

## EFFECTS OF IMMOBILIZATION ON CONTRACTILE PROPERTIES, RECRUITMENT AND FIRING RATES OF HUMAN MOTOR UNITS

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(Received 31 May 1989)

### SUMMARY

1. The contractile properties, recruitment and firing rates of motor units from the human adductor pollicis and the first dorsal interosseous were studied during voluntary isometric contractions after 6–8 weeks' immobilization of the corresponding limbs.

2. In both muscles, motor units of different force thresholds showed a proportionally identical twitch tension decrease and slowing of their time course after immobilization.

3. When expressed as a percentage of the maximal voluntary contraction, more high-threshold motor units were recorded in disused muscles than in control muscles, but the order of recruitment was maintained.

4. The motor unit firing rate at recruitment was identical in control and disused muscles, but the maximal firing rate decreased in all motor units after immobilization. This decrease of the maximal firing rate was greater in motor units of lower threshold than in those of higher threshold.

5. The results further document motoneuronal plasticity in human muscles of different fibre type composition.

### INTRODUCTION

The immobilization of skeletal muscles induces functional alterations which are associated with morphological, biochemical and neurophysiological changes (Booth, 1982; Appell, 1986). In animals, experimental data indicate that disuse is not only associated with decreased muscle force generating capacity (Witzmann, Kim & Fitts, 1982; St Pierre & Gardiner, 1985), but also with alterations of the electromyographic (EMG) activity (Fudema, Fizzell & Nelson, 1961; Fournier, Roy, Perham, Simard & Edgerton, 1983). This last observation suggests that the muscle membrane electrical activity is reduced and/or that neural changes are present. These last changes could result from impaired central drive and/or reduction of proprioceptive afferents on the motoneurons. Possible neural adaptations to disuse are difficult to approach experimentally in animal preparations, but they have been proposed on the basis of experiments performed in humans (Fuglsang-Frederiksen & Scheel, 1978; Sale, McComas, MacDougall & Upton, 1982). In a previous paper (Duchateau & Hainaut, 1987), we compared maximal voluntary contractions

(MVCs) and electrically evoked contractions of the human adductor pollicis and concluded that the functional alterations observed during immobilization resulted from changes in the peripheral processes associated with the contraction and also from changes in central and/or peripheral afferents on the motoneurons.

The effects of immobilization on muscle fibres of different size have been estimated on the basis of histochemical observations (Edström, 1970; Sargeant, Davies, Edwards, Maunder & Young, 1977; MacDougall, Elder, Sale, Moroz & Sutton, 1980), but the contractile adaptation of muscles of different fibre type composition to disuse, and a possible selective effect on type I and II fibres, remains an exciting question (Stokes & Young, 1984).

This paper examines the effects of the immobilization in two human muscles of different fibre type composition (Johnson, Polgar, Weightman & Appleton, 1973), the adductor pollicis and first dorsal interosseous (FDI), on motor unit: (1) contractile properties; (2) order of recruitment; (3) firing rate at recruitment and maximal firing rate.

#### METHODS

The effects of 6–8 weeks' immobilization were investigated in the adductor pollicis of three subjects and in the FDI of two subjects. The subjects (three male students in physical education, one male physical education teacher and one female subject) were 20–42 years old and all were well accustomed to maximal voluntary contractions. Disuse of the adductor pollicis was achieved in two patients after forearm fracture and in one subject without fracture, by immobilization of the thumb at 45 deg abduction with a plaster cast (Duchateau & Hainaut, 1987). For the FDI, the first three fingers of the hand were fixed together with an aluminium splint after injury of the first interphalangeal joint of the third finger. In the four patients, electrical and mechanical properties of the disused muscle were compared with that of the contralateral muscle. In the subject who volunteered to be immobilized, the adductor pollicis of the same hand was compared before and after immobilization. These investigations were approved by the Ethical Committee of the University of Brussels and all subjects gave their informed consent to participate in this study.

