among muscles. Clamann [18] found that larger motor units were located near the surface of the biceps brachii. Whereas, in the first dorsal interosseous, Milner-Brown and Stein [63] found that large and small motor units were uniformly distributed throughout the muscle. As a result of the muscle architecture, a single MUAPT is observed when the fibers of only one motor unit in the vicinity of the electrode are active. Such a situation occurs only during a very weak muscle contraction. As the force output of a muscle increases, motor units having fibers in the vicinity of the electrode become activated and several MUAPT's will be detected simultaneously. This is the case even for highly selective electrodes used by Stålberg et al. [84], which detect action potentials of single muscle fibers. As the number of simultaneously detected MUAPT's increases, it becomes more difficult to identify all the MUAP's of any particular MUAPT due to the increasing probability of overlap between MUAP's of different MUAPT's.

Recording Techniques

A variety of different techniques has been employed by numerous investigators for detecting and identifying MUAPT's. Indwelling needle and wire electrodes as well as surface electrodes with monopolar and bipolar configurations have been used.

The most popular electrode has been the needle electrode which was first used successfully in a monopolar and bipolar configuration by Adrian and Bronk [1], and later brilliantly exploited by Buchthal and his associates. More recently, Gurfinkel' et al. [37], Masland et al. [60], and Kranz and Baumgartner [48] used standard bipolar needle electrodes and visual discrimination to identify one or two MUAPT's per recording. Person and Kudina [75] used a bipolar needle electrode with an interwire distance of 0.02 mm, amplifiers, and an oscilloscope with a high-speed camera to record the myoelectric (ME) signal. Individual MUAPT's were identified visually on the basis of amplitude and shape. Three to six MUAPT's from each needle electrode recording were separated for contractions up to 50 percent maximal voluntary contraction (MVC). Milner-Brown et al. [65] also used a bipolar electrode consisting of two 75 μ m wires fixed with epoxy in the barrel of a 25 gauge needle. An oscilloscope was triggered by the electrical signal from each MUAP and pulse-height analyzers were used to distinguish MUAPT's. Again, only contractile forces up to 50 percent MVC were investigated. De Luca and Forrest [23] devised a special quadrifilar needle electrode consisting of four 25 µm karma wires arranged in the configuration of a square and spaced 25 µm apart. The wires were cemented in the tip of the needle with only the cross section of the wires deinsulated. A special technique was used for reducing electrode impedance. This electrode offers the advantage of selecting one of six pairs of bipolar signals to optimally isolate single MUAPT's. Highspeed photographic recordings of the recorded signal and visual discrimination by shape and amplitude were used to separate three MUAPT's up to 100 percent MVC.

Certain fine wire electrodes have also been used with varying degrees of success. Gurfinkel' et al. [39] and Maton and Bouisset [61] used a monopolar wire electrode and were able to use visual discrimination of pulse shapes to pick out individual MUAP's. However, this type of electrode is not well suited to recording individual MUAPT's, especially during contractions greater than 50 percent MVC. Clamann [18] used a bifilar wire electrode consisting of 27 μ m diameter karma alloy wire inserted via a 27 gauge hypodermic needle. Small hooks at the end of the wire held it in place. (This type of electrode was popularized by Basmajian and Stecko [3].) Separation of individual MUAPT's was accomplished by visual analysis of a

moving photographic record. Accurate identification of MUAPT's was claimed for contractions up to 100 percent MVC. Hannerz [42] used a trifilar (100 μ m silver wire) electrode. Visual separation was again used with accurate separation of MUAPT's, in some cases up to 100 percent MVC. Leifer [53] used a quadrifilar electrode consisting of 25 μ m stainless steel wire. The four wires were arranged in a straight line. The electrode was hooked at its end to anchor it in the muscle after insertion via a 27 gauge hypodermic needle. The individual MUAPT's were separated automatically by a digital computer. The separation scheme was based on amplitude discrimination. Voluntary contractions up to 80 percent MVC were studied.

Another method of recording identifiable MUAPT's has been devised by Gydikov and Kosarov [40]. They used a special surface electrode consisting of an array of small monopolar electrodes. The array is placed over the motor unit end plate region. By using this noninvasive technique, it is difficult to find MUAP's that can be identified and isolated. Their study reports only a total of 30 motor units from 15 different attempts.

Interpulse Intervals

When MUAPT's can be properly identified, it is possible to measure the time between adjacent discharges of a motor unit, i.e., the interpulse interval (IPI). The IPI has been observed to be irregular and can be described as a random variable with characteristic statistical properties [24].

The most general characterization of the IPI is a histogram, which is a discrete representation of the probability distribution function. The histogram should be computed for relatively short durations of the MUAPT (preferably less than 10 s). The shape of the IPI histogram, as reported by various investigators, is not consistent. Buchthal et al. [13], Leifer [53], Clamann [17], and others have reported the shape to have a Gaussian distribution. De Luca and Forrest [24], [25], Person and Kudina [76], and others have reported an asymmetric distribution with positive skewness. Person and Kudina stated that as the mean duration decreased, the IPI histogram became more symmetric, with a substantial decrease in the standard deviation. Gurfinkel' et al. [37] noted that the IPI histogram also becomes more symmetric with a lower standard deviation when visual and/or audio feedback of the motor unit discharges are provided for the subject. The use of different muscles, erroneous discrimination of MUAP's and time-varying firing rates of the MUAPT's could contribute to the differences. Time-varying firing rates of the MUAPT's may be particularly culpable.

