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A Stochastic Model of Muscle Fatigue in Cyclic Heavy Exertions…Formulation

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Abstract

Static muscle contractions when prolonged or frequently repeated result in discomfort, fatigue, and musculosketal injuries. An analytic and quantitative model has been developed in order to expand the working knowledge on muscle fatigue.

In this paper, three Markov models of muscle fatigue are developed. These models are based on motor unit fatigue-recovery characteristics obtained from information on motor unit behavior as it relates to fatigue and graded exertions.

Three successively more realistic models are developed that involve: (1) homogeneous motor units with intensity-dependent fatigue rates and state-independent recovery rates (the HMSI model); (2) homogeneous motor units, intensity-dependent fatigue rates and state-dependent recovery rates (the HMSD model); and (3) non-homogeneous motor units (i.e., Type S and Type F), intensity-dependent fatigue rates and state-dependent recovery rates (the HMSD model).

The result indicate that a simple stochastic model provide a means to analyze the complex nature of muscle fatigue in sequential static exertions.

Key Word: muscle fatigue, % MVC (% of maximum voluntary contraction)
EMG, Type S (Slow twitch-high oxidative muscle fibers)
Type F(Fast twitch-high glycolitic muscle fibers)

INTRODUCTION

The understanding and the avoiding of muscle fatigue problems has been a great concern of many researchers who have examined localized muscle fatigue in various disciplines. Circulatory responses to a working muscle (Lind, 1959; Armstrong, 1976) and biochemical analysis of muscle biopsy samples (Karlsson, et al., 1975; Thortensson, 1976) have been used successfully to explain limited aspects of muscle fatigue. Surface electrode EMG measurements is another frequently used approach to objectively assess the functional state of muscle during both sustained and frequently repeated static contractions (Chaffin, 1969a, 1969b, 1973; Kosarov and Gydikov, 1975).

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One of the earliest techniques, EMG, treated the muscle action potential (MUAP) as a summation of many simpler wave forms, each of which has a varying frequency and amplitude (Chaffin, 1969b). EMG frequency analysis broke down the EMG, a summation of many MUAP's into the basic components occurring in preselected freduency bands. The results contained the amplitude of the components in each of these frequency bands.

Detailed and empirical effects of cyclic work/rest exercise effects on local muscle fatigue were presented by Schutz(1972) who divided the mechanism into two components: a fatigue process and a recovery process. Among the conclusions drawn were the following: (1) very little improvement is gained by very long (greater than 2 minutes) duration rest periods; (2) very long (greater than 2 minutes) duration work periods severely curtail performance; (3) large incremental increases in load sharply limit performance; (4) initial rate of recovery increases as the degree of prior fatigue increases; (5) the net amount or recovery decreases as more and more cycles of work are performed.

A logical consequence was the integration of piecewise knowledge from previous approaches to develop an analytical muscle fatigue model that would not only be conceptually profound but also physiologically compatible with the attributes and structure of muscle itself. Formulated by Lee (1979) the model is quantitative in analysis and is capable of detecting inter and intra-individual differences.

DEVELOPMENT OF MUSCLE FATIGUE MODEL

Concepts of Proposed Model

A motor unit is the body of motoneurons of the anterior horn of the spinal cord, its single axon which leaves the spinal cord in the anterior root and extends through the peripheral nervous system before ramifying to innervate fibers in a particular muscle and the muscle fibers themselves. The motor unit is the element of muscle contraction which includes the mechanism of neural stimulation to the motoneuron and contraction of the muscle fibers which in a motor units are homogenous.

In order to integrate some of the motor unit properties into an analytical model of muscle fatigue, several assumptions (verified by other researchers) have to be made:

1) The train of twitch stimuli arriving at a motor unit decreases the net potential difference between the current level and the threshold level. Thus, a motor unit, once activated, tends to contract continuously throughout the exertion (Milner-Brown and Stein, 1975).
2) Twitch responses of a motor unit are performed almost independently of those of the surrounding motor unit (Sica and McComas, 1971; Stalberg et al., 1976).
3) During a strenuous contraction, each motor unit generates a twitch tetanus, and the muscle tension generated by the recruited units is the sum of these twitch tetani (Coggshall and Bekey, 1970).
4) With independent activities among the motor unit, the maximum tension generated by a muscle at time t, MVC, is equal to the sum of twitch tetani of recruited motor units:

$$\mathrm{MVC}=\sum_{j=1}^{N}\overline{W}_j(t)$$

given that:

$$\overline{W}_j(t)=\sum_{i=0}^{r} w_j(t-t_i)$$

$$=\sum_{i=0}^{r}\int_{-\infty}^{\infty} w_j(t-u)d(u-t_i)du.$$

where

$w_j(t)$: twitch tension of a motor unit at time t,
N : the total number of motor units,
$\overline{W}_j(t)$: tetanus of the motor unit at time t,
$d(t)$: Dirac's delta function,
r : number of stimuli arriving at the motor unit during (0, t).

