Eur J Appl Physiol (1987) 56:306–312

European Journal of
Applied Physiology
and Occupational Physiology


# Electrically evoked contractions of the triceps surae during and following 21 days of voluntary leg immobilization

**C. T. M. Davies, I. C. Rutherford, and D. O. Thomas**

MRC Muscle Group, Department of Physiology and Pharmacology, Queen's Medical Centre, Nottingham, Great Britain

**Summary.** The effects of 21 days voluntary leg (plaster) immobilization on the mechanical properties of the triceps surae have been studied in 11 young female subjects, mean age 19.4 years. The results show that during the period of immobilization the mean time to peak tension (TPT) and half relaxation time (1/2RT) and tension ($P_t$) of the maximal twitch increased significantly ($p<0.001$) but the effects were short lived. Maximal tension and contraction times of the twitch recovered within 2–14 days following the removal of the plaster cast. The electrically evoked tetanic tensions at 10 Hz and 20 Hz did not change significantly ($p>0.1$) during immobilization, but the 50 Hz tetanic tension ($P_{\circ 50}$) and maximal voluntary contraction (MVC) were reduced ($p<0.05$). The fall in $P_{\circ 50}$ and MVC was associated with 10% decrease in the estimated muscle (plus bone) cross-sectional area. The relative (%) change in $P_{\circ 50}$ and MVC following immobilization was related to the initial physiological status (as indicated by the response of the triceps surae to a standard fatigue test prior to immobilization) of the muscle. The rate of rise and recovery fall of the tetanus were slightly but significantly ($p<0.01$) reduced on day 7 of immobilization, but thereafter remained constant. The isokinetic properties of the triceps surae as reflected in the measured torque/velocity relation of the muscle in 4 subjects did not change significantly if account was taken of the slight degree of atrophy present following immobilization. It was concluded that short term voluntary leg immobilization produces atrophy and some loss of isometric twitch and tetanic function, but has little effect on the isokinetic properties of the triceps surae. The changes in the twitch characteristics during and immediately following immobilization may be indicative of a prolongation of the active state of the muscle.

**Key words:** Muscle — Isometric contractions — Atrophy — Isokinetic contractions — Immobilization

## Introduction

It is well known from animal studies that immobilization gives rise to a loss of muscle size and weight due to the disuse of the affected limb (Fischback and Robbins 1969; Tabary et al. 1972; Booth and Kelso 1973). The muscle becomes weaker and the mechanical characteristics of the maximal twitch and tetanus change. The time course of contraction of predominantly slow muscle decreases, whilst that of "fast" muscle increases (Witzmann et al. 1982). This may be due to a change in composition, or at least the myosin component, of the fibre types within the muscle. Unfortunately, in man, few comparable investigations have been undertaken regarding the time course of muscle dysfunction following disuse. In a previous study (White et al. 1984) we have shown that 2 weeks of voluntary immobilization produced a significant increase in the time to peak tension (TPT) of the maximal twitch and a reduction in maximal voluntary contraction (MVC) and muscle (plus bone) cross section area (CSA) but had surprisingly little effect on electrically evoked tetanic tension. The changes in TPT and MVC and CSA recovered within 2, 4 and 14

*Offprint requests to:* C. T. M. Davies, Head of Department, Sport and Exercise Sciences, The University of Birmingham, P. O. Box 363, Birmingham B 15 2TT, Great Britain

days respectively. We postulated that the changes in twitch mechanics may have been due to altered $Ca^{2+}$ release and re-uptake by the sarcoplasmic reticulum, whilst the decrease in MVC relative to the electrically evoked maximal tetanic tension may reflect a reduction in central neural drive resulting from the voluntary inactivity.

The aims of the present investigation were to (i) extend these observations beyond 14 days and (ii) include measurements of both twitch and tetanus mechanics, (iii) assess the influence, if any, of the initial physiological status of the limb on the subsequent magnitude and time course of the observed muscle function changes, and (iv) in 4 of the 11 subjects to relate the changes in electrically evoked twitch and tetani to the isokinetic properties of the muscle.