Two common parameters of the probability distribution function, or the histogram, are the mean and the standard deviation. These two parameters have been used to describe the IPI's. Tokyzane and Shimazu [90] reported that it is possible to differentiate between two types of motor units (tonic and kinetic) by plotting the mean and standard deviation of the IPI's. They found that the standard deviation decreases rapidly as the firing rate increases from its threshold value and reaches a constant value at higher rates. The standard deviation of all motor units is approximately the same when they are initially recruited, but tonic motor units are recruited at

much lower firing rates. Leifer [53], Person and Kudina [76], De Luca and Forrest [24], and Hannerz [42] found no such distinction. They instead found a continuous range of motor unit behavior between these two extremes. The rapid decrease of the standard deviation with increasing firing rate after recruitment is found in the data of Hannerz and of Person and Kudina. The latter investigators proposed that after hyperpolarization (positive afterpotential) is responsible for reducing the standard deviation, and thus increasing the regularity of the intervals.

Gurfinkel' et al. [37] reported several influences on the standard deviation for the IPI's of individual motor units. They found a tendency for the standard deviation to decrease when normal subjects used surrogate means of control (audio or visual feedback) in addition to proprioception. In patients with disturbances of joint perception, the standard deviation was considerably reduced compared to a normal individual, but in patients with cerebellar disturbances, no differences were seen. Sato [79] found that the coefficient of variation (standard deviation divided by the mean) for motor units from the dominant hand of right handed subjects tended to be lower than that of the left hand. Voluntary oscillations were more regular when performed with the right hand. This intimates that a lower coefficient of variation corresponds to greater capability of precision control.

Another statistical parameter of interest for describing the IPI's of a motor unit is their interdependence. The greatest amount of dependence (if any) should occur between adjacent intervals. Dependence may be tested by plotting the values of the adjacent IPI's against each other in the form of a scatter diagram. If the adjacent IPI's are independent and the random process is stationary (time invariant), the points on the scatter diagram will be randomly distributed in a fashion determined by the probability distribution function of the IPI's. In case of dependence, the points on the scatter diagram will have statistically dependent coordinates. An alternative test for dependence is serial correlation. If the average product of the adjacent IPI's is equal to the square of the average of the IPI's, then the serial correlation is zero and the IPI's are linearly independent. Lesser values indicate a negative serial correlation and the tendency of short IPI's to be followed by long IPI's, and vice versa. If the IPI random process is not stationary, the above tests may indicate dependence, when none exists. Therefore, measurements for IPI dependence must be performed over sufficiently short time periods, to reduce time-varying effects.

Several authors have noted weak negative correlations between adjacent IPI's of single motor units. Kranz and Baumgartner [48] found some motor units that exhibited negative serial correlation, some weakly positive, and some with no significant correlation. It should be noted that in their procedure the subjects were provided with audio and visual feedback and were asked to maintain a constant firing rate. Clamann [16] and Masland et al. [60] found no significant serial correlation in most cases during constant force isometric contractions. For similar contractions, Person and Kudina [75], [76] found negative serial correlation only for motor units firing at rates

above 13 pulses/s. At these firing rates they found a constant small standard deviation (5 ms) and symmetric IPI histograms. They attributed these results to the effect of afterhyperpolarization. De Luca and Forrest [24] used a chi-square test on the joint interval histogram for adjacent intervals. No dependence of any statistical significance was found.

Few authors report having made calculations from the IPI data of single motor units to test for higher order interval dependence. The second- through tenth-order serial correlation coefficients computed by Kranz and Baumgartner [48] were of lesser magnitude than the first-order coefficients, and the chi-square test on the third-order joint interval histogram computed by De Luca and Forrest [24] revealed no dependence.

Recruitment

During a constant-force isometric contraction, Gilson and Mills [34], Masland et al. [60], De Luca and Forrest [24], and Grimby and Hannerz [36] have indicated that a motor unit which is active at the beginning appears to remain active throughout a contraction. The issue of time-dependent recruitment during a constant-force isometric contraction is not yet resolved. Edwards and Lippold [30], Vredenbregt and Rau [92], and Person [74] have postulated that time-dependent recruitment should occur to retard fatigue during prolonged contractions. De Luca and Forrest [24] were not able to verify the latter conjecture.

The most consistent observation of motor unit behavior reported in the literature concerns the order of recruitment as a function of size. Henneman et al. [43] observed in decerebrate cats that the order of recruitment during a stretch reflex is from smallest to largest diameter motoneurons. During voluntary contractions, Thomas et al. [89] have observed that limited reversal order of recruitment is possible in muscles that have multiple physiological functions. Since the number of muscle fibers innervated by a motoneuron is proportional to its size, smaller motor units are therefore recruited first and larger motor units last. Freund et al. [31], working with humans, measured the nerve conduction velocities and found that the slower conduction velocities, and thus the smaller nerves, were associated with the lower threshold motor units. Clark et al. [19], working with rhesus monkeys, have also confirmed that motor units recruited at lower force levels have longer contraction times and produce smaller twitch tensions than higher threshold motor units.

Evidence has been presented by Milner-Brown and Stein [63] that in the first dorsal interosseous muscle, the largest contribution of motor unit recruitment occurs at low-force levels. As the force output increases, increasingly larger motor units are recruited [68], [66]. By averaging the force output of the muscle as each pulse from a single motor unit occurred, Milner-Brown et al. [66] were able to determine the twitch tension of each motor unit. They found a linear relationship between twitch tension and recruitment force, indicating that the fractional increment in force $(\Delta F/F)$ is constant. Goldberg and Derfler [35], investigating the masseter muscle, found that motor units with high-recruitment thresholds tend to have larger amplitude MUAP's and twitches with greater

peak tensions than motor units recruited at lower force levels. The larger motor units have been shown to discharge with lower firing rates than other motor units [88], [68].

