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Some Properties of Motor Unit Action Potential Trains Recorded during Constant Force Isometric Contractions in Man

Carlo J. De Luca and William J. Forrest
Anatomy Department, Queen's University, Kingston, Ontario, Canada

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Abstract

A specially designed needle electrode was used to record motor unit action potentials for the complete time duration of constant force isometric contractions varying in discrete steps from minimum to maximum force levels. A total of 70 motor unit action potential trains were recorded and analyzed

Several properties of the motor unit action potentials were observed The inter-pulse intervals between adjacent motor unit action potentials of a particular motor unit action potential train were measured and subsequently analyzed as a real continuous random variable. The distribution of the values of the inter-pulse intervals was described by the Weibull probability distribution function with time and force dependent parameters. Furthermore the Survivor function and the Hazard function of the Weibull probability distribution function described certain characteristics of the motor unit firing intervals. Most important of all, it became possible to derive an equation that would generate a real continuous random variable whose properties would be identical to those of the inter-pulse intervals.

Introduction

A muscle contraction is the result of concurrent contractions of several *motor units*. A motor unit consists of a group of muscle fibers and their innervating terminal branches of one nerve fiber whose cell body is located in the anterior horn of the spinal gray matter. When a motor unit is stimulated, an extra-cellularly placed electrode will record the current distribution in the territory of the motor unit. The recorded pulse is called the *motor unit action potential*. A sequence of motor unit action potentials is known as a *motor unit action potential train* (MUAPT); the time interval between adjacent pulses will be referred to as the *inter-pulse interval* (IPI).

MUAPT's from human skeletal muscles have been analyzed under various conditions by numerous investigators (Bigland and Lippold, 1954; Buchthal *et al.*, 1954; Clamann, 1967; Gilson and Mills, 1941; Gurfinkel *et al.*, 1970; Kaiser and Petersén, 1965; Larsson *et al.*, 1965; Masland *et al.*, 1969; Person and Kudina, 1972). This paper will deal with the properties of MUAPT's recorded at various levels of constant force isometric contraction for the complete time duration of a human skeletal muscle contraction.

Materials and Methods

The following equipment arrangement was used to record the MUAPT's. A sturdy wooden chair with a high back was modified as follows. Two adjustable Velcro straps were fastened to both sides of the back of the chair. A force gauge capable of measuring 50 kg of force with a displacement of 0.1 mm was secured to the chair. A cuff consisting of an adjustable band of cotton webbing 5 cm in width and two pieces of Velcro was connected to the force gauge by a flexible steel cable. The output of the force gauge was attached to one channel of a dual-beam oscilloscope (oscilloscope 1). The differential preamplifier was cascaded with a single-ended amplifier. The output of the amplifier was connected to a separate oscilloscope. The outputs of the amplifier and the force gauge were fed to an *FM* tape recorder. An audio amplifier and a speaker were cascaded to the differential preamplifier. Acoustic representation of motor unit action potentials assisted significantly in detecting the presence of different MUAPT's. A block diagram for the equipment arrangement is presented in Fig. 1.

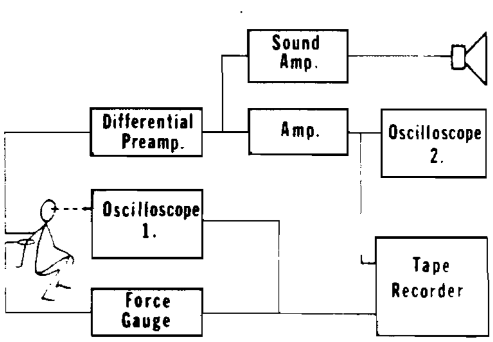

Fig. 1. Block diagram of the equipment arrangement of the experiment

Four right-handed male subjects volunteered for the experiment. Their ages varied from 22–32 years, with an average of 25.3 years. All subjects denied past injury to the right shoulder region. A subject was seated in the chair and the two Velcro straps were fastened over his shoulders. The straps kept the torso of the subject in a fixed position with respect to the force gauge and prevented shrugging of the shoulder by restricting the elevation of the scapula, but did not impede the rotation of the scapula. The cuff was secured snugly about the distal part of the right arm just proximal to the elbow joint.

The maximum force output of the isometric abduction of each subject was measured.

A specially designed quadri-filar electrode (De Luca and Forrest, 1972) was inserted into the central area of the middle fibers of the deltoid muscle. The r electrode was capable of recording distinct MUAPT's from a muscle contracting at any force level (including maximal force). The tip of the electrode penetrated to the middle of the depth of the deltoid muscle. Clamann (1967) pointed out that this region of a muscle contains motor units having a gradation of thresholds from low to high. The electrode was connected to the input of the differential preamplifier. The 3 *dB* points of the bandwidth of the preamplifier were set at 100 and 1600 Hz. The gain of the preamplifier and amplifier was regulated to give the largest possible signal output that could be stored on magnetic tape, thereby optimizing the signal-to-noise ratio.