#### *EMG recording*

Motor unit action potentials were recorded by selective electrodes made of a 40  $\mu\text{m}$  diamel-coated Nichrome wire inserted into the muscle by an hypodermic needle (Desmedt & Godaux, 1977). Motor unit action potentials were amplified by a differential preamplifier and filtered (100 Hz–10 kHz) before being displayed on a Tektronix 565 oscilloscope. The signal was then stored on a Hewlett-Packard 4-channel FM magnetic tape-recorder operated at 15  $\text{in s}^{-1}$ . For the FDI, the electrode was inserted in the mid-part of the belly of the muscle, whereas for the adductor pollicis the needle was inserted through the palmar skin of the hand, in the mid-line between the first and second metacarpal joints, approximately 0.5 cm distally to the border of the opponens pollicis. For each subject, the needle was reinserted in at least three separate locations. For a given site, different depths and angles were explored in order to obtain action potentials from different motor units. In order to check possible motor unit synchronization (Milner-Brown, Stein & Yemm, 1973*a*), surface EMG activity was recorded by means of two surface electrodes, one placed at the motor point of the muscle, the other on the distal tendon. The EMG response was amplified, filtered (10 Hz–1 kHz) and full-wave rectified. Synchronized data were not considered.

#### *Force recording*

The isometric force of the adductor pollicis and FDI muscles was measured with a strain-gauge transducer (Philipps PR 9212; compliance 7.6  $\mu\text{m N}^{-1}$ ; resonance frequency 600 Hz). The analog signal from the transducer was: (1) low-gain DC amplified and unfiltered; (2) high-gain AC amplified after filtering out low-frequency fluctuations (1–100 Hz) by a 3A9 plug-in Tektronix amplifier. For the adductor pollicis the first phalanx of the thumb was connected to the transducer

via an inextensible steel cable so that the hand and the thumb were in the same plane. The forearm and the hand were placed in a clothed Perspex holder in a supinated position and strapped without interfering with the normal blood circulation. For the FDI, the palm of the hand rested on a moulded Perspex plate. The last three fingers were fixed on the plate with a thick rubber band. The thumb was immobilized in abduction and extension by another Perspex plate covered with soft rubber and the first phalanx of the index finger was connected to the transducer. In these conditions, the muscle contraction was nearly isometric.

It would obviously be impossible to identify and test the same motor unit in tests carried out after a 6–8 week interval. Therefore recruitment thresholds were normalized as a percentage of MVC in order to compare motor units that are recruited at the same fractional force relative to MVC in control and disused muscles. Maximum voluntary contraction was determined during three contractions of 4–5 s duration separated by 3 min. The largest of the three contractions was considered as the MVC. During the contractions, the subjects were verbally encouraged and a visual feedback was provided.

#### *Experimental procedure and data processing*

Once a single motor unit action potential was isolated, the twitch force of the motor unit was measured using the spike-triggered averaging method (see Milner-Brown *et al.* 1973*a*). Briefly, the method consists of triggering the sweep of an averager (Nicolet, 4094c) with the motor unit action potential during a steady contraction and recording the evoked isometric force. It is then possible to extract the single motor unit contribution from the whole mechanical force. Since a low steady motor unit firing rate is necessary to avoid mechanical summation (Calancie & Bawa, 1986) subjects were provided with visual and auditory feedback. Moreover, a rate limiter was used to average mechanical responses from the same motor unit. These were separated from each other by at least 100 ms. Thereafter, the subject was required to make 3–5 slow isometric ramp contractions of 5% MVC s<sup>-1</sup> while following a target on an oscilloscope screen (Hewlett-Packard, 1201B). A rest of 5–10 min was allowed between two successive recordings. For each ramp contraction, we determined the motor unit recruitment threshold as the level of force at which the motor unit action potential was first recruited. The instantaneous motor unit firing rate during the steady and ramp contractions was also measured off-line. The raw data stored on magnetic tape (Hewlett-Packard, 3960) were passed through a window discriminator and the instantaneous motor unit firing rate was calculated by an Apple II computer after analog-to-digital conversion. In cases where accurate triggering of the window discriminator was not possible, the EMG was photographed on Kodak 35 mm film and the firing rate was determined by measuring the time between successive spikes. In all experiments, cutaneous temperature was continuously controlled and maintained at 35 ± 0.5 °C with infra-red light.

