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ORIGINAL ARTICLE

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Changes in the action potential and contractile properties of skeletal muscle in human's with repetitive stimulation after long-term dry immersion

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Abstract This paper compares the effects of 7-day *dry* immersion and intermittent muscle contraction on electrical and mechanical failure during muscle fatigue in the human triceps surae muscle electrically stimulated at 50 impulses $\cdot s^{-1}$ via its motor nerve. Intermittent contractions of 60-s duration were separated by 1-s intervals for identical duration of tension development. The 60-s intermittent contractions decreased tetanic force to 57% ($P < 0.05$) of initial values, but force reduction was not significantly different in the two fatigue tests: the fatigue index was 36.2 (SEM 5.4)% versus 38.6 (SEM 2.8)%, respectively ($P > 0.05$). Whilst identical force reduction was present in the two fatigue tests, it would appear that concomitant electrical failure was considerably different. This electromechanical dissociation would suggest that a slowing of conduction along nerve and muscle membranes did not explain the observed mechanical failure. It is suggested that intracellular processes played major role in contractile failure during intermittent contractions after muscle disuse.

Key words Dry immersion · Human triceps surae · Isometric intermittent contraction · Surface action potential · Muscle fatigue

Introduction

It is well known that during muscle contraction mechanical force output decreases gradually. This phenomenon, called fatigue, is probably one of the most intriguing observations associated with contractile activity. Human muscle fatigue studies have been performed under a variety of experimental conditions and, in many cases, the concept of fatigue has been applied to assessing deterioration of muscle performance, i.e. "the failure point" at which the muscle is no longer able to maintain the required force or work output level (Moritani et al. 1981) or as "an inability to maintain the required or expected force" (Edwards 1981). Despite numerous investigations the etiology of muscle fatigue has remained unknown (Fitts et al. 1982).

When a muscle is activated by electrical stimulation at a constant frequency, fatigue is defined as a decrease in tension. Few easily measurable, objective, physiological indices of fatigue exist. These maximally stimulated contractions serve as an index of muscle contractility and have been shown to be independent of central drive (Bigland-Ritchie et al. 1979; Jones et al. 1979). Changes in the surface electromyogram (*EMG*) have been used extensively as indices of fatigue (Edwards and Lippold 1956; Lindstrom et al. 1977; Lindstrom and Magnusson 1977), but the relationship between the *EMG* and fatigue remains unclear and it has been found that *EMG* changes often precede muscle fatigue (Lindstrom et al. 1977), and interpretations of the *EMG* signal and fatigue are made difficult by the complexity of the *EMG* signal. Therefore, in spite of extensive use, the exact relationship between the *EMG* signal and muscle fatigue has not been defined. The *EMG* recorded from a muscle during volitional activation has been described as the result of a summation and interference of the motor unit action potentials from all the active motor units (De Luca 1979) and the characteristics of the *EMG* have been found to depend on the firing patterns of the motor units as well as on the configuration of the motor units action potentials (Lindstrom and Magnusson 1977).

The physiological data within the muscle show a time-dependent changes during the time course of muscle fatigue development. Such changes have been

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shown to be related to hydrogen ion and metabolite accumulation (Witzmann et al. 1983; Wilkie 1986) and to sodium and potassium ion concentration shifts (Jones et al. 1979). It has been suggested that these changes would, in turn, affect the muscle excitation-contraction (E-C) coupling, including the muscle membrane properties, and muscle action potential propagation, leading to *EMG* manifestations of muscle fatigue distinct from mechanical manifestations (Bigland-Ritchie 1981; Moritani et al. 1986). Possibly there is no single cause, and fatigue may take place at several sites independently.

The physiological and biochemical properties of limb skeletal muscle have been shown to adapt to a variety of experimental conditions. Among these has been shown to be the microgravity encountered during spaceflight (Martin et al. 1988; Riley et al. 1990). Foremost among these changes has been found to be a reduction in the force-generating capacity (Witzmann et al. 1982a,b), which is presumably a direct result of the decrease in fibre number (Herbison et al. 1978) and diameter (Maier et al. 1976; Herbison et al. 1978). A decline in fibre number or diameter may coincide with the loss of active cross bridges as has been suggested by the decreased tetanic tension after disuse (Witzmann et al. 1982a, b). Furthermore, disuse has been shown to reduce the functional capacity of the sarcoplasmic reticulum (Kim et al. 1982), and this may in part explain the observed decrease in the rate of tension development and decline (Witzmann et al. 1982a, b). These changes would seem to suggest a spaceflight-induced reduction in muscle work capacity. Thus attention has been focused on the relationship between disuse and changes in intracellular content which contribute to the control of muscle contraction kinetics and the suggestion that changes in muscle membrane ionic processes might contribute to the observed reduction of contraction kinetics after disuse.