## Material and methods

The age, weight and height of the 11 young female subjects studied were 19.4±0.9 years; 54.9±5.1 kg and 165.6±6.4 cm respectively. All the girls were volunteers and gave their informed consent to participate in the experiments. All procedures were approved by the Medical School's Ethical Committee. Complete immobilization of the right leg of each subject was achieved by a full length, non-weight bearing plaster of Paris cast. They were told to use the limb as little as possible, but were given crutches and the use of a wheelchair to aid mobility.

*Isometric dynamometry.* The subjects were allowed to habituate to the electrical stimulation procedures during preliminary visits to the laboratory before definitive control measurements were taken. These were made on at least three occasions prior to immobilization. During the experimental period the electrically evoked and voluntary contractile properties of the triceps surae were measured on the 7th, 14th and 21st day of immobilization, and during the 2nd, 7th, 14th, 21st and 28th day of recovery. On each occasion the subjects were required to sit in a specially designed leg dynamometer with the thigh horizontal and the ankle at 85° (see Davies et al. 1982). Electrical stimulation was applied through two large foil electrodes, one (the anode) placed over the heads of the gastrocnemius and the other over the belly of the soleus. Voltage was increased in a stepwise manner until maximal twitch and tetanic responses were evoked. From the maximal twitch response the force ($P_t$), time to peak tension (TPT) and half relaxation (1/2RT) were measured. Maximal tetanic tensions were recorded at 10 Hz ($P_{o10}$), 20 Hz ($P_{o20}$) and 50 Hz ($P_{o50}$). The criterion for maximal tetanic tension was that force should show no further rise with increasing voltage stimulation, i. e. plateau values to agree within ±5%. Immediately following tetanization a single stimulus at supramaximal voltage was given to elicit the post-tetanic potentiated twitch response. After an appropriate rest period the muscle was stimulated supramaximally for 2 s continuously at 50 Hz and then (later) at 200 Hz. From the responses the rate of rise ($\Delta P_{50}$ and $\Delta P_{200}$) and recovery fall ($\Delta P_{R_{50}}$ and $\Delta P_{R_{200}}$) of tetanic force were measured.

Following these evoked contractions, maximal voluntary contraction (MVC) was measured, and finally, after a further rest period, the fatiguability of the triceps surae was assessed by electrically stimulating the muscles at 20 Hz for 330 ms every second for 2 min. The ratio of the force developed by the 120th train divided by that of the 1st train gave an index of fatigue (FI). Maximal twitch responses were achieved on all subjects, but 3 of the 11 subjects failed to meet the necessary criterion for supramaximal tetanic stimulation, and their data were excluded from the analysis. Anthropometric measurements of the leg were taken either immediately prior or following the stimulation procedure, from which estimates of calf muscle (plus bone) cross-sectional area (CSA) were made (see Davies et al. 1983). Statistical analysis of the data was performed using a student paired $t$ test for significance of variables measured on different occasions.

Finally, on separate occasions immediately before and following immobilization, the isokinetic properties of the triceps surae were measured on 4 subjects using a recently developed technique (Davies et al. 1985). Involuntary isokinetic contractions were measured using a Cybex II dynamometer (Lumex Inc., N.Y., USA), modified by the addition of a strain gauge load cell (TML CLP-1000 kA) to improve the dynamic response of the instrument. The subjects were seated upright with their back tight against the chair of the Cybex, with one leg fully extended. The centre of rotation of the ankle was aligned with the rotational axis of the dynamometer. The foot and thigh were secured by straps to ensure that the heel and knee did not lift from the apparatus during recording.

