

**You might find this additional information useful...**

---

This article cites 29 articles, 6 of which you can access free at:

<http://jn.physiology.org/cgi/content/full/80/3/1373#BIBL>

This article has been cited by 9 other HighWire hosted articles, the first 5 are:

**Ordered Motor-Unit Firing Behavior in Acute Cerebellar Stroke**

C. Sauvage, M. Manto, A. Adam, R. Roark, P. Jissendi and C. J. De Luca  
*J Neurophysiol*, November 1, 2006; 96 (5): 2769-2774.

[Abstract] [Full Text] [PDF]

**Effects of exercise training on {alpha}-motoneurons**

P. Gardiner, Y. Dai and C. J. Heckman  
*J Appl Physiol*, October 1, 2006; 101 (4): 1228-1236.

[Abstract] [Full Text] [PDF]

**Decomposition of Surface EMG Signals**

C. J. De Luca, A. Adam, R. Wotiz, L. D. Gilmore and S. H. Nawab  
*J Neurophysiol*, September 1, 2006; 96 (3): 1646-1657.

[Abstract] [Full Text] [PDF]

**Dominance of the Hand Does Not Change the Phonomyographic Measurement of Neuromuscular Block at the Adductor Pollicis Muscle**

G. Michaud, G. Trager, S. Deschamps and T. M. Hemmerling  
*Anesth. Analg.*, March 1, 2005; 100 (3): 718-721.

[Abstract] [Full Text] [PDF]

**Common Drive in Motor Units of a Synergistic Muscle Pair**

C. J. De Luca and Z. Erim  
*J Neurophysiol*, April 1, 2002; 87 (4): 2200-2204.

[Abstract] [Full Text] [PDF]

Medline items on this article's topics can be found at <http://highwire.stanford.edu/lists/artbytopic.dtl> on the following topics:

Physiology .. Firing Rate  
Engineering .. Biomedical Engineering  
Physiology .. Humans

Updated information and services including high-resolution figures, can be found at:

<http://jn.physiology.org/cgi/content/full/80/3/1373>

Additional material and information about *Journal of Neurophysiology* can be found at:

<http://www.the-aps.org/publications/jn>

---

This information is current as of June 7, 2007 .

# Hand Dominance and Motor Unit Firing Behavior

ALEXANDER ADAM,<sup>1,2</sup> CARLO J. DE LUCA,<sup>1,2,3</sup> AND ZEYNEP ERIM<sup>1</sup>

<sup>1</sup>NeuroMuscular Research Center, <sup>2</sup>Department of Biomedical Engineering, and <sup>3</sup>Department of Neurology, Boston University, Boston, Massachusetts 02215

**Adam, Alexander, Carlo J. De Luca, and Zeynep Erim.** Hand dominance and motor unit firing behavior. *J. Neurophysiol.* 80: 1373–1382, 1998. Daily preferential use was shown to alter physiological and mechanical properties of skeletal muscle. This study was aimed at revealing differences in the control strategy of muscle pairs in humans who show a clear preference for one hand. We compared the motor unit (MU) recruitment and firing behavior in the first dorsal interosseous (FDI) muscle of both hands in eight male volunteers whose hand preference was evaluated with the use of a standard questionnaire. Myoelectric signals were recorded while subjects isometrically abducted the index finger at 30% of the maximal voluntary contraction (MVC) force. A myoelectric signal decomposition technique was used to accurately identify MU firing times from the myoelectric signal. In MUs of the dominant hand, mean values for recruitment threshold, initial firing rate, average firing rate at target force, and discharge variability were lower when compared with the nondominant hand. Analysis of the cross-correlation between mean firing rate and muscle force revealed cross-correlation peaks of longer latency in the dominant hand than in the nondominant side. This lag of the force output with respect to fluctuations in the firing behavior of MUs is indicative of a greater mechanical delay in the dominant FDI muscle. MVC force was not significantly different across muscle pairs, but the variability of force at the submaximal target level was higher in the nondominant side. The presence of lower average firing rates, lower recruitment thresholds, and greater firing rate/force delay in the dominant hand is consistent with the notion of an increased percentage of slow twitch fibers in the preferentially used muscle, allowing twitch fusion and force buildup to occur at lower firing rates. It is suggested that a lifetime of preferred use may cause adaptations in the fiber composition of the dominant muscle such that the mechanical effectiveness of its MUs increased.

## INTRODUCTION

The human motor system adapts to functional requirements with considerable plasticity. Repetitive low-intensity exercise such as that during endurance training results in enhanced aerobic capacity, fatigue resistance, and contractile slowing of muscle. High-resistance training induces muscle fiber hypertrophy and concomitantly increased maximal force output (for detailed review see Faulkner and White 1990). Thus, depending on the use of a particular muscle, its physiological characteristics and mechanical response change. Conceptually, a system of altered mechanical response would require a modification in the way it is controlled if the goal is to maintain similar outputs.

Long-term preferential use of selected muscles can be viewed as a moderate form of exercise. In the past decade,

several researchers reported differences in the physiology between the dominant and the nondominant upper limb. Fugl-Meyer et al. (1982) found a higher percentage of type I muscle fibers in the extensor carpi radialis brevis of the dominant arm compared with the homologous muscle of the contralateral arm. An indication of contralateral differences in fiber composition of the first dorsal interosseous (FDI) muscle was reported by Tanaka et al. (1984), who measured a longer force twitch rise time and higher fatigue resistance in the dominant hand, and Zijdwind et al. (1990), who reported a lesser decline of the fatigue-associated M-wave together with prolonged twitch times in the dominant side. Both results suggested the presence of a higher percentage of slow-twitch type I fibers in the preferentially used muscle. In contrast, a study by Rutherford and Jones (1988) showed no difference between dominant and nondominant FDI in terms of twitch properties or contractile fatigue. Using the same muscle, De Luca et al. (1986) investigated lateral asymmetries in the surface electromyogram (EMG) during voluntary isometric contractions. Right-handed subjects showed a higher rate of fatigue in the nondominant hand as manifested in a greater decrease of the median frequency. Left-handed subjects exhibited no significant lateral difference in median frequency behavior, which was attributed to a high level of ambidexterity among this group. More recently, Tan (1989a,b) reported greater motoneuron excitability in the dominant upper limb as measured by the H-reflex. The H-reflex is mediated via 1A afferents impinging primarily on anterior horn cells of low-threshold motor units (MUs). Because low-threshold MUs are associated with type I fibers, the finding of contralateral H-reflex differences can be viewed as another sign of asymmetric fiber composition. However, evidence exists that the H-reflex is significantly influenced by supraspinal inputs to the  $\alpha$ -motoneuron pool (Kimura 1983), which might point to a more central site for lateral asymmetry. In this regard, Yakovlev and Rakic (1966) published a study that showed a greater number of pyramidal tract fibers to the right hand in nearly 80% of adult human brains.

The question of asymmetries in peripheral nervous pathways was not unequivocally resolved. Friedli et al. (1987) reported a higher detection threshold for cutaneous electrical stimulation in the dominant arm, which they interpreted as a lateral asymmetry in sensory nerves. Sathiamoorthy and Sathiamoorthy (1990) demonstrated higher median nerve conduction velocities in the dominant arm for both left- and right-handed subjects. However, Tan (1985) concluded that motor and sensory nerve conduction velocities for the right and left arm in right- and left-handed subjects did not differ.