## RESULTS

### *Contractile properties*

After 6–8 weeks' immobilization, the comparison between the distribution of the twitch tensions recorded from control and disused adductor pollicis and FDI shows a shift towards a larger number of small tension motor units (Fig. 1). The means are summarized in Table 1. In both muscles, the comparison of the distribution of the motor unit contraction times indicates a mean increase of 16% (range 13–17%) in the adductor pollicis and of 13% (10–15%) in the FDI. Moreover, immobilization also shifts the motor unit twitch time-to-half-relaxation towards larger values of 12% (6–16%) and 13% (9–17%) in the adductor pollicis and FDI respectively (Table 1).

One of the three subjects immobilized by a plaster cast had no fracture, but the findings were the same: the motor unit twitch force decreased by 38% compared to 41 and 42% in the two patients, the contraction time increased by 13% compared to 17 and 16%, and the half-relaxation time increased by 14% compared to 16 and

16%. In this subject, the MVCs of the adductor pollicis of the left hand and the right hand were 90.3 and 92.8 N respectively. Therefore the control values obtained from the same muscle in this subject were pooled with control values obtained from the contralateral muscle in the two patients.

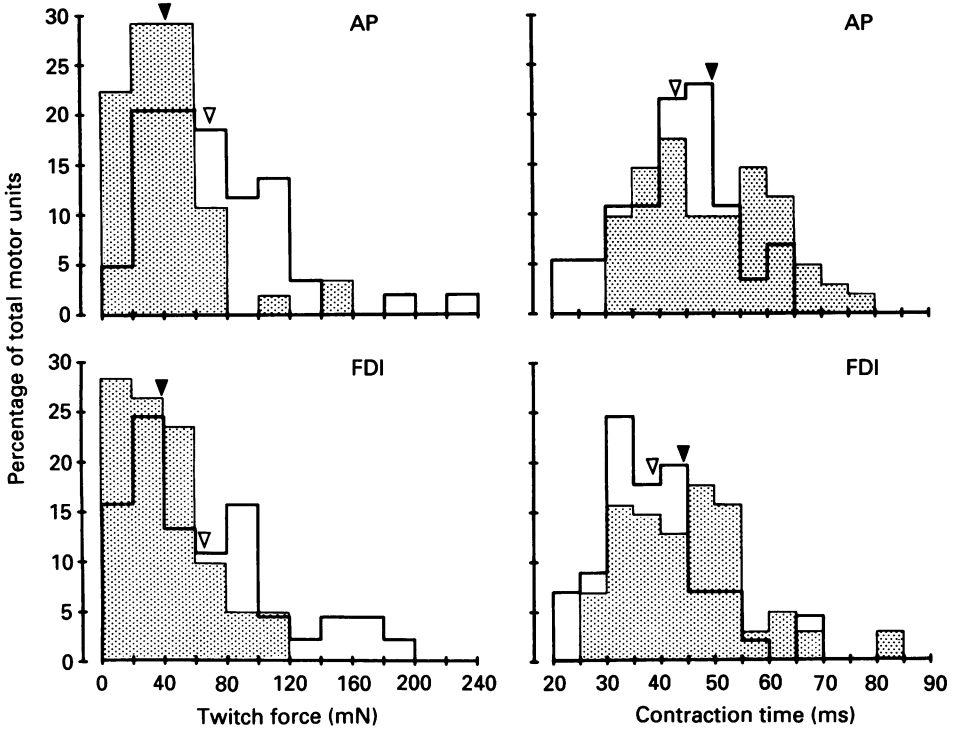


Fig. 1. Histograms showing the distribution of motor units, twitch force and contraction time in control  $\square$  and after immobilization  $\boxtimes$  in adductor pollicis (AP) and FDI for all subjects. The arrows indicate the mean of each distribution. The distributions of the twitch forces are significantly different (Kolmogorov-Smirnov two-sample test) at  $P < 0.01$  and  $P < 0.05$  respectively in adductor pollicis and FDI. The distribution of the contraction time is significantly different at  $P < 0.02$  and  $P < 0.06$  respectively in adductor pollicis and FDI.

