Observations on force enhancement in submaximal voluntary contractions of human adductor pollicis muscle

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Oskouei, Ali E., and Walter Herzog. Observations on force enhancement in submaximal voluntary contractions of human adductor pollicis muscle. J Appl Physiol 98: 2087–2095, 2005. First published February 10, 2005; doi:10.1152/japplphysiol.01217.2004.—It has been observed consistently and is well accepted that the steady-state isometric force after active muscle stretch is greater than the corresponding isometric force for electrically stimulated muscles and maximal voluntary contractions. However, this so-called force enhancement has not been studied for submaximal voluntary efforts; therefore, it is not known whether this property affects everyday movements. The purpose of this study was to determine whether there was force enhancement during submaximal voluntary contractions. Human adductor pollicis muscles (n = 17) were studied using a custom-built dynamometer, and both force and activation were measured while muscle activation and force were controlled at a level of 30% of maximal voluntary contraction. The steady-state isometric force and activation after active stretch were compared with the corresponding values obtained during isometric reference contractions. There was consistent and reliable force enhancement in 8 of the 17 subjects, whereas there was no force enhancement in the remaining subjects. Subjects with force enhancement had greater postactivation potentiation and a smaller resistance to fatigue in the adductor pollicis. We conclude from these results that force enhancement exists during submaximal voluntary contractions in a subset of the populations and suggest that it may affect everyday voluntary movements in the remaining subjects. Subjects with force enhancement had greater postactivation potentiation and a smaller resistance to fatigue in the adductor pollicis. We conclude from these results that force enhancement exists during submaximal voluntary contractions in a subset of the populations and suggest that it may affect everyday voluntary movements in this subset. On the basis of follow-up testing, it appears that force enhancement during voluntary contractions is linked to potentiation and fatigue resistance and therefore possibly to the fiber-type distribution in the adductor pollicis muscle.

Despite this abundance of observations on steady-state force enhancement in electrically stimulated muscle preparations, there is little information on this phenomenon during voluntary contractions. Lee and Herzog (25) studied force enhancement for maximal voluntary contractions in human adductor pollicis muscle, and they found that force enhancement was similar in magnitude to that observed in the same muscle while stimulated electrically and concluded that force enhancement might occur during normal everyday movements. However, everyday movements are performed with submaximal levels of contraction, and there is no evidence whether the results obtained with electrically elicited or maximal voluntary contractions also apply for submaximal voluntary contractions.

The purpose of this study was to determine whether there was force enhancement during submaximal voluntary contractions. We hypothesized that steady-state isometric force after active muscle stretch is greater than the purely isometric steady-state force obtained at the same length for submaximal voluntary contractions and that the amount of force enhancement is the same as that obtained during maximal voluntary contractions. If so, force enhancement would likely also occur in normal everyday movements, and thus it would have to be accounted for in biomechanical models of human movement, in motor control studies of muscle force contributions to net joint moments, and in physiological studies of human performance. The difficulty in performing a study on force enhancement at submaximal levels of voluntary contraction is that activation needs to be carefully controlled, because force enhancement is calculated as the difference in steady-state, isometric force between a test and a reference contraction performed at the same length and the same level of activation. Previously, we showed that steady-state isometric force after active muscle shortening was smaller than the steady-state isometric force obtained at the same length during submaximal voluntary contractions (unpublished observations). In that study, we investigated the reliability of force production and activation at 30% of maximal voluntary contraction in 10 subjects performing 10 repeat trials each in force and in activation control. The mean variations in activation and force for the activation-controlled tests were 5.8 and 9.2%, respectively, while the corresponding values for the force-controlled tests were 9.9 and 3.1%, respectively. These results demonstrate that it is possible to maintain force in an activation-controlled test, and activation in a force-controlled test, within ~10% (i.e., ~3% of maximal voluntary force and activation); thus force enhancement would need to exceed these variations to become clearly apparent.

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**METHODS**

**Subjects**

Seventeen healthy subjects (12 men and 5 women), with a mean (± SD) age of 33 ± 6 yr, height of 166 ± 23 cm, and mass of 74 ± 29 kg, and with no history of neuromuscular disorder and injury to the hand or thumb of the left hand, participated in this study. All subjects were moderately active and were recruited from students and members of the Faculty of Kinesiology at the University of Calgary. Written, informed consent was obtained from all subjects, and the protocol was approved by the University of Calgary Human Ethics Committee.

