Adjustments Differ Among Low-Threshold Motor Units During Intermittent, Isometric Contractions

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1Center for Sensory-Motor Interaction, Department of Health Science and Technology, Aalborg University, Aalborg, Denmark; 2Faculty of Electrical Engineering and Computer Science, University of Maribor, Maribor, Slovenia; 3Laboratorio di Ingegneria del Sistema Neuromuscolare, Politecnico di Torino, Torino, Italy; and 4Department of Integrative Physiology, University of Colorado at Boulder, Boulder, Colorado

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Farina D, Holobar A, Gazzoni M, Zazula D, Merletti R, Enoka RM. Adjustments differ among low-threshold motor units during intermittent, isometric contractions. J Neurophysiol 101: 350–359, 2009. First published November 12, 2008; doi:10.1152/jn.90968.2008. We investigated the changes in muscle fiber conduction velocity, recruitment and derecruitment thresholds, and discharge rate of low-threshold motor units during a series of ramp contractions. The aim was to compare the adjustments in motor unit activity relative to the duration that each motor unit was active during the task. Multichannel surface electromyographic (EMG) signals were recorded from the abductor pollicis brevis muscle of eight healthy men during 12-s contractions (n = 25) in which the force increased and decreased linearly from 0 to 10% of the maximum. The maximal force exhibited a modest decline (8.5 ± 9.3%; P < 0.05) at the end of the task. The discharge times of 73 motor units that were active for 16–98% of the time during the first five contractions were identified throughout the task by decomposition of the EMG signals. Action potential conduction velocity decreased during the task by a greater amount for motor units that were initially active for >70% of the time compared with that of less active motor units. Moreover, recruitment and derecruitment thresholds increased for these most active motor units, whereas the thresholds decreased for the less active motor units. Another 18 motor units were recruited at an average of 171 ± 32 s after the beginning of the task. The recruitment and derecruitment thresholds of these units decreased during the task, but muscle fiber conduction velocity did not change. These results indicate that low-threshold motor units exhibit individual adjustments in muscle fiber conduction velocity and motor neuron activation that depended on the relative duration of activity during intermittent contractions.

INTRODUCTION

A prevailing concept in the study of muscle fatigue is that the adjustments exhibited by the motor system depend on the demands of the task being performed. This concept is known as the task dependence of muscle fatigue (Enoka and Duchateau 2008). According to this scheme, only those physiological processes that are stressed by the physical activity will be challenged enough so that they are eventually impaired and contribute to muscle fatigue. For example, the decline in voluntary activation of muscle differs during maximal sustained, intermittent, and shortening contractions and thus contributes differently to the observed muscle fatigue during these tasks (Babault et al. 2006; Taylor et al. 2006). Similarly, the type of load supported by a limb during a submaximal isometric contraction influences the rate at which the motor unit pool is recruited and the duration that the contraction can be sustained (Enoka and Duchateau 2008; Maluf and Enoka 2005).

The specificity of the adjustments can also be observed among the motor units within a single muscle. For example, Carpentier et al. (2001) found differences in the adjustments exhibited by motor units in the first dorsal interosseus muscle during ramp-and-hold contractions to a target force of 50% of the maximum. The hold phase of each isometric contraction lasted 10 s and the task was performed until the target force could not be reached. Differences were observed between motor units with low (<25% of maximum force) and high (>25%) recruitment thresholds. The low-threshold motor units experienced an increase in mean twitch force, an increase or no change in recruitment threshold, and a decrease in discharge rate, which contrasted with decreases in twitch force and recruitment threshold for the high-threshold motor units. The increase in twitch force for the low-threshold motor units was attributed to a change in muscle stiffness during the task, whereas the changes in discharge rate and recruitment threshold were likely caused by changes in either the intrinsic motor neuron properties or the afferent feedback from the periphery.