5) Each motor unit has a limited contractile capability such that after a constant number of twitch responses a motor unit is fatigued (Magora, et al., 1976).

Therefore the fatigue rate can be assumed to be a function of: 1) the number of motor units recruited, 2) types of motor units recruited, and 3) the number of twitch responses of a recruited motor unit. Similarly, during a recovery period, some motor units which are recruited during the previous contractions repay their deficits. If these motor units recover their cintractile energy, fewer number of motor units need to be recruited at the beginning of the next contraction as compared to the previous.

Table 1 contains the list of variables clarifying the structure of the muscle fatigue model. As seen in the table, the physiological concept of muscle can be represented by numbers and types of motor units. Measurements of these numbers and types are linked to EMG responses of the muscle, and analyses of the EMG responses can be formulated by a simple stochastic process in which fatigue and recovery occur as functions the number of recruited motor units and the number of fatigued motor units, respectively.

Table 1. Variables in Conceptual Muscle Fatigue Model

	PHYSIOLOGICAL PROPERTY OF MUSCLE	PARAMETERS OF THE MODEL
CONCEPT	SOURCE OF ENERGY	TYPE S MOTOR UNITS TYPE F MOTOR UNITS
	AEROBIC ANAEROBIC TWITCH THRESHOLD TWITCH FORCE	NUMBER OF MOTOR UNITS RECRUITED
	STATIC TENSION	PROPORTION OF TYPE S AND TYPE F MOTOR UNITS RECRUITED
	FORCE % MAXIMUM STRENGTH	NUMBER OF EXHAUSTED MOTOR UNITS
	FATIGUE	NUMBER OF RESERVED MOTOR UNITS NUMBER OF ACTIVE MOTOR UNITS

MEASUREMENT	NUMBER OF MOTOR UNITS RECRUITED NUMBER OF TOTAL MOTOR UNITS DURING CONTRACTION	EMG. RMS EMG. REC EMG SPECTRUM ANALYSIS
ANALYSIS	NUMBER OF MOTOR UNITS RECRUITED & PROPORTION OF TYPES & TYPE F MOTOR UNITS RECRUITED RATE OF FATIGUE RATE OF RECOVERY	ESTIMATION OF NUMBER OF RENEWALS DURING FIXED INTERVAL Po(nA), Po(1(t)u)

A stochastic process in muscle contraction

Quantitiatice relationships between EMG and force have been shown by many studies. These studies can be grouped into two; linear relationships (e.g. deVries, 1965, 1968; Milner-Brown et al., 1973, 1975a,b), non-linear relationships (e.g. Person and Libkind, 1969; Coggshall and Bekey, 1970), or both (e.g. see Bouisset, 1973).

Existing myoelectrical and histochemical findings are far from showing dynamic relationships between contractile capability of a motor unit and its electrical changes over time. However, some aspects of the complex relationship can be analytically traced by understanding stochastic models of neuron firing and of chemical transmitter release. Especially, neuron firing models (ten Hoopen and Reuver, 1969, 1970; Srinivasan and Rajamannar, 1970, 1971) showed that arrivals of stimuli to a motoneuron approximates a Poisson process. Vere-Jones (1966) stated that a chemical transmitter (Ach) which is activated by arrivals of neuron firings is released to the muscle by random processes and it can be fitted into $M/M/\infty - M/G/\infty$ tandem queues. t was shown earlier that the output process of an $M/G/\infty$ queue is a Poisson (Mirosol, 1963). Thus arrivals of stimuli to any muscle cell can well be described by a Poisson process.

Suppose an observation is made on a working muscle at time t. Since each motor unit contracts almost independently, the rate at which motor units becomes exhausted during a small interval dt would be equivalent to the departure rate of an M/G/n queue. Arrivals of stimuli to a motor unit is a Poisson because the output process of Poisson arrivals through a linear filter (i.e. the threshold level necessary to initiate motor unit contraction) approximates a Poisson process (Vere-Jones, 1966). The output of the linear filter triggers a sequence of twitches of a motor unit at a 1 to 1 ratio.

It is assumed that the fatigue rate of motor units during dt follows a Poisson distribution. The number of exhausted motor units is distributed with a Poisson density, when the number of active motor units is large (e.g. in the order of 200∼3000 motor units during exertion in major limb muscles; Sica and McComas, 1974).

Thus, the proposed analytic sequence from motor unit fatigue to muscle fatigue can explain many non-linear phenomena such as decreased blood flow rate at heavy exertion, lower lactate level after heavy exertion (e.g. muscle lactate level after 75% of maximum strength exertion was lower than those levels after 25∼50% contractions, etc.). However, limited experimental results in literature prevent wide ranging and accurate estimations of necessary parameters of the proposed model. Therefore, an alternative method of estimation using laboratory experiments should be developed.