**Preparation and Experimental Setting**

Two test protocols involving the thumb adductors of the left hand were performed. Thumb adduction force and carpometacarpal joint angle were measured with a custom-built dynamometer that has been described previously (25). Briefly, subjects sat on an adjustable chair with the forearm slightly abducted and the elbow flexed 90°. Then the left hand was immobilized with a fitted and reusable clinical cast (Eziform, Rehabilitation Division, Smith & Nephew, Germantown, WI) in a neutral position. After hand immobilization, the forearm was placed in a V-shaped metal guide and was secured with Velcro straps (Fig. 1). The center of rotation of the carpometacarpal joint of the left hand was then aligned with the center of rotation of the dynamometer arm. The thumb was strapped to an anatomically shaped aluminum piece at the end of the dynamometer arm. Once attached, the thumb was moved through the full range of abduction and abduction, and proper alignment of the joint axis was confirmed by the lack of slipping of the thumb on the dynamometer arm.

The carpometacarpal joint angle with the fully adducted thumb was defined as 0°. Thumb angles were defined to increase with abduction. All subjects could comfortably perform 30° thumb abduction, and we chose this range (0–30°) as the stretch amplitude.

**Force and Angle Measurement**

Force was measured by the dynamometer via a set of calibrated strain gauges arranged in a full Wheatstone bridge configuration. Thumb angle was measured using an analog encoder and a goniometer that was attached to the dynamometer (25).

**Muscle Activation Measurements**

Muscle activation was measured using electromyography (EMG). EMG recordings were made using a pair of surface electrodes placed over the thenar part of the hand on the adductor pollicis muscle. A reference electrode was placed on the posterior bony side of the metacarpophalangeal joint (Fig. 1). EMG signals were amplified (5,000 times) no further than 10 cm from the recording site, and they were band-pass filtered (10–1,000 Hz). EMG signals were collected at a sampling frequency of 3,000 Hz. The linear envelope of the EMG was obtained by full-wave rectifying and smoothing the EMG signals using a time window of 400-ms sliding average of the rectified signal (Medical Engineering Systems and Ergonomics, Aachen, Germany).

**Twitch Force Measurements**

To produce twitch forces in the adductor pollicis group, two carbon-impregnated rubber electrodes (4.5 × 3.5 cm), thinly coated with conductive gel, were placed on the skin over the ulnar nerve, ~3 cm proximal to the wrist. Once attached, the electrodes were connected to a Grass S88 muscle stimulator (Quincy, MA) via an isolation unit approved for human use. To ensure that all motor units of the ulnar nerve were recruited, single-twitch stimuli (0.8-ms square-wave pulses) were delivered at increasing voltages until further increases failed to produce an increase in twitch force (4, 43). Single-twitch stimulation was used to determine the amount of postactivation potentiation, and doublet-twitch stimulation (2 square-wave pulses of 0.8-ms duration separated by an 8-ms interpulse interval) was used to quantify the twitch force-angle relation.

**Experimental Testing**

**Test 1.** Test 1 was aimed at determining whether there was force enhancement in submaximal voluntary contractions using a 30% of maximal effort. Isometric reference contractions and isometric-stretch-isometric test contractions were performed first at constant (30% of maximal voluntary contraction) activation and then at constant force.

**Activation Control.** Each subject completed 10 sets of trials consisting of an isometric reference contraction and a test contraction. For the isometric reference contractions, subjects performed a 14-s purely isometric contraction at a thumb abduction angle of 30°. For the test contractions, subjects performed a 2-s isometric contraction at 0°, followed by muscle stretch from 0 to 30° at an angular velocity of 9°/s (3.3 s), and followed by an isometric contraction at 30° for another 8.7 s (Fig. 2). Throughout the reference and test contractions, subjects were asked to match a line on the oscilloscope representing an activation level (linear envelope EMG of the adductor pollicis muscle) of 30% of that obtained during the maximal voluntary contraction, thereby keeping activation constant at a submaximal level.

