PASSIVE MUSCLE LENGTH CHANGES AFFECT TWITCH POTENTIATION IN POWER ATHLETES

P. Gago [1,2,3], M.C. Marques [1,2], D.A. Marinho [1,2], M.M. Ekblom [3,4]

[1] Sports Sciences Department, University of Beira Interior, Covilhã, Portugal

[2] Research Center for Sport, Health and Human Development (CIDESD)

[3] Biomechanics and Motor Control laboratory, The Swedish School of Sport and Health Sciences (GIH), Stockholm, Sweden

[4] Department of Neuroscience, Karolinska Institutet, Stockholm, Sweden.

Corresponding author:
Maria Ekblom
Postal address: The Swedish School of Sport and Health Sciences, Box 5626, 114 86 Stockholm, Sweden
Email: maria.ekblom@gih.se
Phone number: +46-812053700

Running head: Dynamic post-activation potentiation

This project was financially supported by the Swedish National Centre for Research in Sports (CIF). Paulo Gago wishes to thank the Fundação para a Ciência e Tecnologia (FCT), Portugal for the Ph.D. Grant (SFRH/BD/79184/2011). The results of the present study do not constitute endorsement by ACSM.

No conflict of interests, financial or otherwise, are declared by the authors.

Abstract

Introduction: A conditioning maximal voluntary muscle action (MVC) has been shown to induce post-activation potentiation, i.e. improved contractile muscle properties, when muscles are contracted isometrically. It is still uncertain how the contractile properties are affected during ongoing muscle length changes. The purpose of this study was to investigate the effects of a 6 s conditioning MVC on twitch properties of the plantar flexors during ongoing muscle length changes.

Methods: Peak twitch, rate of torque development (RTD) and relaxation (RTR), rising time and half relaxation time (HRT) were measured from supramaximal twitches evoked in the plantar flexors of 11 highly trained athletes. Twitches were evoked prior to a 6 s MVC and subsequently on 8 different occasions during a 10-minute recovery, for five different modes: fast lengthening, slow lengthening, isometric, fast shortening and slow shortening of the plantar flexors.

Results: The magnitude and duration of effects from the conditioning MVC were significantly different between modes. Peak twitch, RTD and RTR significantly increased for all modes but more so for twitches evoked during fast and slow shortening as compared to lengthening. Rising time was reduced in the lengthening modes, but slightly prolonged in the shortening modes. HRT was significantly reduced for all modes except fast lengthening.

Conclusion: The findings show that the effects of a conditioning MVC on twitch contractile properties are dependent on direction and velocity of ongoing muscle length changes. This may imply that functional enhancements from a conditioning MVC might be expected to be greatest for concentric muscle actions, but are still present in isometric and eccentric parts of a movement.

Key Words: potentiation; concentric: muscle strength; sports; twitch

Introduction

Post-activation potentiation (PAP) can be defined as the acute enhancement of muscle contractile properties induced by a maximal (MVC), or near maximal, voluntary contraction (5, 21, 24). Such contractions have been shown to increase the peak twitch and rate of torque development (RTD), and to decrease the time to peak (TTP) and half relaxation time (HRT) of an electrically evoked twitch in human muscles for up to 10 min (5, 24, 28, 33). Electrically evoked twitches are used to assess muscle contractile properties since they allow for isolated studies of contractile properties, whereas assessment of sports performance enhancement after a conditioning task can be caused by many factors including psychological placebo-like effects. It has been shown in humans that a brief high-intensity muscle activation can increase the phosphorylation of the myosin regulatory light chains (37) which can ultimately improve the excitation–contraction coupling and thereby modulate the cross-bridge kinetics (7, 8, 40). A few authors have shown that PAP of contractile properties in a twitch is associated with improvements in RTD in voluntary isometric muscle actions (5), and load-relationships in concentric muscle actions (4). Studies erroneously ascribe any performance enhancement found after a conditioning muscle action to changes in contractile properties, although they do not assess contractile properties in isolation (11, 22). The studies that have assessed PAP via the effects of MVCs on electrically evoked twitches have instead been mainly restricted to twitch properties of muscles contracted isometrically (5, 27, 33). In most tasks however, muscles develop force while undergoing length changes. It therefore appears important to investigate effects of PAP on contractile properties not only during isometric muscle actions but also in muscles undergoing length changes.

Caterini *et al* (10) showed that in mouse muscle, a conditioning muscle stimulation enhanced peak twitch more during muscle shortening than in a muscle held isometric. No significant changes were found during muscle lengthening. Furthermore, power production was only enhanced during fast shortening. In slow muscle shortening and lengthening, power production was reduced after a conditioning MVC. In contrast in humans, Babault *et al.* (2) concluded that 5 s after a conditioning MVC, the TTP and RTD of a quadriceps twitch were significantly enhanced both during passive shortening and lengthening. To assess potentiation of twitches performed during muscle lengthening, these authors performed the MVC with the knee set at 20˚ whereas to assess potentiation of twitches performed during shortening they performed the conditioning MVC with the knee set at 96˚. While this may be relevant for ensuring that the thixotropy of the muscle was reset to the current muscle length, it may instead be that the conditioning MVCs were not of the same magnitude for shortening and lengthening. In fact, in the same study it was shown that a twitch response assessed at 56˚ showed less potentiation when the conditioning MVC was performed at 20˚ compared to when it was performed at 96˚. This means that the comparisons between potentiation in passive shortening and lengthening were not entirely valid. Results may have been different if evoked twitch responses assessed during passive shortening and lengthening had been conditioned by an MVC performed at the same muscle length as the evoked twitches. The aim of the current study was to investigate, in athletes, if and how the amplitude and duration of changes in twitch properties seen after an isometric conditioning MVC are dependent on muscle action types (isometric, shortening or lengthening) and muscle length change velocities.

Methods

Subjects

Eleven highly trained male athletes (8 national level sprinters and 3 jumpers (age 21.4±2.6 yrs; height 186 ± 6.1 cm; mass 80.9 ± 7.9 kg; BMI 23.3 ± 1.5 kg/m^2) recruited from athletics clubs in Stockholm participated in the present study. Subjects were free from previous ankle injury and all tests were performed on the plantar flexor muscles of their right leg. All subjects provided their informed written consent prior to participation in the study. The study was approved by the local ethics committee and all procedures adhered to the declaration of Helsinki.

Experimental procedures

The experiment lasted for approximately 2.5 hours, beginning with 10 min of sub-maximal ergometer cycling to warm up. While resting, electrodes were placed on the subjects (see electrical stimulation and EMG protocol). They were then positioned in the isokinetic dynamometer (Isomed 2000, D&R Ferstl Gmbh, Henau, Germany), lying prone with their arms and hands at the side of their body. Their shoulders, hips, legs and right foot were adequately fixated, paying special attention to securely strapping the foot into the foot attachment of the Isomed 2000. The axis of the ankle joint was aligned with the rotational center of the dynamometer's shaft, and a gravity correction of the torques created by the passive weight of the foot was executed using Isomed 2000 built-in software. After these preparations, electric stimulation intensity was set (see electrical stimulation). After resting for 10 min to abolish any kind of remaining potentiation that could influence the data, five separate protocols were executed. Each protocol consisted of three supramaximal twitches, termed control twitches, (see electrical stimulation) followed by a 6-second maximal isometric contraction (6 s MVC) conditioning phase. Finally, during the proceeding 10 min of recovery, 8 subsequent twitches were evoked (Figure 1A). One protocol was performed with the foot at 90˚ (ISO mode), two performed during passive lengthening (at velocities of 30 and 60°/s) (LEN_{fast} and LEN_{slow} modes) and two during passive shortening (at velocities of 30 and 60°/s) (SHO_{fast} and SHO_{slow} modes). For each subject, the order of the five protocols was randomized. After the 10 min of recovery, approximately 2 min of further rest was given before the next protocol was initiated.

Electrical stimulation

Electrical stimulation was applied to the posterior tibial nerve using a single rectangular pulse (1 ms) delivered by a Digitimer stimulator (model DS7A, Hertfordshire, UK). A small cathode electrode (blue sensor, 7-mm diameter, Ag–AgCL Medicotest, Denmark) was positioned in the popliteal fossa after a manual location of the best stimulation zone in that area, using a custom-made stimulating pen. The anode (a 100 x 50 mm carbon rubber electrode, Cefar Medical, Sweden), was placed then taped on the anterior surface of the knee, proximal to the patella. Each subject was initially familiarized with several submaximal electrical stimuli of progressively increased intensity until the compound muscle action potential (M-wave) and the mechanical twitch reached their maximal values. The stimulation intensity was then further increased by 20% to a supramaximal intensity used in the subsequent protocol. Stimulations were always delivered with the foot at 90̊ for the isometric protocol, and at angles previously determined during pilot trials, making sure that the peak twitch occurred as the foot moved through 90̊ for the SHO and LEN modes. These settings resulted in a peak twitch angle variation between modes of 0.68 ± 2.24˚, which is in line with the values presented by Gravel et al. (17).

