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RESEARCH ARTICLE

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Motor unit recruitment order during voluntary and electrically induced contractions in the tibialis anterior

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Abstract The recruitment order of motor units (MU) was compared during voluntary and electrically induced contractions. With the use of spike-triggered averaging, a total of 302 MUs with recruitment thresholds ranging from 1% to 88% of maximal voluntary contraction were recorded in the human tibialis anterior muscle in five subjects. The mean (±SD) MU force was 98.3±93.3 mN (mean torque 16.8±15.9 mNm) and the mean contraction time (CT) 46.2±12.7 ms. The correlation coefficients (r) between MU twitch force and CT versus the recruitment threshold in voluntary contractions were +0.68 and –0.38 ($P<0.001$), respectively. In voluntary contractions, MUs were recruited in order of increasing size except for only 6% of the cases; whereas, during transcutaneous electrical stimulation (ES) at the muscle motor point, MU pairs showed a reversal of recruitment order in 28% and 35% of the observations, respectively, when the pulse durations were 1.0 ms or 0.1 ms. This recruitment reversal during ES was not related to the magnitude of the difference in voluntary recruitment thresholds between MUs. It is concluded that if the reversal of MU recruitment observed during ES is biophysically controlled by differences in their nerve axon input impedance, in percutaneous stimulation at the motor point, other factors such as the size and the morphological organisation of the axonal branches can also influence the order of activation.

Key words Muscle contraction · Electrical stimulation · Motor unit recruitment · Spike-triggered averaging · Human

Introduction

Since the eighteenth century, it has been suggested that the contractile responses of muscle induced by electrical neuromuscular stimulation (ES) are useful in the treatment of paralysed patients and/or the restoration of muscle function before patients are capable of voluntary exercise (Kratzenstein 1744, quoted by McNeal 1976). More recently, ES has been used for strengthening healthy subjects and even trained athletes (for reviews, see Enoka 1988; Hainaut and Duchateau 1992). Some authors claim that ES is as effective for strengthening muscles as voluntary contractions (Canon and Cafarelli 1987; Miller and Thépaut-Mathieu 1990), but other studies that compared these two methods indicate that voluntary contractions are more effective at increasing force and improving resistance to fatigue (Davies et al. 1985; Duchateau and Hainaut 1988). Furthermore, the different effects of ES and voluntary training could be related to differences in motor unit (MU) recruitment during electrically induced responses (Cabric et al. 1988; Enoka 1988; Hainaut and Duchateau 1992). One important difference might be that during voluntary training the discharge frequency of the MUs is modulated throughout the contraction, whereas this does not occur during ES at a constant frequency.

It has been shown from animal experiments (Blair and Erlanger 1933; Solomonow 1984; Fang and Mortimer 1991) and suggested from indirect observations on humans (Trimble and Enoka 1991; Heyters et al. 1994) that, during ES, MUs are recruited in a reversed sequence compared with voluntary contraction. However, the results from human experiments are confusing, because some of these support the reversal of MU recruitment during ES (Trimble and Enoka 1991; Heyters et al. 1994), while others are rather conflicting (Knaflitz et al. 1990; Adams et al. 1993; Binder-Macleod et al. 1995). These controversal observations could be related to differences in experimental approaches and muscles that were studied.

The purpose of the study was to compare the recruitment order among MUs in the tibialis anterior muscle during voluntary and transcutaneous neuromuscular ES. As compared to voluntary contractions, the results indicated a significantly greater number of reversals in MU

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recruitment order during ES. However, the less-than-expected reversal suggests that, in humans, this effect is due not only to differences in nerve axon impedance but also to other factors such as the size and organisation of the axonal branches within a muscle. This difference in recruitment order supports the viewpoint that ES can complement voluntary activation as a modality for muscle training and rehabilitation (for a review, see Hainaut and Duchateau 1992).

