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Muscle Weakness Following Eccentric Work in Man

C. T. M. Davies and M. J. White

Department of Physiology and Pharmacology, Medical School, Queen's Medical Centre, Clifton Boulevard, Nottingham, NG7 2 UH, Great Britain

Abstract. The separate effects of negative (eccentric) and positive (concentric) work on stimulated and voluntary isometric contraction of the triceps surae were studied in five healthy male subjects following the performance of box-stepping for 1 h with a constant leg lead.

The results showed unequivocally that the long-lasting muscle weakness which arises from box-stepping was due to the negative component of the work. The maximal twitch (P_{t_0}) and tetanic (P_0) tensions at 10, 20, 50 and 100 Hz were markedly reduced in the leading ("negative") leg, which was constantly required to absorb the force of body weight as the subject returned from box to floor, whereas the trailing ("positive") leg which lifted body weight from floor to box was relatively unaffected. The decreases in P_{t_0} and P_0 at 20 Hz in the "negative" leg following work were 38N and 765N (25 % and 55 %) respectively and recovery was slow (> 20 h). A 2 min "fatigue" test reflected the changes in P_0; a reduction of absolute force was only seen in the negative leg though the relative (%) decline in tension was the same in both legs and its rate did not differ significantly following exercise from control conditions, which suggests the muscles were weaker but not more fatiguable following exercise. At submaximal voltages of stimulation muscle tensions at 20 and 50 Hz were enhanced in the "positive" leg but depressed in the "negative" leg, the relative (but not absolute) loss of force being greater at 20 Hz than 50 Hz which gave rise to long-lasting fall in the 20/50 tension ratio. The loss of high frequency (50 Hz) force was associated with changes in MVC: $\mathrm{MVC\,(N)} = 507 + 0.937\ P_0\ \mathrm{(N)}$; $r = +0.846$.

It was suggested that repeated stretching of the triceps surae muscles during the eccentric phase of work in the "negative" leg could affect the efficacy of the contractile machinery directly and may cause actual muscle damage. The subjects complained of muscle soreness for 5–7 days after the experiments.

Key words: Electrical stimulation – Negative exercise – MVC – Tetanus and twitch tensions

Introduction

In their study of human muscle fatigue Edwards et al. [6] reported a profound loss of low frequency tetanic tension following exercise. They suggested that this phenomenon may be related to excitation – contraction uncoupling and was probably a feature of recovery from many different forms of dynamic physical activity. In contrast we have found [5] that following running, and uphill walking exercise the fall in electrically stimulated forces is small and recovers within a 2 h period. The only exercise which produced a prolonged significant fall in the 20 Hz stimulated forces was the one originally studied by Edwards and his co-workers namely, box stepping. This was at first surprising, because the energy expenditure and the magnitude of the applied positive forces were similar if not less than those observed in uphill (+ 25 %) gradient work. However, the major differences between box-stepping and uphill walking is the contribution of the negative component of the work. In uphill walking, beyond a gradient of + 15 % the work is wholly positive [7] the centre of gravity is continuously lifted upwards, whereas in stepping the subject is required to lower his body weight within each cycle. The possibility arises, therefore, that the prolonged loss of low frequency force is a consequence of a muscle being repeatedly stretched during its contracted phase.

In order to investigate this problem further we repeated the box-stepping experiments in a way that allowed the negative and positive elements of the work to be studied separately. This was achieved by requiring the subject to lead with the same foot throughout the exercise. This procedure ensures that the lower leg muscles of the trailing leg perform wholly positive work whilst the leading leg absorbs the fall in body weight as it returns from the step to the floor during each cycle.

Materials and Methods

Five male subjects studied were aged 25 ± 4 years, 179 ± 10 cm in height and weighed 75 ± 5 kg. The apparatus used for measurement of the lower leg muscles has been previously described in detail [5]. It consists of a rigid chair and frame in which the subject was seated with thigh horizontal and lower leg held at 85° by a clamp above the knee. The clamp was attached to a fixed steel bar which by means of 2 bonded strain gauges transduced the upward force applied to it when the triceps surae contract. Isometric contractions elicited by electrical stimulation of triceps surae were measured on the left and right legs of each subject. Three twitches at 1 s intervals were recorded, using a 50 µs pulse width, at each level of stimulation with a 1 min rest between increases in voltage. Stimulation was continued until there was no rise in tension with increased voltage. The criterion for supramaximal twitch tension (P_{t_0}) being that at least 3 plateau values agreed within ± 5 %. Following the establishment of P_{t_0}, tetanic stimulation was applied at successively higher frequencies of 10, 20, 50