Our knowledge of the various lateral physiological and anatomic asymmetries in the upper extremities is not

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

matched by that of the lateral differences in the control mechanism of muscle contraction. Only three studies were published. Kamen et al. (1992) described a higher cross-correlation among mean firing rates of pairs of MUs in the dominant FDI for both left- and right-handed subjects. Schmied et al. (1994) reported enhanced short-term MU synchronization, as manifested in stronger and broader cross-correlogram peaks, in the wrist extensor muscles of the dominant arm; Semmler and Nordstrom (1995) found weaker synchronization in the FDI muscle of the dominant hand, but only in right-handed subjects. Whether homologous muscles in preferred and nonpreferred hands differ in MU parameters that directly affect force production, such as recruitment threshold or mean firing rate, is largely unknown.

The current study was aimed at investigating asymmetries in the recruitment and firing rate behavior of MUs in FDI muscle pairs during isometric force generation.

## METHODS

### *Subjects and evaluation of handedness*

Eight healthy males aged 21–39 ( $27.5 \pm 7.5$ , mean  $\pm$  SD) volunteered for this study. All subjects signed an informed consent form that was approved by the local institutional review board. Before the experiments, the hand preference of each subject (in the performance of 10 everyday tasks) was assessed with the use of a modified Edinburgh Handedness Inventory (Oldfield 1971). A laterality quotient (LQ) was computed scoring left to right handedness on a scale from  $-100$  to  $+100$ . Three of the subjects were right-handed ( $LQ > 25$ ), four were left-handed ( $LQ < -25$ ), and one exhibited no hand preference ( $LQ = 0$ ) according to the results of the questionnaire.

### *Experimental setup*

Subjects were comfortably seated at a lab bench with their forearm resting on a flat surface and the hand secured in a restraining device. The device immobilized the hand and the wrist by means of a finger mold and a strap. The FDI was held at maximum length by fixing the thumb at nearly  $90^\circ$  angle to the index finger. Isometric abduction force of the FDI was measured in all trials by placing a high-stiffness force transducer against the proximal interphalangeal joint of the index finger. Force signals were passed through a unity gain force conditioner and low-pass filtered (1-kHz cutoff) before amplification. The filtered force signal was

displayed against a target trajectory on a PC monitor in front of the subject to provide real-time force feedback.

MU action potentials (MUAPs) were recorded with a quadrifilar needle electrode inserted into the belly of the muscle. This needle electrode provided four selective pickup surfaces, each  $50 \mu\text{m}$  in diameter, from which three differential pairs of needle electrode signals were selected and amplified (band-pass 1–10 kHz). A ground strap placed around the forearm as well as a silver disk (5-mm diam) positioned on the middle finger functioned as reference electrodes.

EMG and force signals were recorded on FM tape and digitized off-line on a mini-computer. The three channels of EMG signal were sampled at 50 kHz; the force signal was digitized at 2,048 Hz.

### *Protocol*

During an experimental session subjects performed isometric contractions with each hand at force levels of 30% of their maximal voluntary contraction (MVC). Subjects were instructed to abduct their index finger while avoiding any flexion moment. All measurements were completed for one hand first before testing the other hand, and the order was determined randomly. Without the needle in place, three maximal contractions were performed at intervals of 3 min and the highest value used as the MVC to scale subsequent force trajectories. Subjects were then allowed to practice tracking the trapezoidal force trajectories during several trial runs. When force tracking was stable, the needle electrode was inserted. A digital storage oscilloscope was used to visually check the quality of the EMG signal. Adjustments to the needle position were made to give stable MUAP shapes at varying force levels. Contractions were performed in short succession but with a minimum of 3-min rest in between. Longer recovery times were used when the subject felt fatigued or when the needle was repositioned to record from a different group of fibers. At least three trials with stable electrode position and acceptable force tracking were recorded per hand.

### *Analysis*

MU RECRUITMENT AND FIRING RATE. Impulse trains representing individual MU firing times were obtained from the three channel needle EMG signal by the precision decomposition technique, which is described in detail elsewhere (De Luca 1993; Mambrito and De Luca 1984; Stashuk and De Luca 1989). Briefly, precision decomposition utilizes template matching algorithms and firing rate statistics to reliably identify MUAPs of concurrently active MUs, yielding a time series representation of MU firings. All parameters were derived from the correctly identified MU firing times. The initial firing rate

TABLE 1. Age, contralateral MVC values, and degree of handedness for eight male subjects

Subject	Age	D-MVC, N	ND-MVC, N	MVC-Diff., %	LQ	Handedness
R1	36	38.39	43.38	-13	100	R
R2	24	23.94	33.37	-39	80	R
R3	22	38.26	38.26	0	71	R
N1	23	(L) 46.05	(R) 40.04	13	0	—
L1	21	32.03	26.16	18	-87	L
L2	39	24.29	32.12	-32	-67	L
L3	21	42.71	43.16	-1	-29	L
L4	34	42.04	41.60	1	-78	L
Total	$27.5 \pm 7.5$ (8)	$34.53 \pm 7.91$ (7)	$36.87 \pm 6.53$ (7)	$-7.6 \pm 21.6$ (7)	$-1.4 \pm 82.1$ (7)	

Total values mean  $\pm$  SD with number of motor unit firing records in parentheses.

Degree of handedness is expressed as a laterality quotient (LQ) obtained from handedness questionnaire. Subjects with an LQ  $>25$  are referred to as right-handed (RH), those with an LQ less than  $-25$  are referred to as left-handed (LH). Each maximal voluntary contraction (MVC) value represents the greatest of three consecutive contractions. Mean values for dominant and nondominant hands of LH and RH subjects were not significantly different. ‡ Except for the age variable, *subject N1* was excluded from the calculation of means. D-MVC, dominant MVC; ND-MVC, nondominant MVC; MVC-Diff., MVC difference.

of a MU was computed as the inverse of the average interfering intervals (IFIs) of the first three consistent ( $IFI \leq 200$  ms) firings. The recruitment threshold of a MU was determined as the average force within a window of 15 samples ( $\approx 7$  ms) of the force signal, centered on the first consistent firing of that particular MU. Average firing rates were calculated as the inverse of the average IFI over the first 5 s of a stable target force plateau. The coefficient of variation (CV;  $SD/mean$ ) of the IFIs was calculated over the same time interval as the average firing rate.

The amount of joint fluctuation between mean firing rate signals of concurrently active MUs and the corresponding whole muscle force trace were analyzed with a cross-correlation technique (De Luca et al. 1982b). The same 5-s time interval over which the firing rate statistics were computed for each contraction was chosen for the cross-correlation analysis. Each MU's firing time impulse train was low-pass filtered with a 400-ms Hanning window to produce a continuous-time, mean firing rate signal. The firing rate and the force signals were then high-pass filtered (0.75-Hz corner frequency) to remove any DC bias before computing the cross-correlation function.

**FORCE TRACES.** For each contraction the average force, normalized to the MVC, as well as the CV of force were calculated over the same 5-s interval of the force plateau as the firing rate parameters.

### Statistical tests

Unless otherwise stated, means of parameters were compared by unpaired *t*-tests grouped by hand (dominant vs. nondominant). Significance levels of  $P < 0.05$  (two-tailed) were reported.

## RESULTS

Individual MVC values as well as percent differences in dominant and nondominant MVC values are given in Table 1. Differences between dominant and nondominant hands are at  $\leq 40\%$  but show no consistent trend with respect to degree of handedness (LQ). The mean MVC value of the dominant FDI ( $34.53 \pm 7.91$  N) was not statistically different from that of the nondominant FDI ( $36.87 \pm 6.53$  N,  $P > 0.5$ ).