Materials and method

Subjects and experimental design

Five male subjects aged between 22 and 39 years took part in this investigation and were tested on a number of different (three or four) occasions. All these subjects were well accustomed to the experimental procedure. The tibialis anterior was selected for this study because of the relatively long distance between the motor point and the distal tendon. This distance was sufficient to accommodate a detection electrode and to minimize any interference from the stimulation artefact. The muscle of the left leg (non-dominant side) was tested. This study was approved by the University Ethics Committee, and the subjects gave their informed consent prior to participation in this investigation.

EMG recordings

Motor unit action potentials (MUAP) were recorded by a selective electrode made of two 50-μm diamel-coated nichrome wires inserted into the muscle by means of a hypodermic needle (Duchateau and Hainaut 1990). The electrode was inserted through the skin in the mid-part of the muscle belly. During each experimental session, the electrode was reinserted in at least three separate locations and different depths and angles were explored for any given site in order to record action potentials from different MUs. The MUAPs were amplified by a custom-made differential amplifier and filtered (100 Hz–10 kHz) before being displayed on a Tektronix 565 oscilloscope.

In our experimental conditions using the spike-triggered averaging technique to record MU mechanical response during voluntary activation (Milner-Brown et al. 1973), firing synchronization of a recorded MU with the activity of other muscle MUs would overestimate the force. To check for possible MU synchronization, surface electromyographic activity (EMG) was recorded by means of two silver disk electrodes (8 mm in diameter), placed 2–3 cm apart on either side of the needle electrode. The surface EMG signal was amplified (×1000), filtered (10 Hz–5 kHz) and averaged. A gross estimation (Yue et al. 1995) of MU discharge synchronization was achieved by comparing unrectified and rectified surface EMG signals. If the discharge of several MUs tends to synchronize, the averaged rectified EMG would be broader and greater than expected from the unrectified EMG and the ongoing MU activity (Milner-Brown et al. 1973). According to the criteria proposed by Milner-Brown et al. (1973), a summation of 20% was considered as a reasonable lower limit for synchronized activity. In our experiments, less than 2% of the triggered MUs could have been contaminated by synchronization with other MUs, and they were deleted for further analysis.

Mechanical recordings

Each subject sat on a chair in a slightly reclined position with one foot strapped to a foot-plate, which was inclined at an angle of 45° to the floor. The ankle and knee angles were set at about 90° and 110°, respectively. The isometric force developed by the tibialis anterior was measured by connecting the foot-plate to a strain-gauge transducer (Kulite, TC 2000), and then it was amplified (Tektronix AM 502; bandwidth d.c. to 300 Hz). The transducer was attached at the height of the metatarsophalangeal joint of the big toe with a lever arm of 17 cm. The sensitivity of the force transducer was 30 mV/N (linear range 0–500 N). The force signal was then high-gain-a.c. amplified and filtered (0.1–100 Hz) by means of an AM 502 plug-in Tektronix amplifier to obtain the MU mechanical contribution.

The mechanical recording of the single MUs was assessed by the spike-triggered averaging method (Milner-Brown et al. 1973). Briefly, the method consisted of triggering the sweep of an averager (Nicolet, 4094c) with the MUAP during a steady voluntary contraction and recording the corresponding filtered isometric force. By averaging, the contribution of the MU to the net force was then extracted. Because a low, steady MU firing rate is necessary to avoid mechanical summation of the MU responses (Calancie and Bawa 1986; Nordstrom et al. 1989), subjects were provided with visual and auditory feedback. A hardware rate limiter was also used to average the mechanical responses from the same MU and this separated the individual responses by at least 100 ms (for further details see Milner-Brown et al. 1973). However, for some high-threshold MUs (more than 70% MVC), the rate limiter was set at 90 ms.