### Order of recruitment

Figure 2A illustrates in FDI of one subject the relationship between the recruitment threshold, expressed as a percentage of the MVC, and the motor unit twitch tension in the control muscle *versus* the immobilized muscle. This figure suggests a similar effect on the twitch tension of motor units at different thresholds and also indicates that the size principle (Henneman, Somjen & Carpenter, 1965) does not change in disused muscles. These results are illustrated in one subject but were recorded from all subjects. In the five subjects the linear correlation coefficients of these relations ranged from 0.70 to 0.93 in control and from 0.74 to 0.91 in disused muscles. In these subjects, the slopes of the linear regression in control and disused muscles were respectively 6.3 and 2.6, 5.5 and 2.9, 4.0 and 2.3 in adductor pollicis and

6.0 and 1.3, 7.2 and 3.1 in FDI. Figure 2*B-E* illustrates in the same subject as Fig. 2*A* the twitch electrical and mechanical responses of motor units recruited at different force thresholds in control (*B* and *D*) and disused (*C* and *E*) FDI. The MVC of this subject in the control and the muscle immobilized for 8 weeks was 57.1 and 21.0 N respectively.

TABLE 1. Motor unit contractile properties, recruitment threshold and firing rates for all subjects

	Twitch force (mN)	Contraction time (ms)	Half-relaxation time (ms)	Recruitment threshold (% MVC)	Firing rate at recruitment (Hz)	Maximal firing rate (Hz)
Adductor pollicis						
Control	70 ± 42 (57)	43 ± 10 (57)	35 ± 10 (57)	6.6 ± 5.9 (55)	6.6 ± 16.1 (55)	22.6 ± 7.4 (55)
Immobilized	41 ± 30 (57)	50 ± 11 (57)	39 ± 11 (57)	15.4 ± 13.7 (56)	6.2 ± 15.3 (56)	13.1 ± 3.7 (51)
<i>P</i>	0.01	0.02	0.05	0.003	0.4 (n.s.)	0.001
FDI						
Control	62 ± 46 (44)	39 ± 10 (44)	30 ± 9 (44)	8.6 ± 6.9 (43)	6.5 ± 13.6 (43)	31.0 ± 8.9 (39)
Immobilized	39 ± 27 (41)	44 ± 12 (41)	34 ± 8 (41)	19.2 ± 11.8 (41)	6.1 ± 11.8 (41)	19.0 ± 4.9 (38)
<i>P</i>	0.05	0.06	0.05	0.001	0.2 (n.s.)	0.001

Values are means ± s.d. The number of motor units is indicated in parentheses as well as the level of significance (*P* value).

The comparison, in control and disused muscles, of the recorded motor units' distribution in relation to their recruitment thresholds (Fig. 3) shows a larger number of higher-threshold motor units after immobilization. When expressed as a percentage of the MVC, the means were significantly increased by 133% in the adductor pollicis and by 123% in the FDI (see Table 1).

#### *Electrical activity and firing rates*

The analysis of the motor units' action potentials after disuse indicates an overall decrease of the peak-to-peak amplitude (Fig. 2*B-E*). Although this parameter is influenced by the distance which separates the electrode from the fibres, it always showed a very large decrease of the order of 40–50% when measured in 98 motor units after immobilization and compared with 101 motor units in the control. In both muscles the immobilization did not significantly change the motor units' discharge rate at recruitment, whereas the maximal firing rate was significantly reduced (Fig. 4). The mean of the distribution of the maximal firing rate was reduced in adductor pollicis and FDI by 42 and 39% respectively. The subject without fracture responded like the patients and showed a mean reduction of 43% compared to 44 and 38% in the two patients. Moreover, in control muscles the motor unit fired continuously during the MVC, whereas in disused muscles short periodical interruptions were observed, before the motor unit spontaneously started firing again at the same frequency as before the interruption.

