Signs of muscle thixotropy during human ballistic wrist joint movements

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Axelson, H. W. Signs of muscle thixotropy during human ballistic wrist joint movements. J Appl Physiol 99: 1922–1929, 2005. doi:10.1152/japplphysiol.01370.2004.—A study was conducted on healthy subjects to determine whether voluntary ballistic wrist flexion movements are influenced by immediately preceding conditioning of the forearm muscles. Single rapid wrist flexion movements were made in response to an auditory “Go” signal. Rectified surface EMG was recorded from wrist flexors and extensors, and joint position was measured by a goniometer. The movements were preceded (2–3 s) by four different conditioning routines: 40-s rest (Rest), 10-s voluntary alternating wrist joint flexion and extension movements (Osc), and 10 s of 25° weak isometric wrist extensor (Ext) or flexor contractions (Flex). When subjects made ballistic movements after Osc compared with Rest, peak velocity was higher (P = 0.02) and movement time shorter (P = 0.06), but there was no difference (P = 0.83) in motor reaction time (time between the onset of the first agonist burst and movement onset). If the movements were preceded by Ext compared with Flex, motor reaction time was longer (P = 0.01), indicating a longer electromechanical delay. There were no indications that postconditioning differences in agonist or antagonist muscle activity could explain the results. It was also demonstrated that, after Rest, peak velocity was lower (P < 0.01) for the first than for the second of a series of repetitive ballistic movements. The observations corresponded to results from passive experiments in which the median nerve was electrically stimulated. In conclusion, history-dependent (thixotropic) changes in skeletal muscle resistance seem to have implications for voluntary ballistic wrist movements. The study also provided evidence that muscle conditioning influences the central nervous reaction time preceding ballistic contractions.

motor control; skeletal muscles; history-dependent; mechanical behavior

BALLISTIC MOVEMENTS ARE FUNDAMENTAL parts of normal daily motor activities (walking, chewing, etc.). In sports, for example, small variations in the performance of ballistic movements can be critical (7). Studies of ballistic contractions commonly involve a simple reaction time paradigm to explore central and peripheral aspects of the contractions (e.g., Ref. 13). The premotor reaction time (PMRT; time interval between a given somatosensory stimulus and the onset of agonist activity) depends on central nervous mechanisms (16). The motor reaction time (MRT; time delay between the onset of agonist contraction and movement initiation) and the movement time (MT; the time elapsed during the movement) may, on the other hand, be influenced by the passive mechanical resistance opposing the movement. Much attention has been paid to various factors influencing the muscle activation pattern for ballistic contractions and their central preparation (16, 19). In contrast, there seems to be a lack of detailed information on how changes in passive muscular resistance modify the performance of ballistic contractions.

It is generally accepted that muscular passive forces largely emanate from the muscle sarcomeres. Within the sarcomeres, weakly attached actin-myosin cross bridges and titin filaments seem to be the main sources of passive force production and to be responsible for the so-called history-dependent (or thixotropic) mechanical behavior of the muscles (14, 18). Simply expressed, muscle thixotropy implies that the degree of passive stiffness and resting tension of extra- and intramuscle fibers is critically dependent on the immediately preceding history of contractions and length changes. For example, previous studies on healthy relaxed humans have shown that the amplitude and speed of passive joint excursions produced by imposed forces depend on whether the moving parts have been held in a flexed or extended position immediately beforehand (8, 9) or whether the muscles concerned have been “loosened up” by preceding joint movements (3, 12). Such “afteref fects” observed from the relaxed limbs result from thixotropic alterations in movement resistance formed by the inherent stiffness in extrafusal muscle fibers and by stretch reflex activity (9). The influence of thixotropic variations in intramuscle fibers of the muscle spindles (i.e., stretch reflex activity) is naturally more important during rapid than slow movements.

