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ADAPTATION OF MECHANICAL PROPERTIES OF MUSCLE TO HIGH FORCE TRAINING IN MAN

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SUMMARY

1. The first dorsal interosseus muscle of the hand was trained for 8 weeks using eighty maximal 10 s voluntary isometric contractions per day.

2. As a result of this training the maximal voluntary force increased by 33 %, but electrically evoked tetanic tension increased by only 11 %.

3. In other subjects the muscle was trained using electrical stimulation at 60 Hz to evoke eighty maximal 10 s tetani per day for 8 weeks. This training produced no increase in maximum voluntary force.

4. Our results show that the increase in maximal voluntary force under these conditions may be due to a change in the voluntary neural drive to the muscle.

INTRODUCTION

The maximal voluntary isometric force of a muscle can be increased by training (Darcus & Salter, 1955; Ikai & Fukunaga, 1970), and there is considerable evidence that the most effective stimuli for producing these increases are contractions which are as strong as possible (McDonagh & Davies, 1984). Isometric strength training of this type for 5–12 weeks produces increases in maximal force of 20–40 % (McDonagh, Hayward & Davies, 1983; Komi, Viitasalo, Rauramaa & Vihko, 1978). However, the increase in the cross-sectional area of whole muscle (Ikai & Fukunaga, 1970) and of single muscle fibres (MacDougall, Elder, Sale, Moroz & Sutton, 1980) is only one-quarter of the increase in the maximal voluntary contractile force (m.v.c). This is surprising, as muscle force should be directly proportional to the cross-sectional area of the muscle.

In order to investigate this problem further it would be useful to obtain a measure of muscular force which is independent of the volition of the subject. Therefore, in the present experiments, as well as measuring the response of m.v.c. to training, we have also measured the response of electrically evoked maximal twitches and tetani. Additionally, the effect of muscle exercise by electrically evoked contractions was examined.

A preliminary account of part of this work has been published in the Proceedings of the Physiological Society (Dooley, McDonagh & White, 1983).

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METHODS

Training

Seven men aged 20–36 years, with body weights of 55–76 kg, took part in a training programme using voluntary contraction. Training consisted of a morning and afternoon session of forty maximal voluntary isometric contractions of the first dorsal interosseus muscle of the non-dominant left hand. Each contraction lasted 10 s, with 20 s rest between each contraction. The contractions were performed in sets of ten, with 2 min rest between each set. Training took place 5 days per week for 8 weeks, with Saturdays and Sundays as rest days. This training regime is much more severe than that normally given to human subjects and athletes (McDonagh & Davies, 1984). The objective was to approximate the strenuous training regimes used in animal experiments, in which increases in tetanic tension have been found following training (Exner, Staudte & Pette, 1973).

Three men (ages 26, 36 and 39; weights 80, 76 and 98 kg respectively) took part in a training regime using electrically evoked contractions. These contractions were maximal 10 s tetani, evoked using electrical pulses of 100 μs duration, given at a frequency of 60 Hz. This particular frequency was found to give the maximum area under the tension–time curve for a 10 s contraction. All other aspects of the training protocol were identical to those described for the training using voluntary contractions. The small number of subjects trained using electrically evoked contractions is a reflexion of the extremely arduous nature of this task.

Because of the nature of the training, the subjects were aware of the general purpose of the investigation. However, no information was given to them about changes in the mechanical properties of their trained and untrained muscles.

Mechanical recording

The first dorsal interosseus muscle of the hand produces abduction of the index finger. The isometric force of this abduction was measured by placing the recording head of a force transducer against the lateral side of the proximal interphalangeal joint of the index finger. The transducer (undamped resonant frequency 1·3 kHz) consisted of a mild steel proving ring on which were mounted four foil strain gauges in a Wheatstone bridge arrangement. The output of the transducer was amplified by a bridge balanced d.c. amplifier (C.I.L. Electronics) and displayed on a digital oscilloscope (Iwatsu D.M.S. 6430). The time course and force of contractions were measured from the screen of the oscilloscope using the electronic cursors of the instrument.