The classification of motor units into low- and high-threshold groups by Carpentier et al. (2001) corresponded to the classical distinction between motor units that are fatigue resistant and those that are not (Burke et al. 1973; Kugelberg and Endstrom 1968; Stephens and Usherwood 1977). Despite the terminology, fatigue-resistant motor units can exhibit changes in discharge rate (Mottram et al. 2005), contractility (Nordstrom and Miles 1990), and propagation of the intracellular action potential (Farina et al. 2004) during prolonged voluntary contractions and these adjustments depend on the demands of the task performed (Mottram et al. 2005). For example, the decrease in conduction velocity of motor units in hand muscles during sustained, isometric contractions differs when the motor units discharge at slightly different rates (Farina et al. 2004). Moreover, the neuromodulatory input that contributes to motor neuron excitability in reduced preparations appears to vary with the duration of activation (Heckman et al. 2008) and may influence motor unit activity during voluntary contractions. Changes in individual motor unit properties during fatigue

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contractions may thus be related to differences in the amount of activation experienced by each motor unit during the task.

The hypothesis for the current study was that the duration of activity experienced by low-threshold motor units leads to different adjustments in both the membrane fiber properties and discharge characteristics during a series of intermittent contractions. The purpose of the study was to examine the association between the adjustments exhibited by low-threshold motor units (≥10% of maximum force) and the relative proportion of time each unit was active during ramp increases and decreases in isometric force. Because motor units are recruited at different thresholds, the ramp increases and decreases in force implied that the involved motor units were active for different proportions of the task. The selected target force ensured that all motor units involved were fatigue resistant, so that their muscle fibers and motor neurons had similar properties.

METHODS

Eight healthy men (age, mean ± SD: 27.3 ± 2.2 yr; height, 1.79 ± 0.07 m; body mass, 75.2 ± 7.4 kg) participated in the experiment. The local ethics committee (Regional Committee, Turin, Italy) approved the study and all subjects signed an informed consent form before participation.

EMG recordings

Surface electromyographic (EMG) signals were detected with a two-dimensional grid of 61 silver electrodes (1-mm diameter, 3.5-mm interelectrode distance, 13 rows × 5 columns without the four corner electrodes; Gazzoni et al. 2005) from the abductor pollicis brevis muscle of the right (dominant) hand. The EMG signals were amplified (LISiN-OT Bioelettronica, Turin, Italy), band-pass filtered (3-dB bandwidth, 10–500 Hz), sampled at 1,650 Hz, and A/D converted on 12 bits.

The electrode grid was located with the columns in the direction of the muscle fibers and the last row approximately over the end of the distal tendon. The skin was lightly abraded with abrasive paste (Meditec—Every, Parma, Italy) before the grid was fixed with adhesive tape and a reference electrode was placed at the wrist.

Procedures

A custom-designed brace was used to measure the abduction force exerted by the thumb (Gazzoni et al. 2005). The subject’s wrist was fixed in a padded wood support with the head of the proximal thumb phalanx in contact with a load cell (model 8523-50N, Burster, Germensbach, Germany). The force signal was amplified (Force Amplifier, MISO-II; LISiN), provided as feedback to the subject on an oscilloscope, and recorded concurrently with the EMG signals.

The subjects performed three maximal voluntary contractions (MVCs) separated by a 2-min rest prior to the electrode grid being mounted over the abductor pollicis brevis. The highest peak force was used as the reference MVC for defining submaximal forces. The subject then practiced the ramp contractions, which consisted of a linear increase in force from 0 to 10% MVC in 6 s and then a linear decrease from 10 to 0% MVC in 6 s. The subject received visual feedback of the target force and the force exerted by the thumb. After about 10 min of practice with frequent breaks and then 15 min of rest, the subject performed the 12-s contraction 25 times without resting between trials, which took 5 min. A 5-min isometric contraction of the abductor pollicis brevis muscle at about 5% MVC force has been shown to evoke detectable changes in the fiber membrane properties of low-threshold motor units and the progressive recruitment of motor units (Farina et al. 2004). The MVC was measured at the end of the task so that the amount of fatigue (decline in MVC force) associated with the task could be estimated.