In most normal muscles, motor unit recruitment appears to terminate at approximately 75 percent MVC. Gydikov and Kosarov [41] could only observe minimal recruitment above 60 percent MVC in the biceps brachii. Clamann [18], investigating the same muscle, did not find any recruitment above 75 percent MVC. However, Hannerz [42] noted occasional recruitment above 75 percent MVC in the tibialis anterior.

Although there appears to be generally orderly progression of motor unit recruitment as the force output increases, the neuromuscular control scheme is not absolutely rigid. Grimby and Hannerz [36] found that during bursts of contractions, only motor units that would normally be activated at relatively high-force levels were recruited. Person [74] reported that the recruitment order was stable for a given movement task, but was not stable when the movement task of the same muscle was changed. If the above results are valid, i.e., they are not due to electrode displacement, they imply that the recruitment order is force sensitive.

Firing Rate

In a normal muscle the motor unit does not discharge at constant intervals. Therefore, discharges of a motor unit must be measured in terms of an average firing rate, which is the reciprocal of the average IPI. However, for the average firing rate values to be meaningful, they should be measured over a representative sample of at least six successive IPI's. Measurements made over a smaller number of IPI's may lead to unrepresentatively large values, and measurements made over too many IPI's may obscure meaningful trends in the firing rate.

During a constant-force isometric contraction of the rectus femoris and deltoid muscles, the firing rate of motor units decreases monotonically [76], [24]. Hence, the sequential discharge of a motor unit is a time-dependent process.

The force dependence of motor unit and firing rate during an isometric contraction has been studied by many investigators. The currently available information does not provide a consistent description of the mechanisms involved in force modulation. A frequently studied human muscle is the biceps brachii. Clamann [18] found that the firing rate of motor units recruited at the lowest force levels was 7-12 pulses/s. The firing rate increased with increasing isometric force to a maximum of approximately 20 pulses/s. The minimal firing rate of a motor unit increased linearly with the threshold of recruitment. Almost no motor units fired above 20 pulses/s, even near 100 percent MVC. Leifer [53] found that all motor units fired at approximately 11-16 pulses/s throughout the entire range of contraction force. After a motor unit was recruited, its firing rate increased slightly with increasing force and then remained constant at a preferred rate. He found that this preferred rate increased slightly with increasing threshold of recruitment. As the force level decreased, the firing rate decreased to 30 to 40 percent of the preferred rate before becoming inactive. Gydikov and Kosarov [41], also working with the biceps brachii, found that all motor units had a firing rate of 6-10 pulses/s when they were recruited. For some motor units, the firing rate increased to approximately 13 pulses/s and then remained constant with increasing force. Whereas, for other motor units, the firing rate increased linearly with force up to 100 percent MVC. The former were generally recruited at lower force levels than the latter. Based on their data, they proposed the existence of two types of motor units, tonic and kinetic. However, their small sample source (a total of 30 motor units from 15 subjects) limits the significance of their proposal. Clamann [18] and Leifer [53] never recorded two types of motor units in the biceps brachii, however, the firing rate characteristics found by these two investigators appear to differ slightly. Person and Kudina [76] found that in the rectus femoris muscle, the low threshold motor units began firing at 5-11 pulses/s and reached 18-21 pulses/s at 45 percent MVC. They also found that the higher the recruitment threshold of the motor unit, the less the motor unit increased its firing rate with increasing force. At force levels up to 47 percent MVC the motor units with lower thresholds had higher firing rates.

Hannerz [42] and Grimby and Hannerz [36], working with the tibialis anterior and short toe extensors, found that the minimal firing rate of motor units recruited below 25 percent MVC was 7-12 pulses/s and the maximal firing rate was 35 pulses/s. For motor units recruited above 75 percent MVC, the minimal firing rate was 25 pulses/s and the maximal firing rate was 65 pulses/s in the tibialis anterior and 100 pulses/s in the short toe extensors. Thus, both the average firing rate and the initial firing rate at recruitment increased with force. They also found that all motor units recruited above 80 percent MVC discharged in bursts with pauses of 1 s or more at constantforce levels. In a complementing study on the toe extensor, Borg et al. [6] found that motor units which voluntarily could be driven continuously at firing rates below 10 pulses/s had axonal conduction velocities between 30 and 45 m/s; those that could be driven only in higher firing rate bursts had higher axonal conduction velocities.

Milner-Brown et al. [65] have studied the activity of single motor units in the first dorsal interosseous muscle contracting at force levels below 50 percent MVC. They found that when recruited, motor units began firing at 8.4 ± 1.3 pulses/s and increased their firing rate 1.4 ± 0.6 pulses/s for each 100 g of force output, independent of the force at which each motor unit was recruited. They also found that a change in the force rate affected this result. At slow rates of increasing force (100 g/s), the firing rate had a tendency to reach a plateau, while at faster rates of increasing force (1000 g/s) motor units were recruited at lower force levels, but with higher initial firing rates. This difference was not apparent during decreasing voluntary force contraction.