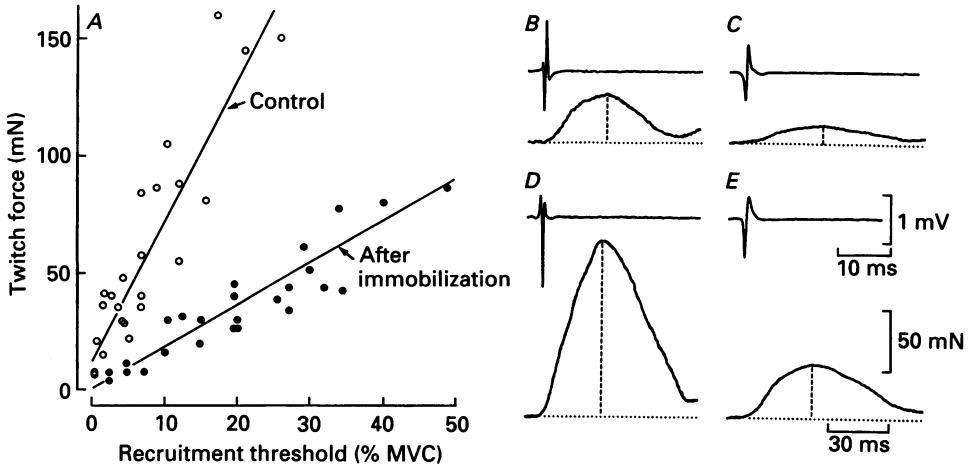


Fig. 2. *A*, twitch force of motor units from FDI of one subject in control (twenty-four motor units) and after 8 weeks' immobilization (twenty-five motor units) plotted as a function of the recruitment threshold (expressed as a percentage of MVC). The linear regression is  $y = 6.02x + 12.0$  ( $R = 0.89$ ;  $P < 0.001$ ) in control and  $y = 1.34x + 4.3$  ( $R = 0.74$ ;  $P < 0.001$ ) after immobilization. The slopes of the regression lines before and after immobilization are significantly different ( $P < 0.01$ ). *B-E*, motor unit action potential and the corresponding isometric twitch of single motor units extracted by spike-triggered averaging (64 sweeps in *B* and *C*; 32 sweeps in *D* and *E*). Motor units in *B* and *D* are control twitches whereas those in *C* and *E* are recorded after immobilization. Motor units in *B* and *C* are recruited at low force thresholds (4.0% and 4.5% of MVC respectively); those in *D* and *E* are recruited at higher force thresholds (26% and 25% of MVC respectively).

