Voluntary activation level and muscle fiber recruitment of human quadriceps during lengthening contractions

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Beltman, J. G. M., A. J. Sargeant, W. van Mechelen, and A. de Haan. Voluntary activation level and muscle fiber recruitment of human quadriceps during lengthening contractions. J Appl Physiol 97: 619–626, 2004. First published April 9, 2004; 10.1152/japplphysiol.01202.2003.—Voluntary activation levels during lengthening, isometric, and shortening contractions (angular velocity 60°/s) were investigated by using electrical stimulation of the femoral nerve (triplet, 300 Hz) superimposed on maximal efforts. Recruitment of fiber populations was investigated by using the phosphocreatine-to-creatine ratio (PCr/Cr) of single characterized muscle fibers obtained from needle biopsies at rest and immediately after a series of 10 contractions (1 s on/1 s off). Maximal voluntary torque was significantly higher during lengthening contractions (270 ± 55 N·m) compared with shortening contractions (199 ± 47 N·m, P < 0.05) but was not different from isometric contractions (252 ± 47 N·m). Isometric torque was higher than torque during shortening (P < 0.05). Voluntary activation level during maximal attempted lengthening contractions (79 ± 8%) was significantly lower compared with isometric (93 ± 5%) and shortening contractions (92 ± 3%, P < 0.05). Mean PCr/Cr values of all fibers from all subjects at rest were 2.5 ± 0.6, 2.0 ± 0.7, and 2.0 ± 0.7, respectively, for type I, Ila, and IIax fibers. After 10 contractions, the mean PCr/Cr values for grouped fiber populations (regardless of fiber type) were all significantly different from rest (1.3 ± 0.2, 0.7 ± 0.3, and 0.8 ± 0.6 for lengthening, isometric, and shortening contractions, respectively; P < 0.05). The cumulative distributions of individual fiber populations after either contraction mode were significantly different from rest (P < 0.05). Curves after lengthening contractions were less shifted compared with curves from isometric and shortening contractions (P < 0.05), with a smaller shift for the type IIax compared with type I fibers in the lengthening contractions. The results indicate a reduced voluntary drive during lengthening contractions. PCr/Cr values of single fibers indicated a hierarchical order of recruitment of all fiber populations during maximal attempted lengthening contractions.

from the literature on animal whole muscle preparations or single fibers, it is well known that force during lengthening contractions increases above the isometric force (13, 19). In human voluntary lengthening contractions, however, this higher torque could, in general, not be demonstrated (3, 12, 22, 27, 36, 37). This divergence from the in vitro relationship is often attributed to a tension-limiting mechanism, which limits motor unit recruitment and/or discharge rate during lengthening contractions (34, 37).

Studies using surface electromyography activity during maximal isometric and isokinetic exercise have shown that electromyography levels during maximal lengthening contractions are lower than during maximal shortening contractions, although higher force output is obtained (1, 20, 22, 35). With the use of superimposed electrical stimulation, it has been demonstrated that the torque of voluntary lengthening contractions can be increased (2, 12, 37). In addition, by means of the twitch interpolation technique, activation levels during maximal voluntary lengthening contractions have been shown to be lower than during isometric contractions (3). These results from studies using different methods support the notion of a reduced neural drive during lengthening contractions compared with isometric and shortening contractions. It has been suggested that the reduction in neural drive could be either due to a lower activation of all recruited fibers as a consequence of inhibition, or due to activation of selective fiber populations (and inhibition or derecruitment of other fiber populations) during lengthening contractions (14). This would lead to a reversal of the normal hierarchy of recruitment (17, 25, 26; but compare Refs. 4, 23, 31, 32).

In the present investigation, we have examined the level of activation during maximal voluntary lengthening, isometric, and shortening contractions and related this to evidence for activation of different fiber-type populations. For this purpose, the ratio of phosphocreatine to creatine (PCr/Cr) was measured in single characterized fiber fragments, which were isolated from needle biopsies obtained at rest and after 10 lengthening, isometric, and shortening contractions. In an earlier study (7), we have demonstrated that this ratio is a useful indicator of fiber activation after very brief exercise involving only a few contractions of 1-s duration. This technique has proven to be a valuable approach for assessing recruitment patterns during isometric contractions at different intensities (6). In the present study, this method enabled us to assess whether type II fibers had been selectively activated (associated with a derecruitment or inhibition of type I fibers), or whether all fibers were activated at a lower level during lengthening contractions.