The triceps surae was stimulated in a manner similar to that described for the isometric contractions. The motor controlling velocity was pre-set to a particular speed, and the triceps surae was maximally activated under isometric conditions using electrically evoked supramaximal tetani at 50 Hz. After a period of 400 ms (to allow maximal activation of the muscle), a relay was automatically triggered switching on the motor and releasing the limb, thus allowing the ankle to plantar flex at the pre-set velocity. Maximal stimulation was continued during the movement and terminated prior to full plantar flexion. Torque and ankle angle were recorded on U-V paper and the torque produced at each velocity (range 0—5.0 rads $s^{-1}$) was measured at a angle of 25° to ensure constant muscle length. An appropriate rest period was given between each stimulation to avoid fatigueing the muscle. The measured torques were normalised for $P_0$ and related to velocity using the equation: $V=(e^{-P/b}-e^{-Po/b})$ a, where P and V are torque and velocity respectively, $P_0$ is the isometric force, and a and b are constants. From the equation the relative torque ($P_4$) at a given V of 4 rads $s^{-1}$ was calculated for each subject.

## Results

The isometric properties of the triceps surae before, during and following immobilization are given in Tables 1 and 2. The period of immobilization is associated with a rise in tension ($P_t$) and an increase in the time of contraction (TPT) and relaxation (1/2RT) of the maximal twitch (Fig. 1), but the effects were relatively short lived. The 1/2RT recovered within 2 days, the $P_t$ within 7 days, and the TPT within 14 days following the immobilization. The evoked tetanic contractions at 10 Hz and 20 Hz were unchanged during the period of immobilization, but there was a significant

**Table 1.** The mechanical properties of the triceps surae. Time to peak tension (TPT), half relaxation time (1/2RT) and tension ($P_t$) of the maximal twitch, tetanic tension at frequencies of 10 Hz ($P_{\circ 10}$), 20 Hz ($P_{\circ 20}$) and 50 Hz ($P_{\circ 50}$), index of fatigue (FI) and maximal voluntary contraction (MVC) before and during 21 days of voluntary immobilization

| Time (days) | TPT (ms) | 1/2RT (ms) | $P_t$ (N) | $P_{\circ 10}$ (N) | $P_{\circ 20}$ (N) | $P_{\circ 50}$ (N) | FI | MVC (N) |
|---|---|---|---|---|---|---|---|---|
| 0 | 130 | 109 | 128 | 566 | 786 | 1068 | 0.64 | 1312 |
| | ±10 | ±19 | ±30 | ±106 | ±149 | ±175 | ±0.20 | ±118 |
| 7 | 144** | 128*** | 143 | 559 | 742 | 960* | 0.63 | 1126* |
| | ±21 | ±28 | ±48 | ±141 | ±174 | ±164 | ±0.15 | ±177 |
| 14 | 148*** | 128*** | 169*** | 547 | 742 | 955* | 0.57* | 1061*** |
| | ±19 | ±29 | ±52 | ±147 | ±191 | ±191 | ±0.15 | ±142 |
| 21 | 148* | 129* | 177*** | 559 | 763 | 956* | 0.60 | 1023*** |
| | ±28 | ±42 | ±55 | ±148 | ±182 | ±191 | ±0.18 | ±178 |

Significance: Control/immobilization * $p<0.05$; ** $p<0.01$; *** $p<0.001$

**Table 2.** The mechanical properties of the triceps surae following voluntary immobilization. Symbols as for Table 1

| Time (days) | TPT (ms) | 1/2RT (ms) | $P_t$ (N) | $P_{\circ 10}$ (N) | $P_{\circ 20}$ (N) | $P_{\circ 50}$ (N) | FI | MVC (N) |
|---|---|---|---|---|---|---|---|---|
| 2 | 134 | 112 | 159*** | 448*** | 678* | 908*** | 0.69 | 1032*** |
| | ±18 | ±34 | ±37 | ±144 | ±160 | ±181 | ±0.14 | ±145 |
| 7 | 144*** | 117 | 137 | 455*** | 680*** | 937* | 0.67 | 1128*** |
| | ±20 | ±29 | ±26 | ±142 | ±152 | ±153 | ±0.14 | ±115 |
| 14 | 139*** | 108 | 142 | 534 | 765 | 1015 | 0.63 | 1210* |
| | ±13 | ±26 | ±50 | ±199 | ±207 | ±196 | ±0.16 | ±170 |
| 21 | 131 | 104 | 142 | 554 | 772 | 1002* | 0.56 | 1273 |
| | ±12 | ±14 | ±40 | ±159 | ±146 | ±151 | ±0.14 | ±190 |
| 28 | 130 | 104 | 139 | 516 | 754 | 996* | 0.52 | 1348 |
| | ± 9 | ±17 | ±38 | ±200 | ±229 | ±217 | ±0.16 | ±254 |