Decomposition of the surface EMG

Multichannel surface EMG signals were used to detect the discharge times of motor units because muscle fiber conduction velocity can be estimated with these recordings. The multichannel surface EMG signals were decomposed with an algorithm that identifies the discharge times of motor units (Holobar and Zazula 2007). Recruitment and derecruitment thresholds for each motor unit were defined as the force at the times when the motor unit began and stopped, respectively, repetitively discharging action potentials (Enoka 1995). Discharge times separated by >200 ms from the nearest neighbor were excluded from the estimation of recruitment and derecruitment thresholds to avoid aligning the thresholds with noise-generated sporadic discharges. Motor units that were continuously active, which was rare, were assigned thresholds of 0% MVC force. The discharge rates at recruitment and derecruitment were defined for the motor units active during the 25 contractions as the average discharge rates of the first and last six discharges and the peak discharge rate was defined as the maximum value obtained from the average rate over six consecutive discharges. The discharge rate was averaged over all discharges during each ramp for the motor units that were recruited after the first ramp.

The accuracy of the surface EMG decomposition algorithm has been previously proven theoretically (Farina et al. 2008) and directly demonstrated with a set of synthetic and experimental signals recorded during ramp contractions (Holobar and Zazula 2004; A. Holobar, D. Farina, M. Gazzoni, R. Merletti, and D. Zazula, unpublished observations). To demonstrate the reliability of the decomposition method in the context of the current study, however, surface and intramuscular EMG signals were concurrently recorded in one subject and the results of the decompositions of the two signals compared. The intramuscular EMG was recorded with a pair of Teflon-coated stainless steel wires (diameter 0.1 mm; A-M Systems, Carlsborg, WA) inserted with a 25-gauge hypodermic needle in a location approximately 10 mm proximal to the surface electrode grid, in line with the central column of the grid. The two wires were cut to expose the cross section and provided one bipolar signal, which was amplified (Counterpoint EMG, Dantec Medical, Copenhagen, Denmark), band-pass filtered (500 Hz to 5 kHz), sampled at 10 kHz concurrently with the surface EMG, and stored after 12-bit A/D conversion. A validated method was used for the decomposition of the intramuscular EMG (McGill et al. 2005).

The two decomposition techniques identified four common motor units (Fig. 1) during the series of ramp contractions. Over the course of the 5-min recording, the two techniques agreed on 96% of the discharge times for these four motor units. The differences between estimates of recruitment and derecruitment thresholds and discharge rates provided by the two decomposition techniques were negligible (Table 1).

Signal analysis

The force signal was low-pass filtered with a fourth-order Butterworth filter with cutoff frequency 5 Hz. The first derivative (slope) of the force signal was computed at the instants of recruitment and derecruitment for each motor unit. The proportion of time that each motor unit was active (PTA) during ramp-up and ramp-down contractions was expressed as the ratio (%) of the time between recruitment and derecruitment of the motor unit relative to the time between its recruitment during two consecutive ramps (Fig. 2).

The action potential of each motor unit was obtained by averaging the multichannel surface EMG signals over all discharges of the motor unit in each ramp (Fig. 3). Muscle fiber conduction velocity was...
estimated for each motor unit from the average action potentials with a multichannel method (Farina et al. 2001, 2002). Three to six channels were used to estimate conduction velocity based on the criterion of a minimal change in shape of the action potential as determined by visual selection (Farina et al. 2002). Although muscle fiber conduction velocity changes with discharge rate (Stålberg 1966), the magnitude of the change was small in abductor pollicis (0.5%/pps; Farina et al. 2004) and it was assumed to be negligible in the observed range of discharge rates.

The dependent variables for the motor units that were active during all ramp contractions were averaged across five consecutive ramp-up and ramp-down contractions to yield five averages for the 5-min task. The averages were normalized to the value for the initial average. The rate of change across the five averages was estimated with a linear regression (normalized rate of change; %/min).

The motor units that were active during all ramp contractions were assigned to eight groups on the basis of the average PTA (Fig. 2) during the first minute of the task (initial PTA). The groups consisted of motor units with initial PTAs of 0–30%, 30–40%, 40–50%, 50–60%, 60–70%, 70–80%, 80–90%, and 90–100%. These groups were chosen to achieve a similar number of motor units in each bin (see RESULTS).