EMG measurements

EMG signals were recorded using circular electrodes (Blue Sensor 7-mm diameter, Ag–AgCL Medicotest, Denmark) positioned in a belly tendon configuration (2 cm below the bifurcation of the gastrocnemii muscles and in line with the achilles tendon) on the soleus muscle and along the belly of the tibialis anterior muscle. A single ground electrode was positioned over the head of the fibula. Low impedance at the skin-electrode interface was obtained by shaving and cleaning the skin with alcohol. The EMG signals were sampled at a rate of 5 kHz, amplified 200 times (NL 824, digitimer, UK), band pass filtered (30 Hz–1 kHz) (NL 125, Digitimer, UK) and converted to digital data using a 16 bit Power 1401 and Spike2 data collection system (version 6.0, Cambridge Electronic Design, UK). Using the soleus EMG signal, the peak-to-peak amplitude of the M wave associated with each twitch response was measured to ensure the effective stimulus of the nerve was not altered during the protocol.

Mechanical measurements

Torque about the ankle was measured by the isokinetic dynamometer Isomed 2000 (D&R Ferstl Gmbh, Henau, Germany) which also controlled the position and angular velocity of the foot. The torque signal was analog-to-digital converted and sampled together with the position and EMG data by a power 1401 (CED, Cambridge, England) in Spike2 software (Spike2, version 6.0, CED, Cambridge, England). The angular impulse of the conditioning MVC was calculated as the area under the torque-time curve from 80% of the peak for the rising and falling of the curve. The torque signal produced as a result of the evoked twitch was analyzed using the same software to extract the following variables: peak twitch, measured as the difference between the maximal twitch torque value and the torque value at the time of the proximal peak of the Soleus M-wave; half relaxation time (HRT), measured as the time from twitch peak torque to the return to 50% of peak torque; maximum rate of torque development (RTD) and relaxation (RTR), measured as the peak of the first derivate of the development of torque (dF/dt) and as the peak of the first derivate of decline of torque (-dF/dt), respectively; and rising time, measured as the time between 10 and 90 % of the peak twitch torque on the ascending side of the twitch (Figure 1B and C).

Statistical analyses

Statistical analysis was performed in Statistical software (Statistica,Version 10, StatSoft Scandinavia AB, Uppsala, Sweden). Normality tests were performed using Shapiro Wilks W-tests. A two-way repeated measures ANOVA was used with the factors time (prior to and at different delays after the conditioning MVC) and mode (ISO, LEN_{fast}, LEN_{slow}, SHO_{fast} and SHO_{slow}). Wherever a significant main effect or an interaction of factors was found, a Tukey HSD post-hoc test was applied. Differences were considered as significant at $p<0.05$. Furthermore, intra-class correlation coefficients (ICC_c) were calculated to assess consistency within the control twitches for each parameter and mode, and to confirm consistency of the conditioning MVC between modes.

INSERT FIGURES 1 A, B and C HERE

Results

Conditioning MVC

The mean of the area under the torque–time curve of the conditioning MVC was 1160.48 ± 50.9 Nms, with no significant differences between modes (F = 1.280; p = 0.294). The ICC_c of the conditioning MVC was 0.767, indicating that the conditioning MVCs were consistent between modes.

Peak twitch

ICC_c for the control twitch peak twitch ranged between 0.930 and 0.996 in the different modes. The absolute value of the peak twitch was significantly different between modes ($F_{4, 40}$ = 190.7), with peak twitch being greater for LEN than SHO. Furthermore, there was a significant interaction between time and mode ($F_{32, 320}$ = 13.3), indicating that the change in peak twitch over time differed between modes. Post-hoc tests showed that compared to the control twitches, the peak twitch was significantly enhanced up to 4 min after the conditioning MVC for all the angular velocities in the SHO and LEN modes, whereas in the ISO mode, the peak twitch was significantly enhanced up to 5 min after the MVC.

Mode-specific peak twitch PAP (expressed as increase in % of control twitch values) at different delays after the conditioning MVC is displayed in Figure 2. Peak twitch PAP differed significantly between modes ($F_{4, 40}$ = 68.2), and relative changes over time also varied significantly between modes ($F_{28,280}$=61.6). The average (mean of all time points) peak twitch PAP after the MVC was highest in the SHO_{fast} mode (37.1 ± 1.2%) and lowest in the LEN_{fast} mode (9.7 ± 9.4%). Post-hoc tests showed significant differences in peak twitch PAP between LEN_{fast} and LEN_{slow} at 5 s after MVC only (Figure 2). For the same angular velocity, peak twitch PAP differed significantly between SHO and LEN from 5 s to 2 min after the conditioning MVC (Figure 2). Finally, in the ISO mode, the peak twitch PAP was 67.0 ± 21.6% at 5 s and 11.0 ± 5.8% at 5 min after the MVC, sustaining significantly higher values than in the LEN_{fast} and LEN_{slow} modes, but significantly lower values than in the SHO_{fast} and SHO_{slow} modes for up to 2 min after the MVC (Figure 2).

INSERT FIGURE 2 HERE

Rate of torque development

ICC_c for the control twitch RTD ranged between 0.948 and 0.994 in the different modes. The absolute values of the RTD were significantly different between modes ($F_{4, 40}$ = 205.0), with higher RTD in LEN than SHO. An interaction between mode and time ($F_{32, 320}$ = 95.6) was also identified and post-hoc tests showed that compared to the control twitches, the RTD was significantly enhanced for 3 min for SHO, 2 min for ISO and LEN_{slow} and 4 min for LEN_{fast}.

RTD PAP (expressed as increase in % of control twitch values) at different delays after the conditioning MVC are displayed in Figure 3. RTD PAP differed significantly between modes ($F_{4, 40}$ = 12.5), and an interaction between mode and time was also identified ($F_{28, 280}$ = 11.0).

The average RTD PAP was highest in the SHO_{slow} mode 35.7 ± 37.47% and lowest in the LEN_{slow} mode 20.2 ± 26.76% (Figure 3). Post-hoc tests showed no significant differences in RTD PAP between LEN_{fast} and $LEN_{slow,}$ or SHO_{fast} and SHO_{slow} (Figure 3). For the slow angular velocity modes, RTD PAP values between SHO and LEN differed significantly from 5 s to 3 min after the conditioning MVC, whereas at the fast angular velocity they differed from 5 s to 1 min (Figure 3). Regarding the ISO mode, the RTD PAP was 102.2 ± 33.3% at 5 s and 19.9 ± 18.2% at 2 min after MVC, sustaining significantly higher values than in the LEN_{fast} and LEN_{slow} modes up to 1 min after the MVC (Figure 3).

INSERT FIGURE 3 HERE

Rate of torque relaxation

ICC_c for the control twitch RTR ranged between 0.919 and 0.984 in the different modes. The absolute values of the RTR were significantly different between modes ($F_{4, 40}$ = 50.1), with RTR being higher for LEN than SHO, and with a significant interaction between time and mode ($F_{32, 320}$ = 5.4). Post-hoc tests showed that compared to the control twitches, the RTR was significantly enhanced for up to 1 min after MVC for $SHO_{fast,}$ 2 min for SHO_{slow} and LEN_{slow}, and 4 min for ISO and LEN_{fast}.

RTR PAP (expressed as increase in % of control twitch values) at different delays after the conditioning MVC are displayed in Figure 4. RTR PAP differed significantly between modes ($F_{4, 40}$ = 6.0), and an interaction was seen between mode and time ($F_{28, 280}$ = 12.2). RTR PAP was highest in the SHO_{slow} mode (30.2 ± 34.24%) and lowest in the LEN_{slow} mode (15.6 ± 16.94%). Post-hoc tests showed significant differences between SHO_{slow} and SHO_{fast} only at 5 s after MVC (Figure 4). For the same angular velocity, SHO and LEN values differed significantly from 5 s to 1 min after the conditioning MVC (Figure 4). Finally, in the ISO mode, the RTR PAP was 66.9 ± 23.5% at 5 s and 11.6 ± 8.9% at 4 min after MVC, sustaining significantly higher values than in the LEN_{fast} and LEN_{slow} modes for up to 1 min, and significantly lower values than in the SHO_{slow} mode for up to 30 s after MVC. No significant differences were identified between the ISO mode and the SHO_{fast} mode (Figure 4).