Significance: Control/recovery period * $p<0.05$; ** $p<0.01$; *** $p<0.001$

($p<0.05$) fall in $P_{\circ 10}$ and $P_{\circ 20}$ on days 2 and 7 of the recovery period (Table 2). $P_{\circ 50}$ and MVC were significantly ($p<0.05$) reduced as a result of immobilization, the recovery in MVC was more rapid than $P_{\circ 50}$. The index of fatigue (FI) remained relatively unchanged (except for a small but significant ($p<0.05$) fall on day 14) during the period of immobilization and recovery. Post-tetanic potentiation of the twitch response was observed before and during immobilization (Fig. 2).

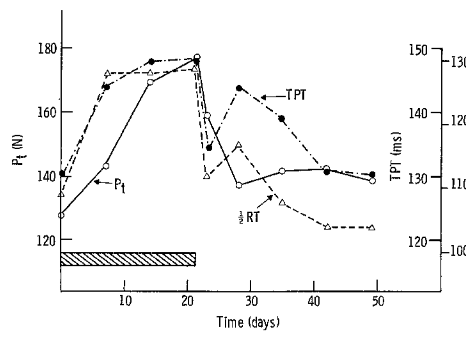


**Fig. 1.** The effect of 21 days of immobilization (hatched bar) on the contraction times and tension of the maximal twitch ($P_t$). TPT (O- · -O), 1/2RT (Δ---Δ) and $P_t$ (O——O). Mean data for 11 subjects. Error bars have been omitted for clarity

The decrease in $P_{\circ 50}$ and MVC was associated with the change in the anthropometric estimate of the muscle (plus bone) cross-sectional area (CSA) of the calf (Fig. 3), and to the initial physiological status (as indicated by the FI) of the muscle (Fig. 4). The % change in $P_{\circ 50}$ and MVC (%) was linearly related to FI:

$$\Delta P_{\circ 50}\ (\%) = 51.58 - 95.93\ \mathrm{FI};\ r = -0.86,\ n = 9$$

$$\Delta \mathrm{MVC}\ (\%) = 12.33 - 53.63\ \mathrm{FI};\ r = -0.62,\ n = 9$$

The rates of rise ($\Delta P_{50}$ and $\Delta P_{200}$) and recovery fall ($\Delta P_{R_{50}}$ and $\Delta P_{R_{200}}$) of the tetanus are summarised in Table 3. $\Delta P_{50}$ remained unchanged, but there was a significant ($p<0.05$) fall in $\Delta P_{200}$ on day 7 of the period of immobilization. Both $\Delta P_{R_{50}}$ and $\Delta P_{R_{200}}$ were significantly ($p<0.01$) reduced on day 7 of immobilization, but thereafter both

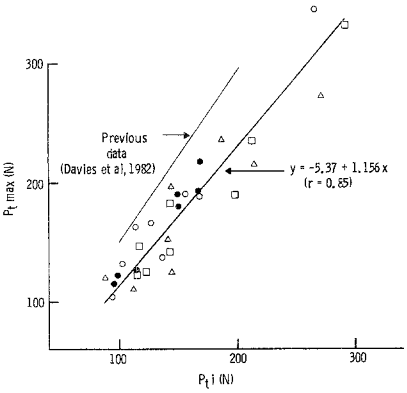


**Fig. 2.** Post-tetanic potentiation before (○) and during 7 days (○), 14 days (△) and 21 days (□) of immobilization. Individual data on 8 subjects who fulfilled the necessary criterion for supramaximal tetanic stimulation (see methods). The relationship between maximal twitch tension ($P_{t\,max}$) after supramaximal tetanic stimulation and the initial twitch tension ($P_{t\,i}$). The regression equation is: $P_{t\,max}(N) = -5.37 + 1.156\,P_t(N)$; $r = 0.85$, $n = 31$

variables remained constant. During the periods of control and voluntary immobilization there were significant ($p < 0.001$) correlations between the rates of rise and fall of the tetanus and the contraction characteristics of the maximal twitch:

$\Delta P_{\circ 50}(\%\ P_0 ms^{-1}) = 0.669 - 0.00213\ TPT(ms)$;
$r = -0.69$, $n = 24$

$\Delta P_{R_{50}}(\%\ P_0 ms^{-1}) = 2.56 - 0.012\ 1/2RT(ms)$;
$r = -0.67$, $n = 24$

Finally, the changes in the isokinetic properties of the triceps surae before and immediately following immobilization are given in Table 4 and illustrated in Fig. 5.

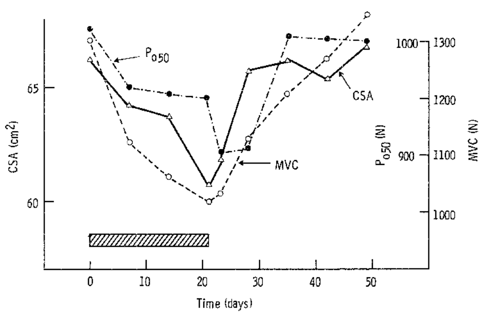


**Fig. 3.** Effects of 21 days of voluntary immobilization (hatched area) on maximal tetanic tension at 50 Hz ($P_{\circ 50}$) (● · — · ●, maximal voluntary contraction (MVC) (○- - -○), and an anthropometric estimate of calf (muscle plus bone) cross-sectional area (CSA) (△——△)

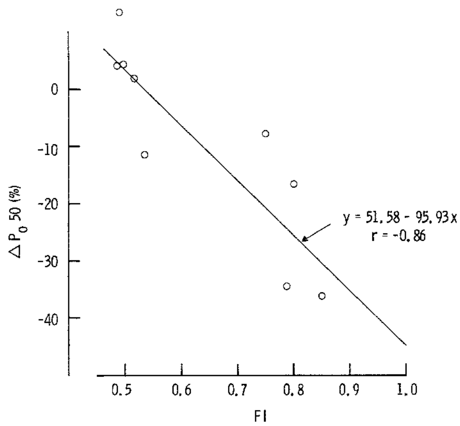


**Fig. 4.** The relationship between the changes in $P_{\circ 50}$ (Δ %) and MVC during the period of immobilization and the control fatigue index (FI) of the triceps surae. ($n = 9$)

The equations given in Table 4 are of the form: $V = (e^{-P/b} - e^{-Po/b})\ a$ (see methods). Immobilization is associated with small reduction in constants a and b and $P_0$ and a significant ($p < 0.05$) decrease in the relative torque ($P_4$) at given velocity of 4 rads $s^{-1}$.

**Table 3.** Rates of rise and recovery fall of tetanus during the period of immobilization (% $P_0$ $ms^{-1}$)

| Time (days) | $\Delta P_{50}$ | $\Delta P_{200}$ | $\Delta P_{R_{50}}$ | $\Delta P_{R_{200}}$ |
|---|---|---|---|---|
| 0 | 0.34<br>±0.07 | 0.41<br>±0.09 | 1.37<br>±0.35 | 1.12<br>±0.33 |
| 7 | 0.32<br>±0.07 | 0.36*<br>±0.07 | 1.10**<br>±0.35 | 0.91**<br>±0.34 |
| 14 | 0.32<br>±0.05 | 0.39*<br>±0.06 | 1.10**<br>±0.44 | 0.92**<br>±0.45 |
| 21 | 0.36<br>±0.06 | 0.40<br>±0.06 | 1.13**<br>±0.44 | 0.91**<br>±0.23 |

Significance: Control/immobilization * $p < 0.05$; ** $p < 0.01$

## Discussion

The results of the present study confirm and extend our previous findings (White et al. 1984) concerning the effects of short-term voluntary immobilization on the mechanical characteristics of the twitch and evoked tetanic tensions of the triceps surae. The time to peak tension (TPT) and half relaxation time (1/2RT) of the maximal twitch ($P_t$) increased significantly ($p < 0.001$) after 7 days, and the change was maintained during the 2nd week of immobilization. The $P_t$ increased