**Statistical analysis**

Relations between variables extracted from individual motor units were investigated with linear correlation analyses. The initial values and normalized rates of change of these variables were analyzed with a one-way ANOVA to identify differences among the eight groups of motor units defined on the basis of the initial PTA. The absolute value of the slope of the force signal was analyzed with a two-way ANOVA (direction of change in force×time). When the ANOVA identified a significant effect, a post hoc Student–Newman–Keuls (SNK) test was used for pairwise comparisons. A paired Student’s t-test was used to compare MVC force before and after the task and the variables of the motor units recruited after the beginning of the task during the first and last ramp contractions in which they were active. Significance was
MVC force decreased from an initial value of 39.2 ± 6.9 to 35.3 ± 5.9 N after 25 contractions, which corresponded to a modest decline in maximal force with considerable variability among participants (−8.5 ± 9.3%; P < 0.05). A total of 73 motor units were identified as active for the entire duration of the task (25 up/down ramps).

The instantaneous discharge rates of two representative motor units for one subject are shown in Fig. 4. In this example, the derecruitment thresholds (5.4 and 8.5% MVC, respectively) were greater than the recruitment thresholds (2.1 and 7.2% MVC, respectively). The derecruitment threshold in the first minute of the task was correlated with the recruitment threshold (n = 73, R² = 0.82, P < 0.001) and the recruitment threshold at the beginning of the task was less than the derecruitment threshold (3.8 ± 1.9 and 5.1 ± 1.8% MVC, respectively; P < 0.001) (Fig. 4). Similarly, the recruitment and derecruitment thresholds were correlated across the five values over the 5-min task (n = 73 × 5 time intervals, R² = 0.78, P < 0.001) (Fig. 5). The absolute slope of the force signal was similar at recruitment (1.72 ± 0.4% MVC/s) and derecruitment (1.68 ± 0.4% MVC/s) for each motor unit (n = 73) during the first minute of the task and did not change during the task (first minute: 1.70 ± 0.5% MVC/s; last minute: 1.73 ± 0.4% MVC/s).

Conduction velocity (3.4 ± 0.6 m/s) and the discharge rates at recruitment (6.4 ± 0.6 pps) and derecruitment (6.5 ± 0.5 pps) during the first minute of the task were not correlated with recruitment threshold (3.8 ± 2.7% MVC), probably due to the narrow range of recruitment thresholds in the sample. Similarly, there was a weak, inverse relation between peak discharge rate (13.9 ± 3.1 pps) and recruitment threshold (n = 73, R² = 0.11, P < 0.05), which indicated that lower threshold motor units experienced a greater increase in discharge rate. The discharge rates at recruitment and derecruitment were similar and less than the peak discharge rate (P < 0.001) (Fig. 4 and Table 2).

PTA values in the first minute ranged from 16 to 98%, where 98% indicates almost continuous activation. To characterize the changes that occurred during the 5-min task, the motor units (n = 73) were assigned to eight groups based on PTA. Because the groups were defined on the basis of the initial PTA and this variable was correlated with the recruitment and derecruitment thresholds, the initial thresholds differed across the groups (F = 62.1, P < 0.05, for recruitment; F = 96.2, P < 0.001, for derecruitment; Table 2). Recruitment threshold differed between all groups (P < 0.05), except between the 40–50 and 50–60% groups and between the 70–80 and 80–90% groups. Derecruitment threshold also differed between all groups (P < 0.05), except between the 50–60 and 60–70% groups. The eight groups were thus distinguished by thresholds of activation in the range 0–10% MVC force, which meant that motor units with the lowest recruitment thresholds were more active during the task than those with higher thresholds.

Although muscle fiber conduction velocity was not related to the initial PTA (n = 73, R² = 0.02; P = 0.95), the changes over time were related to the initial PTA. Figure 6 shows the changes in muscle fiber conduction velocity for three motor units with different initial PTAs detected from one subject. In this representative example, the conduction velocity of a motor unit active for 91% of the time decreased over time by about 10%.
20%, whereas the conduction velocity for the motor unit that was active for only 42% of the time did not change substantially. As suggested by this example (Fig. 6), the change in conduction velocity for all motor units \((\bar{n}/H1100573)\) varied with the initial PTA (ANOVA: \(F/H110052.4, P/H110210.05\)). Motor units that were active for \(90\%\) of the task experienced a larger relative decrease in conduction velocity than motor units that were active for \(70\%\) of the task, and motor units that were active for \(70-90\%\) of the task exhibited a greater decrease than those active for \(60\%\) of the task (Fig. 7B).