INSERT FIGURE 4 HERE

***Rising* time$_{10\text{-}90}$**

ICC_c for the control twitch rising time$_{10\text{-}90}$ ranged between 0.875 and 0.990 in the different modes. The absolute values of the rising time$_{10\text{-}90}$ were significantly different between modes ($F_{4,\ 40}$ = 159.4), with longer rising time$_{10\text{-}90}$ for LEN than SHO. An interaction was found between time and mode ($F_{32,\ 320}$ = 5.4). Post-hoc tests showed that compared to the control twitches, the rising time$_{10\text{-}90}$ was significantly decreased from 5 s to 1 min after the MVC for ISO, LEN_{fast} and LEN_{slow} only.

Change in rising time$_{10\text{-}90}$ (expressed as increase in % of control twitch values) at different delays after the conditioning MVC are displayed in Figure 5. Change in rising time$_{10\text{-}90}$ differed between modes ($F_{4,\ 40}$ = 9.1), and an interaction was found between mode and time ($F_{28,\ 280}$ = 22.9). The mean change in rising time$_{10\text{-}90}$ was rather small, ranging from -7.1 ± 8.8% in the LEN_{fast} to 1.0 ± 2.7% in the SHO_{fast} mode. Post-hoc tests showed significant differences between LEN_{slow} and LEN_{fast} at 5 s after MVC (Figure 5) only, while for the same angular velocity, SHO and LEN values differed significantly from 5 s to 1 min after the conditioning MVC (Figure 5). Finally, in the ISO mode, the change in rising time$_{10\text{-}90}$ was -8.8 ± 8.1%, at 5s and -6.9 ± 6.9% at 1 min after MVC. The change in rising time$_{10\text{-}90}$ was lower in the ISO than the SHO_{fast} and SHO_{slow} modes for up to 30 s after the MVC, and higher in the LEN_{fast} mode for up to 30 s after the MVC. No significant differences were identified between the ISO mode and the LEN_{slow} mode (Figure 5).

INSERT FIGURE 5 HERE

Half relaxation time

ICC_c for the control twitch HRT ranged between 0.918 and 0.964 in the different modes. The absolute value of the HRT was significantly different between modes ($F_{4, 40} = 133.4$), with shorter HRT for LEN than SHO. Furthermore, an interaction between time and mode ($F_{32, 320} = 22.6$) was identified. Post-hoc tests showed that compared to the control twitches, HRT was significantly reduced for 5 min in LEN_{slow}, 30 s in ISO and $SHO_{fast,}$ and for 1 min in $SHO_{slow.}$

The change in HRT (expressed as increase in % of control twitch values) at different delays after the conditioning MVC are displayed in Figure 6. For change in HTR, a main effect of mode ($F_{4, 40} = 3.5$) and interaction between mode and time ($F_{28, 280} = 14.1$) were found. Average change in HRT was the lowest in LEN_{slow} (-9.2 ± 3.8%) and the highest in SHO_{fast} (-0.1 ± 7.3%). Post-hoc tests showed significant differences between SHO_{slow} and SHO_{fast} from 5 to 30 s after the MVC (Figure 6). HRT values during SHO_{slow} and LEN_{slow} differed significantly from 5 s to 5 min, and the same parameter during SHO_{fast} and LEN_{fast} differed from 1 to 3 min after the conditioning MVC (Figure 6). Finally, in the ISO mode, the change in HRT was -13.9 ± 14.6% at 5 s and -13.0 ± 13.1% at 30 s after the MVC, occupying a middle position in relation to $SHO_{slow,}$ presenting higher values up to 30 s and inverting to lower values from 3 to 5 min after MVC (Figure 6). Change in HRT in the ISO mode was not as pronounced as it was in SHO_{fast} mode, being significant only at 3 and 5 min after the MVC. No significant differences were found between the ISO mode and the LEN_{slow} and LEN_{Fast} modes (Figure 6).

INSERT FIGURE 6 HERE

M-wave

ICC_c of the M-Waves associated with the control twitches ranged between 0.995 and 0.999 in the different modes. The absolute value of the M-Wave was significantly different between modes ($F_{4, 40} = 15.6$), and time ($F_{8, 80} = 2.8$). However, there was no significant interaction between mode and time ($F_{32, 320} = 0.41$, $p = 0.99$). Post-hoc tests showed that compared to control values the M-wave was significantly increased by 5.9 ± 1.2% at 5 s after MVC only.

Associations between twitch properties

For all modes, the peak twitch was strongly positively correlated to the RTD and the RTR. Mode-specific correlations between peak twitch, RTD and RTR ranged from r = 0.96 to r = 0.99 ($p < 0.001$). Negative correlations were identified between RTD and rising $time_{10\text{-}90}$, for the ISO (r = -0.87, p = 0.04), LEN_{slow} (r = -0.88, p = 0.04) and LEN_{fast} (r = -0.94, $p < 0.001$) modes, whereas positive correlations were found for the SHO_{slow} (r = 0.79, p = 0.019) and SHO_{fast} (r = 0.74, p = 0.032) modes. Between RTR and HRT, an all modes negative correlation was found (r = -0.66, $p < 0.001$), whereas for the LEN_{fast} mode, no relationship was present (r = -0.005, p = 0.99).

Discussion

The main findings of the present study were that both the extent and the duration of PAP were dependent on direction and velocity of ongoing muscle length changes. Such mode specific potentiation was not found for the supramaximal M-wave. An increase in peak twitch, RTD and RTR after a 6 s MVC was present in all modes, but the largest increase relative to the control twitch values was seen in the SHO modes. There was, however, still substantial PAP during plantar flexor muscle lengthening.

Degree and duration of isometric potentiation

Human studies on muscle contractile properties during ongoing muscle length changes are rare. Therefore only results from the isometric mode could be fully compared between studies. Both the degree and the duration of the isometric potentiation seen in the current study were within the range of what has been demonstrated previously. In the isometric mode, the potentiation of peak twitch, RTD and RTR lasted for 5, 2 and 3 min, respectively. In the same muscle group, the duration of PAP has been shown to range between 5 to 10 min after a conditioning contraction (27, 38). Furthermore the duration of potentiation does not seem to be affected by muscle group since a similar duration of potentiation was observed in both knee extensors (31) and the tibialis anterior (3). The peak twitch in the isometric mode of the power athletes tested in the current study increased by 67.0 ± 21.6%; RTD by 102.2 ± 33.3% and RTR by of 66.9 ± 23.5% 5s after MVC, which appears to be greater than previously reported in most other studies (6, 13, 20, 36, 38). Ereline *et al* (13) and Hamada *et al* (20) compared potentiation in the plantar flexors of different groups of subjects and found increases in peak twitch for sedentary, active and athletic subjects of 20 to 28%; 25 to 38% and 50%, respectively. Other studies with a less homogenous sample of subjects have however reported rather high levels of peak twitch increases – a 68% increase in a mixed population (active and athletes) (35), and a 78% increase in a population of active males (27). It therefore cannot be stated that the athletes participating in the current study have higher degrees of peak twitch potentiation than the general population. Information on the effects of PAP on RTD and RTR in the plantar flexors is limited. Of the above studies, only Shima et al. (36) reported RTD values. They found an enhancement of 86% in peak RTD, i.e. less than what is presented in our study. For the quadriceps muscles of active subjects, peak twitch has been shown to increase by 48%, RTD by 87% and RTR by 102% (33) i.e. lesser increases of peak twitch and RTD but larger increases of RTR compared to our study. The quadriceps muscles are known to have a higher percentage of type 2 fibers compared to the triceps surae (14). A higher percentage of type 2 fibers has been associated with more phosphorylation of the regulatory light chains and larger amounts of PAP (19, 37). The differences seen between our data on the plantar flexors and the above-mentioned study on the quadriceps is therefore more likely related to differences in study population rather than differences in muscle group. Our isometric data further showed a significant decrease in rising time$_{10\text{-}90}$ (-8,8 ± 8,1%) and HRT (-13,9 ± 14,6%) which is consistent with the studies of Belanger *et al.* (6), Vandervoort *et al.* and Hamada *et al*. (20, 38) for contraction time and time to peak twitch. Though not significant in any of the studies investigating HRT, all of them showed a visible trend towards a shorter HRT after conditioning (20, 35, 38).