Thus the first aim was to investigate the voluntary activation level during lengthening, isometric, and shortening contractions by using the superimposed stimulation technique. For this purpose, high-frequency triplets were applied to the femoral nerve during maximal voluntary knee extension contractions and on the relaxed muscle. The second aim was to investigate the activation of different fiber populations during these modes...
of contraction by using PCr/Cr in single fibers. We hypothesized that we would find lower activation levels of lengthening contractions compared with isometric and shortening contractions, as evidenced by superimposed stimulation, and that this would be associated with a lower decrease in PCr/Cr in all fiber types, indicating a maintenance of the normal hierarchy of fiber-type recruitment rather than any reversal of recruitment pattern.

METHODS

Two experiments were performed with the approval of the ethical committee of the Vrije Universiteit Medical Center, Amsterdam, The Netherlands, and in accordance with the Declaration of Helsinki. After the procedures of the experiment were explained, all subjects gave oral and written, informed consent.

Study Design

In experiment 1, the voluntary activation level was determined during lengthening, isometric, and shortening contractions by using superimposed electrical stimulation elicited on maximal efforts. Subjects came to the laboratory for two sessions. In the first session, the torque-angle relationship was determined for each subject. In addition, voluntary activation level during either lengthening, isometric, or shortening contractions was tested. In the second session, which was at least 2 days after the first, the voluntary activation level of the remaining two contraction modes was determined. The order in which the lengthening, isometric, and shortening protocols were carried out was randomized over the two sessions.

In experiment 2, five subjects came to the laboratory for a session in which needle biopsies were obtained after three separate series of 10 contractions performed under lengthening, isometric, and shortening conditions.

Torque Measurements

Isometric and isokinetic knee extension exercise was performed on a specially designed dynamometer, which allowed torque measurements at preset angular velocities. Subjects sat in an upright position with a hip angle of \(\sim 75^\circ\) (0° = full extension), and the axis of rotation of the dynamometer was aligned with the lateral femoral condyle. Straps were applied to the pelvis and torso to stabilize the subject. For isokinetic testing protocols, the axis of rotation was aligned with the lateral femoral condyle. To prevent fatigue, a minimal rest of 2 min was allowed between all maximal efforts.

Experiment 1

Purpose. The aim of the first experiment was to investigate voluntary activation levels of the quadriceps muscle during lengthening, isometric, and shortening contractions by using the superimposed stimulation technique.

Subjects. Ten healthy subjects, six men and four women, with a mean ± SD age of 28 ± 8 yr, height 179 ± 12 cm, and weight 74 ± 9 kg, participated in this experiment. All were regularly active with a mean of 6 training h/wk.

Electrical stimulation. To determine the voluntary activation level of the quadriceps muscle, a superimposed nerve stimulation technique was used. In the present study, a triplet was used instead of a twitch (e.g., Refs. 3, 5), as it has been shown that the variability in superimposed torque is reduced with increasing number of stimuli (33). By using a twitch, superimposed torques may sometimes appear absent, although this may be due to the insensitivity of the method because of the small, transient extra torque rather than complete activation (21). Consequently, this may overestimate the voluntary activation level.