The recruitment threshold of some of the motor units changed during the task. Figure 8 shows an example of one motor unit that slightly increased its recruitment threshold and another that experienced a decrease in recruitment threshold during the same task. The change depended on the initial PTA (ANOVA: \(F = 3.8, P < 0.01\)) (Fig. 7B). Motor units active for \(<70\%\) of the task decreased their recruitment threshold, in contrast to the more active motor units (Fig. 7B). There were similar differences between groups in the change in derecruitment threshold (ANOVA: \(F = 7.5, P < 0.001\)). Motor units with an initial PTA \(>80\%\) increased derecruitment threshold \((P < 0.05; \text{Fig. 7C})\), contrary to the other less active units, and the increase was greater for motor units with an initial PTA \(>90\%\) than those in the range \(80-90\%\) \((P < 0.05; \text{Fig. 7C})\).

Due to the changes in recruitment thresholds, some motor units experienced a change in PTA during the task (ANOVA on normalized rate of change of PTA: \(F = 3.3, P < 0.01\)). PTA decreased over time for motor units with an initial value \(>70\%\), whereas it increased for the other groups (Fig. 7D). Accordingly, PTA at the beginning (first minute) and at the end (fifth minute) of the task was highly correlated \((n = 73, R^2 = 0.77, P < 0.001)\). The linear regression for PTA at the beginning and end of the task had slope 0.78 and intercept 15.0%, which indicated a larger increase in PTA during the task for those motor units with smaller initial PTA. For example, the linear association predicted that a motor unit with
initial PTA of 20% would increase its PTA to 30.7% by the end of the task, whereas a motor unit with an initial PTA of 95% would experience a decrease to 89.7%. Thus the proportion of time during which each motor unit was active during the ramp contractions changed during the task, depending on the initial relative duration of activity.

The individual changes in recruitment thresholds occasionally caused an inversion of recruitment order for pairs of motor units. For example, motor units 3 and 4 in Fig. 8 changed the relative recruitment order from ramp 2 to ramp 25. However, the inversion in recruitment order was observed in only eight motor unit pairs in total and these motor units had relatively small differences in initial recruitment thresholds (1.8 ± 0.5% MVC).

In contrast to the influence of the proportion of activity on recruitment threshold and muscle fiber conduction velocity, the modest changes in peak discharge rate (0.4 ± 4.5%/min) and discharge rates at recruitment (1.2 ± 3.7%/min) and derecruitment (−0.6 ± 3.3%/min) did not depend on initial PTA and were not statistically significant.

In addition to the 73 motor units that were identified during all 25 ramp-up and ramp-down contractions, 18 motor units were recruited after the first minute of the task. After the first detected discharge of an action potential, which occurred at 171 ± 32 s (range, 96–236 s) after the beginning of the task, the newly recruited units were active for the remainder of the task and showed a consistent decrease in recruitment and derecruitment thresholds over time (e.g., motor unit 9 in Fig. 8). The recruitment threshold of these motor units (n = 18) decreased from 9.3 ± 0.6% MVC force during the first ramp contraction in which they were detected to 8.2 ± 1.1% MVC force in the last ramp (P < 0.05). Derecruitment threshold decreased similarly from 9.5 ± 0.4 to 8.6 ± 0.9% MVC force (P < 0.05) from the first to the last activation. Discharge rate and muscle fiber conduction velocity averaged for all discharges in each ramp, however, did not change between the first and last ramps in which the motor units were active (n = 18, average over the first and last ramps, 10.5 ± 0.8 pps and 3.5 ± 0.3 m/s, respectively).

Despite the focus on fatigue-resistant motor units during the performance of a task that produced a modest amount of fatigue, the motor units exhibited different adjustments that depended on the proportion of the task that they were active. Those units active for a large proportion of the contraction at the beginning of the task showed greater decreases in muscle fiber conduction velocity and increases in recruitment threshold. In contrast, less active units experienced a modest change in muscle fiber conduction velocity and a decrease in recruitment threshold during the task. As a consequence, the most active motor units at the beginning of the task became less active by the end of the task, whereas the reverse occurred for the motor units that were less active at the beginning. Thus the low-threshold motor units in abductor pollicis brevis did not experience the same adjustments during the fatiguing task. The adjustments corresponded to the different demands of the task on each motor unit and indicate specificity of the changes even among low-threshold motor units.

