Change in Muscle Fascicle Length Influences the Recruitment and Discharge Rate of Motor Units During Isometric Contractions

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Pasquet, Benjamin, Alain Carpentier, and Jacques Duchateau. Change in muscle fascicle length influences the recruitment and discharge rate of motor units during isometric contractions. J Neurophysiol 94: 3126–3133, 2005. First published July 13, 2005; doi:10.1152/jn.00537.2005. This study examines the effect of fascicle length change on motor-unit recruitment and discharge rate in the human tibialis anterior (TA) during isometric contractions of various intensities. The torque produced during dorsiflexion and the surface and intramuscular electromyograms (EMGs) from the TA were recorded in eight subjects. The behavior of the same motor unit (n = 59) was compared at two ankle joint angles (+10 and −10° around the ankle neutral position). Muscle fascicle length of the TA was measured noninvasively using ultrasonography recordings. When the ankle angle was moved from 10° plantarflexion to 10° dorsiflexion, muscle fascicle length declined by 12.7% (P < 0.001) and the average surface EMG increased (0.47 ± 0.06 mV; P < 0.05). At reduced ankle joint angle, muscle fascicle length declined by 12.7% (P < 0.01) at rest and by 18.9% (P < 0.001) during MVC. Motor units were activated at a lower recruitment threshold for short compared with long muscle fascicle length, either when expressed in absolute values (2.1 ± 2.5 vs. 3.6 ± 3.7 Nm; P < 0.001) or relative to their respective MVC (5.2 ± 6.1 vs. 8.8 ± 9.0%). Higher discharge rate and additional motor-unit recruitment were observed at a given absolute or relative torque when muscle fascicles were shortened. However, the data indicate that increased rate coding was mainly present at low torque level (<10% MVC), when the muscle-tendon complex was compliant, whereas recruitment of additional motor units played a dominant role at higher torque level and decreased compliance (10–35% MVC). Taken together, the results suggest that the central command is modulated by the afferent proprioceptive information during submaximal contractions performed at different muscle fascicle lengths.

INTRODUCTION

The force produced during a voluntary contraction depends on the force generating capacity of muscle and its degree of activation by the CNS. According to the length-tension relationship (Edman and Andersson 1968; Gordon et al. 1966), the force-generating capacity of a muscle varies with its length. In isolated muscle fibers, the active torque decline at short or long fiber length is mainly attributed to a reduced number of attached cross-bridges subsequent to sarcomere shortening or lengthening beyond the optimal actin-myosin overlap (Edman and Andersson 1968; Gordon et al. 1966; Lieber et al. 1994; Rassier et al. 1999).

Human studies that have investigated possible changes in activation level at different joint angles, and thus at different muscle lengths, report contrasting results. At a shorter muscle length, the maximal neural input to the muscle, as estimated from surface electromyography (EMG) or twitch interpolation technique (Merton 1954), either exceeded (Babault et al. 2003; Kasprisin and Grabner 2000; Marsh et al. 1981), matched (Bigland-Ritchie et al. 1992; Newman et al. 2003), or remained lower (Becker and Aviszus 2001; Cresswell et al. 1995) than that recorded at a longer muscle length. In addition to possible length-related changes in electrode-muscle configuration (Farina et al. 2004; Keenan et al. 2005; Kennedy and Cresswell 2001), potential reasons for these discrepancies may include differences in moment-angle relationship between muscles groups and their intrinsic architecture (i.e., angle of pennation; see Maganaris et al. 2001). Furthermore, the balance between excitatory and inhibitory input that can occur with a change in joint position may have also contributed to these divergent results (Kennedy and Cresswell 2001).

Regardless of the exact cause of the discrepancy between studies, change in muscle activation with muscle length must involve modulation in motor-unit recruitment and rate coding. Because the time course of the twitch is reduced with muscle shortening (Bigland-Ritchie et al. 1992; Marsh et al. 1981), it has been hypothesized that higher motor-unit discharge rate would be necessary to produce a given relative torque at a shorter muscle length. Consistent with this hypothesis, Gandevia and McKenzie (1988) observed a shift of the whole muscle force-frequency curve to the right at reduced length. Furthermore, Vander Linden et al. (1991) showed a decrease in motor-unit recruitment threshold and higher discharge rate per change in torque during steady submaximal contractions at shorter muscle length. Tax et al. (1990) also reported higher motor-unit discharge rates in the biceps brachii when the muscle was in a shortened position. In contrast, Bigland-Ritchie et al. (1992) did not observe an increase in motor-unit firing rate of the tibialis anterior (TA) at shorter muscle length during isometric contractions >50% of maximal voluntary contraction (MVC). However, Christova et al. (1998) reported different motor-unit behavior in the biceps brachii with higher discharge rates observed in 52.2% of the investigated motor units at shorter muscle length, but lower rates or no change were present in the remaining units.