Previous studies (1–3) on healthy subjects have shown that history-dependent changes in the passive resistance of the forearm muscles influence the fine motor control of the wrist joint. For instance, in a previous study at this laboratory (3) it was demonstrated that the movement-generating capacity of voluntary wrist extensor contractions varies with history-dependent changes in passive stiffness of the stretched antagonists (i.e., flexors). The voluntary movements in the study (3) were relatively slow and were generated by fairly weak contractions. In contrast, rapid so-called ballistic movements are produced by much stronger contractions, and it is uncertain whether history-dependent variations in opposing muscle resistance are relevant in this context. Nevertheless, it may very well be possible that, for instance, enhanced performance resulting from muscle “limbering up” routines carried out by athletes in their preparations for ballistic actions is partly explained by muscle thixotropy (4). This issue was briefly touched on in a recent report by Castellote et al. (6) and deserves further attention. The aim of the present study was therefore to seek evidence for thixotropic effects during voluntary ballistic movements.

In this study comparisons were made between movement variables obtained from experiments with passive nerve stimulation and voluntary ballistic contractions after different types of muscle-conditioning routines. The rationale for the nerve
stabilization experiments was to provide information about thixotropic variations in the passive mechanical behavior of muscles acting on the wrist joint. The information thus obtained made it possible to search for similar types of changes during voluntary ballistic contractions but under otherwise similar experimental conditions. The PMRT was also measured in voluntary contraction experiments, as it became clear after some preliminary trials that this parameter varied substantially depending on the type of muscle conditioning.

MATERIAL AND METHODS

Subjects

Eleven healthy volunteers (7 women and 4 men, 26–54 yr old) participated in the study. Two subjects were left handed. All subjects gave informed, written consent in accordance with the Declaration of Helsinki, and the project was approved by the Ethics Committee of the Faculty of Medicine at Uppsala University (Dnr 99114).

Experimental Setup

The subjects were seated in a comfortable chair during the trials, which lasted for 60–90 min. The room temperature was around 20°C. The experimental setup is illustrated in Fig. 1 (and partly described in the legend). A torque motor (TQ 34W-22 Aeroflex, Hauppauge, NY) generated a small external force toward wrist dorsiflexion throughout the trials so that the torque motor crank arm was slightly pressed against a metal bar (not shown in Fig. 1) when the forearm muscles were relaxed. The strength of the sustained external torque was 0.25 N·m, which was considered to simulate the gravitational load of the hand opposing the test movements. With this arrangement, the starting position of the hand (3° volar flexed) was always the same for each trial. When the metal bar was removed, the crank arm could be freely rotated within the physiological range of the joint. Surface EMG was recorded from wrist flexors and extensors. Two pairs of disposable surface EMG electrodes (Blue sensor, type N-10-F, Medicotest, Ølstykke, Denmark) were placed 5–6 cm apart in a proximal-distal direction over the flexor carpi radialis and wrist extensor muscles. The amplified surface EMG signal was rectified by analog hardware. The signals were high-pass filtered (30 Hz). Joint movements were sensed by a potentiometer connected to the axis of the torque motor. For practical reasons, all trials were carried out on the left wrist joint. Passive nerve stimulation and ballistic contraction experiments (described below) were performed on two different days.

Nerve Stimulation

The median nerve was stimulated in the distal part of the upper arm (a single supramaximal shock with 0.5-ms duration) to produce a single wrist flexion movement. The subjects were instructed to relax the forearm muscles completely when the stimulus was delivered. To ensure this, the experimenter listened to the EMG through loudspeakers. Supramaximal stimulation was confirmed by inspecting the surface compound motor action potential from the flexor carpi radialis muscle. Some trials were required for optimal placement of the stimulus electrode. The position of the electrode (H636, Nihon-Kohden, Tokyo, Japan) was secured by Velcro straps (electrode placement shown in Fig. 1).