Multichannel surface EMG was used to identify the activity of single motor units because it allows concurrent analysis of muscle fiber properties (conduction velocity) and the recording of many motor units. Theoretical and experimental studies have shown that such recordings provide valid measures of motor unit activity at contractions up to moderate force (Farina et al. 2008). The decomposition method used in the current study has been validated on simulated recordings (Holobar and Zazula 2004, 2007) and on concurrent intramuscular and surface recordings (Holobar et al., unpublished observations). Measurements on one subject confirmed that the approach was appropriate for the current study (Fig. 1 and Table 1).
The results demonstrate that conduction velocity of muscle fiber action potentials belonging to fatigue-resistant motor units (Stephens and Usherwood 1977) can change during a low-force contraction. The changes in conduction velocity were presumably caused by a change in ion concentration gradients across the muscle fiber membranes that influence membrane depolarization. For example, the accumulation of K⁺ in the extracellular space (Sejersted and Sjøgaard 2000), despite an increase in Na⁺-K⁺ pump activity (Everts and Clausen 1994), can cause conduction velocity to decrease (Kossler et al. 1991). Such extracellular accumulation of K⁺ corresponds to an intracellular decrease in K⁺ concentration, even though the initial intracellular concentration of K⁺ is much greater than the extracellular.

<table>
<thead>
<tr>
<th>Initial PTA</th>
<th>0–30% (n = 8)</th>
<th>30–40% (n = 7)</th>
<th>40–50% (n = 7)</th>
<th>50–60% (n = 7)</th>
<th>60–70% (n = 12)</th>
<th>70–80% (n = 13)</th>
<th>80–90% (n = 11)</th>
<th>90–100% (n = 8)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recruitment threshold, %MVC</td>
<td>7.0 ± 0.7</td>
<td>6.4 ± 0.7</td>
<td>5.0 ± 0.6*</td>
<td>4.7 ± 0.4*</td>
<td>3.6 ± 1.1</td>
<td>2.5 ± 0.5†</td>
<td>2.1 ± 0.7†</td>
<td>1.4 ± 0.5</td>
</tr>
<tr>
<td>Derecruitment threshold, %MVC</td>
<td>7.8 ± 0.5</td>
<td>7.3 ± 0.5</td>
<td>6.5 ± 0.4</td>
<td>5.7 ± 0.3**</td>
<td>5.4 ± 0.7**</td>
<td>4.2 ± 0.7</td>
<td>3.6 ± 0.4</td>
<td>2.2 ± 0.6</td>
</tr>
<tr>
<td>Conduction velocity, m/s</td>
<td>3.6 ± 0.4</td>
<td>3.5 ± 0.5</td>
<td>3.5 ± 0.4</td>
<td>3.6 ± 0.5</td>
<td>3.6 ± 0.9</td>
<td>3.3 ± 0.6</td>
<td>3.0 ± 0.5</td>
<td>3.2 ± 0.5</td>
</tr>
<tr>
<td>Discharge rate at recruitment, pps</td>
<td>6.9 ± 0.7</td>
<td>6.4 ± 0.7</td>
<td>6.0 ± 0.6</td>
<td>6.7 ± 0.4</td>
<td>6.6 ± 1.1</td>
<td>6.5 ± 0.5</td>
<td>6.1 ± 0.7</td>
<td>6.4 ± 0.5</td>
</tr>
<tr>
<td>Peak discharge rate, pps</td>
<td>12.3 ± 3.5</td>
<td>13.4 ± 2.1</td>
<td>13.0 ± 1.9</td>
<td>14.3 ± 3.3</td>
<td>14.4 ± 3.3</td>
<td>15.3 ± 3.7</td>
<td>14.8 ± 1.4</td>
<td></td>
</tr>
<tr>
<td>Discharge rate at derecruitment, pps</td>
<td>7.8 ± 0.5</td>
<td>7.3 ± 0.5</td>
<td>6.5 ± 0.4</td>
<td>5.7 ± 0.3</td>
<td>6.4 ± 0.6</td>
<td>6.2 ± 0.7</td>
<td>6.6 ± 0.4</td>
<td>6.2 ± 0.6</td>
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PTA, percentage of time of activity. Recruitment threshold differed (P < 0.05) among the eight groups except for the pairs indicated by * and †. Derecruitment threshold differed (P < 0.05) among the eight groups except for the pair indicated by **. There were no significant differences among the eight groups for the other variables.