The abduction force of the index finger was measured with the subject seated, the hand pronated and the thumb extended. The other fingers, the hand and the thumb were immobilized by a Plasticine mould placed on top of the hand (Garnett & Stephens, 1981). Pressure was exerted on the mould by a clamp. This clamp consisted of a Perspex plate on top of the mould attached by means of four adjustable bolts to a similar plate beneath the hand. Individual moulds were carefully constructed to fit the contours of the dorsal surface of each hand.

The force transducer was attached to the hand clamp. This ensured that force between the hand and the transducer could not be generated by extraneous movements of the wrist, elbow or shoulder joints.

Electrical stimulation

The first dorsal interosseus muscle was stimulated using a Type 3072 isolated stimulator (Digitimer Ltd.). The timing of the 100 μs square-wave stimulating pulses was controlled by a digital timer and gated pulse generator. The stimulating electrodes consisted of two 8 mm diameter silver/silver chloride-coated disks. Good electrical contact with the skin was ensured by coating the electrodes with conducting jelly. The anode was placed over the lateral aspect of the metacarpophalangeal joint of the index finger. The cathode was placed on the skin over the dorsal surface of the muscle at the position of maximum response for a given stimulating voltage, i.e. the motor point. In initial experiments it was shown that larger electrodes covering the whole muscle did not give a greater maximal tetanic force than the 8 mm disk on the motor point. Cadaver dissections revealed that the motor nerve enters the muscle directly below the area of skin physiologically determined as the motor point in the living subject. Motor point stimulation was chosen in preference to ulnar nerve stimulation at the wrist because the former technique allows discrete stimulation of the first dorsal interosseus muscle alone, whereas ulnar nerve stimulation also activates the hypothenar muscles, the medial two lumbricals, the adductor pollicis and all the interossei. Motor point stimulation is also better tolerated by the subject. We found no evidence for spread of the motor point stimulation to the antagonist muscle on the other side of the metacarpal. In initial experiments the palmar interosseus of the index finger was maximally stimulated at a frequency of 100 Hz until index finger adduction force dropped to 2 % of its maximal value. While this antagonist stimulation continued the first dorsal interosseus muscle was given a single maximal tetanus. The force of this tetanus was the same as that recorded during a control period prior to the exhaustion of the antagonist. This indicates that the tetanic force recorded from the first dorsal interosseus muscle is not opposed by actions of the antagonist, and therefore there is no spread of the stimulation to the antagonist muscle.

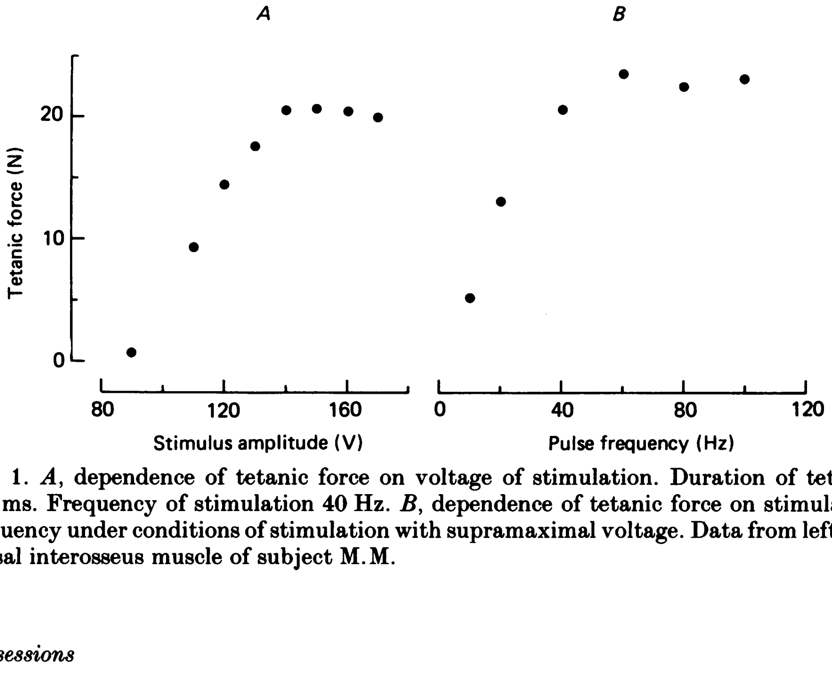

Fig. 1. *A*, dependence of tetanic force on voltage of stimulation. Duration of tetanus 500 ms. Frequency of stimulation 40 Hz. *B*, dependence of tetanic force on stimulating frequency under conditions of stimulation with supramaximal voltage. Data from left first dorsal interosseus muscle of subject M.M.