Electrical stimulation was applied to the femoral nerve during maximal voluntary knee extension efforts (isometric and isokinetic) and when the muscle was relaxed. A constant-current stimulator (model DS7, Digitimer, Hertfordshire, UK) was used with self-adhesive surface electrodes (Schwa-Medico, Nieuw Leusden, the Netherlands) placed on the skin. The cathode (5 × 5 cm) was placed in the trignum femorale to stimulate the nervus femoralis; the anode electrode (8 × 13 cm) was placed on the most prominent part of the m. vastus medialis. The exact location for the stimulating electrode on the nerve was determined by using a ball probe electrode. Pulses of 30–50 mA were applied, and a different electrode position was used for each twitch. The smallest electrode was located at the position of the probe, which gave the largest visible muscle contraction. To determine voluntary activation level during maximal attempts, three square-wave pulses (triplet) of 200 μs were delivered to the muscle at a frequency of 300 Hz, with the use of supramaximal current. Maximal current was determined, by using the triplet, by raising the current until isometric torque at optimum knee angle did not increase further. The current was then increased by a further 20 mA to ensure supramaximality. In the second session, the current was determined again. The mean current used was 162 ± 26 mA, and the applied triplet evoked a muscle contraction of \(\sim 40\%\) of maximal voluntary isometric torque. To increase the reproducibility of the electrode positioning, the positions of the electrodes were marked on the skin before they were removed in the first session.

Most of the subjects had experienced electrical stimulation before. In the subjects who had not, the intensity of stimulation was gradually increased to accustom them to the sensation.

Isometric exercise. In the first session, the torque-knee angle relationship was determined. Subjects performed maximal isometric knee extension contractions at 90, 80, 70, 60, 50, 40, and 30° knee flexion angle (0° = full extension) in a randomized order. One maximal effort lasted \(~3–4\) s. At each knee angle, two attempts were performed. When the torque of these two attempts differed by more than \(~10\%\), a third attempt was performed. The maximal torque reached in these attempts was considered to be the subject’s maximal isometric torque for the specific knee angle. The knee angle at which maximal torque was measured (optimal knee angle) was used for all isometric testing protocols.

Voluntary activation level was determined for isometric contractions by using superimposed stimulation. During maximal isometric knee extension contractions, triplets were elicited \(~1.5–2\) s after the start of the contraction (e.g., see Fig. 1B). Because subjects sometimes had difficulties in performing a maximal effort when a triplet was to be superimposed, several attempts had to be performed until the maximal voluntary torque (before the triplet) did not further increase (usually not more than 5 attempts). For the isometric contractions, the triplets evoked at resting muscle were applied at the same knee angle as the voluntary contractions.

Isokinetic exercise. Shortening and lengthening contractions were performed at an angular velocity of 60°/s and \(~60\)°/s, respectively, with a range of motion between 90 and 30° knee flexion angle. A small preload (25 N-m) had to be overcome to start the movement of the dynamometer lever arm. As this preload was very low, there was no isometric phase before the movement. It has been shown that preload influences the torque magnitude such that, with increasing preload, the torque increases (10). It might be hypothesized that preload could affect the amount of voluntary activation, as it has been found that motor unit activation patterns are influenced by preactivation (25). In the present study, a relatively small preload was chosen, as we aimed to investigate activation patterns of type I and II fibers during three modes of contraction (\(\sim 40\%\) of maximal voluntary preactivation) would have influenced PCr/Cr such that the results from the lengthening and shortening contractions could have been obscured by the changes elicited by the isometric phase.
As the movement was started, the dynamometer accelerated at 1,000°/s² to the preset angular velocity. Subjects performed two to four maximal lengthening or shortening attempts to get accustomed to the movement and to determine the knee angle at which maximal torque was reached. Next, superimposed stimulation was applied on maximal lengthening or shortening attempts (e.g., see Fig. 1, A and C). For each subject, superimposed triplets were triggered such that the effect of the stimulus occurred at optimal knee angle for length- and shortening contractions. For the triplets evoked in resting muscle, the leg was passively moved from 30 to 90° for the lengthening mode and from 90 to 30° for the shortening mode. Similar to the triplets superimposed on maximal efforts, the triplet in resting muscle was elicited a few degrees before optimum knee angle was reached. With the use of this protocol, the highest torque of the triplet was reached at optimum knee angle (optimum angles for the three contraction types were similar; see RESULTS).

As in the isometric contractions, subjects performed lengthening or shortening attempts until voluntary torque did not increase further.