Mode dependent potentiation

In the present study, the peak twitch, RTD and RTR increased in all modes, though to different extents between modes, with potentiation lasting up to 5 min (Figures 2-4). For rising time$_{10\text{-}90}$ and HRT on the other hand, only some of the modes displayed similar behavior (Figures 5-6). Strong positive correlations were found between peak twitch, RTD and RTR, suggesting that the mechanisms underlying these parameters changed in parallel in the investigated modes. Correlations between RTD and rising $time_{10-90}$ were positive for shortning modes and negative for lengthening modes. This is likely due to the rise in peak twitch being greater than the rise in RTD in the shortening modes, whereas for the lengthening modes, the opposite was true. Most previous studies have suggested that an increase in peak twitch is associated with an increase in RTD since increased phosphorylation of the myosin regulatory light chains enhances Ca^{2+} sensitivity and rate of cross-bridge attachment causing an enhanced number of attached cross-bridges (7, 8, 15, 39). The RTR on the other hand has often, but not always, been shown to be enhanced following a conditioning MVC (24). Macintosh *et al.* (24) suggested that an increase in phosphorylation of the myosin regulatory light chains does not cause a substantial increase in the rate of cross-bridge detachment, and when a conditioning contraction enhances RTR, this could instead be linked to an increase in Ca^{2+} uptake. PAP of peak twitch, RTD and RTR were all more pronounced during muscle shortening compared to lengthening. The cross-bridge cycling mechanism has been suggested to differ between muscle lengthening and shortening (8). For example, lengthening increases the proportion of force-generating cross-bridges, possibly due to a higher resistance resulting from the binding of both myosin heads to actin (9), thus causing the twitches induced during muscle lengthening to be larger. Possible causes of differences in PAP between modes include differences in the attached number of cross-bridges in the un-potentiated state, structural differences in the series of elastic components (8, 18, 29), and/or a ceiling effect of contractile properties (29) reducing the potential for PAP during ongoing muscle lengthening. As expected, RTR was negatively correlated with HRT in all modes exept for LEN_{fast}. The reason for the lack of relationship in this mode is unclear. RTR and HRT have been suggested to be associated with the Ca^{2+} reuptake capacity of the sarcoplasmatic reticulum, $[Ca^{2+}]$ in the interfibrillar area, the capacity of troponin C to bind and release calcium (23, 24, 39), and the modulation of cross-bridge kinetics (39). The differences between modes for the HRT and RTR parameters were not expected and rather modest.

To our best knowledge, only one previous study (2) tested and compared PAP of twitches during ongoing muscle length changes in humans. Baubault *et al.* (2) investigated PAP during passive lengthening and shortening of the quadriceps muscle group. Our findings are not expected to be identical to those of Baubault *et al.* since for example: (a) different muscle groups and angular velocities were tested (b) different subjects were used (our highly trained power athletes versus their non athletes), and (c) different conditioning contraction protocols were implemented (our 6s MVC at 90˚ ankle angle versus their 3s MVC in knee flexion or extension). Despite these differences, findings were surprisingly similar with both studies showing that potentiation was indeed present also during ongoing muscle lengthening. Whereas Baubalt *et al.* reported 15% potentiation of peak twitch in slow (30˚/s) lengthening and 10% potentiation in fast (150˚/s) lengthening, the current study reported 43% and 30% for LEN_{slow} (30˚/s) and LEN_{fast} (60˚/s), respectively. One possible explanation for such dissimilarities in potentiation levels may be differences in the muscle length at which the maximal voluntary conditioning contraction was performed. An MVC performed at shorter than optimal muscle length would result in less muscle activation and therefore torque (25), thereby reducing the degree of potentiation (38). The study by Babault *et al.* (2) may therefore have underestimated the degree of potentiation during lengthening and overestimated the degree of potentiation during shortening. Our data further showed that the decay of the induced changes behaved differently between modes for the different analyzed parameters. The difference between modes was especially evident for the rising $time_{10\text{-}90}$ and HRT parameters. A few animal studies also investigated PAP under dynamic conditions (10, 16). Caterini *et al.* (10) suggested that potentiation was greater during the shortening phase than the lengthening phase in a cyclic movement, and that the potentiation was greater with higher shortening velocities. While Caterini *et al.* (10) reported no significant potentiation of peak twitch during ongoing muscle lengthening, we showed that in male power athletes, the potentiation affects contractile properties during ongoing lengthening, though to a lesser extent than in ongoing muscle shortening.

Methodological considerations

To fully understand the implications of the findings presented here a few methodological difficulties need to be discussed.

In the present study, all trials were conducted for each subject in a single session at a stable room temperature. While intramuscular temperature or skin temperature were not assessed in this study, Baudry *et al.* (3) demonstrated that a 6 s MVC did not significantly influence skin temperature, either immediately or 20 min after a conditioning contraction (3). Furthermore, Davis *et al*. (12) found that muscular heating did not significantly impact the supramaximal twitch force. Therefore it seems plausible to assume that the 6 s MVC performed by the subjects in the current study did not change their muscle temperature to a degree that might affect the data.

Another issue worth considering is that a maximal activation performed at a given muscle length could induce thixotrophic and/or hysteresis-like phenomena affecting muscle twitch contractile properties if they are assessed at another muscle length. Proske and Morgan (29, 30) found that a slack effect was generated if a muscle contraction was induced at a higher muscle length than the one tested. However, in the present study, the conditioning MVC was performed at the same angle as where the twitches were tested. Also, in the long resting period between twitches, the foot was passively positioned into the neutral position and subsequently positioned in either the dorsi or plantar flexion position only 30 s prior to a passive shortening or lengthening, respectively. Applying those maneuvers should have minimized any differences between modes in terms of thixotropic and/or hysteresis-like phenomena (1, 29, 30).

Potentiation has been shown to differ between different muscle lengths (8, 24, 32). Therefore, a pilot study was performed to gain information on how the electrical stimulation should be timed for all modes in order for the peak twitch to arrive at the neutral position. These types of adjustments, also performed by Gravel *et al*. (17), resulted in a peak twitch angle variation of 0.68 ± 2.24˚ between all modes. Thus, the differences in PAP between modes in this study are unlikely to be related to variations in muscle lengths.

In the current study, the peak twitch was measured as the difference between the maximal twitch torque and the torque at the time of the proximal peak of the Soleus M-wave. This could mean that the absolute values of the shortening peak twitches are slightly underestimated and that the absolute values of the lengthening peak twitches are slightly overestimated. This may in turn have induced a slight overestimation of potentiation in shortening modes and a corresponding underestimation of the potentiation in lengthening modes.

Implications

The present data, together with previous animal (8, 10, 16, 34), and controlled human studies (2, 4, 5), suggest that PAP is action-type dependent, but still present in all action types. Functional enhancements might therefore be expected to occur not only in isometric and concentric actions, but also in the eccentric part of the movement. Enhanced mechanical efficiency during ongoing muscle length changes might translate into both prolonged endurance (20, 26) in sub-maximal cyclic muscle actions, and into enhanced RTD and power production in explosive tasks, such as a sprint start. Further studies are required to assess if and how enhanced contractile properties seen in muscles during static and dynamic conditions can be functionally exploited for sports performance. The findings of this study also have implications for studies using the twitch interpolation technique to compare voluntary activation between action types and velocities.

Conclusion

The power athletes included in the current study showed a degree and duration of PAP that was dependent on direction and velocity of ongoing muscle length changes. PAP of contractile properties was lower during muscle lengthening than shortening for some, but not all, of the analyzed parameters suggesting that a conditioning MVC may enhance RTD and peak twitch not only in isometric and concentric conditions, but also in eccentric muscle actions for up to approximately 5 min. Future studies trying to link conditioning effects on contractile properties to effects on dynamic sports performance should consider measuring muscle contractile properties during ongoing muscle length changes instead of restricting to isometric conditions only.

Acknowledgement

The authors wish to thank Olga Tarassova for her skillful assistance in data collection for this study. The results of the present study do not constitute endorsement by ACSM.

Grants

This project was financially supported by the Swedish National Centre for Research in Sports (CIF). Paulo Gago wishes to thank the Fundação para a Ciência e Tecnologia (FCT), Portugal for the Ph.D. Grant (SFRH/BD/79184/2011).

Disclosures

No conflict of interests, financial or otherwise, are declared by the authors

References

1. Axelson HW, Hagbarth K-E. Human motor control consequences of thixotropic changes in muscular short-range stiffness. *The Journal of Physiology*. 2001;535(1):279-88.

2. Babault N, Maffiuletti NA, Pousson M. Postactivation Potentiation in Human Knee Extensors during Dynamic Passive Movements. *Medicine & Science in Sports & Exercise*. 2008;40(4):735-43.

3. Baudry S, Duchateau J. Postactivation potentiation in human muscle is not related to the type of maximal conditioning contraction. *Muscle & Nerve*. 2004;30(3):328-36.

4. Baudry S, Duchateau J. Postactivation potentiation in a human muscle: effect on the load-velocity relation of tetanic and voluntary shortening contractions. *Journal of Applied Physiology*. 2007;103(4):1318-25.

5. Baudry S, Duchateau J. Postactivation potentiation in a human muscle: effect on the rate of torque development of tetanic and voluntary isometric contractions. *Journal of Applied Physiology*. 2007;102(4):1394-401.

6. Belanger AY, McComas AJ, Elder GB. Physiological properties of two antagonist human muscle groups. *European Journal of Applied Physiology and Occupational Physiology*. 1983;51(3):381-93.