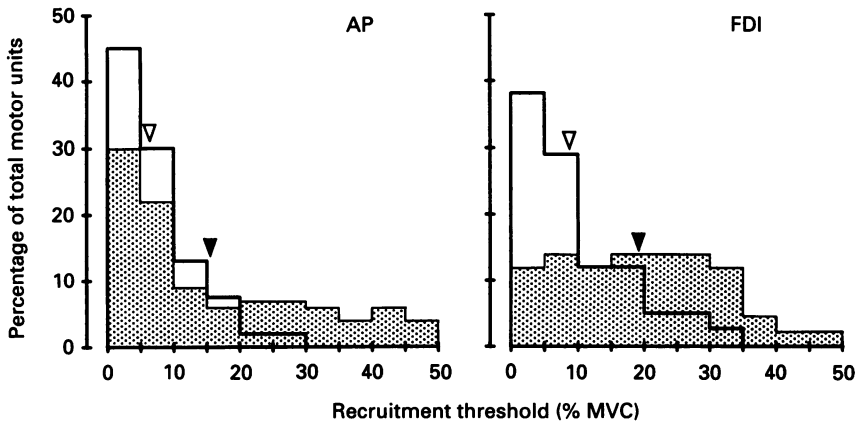


Fig. 3. Histograms showing the distribution of the recruitment thresholds (expressed as a percentage of MVC) in control  $\square$  and after immobilization  $\blacksquare$  in adductor pollicis (AP) and FDI for all subjects. The arrows indicate the mean of each distribution. The distributions are significantly different (Kolmogorov-Smirnov two-sample test) at  $P < 0.003$  and  $P < 0.001$  respectively in adductor pollicis and FDI.

The comparison, in control and disused muscles, of the difference between the maximal firing rate and the firing rate at recruitment ( $\Delta$  firing rate) is illustrated in Fig. 5 for motor units of different recruitment thresholds. In control muscles,  $\Delta$  firing rate decreased with increasing recruitment threshold. In disused muscles it also

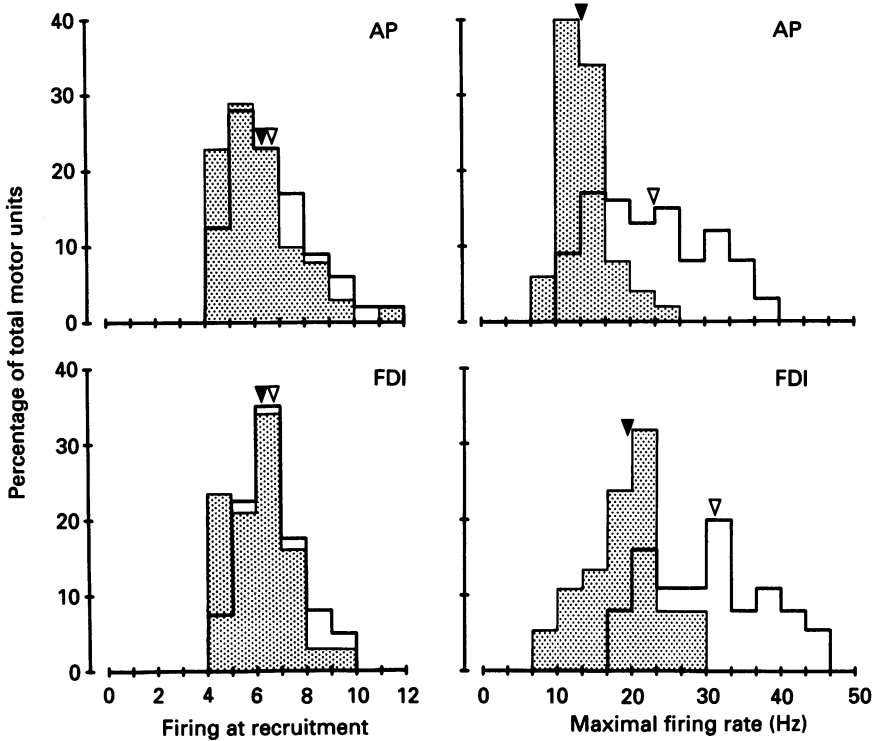


Fig. 4. Histograms showing the distribution of the firing rate at recruitment and the maximal firing rate in control  $\square$  and after immobilization  $\boxtimes$  in adductor pollicis (AP) and FDI for all subjects. The arrows indicate the mean of each distribution. No significant differences were recorded for the firing rate at recruitment before and after immobilization for both muscles, whereas the distributions of the maximal firing rates are significantly different (Kolmogorov-Smirnov two-sample test) at  $P < 0.001$  for adductor pollicis and FDI.

decreased with increasing threshold, but the slope of the regression lines was significantly different from that for control muscles. No significant difference in the decrease in  $\Delta$  firing rate was observed in disused adductor pollicis and FDI when motor units of proportionally similar force thresholds were compared (Fig. 5).