The trace of the isolated second channel of oscilloscope 1 was placed at the equivalent voltage representation of 5 kg above the trace of the other channel which displayed the output of the force gauge. Each subject was instructed to abduct the upper limb in the coronal plane with the arm medially rotated and the forearm pronated. Then he was asked to superimpose the two traces on oscilloscope 1 as quickly as possible with a minimal amount of overshoot. When the desired level of isometric abduction was achieved, the subject was requested to maintain the force output constant until he was no longer capable of doing so. At the end of the contraction, the electrode was removed from the muscle. Each subject had a minimal rest period of two hours between successive contractions. Prior to each contraction, the electrode was reinserted into the deltoid muscle. Hence, different MUAPT's were recorded for each contraction. MUAPT's were obtained for contractions with monitored force outputs of 5, 10, 15, 20 and 25 kg.

The recorded MUAPT's were photographed on a 35 mm film moving at a speed of 250 mm/sec. A 50 Hz square-wave calibration signal was photographed to check the true speed of the camera. A total of 70 MUAPT's were recorded from the four subjects. Two persons independently interpreted the records, thus reducing the probability of allocating a motor unit action potential to the wrong MUAPT. The IPI's of all the MUAPT's were measured. The accuracy of the measurement was ±0.1 msec.

Analysis of Data

A recent study (De Luca, 1972) showed that the relative force contribution of the anterior, middle and posterior fibers of the deltoid muscle and that of the supraspinatus muscle remains constant during isometric abduction. The force contribution of the middle fibers of the deltoid muscle during isometric abduction was calculated from the values of the measured force of abduction by employing a special technique described by De Luca (1972). The force output of the middle fibers of the deltoid muscle was found to be linearly proportional to the measured force of abduction.

The IPI's of a MUAPT were analyzed as a random variable. The following terminology will be used to describe the various tests:

X = a real continuous random variable representing the IPI,
x = the range of all possible values (outcomes) which can be assumed by X,
x_i = a specific outcome of X; the value of a specific IPI,
x_i array = a complete series of outcomes of X; hence, it represents all the IPI's of one MUAPT.

Stationarity

The mean value and the standard deviation of the IPI's for every 5 sec interval of a MUAPT were calculated. These values were calculated for all 70 MUAPT's. The mean values were plotted against the corresponding time. In addition, for each MUAPT, the mean values were plotted against the corresponding standard deviations, and a polynomial least-square regression was performed on all the values for each MUAPT. All the MUAPT's were fitted with a 2nd, 3rd or 4th degree polynomial. The degree of the polynomial which provided the best fit for the values of a particular MUAPT was determined by calculating the residual sum-of-squares between two successive degrees of the polynomial. This procedure has been described by Ostle (1954). The accepted degree was obtained when the values of the residuals was less than 5×10^{-6}.

The histograms of the IPI's for each of the 70 MUAPT's were plotted by a computer program. The mean, standard deviation, skewness, minimum value, maximum value and total number of IPI's were calculated for each MUAPT. Histograms were also plotted for sections of the MUAPT's. Each MUAPT was divided into 10 equal time-sections; 700 histograms were formed.

Probability Distribution Function

The following three probability distribution functions (PDF's) were fitted to the histograms of the IPI's of each MUAPT:

$$\text{Lognormal } f_X(x) = \frac{1}{(x-\alpha)(2\pi K)^{\frac{1}{2}}} \exp\left\{-\frac{\left[\ln\left(\frac{x-\alpha}{\beta}\right)\right]^2}{2K}\right\}$$

$$\text{Gamma } f_X(x) = \frac{1}{\beta\Gamma(K)}\left[\frac{x-\alpha}{\beta}\right]^{K-1} \exp\left[-\frac{(x-\alpha)}{\beta}\right]$$

$$\text{Weibull } f_X(x) = \frac{K}{\beta}\left[\frac{x-\alpha}{\beta}\right]^{K-1} \exp\left[-\left(\frac{x-\alpha}{\beta}\right)^{K}\right].$$

The PDF's are described by three parameters K, β and α; where K = shape parameter, β = scale parameter and α = location parameter. The parameter K has no units, β and α have the units of the IPI's (msec). The parameter α was evaluated by finding the minimum value of x_i. The "best" estimates of K and β were obtained by the Maximum Likelihood method which maximized the function

$$\ln L(K,\beta) = \sum_{i=1}^{n} \ln f(x_i \mid K,\beta)$$

The goodness-of-fit of the three PDF's with the "best" estimates of the parameters was measured by the Kolmogorov-Smirnov test.

The three PDF's were also fitted to the IPI's of sections of a MUAPT. Each MUAPT was divided into consecutive time-sections each containing at least 150 IPI's; this is the minimum number of IPI's that should be used to obtain a meaningful test of the goodness-of-fit of a PDF (Pearson and Hartley, 1954). A total of 225 sections was formed.

