Motor unit behavior during submaximal contractions following six weeks of either endurance or strength training

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[1]*Center for Sensory-Motor Interaction, Department of Health Science and Technology, Aalborg University, Aalborg East, Denmark;* [2]*Universidade do Porto, Faculdade de Engenharia, Porto, Portugal and* [3]*Department of Neurorehabilitation Engineering, Bernstein, Center for Computational Neuroscience, Georg-August University of Göttingen, Göttingen, Germany*

Vila-Chã C, Falla D, Farina D. Motor unit behavior during submaximal contractions following six weeks of either endurance or strength training. *J Appl Physiol* 109: 1455–1466, 2010. First published September 9, 2010; doi:10.1152/japplphysiol.01213.2009.—The study investigated changes in motor output and motor unit behavior following 6 wk of either strength or endurance training programs commonly used in conditioning and rehabilitation. Twenty-seven sedentary healthy men (age, 26.1 ± 3.9 yr; mean ± SD) were randomly assigned to strength training (ST; $n = 9$), endurance training (ET; $n = 10$), or a control group (CT; $n = 8$). Maximum voluntary contraction (MVC), time to task failure (isometric contraction at 30% MVC), and rate of force development (RFD) of the quadriceps were measured before (*week 0*), during (*week 3*), and after a training program of 6 wk. In each experimental session, surface and intramuscular EMG signals were recorded from the vastus medialis obliquus and vastus lateralis muscles during isometric knee extension at 10 and 30% MVC. After 6 wk of training, MVC and RFD increased in the ST group (17.5 ± 7.5 and 33.3 ± 15.9%, respectively; $P < 0.05$), whereas time to task failure was prolonged in the ET group (29.7 ± 13.4%; $P < 0.05$). The surface EMG amplitude at 30% MVC force increased with training in both groups, but the training-induced changes in motor unit discharge rates differed between groups. After endurance training, the motor unit discharge rate at 30% MVC decreased from 11.3 ± 1.3 to 10.1 ± 1.1 pulses per second (pps; $P < 0.05$) in the vasti muscles, whereas after strength training it increased from 11.4 ± 1.2 to 12.7 ± 1.3 pps ($P < 0.05$). Finally, motor unit conduction velocity during the contractions at 30% MVC increased for both the ST and ET groups, but only after 6 wk of training ($P < 0.05$). In conclusion, these strength and endurance training programs elicit opposite adjustments in motor unit discharge rates but similar changes in muscle fiber conduction velocity.

motor unit; surface electromyography; motor training

MOTOR PERFORMANCE IS ENHANCED by repeated exposure to exercise training. Depending on the desired goal, exercise paradigms may include strength, sprint, endurance, or skill training. The muscular and neural adaptations induced by each type of exercise approach are highly specific and may vary for different training paradigms. Typically, endurance training involves generalized muscle activation performed over many repetitions (34, 62). Exercises such as running or cycling are classic examples of endurance training and are known to improve the ability to sustain rhythmic movements for longer periods, mainly due to increased maximal oxygen uptake and increased ability of skeletal muscles to generate energy via oxidative metabolism (28). At the other extreme, strength training typically involves exercises for specific muscle groups that are performed over a short duration, e.g., performing few repetitions at high force levels (34, 58, 62).

Distinct anatomical and physiological adaptations in response to conventional strength and endurance training have been documented (for review, see Refs. 21–23, 28). Because these two types of exercise programs represent extremes of physical activity (58), they may also elicit different neural adaptations. Accordingly, the increases in maximal strength and rate of force development achieved with strength training appear to be impaired when endurance and strength training are applied concurrently (27, 49). This effect has been mainly attributed to an opposite influence of the two training regimes on the neural control of muscles (16, 27). For example, Hakkinen et al. (27) showed that muscle activity at the onset of a rapid isometric explosive contraction was impaired by concurrent endurance and strength training even though similar morphological adaptations occurred with respect to strength training only. In addition to muscular adaptations, the effects of strength and endurance training on motor performance reflect supraspinal and spinal adjustments (6, 15), which ultimately influence the neural drive to the muscles, i.e., the behavior of motor units. However, as recently discussed (15), in vivo data on motor unit properties following training are scarce. Only a few studies have investigated motor unit behavior following strength training (31, 51, 56, 61), and the results remain controversial. For example, increased motor unit discharge rates have been observed after explosive (61) and dynamic strength training (31); however, no changes were observed after isometric training (54, 56). Furthermore, the effects of training on the discharge rates assessed during maximal and submaximal contractions show mixed results (31, 54, 56).

Currently there are no available data on changes in motor unit discharge behavior following endurance training. Although there are speculations on changes in motor unit recruitment and discharge rates with endurance training, these conclusions are largely based on reflex studies (37, 42, 52) and animal experiments (8, 9). For example, Pérot et al. (52) reported an increase of the H-reflex after 8 wk of endurance training, indicating a potential increase in motor neuron pool excitability. Accordingly, for the same relative force level, endurance training was shown to increase the proportion of recruited low-threshold motor units (52). However, it is not possible to draw firm conclusions on changes in motor unit behavior based on the H-reflex response (24, 63).

The specificity of adjustments in motor unit behavior with different types of training is poorly understood, mainly due to

a limited number of studies in this field in addition to a lack of studies that have employed the same methodology to compare changes in motor unit behavior following different training paradigms. Therefore, the purpose of this study was to investigate and compare changes in muscle activity and motor unit behavior of synergistic knee extensor muscles following a strength and an endurance training program. It was hypothesized that differences in motor output (maximal strength, rate of force development, and resistance to fatigue) induced by the two training programs would be associated with different adjustments in motor unit discharge rates. In addition, muscle fiber conduction velocity was measured for individual motor units as an indicator of changes in muscle properties following the training programs.

METHODS

Subjects

Thirty healthy men (age, 26.0 $\pm$ 3.8 yr; mean $\pm$ SD) with no history of lower limb disorders participated in the study. None of the subjects were involved in regular strength or endurance training. All subjects gave their informed consent to the procedures of the study. The study was conducted in accordance with the Declaration of Helsinki and approved by the local ethics committee (N-20090032). After the first experimental session (pretraining session), the subjects were randomly assigned to one of three groups: strength training (ST; $n = 10$), endurance training (ET; $n = 10$), and control (CT; no exercise intervention; $n = 10$).

Training Programs

Progressive endurance or strength training was performed over 6 wk. Subjects attended three training sessions per week. All training sessions were supervised by a study investigator (C. Vila-Chã).

Endurance training. Endurance training was performed on a bicycle ergometer, and the exercise intensity was prescribed based on the percentage of the heart rate reserve (HRR). The lower and upper limits of HRR [target heart rates (THR)] were calculated with the Karvonen method [(maximal heart rate − resting heart rate) × %intensity + resting heart rate] (32). The use of %HRR has been recommended for prescribing exercise intensity in cycling activities (39), since it provides accurate target workloads, especially for individuals with a low fitness level (60).

To maintain the exercise intensity within the required THR, each subject used a pulse meter during the training sessions. From *week 1* to *week 2*, the THR was set between 50 and 60% of the HRR, and each training session lasted 20–30 min. On *weeks 3* and *4*, the duration of the sessions was 30–40 min and THR was 60–70% of the HRR. For the last 2 wk, the time per session increased to 40–50 min and the THR was maintained at 65–75% of the HRR.

Strength training. Each training session involved three bilateral leg exercises (leg press, leg extension, and leg curl) and four additional exercises for the other main muscle groups of the body (lateral pull down, bench press, exercise for the trunk flexors and for trunk extensors). For the leg exercises, the subjects trained with loads of 60–70% of the 1-repetition maximum (1RM) and performed 3 sets of 13–15 repetitions during *weeks 1* and *2*. During *weeks 3* and *4*, the load intensity was increased to 70–75% of the 1RM, and subjects performed 3–4 sets of 10–12 repetitions. Finally, during *weeks 5* and *6*, the load intensity varied in the range 70–85% of the 1RM, and the participants performed 3–4 sets of 8–12 repetitions. The additional exercises for the upper limbs and trunk were performed over 2–3 sets of 13–18 repetitions at an intensity corresponding to 60–70% of the 1RM. The training load

was continuously monitored allowing the necessary adjustments to keep the intensity at the required level.