Freund et al. [31] also performed an extensive investigation of single motor unit activity in the first dorsal interosseous muscle. They found that all motor units, regardless of their recruitment threshold, began firing at approximately the same rate $(6.8 \pm 1.4 \text{ pulses/s})$. However, the lower threshold motor units increased their firing rates with increasing force much

faster than the higher threshold units. The firing rates increased with force asymptotically to a maximum rate which also depended on recruitment threshold. These maximum rates varied from approximately 10 to 25 pulses/s for low to high threshold motor units, respectively. However, none of the studied motor units was recruited above a force of 700 g. The rate of force increase tested by Freund et al. [31] was slower than that tested by Milner-Brown et al. [65]. This difference might account for some of the observed discrepancy.

Posttetanic Potentiation

During repetitive excitation, as is the case in a sustained contraction, the twitch tension of motor units is potentiated (increases). This phenomenon was first observed in mammalian muscles by von Euler and Swank [91]. More recent studies by Standaert [85], Nystrom [71], and Burke et al. [14] have investigated the posttetanic potentiation in the in vivo soleus and gastrocnemius muscles of the cat. Substantial potentiation was always evident in the gastrocnemius muscle, in contrast to relatively little potentiation in the soleus muscle. Olson and Swett [72] localized the effect to muscle fibers of the gastrocnemius which contained a moderate to large number of mitochondria and an ample blood supply. These muscle fibers are very fatigue resistant.

Potentiation of the twitch tension of motor units has been also observed in the human forearm flexors by Gurfinkel' and Levik [38]. However, no correlation has been found between the twitch tension potentiation and the amplitude of the MUAP [45].

Synchronization

All the above properties of the motor units have described the behavior of individual motor units. Synchronization, the tendency for a motor unit to regularly discharge at or near the time that other motor units discharge, describes their behavior with respect to each other. This includes, but is not limited to, MUAPT's which are phase locked or entrained. In a mathematical sense, synchronization can be defined as dependence between MUAPT's. Hence, cross correlation is a sufficient, but not exclusive, condition for synchronization. The latter technique has proven useful for detecting synchronization.

Evidence of the symptoms of synchronization has been reported by several authors. Lippold et al. [57], [58] found that the MUAPT's from different motor units tended to group at the rate of approximately 9 bursts/s. This grouping became more evident when the muscle became fatigued. Missiuro et al. [65] and others have claimed to observe synchronization by noting the appearance of large periodic oscillations in the ME signal as the muscle fatigued. Direct evidence was noted by Mori [69], who observed the motor unit discharges in the soleous muscle synchronized during quiet stance in man. In a later study, Mori and Ishida [70] demonstrated that the discharge of motor units would indeed become synchronized if the feedback from the muscle spindle in the muscle was sufficiently large.

Kranz and Baumgartner [48] and Shiavi and Negin [80] performed a cross-correlation analysis between the MUAP's of

simultaneously recorded MUAPT's. They concluded that during nonfatiguing constant-force isometric contractions of the first dorsal interosseous, flexor digitorum profundus, extensor digitorum indicis, and tibialis anterior, there was no significant cross correlation. However, Buchthal and Madsen [12] and Dietz et al. [27], using the same technique, did find evidence of weak cross correlation in normal muscles. The amount of the cross correlation increased in diseased muscles. The degree of cross correlation also increased as the amplitude of the physiological tremor increased. Milner-Brown et al. [64] have reported that synchronization of MUAPT's is more evident in subjects who frequently exert large brief forces, and that synchronization can be accentuated by performing such contractions.

The phenomenon of motor unit synchronization has not been analyzed and documented as fully as the other motor unit properties. Evidence has been presented that motor units tend to synchronize during fatigue, during physiological tremor, after excercise, and in some disease states. However, no detailed description of the behavior of synchronization as a function of measurable parameters such as force and time has been given. This has been mainly due to the limitations of the recording and analysis techniques. During relatively high-force contractions, currently available electrodes detect too many MUAPT's simultaneously, which cannot be accurately identified and separated for analysis with present techniques.

Summary of Electrophysiological Data

It is clear from the preceding information that at the present time there is no definitive explanation of motor unit behavior during muscle contractions. The apparent contradictions in the reported data are likely due to the disparity in the too few studies that have been performed, and to the varying behavior of different muscles. However, the following description emerges from the currently available information.

During a constant-force isometric contraction the firing rate decreases as a function of contraction time. Motor units which are active at the beginning of a contraction remain active throughout the contraction. Time-dependent recruitment, which might be expected, has not been observed to occur in any significant fashion. However, there is some evidence that the twitch tension of motor units increases as a function of contraction time.

During force-varying isometric contractions the following interplay between firing rate and recruitment occurs. At the beginning of a contraction, recruitment is the dominant factor with the smallest motor units being recruited first. The firing rate at recruitment is unstable and has a minimal value of 5-6 pulses/s. Up to 30 percent MVC recruitment remains the dominant factor, with progressively larger motor units being recruited as the force increases. As a secondary factor, the firing rate also increases. For force levels ranging from 30 to 75 percent MVC, the dominant factor is the increase in the firing rate. Some recruitment of increasingly larger motor units also occurs, but plays a secondary role. At force levels above 75 percent MVC, the further increase in the firing rate continues to be the dominant factor. In most muscles, little (if any) recruitment occurs. In those cases where recruit-

ment has been observed, the firing rate has been irregular. As the innervation ratio of the motor unit increases, the amplitude of the MUAP increases, the twitch tension increases, and the firing rate generally (but not always) decreases. Finally, the force rate of a muscle contraction may have a significant effect on the firing rate and recruitment interplay.

Synchronization of the discharges of motor units has been noted when a muscle fatigues, during both constant-force and force-varying isometric contractions. Finally, the IPI's between adjacent MUAP's have been shown to be independent in most cases, and to have a weak dependence in a few cases.

