Postactivation potentiation in a human muscle: effect on the rate of torque development of tetanic and voluntary isometric contractions

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Baudry S, Duchateau J. Postactivation potentiation in a human muscle: effect on the rate of torque development of tetanic and voluntary isometric contractions. J Appl Physiol 102: 1394–1401, 2007. First published January 4, 2007; doi:10.1152/japplphysiol.01254.2006.—Postactivation potentiation (PAP), a mechanism by which the torque of a muscle twitch is increased following a conditioning contraction, is well documented in muscular physiology, but little is known about its effect on the maximal rate of torque development and functional significance during voluntary movements. The objective of this study was to investigate the PAP effect on the rate of isometric torque development of electrically induced and voluntary contractions. To that purpose, the electromechanical responses of the thumb adductor muscles to a single electrical stimulus (twitch), a train of 15 pulses at 250 Hz (HFT250), and during ballistic (i.e., rapid torque development) voluntary contractions at torque levels ranging from 10 to 75% of maximal voluntary contraction (MVC) were recorded before and after a conditioning 6-s MVC. The results showed that the rate of torque development was significantly increased after the conditioning MVC, but the effect was greater for the twitch (~200%) compared with the HFT250 (~17%) or ballistic contractions (range: 9–24%). Although twitch potentiation was maximal immediately after the conditioning MVC, maximal potentiation for HFT250 and ballistic contractions was delayed to 1 min after the 6-s MVC. Furthermore, the similar degree of potentiation for the rate of isometric torque development between tetanic and voluntary ballistic contractions indicates that PAP is not related to the modality of muscle activation. These observations suggest that PAP may be considered as a mechanism that can influence our contractions during daily tasks and can be utilized to improve muscle performance in explosive sports.

skeletal muscle; contractile properties; electrical stimulation

THE FORCE PRODUCED BY A MUSCLE twitch is history dependent, and its enhancement following a submaximal or maximal contraction has been referred to as postactivation potentiation (PAP; see Ref. 28). Twitch potentiation occurs both in mammalian (1, 16, 26, 33) and human muscles (2, 17, 27, 35) and is usually explained by the phosphorylation of myosin regulatory light chains (16, 26, 31, 38). This mechanism leads to a greater rate of cross-bridge attachment due to an increased sensitivity of the contractile proteins to ionized calcium (Ca^{2+}) that subsequently increases twitch force and its rate of force development (24). PAP has been largely studied in response to single and trains of electrical stimuli in mammalian preparations (1, 16, 23), and its effect on the force appeared to be restricted to twitch and tetanic contractions at low frequency (1, 33). A similar trend has been observed in human muscle as the twitch potentiated to a greater extent than a brief high-frequency train of stimuli (2, 3). This lower PAP in the latter condition can be explained by a saturation process that limits the extent of potentiation of the successive responses within the train (2, 3). A ceiling effect is indeed observed for stimulation frequencies at 20 Hz or above and could, therefore, limit the impact of PAP on voluntary contractions (3).

Compared with electrically induced contractions, less is known about the effects of PAP on voluntary contractions (28). A limited number of studies have investigated the effects of PAP on fast voluntary contractions in humans. Some of them have reported an enhanced jump performance following strong conditioning contractions (11, 13, 37). French and coworkers (11) even observed an increase in torque production during a maximal isometric knee extension without change in the electromyogram (EMG) activity, suggesting that PAP occurred within the muscle. However, a weakness of these studies is that the presence of PAP was not assessed by the recording of twitch potentiation. It is, therefore, difficult to associate these improvements in performance to PAP, especially when the increase in mechanical output occurred ~20 min after the conditioning contraction (13), an elapsed time that is usually sufficient to abolish the PAP effect (2, 22, 35). In contrast, Gossen and Sale (15) did not find any velocity or power improvement during dynamic knee extension performed against various loads, at a time when twitch torque was significantly potentiated.