Procedure

The subjects attended three laboratory sessions, immediately before (*session 1*, *week 0*), 3 wk after the beginning of training (*session 2*, *week 3*), and after completion of the 6-wk training period (*session 3*, *week 6*). To avoid an effect of fatigue on the results, *sessions 2* and *3* were performed at least 48 h after a training session.

In each experimental session, the subject was comfortably seated on an Isokinetic dynamometer (KinCom Dynamometer, Chattanooga, TN) with their trunk reclined to 15° in an adjustable chair and their hip and distal thigh firmly strapped to the chair. The rotational axis of the dynamometer was aligned with the right lateral femoral epicondyle, and the lower leg was secured to the dynamometer lever arm above the lateral malleolus. Maximal and submaximal isometric knee extensions were exerted with the knee flexed to 90°.

After placement of the surface electromyography (EMG) electrodes (as described below), the subject performed two maximal voluntary contractions (MVC) of knee extension over a period of 5 s. These trials were separated by 2 min of rest. The highest MVC value was used as a reference for the definition of the submaximal force levels. In each of the three experimental sessions, the submaximal forces were relative to the MVC measured during the same session. After the maximal contractions, the subjects performed two explosive isometric contractions, and they were encouraged to exert their maximal force as fast as possible.

Intramuscular EMG electrodes were then inserted into the vastus lateralis (VL) and vastus medialis obliquus (VMO), as described below. The subjects performed two isometric knee extensions at 10 and 30% MVC (random order) for 10 s, with 2 min of rest in between. Subjects were provided with online visual feedback of the force exerted, which was displayed on an oscilloscope. Subjects then performed a further isometric knee extension contraction at 30% MVC, maintaining the force for as long as possible. Time to task failure was defined as a drop in force >5% of the target force level for more than 5 s after strong verbal encouragement to the subject to maintain the target force. During the submaximal contractions, knee extension force and intramuscular and surface EMG of the VMO and VL were recorded concurrently (Fig. 1).

EMG Recordings

Surface EMG signals were acquired from the VL, VMO, and biceps femoris (BF) muscles during the maximal and submaximal isometric contractions. Signals from the VL and VMO were detected with adhesive linear arrays of eight electrodes (5 × 1 mm in size, 5-mm interelectrode; SPES Medica, Salerno, Italy). The arrays were located between the innervation zone and the distal tendon, along the direction of the muscle fibers. The tendon regions and innervation zones were identified during preliminary brief knee extensions (45). Signals from the BF were recorded with Ag-AgCl electrodes (Ambu Neuroline; conductive area 28 mm^2), located as recommended by Hermens et al. (29). Before placement of the electrodes, the skin was shaved, lightly abraded, and cleansed with water. A ground electrode was placed around the right ankle. Surface EMG signals were amplified as bipolar derivations (EMG amplifier; LISiN-OT Bioelettronica, Torino, Italy), band-pass filtered (−3 dB bandwidth, 10–500 Hz), sampled at 2,048 samples/s, and converted to digital data by a 12-bit analog-to-digital (A/D) converter board.

Intramuscular EMG signals were recorded from the VMO and VL with two pairs of wire electrodes (50-μm diameter) made of Teflon-coated stainless steel (A-M Systems, Carls, WA). Electrodes were inserted with a 23-G needle 10–20 mm proximal to the surface electrodes. The wires were uninsulated for ~1 mm at the tip to detect intramuscular EMG signals. The angle of insertion of the needle was ~45°, and the depth was a few millimeters below the muscle fascia.
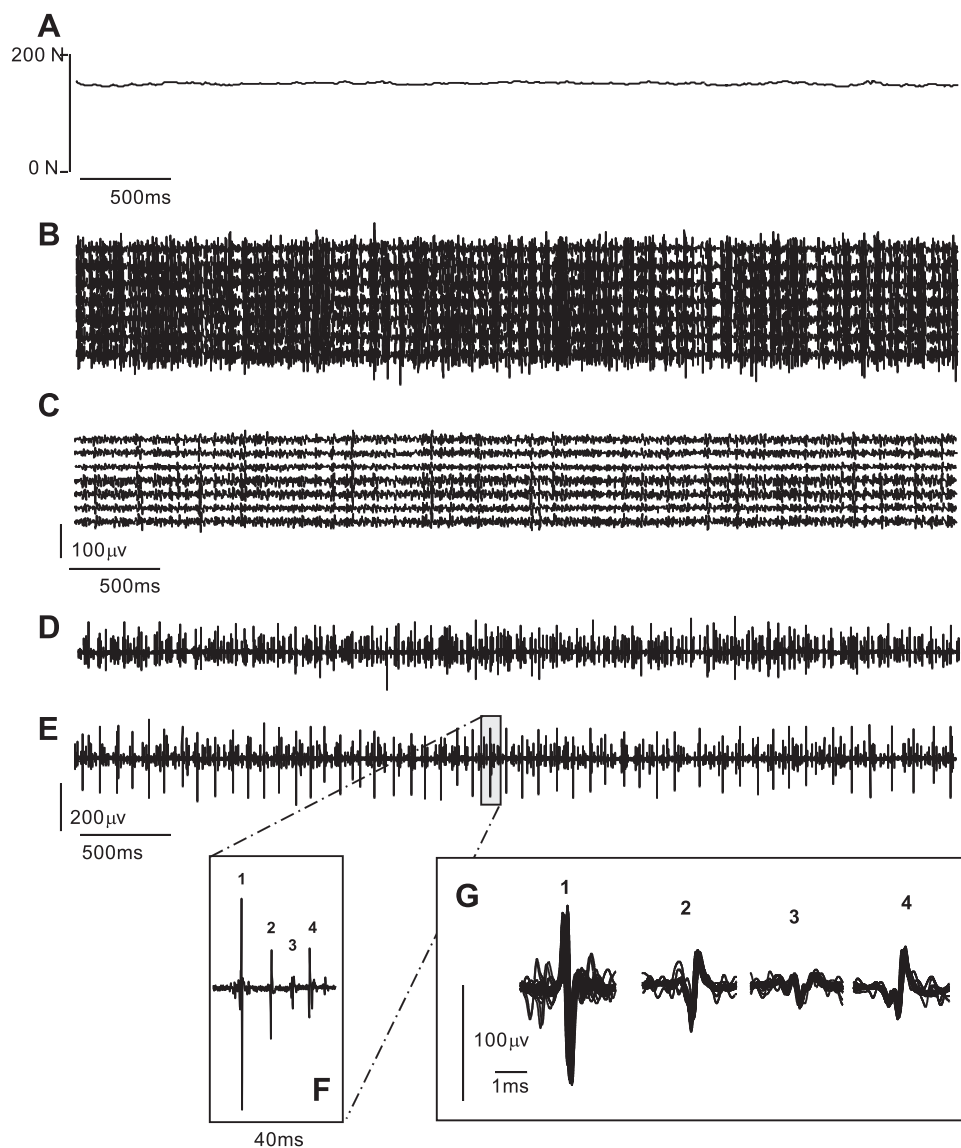
Fig. 1. Representative recordings obtained during an isometric knee extension contraction performed at 30% of the maximum voluntary force. *A*: force exerted by the knee extensors. *B*: surface electromyography (EMG) signals from the vastus medialis obliquus (VMO). *C*: surface EMG signals from the vastus lateralis (VL). *D*: intramuscular EMG signal from the VL. *E*: intramuscular EMG signal from the VMO. *F*: 40-ms interval of intramuscular EMG signal from the VMO. *G*: superimposed action potentials (*1–4*) generated by the target motor units observed in the time interval illustrated in *F*.

