Postactivation potentiation, fiber type, and twitch contraction time in human knee extensor muscles

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Hamada, Taku, Digby G. Sale, J. Duncan MacDougall, and Mark A. Tarnopolsky. Postactivation potentiation, fiber type, and twitch contraction time in human knee extensor muscles. J Appl Physiol 88: 2131–2137, 2000.—In small mammals, muscles with shorter twitch contraction times and a predominance of fast-twitch, type II fibers exhibit greater posttetanic twitch force potentiation than muscles with longer twitch contraction times and a predominance of slow-twitch, type I fibers. In humans, the correlation between potentiation and fiber type distribution has not been found consistently. In the present study, postactivation potentiation (PAP) was induced in the knee extensors of 20 young men by a 10-s maximum voluntary isometric contraction (MVC). Maximal twitch contractions of the knee extensors were evoked before and after the MVC. A negative correlation (r = –0.73, P < 0.001) was found between PAP and pre-MVC twitch time to peak torque (TPT). The four men with the highest (HPAP, 104 ± 11%) and lowest (LPAP, 43 ± 7%) PAP values (P < 0.0001) underwent needle biopsies of vastus lateralis. HPAP had a greater percentage of type II fibers (72 ± 9 vs. 39 ± 7%, P < 0.001) and shorter pre-MVC twitch TPT (61 ± 12 vs. 86 ± 7 ms, P < 0.05) than LPAP. These data indicate that, similar to the muscles of small mammals, human muscles with shorter twitch contraction times and a higher percentage of type II fibers exhibit greater PAP.

action potential; contractile properties; motor unit activation

THE FORCE OF A TWITCH CONTRACTION is increased after a brief maximum voluntary contraction (MVC) (1, 4, 8–10, 12, 13, 22, 25, 29, 30). This enhancement has been termed postactivation potentiation (PAP) (4, 24, 29, 30). The mechanism responsible for PAP is considered to be phosphorylation of myosin regulatory light chains during the MVC, which renders actin-myosin more sensitive to Ca2+ in a subsequent twitch (7, 21, 26).

The magnitude of PAP is influenced both by the methods used to evoke it and the characteristics of the muscle. Maximal (vs. submaximal) voluntary contractions lasting ~10 s cause the greatest PAP (30). The most important muscle characteristic affecting PAP is fiber type. In small mammals, the extent of twitch potentiation is much more pronounced in fast-contracting muscles with a predominance of type II fibers (18). In humans, the data correlating fiber type with PAP have not been consistent. For example, gastrocnemius, with a higher percentage of type II fibers, shows greater posttetanic twitch potentiation than soleus (28), and, in the ankle dorsiflexors, subjects with shorter twitch contraction times (presumed to be associated with a higher percentage of type II fibers) have greater twitch potentiation (19). In contrast, no correlation was found between PAP in knee extensors and the percentage of type II fibers in one knee extensor, vastus lateralis (25).

In view of the contradictory findings in human muscle, the purpose of the present study was to reexamine the correlation between fiber-type distribution and PAP. We chose to study the knee extensors for three reasons. First, it is possible in this muscle group to measure twitch contraction time, an indirect measure of fiber-type distribution, and correlate it with PAP as we had done previously in the ankle dorsiflexors (19). Furthermore, the PAP and twitch contraction time could be measured in the whole knee extensor muscle group. Second, one of the knee extensors, vastus lateralis, is amenable to the muscle biopsy technique, which would allow the correlation between PAP in the entire quadriceps femoris and fiber-type distribution in one of its constituent heads to be tested directly. Third, this was the muscle group in which in a previous study, in contradiction to observations in other muscles, no correlation was found between PAP and twitch contraction time was tested in a group of 20 subjects. Our hypothesis was that, in agreement with our earlier study of ankle dorsiflexors (19), PAP would be greater in muscles with shorter twitch contraction times. In the second phase of the study, the four subjects with the greatest PAP, compared with the four subjects with the lowest PAP, would have a greater percentage of type II fibers and shorter twitch contraction times.