Offprint requests to C. T. M. Davies at the above address

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and 100 Hz for 2 s at each frequency. Two min was allowed between each set of tenani and voltage was increased in a stepwise manner. The criterion for supramaximal stimulation as outlined for the twitch, was applied to the 10 and 20 Hz responses, but at the two higher frequencies, 50 and 100 Hz, the maximal voltage level was subject limited. The procedure resulted in tensions at the higher frequencies which were close to maximal but did not reach supramaximal levels in terms of our applied criterion.

After the final tetanic stimulation three maximal voluntary contractions were recorded and 1 min later an electrically evoked fatigue test. This consisted of short 20 Hz tetani lasting 300 ms, applied 1/s for 2 min at a maximal stimulating voltage. The control measurements were followed by one hour of exercise. This consisted of box stepping at a fixed rate of 20 lifts of the body/min. The height of the box was adjusted in each case to just below patella height. For each subject the work corresponded to approximately 70 % of his predicted maximal aerobic power output. Stepping was carried out in such a way as to ensure that the left leg was raised first and lowered first in each cycle. Stimulated and voluntary contractions on both legs were measured as soon as possible after the end of exercise and at regular intervals thereafter.

Results

The twitch response to normal alternate leg and constant leg lead box stepping are shown in Fig. 1. In alternate leg box stepping the twitch tension is enhanced at submaximal voltages and depressed at supramaximal levels in both legs. The decrease in plateau tension (P_{t_0}) immediately following exercise is of the order of 27 N which represents a 19 % loss of control P_{t_0}. In contrast when the same exercise is performed with a constant (left) leg lead a marked depression in P_{t_0} is only seen in one and not the other leg (Fig. 1). In the right leg which performs wholly positive work (i.e. lifting the body weight onto the box) the twitch tension at submaximal voltages is increased as before, but the decrease in P_{t_0} is less than half (12 N − 7 %) that seen in normal box stepping. In the left ("negative") leg, which absorbs the work performed in lowering body weight from the box to the floor, the tension-voltage curve is displaced to the right, and the fall in P_{t_0} is approximately three times (− 38 N; − 25 %) this value. The combined decrease in P_{t_0} for the two legs in each form of exercise is nearly the same, namely, 54 N and 50.5 N respectively. The recovery of P_{t_0} was slow (> 20 h) following normal box stepping and even slower in the "negative" leg after 1 leg (lead) stepping. The "positive" leg in the latter exercise recovered within 2 – 4 h.

The tetanic tension responses showed similar changes to the twitch. The tetanic force at 20 Hz ($P_{o_{20}}$) was reduced by 315 N and 360 N in the right and left legs respectively following normal stepping and again the tension was enhanced at submaximal voltages in both legs. In constant leg lead stepping, a marked fall (− 765 N, − 55 %) of 20 Hz tetanic force was only seen in the left ("negative") leg. In the "positive" leg the decrease in $P_{o_{20}}$ was − 90 N (− 6 %). In the "negative" leg a marked reduction in the high frequency (100 Hz) stimulated tetanic tension was also apparent (Fig. 2). The absolute fall in tension at 50 and 20 Hz was similar (Fig. 3) however, in relative terms the decrease in force was greater at the lower frequency. Thus if the ratio of the 200 Hz to the 50 Hz tetanic tensions (20/50) was calculated after the