The present work examined in humans the effects of a series of 60-s intermittent contractions separated by intervals of 1 s on mechanical and electrical failure in the triceps surae muscle after a 7-day *dry* immersion. Mechanical and electrical parameters were recorded during electrical stimulation of the muscle motor nerve to dissociate peripheral sites from central level.

Methods

Subjects and immersion procedure

The experiments were performed on six healthy male volunteers. The mean ages, body heights and masses of the groups were 22.7 (SEM 3.5) years. 1.76 (SEM 0.3) m, and 66.4 (SEM 2.3) kg, respectively. All the subjects were habitually active and had a lean body composition. All were familiar with the procedures and gave their informed consent. The study was approved by the Human Ethics Committee at the Institute of Biomedical Problems.

Dry immersion was used to simulate microgravity (see Shulzhenko and Vil-Villiams 1976). During immersion, the subjects remained in a horizontal position continuously for all activities including excretory functions and eating. The exposure lasted 7 days. The subjects were kept under medical observation and all were nonsmokers. Each subject served as his own control.

Experiment procedure

Fatigue was tested in the triceps surae muscle of intact humans during intermittent contraction. Muscle contraction was triggered by supramaximal (+ 40%) rectangular electrical pulses of 1-ms duration delivered through an active monopolar electrode (1-cm diameter) which was placed in the popliteal fossa and a passive electrode placed on the lower third of the thigh. Fatiguability was studied during a standard series of 60-s intermittent isometric contractions separated by 1-s intervals (see Koryak et al. 1975). The stimulation frequency was 50 impulses $\cdot s^{-1}$ during the fatigue tests, because it has been found that this is within the physiological frequency range of activation of muscle cells during the initial part of strong voluntary contractions (Bigland-Ritchie et al. 1983) on the one hand, and estimated to elicit maximal isometric tetanic contraction in response to an electric tetanic stimulation of the nerve, innervating the triceps surae muscle (Koryak 1992, 1994, 1995), on the other.

Force and EMG recordings

The mechanical responses of the triceps surae muscle were recorded by tendometry, which made it possible to measure single muscle contraction force by the degree of tension change in the muscle distal tendon. To ensure standardization of position and fixation of the limb during assessment, a special set-up has been designed (Koryak 1992, 1995). The apparatus maintained the thigh and lower leg in a standard position (knee joint angle between tibia and sole of foot of 900).

Recording of muscle electrical activity called electromyography (*EMG*) or surface action potential (*SAP*) in the test was achieved by means of Ag-AgCl surface electrodes (8-mm diameter). The two recording electrodes were placed longitudinally over the soleus muscle belly, their centres 25 mm apart. The interelectrode impedance was less than 5 kΩ. The earth electrode (7.5×6.5 cm) was fastened on the skin at the shank. Recording of the mechanical and electrical responses of the skeletal muscle during intermittent contractions was made during the 1 s after the start of tetanization of the motor nerve and then for short periods (about 0.2 s) at the end of each contraction and again after 1 s and 121 s.

Measurements and statistics

Experimental *EMG* and force-signals were recorded on magnetic tape and the *SAP* was in addition displayed on a storage oscilloscope. The mechanical twitch and tetanic-tension development (P_t and P_o, respectively) was measured as well as twitch time-to-peak (TPT) and time to half relaxation ($1/2RT$). The maximal rates of twitch tension development (dP_t/dt) were obtained by differentiation of the analogue signal.