The results demonstrate that conduction velocity of muscle fiber action potentials belonging to fatigue-resistant motor units (Stephens and Usherwood 1977) can change during a low-force contraction. The changes in conduction velocity were presumably caused by a change in ion concentration gradients across the muscle fiber membranes that influence membrane depolarization. For example, the accumulation of K⁺ in the extracellular space (Sejersted and Sjøgaard 2000), despite an increase in Na⁺-K⁺ pump activity (Everts and Clausen 1994), can cause conduction velocity to decrease (Kossler et al. 1991). Such extracellular accumulation of K⁺ corresponds to an intracellular decrease in K⁺ concentration, even though the initial intracellular concentration of K⁺ is much greater than the extracellular.
concentration and thus its changes are relatively small. In addition, intracellular calcium ion concentration increases (Gissel and Clausen 1999) and thus the calcium gradient across the membrane also changes with activity and influences membrane depolarization. The influx of Ca\(^{2+}\) can also influence K\(^{+}\) conductance through Ca\(^{2+}\)-dependent K\(^{+}\) channels (Lindinger and Sjøgaard 1991). The decrease in muscle fiber conduction velocity for the most active motor units in the present study is similar to that of a previous study that involved low-force contractions (Farina et al. 2004), which suggests that even at low forces modest changes in ion concentration gradients across the fiber membrane have an influence on conduction velocity.

The rate of change in conduction velocity was related to the proportion of time that the motor units discharged action potentials during the task (Figs. 6 and 7). In contrast to this finding, changes in conduction velocity of all muscle fibers (even those not active) are similar when a contraction is strong enough to occlude blood flow (Gazzoni et al. 2005). One explanation for the individual changes in conduction velocity observed in the current study is the occurrence of more local changes in extracellular ion concentrations compared with the changes that occur during stronger contractions, despite an intermingling of the territories of the active motor units. Alternatively, the changes in intracellular ion concentrations, particularly calcium (Dimitrova and Dimitrov 2003; Gissel and Clausen 1999), may have been more substantial in the more active fibers and been responsible for the individual adjustments. Nonetheless, the result indicates the importance of the type of task in analyzing adjustments in membrane fiber properties.

In addition to the differential influence of the task on the intramuscular adjustments, there were systematic changes in the recruitment and derecruitment thresholds of motor units that were related to the percentage of activity (Fig. 7), even though the motor units had similar initial recruitment thresholds (10% MVC force). The relative changes in recruitment and derecruitment thresholds resulted in the motor units that were most active initially reducing their percentage of activity and, conversely, for the motor units that were less active initially (Figs. 7 and 8). Carpentier et al. (2001) previously observed different adjustments in activation thresholds between motor units that were fatigue resistant (recruitment threshold <25% MVC force) and those that were not (>25% MVC force).

![Graphs](Fig. 7) Changes in motor unit properties over time as quantified by the normalized rates of change over the 5-min task. The normalized rates of change are presented for the 8 groups of motor units (n = 73 in total) classified based on initial PTA. A: normalized rate of change for muscle fiber conduction velocity (CV; the values correspond to a decrease in conduction velocity). B: normalized rate of change for the recruitment threshold. C: normalized rate of change for the derecruitment threshold. D: normalized rate of change for the PTA, where a positive value denotes an increase in the proportion of time the group of motor units was active. In B, C, and D, negative values correspond to decrease and positive values to increase. *: Significantly different, P < 0.05.
MVC force. In the current study, all motor units were likely fatigue resistant (Stephens and Usherwood 1977) and yet they exhibited a range of adjustments. Moreover, the changes in recruitment and derecruitment thresholds observed in the current study for motor units that were active for <70% of the task and had recruitment thresholds in the range of 3.6–7.0% MVC force (Fig. 7 and Table 2) contrasted with those observed by Carpentier et al. (2001) for motor units with recruitment threshold in the range 0–25% MVC force. This indicates that the motor unit recruitment threshold and motor unit type do not determine the specificity of the adjustment.