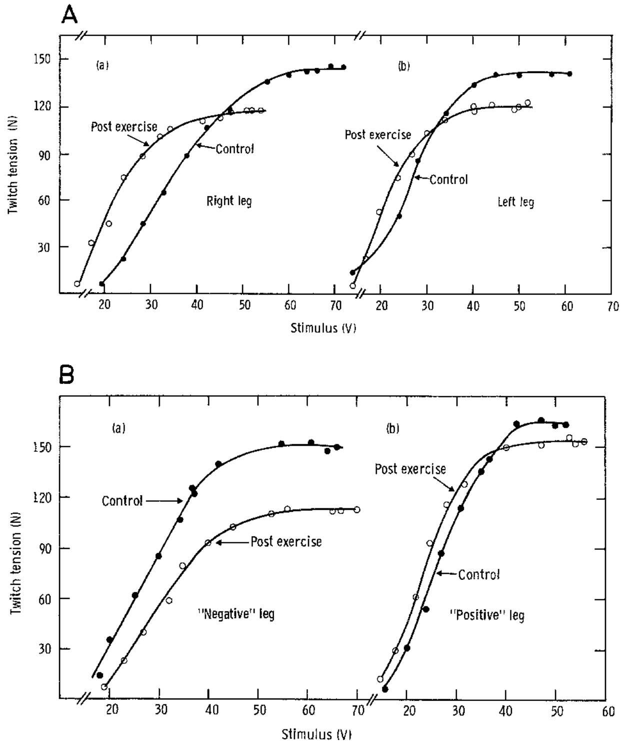

Fig. 1 A and B. (**A**) The twitch tension curves for normal (alternate leg) box-stepping (*a*) right leg, (*b*) left leg. (**B**) Box-stepping with same leg lead (*a*) left ("negative") leg and (*b*) right ("positive") leg. Subject 1

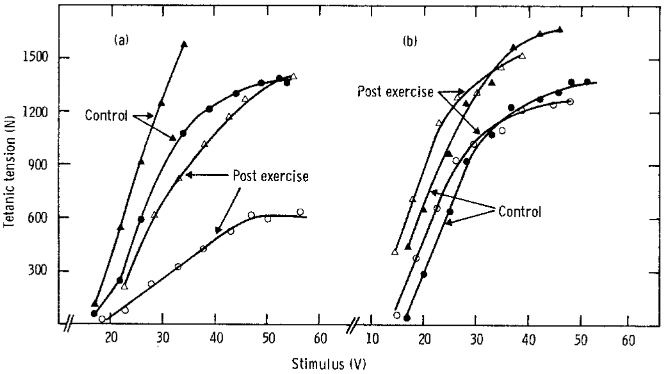

Fig. 2. The tetanic tensions before exercise at 100 Hz (▲) and 20 Hz (●) and following constant leg lead box-stepping, (△) 100 Hz and (○) 20 Hz for (*a*) the "negative" leg and (*b*) the "positive" leg. Subject 1

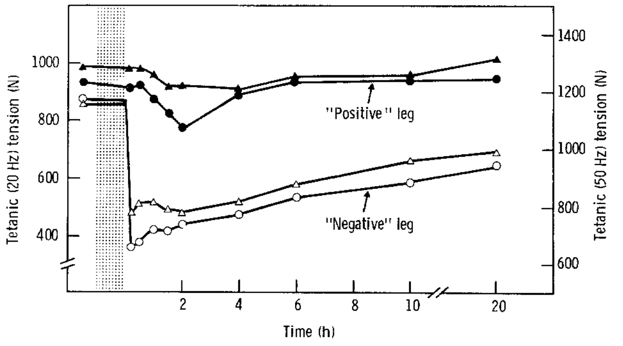

Fig. 3. The time course of high (50 Hz) and low (20 Hz) frequency tension changes during recovery from box-stepping performed with the same leg lead for 1 h. NB. Offset scales. Symbols 50 Hz (▲), (△) and 20 Hz (●), (○) tetanic tensions. Mean data. The *hatched area* indicates the period of exercise

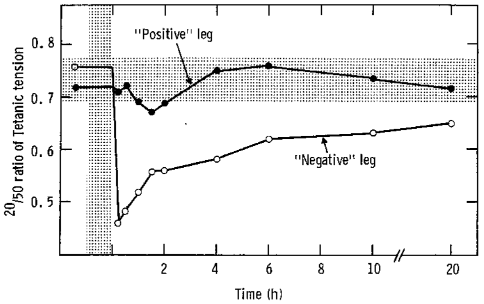

Fig. 4. The time course of the 20/50 ratio changes during recovery from 1 leg lead box-stepping for 1 h. Mean data. The *vertical hatched area* indicates the period of exercise; the *horizontal hatched area* the SD of the control measurements

