Effect of quadriceps femoris muscle length on neural activation during isometric and concentric contractions

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First published November 15, 2002; 10.1152/japplphysiol.00717.2002.—The effect of muscle length on neural drive (here termed “neural activation”) was investigated from electromyographic activities and activation levels (twitch interpolation). The neural activation was measured in nine men during isometric and concentric (30 and 120°/s) knee extensions for three muscle lengths (35, 55, and 75° knee flexion, i.e., shortened, intermediate, and lengthened muscles, respectively). Long (76°), medium (56°), and short (36°) ranges of motion were used to investigate the effect of the duration of concentric contraction. Neural activation was found to depend on muscle length. Reducing the duration of contraction had no effect. Neural activation was higher with short muscle length during isometric contractions and was weaker for shorter than for intermediate and lengthened muscles performing 120°/s concentric contractions. Muscle length had no effect on 30°/s concentric neural activation. Peripheral mechanisms and discharge properties of the motoneurons could partly explain the observed differences in the muscle length effect. We thus conclude that muscle length has a predominant effect on neural activation that would modulate the angular velocity dependency.

Contraction duration; electromyogram activity; twitch interpolation; angular position

THE TORQUE THAT A HUMAN MUSCLE can produce has been shown to depend on the contractile conditions, i.e., contraction mode, angular velocity, and angular position (i.e., muscle length). Similarly, the ability of humans to maximally activate a muscle or a muscular group depends on the different contractile conditions.

In maximal isometric conditions, whether the neural activation generated by the central nervous system depends on muscle length remains an unsettled issue. Gandevia and McKenzie (20) and Bigland-Ritchie et al. (13) found that neural activation stays constant whatever the muscle length, whereas other authors have demonstrated higher (27, 29, 31, 33, 39) or lower neuronal (9) activation with decreasing muscle length. This discordance could partly be attributed to the different experimental designs, including various muscle groups (10) or different techniques for quantifying neural activation. Indeed, conclusions drawn from surface electromyography (EMG activity) (12) and twitch interpolation technique (activation level) (35) can diverge. For instance, Cresswell et al. (16) obtained similar triceps surae activation levels for different muscle lengths whereas EMG activity of both heads of the gastrocnemius muscle was lower for shortened muscle length. Other studies have focused on the discharge properties of the motor units, which yield more convergent results because the motor unit discharge rate has been commonly demonstrated to increase with decreasing muscle length (15, 16, 41).

During maximal concentric actions, neural activation, which is primarily influenced by the angular velocity (e.g., Ref. 2), also depends on muscle length. Yet Komi et al. (31) recently observed enhanced biceps brachii EMG activity with decreasing muscle length during isometric, concentric, and eccentric contractions. However, when muscles are dynamically solicited, duration of contraction could explain at least part of the dependency of neural activation on muscle length. For example, using a release technique, Harridge and White (24) found that triceps surae muscles lack time to develop their maximum tension during fast isokinetic concentric contractions (≥115°/s). Thus it could be expected that reducing the contraction duration by shortening the concentric range of motion would impair neural activation.

Accordingly, these two last-cited studies (24, 31) raised the question of whether neural activation dependency on contraction mode and angular velocity could be biased by either or both the muscle length and the time available for maximal torque generation. Thus the purpose of the present study was to examine the effects of quadriceps femoris muscle length on neural activation during isometric and isokinetic concentric knee extensions (30 and 120°/s). The effect of

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various contraction durations was also investigated during concentric actions by using different ranges of motion. In the present study, the term “neural activation” was used to describe the neural drive and was quantified by means of both the EMG activity and activation level estimated by using the twitch interpolation technique.

**METHODS**

*Subjects.* Nine physically active men without previous knee joint injury participated in the study. Their mean (± SD) age, height, and body mass were 20.6 ± 1.6 yr, 177.3 ± 5.7 cm, and 73.8 ± 6.3 kg, respectively. All subjects were fully informed about the purpose and procedures of the tests, and all gave their written, informed consent before participation. The study was conducted according to the declaration of Helsinki and was approved by the Local Ethics Committee.