**Table 4.** Isokinetic properties of the triceps surae before and after immobilization. The equations are of the form $V=(e^{-P/b}-e^{-Po/b})a$, where P and V are torque and velocity, $P_0$ is the isometric force, a and b are constants, and $P_4$ is the relative torque (%) at a given V of 4 rad/s

| | a | b | $P_0$ (N) | $P_4$ (%) |
|---|---|---|---|---|
| Before | 13.76 | 31.35 | 90.68 | 33.23 |
| | ±3.72 | ±3.99 | ±25.25 | ±8.79 |
| After | 13.06 | 28.98 | 80.48 | 30.78* |
| | ±3.69 | ±3.50 | ±20.67 | ±8.87 |

Significance: Before/after * $p<0.05$

($p<0.001$) after 14 days, and remained elevated during the remainder of the immobilization period (Fig. 1). During the recovery period the maximal tension and contraction times of the twitch returned to control values within 2—14 days. Following tetanic stimulation potentiation of $P_t$ occurred during both the control and immobilization period. The potentiated twitch was related to the initial $P_t$ in a manner similar to that found previously (Davies et al. 1982) when the TPT was changed by heating or cooling. This supports the work of Burke et al. (1973) who found, in contrast to many animal species (Ranatunga 1977), human gastrocnemius fibres do exhibit post-tetanic potentiation independently of their contraction times.

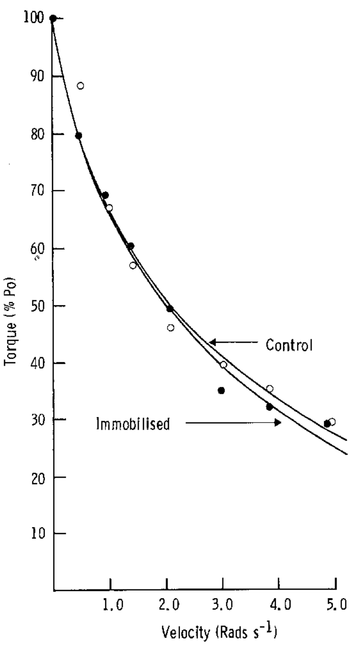


**Fig. 5.** The relationship between electrically evoked torque expressed as % $P_0$ and velocity, control (O) and immobilized (O) leg. For the form of the equation see text and Table 4

The changes in maximal tetanic tension were small compared with those described for the twitch. The mean changes of $P_{\circ 10}$, $P_{\circ 20}$ and $P_{\circ 50}$ during the immobilization period were −1% ($p<0.1$), −2.9% ($p>0.1$) and −10.5% ($p<0.05$) respectively (Table 1). The lack of change of force at low frequencies of tetanic stimulation is surprising when one considers the increase in TPT of the maximal twitch. One would have expected force at 10 Hz (and perhaps 20 Hz) to increase due to better fusion. However this expected rise in force could have been offset by the induced muscle weakness due to the slight atrophy resulting from the immobilisation (Fig. 3). The two effects would tend to cancel each other giving rise to an unchanged evoked force at low frequencies of stimulation. The small (but significant) change in $P_{\circ 50}$ is the same order of magnitude as found for mean changes ($p<0.001$) in the estimated cross-sectional area of the muscle (CSA). Thus the specific tension of the muscle remains unchanged during short-term voluntary immobilization. The greater change in MVC compared with $P_{\circ 50}$ during the period of immobilization (Table 1) is consistent with our earlier findings (White et al. 1984) and suggests either an unwillingness or inability on the part of the subjects to perform a normal MVC. The fact that the subjects were well motivated and experience no pain while performing either voluntary or involuntary contractions, supports our view (op cit) that during a period of immobilization when the leg is deprived of normal voluntary movement, the ability of the central nervous system to activate the triceps surae muscle declines. However, it should be noted that the loss of both voluntary (MVC) and involuntary ($P_{\circ 50}$) contraction force of the triceps surae is confounded by the initial "fatiguability" of the leg being immobilized (Fig. 4). The subjects with a high fatigue index show the greater loss of involuntary force during the period of immobilization. Similar findings have been reported for dynamic aerobic endurance training (Ekblom 1969; Davies and Sargeant 1975) and bed rest (Saltin et al. 1968). This suggests that in future studies in man cognizance must be taken of the initial physiological status of the muscle to be immobilized, in order to assess the extent to which neural and muscle function is affected by loss of voluntary movement.