**Torque analysis.** Maximal voluntary extension torque was the highest measured voluntary torque for lengthening, isometric, and shortening contractions, respectively. For each subject, the optimum knee angle was determined, i.e., the knee angle at which the maximal torque was reached. For the isometric contractions, the torque at the remaining knee angles was expressed relative to this maximal torque. Torque of superimposed triplet (a) for the different contraction modes was determined by subtracting the maximal voluntary extension torque during or after the triplet (just before an effect of the triplet was seen) (b) from the maximal torque evoked by the triplet (c). The superimposed torque was expressed relative to the torque of the triplet evoked on the relaxed muscle in the different modes. Maximal torque generating capacity (MTGC) of the muscle was then calculated by using the following formula:

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MTGC = \frac{b}{1 - a/\text{relaxed}}
\]

Voluntary activation level was determined as the ratio between maximal voluntary torque obtained during the measurements and MTGC. This approach to assess the voluntary activation level has been chosen to allow comparison of activation levels between experiments 1 and 2 (see EXPERIMENT 2, Torque analysis).

It must be noted that we have not corrected for the effect of muscle slack on the torque of the triplet on the relaxed muscle in the shortening mode. Neglecting this effect of muscle slack might have overestimated the MTGC and, consequently, underestimated the voluntary activation level.

Several attempts were made at each contraction mode to perform a maximal effort. For statistical analysis, we have used the attempt in which the highest voluntary torque before the triplet was reached.

**Experiment 2**

**Purpose.** The aim of the second experiment was to assess the activation pattern of type I, IIa, and IIax fibers during only 10 lengthening, isometric, and shortening contractions by using the PCR/Cr of single characterized fiber fragments as a measure for fiber activation.

**Subjects.** Five healthy subjects, four men and one woman with a mean ± SD age of 30 ± 9 yr, height 181 ± 11 cm, and weight 76 ± 8 kg, participated in this experiment. Four of these subjects (three men and one woman) also participated in experiment 1. All were regularly active with a mean of 4 training h/wk.

**Protocol.** The subjects performed three separate series of 10 maximal contractions under lengthening, isometric, and shortening conditions. Each contraction was of 1-s duration followed by 1-s rest before the next contraction. Each protocol was performed with either the right leg or the left leg. The order in which the series were performed and the leg that was tested were randomized, except that, after lengthening exercise, no other protocol was performed with that leg. Rest between series was at least 10 min. To impose the 1-s on/1-s off rhythm, an auditory signal was given during the contraction phase. Immediately after relaxation from the last contraction, a needle biopsy was taken from the m. vastus lateralis. The isometric protocol was performed at optimum knee flexion angle. The preload, range of motion, and angular velocity for lengthening and shortening contractions were the same as used in experiment 1. To be able to relate the

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**Fig. 1.** Example of torque signals of 1 subject during lengthening (A), isometric (B), and shortening (C) contractions. Torque (N•m) is shown in the bottom trace, and knee flexion angle (°) is shown in the top trace of each panel. The characters a, b, and c refer to torque of superimposed triplet, maximal voluntary torque, and maximal torque evoked by the triplet, respectively. Thick line, superimposed triplet. Note that the superimposed torque (a) in lengthening contractions was much higher than in isometric and shortening contractions.
average torque attained during the contractions to the MTGC of the muscle, activation levels during the three contraction modes were determined for both legs. This was performed in two separate sessions (presessions), which were carried out before the session in which biopsies were obtained.

**Muscle biopsy.** With the subject seated on the dynamometer and the knee in the optimum knee flexion angle, small incisions were made after local anesthesia (2% lidocaine) of the skin and fascia. Two incisions were made (one on each leg) at one-third of the distance between the lateral femoral epicondyle and trochanter major. Immediately after local anesthesia (2% lidocaine) of the skin and fascia. Two knee in the optimum knee

Fifteen muscle fragments were obtained. Each fragment was stored desiccated in tubes of which the lid was sealed with laboratory film. Each tube was placed in another small jar with some silica gel, stored desiccated in tubes of which the lid was sealed with laboratory film. Each small jar was stored in liquid nitrogen within a large jar, which was stored desiccated in a vacuum and kept at 10 °C.