Muscle Fatigue and Recovery

Assumptions in the preceeding section state the phenomena of independent activities of the motor unit and additive recruitment for the constant tension in a prolonged exertion. By using the phenomenon, the muscle Eatigue during frequent strenuous exertions can be formulated by estimating fatigue and recovery rates of recruited motor units.

For the assumption of homogeneous motor units, the fatigue rate of a recruited unit and the recovery rate of an exhausted unit are denoted a(fatigue rate) and u(recovery rate). This homogeneity of the motor unit was adopted temporarily for simple notations. Allowing for two types of motor units, a_s and u_s denote the fatigue and recovery rates for the Type S motor units, and a_f and u_f for the Type F motor units.

Suppose that there are N homogeneous motor units in a muscle. Assume that at time t each motor unit is either in the active state (state 0) or in the fatigued state (state 1). For the ith motor unit at time t, the state, $s(i,t)$, is denoted:

$$s(i,t)=\begin{cases}0 & \text{if ith motor unit is active at time } t\\ 1 & \text{if ith motor unit is fatigued at time } t\end{cases} \qquad \cdots\cdots(1)$$

Define $L(t)$ to be the number of fatigued motor units at time t:

$$L(t)=\sum_{i=1}^{N} s(i,t). \qquad \cdots\cdots(2)$$

During an exertion, the number of fatigued motor units at $t+dt$ is greater than or equal to the number at t, $t>0$ and $dt>0$:

$$L(t+dt)\geq L(t). \qquad \cdots\cdots(3)$$

Let a be the fatigue rate of a recruited muscle motor unit and let n be the number of recruiten motor units.

By assumption 2(independent activity of the motor unit), the probability that a motor unit is fatigued among the recruited units during dt is

$$\Pr\{L(t+dt)=m+1 \mid L(t)=m\}=na \qquad \cdots\cdots(4)$$

Given that the initial exertion of the muscle is made at time 0, let T be the first passage time to the state $N-n+1$:

$$T=\text{inf.}\ (t : L(t)>N-n+1) \qquad \cdots\cdots(5)$$

i.e. T is the first passage time to the state of muscle fatigue. The probability that the muscle fatigue occurs at or before time t is:

$$\Pr(T<t)=\Pr\{L(t)>N-n+1\}. \qquad \cdots\cdots(6)$$

The site of fatigue recovery is limited to the already fatigued motor units. By the definition of the recovery rate, u, during a small interval dt of rest:

$$\Pr\{L(t+dt)=m-1 \mid L(t)=m\}=mu. \qquad \cdots\cdots(7)$$

Eq. (5) is simply the fatigue time and equations (4), (7) represent the transition rates of the muscle (i.e. na and mu). By equations (2)-(7), the operational definition of muscle fatigue can be stated by the following probabilistic statements:

1. The state of muscle at time t can be defined by the number of fatigued motor units, $L(t)$.
2. The muscle cannot maintain a required static force at time t if $N-L(t)\leq n$, i.e. $L(t)\geq N-n$.
3. If i motor units are already fatigued at the start of an exertion, the time to muscle fatigue is the first passage time from state i to state $N-n+1$.

By Equations (4) and (7), it is easy to note that the relationship between cumulative work time and intensity of exertion would not be linear. The number of recruited motor units at the onset of exertion is determined by the force of the exertion. During a heavy exertion, n is a large number. And since N is fixed at MVC, the cumulative work time decreases rapidly. Equations (6) and (7) also state that the recovery rate during a rest period is directly related to a number of fatigued motor units.

FIRST PASSAGE TIMES TO THE STATE OF MUSCLE FATIGUE

Suppose that there are N homogeneous motor units in the biceps brachii, and that n active motor units are recruited in order to maintain the desired force. Define the state of the muscle to be equal to the number of fatigued motor units. Then muscle fatigue can be defined to be the state such that the number of fatigued motor units is $N-(n-1)$, i.e. the sum of reserved motor units and currently recruited motor units is equal to $n-1$. Since n is a function of %MVC, a muscle in the state of fatigue at 75 %MVC still may be able to exert 50 %MVC. As seen in Figures 1 and 2, fatigue of recruited motor units during a work period can be defined as a birth-process and the recovery of the new paragraph fatigued motor units during a rest period is considered as a death process.

At the complete resting state, the muscle is in a state 0. When the work begins, the muscle changes its state by making forward (i.e. fatigue) transitions. During the rest period, some of the fatigued motor units recover from fatigue, and the state of the muscle is changed by backward (i.e. recovery) transitions.

The fatigue rate is equal to the rate of forward transition and the recovery rate to the backward transitions. Given these transition rates, the fatigue recovery processes of the muscle can be defined to be a Markov Chain with state space $\{0, 1, 2, \cdots, (N-n+1)\}$, and transition rates a and u.

If the muscle starts out in state i, the net number of forward-transitions to muscle fatigue is $N-(n-1)-i$. Thus the cumulative work time to the muscle fatigue is equivalent to;

A First Passage Time from State i to State $N-(n-1)$.