Figure 1 shows typical force and mean firing rate data obtained from contralateral FDI muscles of a right-handed subject (*subject R3* from Table 1) during two 30% MVC contractions. The force trace and the mean firing rate signals of the nondominant FDI (Fig. 1A) were less stable than those of the dominant FDI (Fig. 1B), reflecting the greater difficulty experienced by the subjects in following a target trajectory with the nondominant hand. From each subject, FDI abduction force, MU recruitment, and firing rate data for an average of four such contractions with each hand were pooled and analyzed.

### Distribution of recruitment thresholds

A total of 235 action potential trains were obtained from MUs that discharged in a stable fashion during the flat portion of the force trajectory. Subtracting the MUs of the subject lacking hand preference, 121 distinct MUs from 30 contractions were analyzed and pooled into the dominant hand group and 101 (from 29 contractions) were analyzed and pooled into the nondominant hand group. Figure 2 shows the distribution of MU recruitment thresholds in dominant and nondominant hands expressed as a percentage of the total number of MUs observed in each hand. To obtain a

reasonable number of data points in each histogram, the data were pooled for all subjects except for the subject that did not exhibit a clear hand preference. The dominant hands clearly had a higher percentage of their FDI MUs recruited at lower absolute force levels ( $< 6$  N), whereas the nondominant hands exhibited a more spread-out recruitment pattern (Fig. 2). Mean recruitment forces in the dominant hands were lower than in the nondominant hands ( $4.05 \pm 2.96$  vs.  $5.11 \pm 3.51$  N,  $P < 0.05$ ).

### Average firing rates at target force

Plotting the average firing rate at the target force versus the recruitment threshold for MUs from all trials of a particular subject revealed a trend toward higher discharge rates in the nondominant hand. Figure 3 depicts the average firing rate values for pooled data from left- and right-handed subjects. Linear regression analysis showed a negative correla-

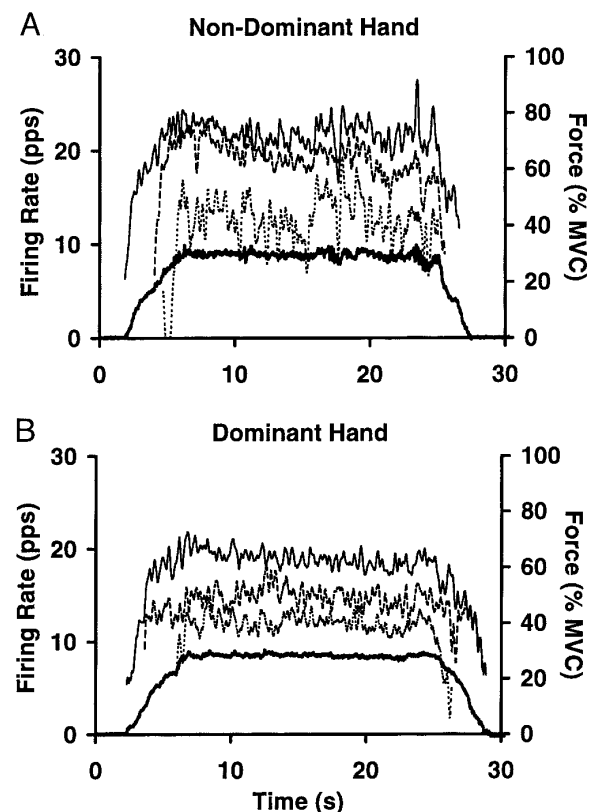


FIG. 1. Example of isometric abduction force and mean firing rate signals of concurrently active motor units (MUs) during submaximal voluntary contraction of nondominant (A) and dominant (B) 1st dorsal interosseous (FDI) in a right-handed subject. Mean firing rates are measured in pulses per second (pps; left ordinate), and the abduction force (bold line) is plotted as a percentage of subject's maximal voluntary contraction (%MVC; right ordinate). For visualization purposes, each MU's firing time impulse train was low-pass filtered with a 400-ms Hanning window to produce a continuous-time, mean firing rate signal (see De Luca et al. 1982b for a detailed description of this technique). Subjects were asked to follow a trapezoidal force trajectory by increasing the abduction force at a rate of 10% MVC/s, holding the force constant at 30% MVC for 20 s, and then decreasing it to 0 again. Force trace of the nondominant FDI (A) was less stable when compared with the dominant muscle (B), reflecting the greater difficulty experienced in following the force trajectory with the nonpreferred hand. Note that firing rate and force signals are related through a common time axis.



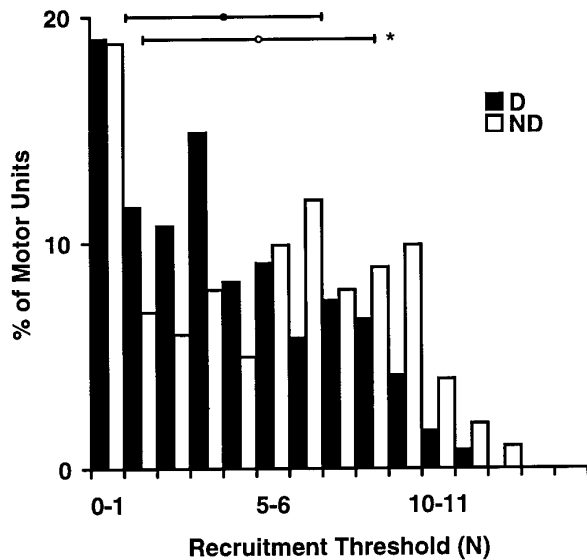


FIG. 2. Distribution of MU recruitment thresholds in dominant (D) and nondominant (ND) hands for pooled data from left- and right-handed subjects. Recruitment threshold is given as absolute force (N). Number of MUs per bin is normalized to the total number of MUs per category (D = 121, ND = 101). Circles and horizontal error bars above the histograms, means  $\pm$  SD; filled circle and bars, dominant hand; open circle and bars, nondominant hand. These data were obtained from isometric, isotonic contractions at 30% MVC. Significance levels of unpaired *t*-test; \*  $P < 0.05$ .

tion between MU firing rate and recruitment threshold within the dominant ( $R^2 = 0.04$ ,  $P < 0.01$ ) and nondominant muscle ( $R^2 = 0.31$ ,  $P < 0.01$ ). Additionally, the nondominant side regression line had a greater negative slope ( $P < 0.01$ ) and a greater intercept ( $P < 0.01$ ) than the contralateral

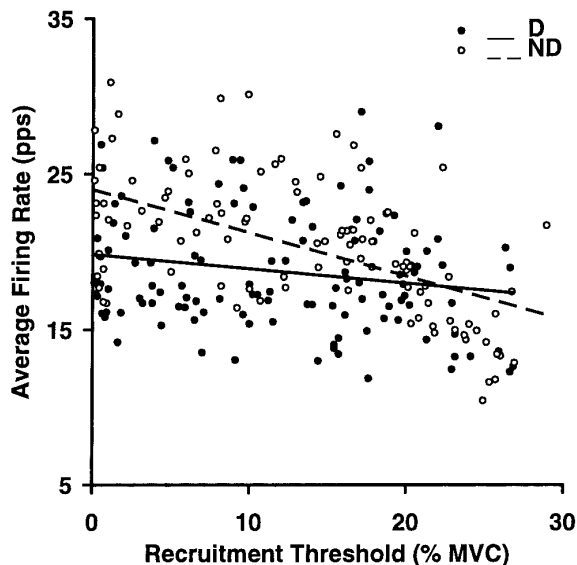


FIG. 3. Scatter plot of average firing rates at target force vs. recruitment thresholds of MUs from all subjects having distinct hand preferences. Average firing rate, calculated over a 5-s interval (see ANALYSIS), is measured in pps; recruitment threshold is plotted as %MVC force. ● and —, MUs from the dominant FDI ( $n = 121$ ); ○ and - - -, MUs from the nondominant FDI ( $n = 101$ ). Firing rates in the dominant hand were generally lower than in the nondominant hand for MUs of similar recruitment threshold. Linear fits through the data points are different for dominant ( $y = -0.09x + 19.83$ ,  $R^2 = 0.04$ ) and nondominant ( $y = -0.28x + 24.01$ ,  $R^2 = 0.31$ ) hands. Both the intercept and the negative slope were greater in the nondominant side ( $P < 0.01$ ).

side. The mean value of the average firing rates across the range of observed recruitment thresholds was 8.0% lower in the dominant FDI when compared with the nondominant muscle [ $18.72 \pm 3.90$  vs.  $20.34 \pm 4.35$  pulses per second (pps);  $P < 0.01$ ].