Based on the current literature, the question of whether at short muscle length a similar torque is reached mainly by the recruitment of additional motor units, the modulation of their discharge rate, or by both mechanisms remains unclear. Part of

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the discrepancy in the previous literature could be explained because change in muscle length has been estimated from the recording of joint position and not from measurement of fascicle length. The purpose of this work was to examine the effect of muscle length change on the recruitment threshold and discharge rate of the same motor unit in the human TA during submaximal isometric contractions of the ankle dorsiflexors. The TA fascicle length was measured using ultrasonography recordings to associate change in muscle architecture with motor-unit behavior.

METHODS

Subjects

Eight subjects (6 men and 2 women) age 22–48 yr old, participated in this investigation and were tested on several occasions for a total of 24 experimental sessions. All subjects were familiar with the experimental procedure, and none had a known neurological or motor disorder prior to testing. They were all volunteers and gave their informed consent before participating in the study. This investigation was approved by the University Ethics Committee and all the experimental procedures were performed in accordance with the Declaration of Helsinki.

Ergometric device

A motor-driven, computer-controlled ergometer (Type HDX 115C6; Hauser Compax 0260M-E2; Offenburg, Germany) was used (Pasquet et al. 2000). This device, which was equipped with a footplate that was fixed to the rotational axis of the motor, recorded the torque generated by the dorsiflexor muscles under static conditions for different ankle joint angles. The subject was secured on an adjustable chair in a slightly reclined position. The right foot was strapped to the plate so that the axis of rotation of the ankle joint was aligned with the shaft of the motor. In neutral position, the plate was inclined at an angle of 45° relative to the floor. The position of the subject was adjusted to obtain a 90° angle for the ankle (neutral position or 0°) and a 120–130° knee angle. This position was duplicated from session to session. The foot was held in place by a 10° plantarflexion (long) and 10° dorsiflexion (short). At each recording site, once a motor-unit action potential was clearly identified, subjects were asked to produce a ramp contraction at the two ankle angle positions at a rate of ~5%/MVCs/s up to the recruitment of the selected unit and then to hold the torque constant to sustain a minimal, repetitive discharge of the unit for ≥5 s (Fig. 1). The subjects received visual feedback of the torque and audio feedback of motor-unit discharge rate. Two successive contractions were separated by ≥5–10 s and 3–5 min of rest was allowed between motor-unit recordings from different electrode locations. To ensure that the same motor unit was compared at the two muscle lengths, its discharge pattern was continuously recorded during the change in ankle position.

Data analysis

Data processing was performed off-line from taped records (Sony PCM-DAT, DTR 8000, Biologic, Clai, France). All signals were

Mechanical and EMG recordings

The torque produced by the dorsiflexor muscles during contractions was measured by a strain-gauge transducer (sensitivity: 0.018 V/Nm; linear range: 0–200 Nm) that was mounted on the rotational axis of the motor. The torque signal was amplified and filtered (AM 502, Tektronix, Beaverton, OR; bandwidth DC: ~300 Hz). Motor-unit potentials were recorded by a selective electrode that comprised 50-μm diam-coated nichrome wires glued into the lumen of a 30-gauge hypodermic needle. The electrode was inserted in the middle part of the TA muscle, and during each experimental session the needle was inserted at different locations. At each location, the needle was manipulated to various depths and angles to obtain a recording site from which the same motor unit was monitored at the two ankle joint positions. The EMG signal was amplified by a custom-made differential amplifier (2,000×) and filtered (100 Hz to 10 kHz) before being displayed on a Tektronix TAS 455 oscilloscope. The surface EMG of the TA was recorded by means of two silver disk electrodes (8 mm diam) placed 2–3 cm apart on either side of the needle electrode. The ground electrodes (silver plate of 2 × 3 cm) for the intramuscular and surface EMG were located over the tibia. The EMG signals were amplified (1,000×) and filtered between (10 Hz and 1 kHz) by a custom-made differential amplifier.