Voluntary Ballistic Contractions

The subjects were instructed to hit a small metal plate by wrist volar flexion as quickly as possible in response to an imperative “Go” signal. The metal plate was placed so that the volar flexion movement was ~45° in amplitude relative to the starting position. The auditory Go signal (100-ms duration, 2,000 Hz) was preceded (500 ms) by three repetitive preparatory “Ready” signals (200-ms interval, 100-ms duration, 5,000 Hz). The signals were generated by a sound circuit connected to a preprogrammed microprocessor (Basic Stamp, Parallax). The subjects were thus mentally alerted for the Go signal, which was considered especially important because one of the conditioning procedures consisted of a 40-s resting period (further described below). Several practice trials were made at the beginning of the ballistic experiments to accustom the subjects to the experimental conditions. In subsequent trials they were instructed to look straight forward while waiting for the Ready-Go signal.

Conditioning Procedures

The first type of experiment consisted of a specific muscle-conditioning routine followed either by delivery of a nerve stimulus to induce a wrist flexion movement (passive tests) or by a Ready-Go command signal for a ballistic wrist movement (active tests). The subjects were exposed to four different conditioning procedures as follows. 1) Rest, i.e., the movements were preceded by a 40-s period of complete relaxation of the forearm muscles with the wrist joint in the starting position (Rest). 2) Alternating wrist extension/flexion movements of ~2–3 Hz within a range of ~50° for 10 s. The subjects were instructed to move the hand as if “loosening up” the joint (Osc). 3) Constant voluntary maintenance of a moderate volar flexed position of ~25° for 10 s by wrist flexor contraction (Flex). 4) Constant voluntary maintenance of a moderate dorsiflexed position of ~25° for 10 s (Ext).

The Osc, Flex, and Ext maneuvers required only minor motor effort and were made without any significant cocontractions. These procedures were terminated by a verbal instruction from the experimenter, and while the subject relaxed the experimenter sometimes gently assisted to restore the hand to the starting position. The time required to regain the starting position after conditioning (Osc, Flex, and Ext) Fig. 1. Schematic drawing of the experimental setup from a horizontal view with the left hand in its relaxed position. The distal forearm rests in a U-shaped wooden block. The hand is fixed to a wooden plate mounted on a torque motor crank arm. If the hand is volar flexed 45°, the torque motor crank arm hits a small metal plate (small solid rectangle) that is fixed on a rubber pad (dashed rectangle). This was the stop position for voluntary ballistic movement trials. The left side of the figure shows the placement, in the distal part of the upper arm, of the bipolar stimulating electrode used in passive nerve stimulation trials (dotted rectangle, electrode straps not shown). Commonly a small wooden block (not shown) was placed between the stimulus electrode and the upper arm support. The electrode was thus firmly pressed against the median nerve so that the nerve could be stimulated supramaximally.
was commonly 1–3 s. As soon as this position was obtained, the experimenter pushed a switch button to deliver the nerve stimulus and auditory command signals. Three consecutive nerve stimulation trials and five ballistic trials were carried out for each type of conditioning. The time between each trial, for data acquisition, was ~30 s. The conditioning procedures were tested in a completely randomized order, and there was an interval of ~1 min between each type of procedure to allow instruction of the subjects about the next task. Differences in movement and reaction time variables were studied for Osc vs. Rest and for Flex vs. Ext. The Flex vs. Ext comparisons were made with the intention of elucidating the effect of postconditioning differences in passive resting joint torque at an intermediate joint position, differences that have previously been demonstrated from the relaxed wrist joint (2). The Osc vs. Rest comparisons were primarily made to investigate the possible effect of reduced so-called muscle short-range stiffness (3, 11) in relaxed parts of the movement opposing antagonists.

In a subsequent type of test, the subjects kept the forearm relaxed for ~1 s and were then given three repetitive (~1-s interval) nerve stimuli or Ready-Go signals. The whole procedure was repeated three times. In this experiment, movement variables were compared between the first and the second movement and between the second and third movement.