The fatiguability of the triceps surae muscle was calculated from the fatigue index (FI) – the percentage ratio of the average force of the five last contractions to that of the five first contractions (Koryak et al. 1975). The *EMG* was analysed from the amplitude of the electrical responses – M-waves [peak-to-peak amplitude of *SAP* (Sica and McComas 1971; Badalyan and Skvortsov 1986)] as well as the amplitude, duration, area of the first phase of the *SAP*

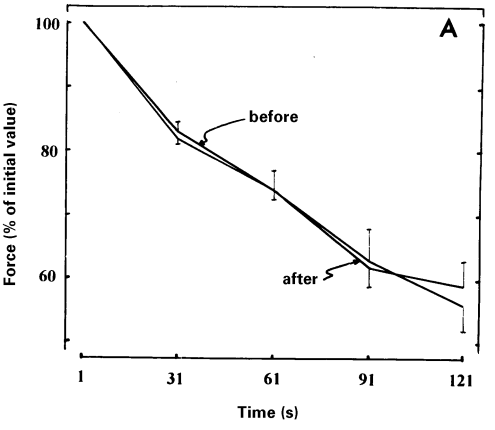
(Skvortsov 1981) at the end of the 1,3,5,121 s of the rhythmic muscle contraction. To determine the relative extent of change in contractile (*C*) and electrical (*E*) M-waves as a result of fatiguability the *E*:*C ratio* was calculated where *E* was the ratio of the amplitude of electrical postimmersion M-wave to the corresponding preimmersion M-wave and C was the ratio of postimmersion to corresponding preimmersion mechanical response of triceps surae muscle. The *E*:*C* ratio was determined from the indices of *E* and *C* at the end of 1,3,5 and 121 s from the start of electrical tetanization.

All values reported are the mean and SEM. Differences between group means were determined by Student's paired *t*-tests and unpaired Wilcoxon tests using the 0.05 level of confidence. The percentage changes for preimmersion and postimmersion were calculated.

Results

Fatigue and tetanic force

The effects of 7-day *dry* immersion on the electrically evoked intermittent contractions, stimulated at 50 impulses $\cdot s^{-1}$ are illustrated in Fig. 1A. In this example, tetanic force decreased gradually to about 57% of its initial value (recorded from the same muscle at 50 impulses $\cdot s^{-1}$). There were no significant differences between the before and after curves: the *FI* was 36.2 (SEM 5.4)% and 38.6 (SEM 2.8)%, respectively ($P > 0.05$, Fig. 1B). The analysis of the time course of the contractile activity of muscle revealed in the main a biphasic nature of the wave. In this case, each succeeding phase was characterized by the appropriate dynamics of changing the contraction force of muscle. There was a more rapid increase in the force of contraction compared to the initial value at 30–31 s (17%–18%) with a subsequent relative slowing-down at 60 –61 s (8%–9%) and again a slight rise in the rate of decreasing the contraction force at 90–91 s (11%–12%) with slowing-down on the last portion of the curve (3%–7%). This observation might seem paradoxical, because it is well known that, during strong isometric contractions the mechanical tension interferes with intramuscular blood circulation and ischaemic processes have been shown to develop (Edwards et al. 1972).



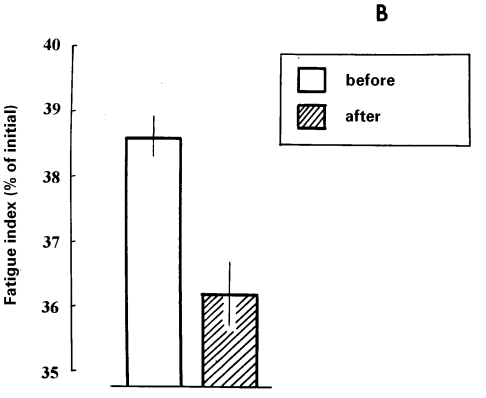


Fig. 1 **A** Comparison of intermittent 1-s contractions separated by 1-s intervals performed before and after *dry* immersion. Values expressed as percentage of initial tetanus force (50 impulses $\cdot s^{-1}$). **B** Fatigue index expressed as percentage in before and after immersion.

Table 1 Electrical and mechanical properties of skeletal muscle before (*b*) and after (*a*) immersion. *E*:*C ratio* Change of rates of electric responses to muscle contraction force

		First		Surface action potential							
				Time from start of electrical stimulation							
				1		3		5		121	
		b	a	b	a	b	a	b	a	b	a
Amplitude	Mean	5.2	5.0	8.6	7.6	10.2	8.1	8.8	8.1	3.4	1.6
(mV)	SEM	1.2	0.2	4.2	1.6	5.6	0.8	3.6	0.5	0.4	0.4
Duration	Mean	6.5	9.7	5.5	6.0	6.0	10.0	6.7	9.7	12.0	17.0
(ms)	SEM	1.5	1.4	0.5	1.0	1.0	3.1	0.3	3.2	2.0	2.0
Area	Mean	20.0	21.2	30.0	19.4	27.8	38.3	28.8	37.8	20.8	13.6
(mV · ms)	SEM	4.1	4.4	4.7	4.4	11.7	8.1	10.6	9.9	5.8	5.4
Ratio E:C	Mean	–	–	–	1.17	–	1.11	–	1.15	–	0.62
	SEM				0.2		0.2		0.2		0.2