METHODS

Subjects

Twenty men served as subjects. Their physical characteristics are given in Table 1. The subjects were free of neuromus-
maximum pre-MVC twitch response was elicited by delivering a series of single stimuli of increasing intensity until a plateau of twitch torque and muscle compound action potential (M wave) amplitude was obtained. The same stimulus intensity was used for subsequent twitches evoked after the MVC. Five minutes after the pre-MVC maximal twitch response was established, the subject performed a 10-s MVC. On the basis of previous research, the 10-s duration was considered optimal for inducing PAP of twitch peak force (30). At 5 s into the MVC, a stimulus was applied to assess the extent of motor unit activation (%MUA) according to the interpolated twitch method (3). Post-MVC twitch responses were evoked immediately (5 s) post-MVC, at 30 s post-MVC, and at 30-s intervals until 5 min post-MVC.

Measurements

MVC, twitch, and EMG responses were analyzed by a custom-designed, computer-based software program. Twitch measurements included peak torque, time to peak torque (TPT), and half-relaxation time (HRT). The peak-to-peak amplitude, duration, and area of the M wave associated with each twitch response were measured.

Muscle Fiber Characteristics

Of the 20 subjects, the four with the highest (HPAP) and the four with the lowest (LPAP) PAP immediately after a 10-s MVC were identified. Percutaneous needle biopsies were obtained from vastus lateralis of these eight subjects by using manual suction and under local anesthesia. Care was taken not to infiltrate the muscle fascia with lidocaine (2%, no epinephrine), and the needle was inserted 15 cm proximal to the lateral knee joint line and inserted 4.5 cm deep to the fascia. With the aid of a stereomicroscope, tissue was mounted on cork blocks (optimum cutting temperature embedding medium) with the fiber orientation perpendicular to the cork base so that cross sections could be cut and frozen in isopentane cooled in liquid nitrogen. Serial sections of 10-µm thickness were made in a cryostat (−40°C) and mounted on glass slides. The samples were then stained for myofibrillar ATPase after separate preincubations of pH 4.3, 4.6, and 10.3 according to the methods described by Brooke and Kaiser (5). Tissue sections were photographed under a light microscope, and measurements were made on projected slides. Cross-sectional fiber areas were measured by using a custom-made computerized digitizer. Fiber-type distribution was determined by counting an average of 1,020 (range 600–1,640) fibers per subject, and fiber areas were measured on an average of 114 ± 43, 103 ± 18, and 87 ± 33 type I, IIa, and IIb fibers, respectively.

Statistics

For the data obtained in all 20 subjects, a one-factor (time) repeated-measures ANOVA was used to test whether the 10-s MVC changed the twitch contractile properties and M-wave characteristics at the various time points post-MVC. When significant main effects were found, Tukey’s post hoc test was used to determine significant differences between the pre- and post-MVC values. To compare the characteristics of the two subgroups of four subjects (LPAP and HPAP), a one-factor (between-group) ANOVA was used. To compare the PAP responses in the two subgroups, a two-factor (between-group, within-time) ANOVA was done on the percent changes from the pre-MVC values. When significant interactions were found, Tukey’s post hoc test was used to determine significant differences between group mean values. Some measures were correlated with others by using the Pearson correlation (r).
Statistical significance was set at \( P \leq 0.05 \). Descriptive statistics include mean and standard deviation (SD) or standard error (SE).

**RESULTS**

Observations in All 20 Subjects

Right knee extensor maximal isometric peak torque (i.e., MVC) and motor unit activation are given in Table 1. Pre-MVC twitch contractile properties and M-wave characteristics are shown in Table 2.

Post-MVC twitch contractile properties. Immediately (5 s) after the 10-s MVC, the PAP of twitch peak torque ranged from 34 to 114\%, with a mean \pm SD of 70.6 \pm 22.5\%. From the initial maximum, peak torque then rapidly declined but was still elevated (\(-12\%\)) above the pre-MVC value after 5 min (Fig. 1A). By comparison, the immediate maximum potentiation of M-wave amplitude was much smaller (\(7 \pm 4\%\)), and it was not significantly elevated beyond the first minute (Fig. 1A). TPT and HRT showed initial decreases, followed by increases back to within a few percent of the pre-MVC values (Fig. 1B).