*Experimental protocol.* Maximal voluntary and evoked twitch torque, activation level, and EMG activity measurements of the right knee extensor muscles were performed on a Biodex isokinetic dynamometer (Biodex, Shirley, NY). Subjects were seated upright with a 90° hip angle on the dynamometer chair. Velcro straps were applied tightly across the thorax and pelvis, with the distal leg fixed to the dynamometer lever arm. The axis of rotation of the dynamometer was aligned to the lateral femoral condyle, indicating the anatomical joint axis of the knee. Isometric and concentric knee extension torque was measured and recorded instantaneously at various preset constant angular velocities. Each subject was familiarized with the dynamometer and stimulation procedure under maximal isometric and isokinetic concentric conditions ±48 h before the experiment.

The test procedure began with a standardized warm-up including both isometric and concentric contractions with increasing intensities until maximal voluntary contraction (MVC). Then, MVCs were performed under isometric and isokinetic concentric conditions. Isometric contractions were ~5 s duration. Two different concentric angular velocities were used: 30 and 120°/s. First, to investigate the effect of the quadriceps muscle length, isometric and concentric torques with the respective neural activation were measured at three different joint angles (35, 55, and 75° knee flexion; full extension = 0°). The term “muscle length,” used hereafter, was retained rather than “joint angle” for clarity in comparing with earlier related studies. Thus a 35° knee joint angle corresponded to shortened quadriceps muscles (L_{35}), 55° (L_{55}) was the intermediate length, and 75° corresponded to lengthened muscles (L_{75}). One concentric trial was performed separately for each muscle length to estimate the respective neural activation estimation. Second, to investigate the effect of the contraction duration on neural activation during concentric efforts, three ranges of motion were considered. The long-duration contraction had a range of motion of 76° from 96 to 20° knee flexion, the medium-duration contraction was 56° from 76 to 20° knee flexion, and the short-duration contraction had a range of motion of 36° from 56 to 20° knee flexion (Fig. 1C). During 30 and 120°/s concentric contractions, the entire contractions lasted 3.20 and 0.94 s for the longest, 2.50 and 0.77 s for the medium, and 1.80 and 0.60 s for the shortest duration. These particular muscle lengths and ranges of motion were chosen as a function of the dynamometer mechanical delay to reach the isovelocity for measuring both activation level and EMG activity. Because of the range of motion modulation, three muscle lengths were tested for the long-duration contraction (L_{35}, L_{55}, and L_{75}), whereas two muscle lengths (L_{35} and L_{55}) were considered for the medium-duration and only one for the short-duration (L_{35}).

The effects of muscle length (L_{35}, L_{55}, and L_{75}) and contraction duration (long, medium, and short) for the different contraction modes (isometric and concentric) and angular
velocities (30 and 120°/s) were tested in a random order. Two consecutive attempts were performed for each experimental condition. At least a 2-min rest period was permitted between each effort to avoid the effects of fatigue. Subjects were consistently informed about the experimental condition considered. Whatever the contraction, subjects were strongly encouraged by the same investigator to push as hard as possible to perform all actions maximally, i.e., during the 5-s isometric contractions and throughout the whole range of motion for concentric contractions.

Measurement of the quadriceps activation level. The voluntary quadriceps femoris activation level was estimated by means of the twitch interpolation technique that involves a single electrical stimulus superimposed during a voluntary effort. Bipolar surface-stimulating electrodes were used. A ball probe cathode (~10-mm diameter) was pressed onto the femoral triangle over the femoral nerve and moved to the position giving the greatest visible contractions of the whole quadriceps muscle group. The anode (self-adhesive electrode, 10 × 5 cm) was positioned midway between the superior aspect of the greater trochanter and the inferior border of the iliac crest. Single square-wave stimuli were delivered with 1-ms duration, 400-V maximal voltage, and intensity ranging from 60 to 130 mA (Digitimer DS7, Hertfordshire, UK). After the warm-up, the maximal stimulus intensity was determined by progressively increasing the current until there was no further increase in the evoked isometric twitch response. Supramaximal stimuli (maximal intensity + 10%) were then applied for all experimental conditions.