As suggested by the authors themselves, the lack of improvement of muscle performance in the study of Gossen and Sale (15) may be due to the relatively long (10 s) conditioning contraction that induced fatigue and thereby have counteracted the benefit derived from PAP. Furthermore, the results could have been influenced by the selected task that involves many different muscles. It is indeed possible that small changes in the coordination between synergist and antagonist muscles contributing to the knee extension could have influenced the mechanical output and suppressed any benefit from PAP. It was thus interesting to investigate whether PAP improves the performance of the muscular system during voluntary contraction by using a shorter conditioning contraction and a smaller muscle group, such as the adductor muscles of the thumb. An advantage of hand muscles is that tetanic contraction at maximal intensity is usually well tolerated by subjects. Therefore, the main purpose of the present study was to examine the effects of PAP and its decay over time on the maximal rate of torque development during ballistic
isometric contractions, induced either voluntarily or by maximal electrical stimulation at high frequency.

MATERIALS AND METHODS

After informed consent was obtained, experiments were conducted on 10 subjects (3 women and 7 men), aged between 24 and 40 yr (28.3 ± 4.7 yr; mean ± SD). None of them presented any signs of neurological disorders. Subjects were all right handed and instructed to refrain from any heavy arm exercise 24 h before testing. They attended the laboratory on two occasions: one session consisted of testing the effect of muscle potentiation on electrically induced tetanic contractions and maximal voluntary contraction (MVC); the second session assessed the effect of muscle potentiation on ballistic isometric voluntary contractions. In the latter condition, the task consisted of brief contractions in which the subject was instructed to reach the target torque as quickly as possible and without correction. The experimental procedure was approved by the local Ethics Committee and performed in accordance with the Helsinki Declaration.

Experimental Apparatus

The subject was seated in a comfortable armchair to achieve shoulder and arm relaxation throughout the experiment. The right hand was placed horizontally and securely held in the prone position by means of a custom-made apparatus. The thumb was maintained in full extension, in the same plane as the palm, by a splint that prevented movement at the phalangeal joints of the thumb. The splint was connected to a transducer (sensitivity: 0.27 V/N; linear range: 0–15 N) to measure the torque produced during the isometric contractions. All electrically induced and voluntary contractions were elicited at a thumb angle of 50° (0° = full adduction). This angle corresponds to the optimum thumb angle for maximal adduction torque (5).

EMG Recordings

The surface EMG from the adductor pollicis muscle was recorded by means of two silver disk electrodes (8 mm in diameter), separated by 1 cm and placed over the muscle belly. The ground electrode was located on the pisiform bone, between the stimulating and EMG recording electrodes. The EMG signal was amplified (1,000×) and filtered (10 Hz–1 kHz) by a custom-made differential amplifier. The torque and the EMG signals were recorded on a computer, at a sampling rate of 2 kHz, and analyzed off-line by using the AcqKnowledge data analysis software (model MP150; Biopac System, Santa Barbara, CA).

Stimulation Procedure

The adductor pollicis muscle was stimulated by rectangular electrical pulses (0.5 ms in duration) delivered through two electrodes (silver disks, 8 mm in diameter), placed over the ulnar nerve at the wrist. A digital timer (Master-8, AMPI, Jerusalem, Israel) was used to trigger the stimulator (Grass S88K, Astra-Med, West Warwick, RI). Maximal electrical stimulation was determined by progressively increasing the intensity until the compound muscle action potential (M-wave) and the mechanical twitch reached their maximal values. The level of stimulation was then set at ~20% above maximum.

Experimental Procedure

Protocol 1: High-frequency train of stimuli. High-frequency trains of stimuli, consisting of 15 pulses delivered at a frequency of 250 Hz (HFT250), were used to induce contractions with the maximal rate of torque development in the adductor pollicis muscle (25). Before performing the conditioning MVC, we recorded the responses to three single twitches (twitch before) and one HFT250 followed after 5 s by one single twitch (twitch after). This last stimulation was used to probe the possible potentiating effect of the testing contraction itself on the twitch (Fig. 1). Thereafter, the subject performed a 6-s conditioning MVC. Its duration was based on previous studies showing that maximum PAP occurred with maximal contractions of 5- to 10-s duration (27, 35). The tests carried out during the recovery period consisted of one single twitch before, one HFT250, and one single twitch after, delivered in the following sequence: 5 s after the conditioning MVC, every min until 5 min, and after 10 min (Fig. 1A).