The needles were removed after insertion, and the wire electrodes were left inside the muscle. Intramuscular EMG signals were amplified as bipolar derivations (Counterpoint EMG; DANTEC Medical, Skovlunde, Denmark), band-pass filtered (500 Hz–4 kHz), sampled at 10,000 Hz, and stored after 12-bit A/D conversion.

Signal Analysis

During the submaximal contractions of 10-s duration, the average rectified value (ARV) was computed from the surface EMG in intervals of 1 s. These values were averaged over the entire duration of the contraction and over all channels of the electrode array. During the explosive contractions, ARV was calculated in two intervals of 50-ms duration and averaged over all channels of the electrode array. The first interval started 70 ms before the onset of force (2, 13). The onset for force was defined as the time instant when force exceeded 8.5 N. The second interval was centered at the time instant of the maximal slope in force (Fig. 2). Rate of force development (RFD) was calculated from the explosive contractions as the maximum slope of the force-time curve (Δforce/Δtime).

The intramuscular EMG signals recorded during the 10-s submaximal contractions were decomposed with a decomposition algorithm (47). The software displays a segment of the EMG signal, the templates of the action potentials of the identified motor units, the discharge patterns, and a close-up of the signal for resolving missed discharges and superimpositions. Accuracy of the automatic decomposition was achieved by inspection of the identified discharge patterns. Full, regular patterns provided confidence that the decomposition was correct, whereas gaps, extra discharges, or uneven intervals provided an indication of possible decomposition errors. To assist in identifying missed discharges, the program displays bars in the signal panel that indicate the expected discharge times of each motor unit. The signal portion can then be viewed in the close-up panel, which displays the signal at an expanded scale and allows matching motor unit templates to be selected. The close-up panel also displays superimpositions at an expanded scale, which allows verification of the result or allows different sets of templates to be selected and adjusted to find the correct fit. Commands are also available for undoing identifications and deleting or merging templates. Unusually short (<20 ms) or long (>200 ms) interspike intervals (ISIs) were manually reanalyzed and corrected when necessary.

The mean discharge rate [pulses per second (pps)] and ISI variability (SD of ISI divided by mean ISI, %) were computed from the motor unit spike trains. For the motor units that could be
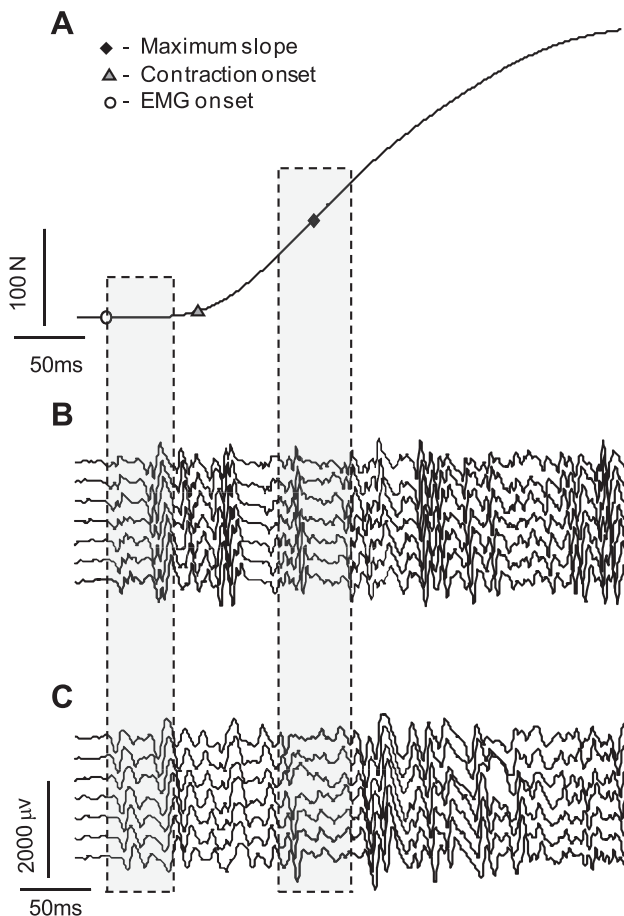
Fig. 2. Representative recordings obtained during the explosive isometric knee extension contraction. *A*: force exerted by the knee extensors. *B*: surface EMG signals recorded from the VMO. *C*: surface EMG signals recorded from the VL. Surface EMG signals were analyzed in 2 intervals of 50 ms (shaded boxes). The first interval started 70 ms before the onset of force (open circle), and the second interval was centered at the time instant of the maximal slope in force (solid diamond). The onset of force was defined as the time instant when force exceeded 8.5 N (shaded triangle).

identified during both the contraction at 10 and 30% MVC in the same session (by visual inspection of superimposed action potential templates), the increment in mean discharge rate between 10 and 30% MVC (ΔMDR) was also computed.

Electrophysiological membrane properties of the muscle fibers of individual motor units were investigated by estimating motor unit conduction velocity (MUCV). This was achieved by extracting the averaged multichannel surface EMG signals with the intramuscular action potentials as triggers (18). The MUCV was estimated from the averaged surface EMG with a multichannel technique previously described (18). MUCV values were obtained from the 10-s isometric knee extensions at 10 and 30% MVC.

Statistical Analysis

The effects of the two training programs on strength (MVC), time to task failure, RFD, and ARV of the BF were assessed with two-way repeated-measures ANOVA with factors group (control, endurance, and strength) and time (*weeks 0, 3*, and *6*). In addition, changes in motor unit discharge rates, ISI variability, ARV of the VMO and VL, and MUCV were evaluated with three-way repeated-measures ANOVA with factors group, time, and muscle. Pairwise comparisons were performed with the Student-Newman-Keuls post hoc test when ANOVA was significant. The significance level was set to $P < 0.05$. Results are reported as means ± SD in the text and means ± SE in Figs. 3–7 and 9.

RESULTS

The three groups initially consisted of 10 subjects each; however, 1 subject from the ST group and 2 subjects from the CT group did not complete the final experimental session and were excluded from the analysis. Thus the results are presented for 9 subjects in the ST group (age, 25.4 ± 4.2 yr; height, 183.4 ± 6.9 cm; weight, 80.3 ± 16.3 kg), 10 subjects in the ET group (age, 26.1 ± 2.8 yr; height, 180.6 ± 6.2 cm; weight, 78.3 ± 14.1 kg), and 8 subjects in the CT group (age, 27.0 ± 5.0 yr; height, 175.3 ± 3.4 cm; weight, 78.0 ± 13.0 kg). No differences were observed between groups for age, height, and weight. Furthermore, no differences were observed between the groups for any of the motor output or electrophysiological parameters assessed in the first experimental session (before training). Although not statistically significant, the ST group showed a trend toward a relatively longer time to task failure compared with both the ET and CT groups (Fig. 3). This was mainly attributed to the values for time to task failure from two subjects, which was substantially above the average of the group at baseline (243.2 and 316.7 s).
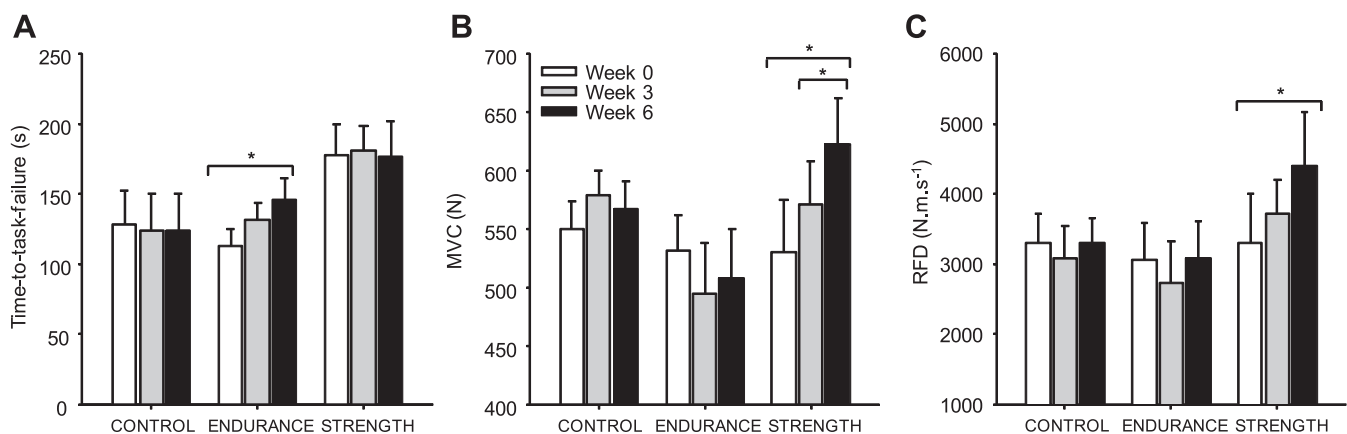