Each trial consisted in a single electrical twitch evoked on relaxed muscles that was immediately followed by a MVC superimposed by single twitch. During isometric contractions (L55, L60, and L75), the superimposed twitch was elicited ~0.5 s after the maximal voluntary torque plateau had been reached. During concentric actions, to deliver the single pulse at a specific muscle length, a trigger was connected to the joint angular position channel. Because of the slightly higher twitch contraction time and electromechanical delay for 120° compared with 30° isometric contractions, the trigger was carefully adjusted to obtain peak twitch responses on relaxed muscles as close as possible to the muscle length desired (L55, L60, and L75). Because the twitch torque evoked on relaxed muscles depends on both angular velocity and muscle length, the superimposed twitch increment (A) was finally expressed as a fraction of the amplitude of the twitch evoked in relaxed muscles (B) under similar conditions to quantify the amount of activation: activation level (%) = 100 − (A/B) × 100.

Torque measurements. During each trial, torque traces were recorded and digitized online (sampling frequency: 5.0 kHz). First, for the twitch evoked on relaxed muscles, the following twitch parameters were measured: 1) peak twitch torque, i.e., the maximal amplitude of the knee extensors twitch torque; and 2) twitch contraction time, the time to peak twitch, calculated from the origin of the mechanical signal. Second, the maximal voluntary torque produced before the superimposed stimulation was collected. Third, the superimposed peak twitch torque during isometric and concentric contractions was calculated by subtracting the torque that would have occurred in absence of stimulation. The latter was estimated by linear extrapolation of the slope of the voluntary torque measured before the stimulation beyond the stimulus artifact. A 50-ms minimal period was used for the extrapolation procedure. Such estimation has already been applied during isometric (5) and concentric MVC (19). Appropriate corrections were made for the gravitational effect of the lower leg for all torque measurements by recording and subtracting the resistive torque of the leg on relaxed subjects under isometric or concentric conditions.

EMG activity measurements. EMG activities from the three superficial knee extensor muscles (vastus lateralis, vastus medialis, and rectus femoris) and one knee flexor (long head of the biceps femoris) were recorded. After the skin was shaved, abraded with sandpaper, and cleaned with alcohol, bipolar surface EMG electrodes (2-cm interelectrode distance) were attached over the respective muscle belly. The reference electrode was placed on the opposite wrist. EMG 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) and recorded with a sampling frequency of 5.0 kHz. The EMG activity was quantified by means of the root mean square (RMS) amplitude, calculated over a 500-ms period for isometric MVC and over a 15° angular displacement before the superimposed stimulation for concentric MVC. All RMS amplitudes were then expressed as a fraction of the L55 isometric RMS value. A mean quadriceps femoris RMS value (aRMS) was finally calculated by averaging the RMS of the three superficial knee extensors. Biceps femoris RMS amplitude was normalized as a percentage of its maximal isometric value when acting as an agonist (L55). EMG peak-to-peak amplitude of the compound muscle action potential (M-wave) associated with the single electrical twitch evoked in relaxed muscles was quantified for each muscle.

Statistical analysis. The two attempts made for each experimental condition were averaged for statistical analysis. Results are expressed as mean values ± SD except in Figs. 2 and 3, in which data are presented as means ± SE for better clarity. Mean values were analyzed by using a two-way ANOVA with repeated measures to test muscle length effect (L55, L60, or L75) and contraction mode or angular velocity (isometric, 30 or 120°/s concentric contractions) for the long-then medium-duration contraction. The neural activation dependency on contraction duration was tested during concentric contractions for both L55 (all three contraction durations) and L60 (long- and medium-duration contraction) by using a one-way ANOVA. F ratios were considered significant at a P level lower than 0.05. A Newman-Keuls post hoc test was conducted if significant main effects or interactions were present.