#### Initial firing rates

For the same subjects as in Fig. 3, the initial firing rates of MUs are plotted as a function of recruitment threshold (Fig. 4). MUs in the nondominant FDI appear to have slightly higher initial firing rates than MUs in the dominant muscle. Over the range of recruitment thresholds of this study, the correlation between initial firing rates and recruitment thresholds in MUs of the nondominant side was not significant but showed a weak positive trend ( $R^2 = 0.02$ ). In the dominant side the observed positive correlation was statistically significant ( $R^2 = 0.11$ ,  $P < 0.01$ ). Regression analysis showed that the slopes of the straight line fits in Fig. 4 are not different, but that the intercept in the dominant hand has a higher value ( $P < 0.01$ ). Disregarding the weak effect of recruitment threshold on initial firing rate, the mean value of initial firing rates for MUs in the dominant FDI ( $10.32 \pm 2.56$  pps) was significantly lower ( $P < 0.01$ ) in comparison to the mean in the nondominant side ( $11.52 \pm 2.62$  pps).

#### Firing rate in the subject without hand preference

The subject lacking hand preference did not express a clear trend toward lower average firing rates in either FDI (Fig. 5A). Although the correlation between average fir-

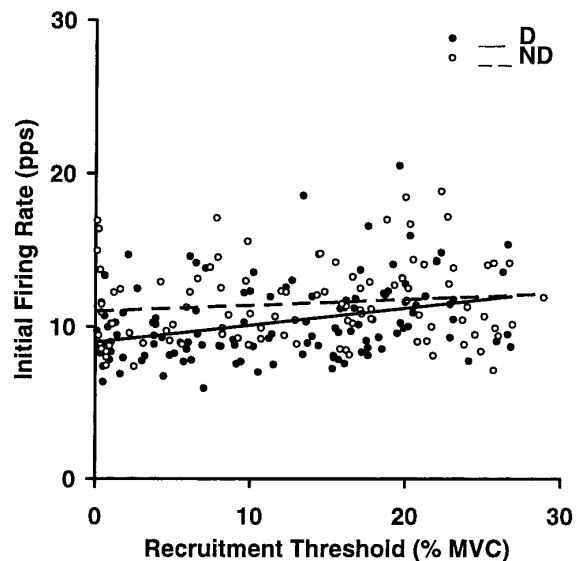


FIG. 4. Scatter plot of initial firing rates vs. recruitment thresholds of MUs from the pool of left- and right-handed subjects. Filled symbols and continuous line, dominant hand data ( $n = 121$ ); open symbols and dashed line, nondominant hand ( $n = 101$ ). Initial firing rates, calculated over the 1st 4 MU discharges, are measured in pps on the y-axis. Normalized recruitment thresholds (%MVC) are plotted on the x-axis. As in the case of average firing rates, initial firing rates tended to be lower in the dominant side compared with the nondominant side. A weak dependence of initial firing rate on recruitment threshold is evident in the dominant ( $y = 0.11x + 8.98$ ,  $R^2 = 0.11$ ) but less in the nondominant ( $y = 0.04x + 11.01$ ,  $R^2 = 0.02$ ) hands.

ing rates and recruitment thresholds in the left and right hand was not statistically significant, straight line fits show a decrease of firing rate with increased recruitment threshold.

A scatter plot of initial firing rates versus recruitment thresholds of MUs is given in Fig. 5B. Although the subject exhibited a significant positive correlation on the right side ( $R^2 = 0.73$ ,  $P < 0.05$ ), regression analysis yielded a dissimilar pattern on the left side caused by a single outlier point. When this outlier (labeled in Fig. 5B) was excluded from the analysis, a weak positive trend was observed between the initial firing rate and the recruitment threshold.

Because only a limited number of MU firing records were available for this case (left hand  $n = 6$ , right hand  $n = 7$ ) and the subject could not be pooled with either left- or right-handed populations, the data were not suited for further statistical analysis.

#### Variability of MU firings

In addition to the lateral discrepancies in firing rates, the variability of the interval between successive firings differed between dominant and nondominant hands (Fig. 6A). The

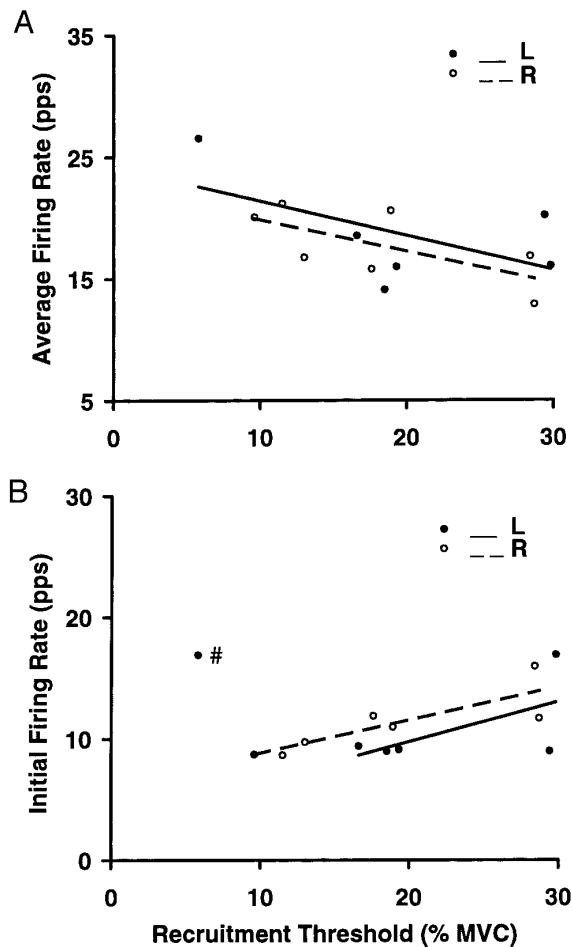


FIG. 5. Scatter plots of average firing rates (A) and initial firing rates (B) vs. recruitment thresholds of the MUs recorded from the subject that lacked hand preference. A: no marked difference in average firing rate/recruitment threshold behavior between MUs in the left (solid circle and lines,  $n = 6$ ) and right (open circle, dashed lines,  $n = 7$ ) hands was observed. In B the outlier (number sign) was excluded from the analysis.