Fig. 3. Values are means ± SE of changes in motor performance across the 6-wk training intervention. *A*: time to task failure assessed during isometric contractions at 30% maximum voluntary contraction (MVC). *B*: MVC of the knee extensors. *C*: contractible rate of force development (RFD). *$P < 0.05$.
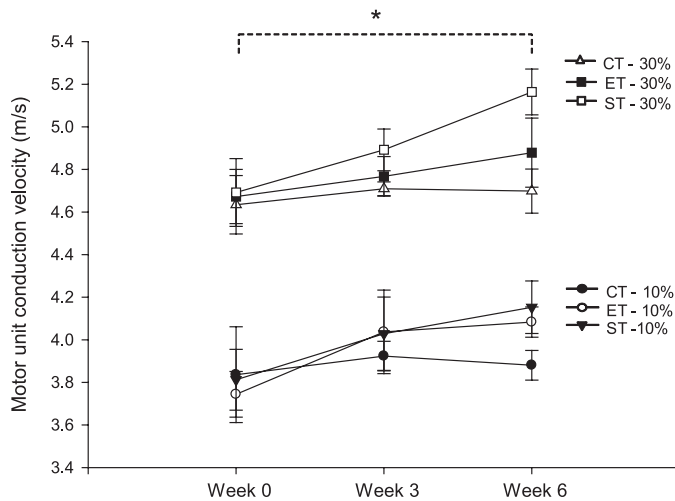
Fig. 4. Values are means ± SE of motor unit conduction velocity (MUCV) for the vasti muscles (average of the VMO and VL) during isometric knee extensions at 10 and 30% MVC for the control (CT), endurance training (ET), and strength training (ST) groups. *P < 0.05.

Motor Output

As expected, endurance and strength training induced specific changes in motor performance over the training period (Fig. 3). Six weeks of endurance training increased the time to task failure by 29.7 ± 13.4% (Fig. 3A) but did not change MVC or maximal RFD (Fig. 3, B and C). In contrast, 6 wk of strength training induced an increase in the MVC force by 17.5 ± 7.5% (Fig. 3B) and in maximal RFD by 33.3 ± 15.9% (Fig. 3C) but did not influence time to task failure (Fig. 3A). None of the motor output parameters changed in the CT group (Fig. 3). Although not statistically significant, both training groups showed changes in MVC after only 3 wk of training. The trend for a decrease in MVC for the endurance group was mainly due to two subjects. These subjects showed a decrease of the MVC

that was much greater (30.0 ± 0.1%) than that for the rest of the group (1.6 ± 10.6%).

Conduction Velocity

Figure 4 shows the MUCV for the VL and VMO (average over both vasti) during the submaximal contractions at 10 and 30% MVC for each experimental session. In the first 3 wk, no statistically alterations of the MUCV were observed ($P = 0.25$). For the contractions at 30% MVC, MUCV increased from baseline to 6 wk posttraining for both training groups ($P < 0.05$; Fig. 4) without differences between the two training groups ($P > 0.11$). Despite the trend for increased MUCV over time for the contractions at 10% MVC, no statistical differences were observed at that contraction level (main effect for time; $P = 0.08$).

Surface EMG

Figure 5 shows the EMG amplitude for the VMO and VL during maximal (MVC) and submaximal isometric knee extension contractions for each experimental session. In the two training groups, the ARV of VMO and VL showed similar changes over the training period (interaction: time × muscle; $P > 0.42$ for all isometric contractions). Furthermore, the activity of the BF muscle did not differ across sessions in any of the groups (interaction: time × group; $P > 0.55$ for all isometric contractions).

For the contraction at 30% MVC, both training groups displayed increased values of VMO and VL ARV after 3 wk of training (Fig. 5, B and C). The ARV increased by 101.8 ± 52.4% (average of both vasti) for the ET group (Fig. 5B) and by 92.6 ± 54.6% for the ST group (Fig. 5C). In the second half of the training program (from *week 3* to *week 6*), the ARV declined in both training groups (average over group and muscles, 45.9 ± 35.0%); however, the changes were only significant for the VMO muscle (Fig. 5, B and C). Despite this

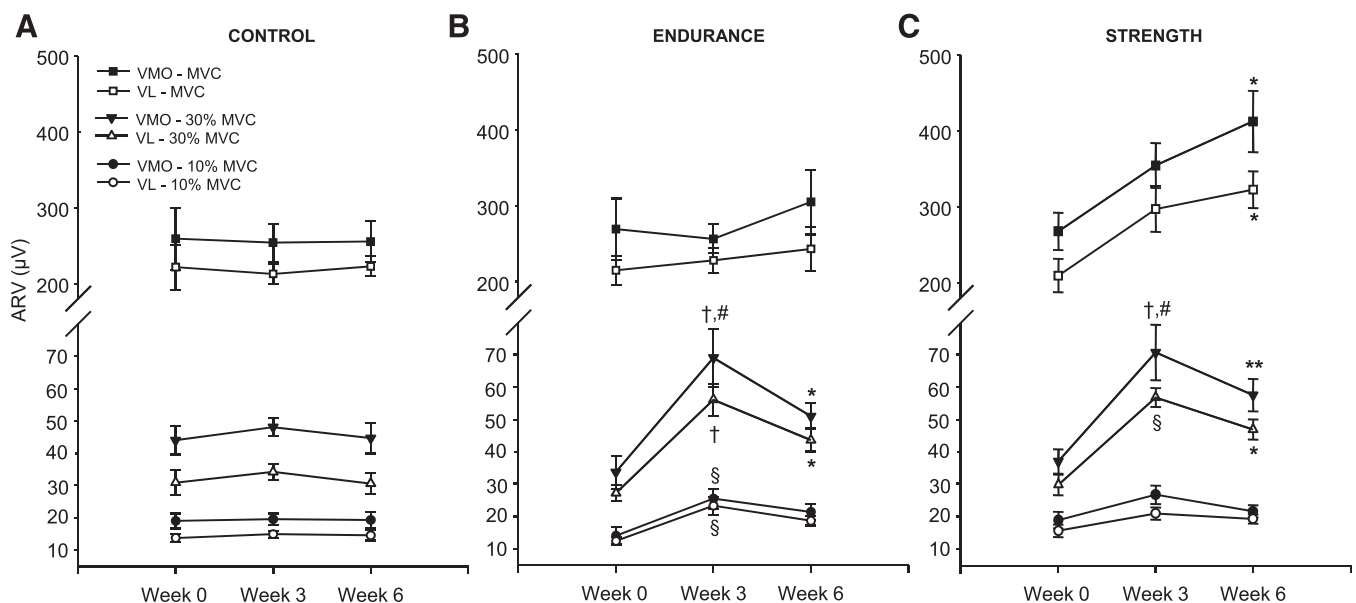Fig. 5. Values are means ± SE for the average rectified value (ARV) of the VMO and VL obtained during maximal (MVC) and submaximal (10 and 30% MVC) isometric knee extension contractions across each experimental session for the CT (A), ET (B), and ST (C) groups. §P < 0.01; †P < 0.0001 from *week 0* to *week 3*. #P < 0.01 from *week 3* to *week 6*. *P < 0.05; **P < 0.001 from *week 0* to *week 6*.
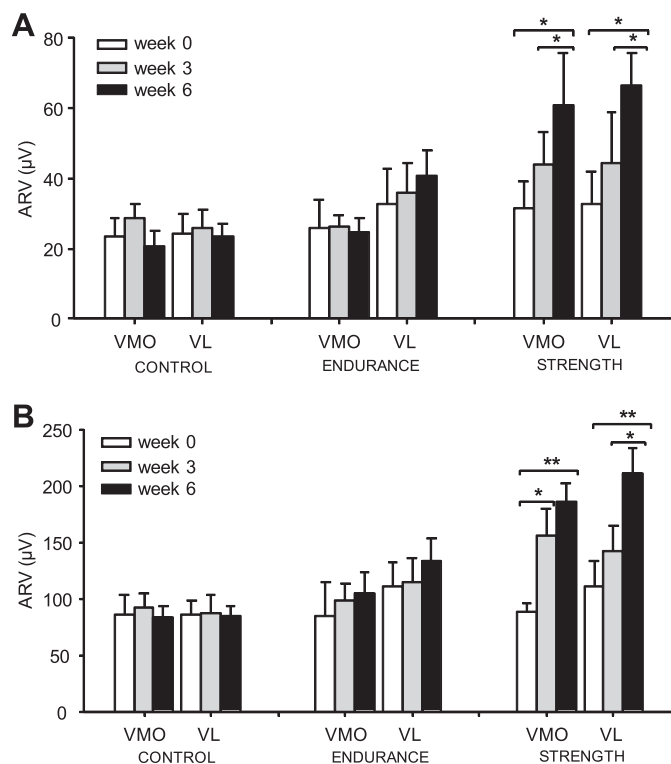
Fig. 6. Values are means ± SE of the EMG ARV for the VMO and VL obtained during the isometric explosive contractions of the knee extensors at *weeks 0*, *3*, and *6* for all groups. *A*: ARV calculated in the time interval from 0 to 50 ms relative to the onset of the EMG. *B*: ARV assessed during a time interval of 50 ms centered at the time instant of the maximum slope. *$P < 0.05$; **$P < 0.001$.