Let $t(i)$ be the first passage time from the initial state i to the fatigue state $N-n+1$. Similarly, let $p(i, N-n+1)$ be the probability of transition from a state i to a state $N-n+1$. The number of transitions required to go from a state i to a state $N-n+1$ is either unity (if the transition is directly made from i to $N-n+1$), or it is $1+t(k)$ (if the initial transition is made from state i to some intermediate k) (Howard, 1971). That is,

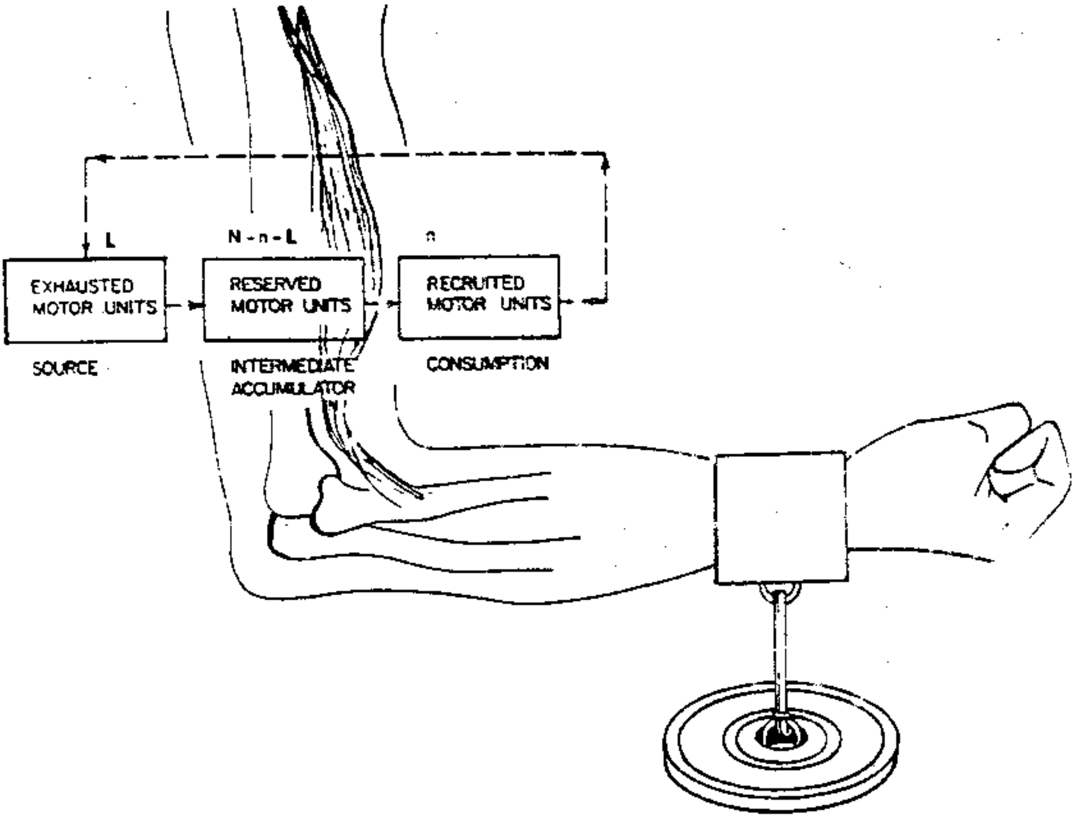


Figure 1. Conceptualized Muscle Fatigue Model.

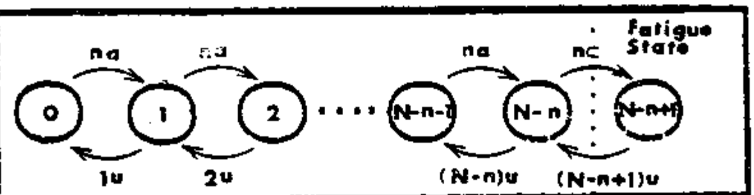
State of the Muscle							
No. of Exhausted Motor Units **L**	0	1	2	...	N-n-1	N-n	N-n+1
No. of Recruited Motor Units	n	n	n	...	n	n	n
No. of Reserved Motor Units **N-n-L**	N-n	N-n-1	N-n-2	...	1	0	-1

Figure 2. Transition Diagram of Muscle Fatigue.

$$t(i)=\begin{cases}1 & \text{with probability } p(i,N-n+1)\\ 1+t(k) & \text{with probability } p(i,k).\end{cases} \qquad \cdots\cdots(8)$$

Using the above equation, the expectation of the first passage times from a state i to a state $N-n+1$, $E\{t(i)\}$, is given by:

$$
\begin{aligned}
&E\{t(i)\}\\
&=p(i,N-n+1)1+\sum_{K=0}^{N-n}p(i,k)[1+E\{t(k)\}]\\
&=\quad 1 \quad +\sum_{K=0}^{N-n}p(i,k)E\{t(k)\} \qquad \cdots\cdots(9)
\end{aligned}
$$

The second-moments of the first passage times, $E\{t^2(i)\}$, can be calculated by use of the second moment of the first passage times.