The HFT250 did not evoke a maximal tetanic torque plateau and consequently did not allow the investigation of the effect of PAP on...
MAXIMAL TETANIC TORQUE

The maximal tetanic torque. To address this issue, additional experiments were conducted in all subjects, during which a contraction consisting of 50 pulses at 100-Hz frequency (HFT100) was substituted for the HFT250 before and after the 6-s MVC. Furthermore, during the same session, additional experiments were carried out to assess the possible fatigue effect induced by the 6-s MVC on the subsequent recordings, and the subject produced a 3-s MVC before and after the conditioning MVC at a timing that was similar to the general experimental protocol, except that twitches were not induced. These last two experiments were performed in a random manner.

Protocol 2: Ballistic voluntary contraction. The experiment began with the recording of three MVCs separated by 2-min intervals. The largest MVC torque was taken as the maximal voluntary torque and served to calculate the target levels used in the various ballistic protocols (see below). The target torque and the actual torque produced were displayed on an oscilloscope in front of the subject. For ~10 min, subjects performed ballistic contractions at four different target levels (10, 20, 50, and 75% of MVC). To minimize any possible fatigue effect induced by this familiarization procedure, subjects were instructed to perform several sets of ~15 contractions with an interval of 3–5 s between contractions, with each set being separated by 1 min of rest. After the familiarization program, subjects rested during the placement of the stimulating and recording electrodes. This procedure lasted ~20 min, an elapsed time sufficient to abolish any potentiating effect induced by the previous contractions (2, 27, 35). Thereafter, subjects performed four distinct protocols in random order at the four previously reported target levels. The testing protocol began with the recording of three twitches (twitchbefore), five ballistic contractions reaching one of the four target levels, and followed 5 s later by a single twitch (twitchafter; Fig. 1B). After these control recordings, subjects performed the conditioning 6-s MVC, followed by one twitchbefore, five ballistic contractions, and one twitchafter. The tests during the recovery period were carried out with the same timing used for the high-frequency train protocol. To ensure that twitch parameters recovered their control values before the beginning of the next target force protocol, a minimum of 10-min rest period was given. Three twitches were elicited and measured, and the subsequent protocol began only if twitch amplitude did not differ by >5% from the initial control values.

Measurements

Electrically induced contractions. The peak torque of the twitch (Pt-before and Pt-after) and tetanus (PT) in response to HFT250, as well as the twitch contraction time (CT) and one-half relaxation time (RT1/2), were measured. The maximal rate of torque development (+dPt/dt or +dPT/dt) and relaxation (−dPt/dt or −dPT/dt) were obtained from the first derivative of the torque signal. The PAP effects on the twitch and HFT250 were measured and expressed as percentage of the control values recorded before the 6-s MVC. The potentiating effect of HFT250 or ballistic contractions, used to prove the extent of PAP on the maximal rate of torque development on the twitchnerve were expressed as percentage of the twitch elicited before (twitchbefore) the HFT250 or ballistic contractions. For electrically induced contractions, the M-wave peak-to-peak amplitude was measured from the EMG signal.

Voluntary contractions. The average torque value during the MVCs and the associated averaged (rectified) EMG activity were measured during 1-s epoch at the torque plateau. The peak torque and maximal rate of torque development computed by the first derivative of each ballistic contraction were measured. The aEMG activity was analyzed from its onset to the time at which the peak rate of torque development was reached. Because the ballistic contractions did not reach precisely the different target levels, we calculated the relation between the peak rate of torque development (expressed as %MVC/ms) and torque achieved during the ballistic contraction (expressed as %MVC) for each subject. As this relation was linear (r² > 0.96), we used this linear relationship for each subject to determine the PAP effect on the rate of torque development associated with the fixed target levels: 10, 20, 50, and 75% MVC.

Statistical Analysis

In protocol 1, the effects of PAP induced by the conditioning 6-s MVC or HFT250 were analyzed by a one-way ANOVA with repeated measures over time. A Dunnett post hoc test was used to identify the significant differences among the selected means when the ANOVA reached a significant value. The effect of PAP on the HFT100 and 3-s MVCs was analyzed by a two-way ANOVA (contraction type × time). In protocol 2, the effect of PAP induced by the conditioning 6-s MVC or ballistic contractions was analyzed by a two-way ANOVA (torque level × time) with repeated measures on both factors. In the last two analyses, a Tukey post hoc test was used to identify the significant differences among the selected means. The linear regressions between torque and rate of torque development for the ballistic contractions were compared by a repeated-measures analysis of covariance (rate of torque development × time, with torque level as covariate) and Dunnett post hoc test. For all comparisons, the level of statistical significance was set at P < 0.05. Data are reported as means ± SD within the text and displayed as means ± SE in Figs. 2, 3, 5, 6, and 7.