#### DISCUSSION

In the present investigation the most striking change of the motor unit behaviour after immobilization is the marked reduction in maximal firing rate. After 6-8 weeks of immobilization, pain could inhibit motoneurons during MVCs (Stokes & Young, 1984) and so explain this reduction in firing rate and the shift towards higher

recruitment threshold. However, during the experiments none of the subjects reported such discomfort during MVC and the decrease in firing rate was also observed in all five subjects during submaximal voluntary contractions. Moreover, the subject without fracture responded to immobilization like the patients. Thus the

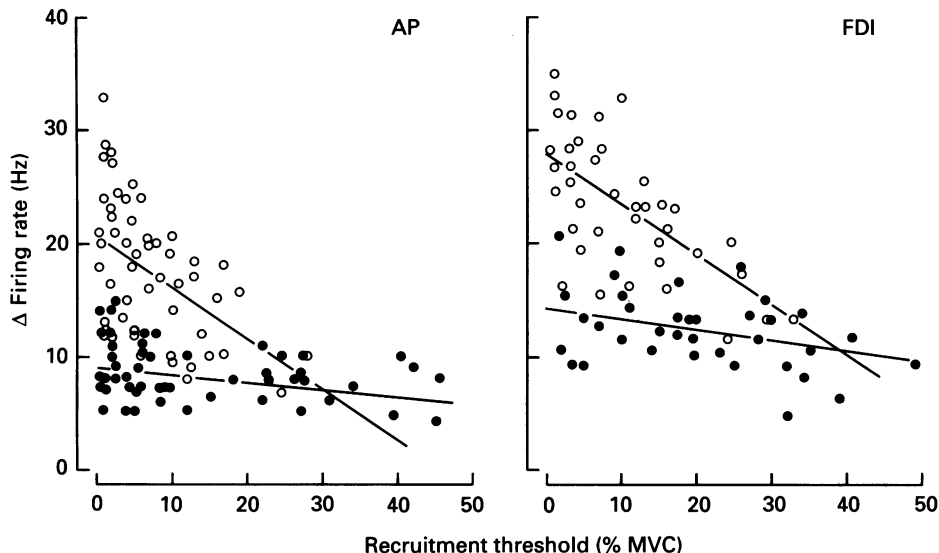


Fig. 5. Difference between the maximal firing rates and the firing rate at recruitment ( $\Delta$  firing rate) in control ( $\circ$ ) and after immobilization ( $\bullet$ ) for all of our subjects, plotted as a function of the recruitment threshold. In adductor pollicis (AP), the linear regressions are respectively  $y = -0.48x + 21.1$  ( $R = -0.51$ ;  $P < 0.001$ ) and  $y = -0.06x + 9.2$  ( $R = -0.29$ ;  $P < 0.05$ ) in control and after immobilization. In FDI, the linear regression are respectively  $y = -0.48x + 28.4$  ( $R = -0.64$ ;  $P < 0.001$ ) and  $y = -0.11x + 14.3$  ( $R = -0.39$ ;  $P < 0.05$ ) in control and after immobilization. The comparison of the slope of the regression lines in the two conditions is significantly different in adductor pollicis ( $P < 0.001$ ) and in FDI ( $P < 0.01$ ).

change in motor unit behaviour reflects a neural adaptation to disuse and should not be related to the fracture or the injury. In the patients, the contralateral muscle served as control whereas in the subject without fracture the same muscle was tested before and after immobilization. In this subject the difference in control MVC recorded from the two adductor pollicis was less than 3% and the motor unit behaviour was not different. Therefore control values of all three adductor pollicis were pooled.

The finding that the maximal firing rate decreases after immobilization without change in the firing rate at recruitment indicates that the motor unit frequency modulation is narrowed in disused muscles. This point is illustrated by Fig. 5 which also shows that the decrease in  $\Delta$  firing rate after immobilization is larger in motor units of low recruitment threshold and large frequency modulation as compared to motor units of higher threshold and lower frequency modulation. Decrease in maximal firing rate could be explained by changes in proprioceptive afferents on the motoneurons (Mayer, Burke, Toop, Hodgson, Kanda & Walmsley, 1981) and/or



reduced ability to activate motor units (Fuglsang-Frederiksen & Scheel, 1978; Sale *et al.* 1982). This last point was suggested by the finding after immobilization of a smaller reflex potentiation which is closely controlled by the central drive (Upton, McComas & Sica, 1971).