7. Brito R, Alamo L, Lundberg U et al. A Molecular Model of Phosphorylation-Based Activation and Potentiation of Tarantula Muscle Thick Filaments. *Journal of Molecular Biology*. 2011;414(1):44-61.

8. Brown IE, Loeb GE. Measured and modeled properties of mammalian skeletal muscle. I. The effects of post-activation potentiation on the time course and velocity dependencies of force production. *Journal of Muscle Research and Cell Motility*. 1999;20(5):443-56.

9. Brunello E, Reconditi M, Elangovan R et al. Skeletal muscle resists stretch by rapid binding of the second motor domain of myosin to actin. *Proceedings of the National Academy of Sciences*. 2007;104(50):20114-9.

10. Caterini D, Gittings W, Huang J, Vandenboom R. The effect of work cycle frequency on the potentiation of dynamic force in mouse fast twitch skeletal muscle. *The Journal of Experimental Biology*. 2011;214(23):3915-23.

11. Chiu LZF,FRY AC, Weiss LW, Schilling BK, Brown LE, Smith SL. Postactivation Potentiation Response in Athletic and Recreationally Trained Individuals. *The Journal of Strength & Conditioning Research*. 2003;17(4):671-7.

12. Davies CT, Mecrow IK, White MJ. Contractile properties of the human triceps surae with some observations on the effects of temperature and exercise. *European journal of applied physiology and occupational physiology*. 1982;49(2):255-69.

13. Ereline J, Gapeyeva H, Pääsuke M. Comparison of twitch contractile properties of plantarflexor muscles in Nordic combined athletes, cross-country skiers, and sedentary men. *European Journal of Sport Science*. 2011;11(1):61-7.

14. Gollnick P, Sjödin B, Karlsson J, Jansson E, Saltin B. Human soleus muscle: A comparison of fiber composition and enzyme activities with other leg muscles. *Pflugers Arch.* 1974;348(3):247-55.

15. Gordon AM, Regnier M, Homsher E. Skeletal and Cardiac Muscle Contractile Activation: Tropomyosin "Rocks and Rolls". *Physiology*. 2001;16(2):49-55.

16. Grange RW, Vandenboom R, Xeni J, Houston ME. Potentiation of in vitro concentric work in mouse fast muscle. *Journal of Applied Physiology*. 1998;84(1):236-43.

17. Gravel D, Bélanger A, Richards C. Study of human muscle contraction using electrically evoked twitch responses during passive shortening and lengthening movements. *European Journal of Applied Physiology and Occupational Physiology*. 1987;56(6):623-7.

18. Hagbarth KE, Hägglund JV, Nordin M, Wallin EU. Thixotropic behaviour of human finger flexor muscles with accompanying changes in spindle and reflex responses to stretch. *The Journal of Physiology*. 1985;368(1):323-42.

19. Hamada T, Sale DG, MacDougall JD, Tarnopolsky MA. Postactivation potentiation, fiber type, and twitch contraction time in human knee extensor muscles. *Journal of Applied Physiology*. 2000;88(6):2131-7.

20. Hamada TS, Digby G.; Macdougall,J. Duncan. Postactivation potentiation in endurance-trained male athletes. *Medicine & Science in Sports & Exercise*. 2000;32(3):403-11.

21. Jubeau M, Gondin J, Martin A, Van Hoecke J, Maffiuletti NA. Differences in twitch potentiation between voluntary and stimulated quadriceps contractions of equal intensity. *Scandinavian Journal of Medicine & Science in Sports*. 2010;20(1):e56-e62.

22. Kilduff LP, Bevan HR, Kingsley MIC et al. Postactivation Potentiation in Professional Rugby Players: Optimal Recovery. *The Journal of Strength & Conditioning Research*. 2007;21(4):1134-8.

23. Kugelberg E, Thornell L-E. Contraction time, histochemical type, and terminal cisternae volume of rat motor units. *Muscle & Nerve*. 1983;6(2):149-53.

24. MacIntosh BR. Cellular and Whole Muscle Studies of Activity Dependent Potentiation Muscle Biophysics. In: DE Rassier editor: Springer New York; 2010, pp. 315-42.

25. Maffiuletti NA, Lepers R. Quadriceps femoris torque and EMG activity in seated versus supine position. *Med Sci Sports Exerc*. 2003;35(9):1511-6.

26. Mettler JA, Griffin L. Postactivation potentiation and muscular endurance training. *Muscle & Nerve*. 2012;45(3):416-25.

27. Miyamoto N, Kanehisa H, Fukunaga T, Kawakami Y. Effect of Postactivation Potentiation on the Maximal Voluntary Isokinetic Concentric Torque in Humans. *The Journal of Strength & Conditioning Research*. 2011;25(1):186-92 10.1519/JSC.0b013e3181b62c1d.

28. O'Leary DD, Hope K, Sale DG. Posttetanic potentiation of human dorsiflexors. *Jornal of Applied Physiology*. 1997;83(6):2131-8.

29. Proske U, Morgan DL. Do cross-bridges contribute to the tension during stretch of passive muscle? *Journal of muscle research and cell motility*. 1999;20(5-6):433-42.

30. Proske U, Morgan DL, Gregory JE. Thixotropy in skeletal muscle and in muscle spindles: a review. *Progress in neurobiology*. 1993;41(6):705-21.

31. Pääsuke M, Saapar L, Ereline J, Gapeyeva H, Requena B, Ööpik V. Postactivation potentiation of knee extensor muscles in power- and endurance-trained, and untrained women. *European journal of applied physiology*. 2007;101(5):577-85.

32. Rassier DE. The effects of length on fatigue and twitch potentiation in human skeletal muscle. *Clinical Physiology*. 2000;20(6):474-82.

33. Requena B, Gapeyeva H, García I, Ereline J, Pääsuke M. Twitch potentiation after voluntary versus electrically induced isometric contractions in human knee extensor muscles. *European journal of applied physiology*. 2008;104(3):463-72.

34. Rijkelijkhuizen JM, de Ruiter CJ, Huijing PA, de Haan A. Low-frequency fatigue, post-tetanic potentiation and their interaction at different muscle lengths following eccentric exercise. *Journal of Experimental Biology*. 2005;208(1):55-63.

35. Sasaki K, Tomioka Y, Ishii N. Activation of fast-twitch fibers assessed with twitch potentiation. *Muscle & Nerve*. 2012;46(2):218-27.

36. Shima N, Rice CL, Ota Y, Yabe K. The effect of postactivation potentiation on the mechanomyogram. *European journal of applied physiology*. 2006;96(1):17-23.

37. Smith JC, FRY AC. Effects of A Ten-Second Maximum Voluntary Contraction on Regulatory Myosin Light-Chain Phosphorylation and Dynamic Performance Measures. *The Journal of Strength & Conditioning Research*. 2007;21(1):73-6.

38. Vandervoort AA, Quinlan J, McComas AJ. Twitch potentiation after voluntary contraction. *Experimental Neurology*. 1983;81(1):141-52.

39. Westerblad H, Lännergren J, Allen DG. Slowed Relaxation in Fatigued Skeletal Muscle Fibers of Xenopus and Mouse : Contribution of [Ca2+]i and Cross-bridges. *The Journal of General Physiology*. 1997;109(3):385-99.

40. Zhi G, Ryder JW, Huang J et al. Myosin light chain kinase and myosin phosphorylation effect frequency-dependent potentiation of skeletal muscle contraction. *Proceedings of the National Academy of Sciences of the United States of America*. 2005;102(48):17519-24.

Figure and table legend

Figure 1.

A) Representation of the overall study protocol. B) Example of an individual twitch showing the analyzed twitch parameters during ongoing muscle length changes: peak twitch (PT), rate of torque development (RTD), rate of torque relaxation (RTR), rising time from 10 to 90 % of the peak twitch (RT_{10-90}) and half relaxation time (HRT). C) Raw data with an example of the effects of a 6 s MVC on plantar flexor twitches in the isometric mode.

Figure 2.

Peak twitch (PT) PAP (% increase from control twitch values) at different delays after the conditioning MVC for the five different modes. Significant ($p<0.05$) differences in degree of peak twitch PAP are indicated by a # for differences between fast lengthening (LEN_{fast}) and fast shortening (SHO_{fast}); a † for differences between slow lengthening (LEN_{slow}) and slow shortening (SHO_{slow}); a **Ø** for differences between isometric and any other mode; and an **ω** for differences between velocities within the lengthening modes.

Figure 3.

Rate of torque development (RTD) PAP (% increase from control twitch values) at different delays after the conditioning MVC for the five different modes. Significant ($p<0.05$) differences in degree of peak twitch RTD are indicated by a # for differences between fast lengthening (LEN_{fast}) and fast shortening (SHO_{fast}); a † for differences between slow lengthening (LEN_{slow}) and slow shortening (SHO_{slow}); and a **Ø** for differences between isometric and any other mode.

Figure 4.

