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Activation of human quadriceps femoris during isometric, concentric, and eccentric contractions

NICOLAS BABAULT, MICHEL POUSSON, YVES BALLAY, AND JACQUES VAN HOECKE
Groupe Analyse du Mouvement, Unité de Formation et de Recherche Sciences et Techniques des Activités Physiques et Sportives, Université de Bourgogne, BP 27877, 21078 Dijon Cedex, France

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Babault, Nicolas, Michel Pousson, Yves Ballay, and Jacques Van Hoecke. Activation of human quadriceps femoris during isometric, concentric, and eccentric contractions. *J Appl Physiol* 91: 2628–2634, 2001.—Maximal and submaximal activation level of the right knee-extensor muscle group were studied during isometric and slow isokinetic muscular contractions in eight male subjects. The activation level was quantified by means of the twitch interpolation technique. A single electrical impulse was delivered, whatever the contraction mode, on the femoral nerve at a constant 50° knee flexion (0° = full extension). Concentric, eccentric (both at 20°/s velocity), and isometric voluntary activation levels were then calculated. The mean activation levels during maximal eccentric and maximal concentric contractions were 88.3 and 89.7%, respectively, and were significantly lower ($P < 0.05$) with respect to maximal isometric contractions (95.2%). The relationship between voluntary activation levels and submaximal torques was linearly fitted ($P < 0.01$): comparison of slopes indicated lower activation levels during submaximal eccentric compared with isometric or concentric contractions. It is concluded that reduced neural drive is present during 20°/s maximal concentric and both maximal and submaximal eccentric contractions. These results indicate a voluntary activation dependency on both tension levels and type of muscular actions in the human knee-extensor muscle group.

twitch interpolation; isokinetic contractions; torque level; neural drive; knee extension

IT IS WELL DOCUMENTED THAT voluntary torque, produced by human muscles, is lower during maximal concentric contractions and equal or higher, depending on training status (4), during maximal eccentric contractions compared with isometric contractions. This muscle behavior is explained by mechanical factors and myoelectrical activity. However, marked differences found between the force-velocity relationship in human and in isolated animal muscles, especially when eccentric or slow concentric contractions are performed, suggest that different activation patterns, depending on both contraction type and angular velocity, would affect the shape of this relationship. Thus it has been postulated that changes in torque could result from a reduction in activation, restricting maximal muscle tension, either during eccentric (13, 35, 36) or slow concentric contractions (10, 29, 38) in humans.

The degree of voluntary activation of the motoneuron pool can be assessed by using the twitch interpolation technique (26). This technique has been frequently applied to isometric contractions of different human muscles such as the adductor pollicis (26), quadriceps femoris (9, 32), elbow flexors (11, 12, 16), and plantar flexors (7). However, voluntary activation during dynamic contractions has received very little attention. To our knowledge, few studies have investigated the extent of activation during eccentric or concentric contractions (4, 5, 15, 22, 28, 36). During maximal eccentric contractions, voluntary activation level (AL) was generally assessed by using tetanical stimulations superimposed on the voluntary contractions. In these conditions, the torque recorded during the superimposed contractions was higher compared with the maximal voluntary torque alone (4, 37). This result would, therefore, suggest that voluntary activation was reduced during maximal eccentric contractions. During slow concentric contractions, the reduced neural drive, hypothesized by numerous authors (10, 13, 29, 38), remains, however, controversial. Indeed, voluntary activation assessed by the twitch interpolation technique during concentric contractions has not confirmed this hypothesis. Some authors (15, 28) have concluded that maximal concentric AL was similar to the maximal isometric level either at slow (20°/s) or at faster angular velocities (150 and 300°/s).

The twitch interpolation technique requires the delivery of one or more supramaximal electrical stimuli to the appropriate motor nerve (or motor point) during an attempted maximal voluntary contraction (MVC). This technique assumes that the motor units that are not recruited or not discharging at their maximal frequency (incomplete activation) should yield a detectable force increment as a consequence of the stimulation of their axons. To improve the signal-to-noise ratio (24) and/or reduce the measurements variability (34), some studies have used multiple rather than single stimuli. However, the enhanced reliability of multiple pulses already observed (21, 24, 34) remains controver-

Address for reprint requests and other correspondence: N. Babault, Groupe Analyse du Mouvement, UFR STAPS, Faculté des Sciences du Sport , Université de Bourgogne, BP 27877 - 21078 Dijon Cedex, France (E-mail: Nicolas.Babault@u-bourgogne.fr).

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sial, as several authors have observed similar results using single stimuli, doublets, or short trains of stimuli (3, 6). Despite some variability from test to test in the voluntary AL (2, 3, 6), Behm et al. (6) have concluded that the technique, associated with a single stimulus to the motor nerve, was reliable in both the plantar flexors and quadriceps femoris. In addition, because spinal reflexes and motor axon antidromic responses are known to influence the interpolated twitch (20), single stimuli seem preferable to minimize the distortions induced by multiple stimuli. However, single stimuli superimposed during concentric contractions have been used in only one study (15), and under no circumstance has this stimulation mode been used to compare voluntary activation during isometric, concentric, and eccentric contractions.