Stimulation procedure

Rectangular pulses of graded intensity were delivered at a frequency of 0.5 Hz from a custom-made stimulator triggered by a digital timer (Digitimer; 4030). Because pulse duration is known to affect the selectivity of stimulation (Solomonow 1984), narrow pulses allowing a more gradual recruitment, two different durations (0.1 ms and 1 ms) were compared. These pulse durations were selected because they are within the range used for percutaneous muscle activation in electrophysiological studies and in physiotherapy. The muscle was stimulated at its motor point by two electrodes, with the cathode (silver disk of 0.8 mm diameter) being placed over the motor point while the anode (silver plate of 2×3 cm) was fastened to the calf muscles. The motor point was defined as the point of stimulation at which a barely perceivable muscle contraction was present at the lowest stimulus intensity. Stimulation was ended when a maximal twitch was obtained or when the subject complained of the discomfort of the electrical stimulus. Stimulus intensity was measured by means of a current probe (Hewlett-Packard; model 1111A).

Experimental procedure

To determine the maximal force of the dorsiflexor muscles, each experimental session began with the subjects performing three MVCs of 4–5 s duration separated by a 2- to 3-min pause. The largest one was used as the MVC. Subsequently, MUs were identified by having the subject perform two or three isometric ramp contractions to identify isolated MUAPs. Once the MUAPs had been clearly identified, the subject maintained a level of force for each MU that was just sufficient to maintain the MU discharge frequency at a constant low rate (5–10 Hz). The mechanical contribution of each MU was then determined using a spike-triggered averaging method (usually two to four MUs at each site). Once this task had been completed, the MU recruitment order during a voluntary contraction was assessed during three to five ramp isometric contractions of 10% MVC/s while following a target on the screen of an oscilloscope. Finally, the recruitment order of the MUs during electrical stimulation was assessed for the two different pulse durations (0.1 ms and 1 ms). The order of stimulus pulse durations was randomised from trial to trial. For the ES, the strategy was to locate the motor nerve branch by moving slightly the cathode, then reduce the stimulus intensity to the level at which the first MUAP was consistently recruited. We then verified that this EMG response corresponded to an “all-or-nothing” response by increasing or decreasing slightly the intensity of stimulation. The stimulus intensity was then gradually increased until the next

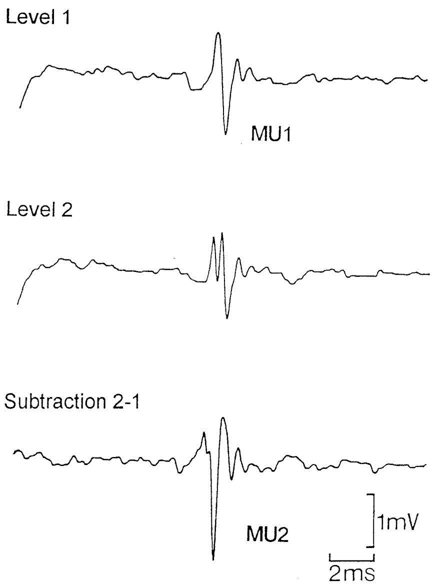

Fig. 1 The subtraction procedure used to identify motor unit action potentials (MUAPs) induced by graded electrical stimulation of the tibialis anterior motor point. *Level 1* corresponds to the first recruited MU (*MU1*), and a small reduction in stimulus strength produced an all-or-none EMG response. *Level 2* was recorded for slightly increased stimulus strength and corresponds to a compound response. MU2 was obtained by subtracting level 1 from level 2

small, obvious change in the EMG was seen, with each change being considered as the result of the recruitment of an additional MU (Fig. 1). Thereafter, a voluntary ramp contraction was performed to check whether the needle electrode did not move during the ES. Three to five minutes' rest was allowed between two successive trials (MU recordings at a given site). The force signals (unfiltered and filtered), the MUAPs, the surface EMG and the current intensity were stored on magnetic tape via an FM 8-channel recorder (Hewlett-Packard; 3960) operating at a speed of 17.78 cm/s.

