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

TAKU HAMADA, DIGBY G. SALE, J. DUNCAN MACDOUGALL, AND MARK A. TARNOPOLSKY

Departments of Kinesiology and Medicine, McMaster University, Hamilton, Ontario, Canada L8S 4K1

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 brief maximum voluntary 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 ms 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.

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

http://www.jap.org 8750-7587/00 $5.00 Copyright © 2000 the American Physiological Society

METHODS

Subjects

Twenty men served as subjects. Their physical characteristics are given in Table 1. The subjects were free of neuromus-
Stimulation and Electromyogram Recording

Twitch contractions of the right knee extensors (quadriceps femoris) were evoked by indirect percutaneous nerve stimulation. Before the stimulating electrodes were attached to the skin, electrode gel was applied to the contact surface. The underlying skin was prepared by shaving, sanding, and rubbing with isopropyl alcohol. Two carbon-impregnated rubber stimulating electrodes were used: the cathode (4 × 7 cm) was placed on the skin over the femoral nerve in the inguinal crease, and the anode (4.5 × 10 cm) was placed over the midpoint of the thigh. The stimuli were rectangular voltage pulses of 200-µs duration, delivered from a stimulator (Devices 3072, Medical Systems). Ag/AgCl electromyographic (EMG) disposable recording electrodes (3.8 mm diameter) were applied to the skin over the belly of vastus medialis (stigmatic), ~20 mm distal and medial to the patella (reference), and on the posterolateral aspect of the thigh (ground). EMG signals were amplified (1,000×) and filtered (10 Hz to 2 kHz). AD conversion and analysis were the same as for twitch torque (see above).

Protocol

After reporting to the laboratory, the subject sat resting for ~30 min before the right leg was placed in the apparatus. A 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.

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%), II A (32%), II B (40%), and mean (I + II, 23%) fiber areas and a greater II to I area ratio than LPAP.

Table 2. Pre-MVC twitch contractile properties and M-wave characteristics in whole group and in LPAP and HPAP subgroups

<table>
<thead>
<tr>
<th></th>
<th>Whole (n = 20)</th>
<th>LPAP (n = 4)</th>
<th>HPAP (n = 4)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Twitch</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peak torque, N·m</td>
<td>44.0 $\pm$ 10.9</td>
<td>49.4 $\pm$ 4.9</td>
<td>40.4 $\pm$ 3.5*</td>
</tr>
<tr>
<td>Twitch-MVC ratio</td>
<td>0.20 $\pm$ 0.06</td>
<td>0.27 $\pm$ 0.08</td>
<td>0.15 $\pm$ 0.02*</td>
</tr>
<tr>
<td>Time to peak torque, ms</td>
<td>73.5 $\pm$ 10.8</td>
<td>85.5 $\pm$ 7.2</td>
<td>61.0 $\pm$ 11.5*</td>
</tr>
<tr>
<td>Half-relaxation time, ms</td>
<td>71.2 $\pm$ 14.2</td>
<td>69.1 $\pm$ 6.5</td>
<td>63.9 $\pm$ 9.8</td>
</tr>
<tr>
<td><strong>M wave</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peak-to-peak amplitude, mV</td>
<td>19.3 $\pm$ 3.1</td>
<td>18.4 $\pm$ 3.9</td>
<td>20.7 $\pm$ 1.7</td>
</tr>
<tr>
<td>Duration, ms</td>
<td>47.4 $\pm$ 7.8</td>
<td>53.2 $\pm$ 4.9</td>
<td>46.3 $\pm$ 6.1</td>
</tr>
<tr>
<td>Area, mV·s</td>
<td>0.19 $\pm$ 0.04</td>
<td>0.19 $\pm$ 0.04</td>
<td>0.20 $\pm$ 0.04</td>
</tr>
</tbody>
</table>

Values are means $\pm$ SD. *$P < 0.05$ for difference between LPAP and HPAP subgroups.
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 PAP (24, 25).

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

<table>
<thead>
<tr>
<th>Fiber area, µm²</th>
<th>LPAP (n = 4)</th>
<th>HPAP (n = 4)</th>
</tr>
</thead>
<tbody>
<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>
</tbody>
</table>
| I/II ratio     | 1.13 ± 0.13| 1.42 ± 0.21*|†
| Distribution, %|            |             |
| Type II        | 38.6 ± 6.9 | 71.8 ± 9.2† |
| Type IIA       | 28.6 ± 2.7 | 45.6 ± 8.8* |
| Type IIB       | 10.1 ± 5.8 | 26.2 ± 7.3* |
| Type II area   | 41.4 ± 8.6 | 78.8 ± 5.6* |

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 \[ CV = (SD/\text{mean}) \times 100 \], 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 \((\text{LPAP} + \text{HPAP})\) 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 \((CV = 31 \text{ vs.} 11\%)\) 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

![Fig. 3. Pre- (solid line) and immediate (5 s) post-MVC (dashed line) twitch (top) and M-wave (bottom) recordings from representative subjects in LPAP (left) and HPAP (right) subgroups. Note larger and more prolonged pre-MVC twitch response in LPAP subject but greater PAP in HPAP subject. These responses were typical of the two subgroups (Table 1 and Fig. 4).](http://jap.physiology.org/DownloadedFrom/)
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-

![Image 4](http://jap.physiology.org/)

**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 (P < 0.05) 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.

samples initially on these eight subjects. If a strong trend toward a significant difference in fiber-type distribution was found, biopsy samples were to be obtained from additional subjects at the two ends of the distribution of PAP to increase statistical power. However, since the findings were so striking and significant even with subsamples of four subjects, it was considered unnecessary to subject additional individuals to biopsies. It might be argued that our design of performing biopsies on the subgroups with the highest and lowest PAP “stacked the deck” in favor of a correlation between PAP and fiber-type distribution. The counterargument is that our approach only ensured a large subgroup difference in PAP. If there was in fact no correlation between PAP and the percentage of type II fibers, we would not have seen the large and significant subgroup difference in percentage of type II fibers actually found.

![Image 5](http://jap.physiology.org/)

**Fig. 5.** Post-MVC M-wave characteristics. A: HPAP had generally greater elevation of M-wave amplitude (main effect, *P < 0.05). B: there was 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.
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 pretetanous 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 Ca\(^{2+}\) 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 Ca\(^{2+}\).

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.

J ohn Moroz and Douglas Oleksuik provided technical assistance. The study was supported by the Natural Sciences and Engineering Research Council of Canada.

Address for reprint requests and other correspondence: D. G. Sale, Dept. of Kinesiology, McMaster Univ., Hamilton, Ontario L8S 4K1 Canada (E-mail: saled@mcmaster.ca).

Received 22 February 1999; accepted in final form 28 January 2000.

REFERENCES