The main purpose of this study was to extend the twitch interpolation technique (single-stimulus mode) to investigate whether the level of voluntary activation of the human quadriceps femoris muscle was dependent on the contractile conditions during both isometric and 20°/s isokinetic contractions (concentric and eccentric contractions). We first determined whether the twitch interpolation technique could give evidence of voluntary activation reduction during slow maximal concentric and eccentric contractions. Second, we tested whether voluntary activation differed among the different contraction modes during submaximal voluntary contractions.

MATERIALS AND METHODS

Subjects. Eight physical education students, with a median age of 25 yr (range: 21.3–33.1 yr), a median body mass of 78 kg (range: 71–95 kg), and a median height of 178 cm (range: 171–186 cm), participated in this investigation. All were volunteers and gave written, informed consent to the experiment.

Torque measurements. Measurements were made for all subjects on the right leg extensors using a Biodex isokinetic dynamometer (Biodex, Shirley, NY), which allowed recording of instantaneous muscle torque at various preset constant angular velocities. Subjects were seated with the trunk vertical and thigh fixed at a 90° hip angle. Velcro straps were applied tightly across the thorax, pelvis, and distal thigh. Voluntary torque was measured at the angular position of 50° knee flexion (0° = full extension), during both isometric and isokinetic contractions. Isokinetic contractions were performed at slow angular velocity (20°/s) during both concentric and eccentric contractions. The range of motion was 60°, from 20 to 80° knee flexion.

Electrical stimulation. A single electrical stimulus was applied percutaneously to the femoral nerve. During both maximal and submaximal contractions, a ball probe cathode (~10 mm diameter) was pressed in the femoral triangle, 3–5 cm below the inguinal ligament. The anode (self-adhesive stimulation electrode, 10 × 5 cm) was located in the gluteal fold. Single square-wave stimulus was used with a 1-ms duration, 400-V maximal voltage, and intensity ranging from 50 to 180 mA (Digitimer DS7, Hertfordshire, UK). The maximal intensity of stimulation was set by progressively increasing the stimulus intensity until the maximal isometric twitch torque and concomitant vastus lateralis M-wave amplitude (determined by averaging four twitch responses elicited every 5 s for a given stimulus intensity) were reached. This maximal intensity was then applied under all experimental conditions (i.e., contraction mode and torque level). To ensure that stimulations were maximally delivered at all times, the resultant vastus lateralis M waves were controlled. No M-wave changes were measured when maximal or submaximal isometric and dynamic contractions were compared. During isokinetic movements, impulses were triggered at a constant 50° knee-flexion angle, corresponding to the middle of the range of motion. Although the maximal torque output did not occur at the same knee angle under eccentric and concentric conditions, the amount of activation was calculated at the same 50° knee flexion. According to Harridge and White (17), for angular velocities <60°/s, muscles would have quite enough time to be as maximally activated as possible.

Voluntary activation. Voluntary AL was calculated by expressing every increment in torque evoked during the contraction (size of superimposed twitch) as a fraction of the amplitude of the response evoked by the same stimulus in the relaxed muscle (twitch size evoked at rest). The AL was then quantified as the percentage AL = [1 − (size of superimposed twitch/twitch size evoked at rest)] × 100.

Twitch evoked at rest. The twitch evoked at rest, to be compared with that superimposed during dynamic contractions, was elicited while the muscle was passively shortened or lengthened for concentric and eccentric movements, respectively. All twitches produced on relaxed muscle were corrected by the resistive torque related to weight of the leg and lever arm and the passive viscoelastic forces. To find the appropriate corrections, the resistive torque was measured as the leg was moved passively at the same constant angular velocity (20°/s) without any stimulation. Muscular relaxation was checked by the absence of the vastus lateralis electromyographic (EMG) signal. A series of four twitches was evoked for each velocity (0, +20, and −20°/s) to obtain a mean evoked response. About 10 s separated each twitch.

Superimposed twitch. During isokinetic contractions, muscle torque was changing over the entire range of motion as a consequence of length, velocity, lever arm changes, and degree of activation. In fact, around the angle of stimulation, voluntary concentric torque decreased, whereas torque increased during the eccentric contractions. For this reason, the superimposed twitch torque was calculated by subtracting the poststimulus twitch torque from the torque that would have occurred in the absence of stimulation for the same angular position. Because the torque-time curve was linear before stimulation (Fig. 1*A*), the torque without stimulation was estimated by linear extrapolation of the slope of the prestimulus voluntary torque beyond the point of stimulation. Such estimation of the interpolated twitch has already been used during isometric contractions (2) and concentric contractions (15). The period used for the extrapolation was at least 50 ms. The application of the twitch interpolation technique during maximal isometric contraction and the estimation of the superimposed eccentric twitch are presented in Fig. 1.