Measurements and Data Acquisition

The passive movements elicited by single nerve stimuli were unrestricted and never reached the stop position. History-dependent variations (after conditioning) in the passive movement response were studied by measuring peak amplitudes and peak velocities. Also, differences in the time delay between nerve stimulation (artifact picked up by the flexor electrodes) and movement initiation were examined. This time delay (denoted stimulus motor reaction time, sMRT) was considered to reflect the electromechanical delay, although it also included the distal latency, i.e., the time taken for the stimulus volley to reach the muscle endplate zone. Three different movement variables (MRT, MT, and peak velocity) were analyzed in the voluntary ballistic experiments. Peak velocities were measured by producing movement derivatives by oscilloscope software. For PMRT measurements, the Go signal was represented by a square-wave pulse in the records that represented the output from the microprocessor feeding the sound circuit.

The amplitude of the rectified wrist flexor and extensor EMG was quantified in an attempt to determine whether postconditioning changes in the movement parameters were caused by variations in agonist and antagonist activity. In both passive nerve stimulation and voluntary contraction experiments, the mean level of the rectified extensor and flexor EMG amplitude between movement onset and half of the movement time (½MT) was measured. The parameters were denoted ExtEMG_½MT and FlexEMG_½MT. These parameters were considered to reflect the amount of extensor and flexor activity that would primarily influence movement speed (and movement amplitude after nerve stimulation). In the voluntary ballistic trials, the mean level of the rectified EMG amplitude was also measured during the MRT interval and denoted ExtEMG_MRT and FlexEMG_MRT. This made it possible to determine whether there were any indications that the MRT was influenced by variations in agonist-antagonist activity. Unfortunately, it was not possible to quantify the amount of extensor EMG activity during the sMRT interval (in the nerve stimulation experiments) because the extensor electrodes picked up the compound nerve action potential from the flexors. This was the only occasion, however, in which cross talk between the recording sites seemed to be a problem. All variables pertaining to the passive and active tests are outlined in Fig. 2.

All signals were displayed on a four-channel digital oscilloscope (Lecroy 9314M, Chestnut Ridge, NY, upgraded with 93XX-MWPM hardware and v.08.2.2 software). After each trial, signals were transferred to a personal computer and stored in a database. In tests that involved specific muscle-conditioning maneuvers (Rest, Osc, Flex, and Ext), the oscilloscope was set to trigger on the nerve stimulus artifact or on the onset of the first flexor EMG burst as soon as the subjects had become relaxed after muscle conditioning. The trigger was time delayed so that the records also encompassed the PMRT period (in active tests). Recordings from subsequent trials for each type of conditioning were averaged offline by using a math function integrated in the oscilloscope software. All measurements were based on the averaged signal except PMRT, which was the mean value of data obtained from individual records. Mean values were also calculated from individual records in tests that involved repetitive movements.

Statistics

The two-tailed paired sample t-test was used for statistical evaluations of differences in the movement and reaction time parameters (amplitude, sMRT, MRT, MT, peak velocity, PMRT, and Go-Stop). All values were expressed as means ± SD. The nonparametric Wilcoxon paired sample test was used to evaluate differences in the EMG parameters (ExtEMG_MRT, FlexEMG_MRT, ExtEMG_½MT, and FlexEMG_½MT). The level of significance was set at P < 0.05.

RESULTS

Approximately 215 nerve stimulation and 320 ballistic trials were carried out on 9 and 11 subjects, respectively. The subjects had no difficulty in fully relaxing during the short (1–2 s) period between the conditioning procedure and delivery of the nerve-auditory stimulus. In the following sections, active movements refer to voluntary ballistic wrist flexor movements and passive movements to those generated by single shocks to the median nerve.

Passive and Active Movements After Conditioning

Osc vs. Rest. Figure 3A shows two superimposed passive movements from the same subject where the nerve stimulations are preceded either by alternating hand movements for 10 s (Osc) or by a resting period of ~40 s (Rest). As illustrated (Fig. 3A), there was no difference (P = 0.20) in the time delay between nerve stimulation and movement initiation (sMRT), but the movement amplitude and peak velocity were higher (P < 0.01 for both) after Osc. In some subjects, extensor reflex activity was observed during the movements, whereas, in general, the flexors were completely relaxed during the trials. There were no differences in flexor and extensor EMG amplitudes (ExtEMG_½MT, P = 0.47; FlexEMG_½MT, P = 0.85) between the two types of conditioning routines.