Thumb adduction force was determined at 4–6 s (i.e., over a 2-s interval) after the stretch to give the mean steady-state isometric force after stretch (Fig. 2). Force enhancement in the activation control protocol was defined as an increase in mean steady-state isometric force in the stretch test contraction at a thumb abduction angle of 30°, compared with the force obtained in the purely isometric reference contraction at 30° (Fig. 2).

**Force Control.** The force control protocol was identical to that used for activation control, except that subjects were asked to match the thumb abduction force (30% of maximal voluntary contraction) rather than activation, thereby keeping force constant and submaximal throughout the reference and test contractions (Fig. 3). Muscle activation was determined at 4–6 s (i.e., over a 2-s interval) after the stretch to give the mean steady-state isometric EMG after stretch (Fig.
3). Force enhancement in the force control protocol was defined as a decrease in steady-state, isometric EMG in the stretch test contraction compared with the EMG obtained in the purely isometric reference contraction (Fig. 3).

Because the activation and force control protocols consisted of 10 reference and 10 test contractions, 20 pairs of trials were available for each subject to determine the amount of force enhancement. In addition, test 1 was repeated by all 17 subjects for reliability several weeks after the initial testing; therefore, 40 individual pairs of reference and test contractions could be analyzed for each subject.

Test 2. After the 2 days of testing for submaximal voluntary force enhancement, all subjects but one (n = 16) performed another set of tests aimed at quantifying selected basic properties of the thumb adductor muscles. Specifically, the goal of test 2 was to determine whether muscle properties of the force enhancement group were the
isometric (0°, 4 s)-stretch (9°/s)-isometric (30°, 5 s) contractions. 12-s isometric contractions at a thumb abduction angle of 30° and then determined by comparing twitch forces before and after maximal assessed by the time period from the start of the test until force had continue the contraction even when they could not hold 60% of subjects were asked to match this force for as long as possible and maximal voluntary contraction force was provided on an oscilloscope and contraction at 30° of thumb adduction and an effort of 60% of contractions, the average of them was used for analysis, and tests were separated by a 2-min rest interval.

Twitch contraction times were determined for twitch contractions at all joint angles, and they were defined by the time period from the onset of the twitch to the attainment of peak force. Half-relaxation times were defined as the time period from peak twitch force until force had decreased to 50% of its peak value. Twitch-to-maximal voluntary contraction ratio was defined as the peak twitch force divided by the maximal voluntary force measured over a 500-ms period.

Fatigue test. For the fatigue test, subjects performed an isometric contraction at 30° of thumb adduction and an effort of 60% of maximal voluntary contraction. Visual feedback of the 60% of maximal voluntary contraction force was provided on an oscilloscope and subjects were asked to match this force for as long as possible and continue the contraction even when they could not hold 60% of maximal voluntary contraction any more. Fatigue resistance was assessed by the time period from the start of the test until force had dropped to 30% of the maximal isometric force (Fig. 4).

Postactivation potentiation. Postactivation potentiation was determined by comparing twitch forces before and after maximal voluntary contractions lasting for 12 s. Each subject performed three 12-s isometric contractions at a thumb abduction angle of 30° and then isometric (0°, 4 s)-stretch (9%)-isometric (30°, 5 s) contractions. Three twitches were given before and after the maximal voluntary contractions. Twitches after the tetanic contractions were given at 5, 10, and 15 s after deactivation of the thumb adductors (Fig. 5).

Data Collection and Analysis

All signals were recorded at a sampling frequency of 3,000 Hz and stored online to a computer for offline analysis. Mean isometric force and mean linear envelope EMG were determined for a 2-s period after steady-state force had been reached in the isometric-stretch-isometric test contractions. Then, the corresponding phase in the isometric reference contractions was located, and the mean isometric force and mean EMG were determined (Figs. 2 and 3). Force enhancement after muscle stretching was calculated by subtracting the mean steady-state force of the isometric reference contractions from the corresponding force after the test contractions. EMG changes after muscle stretching were determined by subtracting the mean steady-state EMG of the test contractions from the corresponding EMG of the isometric reference contractions.