Methods

Before the recording of single motor units, the torque exerted by the dorsiflexor muscles during a MVC was determined. The subject performed three MVCs of 4– to 5-s duration separated by 2- to 3-min rest in a random order at ankle angles of 10° plantarflexion (long) and 10° dorsiflexion (short). At each recording site, once a motor-unit action potential was clearly identified, subjects were asked to produce a ramp contraction at the two ankle angle positions at a rate of ~5%/MVCs/s up to the recruitment of the selected unit and then to hold the torque constant to sustain a minimal, repetitive discharge of the unit for ≥5 s (Fig. 1). The subjects received visual feedback of the torque and audio feedback of motor-unit discharge rate. Two successive contractions were separated by ≥5–10 s and 3–5 min of rest was allowed between motor-unit recordings from different electrode locations. To ensure that the same motor unit was compared at the two muscle lengths, its discharge pattern was continuously recorded during the change in ankle position.

Data analysis

Data processing was performed off-line from taped records (Sony PCM-DAT, DTR 8000, Biologic, Clai, France). All signals were
acquired on a personal computer at a sampling rate of 3 kHz (force), 6 kHz (surface EMG), or 12 kHz (intramuscular EMG) by a MP150 data acquisition system (Biopac Systems, Santa Barbara, CA).

For each ankle angle, the MVC force was determined from the trial that yielded the largest value. The associated average EMG amplitude was measured during a 2-s epoch during the MVC plateau. Motor-unit discrimination was accomplished either with a window discriminator (Duchateau and Hainaut 1990) or when necessary by a computer-based, template-matching algorithm (Signal Processing Systems, SPS 8701, Malvern Victoria, Australia). Single motor-unit action potentials were identified on the basis of amplitude, duration, and waveform shape. Only the motor units that were clearly identified and that differed by <20% in amplitude at the two ankle angles were included in the analysis. These criteria and the technical difficulty to record the same motor unit at the two ankle positions explain the relative low sample of units per session (~3). Motor-unit recruitment threshold, defined as the torque at which the motor unit began to discharge, was determined during each isometric ramp contraction at the two different ankle angles (10° dorsiflexion and 10° plantarflexion). Recruitment threshold was then expressed as a percentage of the MVC torque obtained at the same ankle angle. Motor-unit discharge rate was determined during the sustained contractions and an average value was computed.

Ultrasonography

The architectural changes of the TA at the two ankle angles and for different levels of contraction were investigated in a separate session by ultrasonography (Fukunaga et al. 1997; Maganaris et al. 2001; Reeves and Narici 2003). Fascicle length and pennation angle were assessed by images obtained using real-time B-mode ultrasonographic apparatus (AUS, Esaote Biomedica, Firenze, Italy) with a 1.3-MHz linear-array probe (38-mm scanning length) positioned on the skin along the mid-sagittal plane of the TA muscle over the site corresponding to the location of the needle insertions. Once muscle fascicles had been clearly identified, the probe position was firmly held in place using a self-made resin sheath to provide a standardized measurement site and ensure that measurements were taken from the same position. The probe was coated with a water-soluble transmission gel to provide acoustic contact.

At the two ankle joint angles, images were obtained from rest to isometric MVC, at 10% increments. With the help of visual feedback, subjects had to match the target isometric torque. The contractions lasted 3–5 s and were separated by ≥60 s of rest. Measurements of pennation angle and fascicle length were performed by using digitizing software (Scion Image, National Institutes of Health). The TA is a bipennated muscle with a central aponeurosis. The pennation angle was determined as the angle between the fascicle and its insertion into the central aponeurosis (Ito et al. 1998; Reeves and Narici 2003). Fascicle length was determined as the distance from the central to the superficial aponeuroses. When the superficial end of the fascicle extended off the acquired ultrasound image, fascicle length was determined by trigonometry by assuming a linear continuation of the fascicles (Reeves and Narici 2003).