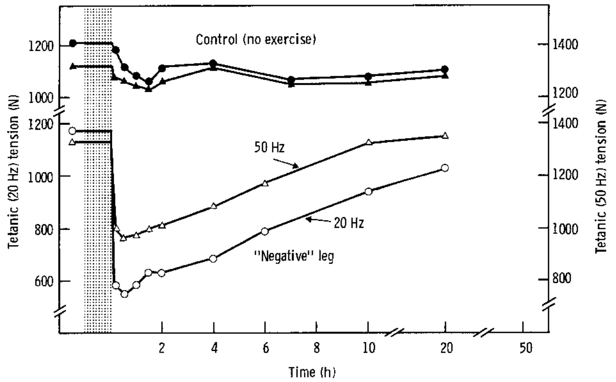

Fig. 5. A comparison of the recovery time course of 20 and 50 Hz forces following control (no exercise) and constant leg lead box-stepping work. Symbols *hatched area* as Fig. 3. Subject 5

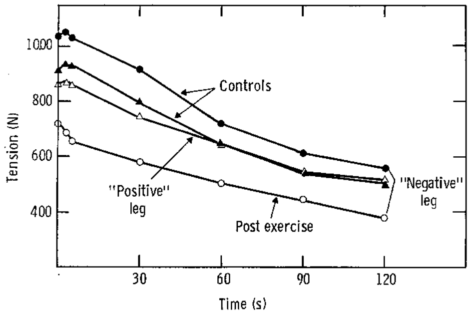

Fig. 6. The relationship between tetanic tension at 20 Hz and time during a 2 min fatigue test applied before and after box-stepping exercise. Subject 1

method of Edwards et al. [6] a marked fall in the ratio could be observed in the "negative" leg. The 20/50 ratio in the positive leg remained relatively unaffected (Fig. 4). In the "positive" leg the 20 and 50 Hz forces return to normal within 2–4 h but in the "negative" leg the high and low frequency forces and 20/50 ratio remained depressed 20 h after the exercise had been completed (Figs. 3 and 4). Part of this depression of 20 Hz and 50 Hz may have been due to the stimulation procedure itself (Fig. 5). Nevertheless, in 2 of the 5 subjects measured, $P_{0_{20}}$ did not return to normal after 50 h of measurement, indeed all subjects complained of muscle weakness and soreness 5–7 days after the experiment. The recovery of high frequency (50 Hz) forces was more rapid than the 20 Hz tensions but in some subjects it was still not complete within the period of measurement. The maximal forces recorded at 50 Hz ($P_{0_{50}}$) showed a close temporal relation with the maximal voluntary contraction (MVC). The association between the two variables is described by the linear regression equation:

$$\mathrm{MVC\,(N)} = 507 + 0.937\,P_{0_{50}}\,(\mathrm{N}); \quad r = +0.846.$$

The results of a fatique test before and after constant leg lead box-stepping exercise are shown in Fig. 6. The initial tension values essentially reflect the changes in P_0 at 20 Hz outlined, a large decrease in force is only seen in the "negative" leg. However, the rate of tension decline during the 2 min test is similar in both the "positive" and "negative" legs following exercise and does not differ significantly ($P > 0.1$) from resting (control) conditions, i.e. if plotted in relative (%Δ) rather than absolute forces the 4 curves shown in Fig. 6 overlap and are statistically identical.

Discussion

The results of the present investigation show unequivocally that the major portion of the muscle weakness which arises as a consequence of box stepping is due to the "negative" component of the exercise. In 1-leg lead box-stepping exercise the muscle tension data obtained on the trailing ("positive") leg is similar to that we obtained previously following uphill walking and level running. In contrast the "negative" leg shows a long-lasting decline in the ability of the triceps surae to develop force.

The maximal twitch tension (P_{t_0}) declines from 150 to 112 N in the "negative" leg following exercise and this is also associated with depression of twitch tension at submaximal voltages. The loss of tension at lower voltages has not been observed by us following other forms of positive work such as running or uphill walking [5] and nor is it apparent in the "positive" leg of the present experiments (Fig. 1). From the results of our previous exercise experiment we have shown that the Q_{10} of twitch tension enhancement at submaximal voltages following work is similar to that found for passive heating and, therefore, it was possible to explain the phenomenon in thermal terms [5]. This is clearly not the case in the present experiments. In negative work muscle temperature (T_m) rises to a greater extent than in positive exercise [9] and though T_m was measured in this investigation it can be estimated from previous work [4] that the T_m of the "negative" leg was of the order of 40° C. A T_m of this magnitude would be expected to enhance the submaximal twitch tension by approximately 18 % rather than depress it. Further, since the half time of T_m decline is $\sim$ 15 min [8] one would not expect the effect to last for at least 20 h (Fig. 1) if it was due to temperature changes. The alterations in the twitch tension-stimulus response curve following concentric exercise is not due to resistance changes of the muscles being stimulated in the lower leg [5]. This is also true for the "positive" and "negative" leg of the present experiments, which suggest that the extreme muscle weakness induced by negative work raises the threshold of motor unit activity involved in force generation independently of the elevation in muscle temperature.