Fig. 2. Relationship between the average maximal voluntary isometric (○), 30°/s concentric (●), and 120°/s concentric (▲) torque and the different muscle lengths (full extension = 0°) using the long-duration contraction (range of motion = 76°). Values are means ± SE. For a given muscle length, significant differences with isometric torque are shown: *P < 0.05, **P < 0.01, ***P < 0.001. For a given contraction mode and angular velocity, L55 maximal voluntary torques were significantly lower than those for L60 and L75: †P < 0.001.
RESULTS

Twitch contractile properties and associated M-waves in relaxed muscles. Peak twitch torque and contraction time of the electrically evoked twitches delivered on relaxed muscles are presented in Table 1. For each angular velocity, the peak twitch was on average 29.2 \pm 9.6 and 21.1 \pm 15.7% lower for \( L_{35} \) \((P < 0.05)\) compared with \( L_{55} \) and \( L_{75} \), respectively. Likewise, whatever the muscle length, the peak twitch torque was 34.4 \pm 7.4 and 27.1 \pm 6.2 depressed under 120°/s concentric conditions \((P < 0.05)\) compared with isometric and 30°/s concentric conditions, respectively (Fig. 1A). These differences were partly due to the lever arm and to the proper torque-length and torque-velocity relationships of the musculoskeletal system. The activation level should therefore be calculated by using a twitch elicited under similar conditions (contraction mode, angular velocity, and muscle length) on both voluntarily active and relaxed muscles.

Changes in peak twitch torque were associated with changes in the twitch contraction time. All three contractile conditions (isometric and concentric 30 and 120°/s) systematically indicate shorter twitch contraction times for \( L_{35} \) than for \( L_{55} \) and \( L_{75} \) muscle length. For the 120°/s concentric condition, the \( L_{35} \) and \( L_{75} \) muscle lengths exhibited significantly lower values compared with both isometric and 30°/s concentric conditions. The \( L_{55} \) twitch contraction time remained unchanged under all contractile conditions.

The M-wave peak-to-peak amplitude was expressed as a fraction of the \( L_{55} \) isometric value. Because no muscle effect was obtained, the average M-wave amplitude was calculated for the three superficial knee extensors (Table 1). Our results indicate no significant M-wave amplitude change for the different muscle lengths and angular velocities.

Maximal voluntary torque. During concentric contractions, the maximal voluntary torque was not significantly different when considering the long-, medium-, or short-duration contraction. For example, during 30°/s maximal contractions, the \( L_{35} \) torque was 148.5 \pm 32.9, 154.2 \pm 39.4, and 157.7 \pm 37.9 N.m, respectively, when the long-, medium-, and short-duration contractions were used. Because no contraction duration effect on maximal voluntary torque was noticed, the following results only consider the torque generated for the three muscle lengths using the same duration, i.e., long-duration contraction.

The analysis of the maximal voluntary torque indicated a dependency on both muscle length and angular velocity (Fig. 2). For the three muscle lengths, the maximal voluntary isometric torque was 41.3 \pm 11.3% higher \((P < 0.05)\) than that produced for the fastest concentric contraction. In the same way, the isometric torque was 33.2 \pm 19.3% higher \((P < 0.05)\) than 30°/s concentric torque for the \( L_{75} \) muscle length. For a given

<table>
<thead>
<tr>
<th>Table 1. Mechanical properties and M-wave amplitudes of single twitch evoked on the relaxed muscles</th>
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<tbody>
<tr>
<td>Isometric</td>
</tr>
<tr>
<td>Peak twitch, N·m</td>
</tr>
<tr>
<td>( L_{35} )</td>
</tr>
<tr>
<td>( L_{55} )</td>
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<tr>
<td>( L_{75} )</td>
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<tr>
<td>Contraction time, ms</td>
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<td>( L_{35} )</td>
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<td>( L_{55} )</td>
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<td>( L_{75} )</td>
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<tr>
<td>M-wave peak-to-peak amplitude</td>
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<tr>
<td>( L_{35} )</td>
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<tr>
<td>( L_{55} )</td>
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<td>( L_{75} )</td>
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</table>