Correlations. There was a significant negative correlation between PAP and TPT; that is, shorter TPT was associated with greater PAP (Fig. 2A). In contrast, the correlation between PAP and HRT was not significant (Fig. 2B). There was a significant negative correlation between PAP and pre-MVC twitch-to-MVC peak torque ratio (\(r = -0.73, P < 0.001\)). There was a significant positive correlation between PAP and MVC peak torque expressed absolutely (\(r = 0.48, P < 0.05\)), but, when peak torque was expressed per kilogram body mass, the correlation was not significant. There was no correlation between PAP and %MUA.

Comparison Between LPAP and HPAP Groups

The four subjects with the lowest (43 \pm 7\%) and highest (104 \pm 11\%) (\(P < 0.001\)) immediate (5 s) PAP formed the LPAP and HPAP groups, respectively. Their physical characteristics, strength performance, and motor unit activation are reported in Table 1. There were no significant group differences in the physical characteristics, although on average HPAP subjects were \(-10\) cm taller and had \(-10\) kg greater body mass. HPAP had greater absolute MVC peak torque but not greater torque expressed relative to body mass. HPAP and LPAP did not differ significantly in %MUA during the MVC.

Pre-MVC twitch contractile properties and M-wave characteristics. As shown in Table 2, LPAP had greater (22\%) twitch peak torque, whereas HPAP had shorter TPT (29\%). The groups did not differ significantly in HRT or M-wave characteristics. LPAP had a greater twitch-to-MVC peak torque ratio.

Muscle fiber characteristics. Table 3 shows that LPAP and HPAP did not differ significantly in type I fiber area of vastus lateralis; however, HPAP had greater type II (36\%), IIA (32\%), IIB (40\%), and mean (I + II, 23\%) fiber areas and a greater II to I area ratio than LPAP.
HPAP had a significantly greater percentage of type II, IIA, and IIB fibers as well as a greater percent type II fiber area.

Post-MVC twitch contractile properties. For representative subjects of the LPAP and HPAP groups, sample recordings of pre- and immediate (5 s) post-MVC twitch responses are shown in Fig. 3. These representative subjects are characteristic of the group results, namely, LPAP’s greater pre-MVC twitch peak torque, but HPAP’s much greater amount of PAP. The group results for the amount of PAP of twitch peak torque are shown in Fig. 4A. HPAP had significantly greater PAP throughout the first 2.5 min of the 5-min testing period. In TPT and HRT, HPAP tended to show greater initial decreases post-MVC and generally lower values relative to the pre-MVC values (Fig. 4, B and C); however, only in TPT was there a significant group difference (Fig. 4B).

Post-MVC M-wave characteristics. Sample pre- and post-MVC M-wave recordings are shown in Fig. 3. HPAP had a greater general increase than LPAP in post-MVC M-wave amplitude (Fig. 5A) and area (Fig. 5C), but not duration (Fig. 5B), during the 5-min post-MVC period.

DISCUSSION

The present study provided two independent lines of evidence indicating a relationship between PAP and fiber-type distribution. The first evidence was that HPAP had a significantly greater percentage of type II fibers and a greater percent type II fiber area than LPAP. It is notable that, although PAP was a measure of the entire quadriceps, fiber-type distribution was determined in only one head of quadriceps, vastus lateralis. When this finding is considered along with the sampling error of determining fiber-type distribution from a single biopsy sample and the small number (4) of subjects per group, the large and highly significant group differences in percentage of type II fibers and type II fiber area are all the more remarkable.

The second evidence indicating a relationship between PAP and fiber-type distribution was the inverse correlation between PAP and pre-MVC twitch TPT found in the entire group of 20 subjects studied. Although TPT is an indirect measure of fiber-type distribution, there is the advantage that TPT, like PAP, is measured in the whole knee extensor muscle group. Our assumption that short TPT reflects a high percentage of type II fibers was supported by the HPAP-LPAP subgroup comparison in these measures; HPAP had both significantly greater percentage of type II fibers and shorter TPT.

Our findings in humans are in agreement with observations in small mammals (18). In the latter, the greater potentiation in type II muscle fibers is associated with greater phosphorylation of myosin regulatory light chains (18), the likely mechanism of potentiation (7, 26). On the other hand, previous observations in humans are equivocal with regard to the correlation between potentiation and fiber-type distribution. Gastrocnemius, which has a higher percentage of type II fibers than soleus (2), has greater posttetanic twitch potentiation than soleus (28). In the ankle dorsiflexors there is an inverse correlation between twitch rise time and postactivation twitch potentiation (10), but this trend is not evident in the quadriceps muscle group.