The effect of negative exercise on tetanic tension is similar but more profound than that described for the twitch. It is clear from the observations given in Fig. 3 that the muscle weakness which is associated with the "negative" leg during box-stepping cannot be regarded solely in terms of low frequency force generation [6]. In absolute terms the decline of tension is similar at high (50 Hz) and low (20 Hz) frequencies of stimulation, though, due to the small forces involved, the relative (%) frequencies decline in force is greater at the lower stimulation. It is for this reason that the (20/50) ratio between the low and high frequency tensions fall in the "negative" leg. In the "positive" leg at lower voltages of stimulation the 20/50 ratio actually increases due to force potentiation (Fig. 2), and therefore does not reflect the measured change in tensions at supramaximal voltages. This we have found to be the case in other forms of positive work such as running and uphill treadmill walking [5]. For this and other reasons [5] we feel, contrary to Edwards et al. [6] that the analysis of muscle weakness and fatigue must be based in man, as in normal animal experimentation, on supramaximal voltage stimulation.

The "fatigue" test [3] results are in accord with our twitch and tetanus findings and show that the initial loss of force is characteristic only of the "negative" leg (Fig. 6). However, the actual relative rate of tension decline during the 2 min test is similar in both legs and in fact does not differ from control conditions. This again suggests [5] that one is investigating muscle weakness rather than fatigue, i.e. the inability to generate, rather than sustain, force. Further, the association of MVC with "maximally" stimulated high (50 Hz) frequency force before and following exercise in both legs suggest that the muscle weakness observed in negative and positive work may have at least one common component. However, the differences between the two forms of work far out-weigh their physiological similarities and it is difficult to conceive that the weakness observed have common origins.

In the "positive" leg following exercise the fall in twitch and tetanic forces were small and recovered rapidly within 2 h but in the "negative" leg muscle weakness was evident from the stimulated muscle tensions the day following the experiments (Fig. 3).

Undoubtedly, a part of the weakness we observed was due to the stimulation procedure itself once the muscle had been made weak by the exercise. Our stimulation protocol was extremely demanding because we wished to gain long term information from both legs of submaximal and supramaximal tetanic and twitch forces. For this reason we performed an additional control experiment in which the subject was not required to exercise but was merely electrically stimulated at the appropriate times throughout the day. It will be seen from Fig. 5 that this procedure produced a small decline in both 20 and 50 Hz tetanic forces which persisted throughout the day but it could not account for the large changes observed during the experimental day. The data from this experiment suggests that the electrically stimulated and voluntary forces were not fully recovered in the negative leg within 20 h (Fig. 5). Indeed the subjects of our investigation complained without exception of muscle soreness in the leg that had performed negative work for 5-7 days after the experiments had been completed. The calf muscles of the "negative" leg were particularly sore and tender on the morning after the exercise day. This suggests that prolonged negative work, during which the muscle is repeatedly stretched in its contracted phase [1], not only impairs the contractile machinery of the muscle responsible for force generation but actually induces muscle damage.

Unfortunately, the actual mechanism of enhanced force generation during an eccentric contraction in man is unknown [2] and the available muscle biopsy data following negative exercise are sparse and not particularly informative. It would seem that ATP concentration remains unchanged following negative work (as one would expect), creatine phosphate decreases within normal limits and lactate accumulation is unexceptionable [10]. These results argue in favour of the maintenance and efficacy of the muscle chemical processes responsible for energy supply during and following negative work. It may well be, therefore, that repeated stretching of the muscle actually damages the contractile protein machinery directly and affects the cycling of cross-bridges within the muscle fibre resulting in a loss of efficiency of the normal contraction processes. However, further research is needed into the precise mechanisms of force generation involved in eccentric work before definitive conclusions can be reached.

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