The time of freezing was taken as the start of the freezing process. From each subject, a resting sample was also obtained. As two biopsies were taken from one leg, the needle was directed either proximal or distal. Biopsies were frozen in liquid nitrogen within an average of 3.8 s (range 2.2–6.7 s) from end of exercise to freezing and they were freeze-dried overnight. The freeze-dried samples were analyzed by a Mann-Whitney U-test for post hoc comparisons. For this analysis, the PCr/Cr of the three fiber populations (type I, IIa, and IIax fibers) were grouped and tested for significant differences compared with rest and among the three contraction modes (lengthening, isometric, and shortening).

To investigate the activation of the individual fiber populations (type I, IIa, and IIax fibers) during lengthening, isometric, and shortening contractions, cumulative distributions of PCr/Cr of individual fiber fragments were calculated for each fiber type, by using intervals of 0.1. To determine significant differences between activation of the fiber populations, Kolmogorov-Smirnov two-sample tests were performed on the cumulative distributions. This test detects differences in both the location and the shape of the distributions (30).

The level of significance for all statistical analysis was set at \( P < 0.05 \).

**RESULTS**

**Experiment 1**

**Optimum knee angle.** In seven subjects, the maximal torque was reached at 60° knee flexion angle. The mean ± SD maximal relative torque was obtained at 60° knee flexion angle (97.8 ± 4.1%). However, there were no significant differences with 70° (97.5 ± 2.6%) and 80° (92.4 ± 4.6%) knee flexion angle. The mean ± SD optimum angles for lengthening, isometric, and shortening contractions were not significantly different (66 ± 4, 64 ± 7, and 63 ± 7° knee flexion angle, respectively).

**Maximal voluntary torque.** Mean voluntary torque during lengthening (270 ± 55 N·m) was significantly higher than mean torque during shortening contractions (199 ± 47 N·m, \( P < 0.05 \)) but not significantly different from mean isometric torque (252 ± 47 N·m) (Fig. 2A). Mean isometric torque was significantly higher than mean torque during shortening (\( P < 0.05 \)).

**MTGC.** Mean MTGC for lengthening contractions (342 ± 68 N·m) was significantly higher than for isometric (273 ± 54 N·m, \( P < 0.05 \)) and shortening contractions (213 ± 53 N·m,
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P < 0.05 (Fig. 2A). In addition, mean isometric MTGC was significantly higher than shortening MTGC (P < 0.05).

**Triplet torque.** Mean torque of the triplet evoked in resting muscle was significantly different between all modes of contraction (respectively, 136 ± 36, 105 ± 22, and 82 ± 18 N·m for lengthening, isometric, and shortening modes; P < 0.05) (Fig. 2A). When triplet torque and maximal voluntary torque for lengthening and shortening contractions were expressed relative to their respective isometric torque, it appeared that mean relative triplet torque (128 ± 11%) was significantly higher than mean relative maximal voluntary torque (106 ± 11%, P < 0.05) for lengthening contractions but not for shortening contractions (79 ± 5 and 78 ± 7%) (Fig. 2B). This implies that voluntary activation was not complete during lengthening contractions.

**Voluntary activation level.** Mean voluntary activation level during lengthening contractions (79 ± 8%) was significantly lower than during isometric (93 ± 5%) and shortening contractions (92 ± 3%) (P < 0.05). There was no significant difference in voluntary activation level of isometric and shortening contractions. There were no differences in voluntary activation level between men and women; both groups had a mean of 79% with a SD of 10 and 6%, respectively.

**Experiment 2**

**Maximal voluntary torque.** Mean maximal voluntary torque data measured in the presessions were not different from the data measured in experiment 1: i.e., 260 ± 58, 235 ± 34, and 208 ± 39 N·m, respectively, during lengthening, isometric, and shortening contractions (one-way ANOVA). Mean maximal torque during the series of 10 lengthening, isometric, and shortening contractions was, respectively, 252 ± 61, 240 ± 20, and 213 ± 36 N·m.