From Eq. (8), $E^2\{t(i)\}$ can be represented by;

$$
\begin{aligned}
&E\{t^2(i)\}\\
&=p(i,N-n+1)1+\sum_{K=0}^{N-n}p(i,k)[1+E\{t(k)\}]^2\\
&=\sum_{K=0}^{N-n+1}p(i,k)+2\sum_{K=0}^{N-n}p(i,k)\ E\{t(k)\}\\
&\quad+\sum_{K=0}^{N-n}p(i,k)\ E\{t^2(k)\}\\
&=1+2\sum_{K=0}^{N-n}p(i,k)E[t(k)]\\
&\quad+\sum_{K=0}^{N-n}p(i,k)E[t^2(k)]
\end{aligned}
$$

Since $E\{t(i)\}=1+\sum_{K=0}^{N-n}p(i,k)E\{t(k)\}$, the above equation can be rearranged into;

$$
\begin{aligned}
&E\{t^2(i)\}\\
&=2E\{t(i)\}-1+\sum_{K=0}^{N-n}p(i,k)E\{t^2(k)\} \qquad \cdots\cdots(10)
\end{aligned}
$$

In the Appendix, expressions for the mean first passage time and for the variance of the first passage times from state i to the state $N-n+1$ are derived for three cases:

1. HMSI Model: Homogeneous Motor Units with State-Independent Recovery Rate
2. HMSD Model: Homogeneous Motor Units with State-Dependent Recovery Rate
3. NMSD Model: Non-Homogeneous (Two Types) Motor Units with State-Dependent Recovery Rates

In the HMSI model, the fatique time is calcuated for n motor recruited from a population of N motor units, using a given fatique rate, a, work period, T_w, a recovery rate, u, and rest period T_r. In this case it was assumed that there are $(N-n)/2$ fatiqued motor units (Appendix A). This model formed the basis for the development of the HMSD and NMSD models. The HMSD model was obtained by modifying the recovery rate of the HMSI model. In the HMSD model a more realistic state-dependent recovery rate (Eq. (7)) is used.

A more physiologically compatible fatigue mechanism, the NMSD, was also modeled. In this model two non-homogeneous motor units, Type S and Type F, are utilized. The structure of the model is presented in Appendix A.3. However, since the first passage time is regenerative (see Eq. A.6), only an approximate solution is obtainable. Because there are two types of motor units, there are many states at which the effective number of fatigued motor units is equivalent to

$N-n+1$: i.e. the fatigue state can not be uniquely defined. Therefore this model was developed by first formulating distinct fatigue and recovery processes and then performing a simulation using input parameters which include numbers of the total motor units(N), numbers of recruited motor units(n), and fatigue and recovery rates of Type S and Type F. The number of fatigued and recovered motor units were obtained by a representative of Poisson random numbers, and then the muscle state was updated. The fatigue state can be defined by:

$$L_sF_s+L_fF_f$$

where

L_f : number of Type S motor units fatigued,
L_f : number of Type F motor units fatigued,
F_s : tetani of a Type S motor unit.
F_f : tetani of a Type F motor unit.

The relative tension of each type of motor units was calculated using the following rationale:

$$f(N_sr_s+N_fr_f)=\mathrm{MVC}$$

where f : a twitch force.

This implies that the tension of a motor unit is proportional to the associated frequency of stimulation. The average of the calculated twitches (f) is about 20 grams, which is within a range of earlier experimental observations made by Sisson(1974) and Sica et al. (1971, 1974); 0.1～50 grams/motorunit.

Discussion

Need for an Analytic Model

In engineering fields, relationships between muscle strength and EMG amplitude have been analyzed mainly by a statistical regression analysis (e.g. see Bigland and Lippold, 1954; deVries, 1965; Bouisset, 1968, Milner-Brown and Stein, 1975). While these statistical analyses show the general scope (i.e. mean, variance) of the relationships, they fail to provide a means to analyze an individual's muscle capabilities.

Therefore, an analytic model to expand a working knowledge of muscle fatigue is needed. This model should be:

(1) Physiologically compatible both in attributes and structure of muscle fatigue,
(2) Quantitative in analysis, and
(3) Capable of detecting inter-and intra-individual differences.

To fulfill these characteristics, one has to clarify the underlying muscle fatigue process by modeling based on analytic, quantitative, and multidisciplinary integrations of knowledge of muscle entities.