Rate of torque relaxation (RTR) PAP (% increase from control twitch values) at different delays after the conditioning MVC for the five different modes. Significant ($p<0.05$) differences in degree of RTR PAP are indicated by a # for differences between fast lengthening (LEN_{fast}) and fast shortening (SHO_{fast}); a **†** for differences between slow lengthening (LEN_{slow}) and slow shortening (SHO_{slow}); a **Ø** for differences between isometric and any other mode; and an **ω** for differences between velocities within the shortening modes.

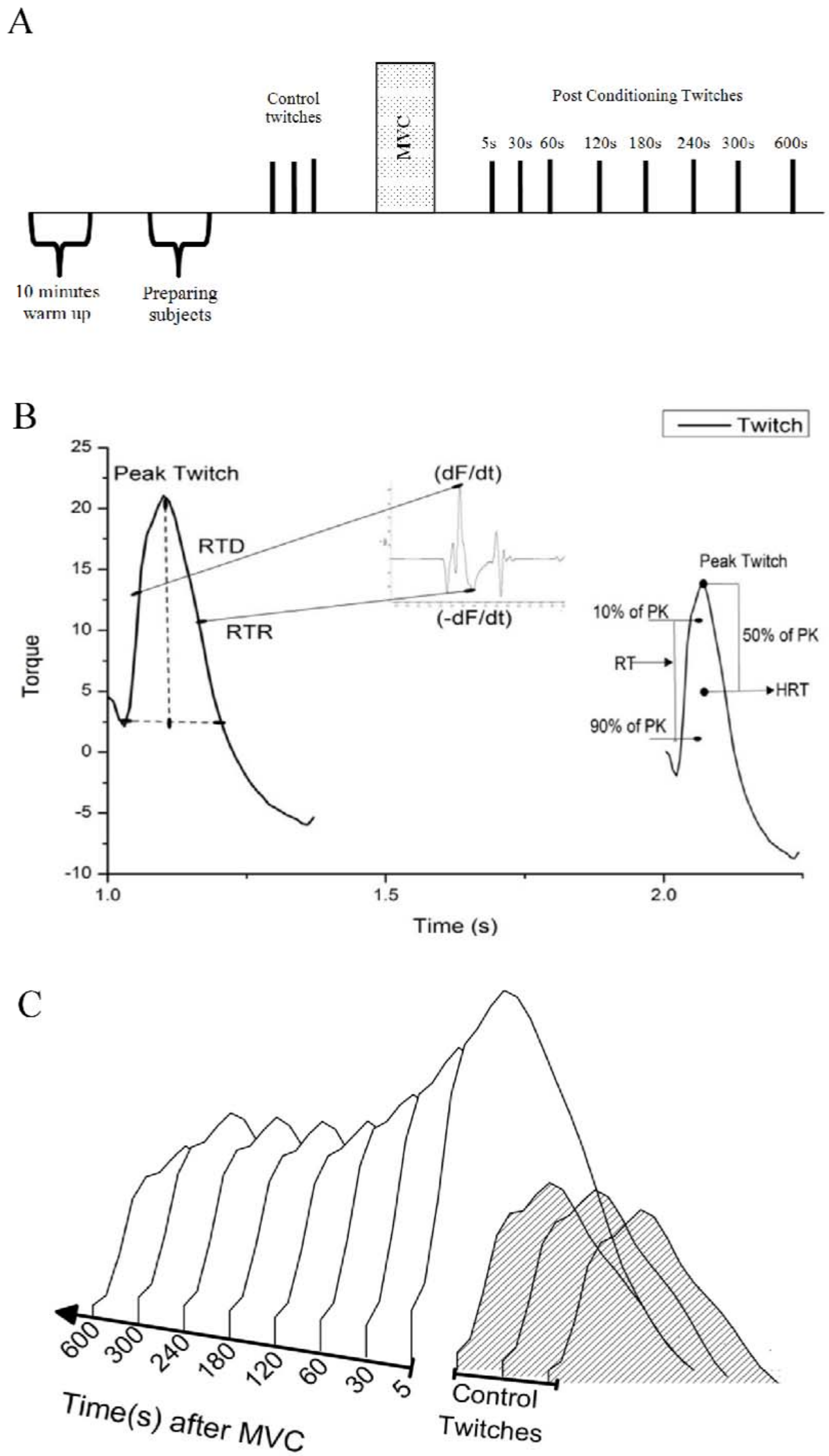
Figure 5.

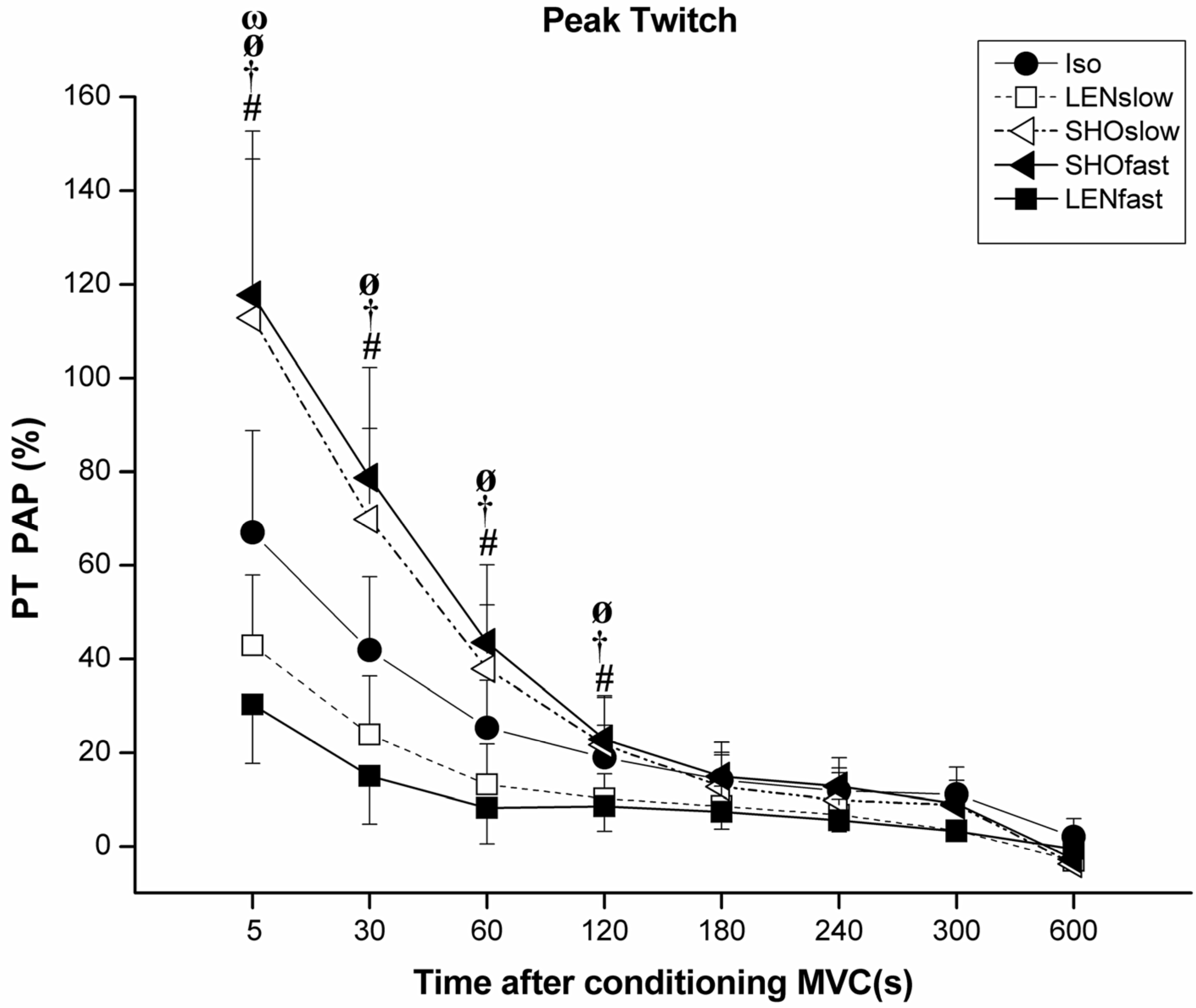
Change in rising time (RT_{10-90}) (expressed as increase in % of control twitch values) at different delays after the conditioning MVC for the five different modes. Significant ($p<0.05$) differences in degree of degree of change in RT_{10-90} are indicated by a # for differences between fast lengthening (LEN_{fast}) and fast shortening (SHO_{fast}); a **†** for differences between slow lengthening (LEN_{slow}) and slow shortening (SHO_{slow}); a **Ø** for differences between isometric and any other mode; and an **ω** for differences between velocities within the lengthening modes.

Figure 6.