Experimental procedure. Maximal isometric contractions (5 s) were first performed at 20, 50, and 80° knee flexion to determine the MVC. Two contractions were made at each angular position. Second, subjects were asked to perform three different tasks. *1*) The first task was maximal and submaximal isometric knee extension at 50° angular position. For submaximal trials, subjects were instructed to keep a specified torque level constant (range from 20 to 100% of the MVC). The stimulation was administered ~3.5 s after the start of the isometric contraction. *2*) The second task was

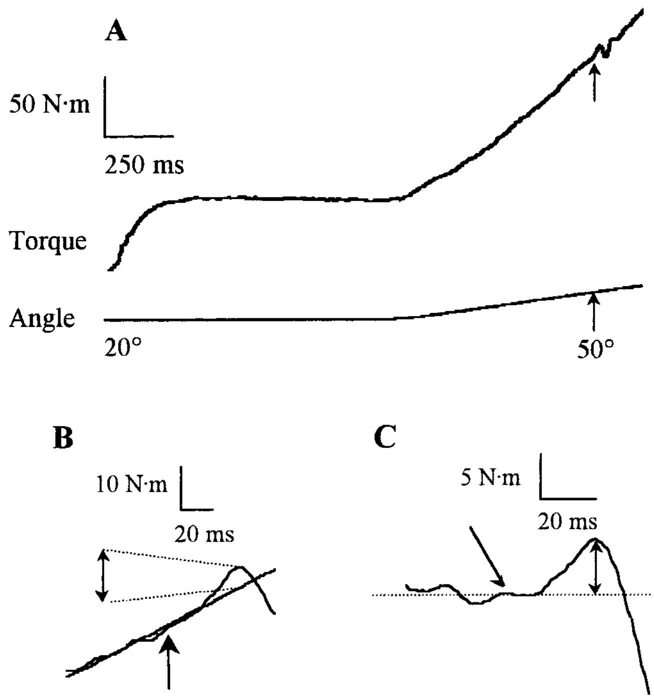

Fig. 1. *A*: effect of single, superimposed electrical stimulus (up arrow) on an eccentric contraction performed at ~80% maximal voluntary contraction (MVC). *Top trace*, torque-time curve; *bottom trace*, knee angle. *B*: estimation of the superimposed twitch response (double arrow) during the same submaximal voluntary eccentric contraction. Superimposed twitch torque was calculated by subtracting the poststimulus torque with the torque that would have occurred without any stimulation (linear extrapolation of the voluntary torque preceding the stimulation) for the same angular position. Up arrow, the time of delivery of the stimulation. *C*: superimposed twitch torque after the subtracting procedure. The twitch size was calculated as the peak torque of the reconstituted twitch. Up arrow, the delivery of the stimulation; double arrow, the estimation of the superimposed twitch response.

maximal and submaximal concentric knee extension; *3*) the third task was maximal and submaximal eccentric knee extension. Contrary to isometric contractions, during maximal and submaximal dynamic contractions, torque could not be maintained constant. Consequently, to be under constant conditions, a vastus lateralis EMG activity control was made. At the onset of the dynamic contraction (20 or 80° knee angle for the eccentric and concentric contractions, respectively), subjects were asked to develop a required torque level during a short isometric preactivation contraction (2 s). Then they were asked to modulate their level of effort during the full range of motion to maintain constant the root-mean-square (RMS) level (range: ±5%) fixed during the preactivation contraction. The RMS level was under visual control via a computer monitor in front of them. Different contraction intensities were obtained by performing preactivation contractions ranging from 20 to 100% of the MVC. Subjects were familiarized with this procedure during a standardized warm-up session. Because subjects succeeded in the task with remarkable ease, during each experiment only two to three trials were excluded from the analysis.

All maximal or submaximal contractions were conducted with superimposed twitch stimulation (Fig. 1*A*). Contraction modes and levels were randomly presented. Three trials were made for each torque level (20, 40, 60, 70, 80, 90, and 100% of the MVC). A 2-min rest period was permitted between each three contractions to avoid the effects of fatigue.

EMG recording. EMG was recorded by using two pairs of silver chloride surface electrodes applied over the belly of the vastus lateralis and biceps femoris. Low impedance of the skin-electrode interface was obtained (impedance <2 kΩ) by abrading the skin. The interelectrode distance was 2 cm (center to center). The reference electrode was attached to the opposite wrist. Myoelectrical signals were amplified with a bandwidth frequency ranging from 1.5 Hz to 2.0 kHz (common mode rejection ratio = 90 dB; impedance = 100 MΩ; gain = 1,000). EMG as well as torque signals were digitalized on-line at a sampling frequency of 1,000 Hz. During isokinetic contractions, vastus lateralis activity was evaluated and directly visualized by means of the RMS amplitude, calculated over subsequent 300-ms period intervals. Vastus lateralis was chosen as it has been suggested that surface EMG recordings from this muscle are more reliable in predicting force output than are those from vastus medialis or rectus femoris muscles (1). The antagonist coactivation (biceps femoris) was evaluated by calculating the RMS over a 300-ms period before the superimposed stimulation. The antagonist RMS was expressed as a fraction of its maximal agonist activity.