RESULTS

Reproducibility of the Conditioning MVC

During the various experimental protocols, each subject had to perform a total of seven conditioning MVCs. Because the MVC torque and associated aEMG did not differ from trial to trial (P = 0.50 and 0.78, respectively), data were collapsed across contractions. The average MVC torque produced by the thumb adductor muscles was 10.3 ± 3.9 N.m, and the aEMG activity was 168.2 ± 136.3 μV.

PAP and Muscle Twitch

The mean characteristics of the twitch before the conditioning 6-s MVC (twitchbefore) are reported in Table 1. Before the conditioning contractions, no significant difference (ANOVA; P > 0.05) was found between the parameters of the twitchbefore recorded in the two protocols (HFT250 and ballistic contractions). Immediately after the conditioning MVC, Pt-before, and its rate of torque development (+dPt/dt), and of relaxation (−dPt/dt), recorded during the HFT250 protocol, were potentiated and reached 280.0 ± 67.8, 297.1 ± 75.8, and 311.6 ± 84.9% of control values, respectively (Dunnett post hoc test; P < 0.001). For the ballistic contractions protocol, there was no significant difference in the extent of PAP (torque level × time: P > 0.05), and, therefore, data were collapsed across intensities. The average potentiation of Pt-before, +dPt/dt, and −dPt/dt recorded immediately after the conditioning MVC reached 254.4 ± 78.8, 281.6 ± 97.8, and 287.9 ± 90.8% of control values, respectively (Dunnett post hoc test; P < 0.001). There was no significant difference in potentiation for these parameters between HFT250 and ballistic contraction protocols (ANOVA; P > 0.05). For both protocols, potentiation was maximal immediately after the conditioning MVC, declined rapidly during the 1st min of the recovery period and then more slowly, to return to control values within 10 min (Fig. 2). In contrast, CT, RT1/2, and M-wave amplitude were not affected by the conditioning MVC (P > 0.05).

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Table 1. Mechanical parameters for the twitch before, tetanic contraction at 250 Hz, and ballistic voluntary contractions for different target levels before the conditioning MVC

<table>
<thead>
<tr>
<th></th>
<th>Twitchbefore</th>
<th>Tetanic Contraction (250 Hz)</th>
<th>Ballistic Voluntary Contraction</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>10% MVC</td>
<td>20% MVC</td>
</tr>
<tr>
<td>Torque, N·m</td>
<td>0.7 ± 0.2</td>
<td>1.6 ± 0.4</td>
<td>3.6 ± 0.9</td>
</tr>
<tr>
<td>CT, ms</td>
<td>72.9 ± 11.3</td>
<td>106.3 ± 14.4</td>
<td>109.7 ± 17.7</td>
</tr>
<tr>
<td>RT1/2, ms</td>
<td>68.8 ± 15.3</td>
<td>81.6 ± 15.0</td>
<td>77.6 ± 8.8</td>
</tr>
<tr>
<td>+dTorque/dt, N·m/s^-1</td>
<td>15.6 ± 2.5</td>
<td>30.8 ± 10.8</td>
<td>62.5 ± 18.7</td>
</tr>
<tr>
<td>–dTorque/dt, N·m/s^-1</td>
<td>6.4 ± 2.2</td>
<td>17.2 ± 6.8</td>
<td>38.1 ± 10.0</td>
</tr>
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</table>

Values are means ± SD for 10 subjects. Twitch data have been collapsed across the different protocols. Twitchbefore, response to Twitches before protocol; MVC, maximal voluntary contraction; CT, contraction time; RT1/2, one-half relaxation time; +dTorque/dt, peak rate of torque development; –dTorque/dt, peak rate of torque relaxation.