Values are means \pm SD. Twitches were evoked for 3 muscle lengths \((L_{35}, L_{55}, \text{and } L_{75}, \text{at 55, 50, and 75° knee flexion, respectively})\) with a 76° range of motion. Twitch mechanical properties were peak twitch torque (N·m) and twitch contraction time (ms). The M-wave amplitude was the average of the 3 superficial knee-extensor muscles and was expressed as a fraction of the \( L_{55} \) isometric value. *\( L_{35} \) values significantly lower \((P < 0.05)\) than both the \( L_{55} \) and \( L_{75} \) quadriceps muscle length for similar action mode and angular velocity. †Concentric 120°/s values significantly lower \((P < 0.05)\) compared with isometric and concentric 30°/s conditions for a similar muscle length.
NEURAL ACTIVATION AND MUSCLE LENGTH

Table 2. Neural activation of the quadriceps femoris during maximal concentric contractions

<table>
<thead>
<tr>
<th>Activation Level</th>
<th>30°/s</th>
<th>120°/s</th>
<th>30°/s</th>
<th>120°/s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medium duration</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L35</td>
<td>81.1±7.2</td>
<td>85.8±4.2</td>
<td>0.95±0.18</td>
<td>1.13±0.17</td>
</tr>
<tr>
<td>L55</td>
<td>83.1±8.9</td>
<td>93.8±3.6</td>
<td>1.02±0.10</td>
<td>1.25±0.11</td>
</tr>
<tr>
<td>Short duration</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L35</td>
<td>85.1±4.9</td>
<td>81.9±6.1</td>
<td>0.93±0.10</td>
<td>1.02±0.13</td>
</tr>
</tbody>
</table>

Mean values (± SD) of the activation level (%) and mean quadriceps femoris root mean square (aRMS; %) are shown as a function of muscle lengths (L35 and L55) using medium- or short-duration contraction (56 and 36° range of motion, respectively). *L35 neural activation significantly lower (P < 0.01) than L55 for the same concentric angular velocity. Concentric 30°/s values statistically lower compared with concentric 120°/s condition for a similar muscle length (†P < 0.05 and ‡P < 0.01).

contraction mode or angular velocity, the L35 maximal voluntary torque was on average 51.4 ± 16.7 and 54.2 ± 16.0% lower compared with L55 and L75, respectively. No difference was observed between the L55 and L75 muscle lengths.

Effect of length on neural activation (long-duration contraction). Surface EMG activity and activation level were used to estimate quadriceps femoris neural activation. Both disclosed neural activation dependency on muscle length (Fig. 3). During maximal isometric contractions, neural activation appeared to be reduced with increasing muscle length (see Fig. 1B). During 30°/s maximal concentric contractions, subjects demonstrated a similar ability to activate their quadriceps muscle group whatever the muscle length. The neural activation measured during 120°/s concentric MVC was, however, lower for shortened muscles (L35) compared with L55 and L75. Nevertheless, this behavior is only significantly revealed when considering activation level results (P < 0.01) and not EMG activity. Concerning EMG data, it is important to note that similar EMG results were obtained when analyzing separately the RMS of the three superficial knee extensors (data not reported).

Effect of angular velocity on neural activation (long-duration contraction). The angular velocity effect on neural activation was then investigated for different muscle lengths (Fig. 3). The results pointed out a specific angular velocity effect for each muscle length. When shortened muscle lengths (L35) were considered, the subjects exhibited a significantly higher activation level for isometric than for the two concentric contractions. The L55 activation level during 30°/s concentric contractions was slightly lower when compared with isometric efforts (P = 0.076) and was significantly increased (P < 0.05) with increasing concentric angular velocity up to 120°/s. Finally, for the L75 muscle length, activation level was higher during 120°/s actions compared with both isometric and 30°/s concentric MVCs. The angular velocity effect was also observed on EMG activity because L55 and L75 aRMS were higher at 120°/s compared with both isometric and 30°/s concentric contractions.