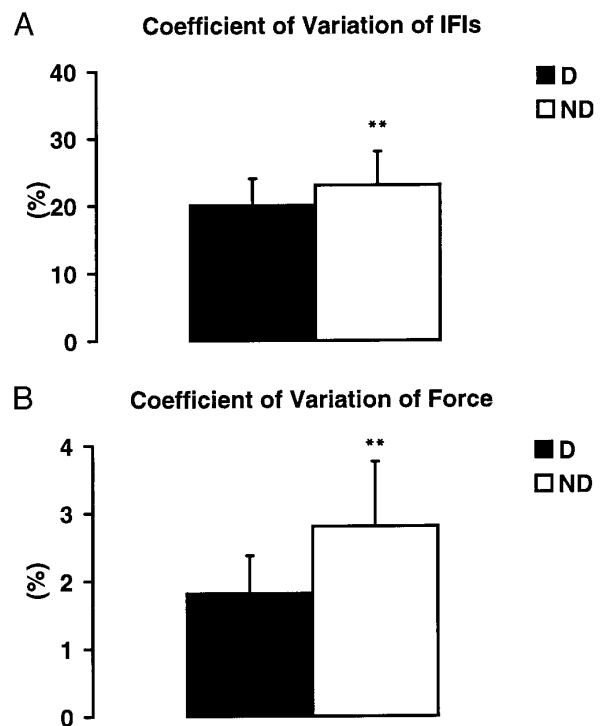


FIG. 6. Variability of MU interfiring intervals (IFIs; A) and force traces (B) for dominant and nondominant hands in left- and right-handed subjects grouped together. Shown are means and SDs of the coefficient of variation (CV; SD/mean) values for MU IFIs and contraction forces. Calculations are based on a 5-s interval at the beginning of the force plateau (see ANALYSIS). A: mean CV of IFIs was significantly smaller in the dominant hand. B: similarly, the mean CV of force was significantly lower in the dominant muscle. Variability of force was  $\sim 1/10$  magnitude of the MU discharge variability. ■, dominant hand (A,  $n = 121$ ; B,  $n = 30$ ); □, nondominant hand (A,  $n = 101$ ; B,  $n = 29$ ). Significance level of  $t$ -test between dominant and nondominant hand; \*\*  $P < 0.01$ .

mean CV of IFIs in the dominant hand was significantly smaller in comparison to the nondominant hand ( $20.17 \pm 3.73\%$  vs.  $23.48 \pm 5.30\%$ ,  $P < 0.01$ ).

#### Variability of force traces

The mean CV of force in the dominant hand of the pool of LH and RH subjects was significantly smaller than the mean value of the nondominant hand ( $1.81 \pm 0.56\%$  vs.  $2.80 \pm 0.96\%$ ,  $P < 0.01$ , Fig. 6B).

Irrespective of the variability of the force traces, left- and right-handed subjects exhibited no difference in force tracing capabilities when the mean force level for each group was compared across contralateral muscle pairs. Overall subjects contracted their dominant FDI at a mean force level of  $29.24 \pm 1.90\%$  MVC and their nondominant FDI at  $29.56 \pm 0.94\%$  MVC.

#### Interaction of firing rate fluctuations with force

Firing rate signals from concurrently active MU were cross-correlated with the force record. No difference in mean peak cross-correlation values was observed between hands, but the cross-correlation latency was significantly greater in the dominant hand ( $138 \pm 33$  ms vs.  $123 \pm 27$  ms,  $P < 0.01$ , Fig. 7).

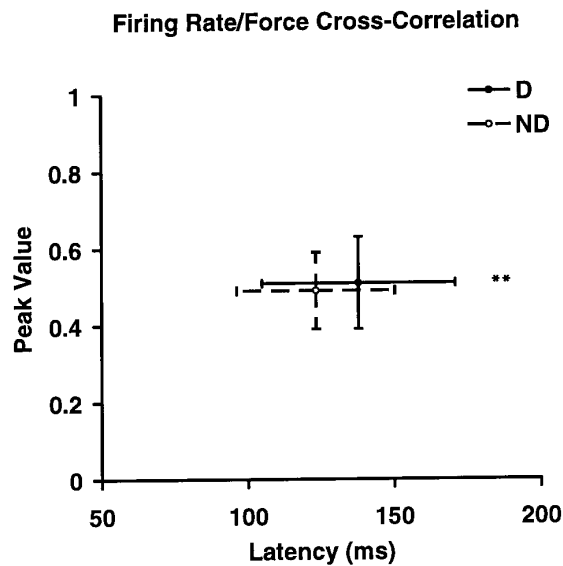


FIG. 7. Results of cross-correlation between mean firing rate and force signals for the pool of left- and right-handed subjects. For each MU, a cross-correlation function was computed between the mean firing rate signal and the contraction force (see ANALYSIS). Mean  $\pm$  SD of the peak values of the cross-correlation function are plotted against mean  $\pm$  SD of the latencies at which the peaks occurred. For physiological reasons and because of the periodicity of the cross-correlation functions, only cross-correlation peaks with latencies in the range of 0–250 ms were examined (88% of the total number of MU had peaks that fell into this range). Positive latency values indicate that fluctuations in the mean firing rate signal lead corresponding fluctuations in the force output. Subjects exhibited no differences in peak values of cross-correlation among contralateral hands but had a significantly longer mean latency in the dominant hand. ● and —, dominant hand ( $n = 106$ ); ○ and - - -, nondominant hand ( $n = 89$ ). Significance level of  $t$ -test comparison between dominant and nondominant hand; \*\*  $P < 0.01$ .

## DISCUSSION

Maximal voluntary force production and MU firing behavior during submaximal contractions were assessed in contralateral FDI muscles of eight male subjects. In the seven subjects that exhibited clear hand preference according to our handedness test, we were able to reliably characterize the firing pattern of an average of 15.9 MUs per subject per hand. We believe that the obtained MU samples adequately represent the MU population in dominant and nondominant muscles for two reasons. First, the EMG recordings were made at various depths within each muscle to record from different MUs and second, fibers belonging to single MUs in the FDI are dispersed throughout much of the muscle cross section, greatly reducing the chance of a sample bias caused by fiber clustering.

Given the number of distinct MUs analyzed in each hand group and the accuracy of the decomposition technique, the relatively small number of subjects was not considered an impediment in detecting the effect of hand preference on neural activation in the FDI muscle. Table 2 qualitatively summarizes the differences between dominant and nondominant hands for all observed MU parameters. The main findings of this study were reduced initial and average firing rates in conjunction with a shift toward lower recruitment thresholds and a greater delay between fluctuations in mean firing rates and muscle force in MUs of the dominant hand. These results are interpreted in terms of an adaptive response

of muscle fibers and motoneurons to increased everyday activity of the preferred hand.

### *Effect of hand preference on recruitment threshold and firing rate of MUs*

The distribution of recruitment thresholds in the dominant hand was skewed toward the low-force end. Accordingly, the mean recruitment threshold in the dominant FDI, measured in Newtons, was 20.7% lower than the mean value in the nondominant side (Fig. 2). Because the sampled MUs are representative of the whole MU population in the FDI, the observation that a higher percentage of MUs in the dominant hand was recruited in the lower threshold range indicates a shift toward lower recruitment thresholds in the preferentially used muscle.

Our data also showed contralateral differences in MU firing rates during isometric contraction of the FDI at a force level of 30% MVC. Two previous studies investigated the effect of handedness on MU firing rates, but they differed from the current investigation in that subjects controlled MU discharge rates, as opposed to force output, and only low-threshold (<4 N or <10% MVC) MUs were considered. Similar to our findings in the FDI, Schmied et al. (1994) reported slightly lower initial firing rates in the extensor carpi radialis muscle of the preferred arm ( $9.56 \pm 0.99$  vs.  $10.09 \pm 1.02$  pps) in two left-handed and two right-handed subjects. In contrast, Semmler and Nordstrom (1995) found no lateral differences in firing rates during low-level contractions of the FDI.