During recovery from immobilization $P_{\circ 50}$ returns to control values slowly. During the immediate post immobilization period, there is a transient decrease in $P_{\circ 50}$ below that found during the experimental period (Table 2). This unexpected decrease in $P_{\circ 50}$ may be a consequence of initial use of the limb once the plaster is removed. The stress of unaccustomed exercise on a previously immobilised limb may give rise to additional weakness and fatigue (see Davies and White 1982) which persists during the early stages of recovery.

The rate of rise and recovery fall of tetanus was related normally (cf. Davies et al. 1987) to the twitch TPT and 1/2RT respectively. The association was unaffected by immobilization. The lack of change (Table 1) in the mechanical properties of the tetanus was also reflected in the dynamic (isokinetic) characteristics of the triceps surae (Fig. 5). Fitting the exponential equation $V=(e^{-P/b}-e^{-Po/b})$ a to the pre- and post torque/velocity data revealed no significant ($p>0.1$) changes in the constant a and a small decrease ($p<0.05$) in constant b following the immobilization period. Normalising the torque data in terms of $P_0$ to account for the degree of atrophy which occurred during the 21 day period removed ($p>0.01$) the pre-and post immobilization difference in the constant b (Fig. 5). The predicted values of the maximal velocity of shortening at zero load ($V_{max}$) remained unchanged, although there was a slight (2.4%) fall ($p<0.05$) in the relative torque at a given V of 4 rads $s^{-1}$ ($P_4$), following immobilization. Thus overall the torque/velocity showed little change as a result of immobilization. This observation is in agreement with that of Witzmann et al. (1982), who showed that there were no significant changes in the $V_{max}$ of rat soleus, extensor digitorum longus or superior vastus lateralis after 21 days of immobilization, and is consistent with the observed relative constancy of the mechanics of the tetanus and current (cross-bridge) theories of muscular contraction. Simmons and Jewell (1974) have proposed that the rising phase of an isometric tetanus is determined by the net rate of cross-bridge attachment, and that the rate constant for the exponential phase of relaxation is equal to that of cross-bridge detachment. The shape of the torque/velocity curve is thus probably governed by the ratio of attachment and detachment of cross-bridges (Simmons and Jewell 1974; Ranatunga 1982), $V_{max}$ being directly proportional to the myosin ATPase activity (Barany 1967; Close 1972). It, therefore, seems reasonable to conclude that short-term immobilization in man has little effect on either cross-bridge cycling or myosin activity. However, one cannot ignore the selective effects of atrophy on the maximal twitch, and the fact that the rate of relaxation (as opposed to the rise — Table 3) of the tetanus is significantly ($p<0.05$) reduced as a result of immobilization.

The TPT and 1/2RT of the maximal isometric twitch is known from the work of Briggs et al. (1977) and Luff (1981) to be associated with the release and re-uptake of $Ca^{2+}$ from the sarcoplasmic reticulum (SR), and that a reduction in calcium re-uptake capacity of the SR also affects adversely the peak relaxation of the tetanus (Fitts et al. 1982). Thus it would be reasonable to assume that the relationship between TPT and $\Delta P_{50}$ and 1/2RT and $\Delta P_{R_{50}}$ and the decline in relaxation rate of the tetanus is due to a change in the rate at which calcium is dissociated from the myofibrillar proteins (Briggs et al. 1977). A decrease in dissociation rate would occur if the re-uptake of $Ca^{2+}$ by the SR proceeded more slowly as a result of immobilization. In immobilized rat soleus Kim et al. (1982) have shown this to be the case. Thus a theory based on a reduction of calcium dissociation from myofibrillar protein would be consistent with the changes in twitch and tetanus mechanics we have observed, and would also explain the significant ($p<0.001$) rise in $P_t$ during the 2nd and 3rd weeks of immobilization (Table 1 and Fig. 1). A reduction in the uptake of $Ca^{2+}$ will enhance cross-bridge formation, and thus the generation of increased force.