Statistical analysis. Descriptive statistics presented in RESULTS or in Figs. 2 and 3 are mean values ± SE. Twitches evoked at rest, torque, AL, and the amount of coactivation obtained during the three MVC trials were averaged for statistical analysis. Because homoscedasticity and normal distribution of the data were verified by means of Levene's and Kolmogorov-Smirnov tests, parametric statistics were used. Thus concentric, isometric, and eccentric conditions were compared by using a one-way ANOVA; subsequent least significant difference test was performed for post hoc analysis to determine differences across velocities. Similarly, average resting twitch torque and average maximal voluntary torque, both normalized with their maximal isometric torque, were compared using a one-way ANOVA. Standard parametric linear regression analysis was used to compare the degree of association between voluntary activation and voluntary torque for all data and for each subject. Slopes of the linear regressions for the three contraction modes (eccentric, isometric, and concentric) were tested by an ANOVA. $P < 0.05$ was taken as the level of statistical significance for all procedures.

RESULTS

Maximal voluntary torque and twitch torque evoked at rest. Knee-extensor maximal voluntary or evoked twitch torque was measured during isometric (0°/s), concentric (+20°/s), and eccentric (−20°/s) contractions. Maximal voluntary concentric torque, measured at 50° constant angular position (236.1 ± 8.1 N·m), was significantly smaller ($P < 0.01$) than isometric and eccentric torques, which were 310.3 ± 11.6 and 313.4 ± 12.8 N·m, respectively. No significant differences were observed between isometric and eccentric maximal voluntary torque values. The mean twitch values evoked on relaxed muscles for eccentric, isometric, and concentric movements were 42.4 ± 4.7, 38.5 ± 4.7, and 38.3 ± 3.8 N·m, respectively. No differences were observed among the three contraction modes. When twitch torque and maximal voluntary torque were expressed as a fraction of their respective isometric torque, relative twitch torque was significantly greater than the

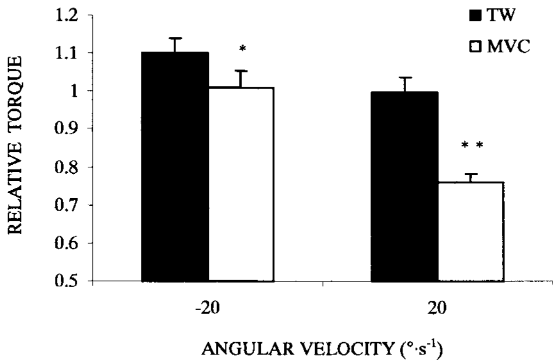

Fig. 2. Normalized torque of the right knee-extensor muscle group during MVC or when contractions were evoked by means of a single twitch (TW) during concentric (+20°/s) and eccentric (−20°/s) contractions. Torque is expressed as a fraction of the respective isometric torque. Values are means ± SE. Significant differences between TW and MVC values at identical velocity: $**P < 0.01$; $*P < 0.05$.

relative maximal voluntary torque. This was observed for both eccentric and concentric conditions (Fig. 2).

AL during maximal contractions. During MVC, an electrical twitch was superimposed to measure the amount of activation. Mean voluntary ALs obtained during the three contraction modes are presented in Fig. 3. The mean voluntary AL during maximal eccentric contractions (88.3 ± 1.9%, range 67.1–99.5%) was significantly lower ($P < 0.01$) than the maximal isometric AL (95.2 ± 1.2%, range 85.6–99.8%). Seven of the eight subjects had a maximal eccentric AL lower than the isometric level. AL during maximal concentric contractions (89.7 ± 1.4%, range 72.9–96.9%) was also significantly lower compared with maximal isometric contractions ($P < 0.05$). During maximal concentric contractions, seven of the eight subjects exhibited a lower AL compared with isometric contractions. No differences were observed between maximal eccentric and concentric AL. For each subject, the coefficient of variation across trials was calculated. Mean coefficients of variation were 4.1 ± 1.1, 1.7 ± 0.6, and 3.1 ± 0.7% for eccentric, isometric, and concentric maximal voluntary activation, respectively.