Statistics

Data are reported as means ± SD within the text and displayed as means ± SE in the figures. Torque and surface EMG during MVCs, and average recruitment threshold and discharge rate of motor units at the two ankle joint angles were analyzed using the Student’s paired t-test. Data from submaximal trials were analyzed by using a two-way ANOVA design with repeated measures to test muscle length effect and torque levels on the EMG-torque ratio, and motor unit and muscle fascicle parameters. Difference in fascicle length for the two ankle joint angles at the different torque levels was tested by using a one-way ANOVA design with repeated measures. A Tukey’s post hoc test was conducted when significant main effects were observed. Significance was set at $P \leq 0.05$.

Results

Maximal torque, EMG activity, and fascicle length

The mean MVC torque produced during dorsiflexion at the two ankle positions was 35 ± 3.3 and 44.3 ± 4.2 Nm at short (10° dorsiflexion) and long (10° plantarflexion) muscle lengths, respectively. As expected, the data indicate that MVC torque is increased ($P < 0.001$) at the longer muscle length. In contrast, the TA EMG activity decreased ($P < 0.05$) with increased muscle length (0.43 ± 0.06 vs. 0.47 ± 0.08 mV). Although small, the changes in EMG during MVC at the shorter muscle length were observed in seven subjects. One subject showed a similar average EMG at both ankle angles.

The effects of the ankle joint position on TA pennation angle and fascicle length are shown at rest and during MVC in Table 1. Both at rest and during MVC, average pennation angle was significantly smaller ($P < 0.001$) at short than at long muscle length. The average fascicle length was significantly greater ($P < 0.001$) at long compared with short muscle length, both at rest and during MVC. When expressed as percentage of their respective resting length, average fascicle length was reduced ($P < 0.001$) by 38.2 ± 5.4 and 42.6 ± 6.0% during MVCs performed at long and short muscle lengths, respectively.

Motor-unit recruitment and discharge rate

Fifty-nine motor units were recorded from different sites in eight subjects at the two ankle joint angles and analyzed during voluntary isometric contractions. A typical example of motor-unit discharge pattern during the isometric ramp-and-hold contraction of the dorsiflexors at the two ankle angle positions is illustrated in Fig. 1. The unit was recruited at a dorsiflexion torque of 4.2 Nm (11.8% MVC) and 6.3 Nm (17.1% MVC) in shortened and lengthened positions, respectively. The decrease of motor-unit recruitment threshold at the shorter muscle length was observed for all units. The average recruitment threshold, expressed as percentage of their respective MVC

<p>| TABLE 1. Pennation angle and fascicle length in the TA at rest and during MVC at short and long muscle lengths |
|---------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|</p>
<table>
<thead>
<tr>
<th></th>
<th>Short</th>
<th>Long</th>
<th>$P$</th>
<th>Short</th>
<th>Long</th>
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<tbody>
<tr>
<td>Pennation angle, °</td>
<td>14.9 ± 2.2</td>
<td>12.8 ± 1.8</td>
<td>0.001</td>
<td>24.5 ± 3.9</td>
<td>20.6 ± 3.6</td>
<td>0.001</td>
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<tr>
<td>Fascicle length, mm</td>
<td>63.6 ± 12.6</td>
<td>72.9 ± 15.6</td>
<td>0.001</td>
<td>36.0 ± 5.6</td>
<td>44.4 ± 6.6</td>
<td>0.001</td>
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Values are mean ± SD. $P$ denotes significant difference between short and long muscle lengths. Regardless of ankle angle, values are significantly different between rest and maximal voluntary force (MVC) ($P < 0.001$). TA, tibialis anterior.
(Fig. 2A), was 5.2 ± 6.1% MVC (range: 0.3–21.2%; 2.1 ± 2.5 Nm, range: 0.1–7.5 Nm) and 8.8 ± 9.0% MVC (range: 0.4–32.8%; 3.6 ± 3.7 Nm, range 0.2–10.5 Nm), at short and long muscle lengths, respectively. These differences indicate a significant reduction (45.5 ± 25.5%; P < 0.001) of the average recruitment threshold when the ankle joint angle was moved from 10° plantarflexion to 10° dorsiflexion.