Effect of the contraction duration on neural activation. Activation level and EMG activity obtained for a given muscle length were similar when the long-, medium-, or short-duration contraction was used (Table 2 and Fig. 3). The neural activation dependency on muscle length and angular velocity, previously presented, was again detected.

Biceps femoris coactivation. The RMS of the biceps femoris was used to quantify coactivation. There was no significant change in coactivation for the three muscles lengths whatever the angular velocity (Table 3). Although slightly higher coactivation values were recorded during 120°/s concentric MVC, no significant difference was obtained among isometric, 30, and 120°/s contractions.

DISCUSSION

The purpose of this work was to investigate the effects of different muscle lengths and contraction durations on neural activation during isometric and concentric MVC. Neural activation was quantified by using both the twitch interpolation technique (activation level) and EMG recordings. Our results indicated a neural activation dependency on muscle length that was not affected by the different concentric contraction durations we used. Both activation level and EMG activity also revealed that neural activation depends on the contraction mode and angular velocity. This latter effect differed as a result of the predominant muscle length dependency.

The twitch interpolation technique demonstrated an inability of our subjects to maximally activate the quadriceps muscle group for all conditions. Activation levels were calculated by averaging two consecutive trials for each experimental condition. No significant difference was obtained between the two trials. Thus mean activation level ranged from 81.1 to 93.8%. These values are somewhat low compared with related studies (e.g., Ref. 19) but are in line with other reports (e.g., Ref. 25). Such differences in activation level can be explained by the high but reasonable intersubject variability previously observed (4) and by the fact that, in the present study, activation levels were estimated by using unpotentiated resting twitches. Indeed, unpotentiated twitches lower activation levels compared with potentiated ones but would likely reveal similar con-

Table 3. Biceps femoris coactivation

<table>
<thead>
<tr>
<th></th>
<th>Isometric</th>
<th>Concentric 30°/s</th>
<th>Concentric 120°/s</th>
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<tbody>
<tr>
<td>L35</td>
<td>20.2±6.1</td>
<td>20.2±6.8</td>
<td>22.2±6.7</td>
</tr>
<tr>
<td>L55</td>
<td>19.3±5.8</td>
<td>20.8±6.2</td>
<td>22.4±6.6</td>
</tr>
<tr>
<td>L75</td>
<td>19.6±6.6</td>
<td>23.0±7.8</td>
<td>22.7±6.8</td>
</tr>
</tbody>
</table>

The biceps femoris coactivation during maximal isometric and 30 and 120°/s concentric contractions is shown as a function of the 3 muscle lengths (L35, L55, and L75). Mean root mean square (RMS) amplitudes (± SD) were expressed as a percentage of the isometric L55 RMS amplitude when acting as an agonistic muscle.
conclusions (unpublished observations). Nevertheless, the twitch interpolation accurately quantifies neural activation during isometric and concentric MVCs (19).

**Neural activation unaffected by the duration of contraction.** Concentric voluntary torque can be measured at a constant muscle length (37) or at the length at which maximal torque occurs (40). However, this latter can dramatically change depending on the angular velocity (6). This last study, together with the indications of Harridge and White (24), points out that a muscle group needs sufficient time for maximal activation with increasing concentric angular velocities. Because these authors (24) did not measure neural activation, their proposition was verified in this study by using different contraction durations. Our results did not confirm this suggestion. Indeed, at least for 30 and 120°/s concentric actions, the different contraction durations did not alter neural activation. Therefore, the neural activation measured for the different muscle lengths did not stem from a dependency on contraction duration; differences in neural activation would mainly disclose a dependency on muscle length (discussed below). Because neural activation was not affected by the duration of the contraction, only the results concerning the long-duration contractions are considered for further discussion.