The results would seem to suggest that these two fatigue phases involve different contractile processes, the second one possibly being sensitive to intramuscular blood circulation. It is of interest that after disuse there were no changes in the curve of reduction in muscle tension. The observation that ischaemia does not modify the initial phase of the relationship between time of contraction and force reduction but considerably reduces the second phase, suggests that different mechanisms are involved in the two phases.

Fatigue and electrical processes

The reduction of muscle force output could be explained by a decrease of electrical activity. Therefore the maximal belly-tendon *EMG* (cf. Table 1, Fig. 2) was also examined. Figure 2A compares the muscle *SAP* measurements recorded during intermittent contractions separated by 1-s intervals and shows that the electrical processes changed differently in the control and disused muscles. After a 7-day immersion the amplitude of the negative *SAP* phase was reduced, whereas duration was increased. These changes developed with the occurrence of the first M-wave and increased at the end of 1-s, 5-s and particularly by the end of the test contractions (Fig. 2A).

Figure 2B shows that in both tests, *SAP* duration decreased significantly during the first 3 s and the corresponding amplitude and area increased (see Table 1). Thereafter, the duration of the negative *SAP* phase increased throughout the test, whereas the time courses of *SAP* amplitude and area were quite different. Their initial increases observed during the first 150 and 250 responses, respectively, were followed not only by a drop to the initial level but by the inversion of the measured parameters as well. At the same time the arrangement of the curves has engaged attention: the increase and/or decrease of the electrical M-waves was greater after immersion compared to control. Thus, after disuse, with fatiguability both the force of the electrically induced contraction and the electrical M-waves reduced significantly. However, if after elimination of the gravitational loading during an intermittent electrically evoked test to fatigue there were no differences in the dynamics of the decrease in triceps surae muscle contraction force, there were significant differences in the dynamics of the changes in electrical responses. The relative extent of the decline in either of these two parameters could be determined from the change in the relationship of the electrical M-wave to the mechanical response of triceps surae muscle (*E*:*C ratio*) (Fig. 3). Analysis of the dynamics of the change of the *E*:*C ratio* revealed a significant difference. As shown by this ratio, during muscle work of the same intensity there may have been different changes in the status of the *contractile* and *electrogenic* elements of the peripheral neuromuscular system. Thus, after