reduction, ARV remained 47–62% higher at *week 6* compared with baseline (significantly different between *week 0* and *week 6* for all muscles in both groups; Fig. 5). A similar pattern was observed for the isometric contractions at 10% MVC, especially for the ET group (Fig. 5*B*). No significant changes in EMG ARV were observed for the CT group for any of the submaximal contractions (Fig. 5*A*).

In contrast to the submaximal contractions, only the ST group showed a significant change in ARV during the maximal contractions (Fig. 5*C*). After 6 wk of strength training, the ARV during MVC increased by 60.7 ± 36.7 and 55.4 ± 30.9% for the VMO and VL, respectively (Fig. 5*C*).

The ARV for the VMO and VL in the early phase of the explosive contractions (0–50 ms) increased progressively over

the 6-wk training period for the ST group (Fig. 6*A*). By the end of the strength training program, the ARV had increased by 167.1 ± 99.8% for the VMO and by 107.2 ± 75.3% for the VL (Fig. 6*A*). The ARV also increased in the second time interval analyzed (50 ms centered on maximum slope) (Fig. 6*B*). Contrary to the ST group, the ET and CT groups did not show any significant change in EMG ARV during the explosive contractions (Fig. 6, *A* and *B*).

Motor Unit Behavior

Discharge rate and ISI variability were obtained from a total of 1,398 motor units during the 10-s isometric contractions at 10 and 30% MVC (Table 1). The number of motor units recorded per subject in each experimental session ranged between 1 and 10 at each force level and for each muscle (average: 4 motor units in each condition).

Figure 7 illustrates the mean motor unit discharge rate for the VMO and VL during the submaximal contractions at 10 and 30% MVC. As observed for the surface EMG ARV, in each group, no differences in the mean motor unit discharge rate were observed between the VMO and VL in each experimental session (interaction: time × muscle; $P > 0.72$ for both contractions).

For the contractions at 10% MVC, the average motor unit discharge rate was not influenced by training, except for the VMO in the ST group (Fig. 7*C*). However, at 30% MVC force, significant changes in motor unit discharge rate were observed at the end of the first half of the training program, in both groups (Fig. 7, *B* and *C*). From *week 0* to *week 3*, mean motor unit discharge rate of the vasti declined by 8.3 ± 4.9% in the ET group (average over VMO and VL; both $P < 0.05$), whereas an increase of 8.4 ± 5.2% was observed in the ST group (for VMO $P < 0.05$; changes did not reach significance for VL, $P = 0.12$). During this period, the small changes in absolute loads applied during the contractions at 30% MVC did not correlate with the changes in discharge rates observed in both training groups ($0.11 < P < 0.79$, for both training programs and muscles). In the following 3 wk (between *weeks 3* and *6*), smaller and nonsignificant changes of the average motor unit discharge rate were observed for both training groups (Fig. 7, *B* and *C*). Over the total training time of 6 wk, the average motor unit discharge rate decreased by 10.9 ± 6.2% (VMO) and 10.6 ± 5.6% (VL) in the ET group and increased by 10.7 ± 4.9% (VMO) and 12.8 ± 4.7% (VL) in the ST group (Fig. 7, *B* and *C*). The ISI variability did not change significantly with training, with the exception of a moderate decrease in the VMO muscle of the ST group (Table 1).

Table 1. *Interspike interval variability for motor units identified for each group, muscle, load, and session*

Group	Load/Muscle, %	Week 0		Week 3		Week 6	
		VMO	VL	VMO	VL	VMO	VL
Control	10	13.5 ± 4.6 (27)	12.8 ± 4.4 (27)	10.4 ± 1.4 (26)	11.5 ± 3.5 (26)	11.9 ± 0.9 (32)	12.6 ± 4.3 (25)
	30	12.9 ± 3.8 (38)	12.4 ± 3.2 (35)	11.8 ± 1.2 (39)	10.5 ± 1.2 (38)	12.9 ± 2.2 (36)	11.8 ± 0.8 (32)
Endurance	10	13.4 ± 2.6 (39)	12.0 ± 3.8 (38)	12.1 ± 3.6 (49)	11.2 ± 3.4 (40)	12.0 ± 4.6 (40)	10.7 ± 4.6 (32)
	30	11.6 ± 2.8 (41)	11.0 ± 2.8 (40)	11.5 ± 1.3 (52)	10.1 ± 1.2 (48)	12.3 ± 3.6 (50)	11.3 ± 2.6 (46)
Strength	10	16.5 ± 4.4 (32)	13.4 ± 3.4 (33)	12.5 ± 2.1* (33)	11.4 ± 3.8 (41)	10.8 ± 1.7† (45)	10.5 ± 2.7 (41)
	30	15.7 ± 2.9 (40)	12.9 ± 3.3 (49)	14.5 ± 3.6 (39)	12.6 ± 2.6 (50)	12.2 ± 3.1‡ (43)	12.5 ± 2.8 (45)