**Changes in neural activation as a function of muscle length during isometric contractions.** As often observed (9, 36, 39), the knee extensor torque produced by human subjects during isometric MVC is significantly lower when the leg is close to full extension (i.e., short muscle length). This reduction in torque could partly be due to mechanical factors such as the reduced number of attached cross bridges subsequent to sarcomere shortening beyond the optimal actin-myosin overlap. Lever arm also influences the knee extension torque. However, the quadriceps lever arm, found to be maximal around 30–50° knee flexion angle and to decrease with increasing muscle length (30), would partly compensate for the detrimental actin-myosin overlap of shortened muscles. Additionally, as indicated by higher surface EMG activities and slightly higher activation levels recorded for shortened muscles, neural activation seems also to compensate for the mechanical disadvantage of the shortened compared with the lengthened quadriceps. However, the EMG signal could be altered by configuration changes of the muscle fibers within the recording volume of the electrodes as a result of the different muscle lengths (22). Nevertheless, as previously reported (32), no M-wave changes were detected as a function of length, suggesting that EMG signals would accurately denote the neural activation dependency on muscle length.

The higher neural activation recorded for short muscle length is in general accordance with previous studies performed on different muscle groups such as the elbow flexors (31) or tibialis anterior (33). These findings were also observed on the knee extensor muscle group (27, 39) and could be partly attributed to forces in the patellofemoral joint. Indeed, joint receptors respond to mechanical events that result in loading the capsule (23) and, together with ligaments receptors (see Ref. 17), could inhibit the α-motoneuron activity. Thus a shortened position (here $L_{35}$) would lessen joint and ligament strain as a consequence of the lower torque, therefore leading to an improved neural activation of the quadriceps femoris muscle. A reduced inhibition of the motoneuron pool via peripheral inputs coming from joint and ligament receptors is therefore partly expected. Besides these effects, muscle length changes are related to modulations of the muscle spindle activity. However, as obtained by Becker and Awiszus (9), muscle spindles would enlarge neural activation for lengthened muscles. Thus muscle spindles would likely have a reduced contribution partly due to a lower sensitivity. Indeed, the muscle spindle sensitivity could be modified by γ-motoneurons that also receive connections from joint and ligament receptors (18). Changes in joint and ligament receptor output as a function of muscle tension might therefore reduce the muscle spindle sensitivity to muscle length changes. This indirect effect of joint receptors on neural activation has a more potent role than its direct action on α-motoneurons (28). Joint and ligament receptors would likely contribute, directly or indirectly (via γ-motoneurons), to neural activation changes as a function of the knee extensor muscle length. Additionally, the enhanced neural activation recorded for $L_{35}$ could result from improved motoneuron excitability. Such excitability increase is partly confirmed by the H reflex enlargement previously recorded in the shortened quadriceps (21). Finally, similar to the findings reported by Cresswell et al. (16), modifications in muscle length produced unchanged soleus M-wave amplitudes. Thus it seems reasonable that the neuromuscular transmission-propagation is not length dependent. In conclusion, the higher level of neural activation observed in shortened muscles performing isometric MVC would result from spinal mechanisms partly compensating for the mechanical disadvantage of short quadriceps muscle length.

**Changes in neural activation as a function of muscle length during concentric contractions.** Neural activation dependency on muscle length is also a relevant factor for the neuromuscular behavior of the quadriceps muscle during dynamic contractions. Indeed, although no muscle length effect was demonstrated for slow concentric angular velocity (30°/s), activation level during 120°/s concentric contractions was found to be lower at the shortest quadriceps length ($L_{35}$). To our knowledge, only one study has measured the activation level for different muscle lengths during concentric, but not isokinetic, contractions (19). These authors obtained unchanged activation levels for two muscle lengths of the elbow flexors, but, because of the range of motion, they could draw no conclusions concerning the muscle length effect. Contrasting with our activation level results, surface EMG recordings did not indicate any muscle length effect. These discrepancies may be consequential to higher inter- and intra-subject variability observed for RMS values than for activation levels (8). Moreover, the fact that the RMS
amplitude was calculated over a 15° angular displacement could mask the effect corresponding to a given muscle length.