Dependence

This test determined if the time duration of a particular IPI affects the time duration of adjacent IPI's. The following procedure is a modification of a test described by Naylor *et al.* (1966). Basically, the procedure consists of constructing a scatter diagram, which is a plot of x_i against x_{i-d} where $d = 1, 2, 3, \ldots$ is the displacement parameter. If the IPI's are independent of each other then the points on the scatter diagram will be randomly distributed. In case of dependence, an above average number of points will be localized in some area(s) of the scatter diagram. Localization of points was detected by dividing the scatter diagram into cells. A convenient way of forming the cells was by dividing the x_i and x_{i+d} axis into equal probability intervals, r, forming r^2 cells. This was accomplished by sorting the x_i array in increasing order of magnitude. Each r interval must contain the same number of sorted values, n/r, where n is the total number of x_i values. The values of x_i which constituted the divisions of the x_i and x_{i+d} axis corresponded to

$$0, x_{n/r}, x_{2n/r}, \ldots, x_{(r-1)n/r}, x_n.$$

The value of r was determined such that the expected number of points, E, in each cell was restricted to

$$5 < E = \frac{n}{r^2} \leqq 10.$$

A χ^2 test was performed on the number of points in each cell with respect to the expected number of points, E. The number of the degrees of freedom was $(r-1)^2$.

If the IPI's of the MUAPT's are nonstationary, this test for dependence must be performed on sections of the MUAPT rather than the complete MUAPT. Each section contained at least 150 IPI's; in most cases a section contained more than 150 IPI's. The lower bound of 150 IPI's was used because this value would divide the scatter diagram into 25 cells, with an average of 6 points per cell. Trial and error experimentation indicated that this was an acceptable number of cells that gave a reasonable test of dependence in a section of the MUAPT.

A detailed account of the above tests has been discussed by De Luca (1972).

Results and Discussion

Direct Empirical Results

As expected, the time duration of a contraction decreased with increasing constant-force levels. Table 1 lists the time durations of each contraction for all the subjects.

Table 1. Time duration (in minutes) of the constant force isometric abductions for all subjects

Subject	Measured force of abduction in kg				
	5	10	15	20	25
LT	2.23	1.50	1.12	0.78	0.77
RW	1.87	1.32	0.50	0.38	0.33
DB	2.52	1.80	0.93	0.65	
WW	2.15	1.72	1.30	0.72	0.62

A MUAPT present at the beginning of the constant force isometric contraction remained active throughout the complete contraction. When a constant force isometric contraction was in progress no additional motor units were recruited throughout the contraction. These findings agree with those of Masland *et al.* (1969) and of Gilson and Mills (1941). Hence, Table 1 also represents the time duration of the MUAPT's. The IPI's of an individual MUAPT were random in nature. The values of the IPI's varied from 1.4 to 1600 msec.

The amplitude of the motor unit action potential was subject to irregular variation throughout the MUAPT. This was very likely due to the inevitable relative displacement of the tip of the electrode with respect to the active fibers during a sustained contraction. However, it is conceivable that the amplitude variability was due to inconsistent excitation of all the muscle fibers in a motor unit territory by the parent motor nerve. Overriding the irregular fluctuations there appeared to be a decreasing trend in the amplitude of most motor unit action potentials with increasing time of the sustained contraction. This decrease in amplitude was not observed in all MUAPT's; in some cases the amplitude increased with increasing time. If the impedance of the electrode-electrolyte interface remains constant, the variation in amplitude may possibly be attributed to physiological processes. However, the impedance of the electrode-electrolyte interface is difficult to control and/or monitor. Therefore, it is not possible to make a definitive statement concerning the cause of the amplitude variation.

Verification of both the decrease and increase in the amplitude of the motor unit action potential can be found in the literature. Knowlton *et al.* (1951) and Stålberg (1966) reported an increase in the amplitude with increasing contraction time. On the other hand, several investigators (Bigland and Lippold, 1954; Lindquist, 1959; Lindsley, 1935; Lippold *et al.*, 1960; Seyffarth, 1940) have reported that the amplitude decreased continuously with increasing time of contraction.