A MODEL FOR THE MUAPT

Several investigators have attempted to formulate mathematical expressions for the MUAPT [4], [54], [21], [20], [86], [8], [32], [22]. Of these investigators, only Libkind [54], De Luca [22], and Gath [32] have employed empirically derived information to construct the model.

As discussed in the previous section, the MUAPT can be characterized by its IPI's and the shape of the MUAP. The most commonly used parameters of the ME signal are the mean rectified value and the root-mean-squared value. To obtain these parameters for the MUAPT, it is only necessary to consider the average firing rate and the shape of the MUAP in the MUAPT.

Evidence has been presented indicating that the firing rate of a motor unit is dependent on the time duration, force, and possibly the force rate of a muscle contraction. Although it has yet to be clearly shown, it is conceivable that it is also dependent on the velocity and acceleration of a muscle contraction. For the purpose of our discussion, the firing rate will be considered to be only a function of time t and force Fand will be denoted as $\lambda(t, F)$. This restriction in the notation is adopted for convenience. However, it should be clearly understood that the derivations which follow apply for any general description of the firing rate. If future investigations reveal definitive relationships between the firing rate and the force rate, velocity and acceleration of a contraction, they can be readily incorporated into the ensuing model with no loss of generality. A systematic way of obtaining a mathematical expression for $\lambda(t, F)$ is to fit the IPI histogram with a probability distribution function $p_x(x, t, F)$. The inverse of the mean value of $p_x(x, t, F)$ will be the firing rate, or

$$\lambda(t,F) = \left[\int_{-\infty}^{\infty} x \, p_x(x,t,F) \, dx \, \right]^{-1}.$$

Alternatively, a mathematical expression of $\lambda(t, F)$ could be obtained by performing a regression analysis of the IPI's as a function of time and force.

On the other hand, it would be extremely difficult to give a unique mathematical description of the MUAP because there are many possible shapes. However, if a MUAPT is isolated and the MUAP can be identified, it would be possible to make a piecewise approximation of the shape. Refer to De Luca [22] for additional information on the mathematical representations.

From a mathematical point of view it is convenient to de-

compose the MUAPT into a sequence of Dirac delta impulses $\delta_i(t)$ which are passed through a filter (black box) whose impulse response is $h_i(t)$. If each Dirac delta impulse marks the time occurrence of an MUAP in a MUAPT, the output of the filter will be the MUAPT or $u_i(t)$. The integer i denotes a particular MUAPT. This decomposition, shown in Fig. 2, allows us to treat the two characteristics of the MUAPT separately.

The Dirac delta impulse train can be described by

$$\delta_i(t) = \sum_{k=1}^n \delta(t - t_k).$$

It follows that the MUAPT $u_i(t)$ can be expressed as

$$u_i(t) = \sum_{k=1}^n h_i(t - t_k)$$

where $t_k = \sum_{l=1}^k x_l$ for k, $l = 1, 2, 3, \dots, n$. In the above expressions, t is a real continuous random variable, t_k represents the time locations of the MUAP's. x represents the IPI's, n is the total number of IPI's in a MUAPT, and i, k, and l are integers which denote specific events.

It is now possible to write the following expressions:

mean rectified value = $E\{|u_i(t,F)|\}$

$$= \int_0^\infty \lambda_i(\hat{t}, F) |h_i(t - \hat{t})| d\hat{t},$$

mean-squared value = $MS \{u_i(t, F)\}$

$$= \int_0^\infty \lambda_i(\hat{t}, F) h_i^2(t - \hat{t}) d\hat{t}$$

where \hat{t} is a dummy variable and E is the mathematical symbol for the expectation or the mean. Although the above equations can be solved, the computation requires the execution of a convolution. De Luca [22] has shown that since $\lambda(t, F)$ is slowly time varying, the above expressions can be greatly simplified to

$$E\{|u_i(t,F)|\} = |\underline{h_i(t)}| \lambda_i(t,F)$$

$$MS\{u_i(t,F)\} = h_i^2(t) \lambda_i(t,F).$$

This approximation introduces an error less than 0.001 percent. The bar denotes an integration from zero to infinity as a function of time. These mathematical computations are displayed in Fig. 3. It should be noted that the first term on the right side of the equations is now a scaling value and is independent of time. Hence, these MUAPT parameters are reduced to the expression of the firing rate multiplied by a scaling factor.

To compute the expression for the power density spectrum (frequency content) of an MUAPT it is necessary to consider additional statistics of the IPI's and the actual MUAP shape. The IPI's can be described as a real-continuous random variable. Only minimal (if any) dependence exists among the IPI's of a particular MUAPT. Therefore, the MUAPT may be represented as a renewal pulse process. A renewal pulse

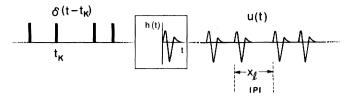


Fig. 2. Schematic model for the MUAPT.

| TERM | DIAGRAM | EXPRESSION |
|---|-----------------------------------|---|
| a) GENERALIZED FIRING RATE OF A TYPICAL MOTOR UNIT | MOTOR UNIT ACTION POTENTIAL TRAIN | $\lambda(\tau,\varphi)^{=}\frac{1}{E(X)}$ |
| b) MOTOR UNIT ACTION POTENTIAL | 1 | $h_{i}(au)$ |
| c) AREA UNDER THE RECTIFIED MOTOR UNIT ACTION POTENTIAL | | $ \underline{h_{j}(\tau)} = \int_{0}^{\infty} h_{j}(\tau) d\tau$ |
| d) AREA UNDER THE SQUARE OF A MOTOR UNIT ACTION POTENTIAL | Ţ | $ h_1^2(\tau) = \int_0^{\infty} h_1^2(\tau) d\tau $ |

Fig. 3. Explanation of some of the terms in the expressions in the text.

process is one in which each IPI is independent of all the other IPI's.