Data analysis

All the data were analysed off-line from the taped records and displayed on a digital oscilloscope (Nicolet; 4094c). The maximal voluntary force was determined from the trial that yielded the largest value. Motor unit discrimination was accomplished with a computer-based, template-matching algorithm (Signal Processing Systems, Australia; SPS 8701). Single MUAPs were identified on the basis of their waveform shapes and were used to trigger the averaging sweeps of the force signal. Usually, 100–300 sweeps were averaged, depending on MU size. For large MUs, 50–100 sweeps were often sufficient, and in this case the contractions were interrupted by one or more small pauses to minimize fatigue. We measured the peak amplitude and the contraction time (CT) on the mechanical response of each MU. The MU recruitment threshold during voluntary activation was defined as the level of force at which the MUAP appeared for the first time on the EMG trace and was measured during the isometric ramp contractions. MU onset activity, obtained from the analog output of the discharge frequency of the discriminator (SPS 8701) and the force signal, were displayed on a digital oscilloscope. The recruitment threshold was expressed as a percentage of the MVC.

During electrical stimulation, the MU recruitment order was assessed by recording the successive EMG levels in response to graded ES. Single MUAPs were then isolated by subtracting the preceding EMG level from each EMG trace (Fig. 1). This procedure was performed several times and we were usually able to record four to eight different MUAPs. These MUAPs were compared on the basis of their shape (number of peaks and their relative size; interpeak latencies) with those recorded in voluntary contraction. Both averaged and single trials were used, depending of the quality of the traces and the difficulty in identifying MUs. MUAPs obtained in ES that were not clearly identified as being the same as those recorded in voluntary contraction were deleted for further analysis. Approximately 75–80% of MU pairs were accurately identified on this basis. For a given site of recording, pairwise comparisons of MUAP recruitment order were made during voluntary ramp and electrically induced contractions. In voluntary contractions, we determined the recruitment order of the MU pairs on the basis of their peak force; the appearance of a MUAP with a large force prior to one with a smaller peak force was considered to represent a reversal of the recruitment order.

Conventional statistical methods were used for calculating means, standard deviations and the coefficient of correlation. The χ^2-test was used to compare the significance of MU recruitment reversal in voluntary and electrically induced contractions.

Results

MUs' mechanical properties of the tibialis anterior

A total of 302 MUs were recorded from five subjects during linearly increasing voluntary contractions, and the recruitment thresholds of these MUs ranged from 1% up to 88% of MVC (Fig. 2). The mean (±SD) dorsiflexion force during MVC was 266.9±25.4 N (torque 45.6±4.4 Nm). The mean MU force was 98.3±93.3 mN (mean torque 16.8±15.9 mNm) and the observed force distribution was rather large (from 3.1 to 456.2 mN). The MU twitch CTs ranged from 21 to 82 ms, with a mean value of 46.2±12.7 ms. The mean MU discharge rate during spike-triggered averaging was 8.1±0.8 Hz. The correlation coefficients (*r*) across all subjects between the MU twitch force and recruitment threshold was +0.68 ($P<0.001$) and between CT and recruitment threshold it was –0.38 ($P<0.001$).

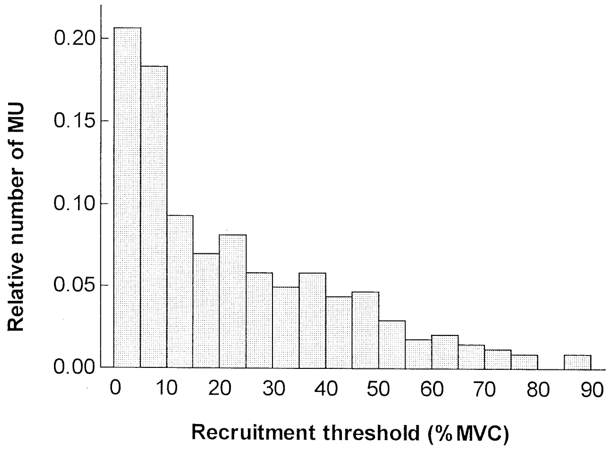

Fig. 2 Histograms showing the distribution of the recruitment thresholds (expressed as percentages of maximum voluntary contraction, *MVC*) of 302 MUs recorded from the tibialis anterior of five subjects. Values ranged from 1 to 88% of MVC