The time duration of the motor unit action potentials of a particular MUAPT remained unchanged during approximately the first half of the constant force isometric contraction. In the second half of the contraction, a variation in the time duration of the motor unit action potential was usually observed. The time duration of the motor unit action potentials of each of the 70 MUAPT's was measured at the beginning and end of each contraction. The histogram of the percentage change of

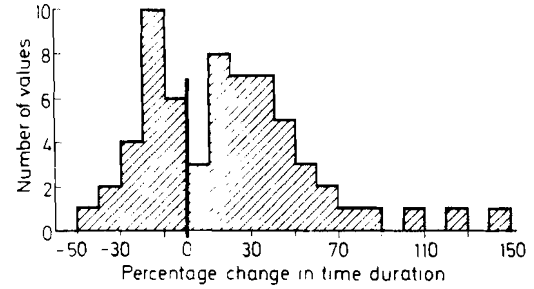

Fig. 2. Percentage change in the time duration of the motor unit action potentials measured at the beginning and end of the constant force isometric contractions

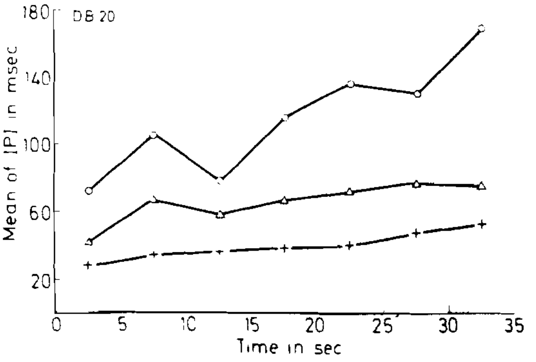

Fig. 3. Time dependence of the mean value of the inter-pulse intervals: the force output of the recorded muscle was 45.3 kg

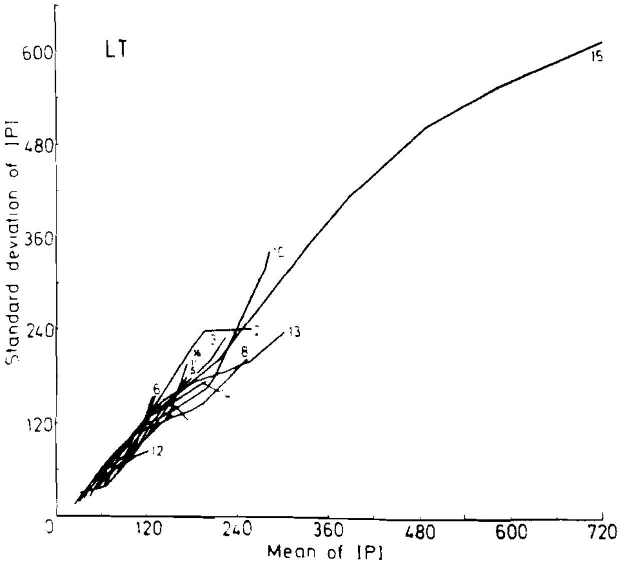

Fig. 4. Relationship of the mean and standard deviation of the inter-pulse intervals of 16 motor unit action potential trains recorded from one subject, contraction force varied from minimum to maximum. The abscissa and ordinate are scaled in milliseconds

the time duration is plotted in Fig. 2. The time duration increased for 40 motor unit action potentials, decreased for 23 and remained unchanged for 7. The group that increased in time duration had a change of (39.4 ± 33.1)% and the group that decreased in time duration had a change of (−18.4 ± 13.2)%. Collectively, the time duration of the 70 MUAPT's increased by (16.7 ± 28.0)%.

Stationarity

Fig. 3 shows the mean value of the IPI's of three simultaneously recorded MUAPT's. The mean value increases with time. This trend was observed for all 70 MUAPT's and agrees with the findings of Person and Kudina (1972). Fig. 4 contains curves for the mean and corresponding standard deviation of the IPI's of 16 MUAPT's recorded from one subject. Another three such plots were formed for the other subjects. The MUAPT's in Fig. 4 were obtained from contractions which ranged from low to maximum force. The mean and standard deviation values vary simultaneously, irrespective of time and force.

A linear least square regression was performed on the mean values against the standard deviation values of the IPI's for every 5 sec interval in all 70 MUAPT's simultaneously; the slope (coefficient of variation) was found to be 0.69 and the correlation coefficient was 0.83. The linear regression intercepted the mean value axis at 16.3 msec.

Fig. 5 shows a typical histogram of all the IPI's of a MUAPT. In 52 histograms, the mean was larger than the standard deviation; in 3, the mean and the standard deviation were approximately equal; and in the remaining 15, the standard deviation was slightly larger than the mean. The envelopes of all the MUAPT's clearly demonstrated a positive skewness. The time dependence of the mean and standard deviation of the IPI's indicate that the histograms of the IPI's should vary throughout the MUAPT. Fig. 6 shows the histograms of a typical, sectioned MUAPT. The following observations can be made:

(a) the positive skewness persists in all sections,

(b) the mean and standard deviation values increase with time.