The power density spectrum of a MUAPT was derived from the above formulation by Le Fever and De Luca [52] and independently by Lago and Jones [50]. It can be expressed

$$S_{u_i}(\omega, t, F) = \frac{\lambda_i(t, F) \cdot \{1 - |M(j\omega, t, F)|^2\}}{1 - 2 \cdot \text{Real } \{M(j\omega, t, F)\} + |M(j\omega, t, F)|^2}$$
$$\cdot \{|H_i(j\omega)|^2\} \quad \text{for } \omega \neq 0$$

where

 ω = the frequency in radians $H_i(j\omega)$ = the Fourier transform of $h_i(t)$ $M(j\omega, t, F)$ = the Fourier transform of the probability distribution function $p_x(x, t, F)$ of the IPI's.

By representing $h_i(t)$ by a Fourier series, Le Fever and De Luca [52] were able to show that in the frequency range of 0-40 Hz the power density spectrum is affected primarily by the IPI statistics. A noticeable peak appears in the power density spectrum at the frequency corresponding to the firing rate and progressively lower peaks at harmonics of the firing rate. The amplitude of the peaks increases as the IPI's become more regular. Beyond 40 Hz, the power density spectrum is essentially determined by the shape of $h_i(t)$, which is in turn dependent on several physiological effects discussed in the first section.

CONCEPTS OF NORMALIZATION AND GENERALIZED FIRING RATE

A generalized representation of the ME signal must contain a formulation which allows a comparison of the signal between different muscles and individuals. This is not a problem in some contractions such as those involving ballistic movements. However, it is a requirement in isometric and anisometric contractions. The formulation for comparison may be obtained by normalizing the variables of the ME signal with respect to their maximal measurable value in the particular experimental procedure. For example, in a constant-force isometric contraction, the time is normalized with respect to the duration that the individual can maintain the designated force level. The contraction force is normalized with respect to the force value of an MVC. The normalized contraction time will be denoted by τ , and the normalized force by ϕ , and their maximal value is 1.

In the model, expressions for the parameters of the ME signal are formed by a superposition of the equations of the MUAPT derived in the previous section. Such an approach requires that the mathematical relationship of the firing rates of all the individual MUAPT's be known. It is difficult to obtain such information from the ME signal. To overcome this barrier, De Luca [21] introduced the concept of the generalized firing rate, and defined it as the mean value of the firing rates of the MUAPT's detected during a contraction. For a detailed description of the calculation of the generalized firing rate, refer to De Luca and Forrest [24]. For constant-force isometric contractions of the middle fibers of the deltoid muscle the generalized firing rate can be expressed as

$$\lambda(\tau, \phi) = \frac{1000}{\beta(\tau, \phi) \Gamma [1 + 1/\kappa(\tau, \phi)] + \alpha} \text{ pulses/s}$$

$$\kappa(\tau, \phi) = 1.16 - 0.19\tau + 0.18\phi$$

$$\beta(\tau, \phi) = \exp(4.60 + 0.67\tau - 1.16\phi) \text{ ms} \quad \text{for } 0 < \tau < 1,$$

$$\alpha = 3.9 \text{ ms} \quad 0 < \phi < 1.$$

It is likely that different relationships exist for other muscles. The above equation is plotted in Fig. 4.

A MODEL FOR THE ME SIGNAL

De Luca [21] modeled the ME signal m(t,F) as a linear, spatial, and temporal summation of the MUAPT's detected by the electrode. Biro and Partridge [5] obtained empirical evidence which justified this approach. The modeling approach was later expanded by De Luca and van Dyk [26] and Meijers et al. [62]. A schematic representation of the model is shown in Fig. 5. The integers represents the total number of MUAPT's which contribute to the potential field at the recording site. Each of the MUAPT's can be modeled according to the approaches presented in Figs. 1 and 2. The superposition at the recording site forms the physiological ME signal $m_p(t,F)$. This signal is not observable. When the signal is detected, an electrical noise n(t) is introduced. The detected signal will also be affected by the filtering properties of the recording electrode r(t) and possibly other instrumentation. The result-

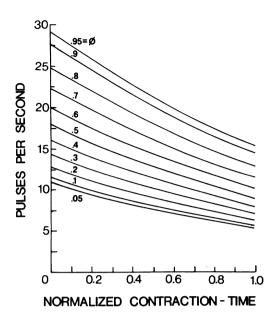


Fig. 4. Generalized firing rate of MUAPT's as a function of normalized contraction time at various normalized constant-force levels of the middle fibers of the deltoid muscle. The force was normalized with respect to the maximal isometric contraction.

ing signal m(t, F) is the observable ME signal. The location of the recording site with respect to the active motor units determines the shapes of h(t), as described at the beginning of this paper.

From this concept it is possible to derive expressions for the mean rectified value, the root-mean-squared value, and the variance of the rectified ME signal. The expressions are presented in Fig. 6. Their derivation can be found in the article by De Luca and van Dyk [26]. In Fig. 6, each of the terms of the expressions is associated with five physiological correlates which affect the properties of the ME signal.