In test 1, mean values of the steady-state isometric force and EMG for each subject were used for statistical analysis (α <0.05) using a paired t-test. The values for each subject across both test days were used for descriptive statistics (mean ± SD). On the basis of the results of test 1, subjects were classified into two groups: one group who showed consistent force enhancement and another group who did not. The pooled values across subjects in each group, presented as means ± SD, were used for statistical analysis. Nonparametric statistics (Mann-Whitney U-test) were used to determine whether there was a difference in force enhancement and EMG deficit between the two groups and whether the two groups differed in any of the muscle properties that were determined in test 2.
RESULTS

Force Enhancement

Statistically significant force enhancement ($P = 0.003$) in the force and activation control tests was observed in 8 of the 17 subjects (Figs. 2, 3, and 6, A and C), and it was not observed in the remaining 9 subjects (Fig. 6, B and D). The group of subjects who exhibited force enhancement did so in 73 of the 80 (91%) activation control trials and in 75 of the 80 (94%) force control trials for an average increase in force from 30 N ($\pm 7$) to 32 N ($\pm 6$) and an average decrease in EMG from 1.08 V ($\pm 0.3$) to 0.91 V ($\pm 0.2$) (Fig. 6, A and C). The group that did not exhibit force enhancement showed an increase in force in 34 of the 90 (38%) activation control trials and a decrease in EMG in 53 of the 90 (59%) force control trials for a net decrease in force from 37 N ($\pm 4$) to 36 N ($\pm 4$) and a net decrease in EMG from 0.91 V ($\pm 0.29$) to 0.87 V ($\pm 0.27$) (Fig. 6, B and D). These changes were not statistically significant.

To ensure the reliability of the force enhancement results, all force enhancement tests were repeated several weeks after the first testing session in an identical manner. The same eight subjects who had statistically significant force enhancement in the first session also had force enhancement in the second session, and all nine subjects who did not exhibit force enhancement also did not show force enhancement in the second testing session (Fig. 6, session 2).

The force-angle (maximal voluntary contractions and twitch contractions) and the force-angular-velocity relations were the same for both groups of subjects (Fig. 7). Similarly, twitch contraction times, half-relaxation times and twitch-to-maximal voluntary contraction ratio did not differ between the group who exhibited force enhancement and the group who did not (Table 1). Twitch characteristics were the same for both groups of subjects.

Postactivation potentiation after isometric reference contractions and stretch test contractions was significantly greater for the group of subjects who exhibited force enhancement (36 ± 21 and 41 ± 21%, respectively) compared with the group that did not (16 ± 20 and 20 ± 22%, respectively) (Figs. 8 and 9). Twitch duration in the potentiated twitches was shorter (169 ± 23 ms) than those observed in the nonpotentiated twitches (199 ± 21 ms) for both groups of subjects ($P < 0.01$).

Fatigue resistance, assessed by the time a 60% maximal voluntary contraction could be maintained, was smaller (75 ± 32 s) for the group who exhibited force enhancement compared with the group who did not (95 ± 42 s) ($P < 0.01$).

DISCUSSION

The primary results of this study were that there is force enhancement for voluntary, submaximal contractions in human skeletal muscles and that this force enhancement was clearly and unequivocally apparent in about one-half of the tested subjects, whereas there was not a hint of force enhancement in the remaining subjects. Although steady-state force enhancement has been observed before in a variety of muscle preparations, ranging from isolated muscles (1, 27) to single fibers (12, 15, 24, 35, 37, 41) and myofibrils (36), force enhancement for electrically stimulated human muscles (11, 25) and voluntary contractions (11, 25) has only been observed in a small number of studies and relatively recently. Here we add the result that force enhancement also occurs in a subpopulation of subjects for voluntary submaximal contractions of the thumb adductors. Therefore, the mechanisms responsible for force enhancement also work for these contractions, at least in some subjects.

One mechanism associated with force enhancement has been associated with the development of sarcomere length nonuniformities (24, 29, 30). According to this theory, force enhancement only occurs on the “unstable” (22) descending limb of the
force-length relation (14), where sarcomeres are stretched by various amounts during active eccentric contractions, some of them ending up on the passive limb of the force-length relation, thereby explaining the enhanced force after active stretch (30). There appears to be no reason why this mechanism should not work during submaximal voluntary contractions; thus, on the basis of this theory, one would expect to observe force enhancement in the experiments performed here, as we did. However, there appears to be no ready explanation why, on the basis of the sarcomere length nonuniformity theory, there should be no force enhancement for some of the subjects.