The reason for the lower $L_{35}$ activation level at our fastest concentric velocity remains unclear but may partly originate from joint receptors that are much more sensitive to extreme positions, i.e., in the terminal phase of the concentric contractions (14). In addition, despite muscle length changes, muscle spindles would have a reduced effect attributable to their lower sensitivity during concentric voluntary contractions. A reduced number of recruited motor units and/or firing rate should bring about the $L_{35}$ activation level reduction (11). Neither the EMG recordings nor the twitch interpolation technique used in the present study was able to distinguish these two recruitment properties.

Nevertheless, as indicated by the reduced twitch contraction time recorded in relaxed muscles with decreasing muscle length, it can be suggested that the firing rate in shortened muscles was insufficient for maximal activation. Effectively, it has already been proposed that a lower twitch contraction time, recorded with shortened muscles, is associated with a higher rate of stimulation needed to achieve maximal tetanic contractions (20). This higher firing rate at short muscle lengths has previously been reported under isometric conditions of the plantar flexor (16) and elbow flexor muscles (15). Thus it could be speculated that the reduced twitch contraction time measured for $L_{35}$ (concentric 120°/s) would require a higher motoneuron discharge rate. This fact leads to the conclusion that the lower activation level in shortened muscles at least at 120°/s could partly lie on suboptimal motor unit firing rates.

**Changes in neural activation as a function of muscle length and angular velocity.** Our results, taken as a whole, demonstrate the dependency of neural activation on muscle length independent of the duration of concentric contractions. This neural activation modulation was due exclusively to agonistic muscles. Indeed, we observed a similar biceps femoris coactivation for all the muscle lengths, contraction modes, and angular velocities tested. Analogous findings have been reported by Aagaard et al. (1) during 30°/s isokinetic knee extensions. These authors obtained the highest coactivation close to extreme knee extension (10–30° knee flexion) that was suggested to assist the mechanical and proprioceptive roles of the anterior cruciate ligament.

In our hands, neural activation dependency on both contraction mode and angular velocity was also observed for agonistic muscles. This latter effect was predominantly modulated by the muscle length dependency. Indeed, shortened muscles revealed higher activation level during isometric than during concentric MVC. The lengthened quadriceps, however, produced higher activation level during fast concentric contractions (120°/s) compared with the two other conditions. Nevertheless, as a general trend, when the activation level is averaged over the three muscle lengths, the value recorded during 30°/s concentric MVC was lower compared with isometric and 120°/s concentric MVC (83.5 ± 6.8, 88.9 ± 6.2, and 89.6 ± 5.1%, respectively). Such a small reduction in activation would indicate a quite larger reduction in excitation of the motoneuron pool (26). This lesser amount of voluntary activation, already demonstrated by others (7, 38), would contribute to reduce the maximal tension. Either or both central and peripheral mechanisms may be involved in the low neural activation for the slow concentric velocity. Cortical drive reductions, investigated by means of magnetic cortical stimulation, may explain the drop in neural drive observed during maximal voluntary contractions (25). Nevertheless, changes in excitability of the cortical neurons play only a minor role during shortening and lengthening tasks (3). Thus this low neural activation might arise primarily from spinal mechanisms, including an increased joint and ligament receptor inhibitory input and a lower α-motoneuron excitability (e.g., Ref. 42). It is hypothesized that the higher neural activation observed at 120°/s compensates for the mechanical disadvantage of the concentric velocity increase (e.g., viscoelastic force loss; Ref. 34) and may be primarily regulated by additional recruited motor units (8).

In conclusion, the present neural activation results confirm previous reports concluding that neural drive is dependent on muscle length. Nevertheless, changing the contraction duration by reducing the range of motion does not significantly alter the voluntary torque and the ability of the subjects to activate their muscle group. The length dependency may largely influence the commonly observed contraction mode and angular velocity effect. In fact, muscle length-related changes in neural activation differed according to either the contraction mode (isometric and concentric MVC) or angular velocity (30 and 120°/s concentric velocities). Further thorough studies are needed to identify neural mechanisms involved in neural activation changes as a function of muscle length and angular velocity.

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**REFERENCES**


6. Amiridis IG, Martin A, Morlon B, Martin L, Cometti G, Pousson M, and Van Hoecke J. Co-activation and tension-