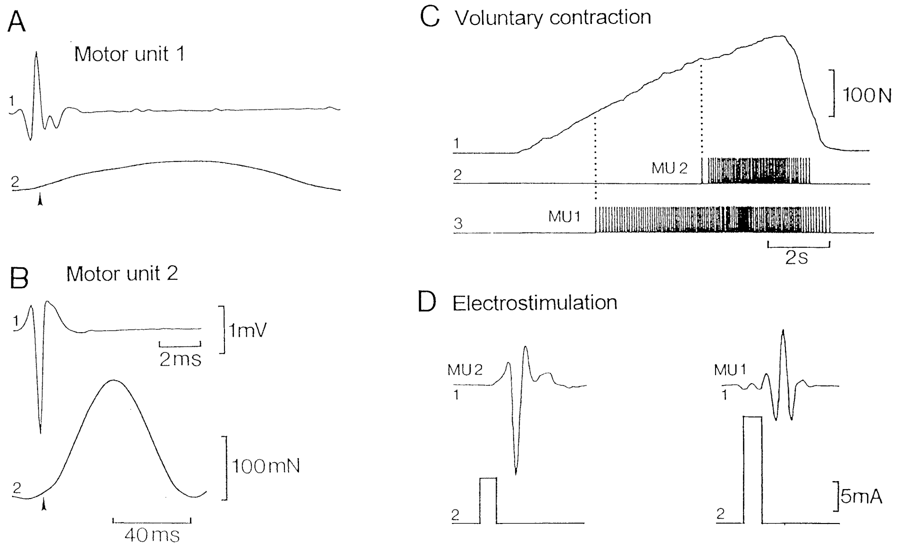

Fig. 3A–D The recruitment order of two MUs (**A,B**) with different MUAPs (*1*) and mechanical properties (*2*) during voluntary (**C**) and electrically induced (**D**) contractions. Traces in **A** and **B** are averaged waveforms (117 and 66 sweeps, respectively), whereas in **D** single trials are illustrated. In voluntary isometric ramp contractions (**C**), these MUs were recruited according to their sizes (recruitment thresholds were 87 N and 203 N, respectively, for MU1 and MU2). In electrically induced contractions (pulse duration of 1 ms), a reversal in the order of activation occurred (**D**) and MU2 was recruited at a lower level of stimulation than MU1 (7 vs 17 mA, respectively)

Recruitment reversal during ES

Figure 3 illustrates the recruitment of two MUs in one subject. MU1 and MU2 were identified by the shape of their MUAP and twitch time course (Fig. 3A,B, 1 and 2, respectively). MU1 was recruited at 87 N threshold during a voluntary ramp contraction, whereas MU2 was activated at a higher force level (203 N; cf. Fig. 3C). The sequence of activation was reversed during electrically induced contractions, with MU2 appearing at a lower level of stimulation compared with MU1 (7 and 17 mA, respectively; cf. Fig. 3D). Such reversals during ES were observed in 28% of the comparisons for a pulse duration of 1 ms across all subjects. These reversals were also observed during voluntary contractions, but in only 5.7% of the comparisons and only when the recruitment thresholds of the MUs pairs differed by less than 12%.

Effect of pulse duration

Figure 4 compares the recruitment reversal induced by two different pulse durations (1.0 ms and 0.1 ms). During ES the recruitment order was studied in 235 and 231 MUs pairs, respectively, for 1.0 ms and 0.1 ms; whereas 249 MUs pairs were analysed during voluntary contractions. Consistent results were recorded from all the subjects, and the mean results indicate that the number of reversals was significantly greater ($P<0.01$) during ES than in voluntary activation. It also appears from the data in Fig. 4 that the reversal has a tendency to be greater at 0.1 ms pulse duration than 1.0 ms (respectively, 35% and 28%), but this observation was not statistically significant ($P>0.05$). However, these values varied across subjects and ranged from 28% to 40% for 0.1 ms of pulse duration and from 22% to 36% for 1 ms.