Testing sessions

Testing of the trained hand and the untrained contralateral hand took place every 2 weeks. The hand and the Plasticine packing of the pressure plate were first heated for 8 min in a water bath maintained at 45 °C. Preliminary experiments showed that this technique raises the muscle temperature to 37 ± 2 °C, which is well maintained throughout the experimental period of 40 min. The hand was then positioned in the apparatus on an outline of the subject's hand drawn during a pre-training control period. This ensured identical positioning of both the hand and transducer from session to session, and enabled the isometric forces to be measured at a standardized muscle length. The anode was then attached, and the position for the cathode was found by using a probe electrode to find the position of maximal response for a given stimulating voltage. Muscle twitch forces were recorded at progressively higher voltages until a plateau was obtained in the graph of force against voltage. The force and time-to-peak tension of the twitch used for further analysis were then recorded using supramaximal stimulation.

A similar stepwise increase in voltage was then performed using 500 ms tetani evoked by stimulation at 40 Hz (Fig. 1*A*). Once a plateau in the force–voltage curve was obtained, voltages equal to 1·2 times that required to produce maximal force were used to elicit tetani at stimulating frequencies of 40, 60, 80 and 100 Hz. This voltage of stimulation was well tolerated by the subjects, and checks showed that the stimulation remained supramaximal during the whole testing period. Maximal tetanic force was usually evoked in the range 60–100 Hz (Fig. 1*B*). Fatigue or potentiation of the muscle during the testing session was avoided by allowing 30 s rest between twitches and 2 min rest between tetani. Following the tetani the muscle was allowed 5 min rest, and the subject was asked to perform three 3–5 s m.v.c.s with an interval of 2 min between each. The force of the strongest contraction was recorded for further analysis.

Informed consent was obtained from all subjects. All the procedures were approved by the Ethical Committee of Nottingham University Medical School.

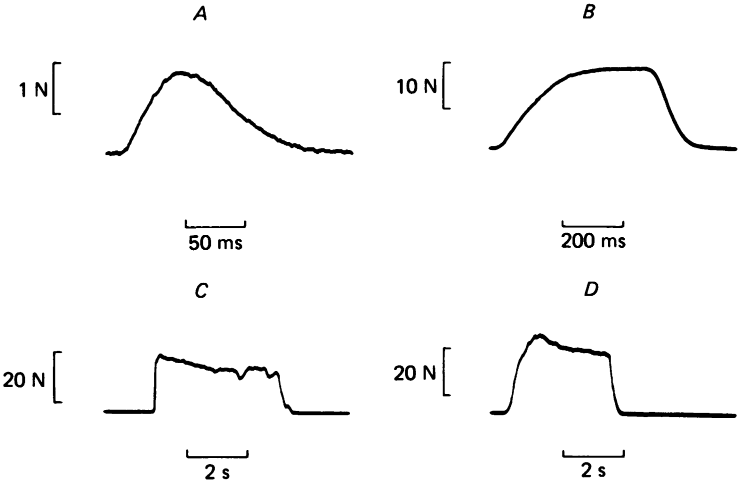

Fig. 2. A typical set of records from the first dorsal interosseus muscle of the left hand. Upper frame: *A*, isometric twitch; *B*, isometric tetanus, taken from the subject prior to training. The tetanus was evoked by supramaximal electrical stimulation at a frequency of 100 Hz. Lower frame: m.v.c.s taken before (*C*) and after (*D*) the 8 week training period. All records from subject M.B. (left hand).

RESULTS

Training using voluntary contractions

A representative set of myograms from a first dorsal interosseus muscle is illustrated in Fig. 2. Summarized in Table 1 are the results from the trained muscles and their contralateral controls, taken before and after 8 weeks training. In the muscles of the trained hands there was no significant change in twitch tension or time-to-peak of the twitch. In contrast, the m.v.c. of these muscles showed a mean increase of 33 %. The progressive increase in m.v.c. over the 8 weeks is illustrated in the upper portion of Fig. 3. The increase first became statistically significant at week 4. The lower part of Fig. 3 illustrates the tetanic tension of these muscles over the training period. Tetanic tension increased less than maximal voluntary force and first became statistically significant at week 6, when it was 11 % greater than that found in control muscles ($P < 0{\cdot}05$). However, at week 8 tension was not significantly different from control values.