Another mechanism that has been proposed to explain force enhancement is associated with an increase in the passive force after stretch of activated muscles. This suggests that part of the force enhancement was caused by a passive structural element (passive force enhancement) as described previously for the cat soleus (19). No such passive force enhancement was observed in this study; thus this mechanism does not seem to have been at work here. Passive force enhancement has been observed at long muscle length only; in fact in the cat soleus, where most of these observations were made, passive force enhancement was only observed at lengths beyond those encountered physiologically during everyday movements (19). Because all our experiments were performed at around the plateau of the force-length relation and well within the physiological range, it is not surprising that passive force enhancement did not play a role in the present experiments.

Aside from an increase in the steady-state force in the force enhanced state compared with the isometric reference force, force enhancement has also been associated with an increase in muscle stiffness (18) and a decrease in the rate of force decay after deactivation of the muscle (34). Within the framework of the cross-bridge theory, an increased force and stiffness and a decreased rate of force decay could be explained with a decrease in the rate of cross-bridge detachment [the function $g(x)$ in Huxley’s 1957 cross-bridge notation (23)]. If force enhancement was truly associated with a decrease in $g(x)$, it is not immediately apparent why this should have happened for some subjects in our study but not for others. Therefore, we believed that more needed to be known about the mechanical properties of the muscles from the two subject groups. To address this issue, a series of tests, as outlined in METHODS, was performed after the results of the force enhancement experiments showed such a distinct dichotomy between subjects: some had great force enhancement that was consistent across trials and for the two repeated experiments, whereas others showed no hint of force enhancement in any of the tests.

In these follow-up tests, two results were statistically significant: those subjects who showed force enhancement had greater postactivation potentiation and a smaller resistance to fatigue (Figs. 8 and 9). Both these results suggest that the group showing force enhancement might have had a greater percentage of fast-twitch fibers than the group who showed no force enhancement, because it is known that postactivation potentiation is greater in fast-twitch fibers than in slow-twitch fibers (10, 16, 46). Therefore, this result suggests that force enhancement might occur exclusively (or to a greater extent) in fast-twitch fibers than in slow-twitch fibers. We are not aware of any previous evidence that would link force enhancement to fast rather than slow-twitch fibers. However, several studies demonstrated a correlation between the magnitude of potentiation and myosin regulatory light chain phosphorylation (26, 31), the mechanism that is often considered to play a major role in postactivation potentiation (7, 26, 31, 38, 39, 45). Furthermore,
it has been shown in skinned fiber preparations that force at a given Ca\(^{2+}\) concentration is increased after potentiation (32, 44). These two observations, together with the present finding that postactivation potentiation is greater in the group showing force enhancement compared with the group who had no force enhancement, provide support for the idea that force enhancement is associated with fiber type. However, if force enhancement was associated with fiber type, one would also expect twitch characteristics and the force-velocity relation to differ among the two groups. But they did not, and from the results of this study, it is hard to draw firm conclusions for the reason of why some subjects had clear and repeatable force enhancement, whereas others did not.

One might expect that gender might have influenced the results, because it has been suggested that women tend to have smaller percent type II fiber area in selected muscles compared with men (40) and that women have specific features of fatigue resistance that are better than those of men (21). However, men and women were nearly equally distributed in the two groups (2 and 3 women, and 6 and 6 men in the force enhancement and no force enhancement groups, respectively); therefore, gender is likely not a factor that could explain these findings.