The muscle twitches (twitchafter) that followed each HFT 250 and ballistic contractions were also affected by this previous activity. In the control conditions, Pafter reached 133.3 ± 5.4% of the Pbefore after the HFT 250 (Dunnett post hoc test, P < 0.01). A similar finding was observed after the ballistic voluntary contractions. However, PAP extent of the twitchafter was greater (Tukey post hoc test; P < 0.01) for contractions at 75% MVC (149.7 ± 32.3%; P < 0.01) compared with that at 50% MVC (118.1 ± 8.1%; P < 0.01), 20% (118.4 ± 22.2%; P < 0.01), and 10% MVC (107.3 ± 11.1%; P > 0.05; Fig. 3). Following the 6-s MVC, the extent of twitchafter potentiation induced by the HFT 250 and ballistic contractions at 75% MVC dropped to 91.2 ± 8.1% (P < 0.01) and 89.2 ± 12.5% (P < 0.01) of Pbefore, respectively, with similar patterns for ballistic contractions at lower target levels. Except for ballistic contractions at 75% MVC (Fig. 3) that remained reduced until the 5th min of the recovery period (Tukey post hoc test; P < 0.001), the potentiating effect of HFT 250 and ballistic contractions returned to their initial values (Dunnett and Tukey post hoc tests; P > 0.05) within 1 min after the conditioning MVC.

PAP and HFT 250

Figure 4A illustrates the mechanical and electrical responses to a 15-pulse, 250-Hz train before and 1 min after the 6-s MVC. Before the conditioning MVC, the average torque was 7.0 ± 1.8 N·m (~68% MVC), and the associated rate of torque development reached 107.8 ± 9.3 N·m·s^-1 (Table 1). Immediately after the conditioning MVC, the tetanic torque did not change significantly, whereas 1 min later, the torque increased to 112.5 ± 6.6% of the control value (Dunnett post hoc test; P < 0.01) and remained potentiated until 5 min after the MVC.

![Fig. 2. Time course of postactivation potentiation for peak torque of twitchbefore (Pbefore, A) and its first derivative (+dP/dt:before, B) during HFT 250 (○) and ballistic (●) protocols. Data from the protocol using voluntary contractions have been collapsed across intensities. In inset, twitch torque traces before and 5 s after a 6-s MVC from one subject are superimposed. Values are means ± SE; n = 10 subjects. *Significant difference (P < 0.01) with control values.](http://jap.physiology.org/)

![Fig. 3. Time course of postactivation potentiation for peak torque of twitchafter (Pafter, A) and its first derivative (+dP/dt:after, B) both expressed as percentage of the twitchbefore during HFT 250 (○) and ballistic contractions at 75% MVC (●) protocols. CON, control. Values are means ± SE; n = 10 subjects. Significant difference (P < 0.01) with control values for ✱HFT 250 and ✱voluntary protocols.](http://jap.physiology.org/)
decreased exponentially as the torque attained during the ballistic contraction increased (Fig. 7). In addition, the rate of torque development for ballistic contractions at 10 and 20% MVC was still potentiated 2 min after the conditioning MVC (Tukey post hoc test; \( P < 0.01 \)), whereas those for contractions at 50 and 75% MVC were only significantly (\( P < 0.05 \)) potentiated up to 1 min after the conditioning MVC (Tukey post hoc test; \( P < 0.05 \)).

**PAP and MVC or HFT\(_{100}\)**

In control condition, the average maximal torque developed in response to a 50-pulse 100 Hz was \( 7.8 \pm 2.1 \) N.m and corresponded to \( \sim 73\% \) of the 3-s MVC torque (10.7 \pm 2.3 N.m). This MVC torque value did not differ from the torque recorded during the 6-s MVC. Immediately after the conditioning 6-s MVC, the torque developed during the HFT\(_{100}\) and the 3-s MVC was reduced (time effect; \( P < 0.001 \)) to 92.3 \pm 3.8 and 88.6 \pm 4.3\%, respectively (Dunnett post hoc test; \( P < 0.01 \)). These changes were transient since, 1 min later, the torque of both contraction types returned to control values. No potentiation of these contractions was observed throughout the recovery period.