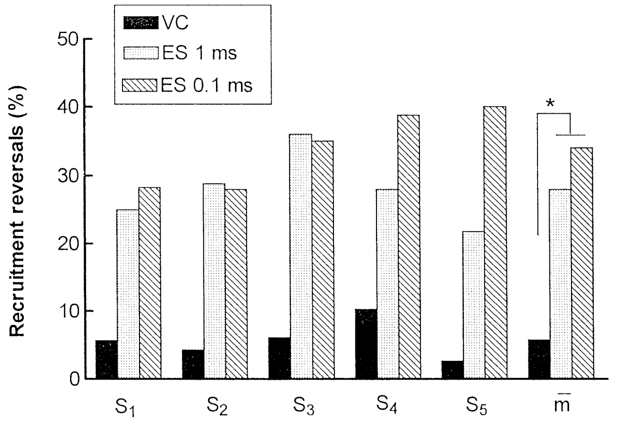

Fig. 4 Comparison of the recruitment reversal of MU pairs, expressed as percentages, during voluntary contraction (*VC*) and electrical stimulation (*ES*) for our five subjects (*S1–S5*) and the whole MU population ($\bar{m}$). In ES, two pulse durations (0.1 and 1 ms) were compared. * Significant difference at $P<0.01$

Effect of recruitment threshold difference

The effect of the difference in recruitment threshold between pairs of MUs on the frequency of the recruitment reversals during ES was tested for differences that ranged from less than 10% to as much as 50–60% during voluntary contractions. The results indicate that there is no significant tendency for reversal during ES to be related to the difference in MU recruitment threshold observed during voluntary contractions (Fig. 5). Similar data were recorded from experiments performed with 1.0-ms and 0.1-ms durations during ES.

Discussion

The present work compared, for the first time by direct recording, the recruitment order of single MU during voluntary and electrically induced contractions. The ex-

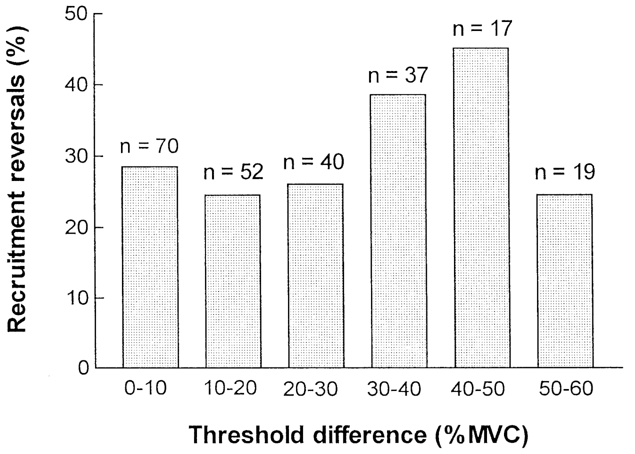

Fig. 5 Percentage of recruitment reversals in all MU pairs during electrical stimulation as a function of the difference in the recruitment threshold. Data are shown for a pulse duration of 1 ms, but similar results were obtained for a pulse duration of 0.1 ms. Number of MU pairs in each class is indicated *above bars*. Note the absence of any association between these two parameters

perimental results indicate that, in tibialis anterior muscle, although reversal of MU recruitment order during ES should be fundamentally controlled by the axon's input impedance, it is also probably affected by other factors such as the size of the axonal branches as well as their location and orientation in the current field (Knaflitz et al. 1990). Furthermore, this investigation made on 302 MUs of the tibialis anterior confirms and extends previous studies of human upper limb muscles and indicates that, during voluntary contractions, MUs are activated according to the Henneman "size principle" (Henneman et al. 1965; Milner-Brown et al. 1973; Desmedt and Godaux 1977; Romaiguère et al. 1989).