Theoretical Extension

The Study was conceptualized on the bases of physiological, histochemical and myoelectrical experiments. These findings were organized into a known sequence of contractile processes by mathematical equations. Based on these functional relations, methods to estimate fatigue rates and recovery rates can be formulated. Estimations of fatigue andrecovery rates can be made from laboratory experiments. More specificly, major estimations can be made on the basis of surface EMG changes at constant exertion. From these EMG analyses, relative numbers of motor units recruited in successive exertions have been calculated.

The model can be used to provide insights to help clarify some of popular topics of discussion. For example, by estimating relative numbers of a subject's motor units which were recruited during a contraction, the phenomenon of decreased local blood flow or working muscle at high exertion can be re-evaluated not only in terms of the "meachanical occlusion" or "nipping" effect, but also in terms of decreased activity of aerobic process, and thus, an increased role of Type F motor units.

The inhibitory role of the muscle lactate level can also be reviewed. After analyzing his relative importance of Type S and Type F motor units during the subject's exertion, estimations of his relaitve muscle lactate level can be checked against the related literature. It is known that a high gradient exists between an individual's muscle lactate and his blood lactate(Mitchell et al., 1970). Increased blood flow after static exertion would remove only the blood lactate and thus a larger concentration gradient between muscle lactate and blood lactate would then facilitate removal of muscle lactate. The muscle lactate level after 75% exertion was lower than the levels after 25% and 50% exertions. This indicates that muscle fatique in heavy exertion occurs because of loss of some contractility of each motor unit for almost all motor units. Therefore, during 25%MVC and 50% MVC exertions, a larger number of Type F motor units would be reserved initially than during 75 %MVC exertions.

The presence of many renewable Type F motor units during 25% MVC and 50% MVC exertions will lead to the production of more muscle lactate than is produced in 75% MVC exertion. The above assertion can be partially proved by comparing the numbers of the two types of motor units at different force levels.

It has been observed that people who exert high maximum strength show shorter endurance time (e.g. Armstrong, 1976). These observations can be explained by arguments similar to the above, i.e., the relative distribution of Type S and Type F motor units of an individual. People who can exert high initial strength would have a large percentage of Type F motor units. Consequently, the role of Type F motor units in exertion increases in individuals who can exert high initial strength, and these units are more easily recruited. This analysis has a significant implication for industrial applications: workers who have a higher initial strength capability may be adversly affected by even slight increase of work period more readily than workers who have a low strength capability.

Using the model, this implication can be evaluated experimentally, by comparisons of the estimated numbers of the types of the subject's motor units and his endurance times.

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Appendix A

First Passage Time To The State of Muscle Fatigue

A. 1 Homogeneous Motor Units, State-Independent Recovery: The HMSI Model

Let a be the fatigue rate of a single recruited motor unit and u the recovery rate of a single fatigued motor unit respectively. Since activities of motor units are approximately independent, the fatigue rate of a muscle during contraction of n motor units would be na. Under the assumption of a state-independent recovery rate, the recovery rate of the muscle can be set to the average number of all fatiguable motor units, $0.5(N-n)$; i.e. $0.5(N-n)u$.

Using the standard Birth-Death results, the expectation of the first passage times is obtained:

$$E\{t(i)\}$$

$$=\sum_{j=1}^{N-n+1}\sum_{K=1}^{i} 1/(\mathrm{na})[\{0.5(N-n)u\}/(\mathrm{na})]^{K-i}$$

$$=1/(\mathrm{na})\sum_{j=1}^{N-n+1}\sum_{K=1}^{j}[\{(N-n)u\}/(2\mathrm{na})]^{K-1}$$

$$=1/(\mathrm{na})\sum_{K-1}^{N-n+1}(N-n+1-k)[\{(N-n)u\}/(2\mathrm{na})]^{K-1} \qquad \cdots\cdots(\mathrm{A.1})$$

By Eq. A.1, the second moment of the first passage times from one state to another is:

$$E\{t^2(i)\}$$

$$=\sum_{j=i}^{N-n}2/[\{\mathrm{na}\}\sum_{L=j}^{N-n}\sum_{K=1}^{L}1/\{\mathrm{na}\}]$$

$$[\{N-n)u\}/\{2\mathrm{na}\}]^{K-1}$$

$$+\sum_{K=i-1}^{N-n-1}\sum_{j=1}^{K}[2\{0.5(N-n)u\}^{j}]/(\mathrm{na})^{j+1}$$

$$\sum_{L=i-j}^{N-n}\sum_{K=1}^{L}1/(\mathrm{na})[\{0.5(N-n)u\}/(2\mathrm{na})]^{K}$$

$$-\sum_{j=i}^{N-n}\sum_{K=1}^{j}[\{0.5(N-n)u\}]^{K}/(\mathrm{na})^{K-1}]$$

$$-(N-n+1-i)/(\mathrm{na}) \qquad \cdots\cdots(\mathrm{A.2})$$

A. 2 Homogeneous Motor Units, State-Dependent Recovery: The HMSD Model

The model of a state-dependent recovery process involves the use of motor unit recovery rates ku, where k is a number of fatigued motor units.