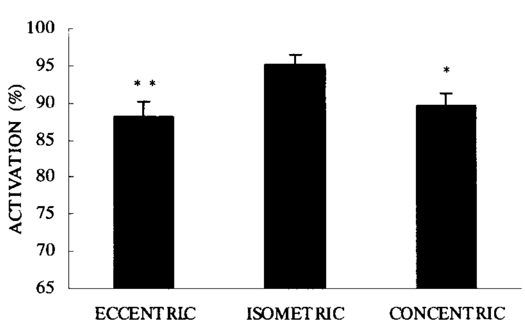

Fig. 3. Mean maximal voluntary activation level measured during maximal eccentric, isometric, and concentric contractions. Maximal voluntary activation (100%) corresponds to no detectable force increment consecutive to the superimposed twitch. Values are means ± SE. Activation during maximal eccentric and concentric contractions is significantly lower than maximal isometric activation: $**P < 0.01$; $*P < 0.05$.

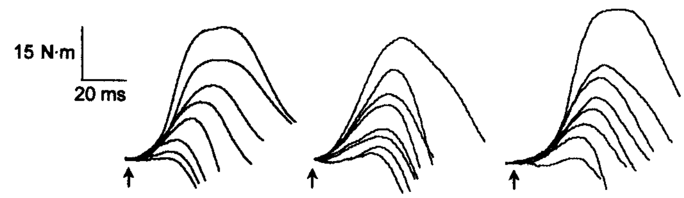

Fig. 4. Torque-time profile of the superimposed twitch response during isometric (*left*), concentric (*center*), and eccentric contractions (*right*). The twitches are presented from relaxed muscle to MVCs (*top* to *bottom traces*). Control and superimposed twitches have been aligned so that time of stimulus (arrows) and force offset of the superimposed twitch are coincident.

The amount of coactivity (biceps femoris) was also measured and averaged 25.1 ± 3.0, 23.0 ± 2.7, and 26.1 ± 3.5% of its agonist activity for eccentric, isometric, and concentric MVC, respectively. No significant differences were recorded among the different angular velocities.

Submaximal voluntary torque and AL. The extent of activation was evaluated for different levels of effort. As expected and whatever the contraction mode, the superimposed twitch torque decreased with increasing voluntary torque (Fig. 4). Consequently, voluntary activation increased as a function of torque. Plots of average AL and average voluntary torque during muscular contractions for one subject are shown in Fig. 5. When individual data are considered, a linear fit ($P < 0.001$) was obtained for each contraction mode. Across the subjects, correlation coefficients ranged from 0.69 to 0.95 for eccentric contractions, 0.86 to 0.95 for isometric contractions, and 0.76 to 0.96 for concentric contractions. On the average, the slopes of the AL-voluntary torque relationships were 0.72 ± 0.44 for the eccentric condition and were significantly lower than those obtained for the concentric (1.02 ± 0.05) and isometric (0.90 ± 0.05) relationships. Five of the eight subjects had an eccentric slope lower than the concen-

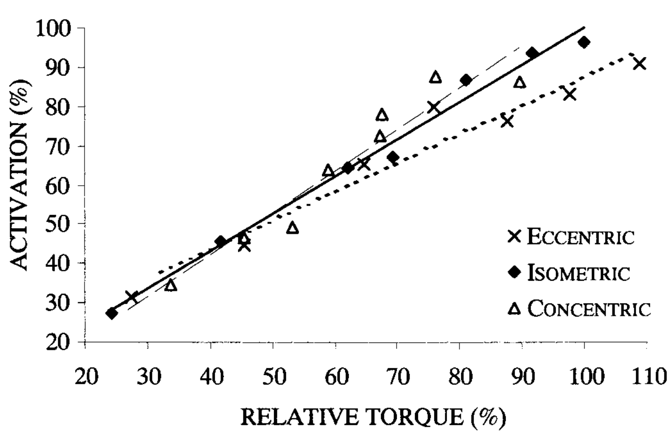

Fig. 5. Relationship between activation level and relative torque (normalized with respect to the maximal isometric torque) for 1 subject. Slow concentric (dashed line), isometric (solid line), and slow eccentric (dotted line) relationships are best fitted by linear regressions. Equations for concentric, isometric, and eccentric contractions are $y = 1.07x - 0.81$ ($r = 0.96$), $y = 0.94x + 5.15$ ($r = 0.95$), and $y = 0.73x + 14.11$ ($r = 0.95$), respectively. Eccentric slope is significantly lower than isometric and concentric slopes ($P < 0.001$).

tric slope. Four of them had an eccentric slope lower than the isometric slope. No significant difference was observed between isometric and concentric slopes.

DISCUSSION

In this study, the twitch interpolation technique, associated with single stimuli, was adapted for application during dynamic contractions. The AL was 88.3 and 89.7% for maximal eccentric and concentric contractions, respectively, and 95.2% for maximal isometric contractions. A majority of studies using this technique during isometric MVC have concluded that human subjects can maximally or near maximally (voluntary activation >95%) activate their muscles (2, 3, 7, 11, 15, 16, 26, 28, 39). Under isometric conditions, our results would confirm these findings. However, as for other studies, AL estimation implies some variability. The range of maximal activation values obtained here was similar to previous results obtained during isometric (2) and concentric contractions (15). The mean coefficient of variation was 1.7% for isometric MVC and was identical to that obtained by Allen et al. (2). These authors concluded that voluntary activation, measured during maximal voluntary efforts, was similar from session to session. Nevertheless, because variability seems to increase during dynamic contractions (see Fig. 3*B* in Ref. 15), the resolution of the technique would decrease slightly. Thus multiple measures are required to enhance the technique reliability.