The mean MU torque, recorded in our experiments using the spike-triggered averaging method in tibialis anterior, however, was larger (16.8 vs 5.7 mNm) and the CTs were shorter (46 vs 61 ms) than those reported for the same muscle during microstimulation (Andreassen and Arendt-Nielsen 1987). These differences could be explained by a difference in muscle compliance related to the experimental setup and/or to the method, since in spike-triggered averaging MU activity is recorded during a voluntary contraction and the elastic muscle elements are stretched by the contraction of other MUs, whereas it is not the case during microstimulation of a single MU. Another explanation is that, during voluntary contraction, the repetitive activation of an MU induces a twitch potentiation that is not present during microstimulation because MU response is averaged at low frequency. Such twitch potentiation associated with a decreased CT has been observed in both human muscle (Desmedt and Hainaut 1968) and single frog fibre (K. Hainaut, unpublished work). However, according to Kossev et al. (1994), spike-triggered averaging and intramuscular microstimulation produced similar MU forces in the first dorsal interosseous, but CT appeared to be underestimated in the first method. Thomas et al. (1990) also found comparable MU forces when studied by intraneural motor-axon stimulation and spike-triggered averaging in the thenar muscles, but a slightly longer CT was observed in the latter method.

The recruitment reversal of MUs during ES as compared with MU activation during voluntary contractions has been suggested by the finding of a close, positive correlation between MU excitability and axon diameter during electrical stimulation of a whole nerve trunk in animals (Blair and Erlanger 1933). Furthermore, during voluntary contractions an MU is activated by a synaptic current passing into the motoneuron, with the result that smaller motoneurons, which have a higher input impedance, are recruited more easily (Henneman et al. 1965; Burke and Edgerton 1975). During ES, however, the MU is activated by an electric current that is applied externally to the nerve axons, and larger cells with low axonal input impedance are thus more excitable (Blair and Erlanger 1933; Solomonow 1984; Fang and Mortimer 1991).

The discussion of the reversal in humans is more confusing because there is no consensus. Reversal during ES is supported by some observations (Cabric et al. 1988; Trimble and Enoka 1991; Heyters et al. 1994) but contested by others (Brown et al. 1981; Knaflitz et al. 1990; Adams et al. 1993; Binder-Macleod et al. 1995). Most studies on human muscles, however, have involved indirect experimental approaches: (a) EMG power spectrum and conduction velocity (Knaflitz et al. 1990); (b) muscle twitch time-to-peak (Trimble and Enoka 1991; Heyters et al. 1994); (c) force-frequency relationship and fatigability at different intensities (Binder-Macleod et al. 1995); and (d) muscle biopsies before and after a training program (Cabric et al. 1988; Delitto et al. 1989). The present study compares MU activation sequences during ES-induced responses versus voluntary contractions and is based on direct recordings of MU activity using the spike-triggered averaging technique (Milner-Brown et al. 1973).

Given the size-related differences in input impedance, our observation of a rather limited reversal during ES in the tibialis anterior is surprising, but in line with the results of Knaflitz et al. (1990), who observed a reversal in only 28% of their experiments. In addition, in humans, recruitment thresholds of MUs participating in a voluntary contraction could be altered by the fact that the stimulation of cutaneous receptors induces excitatory afferents in motoneurons of type F (fast) MUs and inhibitory ones in those of type S (slow) MUs (Garnett and Stephens 1981). Trimble and Enoka (1991) documented such a viewpoint for reflex activation in the presence of sub-motor threshold ES and suggested that recruitment order change was related to an alteration of the sensory input to the motoneuron pool induced by the stimulus. However, in our experimental conditions, the nerve axons are directly activated, and those that are closer to the electric field should be recruited more easily than those deeper in the muscle mass. This interpretation and our