The expected value of the first passage times from a state i to the state $(N-n+1)$ was obtained as:

$$E\{t(i)\}=(N-n+1-i)/(\mathrm{na})+1/\{\mathrm{na}\}$$

$$\sum_{L=i}^{N-n}\sum_{k=1}^{L}Q(1,k)[u/(\mathrm{na})]^{k}$$

$$\text{where } Q(1,k)=1(1-1)(1-2)(1-3)\cdots(1-k+1). \qquad \cdots\cdots(\mathrm{A.3})$$

By applying the similar induction procedure, the general from of the second moment of the first passage times, $E\{t^2(i)\}$ is:

$$E\ \{t^2(i)\}=\sum_{L=i}^{N=n}2/(\mathrm{na})E\{t(1)\}$$

$$+\sum_{k=1}^{L}Q(1,k)[u/(\mathrm{na})]^{k}E\ \{t(1-k)\}$$

$$-\sum_{L=i}^{N-n}1/(\mathrm{na})(1+\sum_{k=1}^{L}Q(1,k)[u/(\mathrm{na})^{k}]) \qquad \cdots\cdots(\mathrm{A.4})$$

A. 3 Non-Homogeneous Motor Units, State-Dependent Recovery: TheNMSD Model

Under the hypothesis of differential recruitment for the two types of motor units, computing the first passage times to the point of muscle fatigue is not straight-forward. The difficulty arises from the fact that recruitment of motor units now depends on the availability of two types of motor units. For example, the number of Type S motor units and Type F motor units which are to be recruited during an exertion not only depend on the level of exertion, but also depend on the availability of each type of motor unit at the time of recruitment. However, an approximation to the first passage times can be made by considering the following physiological findings.

It is well known that there exists orderly recruitment during a sternuous exertion (Grimby and Hannerz, 1976, 1977; Milner-Brown et al., 1973, 1974, 1975; Cerretelli et al., 1976; Yemm, 1977 etc.). Type S motor units are more easily recruited than Type F motor units (Milner-Brown et al., 1973, 1975; Gollnick et al., 1974). The differential recruitment of motor units can be related to the distinct difference in the threshold levels of recruitment between low threshold level of Type S motor units and high threshold level of Type F motor units (Robinson, 1976). Therefore it is reasonable to assume that, at least in the case of strenuous exertion, all Type S motor units would be recruited at the onset of an exertion, followed by Type F motor units.

Furthermore, fatigue rates and recovery rates for the two types of motor units are quite distinct. Type F motor units show both faster fatigue and recovery rates than Type S motor units. Type Fmotor units rely for their energy supply on anaerobic processes, while Type S motor units utilize aerobic processes. Therefore, it can be assumedthat the recovery rate of each type of motor unit depends on the number of fatigued motor units of the same type, and is approximately independent the other type.

Thus, the following assumptions can be made:

1. During a strenuous exertion, all Type S motor units are initially recruited and then some of Type F motor units are additionally recruited.
2. During a small interval of work dt, at mostone motor unit of either type can make a shift from an active state to fatigued state, and fatigue processes between types and among motor units are independent.
3. During a small interval of rest dt, only one motor unit of either type can be recovered from fatigue, and recovery process between types and among motor units is independent.

Using these assumptions and for $dt=1$:

$$\begin{cases} p(i,i-1;j,j)=iu_s \\ p(i,i+1;j,j)=a_s \\ p(i,i;j,j)=1-[a_s+a_f+iu_s+ju_f] \\ p(i,i;j,j-1)=ju_f \\ p(i,i;j,j+1)a_f \end{cases}$$

where

$(i,i;.,.)$: states of Type S motor units at time t and $t+dt$,

$(.,.;j,j)$: states of Type F motor units at time t and $t+dt$, respectively. ……(A.5)

With these rates the probability rate matrix is shown in Figure A.1 where:

N_s represents the total number of Type S motor units and N_f represents the total number of Type F motor units.

Suppose that state $j, N_s \leq j < (N_s+N_f)$, represents the point of muscle fatigue (i.e. there are j fatigued motor units). Suppose that (n_s+n_f) motor units are necessary to reach to a required level of exertion. Then the following relation holds between j and (N_s+N_f);