Figure 3B shows two superimposed ballistic movements made in response to Go signals delivered after the same types of conditioning routines. There was no difference in MRT (P = 0.83), and, also in conformity with the passive tests, movement peak velocity was significantly higher (P = 0.02) after the Osc procedure. MT clearly tended to be reduced (P = 0.06). There were no differences in the mean amplitudes of the extensor and flexor EMGs recorded during the MRT interval and those recorded during ½MT [ExtEMG_MRT (P = 0.96), FlexEMG_MRT (P = 0.33), ExtEMG_½MT (P = 0.92), and FlexEMG_½MT (P = 0.14)]. Table 1 summarizes data obtained from the passive and active experiments after Osc and Rest.

Flex vs. Ext. Comparisons were also made between passive movements elicited by nerve stimulation after the wrist joint had been voluntarily held either in a flexed (Flex) or extended...
Fig. 2. In both $A$ and $B$, dashed vertical lines indicate limits for different variables. The 2 top traces show the rectified extensor and flexor surface EMG. Movement onset was defined as a time point at which the joint had reached a 0.5° volar flexed position relative to the starting position. $A$: a passive volar flexion movement elicited by delivery of a single stimulus to the median nerve. Cross-talk activity appears in the extensor trace. Amp, movement amplitude; sMRT, stimulus motor reaction time, which was the time period between stimulation and movement onset. ExtEMG_1⁄2MT and FlexEMG_1⁄2MT, mean level of rectified extensor and flexor EMG activity, respectively, during half of the movement time. $B$: a single ballistic volar flexion movement. The extensor EMG trace shows the square-wave signal that represents the "Go" stimulus. Vertical dashed lines indicate time parameters: PMRT, interval between the positive edge of the square-wave pulse and the onset of the first flexor burst; MRT, movement reaction time, i.e., interval between the onset of the first flexor burst and movement onset; MT, interval between movement onset (as defined above) and the 45° volar flexed stop position; Go-Stop, sum of all the parameters. ExtEMG_MRT and FlexEMG_MRT, mean level of rectified extensor and flexor EMG activity, respectively, during the MRT interval. EMG was also quantified during half of the MT as in the nerve stimulation trials ($A$). As shown, the movement exceeds 45°, indicating that the rubber pad was squeezed by the impact.

Fig. 3. Superimposed single (nonaveraged) recordings after 10-s voluntary alternating wrist joint flexion and extension movements (Osc) and 40-s rest (Rest). Vertical dashed lines indicate limits for relevant variables. Horizontal dotted lines in the flexor EMG traces indicate oscilloscope trigger levels for averaging. $A$: passive volar flexion movements from 1 subject after Osc (black) and Rest (gray). There is no apparent difference in sMRT, but after Osc the peak amplitude is higher. $B$: ballistic contractions from one subject after Osc (black) and Rest (gray). There is no difference in MRT, but MT is shorter after Osc. The difference in MT is highlighted by the vertical dotted line in the post Rest goniometer signal. Dotted horizontal line indicates stop position. The larger amplitude (exceeding the predefined stop position) after Osc indicates that the rubber pad was more depressed by the movement.
and flexors, respectively. *Significant difference Osc vs. Rest (P < 0.05).

Amp, ° 28 ± 7 19 ± 7*
MT, ms 86 ± 23 94 ± 32
EXTEMG_MRT, μV 27 (4–66) 27 (2–86)
EXTEMG_1/2MT, μV 2 (0–80) 2 (0–22)
FlexEMG_MRT, μV 35 (6–229) 32 (8–176)
FlexEMG_1/2MT, μV 428 (179–986) 398 (183–918)
FlexEMG_MRT, ° 393 (214–893) 392 (179–588)
PV, °/s 197 ± 48 172 ± 55*

Values are expressed as means ± SD or median (range). *Significant difference Osc vs. Rest (P < 0.05).