Although we saw lower average firing rates and lower recruitment thresholds in the dominant FDI when compared with the nondominant side, data for individual muscles are in agreement with the “onion skin phenomenon” (De Luca 1989; De Luca and Erim 1994), which indicates that earlier recruited MUs maintain higher mean firing rates than later recruited MUs at any point throughout a contraction. Plots of average firing rates as a function of MU recruitment force for our subjects show that within each muscle (e.g., the nondominant FDI in Fig. 2A) MUs recruited at lower thresholds indeed discharged at a higher rate than higher threshold units. Furthermore, initial firing rates showed a weak trend to increase with recruitment threshold for both the dominant

TABLE 2. Summary of contralateral differences in whole muscle performance and MU firing parameters of the FDI

Whole muscle performance	
MVC	D = ND
Force variability	D < ND**
MU parameters	
Recruitment thresholds	D < ND*
Average firing rates	D < ND**
Initial firing rates	D < ND**
Discharge variability	D < ND**
Firing rate/force cross-correlation latency	D > ND**

Results of the comparison of mean parameter values between dominant (D) and nondominant (ND) hands for the group of left- and right-handed subjects are shown qualitatively by the symbols <, >, and =. Significance level of  $t$ -test comparison between mean values; \*  $P < 0.05$ , \*\*  $P < 0.01$ . See Table 1 for other definitions.

and nondominant groups of MUs (Fig. 4). This finding is consistent with previous reports of a positive correlation between initial firing rate and recruitment threshold (Clamann 1970; De Luca and Erim 1994). Although the relationship between the firing rate and the recruitment threshold of a single MU is noisy and by no means deterministic, the firing rate behavior of the MU pool appears to be organized in a hierarchical manner with respect to recruitment threshold. Thus although the activation patterns of MUs in the dominant and nondominant FDI are distinct, our results confirm that within each muscle the MU pool follows the rank-ordered recruitment and firing rate organization described most recently by Erim et al. (1996).

#### *Adaptations in response to preferential use*

The observed contralateral firing rate differences are consistent with reports of slow muscle twitch characteristics in the FDI of the dominant hand (Tanaka et al. 1984; Zijdwind et al. 1990) and support the hypothesis that preferred use of the dominant hand alters the mechanical properties of the FDI muscle such that relatively more force is built up at lower firing rates. Because force output was the controlled variable in our study, firing rates in the dominant FDI apparently did not need to be as high as in the nondominant FDI to produce the same amount of force.

There are three apparent adaptations to repeated use that could potentially augment the force produced by the pool of lower threshold MUs in the dominant hand: 1) greater force output for the low-threshold MU through selective hypertrophy of slow fibers, 2) longer twitch duration times resulting in greater twitch fusion at low firing rates, and 3) greater number of MUs recruited at low force levels. Very little evidence for selective hypertrophy of low-threshold slow-twitch fibers in response to endurance exercise can be found in the literature (see review by Edström and Grimby 1986). Intensive endurance training and repetitive low-frequency stimulation typically promote increased oxidative capacity and reduced mean fiber cross-sectional area of the whole muscle. Hypertrophy of fibers occurs as a result of increased muscle load (i.e., weight training, compensatory overload) and affects all fiber types (Faulkner and White 1990; Gardiner 1991). Thus selective hypertrophy of slow-twitch, low-recruitment threshold MUs does not appear to be a very likely outcome of daily preferential use. Direct and indirect evidence for options 1 and 2 can be found in morphological (Fugl-Meyer et al. 1982) and physiological (De Luca et al. 1986; Tanaka et al. 1984; Zijdwind et al. 1990) studies that reported a higher percentage of type I fibers, slower contraction times, and higher fatigue resistance for muscles of the dominant upper limb. The shift in the histogram toward lower recruitment thresholds observed in the dominant hand in this study directly supports option 3, an increased number of MUs recruited at low force levels. A higher percentage of low-threshold MUs and a higher percentage of slow-twitch fibers are most likely not separate phenomena for the reason that the muscle fibers innervated by a single motoneuron have somewhat similar contractile characteristics, which in addition are matched to the motoneuron properties such as threshold and conduction velocity (Kernell 1992). As previously reported, the latency of the peak in the cross-correlation function between mean firing

rate and force signals is indicative of the electromechanical coupling within a muscle (De Luca et al. 1982b). By revealing longer cross-correlation latencies between firing rates and force in the dominant muscle (Fig. 7), this study presents further evidence of contralateral fiber type disparity in the upper limb.

Induced fiber type disparity was studied in abundance in animal models (Faulkner and White 1990; Kernell 1992; Salmons 1994). In particular, prolonged repetitive activation of muscle, either through electrical stimulation or through exercise training, was observed to increase the percentage of slow-twitch fibers. The extent to which such transformations occur in humans as a result of exercise is not yet well documented (Gardiner 1991; Salmons 1994).

Temporary changes to recruitment threshold and firing rate of individual MUs were reported for different experimental paradigms (Datta and Stephens 1981; De Luca 1989; Garnett and Stephens 1981; Masakado et al. 1991). In these independent studies, the afferent input from skin receptors was either reduced (skin desensitization through topical anesthesia) or increased (percutaneous electrical stimulation), producing a differential effect on low-threshold ( $\leq 20\%$  MVC) and high-threshold ( $\geq 30\%$  MVC) MUs. In both cases, changes in recruitment threshold were accompanied by complementary changes in firing rate, preserving the normal recruitment/firing rate interplay. In the current study, reduced recruitment thresholds in the dominant muscle were accompanied by decreased, not increased, average firing rates, suggesting a more profound adaptation of the MU pool, one not likely mediated by the skin receptors.

It was not surprising to find that the firing rate disparity was more prominent among lower threshold MUs (plots of average firing rate vs. recruitment threshold showed a greater negative slope in the nondominant hand; see Fig. 3) because these MUs most likely adapted to preferred use by reducing the firing rate output for a given excitation level to potentially match the mechanical slowing of the muscle. Another way of looking at these data is to say that the change in the distribution of recruitment thresholds in the dominant hand resulted in a higher number of low-threshold MUs being activated at a given force level when compared with the nondominant side. A higher number of active MUs allowed for lower individual firing rates without compromising total force output. Nevertheless, it is possible that, apart from changes to the recruitment and firing characteristics of the dominant MUs, the drive to the dominant MU pool was also lower. A CNS drive pattern different from that of nondominant side is to be expected because the mechanical characteristics of the muscle are different. Thus for the subjects of this study, MUs in the dominant hand appear to become more effective in generating force at submaximal contraction levels.

#### *Effect of hand preference on regulation of force*

The variability of the abduction force during the attempted constant force task was significantly higher in the nondominant hand (Fig. 6B). An explanation of this phenomenon may be found in the work of Keen et al. (1994), who found that strength training reduced the amount of force variability by 30% in submaximal contractions of the FDI in elderly