These observations were confirmed in the remaining 690 histograms of the sectioned MUAPT's. The shape and time dependence of the histograms in Figs. 5 and 6 are compatible with the histograms of MUAPT's that Lippold *et al.* (1960) recorded from the human triceps muscle and the histograms that Person and Kudina (1972) obtained for low-level constant-force isometric contractions from the human rectus femoris muscle. Person and Kudina (1972) maintained that for motor unit firing rates greater than 10–13 pulses per sec. the IPI histograms were symmetrical. Clamann (1967), recording from the human biceps brachii muscle, found that the IPI histograms had a Gaussian distribution. No evidence of symmetry was detected in the IPI histograms obtained in this study. It is interesting to note that IPI's of neural motor activity in the central nervous system of mammals have histograms with large positive skewness and a shape similar to the histograms of Figs. 5 and 6. Martin and Branch (1958) obtained histograms of spontaneous activity from single Betz cells in the motor cortex of anesthetized cats with midbrain lesions. Evarts (1964) recorded action potentials from pyramidal tract neurons in the precentral gyrus of intact, unanesthetized monkeys at rest and during movements.

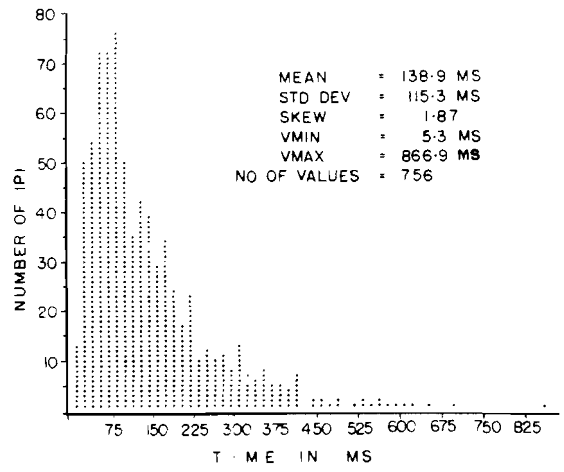

Fig. 5. Histogram of the inter-pulse intervals of a motor unit action potential train which was recorded during an isometric contraction. The contraction was sustained until the pre-set constant force could no longer be maintained. The force from the monitored muscle was 26 kg

The time dependence of the mean, standard deviation and shape of the histograms of the IPI's strongly indicate that the IPI's of a MUAPT are nonstationary. This result agrees with that of Masland *et al.* (1969).

Probability Distribution Function

The results of the goodness-of-fit of the three PDF's to the IPI's of the complete MUAPT are listed in Table 2. A large Kolmogorov-Smirnov probability level indicates a good fit.

The Gamma PDF provides by far the worst fit for the IPI's of the complete MUAPT's; 83% of the MUAPT's had a $p \leq 0.05$. The results for the Lognormal and Weibull PDF's are quite similar with the Weibull PDF providing a slightly better fit than the Lognormal. Even in the best case, 39% of the MUAPT's have a $p \leq 0.05$ which indicates that none of the three PDF's provides an acceptable fit for the IPI's of the complete MUAPT's. This is not a sur-

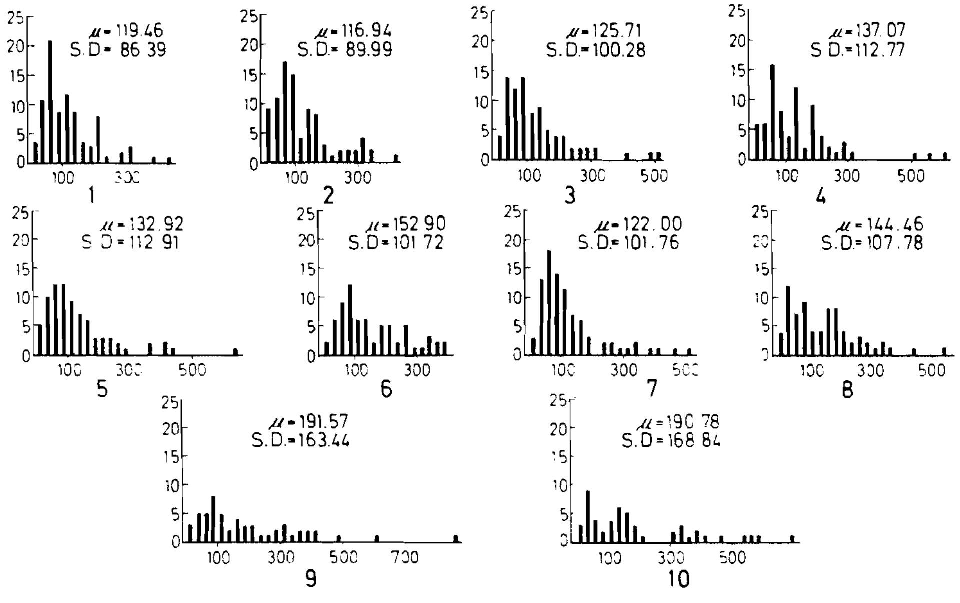

Fig. 6. Histograms of ten equal and consecutive time-sections of a motor unit action potential train that was recorded during an isometric contraction. The contraction was sustained until the pre-set constant force could no longer be maintained. The abscissa is scaled in milliseconds

prising result because the IPI's of a MUAPT are nonstationary; therefore, one would expect that the tests made on the sectioned MUAPT would be more indicative. The results of such a test (Table 3) show a clear delineation between the goodness-of-fit of the Weibull PDF and of the other two PDF's. A χ^2 test with nine degrees of freedom was performed to measure the uniformity of the MUAPT sections at various probability levels. The Gamma and the Lognormal PDF's still provide very bad fits with $p < 0.00001$. The results for the Weibull PDF have a significance level of $p = 0.41$. This is very strong evidence that the Weibull PDF provides a good fit for the IPI's of the MUAPT's recorded at all levels of constant force isometric contraction.