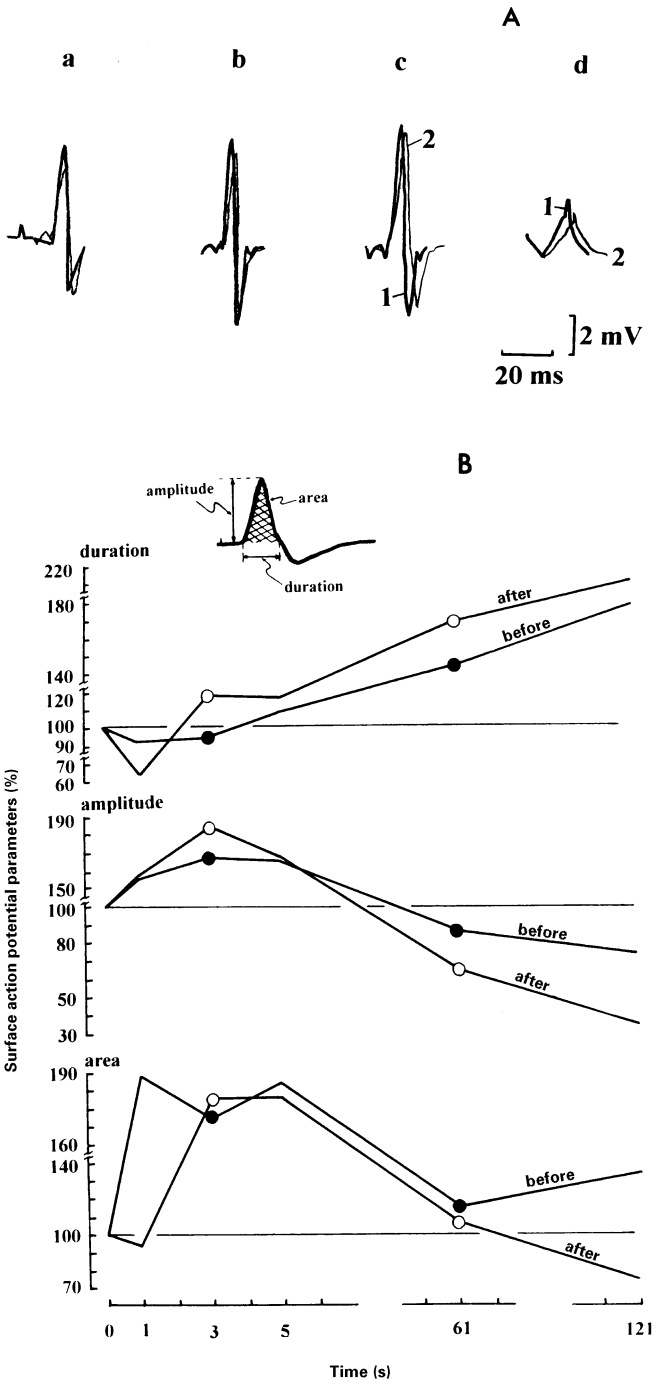


Fig. 2 **A** Superimposition of surface action potentials: the first in the intermittent tetanic (50 impulses · s^{-1}) series of contractions (*a*) at the end of 1, 5, 121 s (*b*, *c*, *d*, respectively) before (1) and after (2) immersion. **B** Comparison of time course of changes in surface action potential parameter during intermittent 1-s contraction series separated by 1-s intervals. Changes are expressed as percentage of the initial value the surface action potentials

immersion during the initial 5 s of the test contraction, there was a relatively more marked decrease in the contraction force than of the electrical M-waves. With increasing duration of the work performed there was a

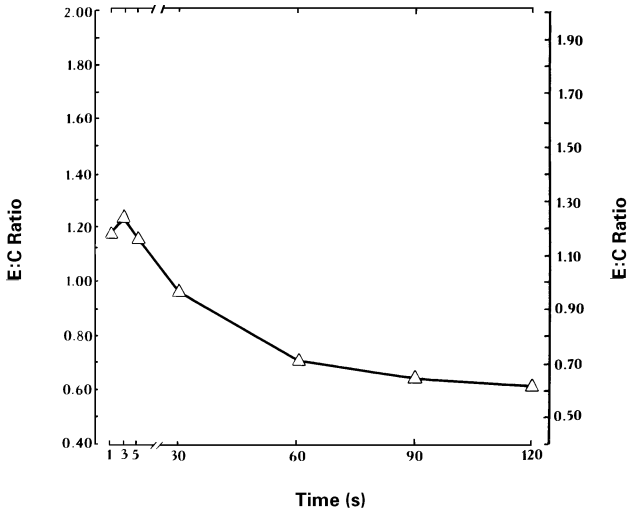


Fig. 3 Change of ratio of electric responses to muscle contraction force (the *E*:*C ratio*) during 60 intermittent 1-s electrically evoked contractions (50 impulses $\cdot$ s^{-1}) with a 1-s interval between contractions after immersion

relatively more marked decrease in the muscle electrical responses.

Fatigue and E–C coupling

Experimental results reported in the preceding section would indicate that intermittent contractions reduce tetanic force and change the electrical processes triggering muscle contraction. This suggests that some stage of muscle E–C coupling beyond membrane ionic processes must be involved in these fatigue tests.

The E–C coupling can be studied in intact humans by simultaneously recording P_t and the corresponding *SAP* in response to a single supramaximal stimulus of short duration and by studying the maximal twitch electrical response and the corresponding mechanical twitch. Table 2 compares E–C coupling in extreme situations, before and after immersion. Study of the mechanical twitch shows a constant P_t and TPT of muscle but significantly decreased dP_t/dt and $1/2RT$ ($P < 0.05$). It is interesting that comparison of these mechanical twitches showed no significant difference. These electromechanical dissociations suggested that not only failure of electrical propagation was present, but that some stage beyond the membrane processes was changed.