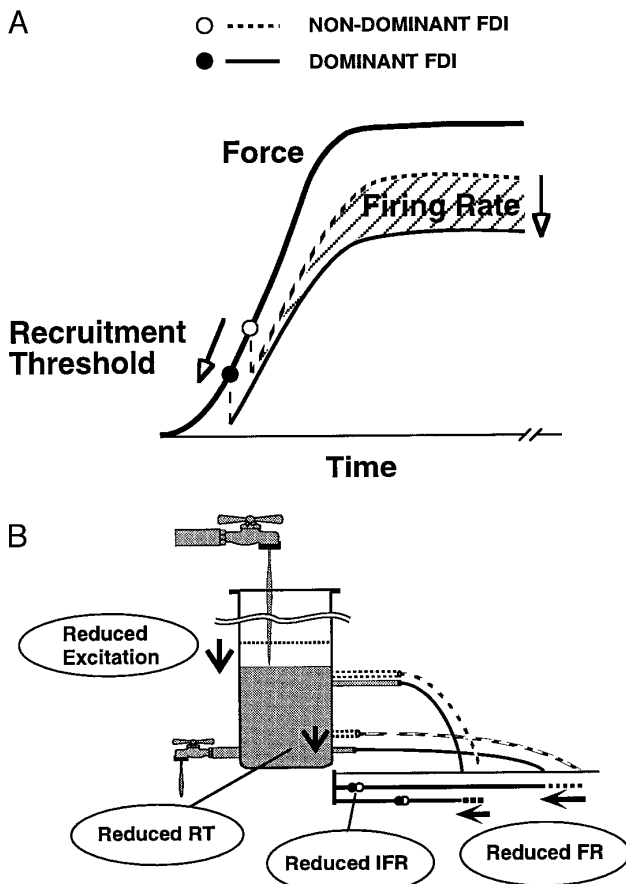


FIG. 8. *A*: schematic representation of differences in MU firing rates and recruitment thresholds (RTs) for contralateral FDI muscle pairs during submaximal voluntary contractions. One MU, representative of the whole pool of MUs, is shown for each the dominant and the nondominant side. Abduction force (bold solid line) was the same for both hands, but the firing rates for MUs of the dominant hand (solid line) were lower than for MUs in the nondominant hand (dashed line), as indicated by the hatched area between the firing rate curves. In addition, the MU recruitment thresholds were lower in the dominant FDI (filled circle) than in the nondominant FDI (open circle). *B*: simple hydraulic model summarizing firing rate and recruitment adaptations in the dominant hand as a result of daily preferential use. Refer to De Luca and Erim (1994) for complete details of the model. Inflow of water from the top spigot into a vat represents the drive to the MU pool, and the outflow through the bottom spigot represents inhibitory inputs. Height of spouts and the distance water travels along the horizontal line symbolize recruitment threshold and firing rate of MUs. For each MU, the length of the horizontal line represents the firing rate, whereas the length of the spout determines the initial firing rate, which is indicated below by a filled circle. Net accumulation of water in the tank corresponds to the common drive. The figure depicts the firing rate behavior of a higher and a lower recruitment threshold MU in the nondominant (dotted lines) and the dominant (solid lines) muscle during a submaximal contraction. In the dominant hand, the RT and initial firing rate of the 2 MUs were reduced when compared with the contralateral side. When performing the same submaximal contraction, the dominant hand operates at a lower excitation level, resulting in lower firing rates in comparison with the nondominant hand. No crossover occurs between firing rates of the dominant and nondominant hand because the drop in net excitation is larger than the decrease in recruitment thresholds. Differences in firing rate and recruitment behavior in contralateral sides are interpreted in terms of an adaptation in the muscle of the dominant hand as a result of daily preferential activity. IFR, initial firing rate; FR, firing rate.

subjects. They attributed this modification to neuronal conditioning caused by practice and not to muscle plasticity, because the greatest improvements occurred on a short time-scale ( $\leq 4$  wk) and during low-force contractions without

a change in the distribution of low-threshold MU forces (estimated by spike-triggered averaging). In support of this argument, our data revealed matching lateral difference in the variability of the IFIs (Fig. 6A). Consequently, it is plausible that the spinal and/or supraspinal asymmetries and not the mechanical properties of the MUs are responsible for the diminished ability of the nondominant muscle to produce a constant force. This speculation is consistent with the results of Yakovlev and Rakic (1966), who found that a greater number of pyramidal tract fibers innervate the dominant hand.

In contrast, Semmler and Nordstrom (1995) reported no contralateral differences in MU discharge variability or force tremor amplitude. Schmied et al. (1994) also found no relation between mean IFI variability and handedness. These partially contradicting results might be attributable to inherent differences in the muscles under investigation or differences in the experimental paradigm, such as contraction level and whether subjects controlled firing rates or force. In particular, experiments that asked subjects to maintain steady MU firings with the use of firing rate feedback may introduce an unusual regularity to the MU firings.

Our result that mean MVC values did not differ between dominant and nondominant hands agrees with the findings of Tanaka et al. (1984), Rutherford and Jones (1988), and Semmler and Nordstrom (1995); the only other studies reported that dealt with this subject to the best of our knowledge. Mean MVC values for the FDI of the dominant and nondominant hand were similar to those found by Tanaka et al. (1984) but  $\sim 20\%$  lower than in the other two studies. This minor discrepancy may be accounted for by differences in the methods used for measuring the force. The lack of an effect of handedness on MVC values, a common result to all the previous studies in the FDI, is not surprising because the effect of everyday usage on maximal contraction strength is expected to be low. Maximal strength is in large part determined by the force output of high-threshold MUs, but these are rarely used in everyday activities and thus should not adapt to preferred use of one hand.

In light of results from other investigations on the fiber type distribution, twitch response, and fatigue characteristics of hand muscle pairs, the effect of handedness is interpreted as an adaptation of the MU pool in the dominant FDI to daily preferential use (exercise) over many years. The adaptation allows for more effective force production at low firing rates, most likely caused by an increased percentage of slow fibers resulting in greater twitch fusion at lower MU firing rates. The observations of higher force and MU discharge variability in the nondominant hand may have been caused in part by any inexperience subjects had using the nondominant muscle for skilled tasks, but the influence of genetic factors on the lateralization of the motor system cannot be ruled out.

Whether the above differences in recruitment and firing behavior of MUs between dominant and nondominant hands indeed represent the result of preferred use will have to be determined by studying, for example, young children whose muscles presumably did not yet adapt to hand preference or, better yet, by testing whether dominant muscle characteristics can be achieved in the nondominant side through chronic, low-intensity exercise.

### Conceptual model for MU modifications in the dominant hand

Figure 8A schematically summarizes our findings related to the MU recruitment threshold and firing rate differences among FDI muscle pairs during submaximal contractions. Although the force output in both muscles had the same magnitude (bold solid line), the recruitment thresholds (circles) and firing rates (solid line) of MUs possessed lower mean values in the dominant hand.

To summarize the observed effects on MU control properties, we make use of a model that was previously described by De Luca and Erim (1994). This "vat model" is helpful in visualizing the differences in MU control strategies among contralateral muscles. Figure 8B shows the model of the MU firing behavior in the dominant muscle (solid lines) operating at the same target force level as the nondominant FDI (dotted lines). The inflow of water into a tank represents the drive to the MU pool, and the outflow through the spouts represents the firing rate response of individual MUs. An outlet valve symbolizes the inhibitory inputs to the MU pool. Thus the water level in the vat represents the net excitation level seen by all the MUs. The height of the spouts and the distance the water travels horizontally are proportional to the recruitment threshold and the firing rate (indicated by horizontal bars) of MUs. For simplicity, only two MUs are shown for each muscle. The MU having the lower recruitment threshold (spout) also has a shorter spout, which correlates with a lower initial firing rate (indicated by a dot on the firing rate bar). Water from the lower spout travels further than from the upper spout, corresponding to the observation that within one muscle lower threshold MUs have a higher average firing rate than higher threshold units. Modifications made to the nondominant hand model correspond to altered MU firing rate and recruitment behavior of the dominant muscle. The height of the spouts, corresponding to the recruitment thresholds, and their lengths, corresponding to the initial firing rates, are decreased for the MUs in the dominant muscle model. The horizontal displacements of water from the spouts, corresponding to the firing rates from both higher and lower threshold MUs, are less in the dominant than in the nondominant hand. This decrease of firing rates is achieved as a result of a diminished net excitation shown as a decreased water level in the vat, assuming the vat size is unchanged. The effect of the reduction in net excitation must be larger than the change in recruitment thresholds because firing rates of corresponding dominant and nondominant MUs do not cross over. Thus the vat model incorporates the observed firing rate discrepancies among contralateral muscle pairs by necessitating different excitation levels of the respective MU pools.