Table 3. Vastus lateralis muscle fiber characteristics in LPAP and HPAP groups

<table>
<thead>
<tr>
<th></th>
<th>LPAP (n = 4)</th>
<th>HPAP (n = 4)</th>
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<tbody>
<tr>
<td>Fiber area, µm²</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type I</td>
<td>4544 ± 240</td>
<td>4923 ± 266</td>
</tr>
<tr>
<td>Type II</td>
<td>5130 ± 730</td>
<td>6964 ± 749*</td>
</tr>
<tr>
<td>Type IIA</td>
<td>5495 ± 734</td>
<td>7261 ± 724*</td>
</tr>
<tr>
<td>Type IIB</td>
<td>4764 ± 781</td>
<td>6666 ± 823*</td>
</tr>
<tr>
<td>Mean (Ⅰ+Ⅱ)</td>
<td>4837 ± 472</td>
<td>5943 ± 264†</td>
</tr>
<tr>
<td>II/I ratio</td>
<td>1.13 ± 0.13</td>
<td>1.42 ± 0.21*</td>
</tr>
<tr>
<td>Distribution, %</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type II</td>
<td>36.6 ± 6.9</td>
<td>71.8 ± 9.2†</td>
</tr>
<tr>
<td>Type IIA</td>
<td>28.6 ± 2.7</td>
<td>45.6 ± 8.8*</td>
</tr>
<tr>
<td>Type IIB</td>
<td>10.1 ± 5.8</td>
<td>26.2 ± 7.3*</td>
</tr>
<tr>
<td>Type II area</td>
<td>41.4 ± 8.6</td>
<td>78.8 ± 5.6*</td>
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Values are means ± SD. *P < 0.05, †P < 0.01, ‡P < 0.001 for difference between LPAP and HPAP subgroups.
and posttetanic twitch potentiation (19). In contrast, no correlation was found between PAP in knee extensors and the percentage of type II fibers or amount of myosin phosphorylation in vastus lateralis; moreover, similar increases in phosphorylation in one fast and two slow myosin light chains were observed (25).

In regard to the correlation between PAP and fiber-type distribution, the contrast in results between the present study and the aforementioned study of knee extensors (25) is of interest because both studies used the same method for inducing potentiation (10-s MVC), recorded maximal twitch responses at the same joint angle (90°), evoked the first post-MVC twitch almost immediately after the MVC (2 vs. 5 s), and obtained biopsy samples from the same muscle (vastus lateralis). It is therefore difficult to account for the contradictory findings and conclusions of the two studies. Some differences between the studies can be identified, however. First, in a sample of 22 subjects, Stuart et al. (25) observed a mean (± SD) PAP of 60 ± 10% (estimated from their Fig. 1, 90° angle). The coefficient of variation (CV = (SD/mean) × 100), an indication of intersubject variability, was ~ 15%. In our study of 20 subjects, PAP was 71 ± 23% with a larger CV of 32%. In the LPAP and HPAP subjects combined (n = 8), mean PAP was 73 ± 34% with a large CV of 46%. In the study of Stuart et al. (25), the percentage of type II fibers was determined in 18 subjects; the mean was 47 ± 6% with a CV of 13% and a range of 37–65%. In the present study, the corresponding mean in eight subjects (LPAP + HPAP) was 55 ± 19% with a CV of 35% and a range of 30–84%.

Thus, in both PAP and fiber-type measures, the present study had a greater range and/or overall intersubject variability. If a correlation exists between two variables, it is more likely to be revealed in subject samples with a larger intersubject variability and range. Therefore, our success and the previous study’s failure to find a significant correlation between PAP and percentage of type II fibers may be partly due to our greater intersubject variability in both measures.

A second difference was that the present study used male subjects, whereas in the other study (25) all but 2 of 22 subjects were female. It is not clear how gender might have affected the correlation between PAP and fiber-type distribution. In ankle dorsiflexors, men and women had similar posttetanic potentiation, but the intersubject variability (CV = 31 vs. 11%) and range were much greater in the men (20). Therefore, the larger intersubject variability and range in PAP seen in the present study compared with the study of Stuart et al. (25) may relate partly to our use of men and their use of mainly women as subjects. On the other hand, there is no evidence that women have greater intersubject variability in fiber-type distribution (23).