The untrained muscles showed no significant change in any of the variables measured. In six of seven subjects, the tetanic tension of the untrained muscle increased between week 6 and week 8. However, the increase of the average among the subjects was not statistically significant. A similar response could be discerned in the m.v.c. data, but this also was not significant. Training produced a significant

TABLE 1. Mechanical properties of experimental and contralateral control muscles before and after training with m.v.c.s (A) and electrically evoked tetanic contractions (B)

	Untrained hand		Trained hand	
	Pre-training	Post-training	Pre-training	Post-training
A, $n = 7$				
Twitch tension (N)	2·5±0·3	3·0±0·4	2·9±0·4	2·9±0·3
Time-to-peak (ms)	64±3	63±3	71±4	66±3
Tetanic tension (N)	23·4±1·7	27·3±2·1	23·0±1·7	25·0±2·2
Maximal voluntary force (N)	37·6±4·4	41·7±4·7	31·8±2·8	40·8±3·8*
B, $n = 3$				
Twitch tension (N)	2·8±0·5	2·7±0·1	3·6±0·6	3·4±0·5
Time-to-peak (ms)	63±5	63±7	67±5	68±6
Tetanic tension (N)	21·6±3·3	24·8±3·2	25·3±1·4	23·9±5
Maximal voluntary force (N)	33·2±3·7	33·4±1·5	32·4±4·4	28·7±1·2

Each value is given as mean ± S.E. of mean. All forces measured at the first interphalangeal joint of the index finger. A Student's *t* test (two-tailed) for paired values was performed on the pre-training and post-training data. $^*P < 0{\cdot}02$.

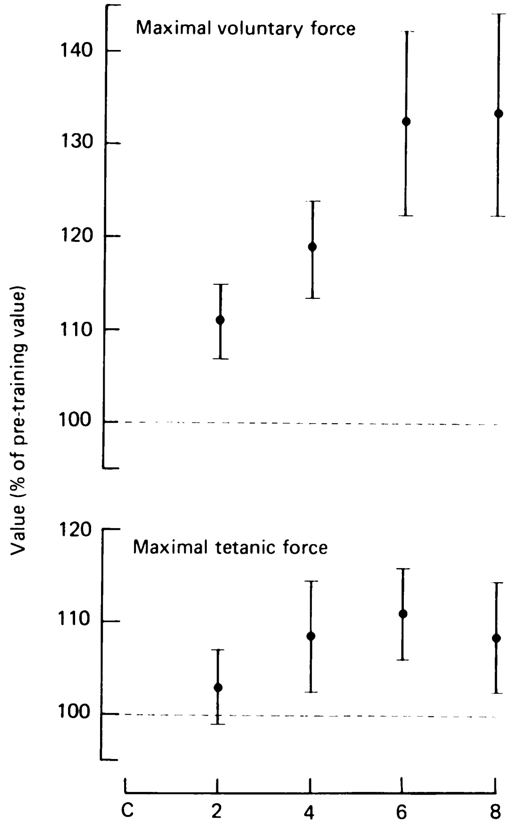

Fig. 3. Force of maximal voluntary contraction (m.v.c.) (upper graph) and maximal tetanic force (lower graph) of the trained first dorsal interosseus muscle during training using m.v.c.s. Each point represents the mean of determinations from seven subjects ± S.E. of mean.

($P < 0{\cdot}005$) increase in the ratio of the m.v.c. of the trained hand to the m.v.c. of its contralateral control. However, none of the other variables showed such a relative increase.

Although the untrained hand showed no statistically significant changes in force, a plot of the percentage increase in m.v.c. in this hand against that in the trained hand revealed a significant correlation ($r = 0{\cdot}94$, $n = 7$, $P < 0{\cdot}005$, $y = 0{\cdot}442x - 2{\cdot}45$), suggesting the possibility of an underlying contralateral training effect equal to about 40 % of the ipsilateral training effect. No significant correlation was found for a similar plot of maximal tetani in trained and contralateral muscles.