## References


Barany M (1967) ATPase activity of myosin correlated with speed muscle shortening. J Gen Physiol [Suppl] 50:197—218

Booth FW, Kelso JR (1973) Effect of hindlimb immobilization on contractile and histochemical properties of skeletal muscle. Pflügers Arch 342:231—238

Briggs FN, Poland JL, Solaro RJ (1977) Relative capabilities of sarcoplasmic reticulum in fast and slow mammalian skeletal muscles. J Physiol 266:587—594

Burke RE, Levine DN, Tsairis P, Zajac FE (1973) Physiological types and histochemical profiles in motor units of the cat gastrocnemius. J Physiol 234:723—748

Close RI (1972) Dynamic properties of mammalian skeletal muscles. Physiol Rev 52:129—197

Davies CTM, Sargeant AJ (1975) Effects of training on the physiological responses to one- and two-leg work. J Appl Physiol 38:377—381

Davies CTM, White MJ (1982) Muscle weakness following dynamic excuse in humans. J Appl Physiol 53:236—241

Davies CTM, Mecrow IK, White MJ (1982) Contractile properties of the human triceps surae with some observations on the effects of temperature and exercise. Eur J Appl Physiol 49:255—269

Davies CTM, White MJ, Young K (1983) Muscle function in in children. Eur J Appl Physiol 52:111—114

Davies CTM, Thomas DO, White MJ (1985) Measurement of human muscle torque under isokinetic conditions using electrically evoked tetani. J Physiol 361:9P

Davies CTM, Thomas DO, White MJ (1987) Mechanical properties of young and elderly human muscle. Acta Med Scand (in press)

Ekblom B (1969) Effect of physical training on oxygen transport system in man. Acta Physiol Scand [Suppl] 328:1—45

Fischbach GD, Robbins N (1969) Changes in contractile in contractile properties of disused soleus muscles. J Physiol 201:305—320

Fitts RH, Courtright JB, Kim DH, Witzmann FA (1982) Muscle fatigue with prolonged exercise: contractile and biochemical alternations. Am J Physiol 242:C65—73

Kim DH, Witzmann FA, Fitts RH (1982) Effect of disuse on sarcoplasmic reticulum in fast and slow skeletal muscle. Am J Physiol 243:X156—160

Luff AR (1981) Dynamic properties of the inferior rectus, extensor digitorum longus, diaphragm and soleus muscles of the mouse. J Physiol 313:161—171

Ranatunga KW (1977) Influence of temperature on the characteristics of summation of isometric mechanical responses of mammalian skeletal muscle. Exp Neurol 54:513—532

Ranatunga KW (1982) Temperature-dependence of shortening velocity and rate of isometric tension development in rat skeletal muscle. J Physiol 329:465—483

Saltin B, Blomqvist G, Mitchell JH, Johnson RL, Wildenthal K, Chapman CB (1968) Response to exercise after bed rest and after training. Circulation [Suppl] 38 7:1—78

Simmons RM, Jewell BR (1974) Mechanics and models of muscular contraction. Rec Adv Physiol 9:87—147

Tabary JC, Tabary C, Tardieu C, Tardieu G, Goldspink G (1972) Physiological and structural changes in the cat's soleus muscle due to immobilization at different lengths by plaster casts. J Physiol 224:231—244

White MJ, Davies CTM, Brooksby P (1984) The effects of short-term voluntary immobilization on the contractile properties of the human triceps surae. J Exp Physiol 69:685—691

Witzmann FA, Kim DH, Fitts RH (1982) Recovery time course in contractile function of fast and slow skeletal muscle after hind limb immobilization. J Appl Physiol 52:677—682

Accepted December 16, 1986