The average discharge rate across all contraction intensities was 11.4 ± 2.3 and 11.1 ± 2.0 Hz, for short and long muscle lengths, respectively (Fig. 2B). The data did not differ statistically. In Fig. 3, the motor-unit discharge rate-torque ratio, at short and long muscle lengths, has been expressed relative to its respective MVC torque. At low torque level (0–5% MVC), the ratio was roughly twice (10.8 ± 6.0 vs. 5.6 ± 3.0 Hz/Nm; P < 0.001) at short compared with long muscle lengths. However, as torque increased, motor units displayed a rather pronounced drop at short muscle length. At torque >10% MVC no significant difference was observed between both ankle joint angles.

In 15 trials, an additional motor unit was recruited (average threshold: 14.2 ± 5.0% MVC) at short muscle length but not at long muscle length when the same absolute torque level was produced. These units, collected in five of the eight subjects, were only recruited at the longer muscle length for higher relative torque (22.8 ± 5.7% MVC). Such additional recruitment of motor units is displayed by Fig. 4. The graph illustrates the recruitment of a second unit although the discharge rate of the first unit was similar for short and long muscle lengths (13.5 ± 1.3 and 13.3 ± 1.8 Hz, respectively). Interestingly, the recruitment of additional motor units at short muscle lengths was mainly observed (89.4%) at dorsiflexion torque above 10% MVC, and their average discharge rate was 10.8 ± 2.4 Hz.

FIG. 2. Motor-unit recruitment threshold (means ± SE; n = 59), expressed as % MVC torque (A) and discharge rate (B) of the TA muscle at short and long muscle lengths. Significant difference between the 2 conditions: ***P < 0.001.

The modulation in motor-unit activation pattern was associated with change in surface EMG activity. The EMG-torque ratio (Fig. 5) illustrates change in muscle activation relative to the torque produced during isometric dorsiflexions at different intensities for the two ankle joint angles. When computed across all torque levels (0 and 35% MVC), the mean ratio at short muscle length was about twice that at long muscle length (0.028 ± 0.012 vs. 0.013 ± 0.005 mV/Nm; P < 0.001). For both ankle angles, the ratio was greater at low torque (<10% MVC) than at higher torque levels (10–35% MVC; Fig. 5).

**Muscle architecture**

The effects of change in ankle position on the pennation angle and fascicle length, at different voluntary contraction intensities, are illustrated in Fig. 6. Regardless of torque level, the average pennation angle at the central aponeurosis was greater (P < 0.001) and fascicle length shorter (P < 0.001) when the ankle joint angle was moved from 10° plantarflexion to 10° dorsiflexion. The pennation angle increased from rest to MVC by 61.2 and by 64.4% at long and short muscle lengths, respectively. The changes in pennation angle were greater (P < 0.001) during contractions between 0 and 10% MVC (Fig. 6B). For isometric dorsiflexion at 10% MVC, fascicle length was significantly reduced (P < 0.001) from 72.9 ± 15.6 to 55.4 ± 8.4 mm (−23.0%) and from 63.6 ± 12.6 to 44.9 ± 7.8 mm (−28.7%) at long and short muscle lengths, respectively. From rest to MVC, fascicle length decreased by 38.2 and 42.7% at long and short muscle lengths, respectively. As illustrated by Fig. 6D, the greatest difference in fascicle length between the two joint angles was obtained at 10% MVC.

**DISCUSSION**

Previous investigations have reported that the pattern of motor-unit activity is related to muscle length (Christova et al. 1998; Kennedy and Cresswell 2001; Tax et al. 1990; Vander Linden et al. 1991). The present work represents the first attempt to associate changes in muscle fascicle length with changes in recruitment threshold and discharge pattern of the same motor unit recorded during voluntary isometric contrac-
tions in human. The results indicate that a given absolute or relative torque is reached with higher discharge rate and increased motor-unit recruitment when muscle fascicles are shortened. The main finding is that increased rate coding is preponderant at low torque (<10% MVC) when the muscle-tendon complex is compliant, whereas motor-unit recruitment plays a dominant role at higher torque (10–35% MVC) and decreased compliance.