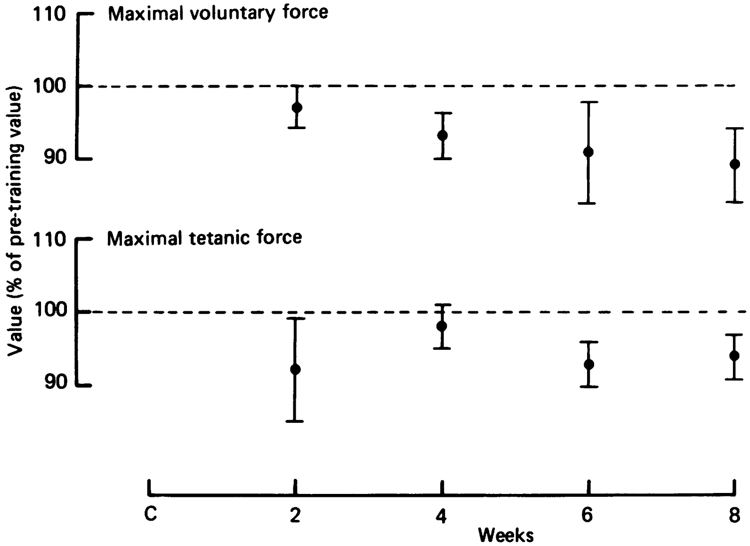

Fig. 4. Force of maximal voluntary contraction (m.v.c.) (upper graph) and maximal tetanic force (lower graph) of the trained first dorsal interosseus muscle during training using maximal electrically evoked tetani. Each point represents the mean of determinations from three subjects ± S.E. of mean.

Training using electrically evoked contractions

The results from the three subjects trained using electrically evoked contractions (see Methods) show no over-all increase in any of the measured variables (Table 1). Indeed m.v.c. showed a tendency to decrease in the trained hand (Fig. 4). One subject (M.M.) was involved in both training programmes. A rest interval of 6 months was allowed between each programme. The same muscle of this subject showed a clear increase in m.v.c. with the training involving voluntary contractions, but no increase in force following training using electrically evoked contractions.

DISCUSSION

Our results show that training using maximal voluntary isometric contractions produced little if any change in the time-to-peak of the evoked twitch contractions, confirming findings in previous studies (McDonagh *et al.* 1983; Duchateau & Hainaut, 1984). Interestingly, training with electrical stimulation also did not produce a change in the time course of the twitch. This particular finding contrasts with that of Edwards, Jones & Newham (1982), who reported that electrical stimulation of human muscle leads to lengthening of the twitch time-to-peak. The discrepancy is probably due to the different protocols adopted in the two studies.

It is clear from this current work and from our previous findings (McDonagh *et al.* 1983; Davies & Young, 1983) that increases in m.v.c. following training are much greater than the increases in electrically evoked force. This result fits well with other data which indicate a discrepancy between increases in the cross-sectional area of muscle tissue and the increases in m.v.c. following high force training (see Introduction). Further evidence for some dissociation between hypertrophy and increased m.v.c. comes from the observations that m.v.c. increases most during the early weeks of training, whereas muscle cross-sectional area increases most during the later stages of training (Häkkinen, Komi & Tesch, 1981; Fukunaga, 1976).

The training using electrically evoked contractions produced no increases in m.v.c., suggesting that neural drive has to be present in the exercises in order to produce large increases in m.v.c. The simplest conclusion from the results of both forms of training is that the voluntary neural drive to muscles is increased following training using voluntary contractions. However, if the first dorsal interosseus is alone in producing the voluntary force, then this explanation would seem to entail that tetanic tension be greater than m.v.c. prior to training. The opposite was found. This suggests that additional muscles make a contribution to the m.v.c. The increase in voluntary force with training could, therefore, also arise from increased tension in assisting muscles as training progressed.

In conclusion, we have shown that training using m.v.c.s produces a much smaller increase in tetanic force than in maximal voluntary force. Further, we have argued that the increase in maximal voluntary force may be due to a change in voluntary neural drive to the muscle tissue.

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