**Voluntary activation level.** The mean activation levels during the series of lengthening (76 ± 12%), isometric (90 ± 9%), and shortening (91 ± 10%) contractions were not different from the voluntary activation level of the three modes of exercise obtained in experiment 1 (one-way ANOVA).

**PCr/Cr.** A total of 720 single-fiber fragments (293 type I, 289 type IIA, and 138 type IIX) was characterized and analyzed for PCr and Cr content. Figure 3A shows an example of the PCr/Cr of the different fiber fragments of one subject at rest and after exercise.

The mean PCr/Cr of all type I fibers from all subjects at rest (2.5 ± 0.6, n = 94) was significantly different from the resting values of type IIA (2.0 ± 0.7; n = 95) and type IIX fibers (2.0 ± 0.7; n = 43) (P < 0.05). There were no significant differences at rest between type IIA and IIX fibers. After the series of lengthening, isometric, and shortening contractions, the mean PCr/Cr values for the grouped fibers (regardless of type) were 1.3 ± 0.2 (n = 146), 0.7 ± 0.3 (n = 158), and 0.8 ± 0.6 (n = 184), respectively. These were all significantly different from resting values (P < 0.05) and between contraction modes (P < 0.05).

Cumulative distributions of the PCr/Cr of the individual fiber populations are shown in Fig. 4. Kolmogorov-Smirnov
and IIA fibers after shortening contractions show only a moderate rate of increase above the PCr/Cr of ~1.0. This is caused by the results of two subjects (e.g., see Fig. 3B), who show a relatively large variation in the PCr/Cr after shortening exercise compared with the other three subjects (e.g., see Fig. 3A).

**DISCUSSION**

The present study has two main findings. First, the voluntary activation level during lengthening contractions was significantly lower than during isometric and shortening contractions, without a difference between the latter two. Second, PCr/Cr values of single characterized fiber fragments obtained from needle biopsies were decreased in all fiber types after 10 brief contractions, and there was no evidence for a selective activation of type II fibers during lengthening contractions. In fact, it is quite the reverse: associated with lower voluntary activation (~76% MTGC), there was a less marked change in the PCr/Cr in the higher hierarchy type IIA fibers, as might be normally expected from the size principle (see Fig. 4).

**Neural Inhibition**

In the present study, voluntary torque during maximal lengthening contractions was not higher than isometric torque. This is in contrast to what could be expected from force-velocity relationships of isolated muscle fibers (13) and whole muscle preparations (19) in which torque during lengthening has been shown to be higher than during isometric contractions. On the other hand, our results are comparable with studies on humans that also did not find an increased torque during maximal lengthening contractions (3, 12, 36, 37). A reduced neural drive during lengthening contractions compared with isometric and shortening contractions is suggested to limit maximal voluntary torques (34, 37). Several results from the present study confirm the notion of a limited neural activation during lengthening contractions. First, direct evidence comes from the voluntary activation level calculated from superimposed stimulation. Our data show that the voluntary activation level for lengthening contractions was lower than for isometric and shortening contractions. Second, whereas voluntary torque during lengthening was not different from isometric torque, triplet torque during lengthening was 30% higher than the isometric triplet torque (Fig. 2B). Third, the triplet torque during lengthening contractions was 20% higher compared with maximal voluntary torque when they were expressed relative to isometric torque (Fig. 2B), whereas there was no difference for shortening contractions. Fourth, estimated MTGC was 27 and 62% higher in lengthening contractions compared with isometric and shortening contractions, respectively (Fig. 2A, P < 0.05).

A comparison of the data from experiment 1 can be made with a study from Babault et al. (3). They also found lower activation levels during lengthening (88.3%) compared with isometric contractions (95.2%). Although in contrast to the present findings and previous studies (2, 30), they also found a significant difference in activation levels during isometric compared with shortening contractions (89.7%).