Values are interspike interval (ISI) variability for the motor units identified for each group, muscle [vastus medialis obliquus (VMO) and vastus lateralis (VL)], load (10% and 30% maximum voluntary contraction), and session (*weeks 0*, *3*, and *6*). *$P < 0.05$, *week 0* compared with *week 3*. †$P < 0.01$, *week 0* compared with *week 6*. ‡$P < 0.05$, *week 0* compared with *week 6*.
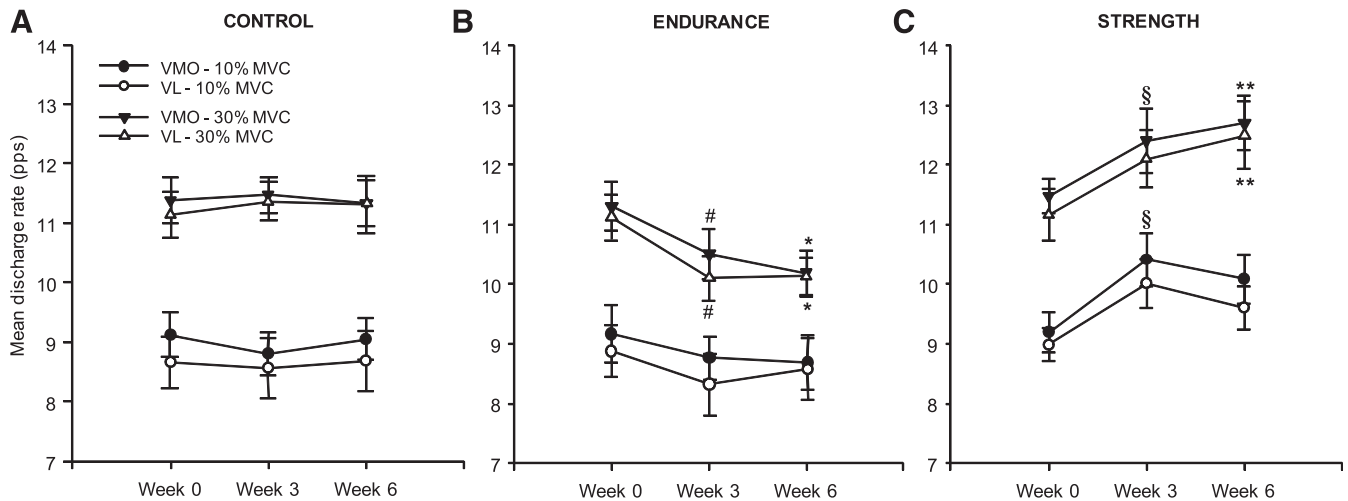
Fig. 7. Values are means ± SE of motor unit discharge rate for the VMO and VL obtained during submaximal isometric contractions of the knee extensors across experimental sessions for the CT (*A*), ET (*B*), and ST (*C*) groups. Significant changes were only observed at 30% MVC. #$P < 0.05$; §$P < 0.01$ from *week 0* to *week 3*. *$P < 0.05$ from *week 0* to *week 6*. from week 0 to week 3. **$P < 0.01$ from *week 0* to *week 6*.

A subset of 242 motor units were identified during contractions at both 10 and 30% MVC within the same experimental session. For each experimental session and muscle, the number of motor units identified at both force levels ranged between 9 and 22. At least one motor unit was identified at both contraction forces for each subject and experimental session.

Figure 8 shows motor unit data recorded from the VMO during the contractions at 10 and 30% MVC, both pre- and posttraining, from a representative subject of each group. In

this example, the difference in rate between the lower and the higher force (ΔMDR) decreased following endurance training (Fig. 8*B*) and increased following strength training (Fig. 8*C*). Accordingly, the group data showed that 6 wk of endurance training decreased the ΔMDR of the VMO by 1.12 ± 0.8 pps (Fig. 9), whereas strength training evoked an increment of 1.28 ± 0.7 pps in the same muscle (Fig. 9). For the VL muscle, ΔMDR increased by 1.60 ± 0.8 pps in the ST group and decreased (although nonsignificantly) by 0.7 ± 0.6 pps in the
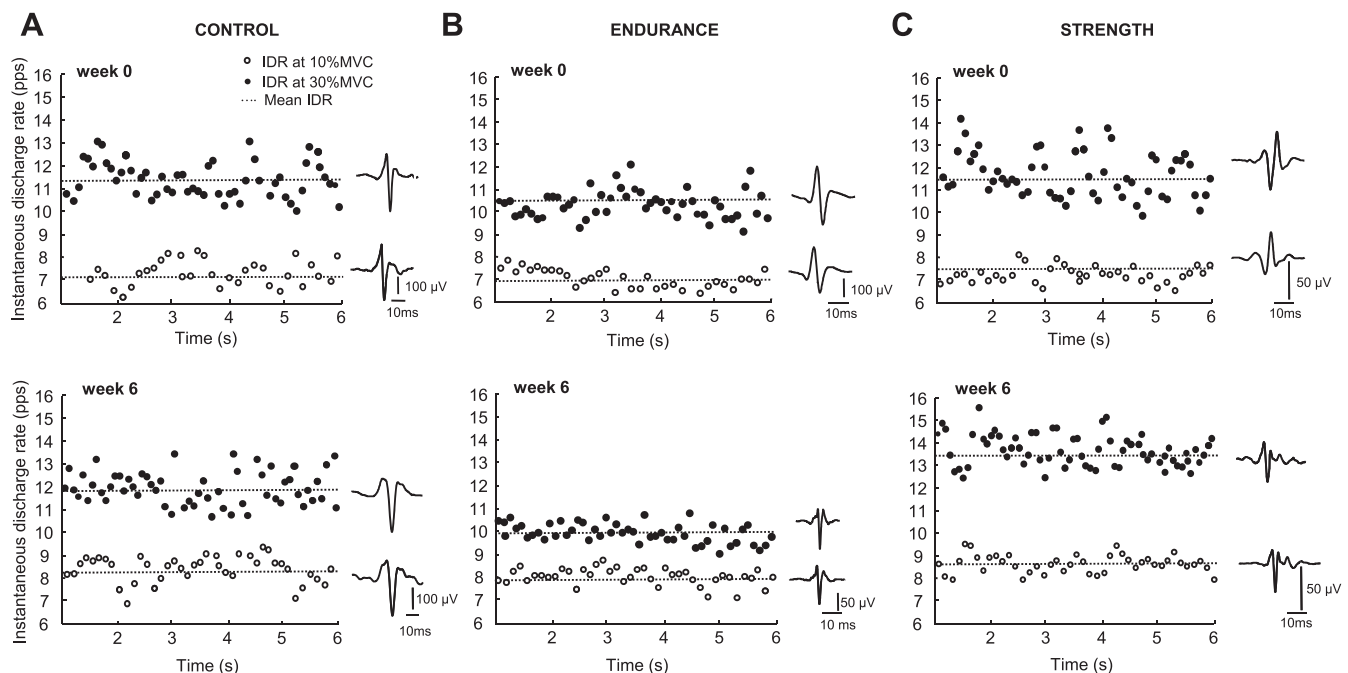

Fig. 8. Instantaneous discharge rate of motor units identified for the VMO muscle during isometric contractions at both 10 and 30% MVC in the experimental session before (*week 0*) and after training (*week 6*) for representative subjects in the CT (*A*), ET (*B*), and ST (*C*) groups. Motor unit action potential templates are provided at *right* of each graph confirming that within the same experimental session (*week 0* or *week 6*), the action potentials are presumably generated by the same motor unit monitored for both the 10 and 30% MVC contractions. In the pretraining session, the interspike interval (ISI) variability, quantified as coefficient of variation of the ISI, for the motor units shown for the CT, ET, and ST groups was 21.9, 9.6, and 16.5% at 10% MCV and 17.1, 9.3, and 12.4% at 30% MVC, respectively. In the posttraining session and for the same groups, the coefficient of variation of the ISI was 10.1, 6.1, and 8.9% at 10% MVC and 9.8, 5.2, and 8.3% at 30% MVC, respectively.
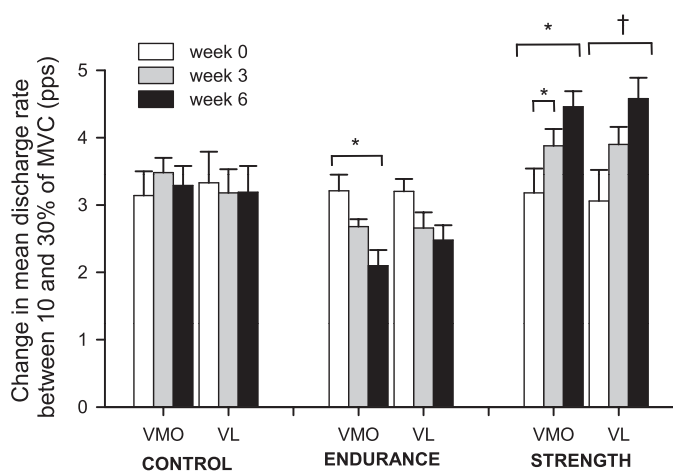
Fig. 9. Values are means ± SE of the change in mean discharge rate for motor units detected at both 10 and 30% MVC (ΔMDR) for the VMO and VL, in all groups. Data are presented only for motor units that could be identified during both the contraction at 10 and 30% MVC in the same session (by visual inspection of superimposed action potential templates). $*P < 0.05$; $†P < 0.001$.