This work was supported by the Rehabilitation Research and Development Service of Veterans Affairs and the Liberty Mutual Insurance Company.

Address for reprint requests: C. J. De Luca, Boston University, Neuro-Muscular Research Center, 44 Cummington St., Boston, MA 02215.

Received 14 January 1998; accepted in final form 28 May 1998.

### REFERENCES

- CLAMANN, H. P. Activity of single motor units during isometric tension. *Neurology* 20: 254–260, 1970.
- DATTA, A. K. AND STEPHENS, J. A. The effect of digital nerve stimulation on the firing of motor units in human first dorsal interosseous muscle. *J. Physiol. (Lond.)* 318: 501–510, 1981.
- DE LUCA, C. J. Control properties of motor units. Evolving concepts. In: *Computer-Aided Electromyography and Expert Systems*, edited by J. E. Desmedt. Amsterdam: Elsevier, 1989, p. 103–109.
- DE LUCA, C. J. Precision decomposition of EMG signals. *Methods Clin. Neurophysiol.* 4: 1–28, 1993.
- DE LUCA, C. J. AND ERIM, Z. Common drive of motor units in regulation of muscle force. *Trends Neurosci.* 17: 299–305, 1994.
- DE LUCA, C. J., LEFEVER, R. S., MCCUE, M. P., AND XENAKIS, A. P. Behavior of human motor units in different muscles during linearly varying contractions. *J. Physiol.* 329: 113–128, 1982a.
- DE LUCA, C. J., LEFEVER, R. S., MCCUE, M. P., AND XENAKIS, A. P. Control scheme governing concurrently active human motor units during voluntary contractions. *J. Physiol.* 329: 129–142, 1982b.
- DE LUCA, C. J., SABBAAH, M. A., AND ROY, S. H. Median frequency of the myoelectric signal. Effects of hand dominance. *Eur. J. Appl. Physiol.* 53: 457–464, 1986.
- EDSTRÖM, L. AND GRIMBY, L. Effect of exercise on the motor unit. *Muscle Nerve* 9: 104–126, 1986.
- ERIM, Z., DE LUCA, C. J., MINEO, K., AND AOKI, T. Rank-ordered regulation of motor units. *Muscle Nerve* 19: 563–573, 1996.
- FAULKNER, J. A. AND WHITE, T. P. Adaptations of skeletal muscle to physical activity. In: *Exercise, Fitness and Health A Consensus of Current Knowledge*, edited by C. Bouchard, R. J. Shepard, T. Stephens, J. R. Sutton, and B. D. McPherson. Champaign, IL: Human Kinetics, 1990, p. 265–279.
- FRIEDLI, W. G., FUHR, P., AND WIGET, W. Detection threshold for percutaneous electrical stimuli: asymmetry with respect to handedness. *J. Neurol. Neurosurg. Psychiatry* 50: 870–876, 1987.
- FUGL-MEYER, A. R., ERIKSSON, A., SJÖSTRÖM, M., AND SÖDERSTRÖM, G. Is muscle structure influenced by genetic or functional factors? *Acta Physiol. Scand.* 114: 227–281, 1982.
- GARDINER, P. F. Effects of exercise training on components of the motor unit. *Can. J. Sport Sci.* 16: 271–288, 1991.
- GARNETT, R. AND STEPHENS, J. A. Changes in the recruitment threshold of motor units in human first dorsal interosseous muscle produced by skin stimulation. *J. Physiol. (Lond.)* 311: 463–473, 1981.
- KAMEN, G., GREENSTEIN-SOLAR, S., AND DE LUCA, C. J. Lateral dominance and motor unit firing behavior. *Brain Res.* 576: 165–167, 1992.
- KEEN, D., YUE, G., AND ENOKA, R. Training related enhancement in the control of motor output in elderly humans. *J. Appl. Physiol.* 77: 2648–2658, 1994.
- KERNELL, D. Organized variability in the neuromuscular system: a survey of task-related adaptations. *Arch. Ital. Biol.* 130: 19–66, 1992.
- KIMURA, J. The H-reflex and other late responses. In: *Electrodiagnosis in Diseases of Nerve and Muscle*, Philadelphia, PA: Davis, 1983, p. 379–398.
- MAMBRITO, B. AND DE LUCA, C. J. A technique for the detection, decomposition and analysis of the EMG signal. *Electroenceph. Clin. Neurophysiol.* 59: 175–188, 1984.
- MASAKADO, Y., KAMEN, G., AND DE LUCA, C. J. Effects of percutaneous stimulation on motor unit firing behavior. *Exp. Brain Res.* 86: 426–432, 1991.
- OLDFIELD, R. C. The assessment and analysis of handedness: the Edinburgh Inventory. *Neuropsychologia* 9: 99–113, 1971.
- RUTHERFORD, O. M. AND JONES, D. A. Contractile properties and fatigability of the human adductor pollicis and first dorsal interosseous: a comparison of the effects of two chronic stimulation patterns. *J. Neurol. Sci.* 85: 319–331, 1988.
- SALMONS, S. Exercise, stimulation and type transformation of skeletal muscle. *Int. J. Sports Med.* 15: 136–141, 1994.
- SATHIAMOORTHY, A. AND SATHIAMOORTHY, S. S. Limb dominance and motor conduction velocity of median and ulnar nerves. *Indian J. Physiol. Pharmacol.* 34: 51–53, 1990.
- SCHMIED, A., VEDEL, J.-P., AND PAGNI, S. Human spinal lateralization assessed from motoneuron synchronization: dependence on handedness and motor unit type. *J. Physiol. (Lond.)* 480: 369–387, 1994.
- SEMMLER, J. G. AND NORDSTROM, M. A. Influence of handedness on motor unit discharge properties and force tremor. *Exp. Brain Res.* 104: 115–125, 1995.
- STASHUK, D. AND DE LUCA, C. J. Update on the decomposition and analysis of EMG signals. In: *Computer-Aided Electromyography and Expert Systems*, edited by J. E. Desmedt. Amsterdam: Elsevier, 1989, 39–47.
- TAN, U. Velocities of motor and sensory nerve conduction are the same

- for right and left arms in right- and left-handed normal subjects. *Percept. Mot. Skills* 60: 625–626, 1985.
- TAN, U. The H-reflex recovery curve from the wrist flexors: lateralization of motoneuronal excitability in relation to handedness in normal subjects. *Int. J. Neurosci.* 48: 271–284, 1989a.
- TAN, U. Lateralization of the Hoffmann reflex from the long flexor thumb muscle in right- and left-handed normal subjects. *Int. J. Neurosci.* 48: 313–315, 1989b.
- TANAKA, M., McDONAGH, M.J.N., AND DAVIES, C.T.M. A comparison of the mechanical properties of the first dorsal interosseous in the dominant and non-dominant hand. *Eur. J. Appl. Physiol.* 53: 17–20, 1984.
- YAKOVLEV, P. I. AND RAKIC, P. Patterns of decussation of bulbar pyramids and distribution of pyramidal tracts on two sides of the spinal cord. *Trans. Am. Neurol. Assoc.* 91: 366–367, 1966.
- ZIJDEWIND, C., BOSCH, W., GOESSENS, L., KANDOU, T.W.A., AND KERNELL, D. Electromyogram and force during stimulated fatigue tests of muscles in dominant and non-dominant hands. *Eur. J. Appl. Physiol.* 60: 127–132, 1990.