In the equation of the mean rectified value, the term J(t,F) is a nonpositive term which accounts for the cancellation in the signal due to the superposition of opposite phases of the MUAPT's. In a sense, the superposition term represents the ME activity which is generated by the muscle, but is not available in the observed ME signal. The expression for the mean rectified value confirms that this parameter of the ME signal is dependent on the number and firing rates of the MUAPT's detected by the electrode, the area of the MUAP's, and the amount of cancellation occurring from the superposition of the MUAPT's.

The integral of the mean rectified value is a commonly used parameter in electromyography. By definition, it will be dependent on the same physiological correlates as the mean rectified value. It is often used to obtain a relationship between the ME signal and the force output of the muscle. A linear relationship has been reported often. Considering all the physiological correlates involved, the nonlinearity of the motor unit behavior, and the viscoelastic properties of muscle tissue, a linear relationship is unlikely. A nonlinear relationship as that

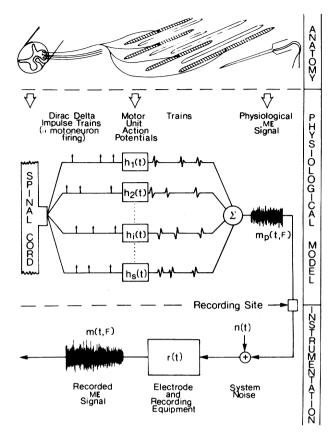


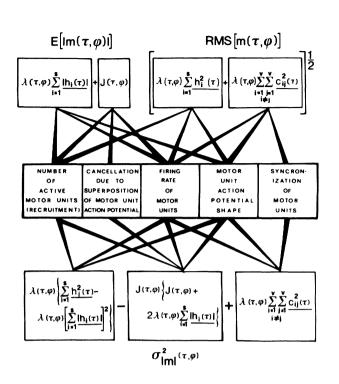
Fig. 5. Schematic representation of the model for the generation of the ME signal.

observed by Vredenbregt and Rau [92], Komi and Viitasalo [47], and others is more plausible.

The root-mean-squared value is also dependent on the number and firing rates of the MUAPT's and the area of the MUAPT's, but is not affected by the cancellation due to the MUAPT superposition. However, it is affected by the cross-correlation (due to synchronization) between the MUAPT's, represented by the $c_{ij}^2(\tau)$ terms. In the corresponding equation in Fig. 6, the integer v denotes the number of MUAPT's that are cross correlated. Note that any two MUAPT's can still be synchronized even if their cross-correlation term is zero, since the lack of cross correlation at $\tau = 0$ is not sufficient to prove independence. Under this condition, their synchronization has no effect on the root-mean-squared value.

The expression for the variance of the rectified signal is more complicated, containing all the terms which are present in the previous two parameters. Therefore, it reflects the combined effect of all the physiological correlates. This parameter represents the ac power of the rectified ME signal and should prove to be useful in analyzing the ME signal. However, it has been used sparingly. Most of the past investigations have dealt with the dc level of the ME signal.

The approach used thus far has been directed at relating the measurable parameters of the ME signal to the behavior of the individual MUAPT's. However, when the recording MEAN RECTIFIED



AND

RMS VALUES

VARIANCE OF THE RECTIFIED SIGNAL

Fig. 6. Theoretical expressions for parameters of the ME signal and their relation to physiological correlates of a contracting muscle.

electrode detects a large number of MUAPT's (greater than 15), such as would typically be the case for a surface electrode, the law of large numbers can be invoked to consider a simpler, more limited approach. In such cases, the ME signal can be effectively represented as a signal with a Gaussian distributed amplitude. By using this approach, Hogan [44] was able to demonstrate that the mean rectified value of the ME signal can be expressed as

$$E\{|m(\tau,\phi)|\}=\sqrt{2/\pi}\ \sigma(\tau,\phi)$$

where $\sigma(\tau, \phi)$ is the standard deviation of amplitude distribution.

A TEST FOR THE MODEL

According to the model, the power density spectrum of the ME signal can be formed by the summation of the power density spectrum of each of the MUAPT's if they are independent. By considering the spectral analysis of a MUAPT discussed previously, it can be shown that if the ME signal contains several independent MUAPT's with MUAP's of approximately the same amplitude, but different firing rates, the region below 40 Hz is relatively smooth. The peaks and valleys which exist in this region of the individual power density spectra will be smoothed by cancellation. Such is the case in most ME signal spectra. However, in some cases De Luca [21] and Hogan [44] have noted a large peak that occurs between 8 and 20 Hz, with no significant muscle

tremor. The model predicts this situation under the following two conditions: if the ME signal contains a predominance of regularly firing MUAPT's with somewhat similar firing rates, or if the ME signal is dominated by a high-amplitude MUAPT. In fact, Hogan [44] has shown that as successively more motor units are detected by the recording electrode during increasing force level contractions, the amplitude of the peak in the 8-20 Hz region diminishes with respect to the remainder of the spectrum. Above 40 Hz the shape of the power density spectrum is determined by the shapes of the MUAP's of the constituent MUAPT's. The amplitude of the power density spectrum increases as the number of MUAPT's and their firing rates increase.

Before testing the remainder of the parameters derived by the model, it is necessary to comment that the neuromuscular system is an extraordinary actuator. It is capable of generating and modulating force under a wide variety of static (isometric) and dynamic (velocity, acceleration) conditions. It has been shown that the behavior of the MUAPT's varies for different types of contractions. However, it is possible to test the model for the ME signal recorded during constant-force isometric contractions.