**DISCUSSION**

To investigate the effect of a conditioning MVC on the peak rate of torque development of a subsequent contraction, we recorded the mechanical responses to a single stimulus (twitch), HFT\(_{250}\), and ballistic voluntary contractions at different torque levels. Our results show that 1) the increase of the.
rate of torque development was larger for the twitch (~200%) compared with HFT250 (~17%) or ballistic contractions (from 9 to 24% for torque levels ranging from 75 to 10% MVC); 2) twitch potentiation was maximal immediately after the conditioning MVC, whereas the rate of torque development for HFT250 and ballistic contractions was maximally potentiated 1 min post-MVC; and 3) whereas twitch potentiation declined nearly exponentially over time to disappear within the following 10 min of recovery, the rate of torque development for HFT250 and ballistic contractions declined more progressively and remained significantly potentiated during 5 and ~2 min, respectively. Although relatively small compared with the twitch, the similar extent of potentiation for the rate of torque development between electrically induced (HFT250) and ballistic voluntary contractions indicates that PAP is not related to the modality of muscle activation. To our knowledge, this is the first detailed study that reports an increased maximal rate of torque development of voluntary contractions in the presence of twitch potentiation.

**PAP and Muscle Twitch**

Muscle twitch was recorded and analyzed because it represents the most common tool to establish the presence of PAP. In the present study, twitch torque recorded after the conditioning MVC (twitch\_before) and its peak rate of torque development and of relaxation were significantly increased during 5 min following the conditioning MVC, the greatest effect being obtained immediately after the MVC. These results are in agreement with those of previous studies that reported a similar degree of PAP and decay over time (2, 3, 17, 30, 35). In our study, the time course of the potentiated twitch did not differ from the control twitch, whereas it was shown to be shortened in some previous studies (17, 27). Although we do not have a clear explanation for these contrasting results, it must be mentioned that other studies did not observe changes in twitch CT and RT\_1/2 after a conditioning contraction (2, 3, 35). Regardless, the causes of this divergence between studies, the observation that M-wave peak-to-peak amplitude was unchanged during PAP, confirms that potentiation is mainly related to intramuscular mechanisms (2, 3, 24, 26).

In control conditions, the twitch (twitch\_after) recorded after each HFT250 and ballistic contractions was used to probe the possible potentiating effect of the testing contraction itself on the twitch. Our results shows that the size of twitch\_after was also increased by these previous contractions. Such twitch enhancement, following low- or high-frequency trains of stimuli, has already been reported in mammalian (1, 16) and human muscles for various frequencies and durations of stimulation (4, 7). However, the potentiation of the twitch\_after observed after the ballistic contractions performed at intensities as low as 20% of MVC was unexpected, because Vandervoort and coworkers (35) reported that brief, voluntary isometric contractions below 75% MVC produced little or no potentiation. Our observation
that ballistic contractions at 20% of MVC induced twitch potentiation could be related to the involvement of a greater number of motor units during fast voluntary contractions compared with sustained submaximal contractions performed at similar intensities (6, 9). This enhanced motor unit recruitment involves higher force-threshold motor units (comprised of faster twitch fibers) that display greater PAP capacity than lower threshold motor units (14, 27). This potentiating effect of the testing contraction may explain why \( P_{t\text{-before}} \) did not follow a strict exponential decline during the recovery period in the present study (Fig. 2), as is the case when PAP decay is tested by single twitches only (2, 3, 17, 30). Indeed, each short train of electrical stimuli (HFT250) and the five ballistic contractions could have contributed to maintaining potentiation at a higher level and partly affected the normal PAP decay.

**PAP and Rate of Torque Development**

The most important result of this study is the potentiating effect of a 6-s MVC on the maximal rate of torque development during ballistic voluntary contractions. This finding contrasts with the lack of increase in knee extension velocity after PAP in the study of Gossen and Sale (15). The shorter conditioning contraction in our study (6 vs. 10 s) and the greater percentage of fatigue-resistant fibers in the adductor pollicis compared with the quadriceps (19) may have reduced the counteracting effects of fatigue on the benefit derived from PAP in our experimental conditions. However, our results are in agreement with results from mammalian models showing an enhanced maximal rate of isometric force development (34) and an upward shift of the load-velocity relation (16) after a 5-Hz, 20-s conditioning contraction. Furthermore, our results indicate that PAP was greater for contractions at low-torque levels, since the ballistic contractions at 10% MVC exhibited a greater potentiation of the peak rate of torque development compared with contractions at 50 and 75% of MVC. This original observation indicates that the potentiating effect on the rate of torque development is related to the torque achieved during the ballistic contraction (Fig. 7).