Change in half relaxation time (HRT) (expressed as increase in % of control twitch values) at different delays after the conditioning MVC. Significant ($p<0.05$) differences in degree of change in HRT are indicated by a # for differences between fast lengthening (LEN_{fast}) and fast shortening (SHO_{fast}); a **†** for differences between slow lengthening (LEN_{slow}) and slow shortening (SHO_{slow}); a **Ø** for differences between isometric and any other mode; and an **ω** for differences between velocities within the shortening modes.

Figure 1


A
Control twitches
MVC
Post Conditioning Twitches
5s 30s 60s 120s 180s 240s 300s 600s
10 minutes warm up
Preparing subjects
B
Twitch
Peak Twitch
(dF/dt)
RTD
RTR
(-dF/dt)
Peak Twitch
10% of PK
50% of PK
RT
HRT
90% of PK
Torque
Time (s)
C
600 300 240 180 120 60 30 5
Time(s) after MVC
Control Twitches



Peak Twitch
Iso
LENslow
SHOslow
SHOfast
LENfast
ω
ø
†
#
160
140
120
100
80
60
40
20
0
PT PAP (%)
5
30
60
120
180
240
300
600
Time after conditioning MVC(s)

Figure 2

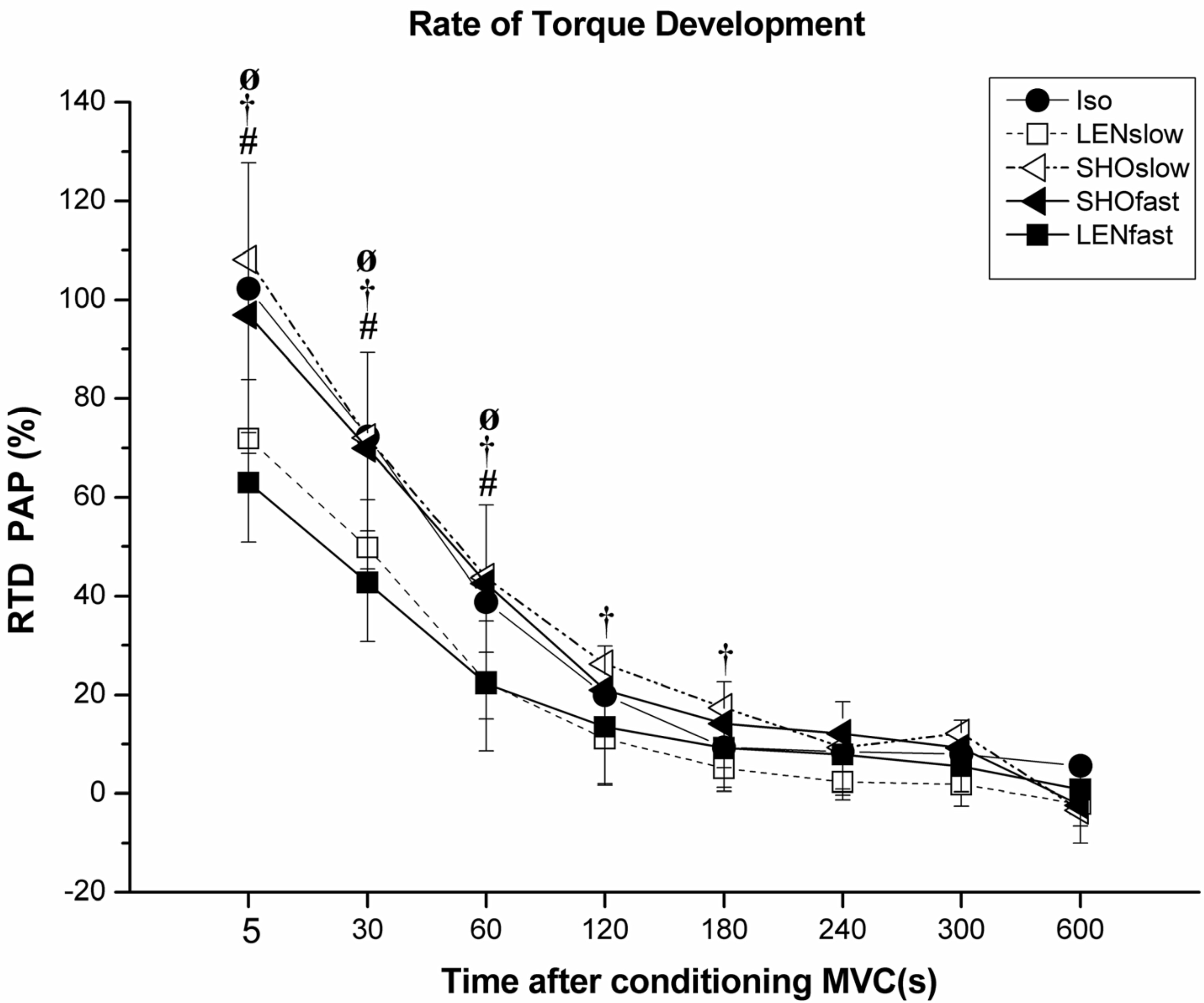
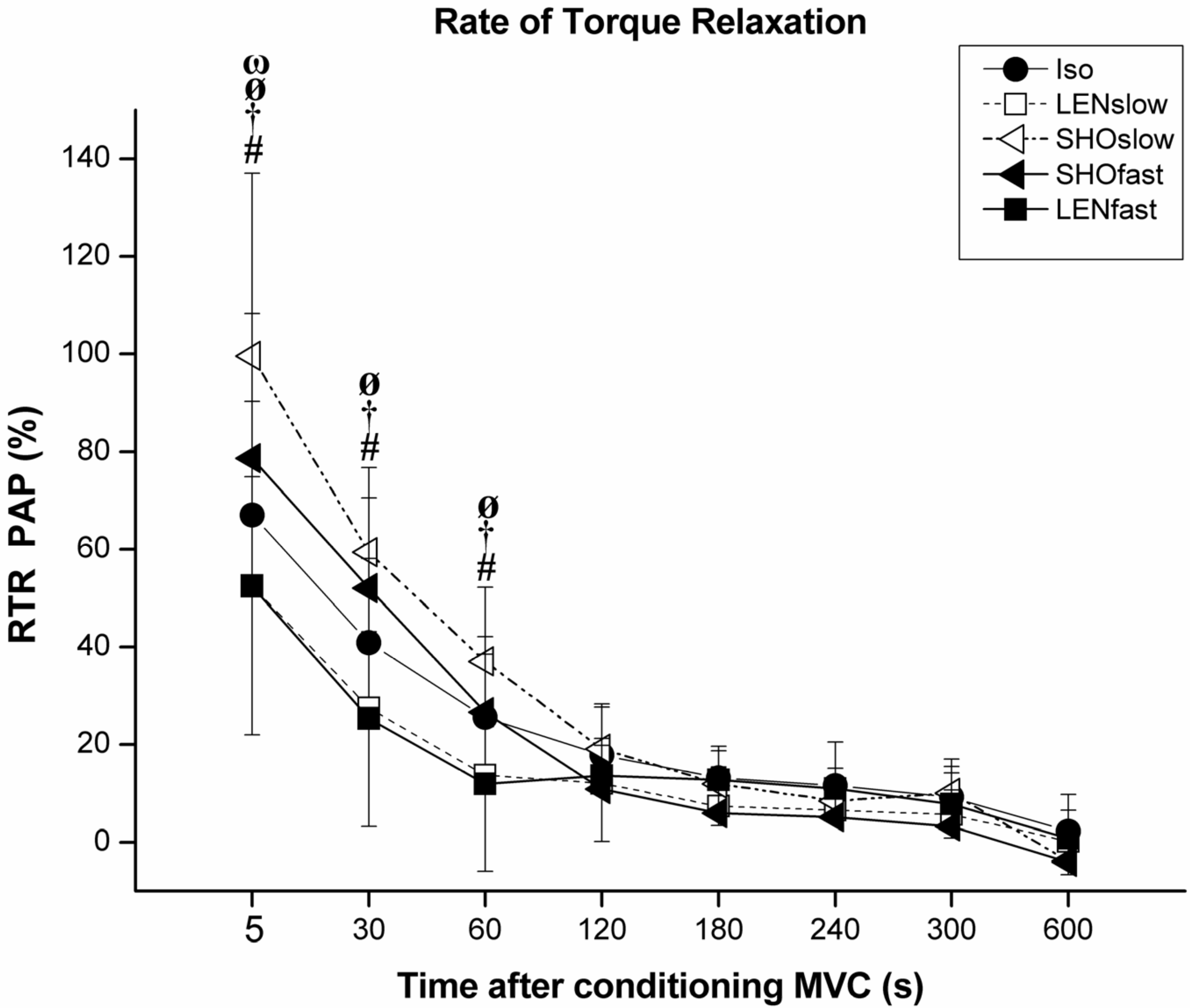