Results of the twitch interpolation technique indicate that, during maximal eccentric and concentric contractions, voluntary activation was lower compared with maximal isometric contractions. Thus application of single stimuli for assessment of the voluntary activation during eccentric contractions corroborates the reduced neural drive previously hypothesized with different approaches such as EMG (4, 36) or artificial activation evoked on relaxed muscle or superimposed to the voluntary contraction (4, 13, 30, 37). During concentric contractions, as already suggested without employment of superimposed stimulation (18, 29, 30, 36), the same effect was also found. However, previous findings using twitch interpolation during concentric contractions (15, 28) did not confirm this result. Tetanical stimulation superimposed to maximal concentric contraction on the knee extensors did not indicate reduction of AL during slow concentric contractions (37). Because it has been demonstrated that training status did influence the reduction of neural drive (4), the differences with our results could be attributed to the population tested. Indeed, our experimental group, including normally active subjects, was less accustomed to perform maximal efforts than the subjects tested by Westing et al. (37), who were, among others, wrestlers and weightlifters. Furthermore, the velocity tested was threefold greater than those considered in the present investigation and may contribute to the different results. Gandevia et al. (15) calculated maximal voluntary activation during isometric and concentric contractions (until 300°/s) using single electrical stimulation and observed similar activation for the different angular velocities. The fact that nonisokinetic contractions were considered and that the authors did not ensure constant EMG activity during the full range of motion might in part explain the differences from our findings. Another reason for the different results could be that their study was performed on the elbow flexors. Indeed, in another study (28) performed on the quadriceps muscle group under isokinetic conditions (20 and 150°/s), results tended toward our findings. A reduction of activation was effectively observed in more subjects at the slowest velocity than during isometric or 150°/s concentric contractions.

The conclusion supported by the twitch interpolation technique during maximal voluntary efforts appears to be confirmed by the comparison between the relative changes in maximal voluntary torque or twitch torque evoked on resting muscles (see Fig. 2). Indeed, identical maximal voluntary and evoked twitch torque (both normalized with respect to isometric torque) would have revealed similar activation of the knee-extensor muscle group by the central nervous system whatever the angular velocities. However, our results indicate that maximal voluntary torque is not dependent only on the mechanical properties and suggest that ALs would restrain the maximal voluntary concentric and eccentric torque. Thus maximal ALs depend on the types of muscle actions performed. Neural drive inhibition (incomplete motor unit activation) seems to be active to limit high tension levels during 20°/s maximal concentric and eccentric voluntary efforts. Initially, it has been suggested (e.g., Ref. 4) that the neural drive reduction would contribute to the limitation of maximal tension and the preservation of the musculoskeletal integrity (patella dislocation, tendon rupturing, etc.). According to this hypothesis, maximal concentric contractions should have induced higher ALs than those measured in our study, compared with isometric ones. Nevertheless, it is possible to explain this apparent contradiction by the fact that the "tension-limiting mechanism" would be mostly dependent on the type of muscular actions (i.e., isometric or dynamic) rather than on the maximal torque output. This mechanism would be more efficient during maximal dynamic than isometric contractions, as a higher AL was obtained during isometric compared with the concentric and eccentric contractions. Moreover, regarding the magnitude of change of voluntary activation and maximal voluntary torque recorded during maximal eccentric and concentric efforts, activation may not be the only mechanism responsible for torque limitations. Indeed, the similar concentric and eccentric ALs contrast with the considerable variations between relative voluntary and resting twitch torque, particularly observed during concentric contractions. One must, therefore, keep in mind that complementary mechanisms, dependent on the type of contraction, should contribute to these discrepancies. For example, the resultant concentric torque is more affected (i.e., reduced) by the antagonist coactivation than during eccentric actions (23). Indeed, although antagonist EMG activity is similar whatever the angular velocity, during concentric knee extensions, antagonist muscles act eccentrically, thus producing a greater torque in opposition to the agonist action. Similarly, it can be postulated that maximal voluntary concentric contractions could induce more viscoelastic force loss than gain obtained during eccentric contractions (25).