It was previously shown in the human tibialis anterior that the extent of PAP on the successive responses of an electrical train of stimuli declined with increased frequency of stimulation (3). Furthermore, Desmedt and Godaux (6) reported that motor unit discharge rate during ballistic isometric contractions increases with the torque reached. These observations might partly account for the slightly greater PAP effect on ballistic contractions at 10% MVC compared with ballistic contractions of higher torque levels or HFT250 (Figs. 5 and 7), since a lower motor unit discharge rate would magnify the effect of potentiation on the summation of the successive contractions compared with higher frequencies. Therefore, PAP appears to be more effective during ballistic contractions at low- than high-torque levels for the thumb adductor muscles. Because potentiation is greater for high-threshold compared with low-threshold motor units (14, 29), the greater PAP effect for ballistic contractions of low-torque level could be surprising at first. However, it has been shown that most motor units are recruited at a \( \sim 33\% \) maximal torque during a ballistic contraction in the tibialis anterior (6). As the adductor pollicis displays a narrower range of recruitment than the tibialis anterior during slow contractions (8, 32), one can expect that most motor units are recruited below a torque level of \( \sim 20\% \) during ballistic contractions. A clear understanding of PAP modulation during ballistic voluntary contractions requires further studies in relation to motor unit recruitment and rate coding.

**PAP Time Course**

Twitch torque and its peak rate of torque development (\( \text{twitch}_{\text{before}} \)) were maximally potentiated immediately after the conditioning MVC. In contrast, for both HFT250 and ballistic contractions, maximal potentiation of their rate of torque development occurred 1 min after the conditioning MVC (Figs. 5 and 6). This delayed effect could be explained by a saturation process that limits the extent of potentiation on the summation of contractions immediately after the conditioning contraction (2, 3, 7). For example, recent studies (2, 3) reported that the contribution of the third pulse in a three-pulse train (100 Hz) was depressed immediately after a 6-s MVC but slightly potentiated from the 1st to the 4th min of the recovery period. This observation suggests a ceiling effect, probably linked to the level of free cytosolic Ca\(^{2+}\) concentration immediately after the conditioning contraction (24). In the present study, this ceiling effect could have contributed to delay the increase of the torque and its rate of development by limiting the potentiation of the successive muscle activations within a HFT250 or a ballistic contraction performed immediately after the 6-s MVC. Moreover, this saturation effect may explain the delayed potentiation of the torque compared with the rate of torque development, because the greatest effect of myosin regulatory light-chain phosphorylation on isometric torque potentiation is obtained at low Ca\(^{2+}\) activation level, whereas, for the rate of torque development, it is reached at higher Ca\(^{2+}\) concentration (24).

The above discussion of a possible ceiling effect cannot, however, account entirely for the decrease of \( P_{t\text{-after}} \) compared with \( P_{t\text{-before}} \) after the 6-s MVC, because at that time the tetanic and MVC torques are also reduced. It could, therefore, be hypothesized that some other mechanisms may have interfered with PAP during the few seconds that follow the conditioning MVC. The fact that PAP may coexist with fatigue, the former delaying the latter (10, 12, 18), and the reduced torque recorded in response to the HFT100 and 3-s MVC immediately after the conditioning 6-s MVC in the present study, suggest that fatigue could have also contributed to reduce the extent of potentiation. This proposal is in agreement with a previous study showing a substantial reduction in torque output after a 10-s MVC in the adductor pollicis muscle (21). This loss in MVC torque was associated with a reduction of the torque produced in response to a 3-s tetanic contraction at 80 Hz, whereas no impairment was found in response to a tetanic contraction of similar duration at 20 Hz. Because high-frequency fatigue is transient (20, 36), it could partly explain the reduced MVC and twitch (\( P_{t\text{-after}} \)) torque immediately after the conditioning MVC, as well as the delayed maximal PAP observed for HFT250 and ballistic contractions. Regardless of the underlying mechanisms, our results indicate that the extent and time course of PAP are different for the twitch and HFT250 or ballistic contractions.

In conclusion, the main finding of the present study is the significant enhancement of the rate of torque development of tetanic and ballistic voluntary contractions associated with
PAP. Although twitch potentiation is maximal immediately after the conditioning MVC, the rate of torque development of electrically induced and ballistic voluntary contractions is maximally enhanced 1 min after the MVC and remained significantly potentiated during, respectively, 5 and 2 min. These findings suggest that PAP may be considered as a mechanism that can influence our contractions during daily tasks and can be utilized to improve muscle performance in explosive sports.

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