As previously reported, reduced ankle angle is associated with decreased MVC torque produced by the dorsiflexor muscles (Bigland-Ritchie et al. 1992; Gandevia and McKenzie 1988; Marsh et al. 1981; Vander Linden et al. 1991). The decline in torque at short muscle length is mainly attributed to a reduced number of attached cross bridges subsequent to sarcomere shortening beyond the optimal actin-myosin overlap (Edman and Andersson 1968; Gordon et al. 1966; Lieber et al. 1994; Rassier et al. 1999). In our study, with decreased ankle angle (from 10° plantarflexion to 10° dorsiflexion), the average TA fascicle length decreased by 9.3 mm (12.7%) at rest and by 8.4 mm (18.9%) during MVC. Furthermore, the fascicle shortening between rest and maximal isometric contraction was greater at 10° dorsiflexion compared with 10° plantarflexion. A similar observation has been recently reported by Reeves and Narici (2003) and by Hodges and co-workers (2003) in the same muscle. Such reduction in fascicle length, when the ankle was moved from 10° plantarflexion to 10° dorsiflexion, was sufficient to reduce muscle force because the muscle fibers would presumably operate in the ascending limb rather than at the plateau region of the length-tension relationship (Lieber et al. 1994; Rassier et al. 1999). In addition, with reduced muscle length, the pennation angle of TA muscle fibers was increased by 2.1 and 3.9°, at rest and MVC, respectively. Such changes would place the muscle fibers in a less optimal angle, in relation to the line of action of the muscle, to generate maximal torque (Ito et al. 1998; Maganaris et al. 2001; Narici 1999).

At a short muscle length, MVC was associated with a greater average surface EMG. This enhanced EMG activity at a short muscle length is in agreement with previous studies performed in the same muscle (Marsh et al. 1981), elbow flexors (Kasprisin and Graber 2000; Komis et al. 2000), and knee extensors (Babault et al. 2003). However, these observations are in contrast with the studies of Cresswell et al. (1995) and Pinniger et al. (2000), showing a significant reduction in EMG activity from the two heads of the gastrocnemius muscle at shortened muscle length. Surface EMG reflects both peripheral and central properties of the neuromuscular system that are modulated, respectively, by fiber membrane and motor neuron activation. The changes in TA EMG activity with muscle length could also be modified by nonphysiological factors such as changes in electrode-muscle configuration (Farina et al. 2004; Keenan et al. 2005; Kennedy and Cresswell 2001). Another potential factor that could have influenced the EMG-torque relationship is a possible difference in the contribution of synergistic muscles at the two ankle joint angles. In addition to the TA muscle, which is the main contributor to the dorsiflexion torque, other muscles such as the extensor hallucis longus, the extensor digitorum longus, and the peroneus tertius also contribute to dorsiflexion. Although we cannot rule out the possibility of a greater contribution of any one of these muscles at the longer muscle length, which could have reduced the contribution of the TA muscle at a given torque level, this should have minor effect on our results. Indeed, all these muscles are monoarticular, and due to the retinaculum systems surrounding the distal tendons of the dorsiflexors, their lever arms should not change differently during small (20°) ankle

FIG. 5. EMG-torque ratio for different torque levels (expressed as % MVC torque) at short and long muscle lengths. Each value represents the average (+SE) over 5% range of their relative MVC torque. Significant differences between the 2 conditions: *P < 0.05; **P < 0.01; ***P < 0.001.

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rotation. Furthermore, these muscles have a similar excursion range in most of our movements and therefore their length-tension relationships should not differ too much (Rassier et al. 1999). Regardless of the reasons for the differences between studies, the change in surface EMG observed in the current work did not result from a submaximal voluntary activation because it has been shown by means of the twitch interpolation technique that the TA can be maximally activated in most subjects regardless of the ankle joint angle and the type of contraction (Bigland-Ritchie et al. 1992; Klass et al. 2005).