ET group (Fig. 9). No changes were observed over time for the CT group (Figs. 8A and 9A).

DISCUSSION

This study shows distinct adjustments in motor unit discharge rates and similar changes in MUCV for the knee extensors following strength and endurance training.

Training Programs

Conventional endurance and strength training programs were used in this study because they represent common training programs applied in both conditioning and rehabilitation fields. Typically, endurance training implies alternated rhythmic extension and flexion of the limbs, such as running or cycling, which are performed for long periods at low force levels (27, 58). On the other hand, common strength training programs involve rhythmic extension and flexion of either one or both limbs, performed at high force levels for short periods of time (27, 58). Given these differences between strength and endurance training, the changes in motor performance are also expected to be divergent (27). Manipulation of specific training stimulus variables, such as intensity and time of exposure, evokes multiple physiological and neurological adaptations, contributing to motor performance enhancement. Furthermore, the magnitude of these alterations is strongly dependent on the progressive increment of training variables. In the present study, both training programs were designed to introduce progressive increments in volume and intensity to allow progressive adaptation, avoiding the risk of overtraining. Moreover, a systematic increase of demands placed on the body is necessary for progressive improvement (36). This model of training may have contributed to differences between our results and those of previous studies on motor unit adaptations to strength training (31, 54, 56). Another important consideration is the type of movement pattern used in the different studies. Previous studies on motor unit adaptations to training involved only unilateral and single-joint exercises (31, 54, 56),

whereas in the present study, bilateral and multi-joint exercises were selected. Although both training programs in the present study involved rhythmic flexion and extension of both lower limbs, in the strength training program the movement was performed simultaneously with both legs, whereas in the endurance training the task involved alternated leg movements. It cannot be excluded that this difference in the tasks had an effect on the different adaptations (see also *Limitations*).

Motor Output

Six weeks of either strength or endurance training induced significant changes in motor performance. In the ET group, resistance to fatigue was enhanced, but maximal force and RFD remained unchanged. In contrast, the ST group experienced increases in MVC and RFD and no change in the resistance to fatigue. These distinct effects on motor output following strength and endurance training are in agreement with previous results (27, 46) and demonstrate the efficacy of the applied training programs.

Maximal Contractions and Surface EMG Amplitude

The EMG amplitude of the VMO and VL muscles measured during maximal and explosive knee extension was affected by strength but not by endurance training (Figs. 5 and 6A). Six weeks of strength training induced marked increments in the EMG amplitude of the VMO and VL muscles that were accompanied by increments in MVC and maximal RFD. Furthermore, the ARV of the VMO and VL increased at the onset of the explosive contractions for the ST group (Fig. 6A). Since gains in force have been observed in the early phase of strength training in the absence of morphological changes of the muscle (23, 57), it has been suggested that neural factors, such as increased agonist muscle activation (3, 48, 57) and decreased antagonist muscle activation (11), are the main determinants of the increase in force. However, these effects have not been demonstrated consistently for either the agonist (30, 56) or antagonist (4, 27) muscles.

In the present study, the gains in force output were accompanied by marked increments in the EMG amplitude of the agonist muscles (VMO and VL) without changes of the antagonist muscle (BF). The changes observed in the surface EMG amplitude may reflect both neural (e.g., motor unit behavior) and muscular (e.g., increased fiber CSA, sarcolemmal excitability) adaptations. Some studies have reported early changes (i.e., after 5–14 wk) in the muscle architecture, such as increased fiber CSA and pennation angle (10, 35, 59) in response to high-intensity strength training. However, in the current study, high-intensity loads were only used in the last 2 wk of training; therefore, significant alterations of the muscle architecture were not expected. Nonetheless, changes in the conduction velocity of motor unit action potentials (MUCV) were observed during submaximal contractions at 30% MVC after 6 wk of training. Therefore, both training programs had an influence on the muscle fiber electrophysiological properties, which indicates that some peripheral adaptations occurred in response to training. The changes in MUCV were in the same direction for the two training programs, which may be explained by similar changes at the membrane level. For example, MUCV depends on the Na^+-K^+ pump capacity (12, 19),

and both strength and endurance training upregulate the Na^+-K^+ pump capacity in the skeletal muscle (12, 41).

Although muscle fiber conduction velocity has been shown to be associated with fiber diameter and correlated to the peak of the fiber twitch force (7), changes in MUCV do not necessary imply changes in the contractile properties (see e.g., Ref. 17); therefore, it is not possible to infer changes in contractility from the current data (see also *Limitations*).

Submaximal Contractions and Motor Unit Behavior

After training, the ET and ST groups showed similar changes in surface EMG amplitude (Fig. 5, *B* and *C*) but opposite adjustments in motor unit behavior (Fig. 7, *B* and *C*). After 6 wk of training, the average motor unit discharge rate decreased in the ET group (Fig. 7*B*) and increased in the ST group (Fig. 7*C*). The same trends were also observed for the increment in discharge rate from 10 to 30% MVC following training (Fig. 9). These observations suggest that the motor training programs used in this study evoked specific adjustments in the behavior of motor units. Furthermore, these changes were observed after only 3 wk of training for both training approaches. The potential mechanisms involved in these early and opposite adaptations is discussed below for each training program.

Endurance training. This is the first study that investigates motor unit adaptations to endurance training in humans in vivo. The main observation is that for the same relative submaximal force level, the motor unit discharge rate decreased following training. Despite the decrease in discharge rate, the surface EMG amplitude increased. An increase in EMG amplitude reflects an increase in the motoneuron pool output (20). Thus, because the discharge rate of individual motor units decreased, it is likely that more motor units were active. However, alterations of the surface EMG signals should be interpreted with caution and may also be associated, e.g., with changes in the intracellular action potential shape or volume conductor (for review, see Ref. 20).

Interestingly, Adams et al. (5) observed a similar difference in motor unit discharge rate during submaximal contractions of the dominant vs. the nondominant hand of healthy volunteers. In addition to a reduction in discharge rate, the motor units of the dominant hand showed lower and more clustered recruitment thresholds (5). Their results were interpreted as the effect of long-term preferential use of the dominant hand, which can be viewed as a moderate form of exercise (5). Those observations are in agreement with the results of the current study, although important differences, such as the range of motor unit recruitment in hand and leg muscles, exist between the two studies.

Increased net motoneuron excitability, assessed by classic H-reflex techniques, has been shown in endurance-trained athletes compared with power-trained athletes (37, 42) and has also been observed after a short period of endurance training (52). On the basis of these results, it was suggested that a larger proportion of low-threshold motor units would be recruited for the same relative force level after endurance training (37, 52). However, an increased H-reflex has also been observed after strength training (3) and immobilization (40). Since the H-reflex is modulated by several neural mechanisms that can alter motor unit behavior, its interpretation is limited. In addition to

studies on the H-reflex, animal studies have also directly analyzed motor neuron properties following endurance training and have shown that moderate training results in a more hyperpolarized resting membrane potential and voltage threshold, greater afterhyperpolarization amplitude, and decreased spike rise time in low-threshold motor neurons (8, 9). Although their functional consequences are not fully known (24), a greater afterhyperpolarization amplitude and decreased spike rise time in low-threshold motor neurons would alter the motor neuron frequency-current relation and decrease the discharge rates (25), in agreement with the present results.