After Flex, sMRT was significantly shorter (P < 0.01) and the movement amplitude and peak velocity were higher (P < 0.01, for both). In the majority of trials the flexor muscles were completely relaxed during the passive movements. Extensor reflex activity was evident in several individuals (but not in the records shown in Fig. 4A). There were no differences in flexor or extensor EMG amplitudes between the two types of conditioning procedures [ExtEMG_MRT (P = 0.08) and FlexEMG_MRT (P = 0.45)].

Figure 4B exemplifies movements from corresponding ballistic experiments. Movement onset (MRT) was earlier (P = 0.01) after Flex, but in contrast to that in the passive test, peak velocity was reduced (P = 0.02). There was no indication that the reduction in peak velocity was due to increased antagonistic extensor activity. On the contrary, the extensor amplitude (ExtEMG_MRT) was lower (P = 0.02) after a Flex procedure. There were no significant differences in the other EMG parameters [ExtEMG_MRT (P = 0.56), FlexEMG_MRT (P = 0.65), and FlexEMG_1/2MT (P = 0.58)]. There was no significant difference in MT (P = 0.20). Table 2 summarizes data obtained from the passive and active experiments after Flex and Ext.

**Repetitive Passive and Active Movements**

In a previous study (3) on muscle thixotropy, it was demonstrated that passive opposing muscle stiffness is higher for the first than for the second movement in a series of three repetitive wrist joint movements. It was also shown (3) that the stiffness recovered during a resting interval (see also Ref. 11). In the present study a similar protocol was used primarily to determine whether the first in a series of passive and voluntary ballistic repetitive movements made after 40 s of rest was slower than the subsequent movement (see Methods). Offline inspection of the EMG trace confirmed that in the majority of trials the forearm muscles were relaxed before the stimulations. The amplitude of the first in a series of three consecutive passive movements was lower than that of the second movement (20.0 ± 4° vs. 21.4 ± 4.6°, P < 0.01). There was no difference in amplitude between the second and the third
movement (21.4 ± 4.6 vs. 20.0 ± 4.2°, \(P = 0.80\)). Amplitude data indicated a loosening-up effect of the first passive movement on the next one in a series. There were no significant differences in peak velocities between the first and the second movement (178 ± 37 vs. 183 ± 38°/s, \(P = 0.12\)) and between the second and the third movement (183 ± 38 vs. 181 ± 33°/s, \(P = 0.33\)).

In corresponding active experiments the subjects were given three repetitive Ready-Go commands for ballistic contractions. The peak velocity of the first ballistic movement was lower than that of the second one (741 ± 139 vs. 792 ± 182°/s, \(P < 0.01\)), but there was no difference between the second and the third movement (792 ± 182 vs. 778 ± 167°/s, \(P = 0.36\)). Apparently, a single ballistic movement made after a period of muscle relaxation is sufficient to produce a faster immediately succeeding movement.

Premotor Reaction Time

Usually the subjects had no particular problems with the imperative Ready-Go signals. In ~2% of the ballistic trials the first flexor burst preceded the Go signal. Such trials were defined as false starts and naturally were excluded from the PMRT measurements. It seemed necessary to include the PMRT parameter in the study, because some preliminary trials had indicated variations depending on the type of muscle conditioning procedure. In addition, the total time taken to reach the stop position after the Go signal (Go-Stop) was calculated by adding the central reaction time (PMRT) to the “peripheral” parameters MRT and MT (legend, Fig. 2B).

The Go-Stop interval was, on average, 31 ms shorter after Osc than after Rest (276 ± 40 vs. 307 ± 56 ms, \(P = 0.01\), and PMRT was 25 ms shorter (141 ± 40 vs. 166 ± 51 ms, \(P = 0.01\)). In relative terms, 80% of the reduction in Go-Stop latency after Osc was due to a reduction in PMRT and the remaining 20% was due to shorter MRT and MT. Furthermore, the Go-Stop interval was 32 ms shorter after Flex than after Ext (283 ± 40 vs. 315 ± 67 ms, \(P = 0.04\)). The PMRT was 31 ms shorter (Flex, 143 ± 40; Ext, 174 ± 60; \(P = 0.04\)), indicating that most (if not all) of the reduction in Go-Stop latency after Flex was caused by a reduction in PMRT.