During submaximal eccentric, isometric, and concentric voluntary contractions, the AL increased linearly with increasing tension level. The significantly weaker slope of the AL-torque relationship obtained during eccentric contractions indicates that the voluntary activation reduction is not limited to maximal eccentric efforts but may be an inherent characteristic of the command to activate lengthening muscles voluntarily. It, therefore, supports the fact that, during eccentric contractions, less neural drive (number or discharge rate of the motor unit) is needed to develop a given submaximal muscle tension (8). Identical findings have recently been obtained on human soleus muscle using a different technique, i.e., comparison between submaximal electrical activation and maximal and submaximal voluntary efforts (30). Nevertheless, according to Pinniger et al. (30), this activation reduction would happen at least for torque levels >30% of the MVC and not for the whole eccentric torque range. The reduction of the motoneuronal excitability during eccentric contractions (31), possibly originating from presynaptic inhibition changes, may explain this result. Indeed, it has already been reported that, during submaximal lengthening contractions, high-threshold motor units may be preferentially activated (27). However, contrary to the eccentric condition, submaximal concentric efforts indicate a similar relationship to that fitted during isometric contractions. Such similarity has already been observed using short trains of stimuli (28). Thus a discontinuity between submaximal and maximal concentric contractions is revealed that is probably due to different neural mechanisms intervening in the activation regulation for the different tension levels.

Mechanisms responsible for the reduced central motor drive during maximal dynamic contractions remain unclear but would probably originate from supraspinal, spinal, and peripheral pathways. As indicated using magnetic cortical stimulation, cortical drive may be one cause of the incomplete activation during MVC (14, 19). A lower α-motoneuron excitability, induced by an increased inhibitory feedback from joint receptors of a Golgi type (33), free nerve endings in the muscle, and cutaneous and joint receptors, might also be at the origin of the activation reduction (37). However, it is reasonable that different mechanisms or effectiveness of the peripheral and/or central motor drive would act to reduce the voluntary AL during maximal concentric and maximal and submaximal eccentric contractions.

In conclusion, the twitch interpolation technique associated with single stimuli may provide a direct measure of the voluntary AL during isometric and dynamic contractions. The results indicate reduced activation during both maximal and submaximal eccentric contractions and only maximal concentric contractions at a 20°/s constant angular velocity. The pattern of voluntary activation of the human knee-extensor muscle group would, therefore, depend on the type of muscular actions performed. Neural drive inhibition can be one possible cause of the reduced activation during maximal dynamic contractions.

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REFERENCES

1. **Alkner BA, Tesch PA, and Berg HE.** Quadriceps EMG/force relationship in knee extension and leg press. *Med Sci Sports Exerc* 32: 459–463, 2000.
2. **Allen GM, Gandevia SC, and McKenzie DK.** Reliability of measurements of muscle length and voluntary activation using twitch interpolation. *Muscle Nerve* 18: 593–600, 1995.
3. **Allen GM, McKenzie DK, and Gandevia SC.** Twitch interpolation of the elbow flexor muscles at high forces. *Muscle Nerve* 21: 318–328, 1998.
4. **Amiridis IG, Martin A, Morlon B, Martin L, Cometti G, Pousson M, and Van Hoecke J.** Co-activation and tension-regulating phenomena during isokinetic knee extension in sedentary and highly skilled humans. *Eur J Appl Physiol* 73: 149–156, 1996.
5. **Beelen A, Sargeant AJ, Jones DA, and De Ruiter CJ.** Fatigue and recovery of voluntary and electrically elicited dynamic force in humans. *J Physiol (Lond)* 484: 227–235, 1995.
6. **Behm DG, St. Pierre MM, and Perez D.** Muscle inactivation: assessment of interpolated twitch technique. *J Appl Physiol* 81: 2267–2273, 1996.
7. **Belanger AY and Mc Comas J.** Extent of motor unit activation during effort. *J Appl Physiol* 51: 1131–1135, 1981.
8. **Bigland B and Lippold OCJ.** The relation between force, velocity and integrated electrical activity in human muscles. *J Physiol (Lond)* 123: 214–224, 1954.
9. **Bigland-Ritchie B, Furbush F, and Woods JJ.** Fatigue of intermittent submaximal voluntary contractions: central and peripheral factors. *J Appl Physiol* 61: 421–429, 1986.
10. **Caiozzo VJ, Perrine JJ, and Edgerton VR.** Training-induced alterations of the in vivo force-velocity relationship of human muscle. *J Appl Physiol* 51: 750–754, 1981.
11. **De Serres SJ and Enoka RM.** Older adults can maximally activate the biceps brachii muscle by voluntary command. *J Appl Physiol* 84: 284–291, 1998.
12. **Dowling JJ, Konert E, Ljucovic P, and Andrews DM.** Are humans able to voluntarily elicit maximum muscle force? *Neurosci Lett* 179: 25–28, 1994.
13. **Dudley GA, Harris RT, Duvoisin MR, Hather BM, and Buchanan P.** Effect of voluntary vs. artificial activation on the relationship of muscle torque to speed. *J Appl Physiol* 69: 2215–2221, 1990.
14. **Gandevia SC, Allen GM, Butler JE, and Taylor JL.** Supraspinal factors in human muscle fatigue: evidence for suboptimal output from the motor cortex. *J Physiol (Lond)* 490: 529–536, 1996.
15. **Gandevia SC, Herbert RD, and Leeper JB.** Voluntary activation of human elbow flexor muscle during maximal concentric contractions. *J Physiol (Lond)* 512: 595–602, 1998.
16. **Gandevia SC and McKenzie DK.** Activation of human muscles at short muscle lengths during maximal static efforts. *J Physiol (Lond)* 407: 599–613, 1988.
17. **Harridge SD and White MJ.** Muscle activation and the isokinetic torque-velocity relationship of the human triceps surae. *Eur J Appl Physiol* 67: 218–221, 1993.
18. **Harris RT and Dudley GA.** Factors limiting force during slow, shortening actions of the quadriceps femoris muscle group in vivo. *Acta Physiol Scand* 152: 63–71, 1994.
19. **Herbert RD and Gandevia SC.** Muscle activation in unilateral and bilateral efforts assessed by motor nerve and cortical stimulation. *J Appl Physiol* 80: 1351–1356, 1996.