**Activation Pattern**

A reduced neural drive during maximal attempted lengthening contractions, as demonstrated by the present study, has

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**Fig. 4.** Cumulative distribution of single-fiber PCr/Cr in type I (A), IIA (B), and IIX (C) fibers at rest (solid lines) and after a series of 10 lengthening (long dashed lines), isometric (short dashed lines), and shortening (dashed and dotted lines) contractions. At rest, curves of all fiber types were significantly different (P < 0.05). After each contraction mode, the curves of all fiber types were significantly different from rest (P < 0.05) and significantly different between contraction modes (P < 0.05). Shaded areas show that there is a less marked change in PCr/Cr after lengthening contractions for type IIX fibers compared with type I fibers.
been attributed to either preferential recruitment of type II motor units (that is, with a concomitant inhibition of type I fiber recruitment) or lower activation levels of all activated fibers (14, 34). In the present study, PCr/Cr values of single characterized fiber fragments were used to investigate the activation pattern of different fiber populations during maximal lengthening, isometric, and shortening contractions. We have calculated cumulative distributions, and a significant shift in the curve of a fiber type after exercise was interpreted as an activation of that fiber type (Fig. 4). The data show that all fiber types were active during attempted maximal lengthening, isometric, and shortening contractions because, in each fiber type, there was a significant shift in the distribution after each contraction mode. In addition, for all fiber types, there were significant differences between curves of the three modes of contractions. This was also seen in the mean decline of the PCr/Cr of grouped fiber populations, which was significantly smaller for lengthening (37%, P < 0.05) than for isometric (66%, P < 0.05) and concentric contractions (67%, P < 0.05). For lengthening contractions, it might have been expected that the cumulative distribution would show a smaller shift in the curve, because, in an earlier study on maximally stimulated rat muscle, we have shown that the PCr/Cr after 10 maximally stimulated lengthening contractions was smaller compared with shortening contractions (unpublished observation). Moreover, the mechanical data of the present study already showed that subjects had lower voluntary activation levels during lengthening contractions.

The fact that the distributions of the PCr/Cr after isometric and shortening contractions were also significantly different was less expected because voluntary activation levels were not different. Furthermore, in a study on rat muscle, we showed that there was no difference in the PCr/Cr after isometric and shortening contractions at similar relative contraction velocities of approximately one-third of optimum velocity (7a). It should, however, be noted that the cumulative distribution curves for shortening contractions are different in shape compared with lengthening and isometric contractions. This is attributed to the data of two subjects, who showed an unusually large variation in the PCr/Cr after shortening exercise (for example, see Fig. 3B). As the Kolmogorov-Smirnov two-sample test assesses the difference in both position and shape, it is most likely that the significant difference between isometric and shortening curves is caused by the change in shape. The difference in shape is mostly attributable to a lower number of fibers with PCr/Cr values around 1.0. Therefore, no strong conclusions can be made on the recruitment of fiber types during shortening contractions.

It has been suggested that, during submaximal lengthening exercise, there would be a selective activation of type II fibers and deactivation of type I fibers (17, 25, 26). However, the present study could not find evidence for this concept in attempted maximal exercise. In contrast, as can be seen in Fig. 4, the gray areas for the three fiber populations decreases from type I to Ila to IIX fibers. Thus, if there were a difference in activation between fiber types, our data seem to suggest that, in maximal attempted lengthening contractions, there is less activation of type IIX compared with type I fibers. This observation is entirely consistent with a hierarchy of fiber-type recruitment from type I to Ila to IIX.

Conclusion

The present study investigated the voluntary activation level during maximal attempted lengthening, isometric, and shortening contractions. In addition, the activation pattern of muscle fiber types was studied by using the PCr/Cr of single characterized fiber fragments as a measure of fiber activation. It was demonstrated that the voluntary activation level during maximal attempted lengthening contractions was significantly lower than during isometric and shortening contractions, whereas the degree of voluntary activation was not different between isometric and shortening contractions. The PCr/Cr of single fibers showed that there was no evidence for selective recruitment of type II fibers with concomitant derecruitment of type I fibers. In contrast, the data seem to suggest that, during maximal attempted lengthening contractions, all fiber populations were recruited, albeit at a lower rate. Furthermore, the PCr/Cr depletion pattern indicated a hierarchical pattern of motor unit recruitment.

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