DISCUSSION

The present study provides evidence that voluntary ballistic wrist joint movements are influenced by thixotropic, i.e., history-dependent, variations in passive muscular forces opposing the movements. The results are relevant for many common situations in which ballistic voluntary contractions encounter loads primarily consisting of inherent muscle resistance and gravitation (“free movements”). The results from the nerve stimulation experiments corroborate previous observations that the amplitude and speed of passive movements elicited by nerve stimulation (12) or external torque pulses (8, 9) are highly dependent on the type of immediately preceding muscle-conditioning procedure. Most of the postconditioning differences (Flex vs. Ext and Osc vs. Rest) in the passive movement parameters could be found in corresponding voluntary ballistic movement experiments. The observed history-dependent differences in the voluntary movement parameters could not be explained by postconditioning variations in the strength of flexor or extensor muscle activity. Somewhat unexpectedly, the ballistic contraction experiments also revealed that history-dependent variations in the peripheral time parameters (MRT and MT) after muscle conditioning were relatively modest compared with changes in the central nervous reaction time (PMRT).

Although the results obtained indicate that history-dependent changes in the passive mechanical properties of the relaxed forearm muscles influence the onset and speed of movements elicited by nerve stimulation and ballistic contractions, other mechanisms may also be involved. For instance, postactivation potentiation (PAP) occurs in recently recruited muscles, leading to enhanced force production at a given level of muscle activation (for review, see Ref. 15). PAP is considered to be the effect of phosphorylation of myosin regulatory light chains during a conditioning contraction. This mechanism increases the sensitivity of actin-myosin filaments to Ca²⁺ in a subsequent contraction. It may be argued that PAP explains, for instance, why the flexor movement response to median nerve stimulation was enhanced after the wrist joint had been voluntarily held in a moderately volar flexed (Flex) compared with dorsiflexed (Ext) position. Furthermore, alternating hand movements (Osc vs. Rest) naturally engage the flexor muscles, and PAP in those muscles might explain the increased movement speed after Osc in both the nerve stimulation and voluntary contraction experiments. It must be pointed out, however, that PAP is particularly pronounced after maximal voluntary contractions and that the conditioning contractions (Flex, Ext, and Osc) in the present study were rather weak (see METHODS).

It seems likely that history-dependent changes in the mechanical behavior of unrecruited parts of the muscles were more important in the present experiments (Flex vs. Ext and Osc vs. Rest) and that PAP is more relevant in situations where conditioning contractions are more forceful. Hence, it may be possible that PAP, to some extent, explains the increased movement speed after the first voluntary ballistic contraction in the series of repetitive contractions. Nevertheless, the results from the repetitive movement trials are consistent with previous findings in human and animal-based studies (3, 5) on muscle thixotropy, which have clearly demonstrated that one single stretch movement of the antagonists is sufficient to reduce their so-called short-range stiffness component, a particular stiffness that does not reappear completely until the muscles are left “undisturbed,” i.e., relaxed for 10–20 s (11). The present study suggests that a reduction in passive muscular short-range stiffness has implications not only for slow voluntary wrist joint movements (3) but also for the movement-generating capacity of voluntary ballistic contractions.