20. **Herbert RD and Gandevia SC.** Twitch interpolation in human muscles: mechanisms and implications for measurement of voluntary activation. *J Neurophysiol* 82: 2271–2283, 1999.
21. **Herbert RD, Gandevia SC, and Allen GM.** Sensitivity of twitch interpolation. *Muscle Nerve* 20: 521–522, 1997.
22. **James C, Sacco P, and Jones DA.** Loss of power during fatigue of human leg muscles. *J Physiol (Lond)* 484: 237–246, 1995.
23. **Kellis E and Baltzopoulos V.** The effects of the antagonist muscle force on intersegmental loading during isokinetic efforts of the knee extensors. *J Biomech* 32: 19–25, 1999.
24. **Kent-Braun J and Le Blanc R.** Quantitation of central activation failure during maximal voluntary contractions in humans. *Muscle Nerve* 19: 861–869, 1996.
25. **Martin A, Morlon B, Pousson M, and Van Hoecke J.** Viscosity of the elbow flexor muscles during maximal eccentric and concentric actions. *Eur J Appl Physiol* 76: 157–162, 1996.
26. **Merton PA.** Voluntary strength and fatigue. *J Physiol (Lond)* 123: 553–564, 1954.
27. **Nardone A, Romano C, and Schieppati M.** Selective recruitment of high-threshold human motor units during voluntary isotonic lengthening of active muscle. *J Physiol (Lond)* 409: 451–471, 1989.
28. **Newham DJ, McCarthy T, and Turner J.** Voluntary activation of human quadriceps during and after isokinetic exercise. *J Appl Physiol* 71: 2122–2126, 1991.
29. **Perrine JJ and Edgerton VR.** Muscle force-velocity and power-velocity relationships under isokinetic loading. *Med Sci Sports Exerc* 10: 156–166, 1978.
30. **Pinniger GJ, Steele JR, Thorstensson A, and Cresswell AG.** Tension regulating during lengthening and shortening actions of the human soleus muscle. *Eur J Appl Physiol* 81: 375–383, 2000.
31. **Romanò C and Schieppati M.** Reflex excitability of human soleus motoneurones during voluntary shortening and lengthening contractions. *J Physiol (Lond)* 390: 271–284, 1987.
32. **Rutherford OM, Jones DA, and Newham DJ.** Clinical and experimental application of the percutaneous twitch superimposition technique for the study of human muscle activation. *J Neurol Neurosurg Psychiatry* 49: 1288–1291, 1986.
33. **Solomonow M, Baratta R, Zhou BH, and D'Ambrosia R.** Electromyogram coactivation patterns of the elbow antagonist muscle during slow isokinetic movement. *Exp Neurol* 100: 470–477, 1988.
34. **Suter E and Herzog W.** Effect of number of stimuli and timing of twitch application on variability in interpolated twitch torque. *J Appl Physiol* 90: 1036–1040, 2001.
35. **Webber S and Kriellaars D.** Neuromuscular factors contributing to in vivo eccentric moment generation. *J Appl Physiol* 83: 40–45, 1997.
36. **Westing SH, Cresswell AG, and Thorstensson A.** Muscle activation during maximal voluntary eccentric and concentric knee extension. *Eur J Appl Physiol* 62: 104–108, 1991.
37. **Westing SH, Seger JY, and Thorstensson A.** Effects of electrical stimulation on eccentric and concentric torque-velocity relationships during knee extension in man. *Acta Physiol Scand* 140: 17–22, 1990.
38. **Wichiewicz TL, Roy RR, Powell PL, Perrine JJ, and Edgerton VR.** Muscle architecture and force-velocity relationship in humans. *J Appl Physiol* 57: 435–443, 1984.
39. **Yue GH, Ranganathan VK, Siemionow V, Liu JZ, and Sahgal V.** Evidence of inability to fully activate human limb muscle. *Muscle Nerve* 23: 376–384, 2000.