During voluntary isometric dorsiflexion, the ankle joint angle has a substantial effect on motor-unit discharge pattern at recruitment. In our study, motor units were recruited at a lower torque level at short than at long muscle length. This is in agreement with the study of Miles et al. (1986), showing an increase in motor-unit recruitment threshold in the human masseter muscle when the jaw opening approached the maximal gape. Furthermore, at low torque levels, motor units exhibited a greater discharge rate per unit torque at short compared with long fascicle length. These results are consistent with the increased motor-unit discharge rate at recruitment observed by Vander Linden et al. (1991) in the TA when the muscle was shortened. Other studies that focused on motor-unit discharge characteristics observed an enhanced discharge rate at short muscle lengths (Tax et al. 1990). These findings contrast, however, with those of Kennedy and Cresswell (2001), who reported an increased recruitment threshold of motor units in the medial gastrocnemius at short muscle length (flexed vs. extended knee). From these observations, the authors suggested that once the muscle fiber reached a critical level of shortening, the muscle became “actively insufficient,” even if fully activated, leading to a reduction of the neural drive to the spinal motor neurons. They concluded that an increased inhibition of the motor neurons pool related to a diminished force-producing capabilities of motor units was present at reduced muscle length. In contrast, our results suggest a greater excitability or a smaller inhibition of TA motor neuron pool at short muscle length. These opposite results may be explained by specific changes in muscle architecture of the monoarticular TA and the biarticular medial gastrocnemius during lengthening (see Kawakami et al. 1998; Reeves and Narici 2003). The observation that the TA muscle did not become “actively insufficient” at an ankle joint angle of 10° dorsiflexion presumably indicates that it operates closer to the plateau of the length-torque relationship than the medial gastrocnemius when the knee is flexed at 90°. This study was not designed to determine the mechanisms of the decreased recruitment threshold and increased discharge rate of motor units at short muscle fascicle length. However, the data are consistent with the view point that the CNS motor command can be modulated by the integrated afferent proprioceptive information at a given joint position (Kennedy and Cresswell 2001; McNulty and Cresswell 2004). The increased discharge rate observed when the muscle is compliant could be related to increased reflex responsiveness, as was reported in contractions performed against an unstable mechanical load (Akazawa et al. 1983).

The enhanced activation during submaximal contractions at short muscle length would obviously compensate for the length-dependent changes in the time course of the mechanical twitch. The reduction in both twitch contraction time and peak torque (Babault et al. 2003; Bigland-Ritchie et al. 1992) would require a higher motor-unit discharge rate to produce a similar level of force in the shortened compared with the lengthened position (Bigland-Ritchie et al. 1992). Therefore when the torque was increased ≤10% MVC, the rate of change in discharge rate was greater than at higher torque levels with a more rapid decrease in motor-unit discharge per unit torque at short muscle length. In parallel, ultrasonographic measurements indicate that fascicle length displayed the greatest shortening at low torque (<10%) with a greater magnitude at the dorsiflexed ankle position. Both observations should be related to the enhanced compliance of the musculo-tendinous structure at low torque levels. The increased motor-unit discharge rate at recruitment, would compensate for the greater slack in the passive elastic
components of the muscle-tendon complex. Such compensation at short muscle lengths would increase stiffness and contribute to facilitate transmission of the force generated by the muscle (Ito et al. 1998; Parmiggiani and Stein 1981).

In agreement with the study of Bigland-Ritchie et al. (1992), we did not observe a greater motor-unit discharge rate at short compared with long muscle length when the contraction was performed at high isometric torque intensities. Although there was no significant difference in discharge rate per unit torque at both muscle lengths, for torque comprised between 10 and 35% MVC, the EMG-torque ratio was larger at short length. This greater average EMG activity is probably related to the recruitment of additional motor units, which would be necessary to generate comparable absolute or relative torque than that recorded at long muscle length. This suggestion is consistent with the observation that motor units were recruited at lower recruitment threshold and that, at the same absolute torque, more motor units were activated at short compared with long muscle fascicles. Therefore recruitment of additional motor units appears to be the main mechanisms to generate the required torque at short muscle lengths, at least for contractions ranging between 10 and 35% MVC. Considering the curvilinear shape of the length-tension relationship of the aponeurosis and tendon (Magnusson et al. 2001), the greater compliance would contribute to a larger change in fascicle length, mainly at low forces and may explain why the discharge rate per unit torque did not differ between muscle lengths at higher torque levels.

In conclusion, the current study demonstrates that during submaximal isometric voluntary contractions, motor-unit recruitment and discharge rate are greater at short compared with long muscle fascicle length. Furthermore, the data indicate that rate coding and motor-unit recruitment are related to the compliance of the muscle-tendon complex. Rate coding appeared to be the major contributor at small torque intensities, whereas the functional significance of recruitment increased with increasing torque and decreasing compliance.

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