The present study provides additional information about the effects of limbering up of muscles on motor performance (4). For instance, alternating joint movements (Osc) or a single rapid prestretch of the antagonists (repetitive trials) increases the movement velocity if such a procedure is carried out a few seconds before a ballistic contraction. However, after a relatively short period of muscle relaxation (30–40 s), this beneficial effect is lost. It is perhaps even more effective to keep the muscles in motion in preparation for a ballistic movement. This issue was partly addressed in a recent study by Castellote et al. (6), who examined changes in reaction time and movement and EMG variables during different motor tasks. Their study cannot easily be compared with the present study, in which the test movements were examined after conditioning maneuvers.
Nevertheless, it is of interest to comment on some similarities and discrepancies in the results. In the study by Castellote et al., the subjects performed rapid movements about the wrist joint that were quite similar to the Osc routine carried out in the present study. In agreement with their observations, the present study demonstrated that peak velocities were increased after oscillating hand movements. In addition, Castellote et al. found a shorter electromechanical delay (MRT) for a ballistic movement made during rapid 5° oscillating hand movements compared with when the muscles were at rest. This was not observed in the present experiments (Osc vs. Rest). It may seem reasonable to assume that if the peripheral resistance to a movement has been reduced by oscillating hand movements, the ballistic movement onset should occur at an earlier stage during the contractions. It may be speculated, however, that although the passive tension is reduced in the muscles opposing movement initiation (agonists) by such a procedure, tension reduction also occurs in unrecruited muscle fibers that will later be activated to generate the ballistic movement (agonists). This reduction in resting tension of the agonists prolongs the buildup of active tension (14). Simultaneous reduction in the resting tension of both antagonist and agonist may therefore not produce a net effect in the electromechanical delay studied from the whole joint.

It was also of interest to note that the electromechanical delay preceding both passive and ballistic movements was shorter after Flex than after Ext. In conformity with previous observations (Fig. 2B in Ref. 2) on muscle thixotropy, such procedures give rise to history-dependent variations in passive torque resistance at intermediate joint positions, which most likely explain why the movement onset was shorter after a Flex procedure. However, the slower peak velocity of voluntary ballistic movements after Flex was an unexpected finding and inconsistent with the results of the passive tests. This discrepancy between the passive and the active tests may be considered to reflect the fact that nerve stimulation and voluntary contractions differ in the way in which they activate the muscles. Ballistic movements are preprogrammed by the central nervous system but seem to be under some proprioceptive feedback (10, 19). Thus there is a possibility that the muscle conditioning procedures give rise to reflex-induced changes in central motor output to the muscle. This may explain why the extensor EMG activity (EX\text{EMG, }\text{\%MT}) was decreased after Flex (vs. Ext) during the voluntary ballistic movements. However, this was the only occasion in which there was a significant difference in EMG activity in the comparisons (Flex vs. Ext and Osc vs. Rest), and the finding did not explain why the movement velocity was increased after Flex. Decreased extensor activity after a Flex procedure would rather produce a faster voluntary flexion movement, but this was not observed.

It was not the intention in the present study to explore the central processing of ballistic contractions. Nevertheless, the rather pronounced variations in PMRT depending on the type of conditioning deserves attention. It was shown, for instance, that changes in the overall performance of the ballistic contractions, in terms of time delay between the delivery of the auditory stimulus and the time point at which the subjects reached the stop position, was largely attributable to a reduction in PMRT. Apparently, preceding voluntary movements compared with rest (Osc vs. Rest) and preactivation of the agonists compared with the antagonists (Flex vs. Ext) facilitate the central processing of ballistic contractions. Perhaps such observations can be explained by changes in motor cortex excitability (17) owing to postconditioning variations in resting spindle afferent activity.

Previous studies by the author (1–3) have clearly demonstrated that the motor nervous system fully compensates for history (thixotropy)-dependent changes in passive stiffness and muscular resting tension in its precise control of slow repetitive movements and steady position maintenance, respectively. Such motor adjustments in response to thixotropic changes in short-range stiffness and resting tension seem to be made partly “automatically” and rely on intact proprioceptive pathways (1–3). In the present study, the subjects were asked to perform fast movements with no other instructions than to reach a certain position as quickly as possible. However, if it is the intention to make rapid movements with high precision in terms of speed and amplitude, the motor nervous system must somehow be capable of compensating for history-dependent changes in the peripheral resistance (i.e., for muscle thixotropy). This issue remains to be investigated.

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