Discussion

Mechanical failure (fatigue) during contraction is probably one of the most intriguing physiological phenomena of muscle capacity. The present work is a contribution to the discussion of this problem. It examined the specific effects of disuse on the electrical and mechanical changes in intact human triceps surae muscle, during intermittent contractions elicited by electrical stimulation of its motor nerve. The possible effects of central (motor) nerve command during these fatigue tests have been excluded by the experimental procedure.

The results showed that:

1. The rate of decrease in the force of muscle contraction during rhythmic fatigue stimulation did not vary between before and after disuse.
2. On stimulation the *SAP* showed a marked decline in amplitude and increase in duration, reflecting changes in the peripheral generation of the action potentials by the muscle fibres.
3. A correlation between the electrical and mechanical responses of the muscle (*ratio E*:*C*) indicated that the specific role in fatigue of *electrogenic* and *contractile* elements of the neuromuscular system is changed during the development of peripheral fatigue.

Our findings (see Fig. 1A) did not reveal any difference in the reduction of the working capacity after disuse which is in good agreement with previously obtained data (White and Davies 1984; St-Pierre and Gardiner 1985) and confirm the point of view of Merton (1954) that peripheral mechanisms play an

Table 2 Twitch and surface action potential (*SAP*) parameters before and after 7-day immersion. P_t Twitch contraction, TPT time to peak twitch, $1/2RT$ time to half relaxation, dP_t/dt rate of force development, V and D amplitude and duration of *SAP* first phase, respectively, A area of *SAP* first phase

		Twitch				*SAP*		
		P_t (N)	TPT (ms)	$1/2RT$ (ms)	dP_t/dt (% P_t/ms)	V (mV)	D (ms)	A (mV $\cdot$ ms)
Before	Mean	125.6	118.2	93.7	2.06	4.1	10.4	21.6
($n = 6$)	SEM	13.7	3.6	3.3	0.29	0.6	1.0	3.6
After	Mean	139.3	118.8	88.7*	1.77*	3.5*	12.8**	21.0**
($n = 6$)	SEM	18.6	3.4	3.8	0.19	0.5	0.7	3.4

*, ** Statistically significant ($p < 0.05, 0.01$, respectively) between before and after immersion.

important role in force reduction. Peripheral fatigue probably results from a deterioration in the excitability of the muscle fibres. It has been found that failure of propagation of action potentials may occur:

1. Along the terminal branches of motor nerves (Krnjevic and Milidi 1958)
2. At the neuromuscular junction (Krnjevic and Miledi 1958)
3. Along the surface of muscle fibres (Krnjevic and Miledi 1958; Bigland-Ritchie et al. 1979), and along the T-tubules (Bezanilla et al. 1972)

The blocking of the fibre action potentials during stimulation would indicate a failure of excitation, but the location cannot be determined. Blocking of an *SAP* was invariably preceded by a major change in the amplitude and duration of the fibre action potential.

An integral index of the state of the *electrogenic* element of the neuromuscular system can be the size (amplitude and area) of the recorded *SAP*. Comparison of electrical and mechanical failures during intermittent contractions was interesting because this comparison indicated that identical tetanic force reduction after and before disuse (cf. Fig. 1A) was associated with complex *SAP* changes (cf. Fig. 2B). This observation would suggest that muscle intracellular processes must have played a major role in the observed contractile failure.

Recorded *SAP* changes during fatigue indicated that different peripheral mechanisms may have been involved. The comparison between control and disused muscle indicated that the failure of the electrical processes was different in the two fatigue tests. It would appear from Fig. 2B that during the first 3 s of contraction, the *SAP* duration decreased in both tests while the corresponding amplitude and area of the *SAP* increased significantly. These data would suggest that presynaptic and/or end-plate potentials were facilitated, and that the propagation velocity of the action potential increased along the muscle membranes (see Stalberg 1966) and that the dispersion between the fibre action potentials was reduced (see Desmedt 1958; Desmedt et al. 1968). The subsequent increase in *SAP* duration and area, observed without any reduction in *SAP* amplitude, must have been due mainly to the slowing of the conduction velocity along membranes of muscle as shown by fibres (Bigland-Ritchie et al. (1979) and Milner-Brown and Miller (1986) so the *SAP* broadened in shape (cf. Fig. 2A).