$$(N_s+N_f)-j<(n_s+n_f).$$

$$
P = \left(\begin{array}{cc|ccccccc|cccccccc}
 & \text{STATE AT TIME } (t+\Delta t)\ \text{Type S} & 0 & & & & & & & 1 & & & & & & & \\
\text{STATE AT TIME } t\ \text{Type S} & \text{Type F} \backslash \text{Type F} & 0 & 1 & 2 & 3 & \cdots & N(f)-n(f) & N(f)-n(f)+1\ (\text{Fatigue State}) & 0 & 1 & 2 & 3 & \cdots & N(f)-n(f) & N(f)-n(f)+1 & \\
\hline
0 & 0 & 1-A(s)-A(f) & A(f) & 0 & 0 & \cdots & 0 & 0 & A(s) & 0 & 0 & 0 & \cdots & 0 & 0 & \\
 & 1 & U(f) & 1-A(s)-A(f)-U(f) & A(f) & 0 & \cdots & 0 & 0 & 0 & A(s) & 0 & 0 & \cdots & 0 & 0 & \\
 & 2 & 0 & 2U(f) & 1-A(s)-A(f)-2U(f) & A(f) & \cdots & 0 & 0 & 0 & 0 & A(s) & 0 & \cdots & 0 & 0 & \\
 & 3 & 0 & 0 & 3U(f) & 1-A(s)-A(f)-3U(f) & \cdots & 0 & 0 & 0 & 0 & 0 & A(s) & & 0 & 0 & \cdots \\
 & \vdots & \vdots & \vdots & \vdots & \vdots & \cdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \cdots & \vdots & \vdots & \\
 & N(f)-n(f) & 0 & 0 & 0 & 0 & & 1-A(s)-A(f)-[N(f)-n(f)]U(f) & A(f) & 0 & 0 & 0 & & & A(s) & 0 & \\
 & N(f)-n(f)+1\ (\text{Fatigue State}) & 0 & 0 & 0 & & \cdots & [N(f)-n(f)+1]U(f) & 1-A(s)-A(f)-[N(f)-n(f)+1]U(f) & 0 & 0 & 0 & 0 & & & A(s) & \\
\hline
1 & 0 & U(s) & 0 & 0 & 0 & & 0 & 0 & 1-A(s)-A(f)-U(s) & A(f) & 0 & 0 & \cdots & 0 & 0 & \\
 & 1 & 0 & U(s) & 0 & 0 & & & 0 & U(f) & 1-A(s)-A(f)-U(s)-U(f) & A(f) & 0 & \cdots & 0 & 0 & \\
 & 2 & 0 & 0 & U(s) & 0 & & 0 & 0 & 0 & 2U(f) & 1-A(s)-A(f)-2U(f)-U(s) & A(f) & \cdots & 0 & 0 & \\
 & 3 & 0 & 0 & 0 & U(s) & & 0 & 0 & 0 & 0 & 3U(f) & 1-A(s)-A(f)-U(s)-3U(f) & \cdots & 0 & 0 & \cdots \\
 & \vdots & \vdots & \vdots & \vdots & \vdots & & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \cdots & \vdots & \vdots & \\
 & N(f)-n(f) & 0 & & 0 & 0 & U(s) & 0 & 0 & 0 & 0 & 0 & & [N(f)-n(f)]U(f) & 1-A(s)-A(f)-U(s)-[N(f)-n(f)]U(f) & A(f) & \\
 & N(f)-n(f)+1 & 0 & 0 & 0 & 0 & & U(s) & 0 & 0 & 0 & 0 & 0 & \cdots & [N(f)-n(f)+1]U(f) & 1-A(s)-A(f)-[N(f)-n(f)+1]U(f) & \\
\hline
 & & & & & \vdots & & & & & & & & & & & \ddots
\end{array}\right)
$$

FIGURE A1 TRANSITION PROBABILITY OF FATIGUE AND RECOVERY PROCESSES UNDER ASSUMPTIONS OF TWO TYPES OF MOTOR UNITS, STATE - DEPENDENT RECOVERY : (NMSD)

In other words, the number of active motor units in the muscle must be less than the required number of recruitment at the point of muscle fatigue.

From Figure A.1, probabilities of transitions are considered in two dimensions, i.e. transitions within Type S motor units and transitions within Type F motor units. A forward transition rate could be either $N_s a_s$ within Type S motor units or $n_f a_f$ within Type F motor units. Once the matrix in Figure A.1 is prepared, the derivations of the first moment of the first passage times and the second moment are straight-forward.

By plugging transition probabilities in Eq. A.5, into Eq. 9, and then by applying the similar induction procedure, the first moment of the first passage times, $E\{t(i,j)\}$ can be obtained:

$$\begin{aligned} &E[t(i,j)]=1/[a_s+a_f+iu_s+ju_f] \\ &\quad \{[1+iu_sE[t(i-1,j)]+ju_fE[t(i,j-1)] \\ &\quad +a_sE[t(i+1,j)]+a_fE[t(i,j+1)]]\} \qquad \cdots\cdots(A.6) \end{aligned}$$

As seen in Eq. A.6, the terms in the right hand side of the equation is regenerative. Thus only approximate solution can be obtained.

Eq. A.6 is the general form for the expected first passage time to muscle fatigue. Computing the expected time by this equation requires additional assumption because the fatigue state cannot be uniquely defined. In other words, the fatigue state can be reached by combinations of different numbers of Type S and Type F motor units. In order to determine a unique fatigue state, the twitch tension of each type of motor units was assumed to be proportional to the associated frequency of stimulation.