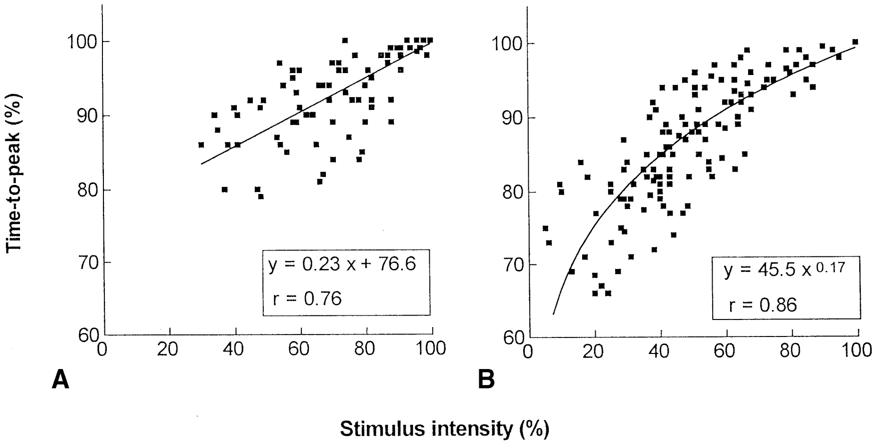

Fig. 6 Comparison of the relationship between the time to peak of a muscle twitch and the stimulus intensity in **A** the tibialis anterior (seven subjects) and **B** the lateral gastrocnemius (ten subjects) muscles in response to electrical stimulation at the motor point. Values are expressed as percentage of twitch time-to-peak and the corresponding stimulus relative to the maximal response. The data are best fitted by a linear regression and power curves for the tibialis anterior and the lateral gastrocnemius, respectively. Data for lateral gastrocnemius were taken from Heyters et al. 1994

observation of limited reversal during ES in tibialis anterior could be explained by the argument that, in the tibialis anterior, larger diameter axons appear to be located deep within the muscle mass and not near its surface (Henriksson-Larsen et al. 1985). It is also consistent with an indirect experimental approach showing that the range of twitch time-to-peak was greater in muscles with a larger proportion of fast MUs at their surfaces (Heyters et al. 1994). With respect to this last experimental approach, Fig. 6 illustrates the relation between twitch time-to-peak and the intensity of stimulation in the tibialis anterior and the lateral gastrocnemius, a muscle that is known to have a larger proportion of fast MUs located at its surface (Johnson et al. 1973). In the tibialis anterior, the relation is linear and the range of twitch time-to-peak is more narrow than in the gastrocnemius (cf. Fig. 6). Such a finding is consistent with a smaller proportion of fast MUs located at the surface of this muscle, and thus a rather limited recruitment reversal can be explained, not because larger MUs are less excitable than smaller ones during ES, but because they are more distally located in the electric field. This discussion is in line with our observation that, although the recruitment reversal tended to increase with a reduction in pulse duration (from 1.0 ms to 0.1 ms), the difference was not statistically significant. If the excitability of the nerve axons played the dominant role in the order of MU recruitment during ES, one would expect, on the basis of the strength-duration relationship, a greater reversal to occur for the short-duration pulse (Blair and Erlanger 1933; Solomonow 1984).

Our observation that the reversal recruitment during ES was not related to the difference in recruitment thresholds between MUs observed in voluntary contractions further supports the viewpoint that the axonal excitability threshold is not the only factor that determines MU recruitment order. Indeed, if the reversal of MU recruitment during ES was mainly related to the difference in its axonal input impedance, it should have been augmented with an increased difference in activation threshold because of the greater input impedance between MUs in a pair. Whatever the pulse duration, however, this was not the case in our experimental conditions, which means that, in transcutaneous ES, other factors such as the size of the axonal branches and their orientation in the current field also play an important role (see Knaflitz et al. 1990; Binder-Macleod et al. 1995). It has been suggested that some terminal branches of large MUs could be smaller than those of small ones and, therefore, would only be activated by higher current levels than smaller MUs (Knaflitz et al. 1990).

It is concluded from these direct observations of MU activation during voluntary and electrically induced contractions that the reversal of MU recruitment order during ES is controlled not only by differences in axonal input impedance, as is clearly shown from direct observations on animals, but also by other factors probably related to the size and the morphological organisation of the axonal branches within the muscle.

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