Table 2. Percentage of complete motor unit action potential trains at various levels of probability determined from the Kolmogorov-Smirnov statistics

Probability level	Gamma (in %)	Lognormal (in %)	Weibull (in %)
$p \leqq 0.05$	83	44	39
$p \leqq 0.10$	89	54	53
$p \geqq 0.90$	0	1.4	0
$p \geqq 0.95$	0	0	0

Total number of motor unit action potential trains = 70.

Table 3. Number and percentage of motor unit action potential train sections at ten levels of probability determined from the Kolmogorov-Smirnov statistics

Probability level	Gamma	Lognormal	Weibull
0 -0.1	98 44 %	91 41 %	25 11 %
0.1-0.2	37 17 %	30 13 %	19 8.5%
0.2-0.3	26 12 %	17 7.6%	21 9.4%
0.3-0.4	23 10 %	11 4.9%	30 13 %
0.4-0.5	8 3.6%	12 5.4%	26 12 %
0.5-0.6	6 2.7%	10 4.5%	28 13 %
0.6-0.7	12 5.4%	12 5.4%	18 8.0%
0.7-0.8	4 1.8%	10 4.5%	23 10 %
0.8-0.9	6 2.7%	13 5.8%	19 8.5%
0.9-1.0	4 1.8%	18 8.0%	15 6.7%

Total number of sections = 224.

The above results do not prove that the Weibull PDF provides the best possible fit. It is conceivable that some other PDF that provides a better fit exists. However, the fit provided by the Weibull PDF is highly significant. Furthermore, the Weibull PDF is a relatively simple mathematical expression which can be manipulated to investigate some properties of the MUAPT, which will be discussed in subsequent sections.

Trends in the Parameters of the Weibull Probability Distribution Function

A multiple linear least-square regression was performed on the values of $\varkappa$ and the natural logarithm of β calculated for the sectioned MUAPT's with respect to time and constant force. MUAPT's recorded from all four subjects were used. The time duration of the MUAPT's varied considerably for different subjects and force levels of the sustained contraction (see Table 1). Hence, it was necessary to normalize the time and force. Time was expressed as a fraction of the total time duration of the MUAPT, and the constant force as a fraction of the maximum force output of the middle fibers of the deltoid muscle. Table 4 lists the results of the multiple linear least-square regression. The parameter $\varkappa$ is unitless; β has units of msec.

The mean and standard error of the time and constant-force coefficients were calculated. A t-test was performed to establish the significance level of the time and constant-force coefficients; in all cases, the t-test indicated highly significant results. To elucidate the validity of the linear relationship, the residuals of $\varkappa$ and $\ln\beta$ were separately plotted against their corresponding (a) predicted value, (b) normalized time, and (c) normalized constant-force. In all six plots, the plotted values were randomly dispersed indicating that a linear relationship is as good as any other relationship.

Table 4. Time and force dependence of the Weibull probability distribution function parameters

		Regression coefficients					
		Time coefficient			Constant-force coefficient		
Parameter	Constant	Mean	Standard error	p value of t-test	Mean	Standard error	p value of t-test
$\varkappa$	1.16	−0.19	0.03	0.000001	0.18	0.05	0.0001
$\ln(\beta)$	4.60	0.67	0.12	0.000001	−1.16	0.17	0.000001

The average time and force dependence of $\varkappa$ and β can be expressed by the following equations:

$$\begin{aligned} K(\tau,\phi) &= 1.16 - 0.19\,\tau + 0.18\,\phi \\ \beta(\tau,\phi) &= \exp(4.60 - 0.67\,\tau - 1.16\,\phi)\ \text{msec} \end{aligned} \quad \text{for} \quad \begin{aligned} &0<\tau<1 \\ &0<\phi<1 \end{aligned}$$

where τ = normalized time duration of the MUAPT,
ϕ = normalized constant force.

The above equations are general expressions valid for all MUAPT's. τ and ϕ were found to be independent with no significant interaction term. The average value of the parameter, α, calculated for the complete MUAPT's was found to be 3.89 ± 2.82 msec.

Stochastic Properties of Motor Unit Action Potential Trains

Some properties of the Weibull PDF yield useful information about the MUAPT. The following properties are valid for all MUAPT's recorded during a voluntary constant force isometric contraction from the deltoid muscle.