Carpentier et al. (2001) used ramp-and-hold contractions that made it difficult to quantify the proportion of activity, which was thus not associated with the adjustments. Because the ramp-up and ramp-down phases each lasted 3 s and the hold phase had a duration of 10 s, however, the high-threshold motor units should have been active for a lesser proportion of each contraction than the low-threshold units, which is in agreement with the specificity of the adjustments observed in the current study for motor units with different durations of activity. Longer hold phases, such as 50 s at a target torque of 20% of maximum, resulted in motor units in vastus lateralis being active for similar durations and displaying reasonably similar adjustments (Adam and De Luca 2003). Because the motor units analyzed in this study likely received similar descending drive and afferent feedback from the periphery, the individual adjustments in activation thresholds could be due to individual changes in the twitch forces expressed by each motor unit or in motor neuron excitability. The recruitment threshold of a motor unit is not a measure of motor neuron excitability, but depends on the sum of the forces developed by the units activated prior to the test unit. When the forces exerted by the previously activated motor units decrease, the recruitment threshold of the test unit will decrease. Conversely, potentiation of twitch force will increase the force exerted by the units that are already active and result in an increase in the recruitment threshold of the test unit. Accordingly, Carpentier et al. (2001) observed an increase in twitch force for lower-threshold motor units and a decrease for higher-threshold units that were accompanied by an increase in threshold for low-threshold units and a decrease for higher-threshold units.

Alternatively, the excitability of the motor neurons may have changed differently depending on the duration of motor unit activation and have caused the individual adjustments in activation thresholds. The extrinsic synaptic input needed to recruit a motor neuron may change during a fatiguing contraction. Over short time intervals of motor unit activity, persistent inward currents in the dendrites may reduce the current required from extrinsic synaptic sources to reach recruitment threshold (Fuglevand et al. 2006; Gorassini et al. 2002; Heckman et al. 2005; Nordstrom et al. 2007). Longer intervals of motor unit activity, however, may elicit slow inactivation of Na + and Ca 2+ persistent inward currents that conversely increase the synaptic current required to reach threshold (Heckman et al. 2005). Additionally, slow inactivation of Na + channels and a slowing of the transmembrane Na + -K + pump activity may increase the recruitment threshold (Miles et al. 2005; Vilin and Ruben 2001). Because these mechanisms depend on the duration of activation and are particularly relevant in low-threshold motor neurons (Heckman et al. 2005), they may have contributed to the differential adjustments in motor unit activity observed in the current study.

The individual adjustments in motor unit activity occurred during a progressive increase of the central drive to the motor neuron pool, as evidenced by the additional recruitment of motor units during the current task and as observed previously (Farina et al. 2004). The motor units that were recruited after the first minute of the task exhibited a progressive decrease in activation thresholds and did not change either muscle fiber conduction velocity or discharge rate due to the relatively

FIG. 8. Discharge times of motor units identified from one subject during 3 ramp-up contractions (ramps 2, 14, and 25). The changes in recruitment thresholds are illustrated for 2 motor units. The first motor unit (initial PTA = 94%) slightly increased its recruitment threshold (open triangles) over time, whereas the second (initial PTA = 42%) decreased its threshold (filled triangles). Motor unit 9 was first recruited in ramp 14.
shorter duration of activation. These adjustments were consistent with those observed for the motor units that were less active during the first minute of the task.

In summary, low-threshold motor units in abductor pollicis brevis exhibited different adjustments during a fatiguing contraction that depended on the relative duration that each motor unit was active during the task. Motor units that were initially active for most of the task displayed a larger decrease in muscle fiber conduction velocity and an increase in recruitment and derecruitment thresholds, whereas less active and newly recruited motor units experienced decreases in recruitment and derecruitment thresholds and less or no decrease in conduction velocity. The results indicate that the relative duration of activity evoked differential adjustments in a homogeneous group of motor units during intermittent, isometric contractions.

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