In a recent study performed by Stulen and De Luca [87], ME signals were simultaneously recorded differentially with bipolar surface and needle electrodes while 11 subjects performed sustained constant-force isometric contractions at 25, 50, and 75 percent MVC. The empirical values of the parameters corresponding to those derived previously were calculated and compared. Let us consider the empirical root-mean-squared parameter which is plotted in Fig. 7. The solid lines represent the average value for the 11 subjects. The vertical lines indicate one standard deviation about the average. For convenience, the magnitude of the values has been normalized with respect to the largest value of the average.

Note that the amplitude of the root-mean-squared parameter increases as a function of time when the ME signal is detected with surface electrodes and decreases when detected with indwelling electrodes. Why? These signals were recorded simultaneously from the same area of the same muscles. To explain this apparent paradox we must turn our attention to the model.

It is possible to solve the equation for the root-mean-squared parameter in Fig. 6, with the following restrictions: 1) no recruitment occurs during a constant-force contraction, 2) the areas of the MUAP's do not change, and 3) the MUAPT's are not cross correlated. With these assumptions, the root-meansquare parameter is directly proportional to the square root of the generalized firing rate. In fact if the generalized firing rate of Fig. 4 is normalized, it provides an exceptionally good fit to the mean value of the root-mean-squared parameter of the ME signal recorded with indwelling electrodes at 25 and 50 percent MVC, but not at 75 percent MVC. It appears that the decrease in the ME signal from contractions executed at less than 50 percent MVC is due to the decrease in the firing rates of the motor units, and that recruitment and synchronization do not play a significant role. But at 75 percent MVC, other physiological correlates affect the ME signal. Earlier in this article, observations were presented indicating that in

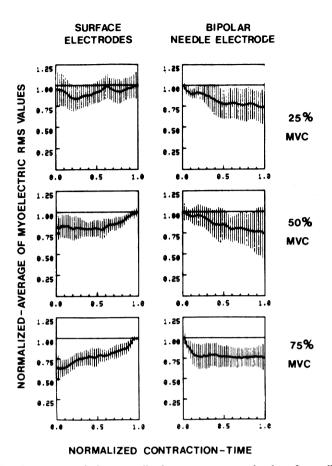


Fig. 7. Average of the normalized root-mean-squared values from all subjects, plotted as a function of contraction time. Both the amplitude and time duration are normalized to their respective maxima. The vertical lines indicate one standard deviation about the average. The acronym MVC stands for maximal voluntary contraction.

general, there is no recruitment at a 75 percent MVC. It appears that synchronization is the likely candidate to explain the different behavior of the root-mean-squared curves at 75 percent MVC. This indication is also implied in the behavior of the empirical mean rectified parameter and the variance of the rectified signal [87]. However, it is necessary to emphasize that this result does not provide direct evidence of synchronization.

During a muscle contraction maintained at a constant force, if the firing rate of the motor units decreases and there is no significant recruitment, a complimentary mechanism must occur to maintain the constant-force output. One possible mechanism is the potentiation of twitch tension of the motor units as a contraction progresses. Evidence for potentiation of twitch tension caused by sustained repetitive stimulation has been presented by Gurfinkel' and Levik [38] in situ in the human forearm flexors, and by Burke et al. [14], Olson and Swett [72], and others in vivo in the cat gastrocnemius. The studies performed on cats indicate that substantial potentiation occurs only in the fatigue resistant muscle fibers of the gastrocnemius, and to a much lesser extent in the fatigue resistant muscle fibers of the soleus. If this muscle and fibertype dependence also exists in the human, then the amount of complimentary decrease in firing rate will also be muscle dependent. This point requires verification.

Now, let us consider the ME signals recorded with surface electrodes. Why is the root-mean-squared value increasing during all three force levels when the firing rate is decreasing? The behavior of the firing rate is not affected by the type of electrodes used to record the signal. One possible explanation is as follows. During a sustained contraction, the conduction velocity along the muscle fibers decreases [81], [56]. As a result, the time duration of the MUAP's increases [24]. This change in the shape of the MUAP's is reflected in the power density spectrum as a shift towards the lower frequencies which has been documented by Kadefors et al. [46] and others. Hence, more signal energy passes through the tissue between the active fibers and the surface electrodes. Lindstrom et al. [56] has made theoretical calculations which show that the muscle tissue and differential electrodes act as lowpass filters. As the distance between the active fibers and the electrodes increases, the bandwidth of the tissue filter decreases. The increasing effect on the signal due to the tissue and electrode filtering overrides the simultaneously decreasing effect of the firing rate. The filtering effect is not seen in the signal recorded with the indwelling electrodes because the active fibers are much closer to the recording electrode.

Hence, the apparent paradox in the behavior of the ME signal recorded with surface and indwelling electrodes is resolved by considering the recording arrangement.

It has been shown that the modeling approach is in agreement with the empirical results that could be tested. The model has also helped to resolve some ambiguities as well as to give insight into the information contained in the ME signal. The limited discussion and arguments based on the describable known MUAPT behavior that have been presented are not sufficient to establish the generality of the model. However, as additional information describing the behavior of MUAPT's becomes available (especially the force dependence), the model should prove to be more useful and revealing.

ACKNOWLEDGMENT

I wish to thank Dr. J. V. Basmajian for acting as the catalyst that persuaded me to unify my thoughts on electromyography. Thanks are also due to F. B. Stulen and R. S. Le Fever; my students and colleagues, who performed a significant part of the work reported herein. Special thanks are also due to N. W. Vignone who was instrumental in the preparation of the manuscript.

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Carlo J. De Luca (S'64-M'72-SM'77) for a photograph and biography, see p. 237 of the April 1979 issue of this Transactions.