If we assume that force enhancement occurs primarily in fast-twitch but not slow-twitch fibers, why would this property only have been observed here and not in the dozens of studies performed in the past half century since the pioneering work of Abbott and Aubert (1) on this topic? First, most studies on force enhancement were performed for maximal contractions that were elicited through electrical stimulation of the muscle or the nerve supplying the muscle. During maximal contraction, all motor units are recruited; thus force enhancement would have been observed as the fast motor units were acti-

Table 1. Twitch contraction times, half-relaxation times, and twitch-to-maximal voluntary contraction ratio of thumb adductor pollicis muscle for the force enhancement and no force enhancement groups

<table>
<thead>
<tr>
<th>Subject No.</th>
<th>Contraction Time, ms</th>
<th>Half-Relaxation Time, ms</th>
<th>Twitch-to-Maximal Voluntary Contraction Ratio, %</th>
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<tr>
<td>Force enhancement group</td>
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<tr>
<td>1</td>
<td>89±4</td>
<td>64±4</td>
<td>09±2</td>
</tr>
<tr>
<td>2</td>
<td>90±4</td>
<td>69±6</td>
<td>10±1</td>
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<td>7</td>
<td>84±3</td>
<td>62±5</td>
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</tr>
<tr>
<td>Means ± SD</td>
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<td>12±2</td>
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<tr>
<td>No force enhancement group</td>
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<tr>
<td>Means ± SD</td>
<td>96±11</td>
<td>78±16</td>
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</tr>
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</table>

Values are means ± SD across all joint angles. Twitch contraction times were defined by the time period from the onset of the twitch to the attainment of peak force. Half-relaxation times were defined as the time period from peak twitch force until force had decreased to 50% of its peak value. Twitch-to-maximal voluntary contraction ratio was defined as the twitch amplitude divided by the maximal voluntary force (over 500 ms).
vated. Also, for submaximal nerve stimulation, it is well known that the fast motor units are recruited first (3, 6); thus one would also expect to observe force enhancement associated with fast-twitch fibers in these experiments. However, for submaximal voluntary contractions, one would expect the slow motor units to be recruited first, and only once a certain force threshold was exceeded would the fast motor units be recruited (2, 8, 17, 28). If some of the subjects had sufficient slow motor units in the thumb adductor muscles, then 30% of maximal voluntary contraction might not have required the recruitment of fast-twitch fibers; thus there would have been little or no force enhancement. However, in subjects with few slow-twitch fibers, 30% of maximal voluntary contraction might have required the recruitment of fast motor units that produced the observed force enhancement. Obviously, this study was not designed to test whether force enhancement was associated with fiber type. However, it should be quite straightforward to test this hypothesis noninvasively, that is, without the need for muscle biopsies.

For example, imagine we were to repeat the experiments that were performed as part of this study at submaximal levels of testing of 10 and 60% of maximal voluntary contraction. At 10% of maximal voluntary contraction, one would expect that none of the subjects would need to recruit any fast motor units, and therefore one would predict that, at this low level of contraction, there would be no force enhancement for any of the subjects, independent of whether they had force enhancement at the 30% of maximal voluntary contraction level or not. Similarly, it is quite well accepted that at 60% of maximal voluntary contraction, most or all of the motor units in the small hand muscles are recruited (5). Therefore, all subjects would have recruited some fast motor units at this level of contraction, and they all should show force enhancement at 60% of maximal voluntary contraction, independent of whether they had force enhancement at 30% of maximal voluntary contraction or not. This last experiment is partially supported by the results of previous work in which our laboratory observed clear and repeatable force enhancement for all subjects performing active stretch contractions for voluntary contractions at 100% of maximal voluntary contraction (25).

Needless to say that the idea that force enhancement should only occur in fast-twitch fibers has its limitations. For example, our laboratory has observed consistent force enhancement in the cat soleus (19, 20), a muscle that is composed virtually exclusively of slow-twitch fibers (8, 9). Similarly, there is an abundance of observations of force enhancement in single-fiber preparations, and it seems unrealistic to expect that all these fibers were of the fast-twitch type. However, for lack of better explanation, it appears that force enhancement for submaximal voluntary contractions might be linked to fiber type.

Thus we conclude from the results of this study that force enhancement exists for submaximal voluntary contractions, and we hypothesize that force enhancement might be associated primarily with fast-twitch muscle fibers. Therefore, very small levels of contraction (i.e., less than ~10% of maximal voluntary contraction) would not be associated with force enhancement, whereas force enhancement would become more prominent with increasing levels of contraction, as fast motor units make up an increasing proportion of the activated muscle fibers.

REFERENCES