The decrease in the motor unit twitch force observed in these experiments after immobilization is coherent with previous results which showed a decrease of the maximal force during voluntary contractions (Sale *et al.* 1982) and electrically evoked contractions (White & Davies, 1984; Davies, Rutherford & Thomas, 1987; Duchateau & Hainaut, 1987). The finding in all five subjects of a proportionally identical decrease in twitch force in motor units of different force thresholds does not support the proposition that red fibres are more affected by reduced use than white fibres (Edström, 1970). Our results are in agreement with those of Sargeant *et al.* (1977) and MacDougall *et al.* (1980) and indicate that immobilization has the same effect on motor units of different force thresholds. Under our experimental conditions the subject performed sustained isometric contractions as large as 50% of the maximum in control and 70% after immobilization. Thus it is assumed that nearly all motor units were recruited (Kukulka & Clamann, 1981; De Luca, Lefever, McCue & Xenakis, 1982) and that the larger motor units were also tested in disused muscles. The slowing of the motor unit twitch time course is in line with previous observations of a slower muscle twitch time course after immobilization (Sale *et al.* 1982; Davies *et al.* 1987; Duchateau & Hainaut, 1987). Although the analysis of the motor unit action potential amplitude is of limited value (Bellemare, Woods, Johansson & Bigland-Ritchie, 1983), our results are coherent with previous observations of the effects of immobilization on the muscle twitch action potential recorded via surface electrodes and voluntary EMG recorded with a coaxial needle (Fuglsang-Frederiksen & Scheel, 1978). After immobilization the amplitude of the motor unit action potential is smaller because fibre atrophy is present (Fudena *et al.* 1961) and the motor unit cannot fire consistently throughout the MVC. Thus the EMG is not only reduced in amplitude but silent periods appear (Duchateau & Hainaut, 1987, Fig. 2).

The observed shift of the motor units' distribution towards higher muscle force thresholds could be explained by the fact that after immobilization it is technically easier to record motor units of larger threshold because the maximal firing frequency is decreased and the interference of motor units is smaller. Our interpretation is that in disused muscles a larger number of motor units is needed to develop a submaximal force of contraction because all motor units have lost a part of their contractile tension. This point of the discussion is coherent with the finding that after exercise training the contractile tension of the motor units is increased and fewer high-threshold motor units are recruited during submaximal voluntary contractions (Hainaut, Duchateau & Desmedt, 1981, Figs 3 and 4). Moreover, the observation in all subjects of a positive correlation between the recruitment threshold and the twitch tension of the motor units after immobilization extends Henneman's size principle to disused human muscles. This concept, which was originally proposed in the decerebrated cat (Henneman *et al.* 1965), has been confirmed in humans during isometric and dynamic contractions (Milner-Brown, Stein & Yemm, 1973*b*; Stephens & Usherwood, 1977; Desmedt & Godaux, 1977) and more recently after 3 months' exercise training (Hainaut *et al.* 1981).

It is concluded that immobilization not only alters the peripheral electrical and mechanical processes of the muscle contraction, but also similarly changes the motor units' behaviour in human adductor pollicis and FDI. In both muscles the motor unit frequency modulation is narrowed by a decrease in the maximal firing rate, which appears to be larger in motor units of low recruitment threshold, although all motor units show similar contractile adaptations to immobilization.

This work was supported by the Fonds National de la Recherche Scientifique of Belgium, the Conseil de la Recherche of the University of Brussels and the Reckitt and Colman Foundation. The authors thank Miss A. Deisser and Miss L. de Montigny for assistance in the preparation of the manuscript.

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