In the second half of the intermittent contractions, the reduction in *SAP* amplitude would suggest that presynaptic and/or end-plate failure was then present in the intermittent fatigue. This view is consistent with the finding that the *SAP* area which was previously found to have increased now decreased, although the duration of the *SAP* kept increasing throughout the test. It was also consistent with the previous observations that the rise time of the end-plate current has been found to decrease during disuse (Ruzzier et al. 1982; Khristova et al. 1986), although the decrease in contraction force was identical in both fatigue intermittent tests. This difference in behaviour between nerve and muscle membranes is not surprising, since their architectures are quite different, and recovery of control ionic concentrations must be slower in the muscle T (transverse) system compared with nerve membranes. It has been suggested that the presence of a T tubular system plays an important role in muscle electrical fatigue (Bianchi and Narayon 1982; Lannergen and Westerblad 1982).

The study of muscle E-C coupling was achieved by comparison of twitch *SAP* and tension development. The results showed that dP_t/dt was reduced, but P_t was not significantly changed after disuse, whereas changes of corresponding *SAP* were considerably different. This electromechanical dissociation would suggest not only failure of electrical propagation, but that some stage beyond membrane processes changed and played a predominant role as suggested by Merton (1954) Jones et al. (1979) and Bianchi and Narayon (1982). Changes in the configuration of the action potential have been associated with a depletion in extracellular $[Na^+]$, increased $[K^+]$, and an increase in $[H^+]$ ion of muscle fibres (Bigland-Ritchie et al. 1979; Jones et al. 1979; Lannergen and Westerbload 1982). In addition, these suggest that muscle energy metabolism can play an important role in regulating the muscle membrane excitability. An additional factor in enhancing the electrolyte excretion could be that disuse significantly impairs electrolytic homeostasis as suggested by Noskov et al. (1985) and thus affording the reduction of muscle membrane excitability as proposed by Lindstrom et al. (1977), Birland-Ritchie et al. (1979) Jones et al. (1979) and Edwards (1981). In the present case, the surface *EMG* shown in Fig. 2A strongly supports this hypothesis.

As is evident from the present findings, the reduction in the contraction force of the muscle during the intermittent fatigue test was similar before and after disuse suggesting, on the one hand, that the fatigue developed cannot be explained by the changes in the contractile apparatus itself as a result of an active factor and, on the other, that one of the components (if not the only cause) of developing peripheral fatigue could be a disorder in the *electrogenic* element of the neuromuscular system. The comparison of the changes in mechanical response with the corresponding alteration of electrical response (*ratio* $E:C$) enables the determination of the specific role of the *electrogenic* and *contractile* elements in the development of peripheral fatigue. Analysis of the *ratio* $E:C$ before and after disuse indicated that there occurred different dynamics of changes in the state of contractile and electrical elements of the peripheral neuromuscular system (see Table 2).

These results do not contradict the above discussions because an interpretation of the $E:C$ *ratio* suggests

a linear relationship between mechanical responses of muscle, but the relationship between the *EMG* and fatigue has remained unclear (Lindstrom et al. 1977), especially when developing fatigue can be impaired. It has been shown that during contraction triggered by electrical stimulation of the motor nerve, the decrease in the contractile force of the muscle cannot be compensated by a modulation of the motor unit firing frequency (Woods et al. 1987). The study of electrically evoked fatigue showed that the decrease in force observed during intermittent contractions was no different in control and disused muscles and indicated that fatigue was no larger after immersion. In addition, it has been reported that the normal action potential of muscle fibre is several times higher than the threshold value required for activation of the contractile apparatus (Sandow 1965). Due to this, even reduced action potentials are capable of triggering normal contractions of muscle fibres.

Conclusions

During exercise of short duration the decreased muscle force appeared to result essentially from peripheral neuromuscular changes. The study of electrically evoked contractions contributes to the understanding of the underlying mechanisms of peripheral fatigue in the neuromuscular system, since it avoids the complications resulting from changes in the motor unit firing frequency.

Mechanical failure during intermittent muscle contraction involved peripheral sites and mechanisms associated with membrane and intracellular processes. The comparison of peripheral electrical and mechanical changes during intermittent electrically triggered contractions in both contractions indicated that a slowing of action potential conduction along nerve and muscle membranes did not explain the observed mechanical failure.

The comparison between the electrical and mechanical responses, recorded in control and disused muscle, supported the proposition that electrical changes do not closely control the mechanical failure. Thus among the peripheral neuromuscular changes observed during short duration exercises, it is suggested that muscle intracellular processes must play the dominant role in the observed force decrease during fatigue after disuse.

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