The mean value of the time and force dependent Weibull PDF is given by:

$$\mu(\tau,\phi) = \beta(\tau,\phi)\,\Gamma\left(1 + \frac{1}{K(\tau,\phi)}\right) + \alpha$$

where Γ = the Gamma function
$\beta(\tau,\phi)$ time and force dependent parameters of the
$\varkappa(\tau,\phi)$ = Weibull PDF
α = minimum value of the IPI's.

The *generalized firing rate* may be expressed as the inverse of the mean

$$g(\tau,\phi) = \frac{1000}{\beta(\tau,\phi)\,\Gamma\left(1 + \dfrac{1}{K(\tau,\phi)}\right) + \alpha}\ \text{pulses per sec.}$$

The *generalized firing rate* represents the expected dependence of the firing rate of a typical motor unit with respect to time during a constant force isometric contraction. The family of curves for the *generalized firing rate* is plotted in Fig. 7.

Near the end of a very weak contraction $\tau \simeq 1$ and $\phi \simeq 0$, then $\varkappa(\tau,\phi) \simeq 1$ and $\beta(\tau,\phi) \simeq 195$ msec. At these parameter values the Weibull PDF approaches the Exponential PDF and the scale parameter $\beta(\tau,\phi)$ becomes the mean value of the IPI. Hence the lowest firing rate of a typical motor unit is approximately 5 pulses per sec. This result corresponds with observations made by Bigland and Lippold (1954) and Person and Kudina (1972).

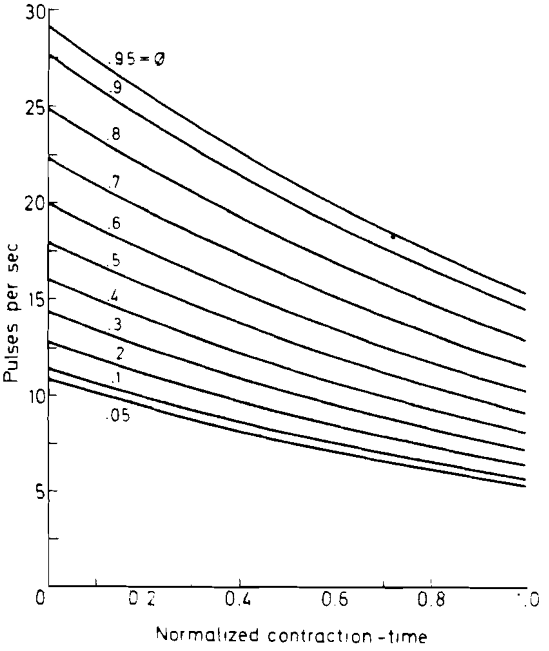

Fig. 7. Generalized firing rate of motor unit action potentials as a function of normalized contraction-time at various normalized constant-force levels. The force was normalized with respect to the maximum isometric contraction

The Survivor function of the time and force dependent Weibull PDF is

$$S_H(\eta,\tau,\phi) = \exp\left[-\left(\frac{\eta - \alpha}{\beta(\tau,\phi)}\right)^{K(\tau,\phi)}\right]$$

This function gives the probability that a motor unit has not fired up to time η measured from the time of the previous firing. The equation indicates that the probability of a motor unit not having fired after a previous firing decreases exponentially with respect to the amount of time that elapses.

The negative derivative with respect to η of the logarithm of the Survivor function describes another useful function known as the Hazard function that can be expressed as

$$O_H(\eta,\tau,\phi) = \frac{K(\tau,\phi)}{\beta(\tau,\phi)}\left(\frac{\eta - \alpha}{\beta(\tau,\phi)}\right)^{K(\tau,\phi)-1}$$

This function gives the probability per unit time of an immediate firing when no firing has occurred for η time. The quantity $O_H(\eta,\tau,\phi)\,\Delta\eta$ is the probability that a motor unit will fire during the small time interval $\Delta\eta$, given that the motor unit has not fired for η time.

For $K(\tau,\phi) > 1$, which is usually the case for the IPI's of the MUAPT's, there is positive "aging" with $O_H(\eta,\tau,\phi)$ varying from zero to infinity as η increases. This indicates that the longer the elapsed time since the previous motor unit firing, the greater the probability that the motor unit will fire. This is known as the "wear effect". Near the end of a very weak contraction, $K(\tau,\phi) \simeq 1$ and the wear effect will disappear. The Hazard function attains the constant value of $(195\ \text{msec})^{-1}$.

The Cumulative probability distribution function of the Weibull PDF is

$$F_X(x,\tau,\phi) = 1 - \exp\left[-\left(\frac{x-\alpha}{\beta(\tau,\phi)}\right)^{\kappa(\tau,\phi)}\right]$$

where X represents the IPI. In the above equation, replace the term $1 - F_X(x,\tau,\phi)$ by a real continuous random variable, D, whose values have a Uniform PDF between 0 and 1; take the logarithm of both sides and by rearranging the equation it follows that

$$X = +\beta(\tau,\phi)\,[-\ln D]^{\frac{1}{\kappa(\tau,\phi)}} + \alpha$$

This equation is completely defined and can be used to generate a real continuous random variable which will behave similarly to the IPI's of a MUAPT. The values of D can be obtained from random number generator such as a digital computer or specialized instrumentation.