Rate of Torque Development
RTD PAP (%)
140
120
100
80
60
40
20
0
-20
5
30
60
120
180
240
300
600
Time after conditioning MVC(s)
Iso
LENslow
SHOslow
SHOfast
LENfast
Ø
†
#

Figure 3

Figure 4



Rate of Torque Relaxation
Iso
LENslow
SHOslow
SHOfast
LENfast
RTR PAP (%)
140
120
100
80
60
40
20
0
5
30
60
120
180
240
300
600
Time after conditioning MVC (s)
ω
ø
†
#

Figure 5

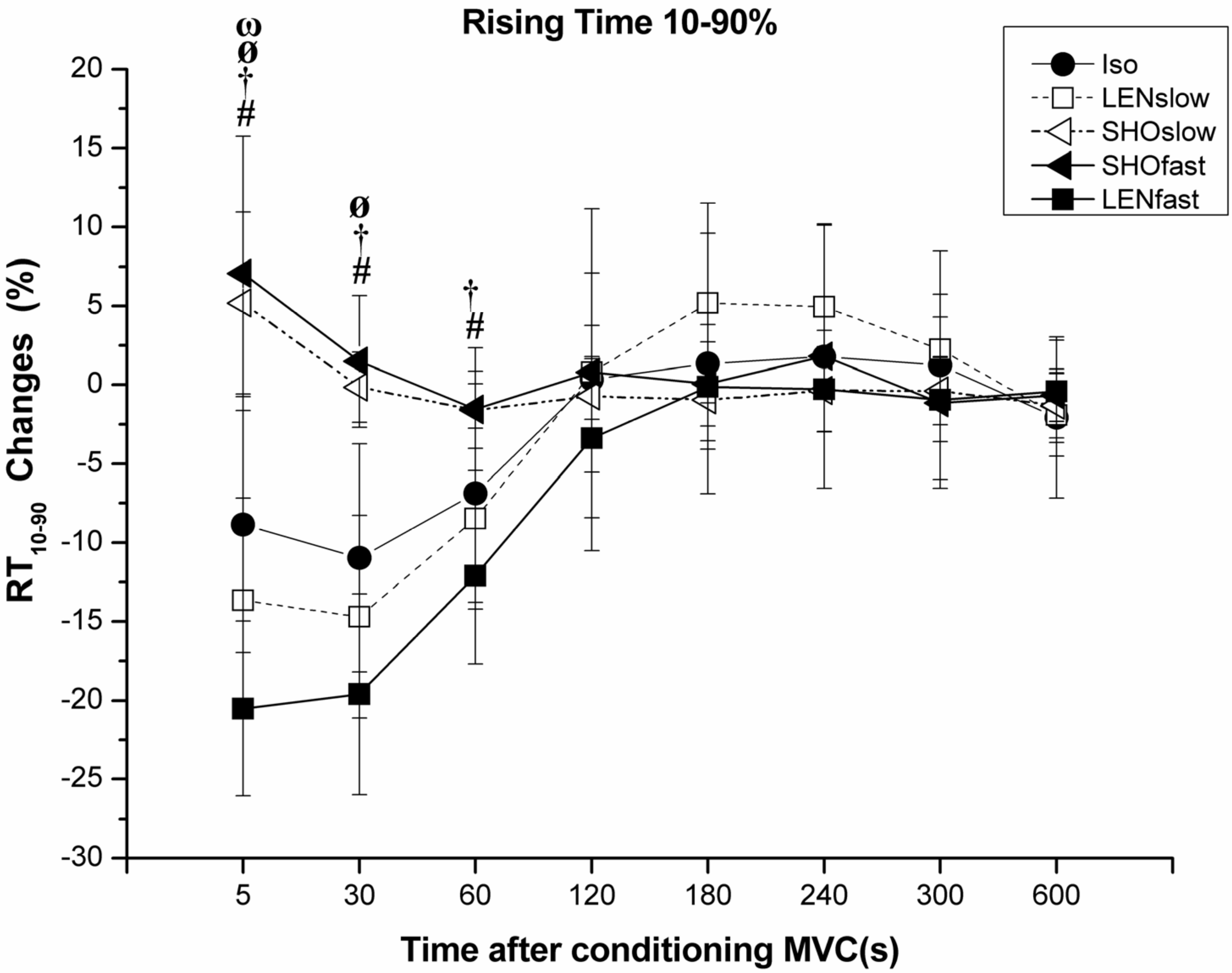
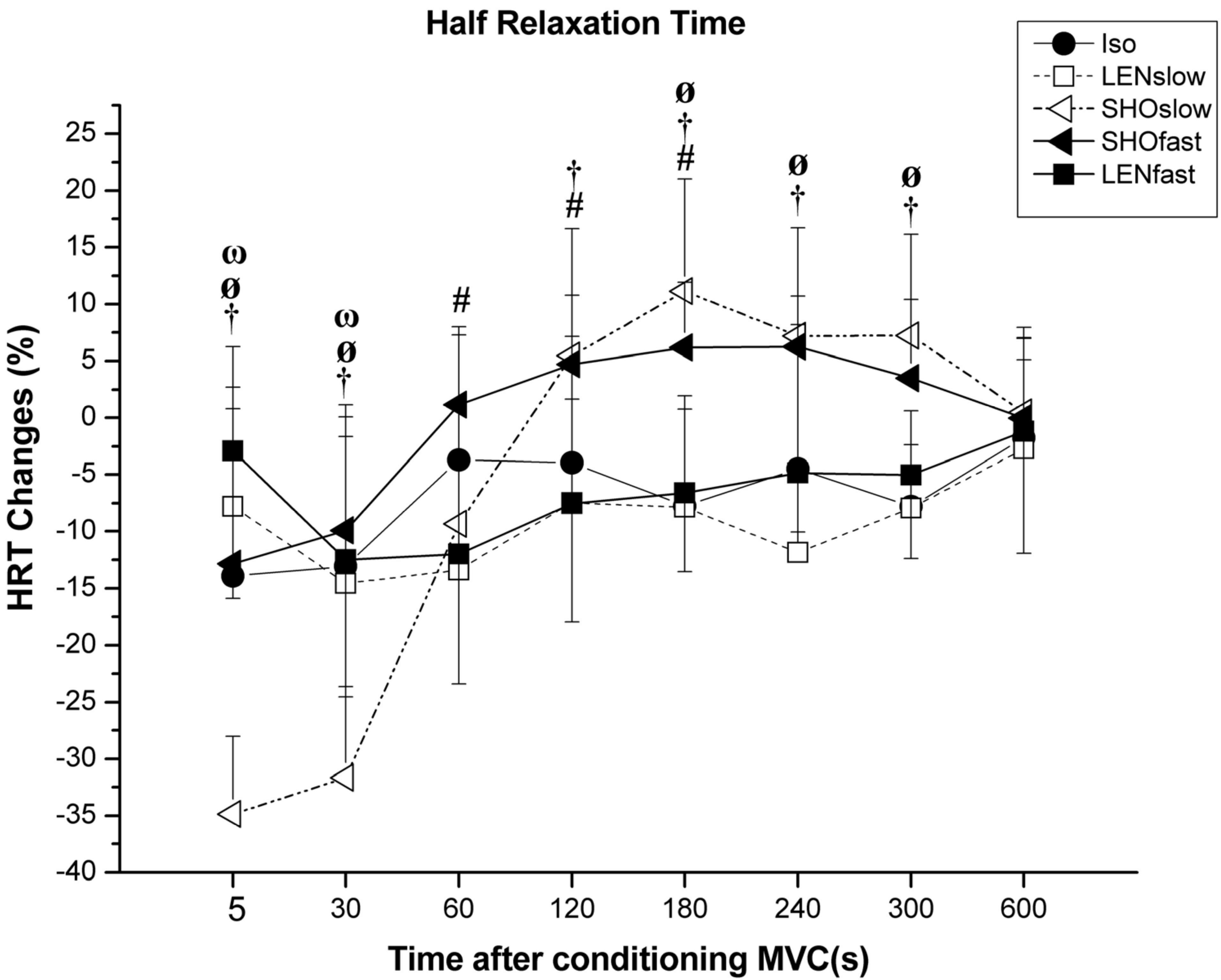

Rising Time 10-90%
Iso
LENslow
SHOslow
SHOfast
LENfast
RT10-90 Changes (%)
Time after conditioning MVC(s)
20
15
10
5
0
-5
-10
-15
-20
-25
-30
5
30
60
120
180
240
300
600
ω
ø
†
#

Figure 6



Half Relaxation Time
Iso
LENslow
SHOslow
SHOfast
LENfast
HRT Changes (%)
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
-40
5
30
60
120
180
240
300
600
Time after conditioning MVC(s)
ω
ø
†
#