The third and perhaps most important difference between the studies was the selection of subjects for muscle biopsies. Stuart et al. (25) obtained muscle biopsies in 18 of their 22 subjects, whereas only 8 of 20 subjects underwent biopsies in our study. Furthermore, these eight subjects were the four with the lowest and highest PAP. The design ensured the greatest possible differences in PAP. Our plan was to obtain biopsy
When MVCs are used to induce PAP, the %MUA achieved during MVCs would be expected to affect the magnitude of PAP (30). In particular, failure to fully activate high-threshold motor units composed of type II fibers would reduce the magnitude of PAP. In the present study, most subjects achieved a high level of motor unit activation, and there was relatively small intersubject variability. Probably as a consequence of this, no correlation was found between %MUA and PAP in the entire group of 20 subjects. In addition, HPAP and LPAP subgroups did not differ significantly in %MUA.

PAP is usually accompanied by a decrease in TPT and HRT (1, 8, 15, 16, 19, 22), and this was also observed in the present study. Like the potentiation of twitch force, the decrease in TPT was more pronounced in the HPAP group, suggesting that this feature of PAP is also affected by fiber-type distribution. The mechanism responsible for the correlation between percent-

![Fig. 4. A: effect of 10-s MVC on PAP of twitch peak torque in 5-min post-MVC period. There was a significant group × time interaction (P < 0.001). *P < 0.05, significantly different from pre-MVC value. **P < 0.01, significantly different from LPAP value. B: effect on TPT. There was a significant group main effect but no group × time interaction; therefore, no mean comparisons were made. C: effect on HRT. There was no significant group main effect or group × time interaction. Values are means and SE.

![Fig. 5. Post-MVC M-wave characteristics. A: HPAP had generally greater elevation of M-wave amplitude (main effect, *P < 0.05). B: no group main effect or group × time interaction in M-wave duration. C: in M-wave area, there was a significant group × time interaction (P < 0.001). *P < 0.05, significantly different from pre-MVC value. **P < 0.01, significantly different from LPAP value. Values are means and SE.](http://jap.physiology.org/)
age of type II fibers and greater shortening of TPT (i.e., greater rate of twitch force development) is likely the same as for greater potentiation of twitch force; namely, greater phosphorylation of myosin regulatory light chains (27). In contrast, the decrease in HRT was not greater in HPAP. Also in contrast to what was found for pre-MVC TPT, pre-MVC HRT did not differ significantly between HPAP and LPAP, and there was no correlation between pre-MVC HRT and PAP in the whole group or 20 subjects. In the human dorsiflexor muscles, there is a significant negative correlation between pretetanus HRT and posttetanic potentiation of twitch force, but the correlation is smaller than for TPT (19). At present we cannot explain why no correlation was found between HRT and PAP in the present study or why HPAP and LPAP did not differ significantly in HRT. The difference in results between TPT and HRT may be related to the fact that TPT is influenced by the rate of release of Ca²⁺ from the sarcoplasmic reticulum and/or its interaction with the regulatory protein troponin, whereas HRT is influenced by the rate at which the sarcoplasmic reticulum can sequester Ca²⁺.

As observed previously (11), we found an increase in the amplitude of the muscle compound action potential (M wave) after a voluntary contraction. Furthermore, the increase in M-wave amplitude was greater in the group (HPAP) with the greater PAP and higher percentage of type II fibers. The mechanism of M-wave potentiation is likely stimulation of the fiber membrane’s Na⁺-K⁺ active transport mechanism (17). Therefore, probably some characteristic of type II fiber membrane properties, such as a greater density of Na⁺-K⁺ pumps (6), may be implicated in the correlation between percentage of type II fibers and the amount of M-wave potentiation.

In conclusion, the present study has confirmed, in human skeletal muscle, the correlation between fiber-type distribution and PAP that is well established in the skeletal muscles of small mammals. Two other features of PAP, namely, shortening of twitch contraction time and amplification of the muscle action potential, are also correlated with fiber-type distribution.

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REFERENCES


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