Dependence

The scatter diagram of the IPI's of a complete MUAPT revealed a grouping of points along the diagonal of the scatter diagram. This result was expected because the IPI values at the beginning of the MUAPT's are smaller than those at the end. Hence the relatively smaller IPI's at the beginning of the MUAPT's will be followed by other smaller IPI's; near the end of the MUAPT, the relatively larger IPI's will be followed by larger IPI's. Such a trend is evident in Fig. 3. The test for dependence of the IPI's performed on the sections of MUAPT's greatly reduced the effect of nonstationarity. Ideally, if the IPI's were independent, the χ^2 test statistic should have a χ^2 distribution; this means that approximately 5% of the sections should have a probability level of $p \leqq 0.05$; $10\% \leqq 0.10$; etc. Table 5 lists the number and percentages of sections which have the indicated probability level. A χ^2 test with nine degrees of freedom was performed to test the uniformity of the results. It was only necessary to consider the displacement parameters $d = 1, 3$. For $d = 1$, the probability significance level was $p = 0.45$ and for $d = 3$; $p = 0.77$. These probability significance levels imply that the IPI's of a section of the MUAPT's can be considered to be locally independent within the limitations of the test. A contingency table (Kendall and Stuart, 1967) was set up to measure the similarity between the results of $d = 1, 3$. The probability significance level of the contingency table was $p = 0.79$. This value provided strong evidence that there is no significant difference between the results for $d = 1, 3$.

Table 5. Number and percentage of motor unit action potential train sections at ten levels of χ^2 probability for two values of the displacement parameter

Probability	Displacement parameter			
level	$d = 1$		$d = 3$	
0 –0.1	29	12.9%	22	9.8%
0.1–0.2	15	6.7%	21	9.4%
0.2–0.3	26	11.6%	30	13.4%
0.3–0.4	19	8.5%	24	10.7%
0.4–0.5	22	9.8%	26	11.6%
0.5–0.6	22	9.8%	24	10.7%
0.6–0.7	26	11.6%	20	8.9%
0.7–0.8	28	12.5%	20	8.9%
0.8–0.9	18	8.0%	17	7.6%
0.9–1.0	19	8.5%	20	8.9%

Total number of sections = 224.

Previous reports in the literature contain conflicting statements about the statistical dependence of the IPI's recorded during voluntary isometric constant force contractions. The results of Clamann (1967) agreed with those of this study. He demonstrated that IPI's are statistically independent. Masland *et al.* (1969) stated that the majority of MUAPT's which they recorded contained IPI's which by their criteria were statistically independent; however, all the MUAPT's had some IPI's which were dependent at some time during their recording. Person and Kudina (1972) found no correlation between adjacent IPI's for motor units firing below 10 pulses per sec. At firing rates above 10–13 pulses per sec, they found a negative correlation between adjacent IPI's.

The observed and derived properties that have been presented are only valid for MUAPT's recorded from the middle fibers of the deltoid muscle. It remains to be proven that these properties are valid for MUAPT's recorded from other muscles.

Conclusion

Motor unit action potential trains (MUAPT's) were recorded from the middle fibers of the deltoid muscle for the complete time duration and force range of a constant force isometric abduction of the upper limb.

A motor unit remains active throughout the complete time duration of a constant-force contraction. Near the end of a sustained contraction the amplitude of a motor unit action potential appears to decrease and the time duration of a motor unit action potential has a tendency to increase, although 33% of the motor unit action potentials displayed a decrease in time duration.

The inter-pulse intervals (IPI's) of a MUAPT may be considered as a nonstationary and locally independent real continuous random variable. The Weibull probability distribution function with time and force dependent parameters provides a good fit for the distribution of the IPI's of a MUAPT. The Weibull PDF may be used to obtain equations for the following expressions which give insight into the firing pattern of a motor unit.

a) The *generalized firing rate* or the expected firing rate of a typical motor unit decreases with increasing contraction time. The *generalized firing rate* decreases for isometric contractions elicited at lower constant-force levels.

b) The Survivor function indicates that the probability of a motor unit not having fired after a previous firing decreases exponentially with respect to the elapsed time.

c) The Hazard function indicates that the probability per unit time of an immediate firing of a motor unit increases nonlinearly with the elapsed time since the previous motor unit firing; this is known as the "wear effect".

d) A time and constant-force dependent equation for generating a continuous random variable having the same properties as the IPI's can be derived.

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Carlo J. De Luca
Department of Anatomy
Queens University
Kingston, Ontario, Canada