In addition to this interpretation, the changes in motor unit behavior may also be a consequence of changes in contractile properties of the muscle fibers following training. The time course of the twitch force partly reflects the time course of rise and fall of calcium released from the sarcoplasmic reticulum (33). It has been shown that 5 wk of endurance training induces a downregulation of the calcium cycling due to a reduction of the Ca^{2+}-ATPase activity (43). These adaptations might contribute to a lengthening of the twitch duration, which would result in a similar twitch fusion at lower discharge rates. In this study the contractile properties of the muscle were not directly assessed, which represents a limitation of the study. However, Grosset et al. (26) did not observe changes in the muscle twitch contraction time or half relaxation time after 10 wk of endurance training. Furthermore, the unloaded shortening velocity (V_0) of type I fibers increases after 13 wk of endurance training (21, 44). These previous results indicate that it is unlikely that muscle contractility changes caused the observed changes in motor unit discharge rate after only 3 wk of training. In addition, in this study we measured the conduction velocity in individual motor units. This measure provides information on the muscle fiber electrophysiological membrane properties at the single motor unit level. Although the measure MUCV did not change during the first 3 wk of training, a significant increment in MUCV was observed at the end of the training program, although only for the contractions at 30% MVC. Therefore, some peripheral adaptations did eventually occur after 6 wk of training. However, the time course of these adaptations was different from the observed changes in discharge rates.

Finally, it is worth noting that the MVC decreased slightly for the ET group after 3 wk of training, albeit not significantly. Consequently, the absolute load applied during the relative submaximal force contractions was smaller. This difference might have contributed to the observed changes in motor unit discharge rates. However, the small change in absolute loads applied during the contractions at 30% MVC did not correlate with the change in discharge rates observed in both training groups.

Strength training. Motor unit discharge rates of the vasti increased following strength training during contractions performed at 30% MVC and were accompanied by an increase of the surface EMG signal amplitude. The increase in motor unit discharge rate during submaximal contractions following strength training was also in agreement with the increase in EMG signal amplitude during the maximal contractions. These results suggest that the changes in motor unit discharge rates contributed to changes in force output, at least in the initial phase of training (1, 51, 61).

Maximal discharge rates have been shown to increase during both ballistic contractions (61) and maximal isometric contractions (31, 51) following strength training. Nevertheless, for submaximal contractions, these observations are not confirmed by all studies (31, 56). The different results observed in the present study compared with those of some previous studies (31, 56) are likely due to differences in the exercise paradigms. For example, in the studies by Kamen and Knight (31) and Rich and Cafarelli (56), the training paradigm involved one unilateral exercise (leg extension) and the training variables (load intensity, number of repetitions and series) were maintained constant across the entire training program. On the contrary, in the present study we applied a progressive strength training program across the 6-wk period. The total volume of training reached at the end of the 6-wk training period was higher in the present study compared with that in the aforementioned studies. Differences in exercise paradigms are relevant, since the intensity and time of exposure to exercise influence motor neuron properties and, consequently, the motor unit behavior (25). Other training variables, such as the type of exercise (single-joint vs. multijoint exercise) or type of contraction (isometric vs. dynamic), may also contribute to different training outcomes. The strength training program employed in this study involved both single-joint (leg extension) and multijoint (leg press) exercises of the quadriceps, performed during dynamic contractions (both concentric and eccentric actions). In addition, the subjects performed a single-joint exercise for the hamstring muscles.

Changes in motor unit behavior following strength training may include changes in the recruitment threshold of motor units. Van Cutsem et al. (61) reported lower recruitment thresholds and higher discharge rates after 12 wk of explosive training in the absence of changes in the contractile properties of the motor units. In another study, 3 wk of isometric training were shown to increase the maximal surface EMG of the VL, M-wave, and maximal activation (measured with twitch interpolation techniques), whereas the discharge rate of motor units remained unchanged (54).

Despite limitations associated with surface EMG, the increased EMG amplitude observed in this study with strength training is in accordance with the observed increased motor unit discharge rates. Changes in MUCV may also contribute to changes in the surface EMG signal amplitude (20). However, MUCV did not change after 3 wk of training, contrary to surface EMG amplitude and motor unit discharge rates.

Early Adaptations to Training

Both training programs showed significant changes in motor unit behavior after only 3 wk of training. In this period, MUCV did not change significantly, thus the electrophysiological membrane properties were not influenced by training. Only a few other studies have assessed changes in motor unit behavior across a training period (31, 51). In these studies, maximal motor unit discharge rates of the abductor digiti minimi and VL increased after 2 and 7 days of strength training, respectively (31, 51). Interestingly, after this peak, maximal discharge rates decreased returning to baseline levels after 6 wk of training (51). In the current study, the greatest rate of change in motor unit discharge rate occurred in the first 3 wk of training. In the subsequent 3 wk, smaller changes were observed; however,

neither the ST nor the ET group showed a reversal of the adaptations that had occurred within the first half of the training program. The surface EMG amplitude of the vasti also showed a rapid increment in the first half of the training program but was followed by a decrease in the second half of training; nevertheless, by the end of *week 6*, the EMG amplitude still remained greater compared with baseline values. These results are in agreement with previous observations on more rapid changes in the early phase of strength training with respect to later phases (22). These early adaptations likely involve changes in supraspinal excitability, spinal pathways, or changes in the membrane properties of the motoneurons (15). However, the nature and exact sites of the neural adaptations to strength training in this early phase remain unknown (6, 15).

Synergistic Muscles

Both the VMO and VL showed similar neural adaptations to strength training. Some studies have reported differences in the magnitude and time course of muscle architecture adaptations of the VL and VMO to high-intensity strength training (10, 59). A significant increase of the cross-sectional area of the VL was observed following 20 days of training (equivalent of 6.5 wk of training), whereas it was only observed after 35 days (equivalent of 11 wk) for the VMO muscle (59). It has been suggested that this dissimilarity is related to differences in activation of the muscles within the quadriceps group depending on the speed and angle of the contraction (10). Conversely, in the present study no differences in the surface EMG, motor unit behavior, or MUCV were observed between the VMO and VL in any subject group. However, in this study the vasti were investigated during knee extension contractions performed with the knee in 90° of flexion, a condition that corresponds to a similar level of activity of the vasti (50, 53).

Limitations

Training-induced improvements in motor output are dependent on a number of physiological, morphological, and neural factors (62). In the present study we mainly investigated changes in motor unit discharge rate and MUCV, which constitute only a part of a number of possible adaptations. Adjustments in motor unit discharge rate are also dependent on several factors, including muscle contractile properties and motor unit recruitment thresholds. Although MUCV partly correlates to the force expressed by the motor units (7), changes in the MUCV do not necessarily reflect alterations of the contractile properties, and direct measures of contractility would provide further clarification on motor unit adaptations to training programs. Alterations of the discharge rates may indeed represent an adjustment to the modified contractile properties of the muscle fibers. For example, in endurance training there may be a lengthening of the twitch force so that twitch fusion force can be produced at lower discharge rates. This hypothesis cannot be tested from the current data.

The different types of exercise used in each training program (i.e., alternating vs. simultaneous flexion and extension of the lower limbs) might have accounted for the opposite adaptations observed at the motor unit level, since they involve different motor control strategies. Cycling is generated by the integrated activity of several control systems at various levels of the central nervous system, and differences exist when the soleus

H-reflex and motor-evoked potentials are compared during cycling and tonic plantar flexion (55).

Finally, changes in voluntary activation may have an influence on motor unit discharge rates. Voluntary activation has been reported to change with training in some studies (14, 54), although in other studies this was not observed (38, 61). The current study did not include the measure of voluntary activation, whose potential changes with training may explain some of the results presented.

Conclusion

The findings in this study suggest that two specific endurance and strength training programs elicit early and opposite adjustments in motor unit discharge rates. Endurance training increased resistance to fatigue and was accompanied by a decrease in motor unit discharge rates. In contrast, strength training enhanced maximum force output and was accompanied by an increase in motor unit discharge rates. By the end of 6 wk of training, both programs elicited increases in MUCV, revealing electrophysiological adaptations of the muscle fiber membrane properties in similar directions. However, in the first 3 wk of training, when changes in motor unit discharge rates were most marked, changed in MUCV were not observed. These findings reveal different time courses of some of the neural and peripheral adaptations in response to different motor training programs.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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