Chapter 3

Vastus lateralis surface and single motor unit
EMG during shortening, lengthening and
isometric contractions corrected for mode
dependent strength differences
Abstract

Knee extensor neuromuscular activity was investigated during isometric (60° knee angle), shortening and lengthening contractions (50-70°, 10°·s⁻¹) corrected for force-velocity related differences in intrinsic muscle strength. However, during dynamic contractions additional factors such as shortening induced force losses and lengthening induced force gains may affect muscle strength and thereby neuromuscular activity. Therefore, even after correction for force-velocity related differences in muscle strength we expected neuromuscular activity to be higher and lower during respectively shortening and lengthening compared to isometric contractions. Neuromuscular activity was determined using rectified surface electromyography (rsEMG) of the three superficial muscle heads in a first session (10 and 50 % MVC) and additionally with EMG of (46) vastus lateralis (VL) motor units recorded during a second session (4-76 % MVC). RsEMG behaved similar (P > 0.05) during both sessions. Using superimposed electrical stimulation, muscle strength independent of voluntary activation for shortening and lengthening contractions was found to be respectively 0.96 and 1.16 times the isometric (Iso) strength. Therefore, neuromuscular activity during submaximal shortening and lengthening was compared with isometric contractions of respectively 1.04Iso (= 1/0.96) and 0.86Iso (= 1/1.16). RsEMG and discharge rates were normalized to isometric values. Shortening rsEMG (1.30 ± 0.11) and discharge rate (1.22 ± 0.13) were higher (P < 0.05) than 1.04Iso values (respectively 1.05 ± 0.05 and 1.03 ± 0.04), but lengthening rsEMG (1.05 ± 0.12) and discharge rate (0.90±0.08) were not lower (P > 0.05) than 0.86Iso values (0.76 ± 0.04 and 0.91 ± 0.07 respectively). Thus when force-velocity related differences in muscle strength were taken into account, neuromuscular activity was not lower during lengthening but was still higher during shortening compared to isometric contractions.
Introduction

Maximal torque production of a muscle can be regulated by the recruitment of motor units and changing the discharge rate of the recruited motor units. Furthermore, it can be influenced by the length of the muscle, the mode (isometric, shortening or lengthening) and the velocity of the contraction and the contraction history. From animal single fibre, animal whole muscle and human experiments it is known that stimulated torque is lower during shortening and higher during lengthening compared to isometric contractions (de Ruiter et al, 1998; de Ruiter et al, 2000; Edman et al, 1978; Katz, 1939). However, in human studies the maximal voluntary lengthening torque does not always exceed the isometric torque, which has been attributed to incomplete voluntary muscle activation due to a neural inhibitory mechanism (Babault et al, 2001; Beltman et al, 2004a; Pinniger et al, 2000; Westing et al, 1990). Nevertheless, according to the force – velocity relationship skeletal muscles are intrinsically stronger during lengthening and conversely, weaker during shortening contractions (Edman et al, 1978; Katz, 1939).

In addition to the differences in force – velocity related differences in intrinsic muscle strength, it is also known that force is depressed during and following shortening compared to purely isometric contractions which is referred to as shortening induced force depression (de Ruiter and de Haan, 2003; de Ruiter et al, 1998; Lee et al, 1999). This has been suggested to be a consequence of a stress-induced inhibition of cross bridge attachment within the new zone of overlap between the thick and thin filaments (Granzier and Pollack, 1989). Shortening induced force depression develops during shortening and increased surface electromyography (EMG) has been found to compensate for the decreased force generating capacity of muscle fibres during and following shortening contractions. Another reason why higher neuromuscular activity (defined as the number of motor units recruited and their discharge rates) during shortening may be expected is shown by de Haan (1998) who found that higher stimulation frequencies are needed to obtain maximal torque during maximal shortening compared to isometric contractions, suggesting that a higher intracellular calcium concentration was needed for the shortening contractions. In contrast and in addition to the higher intrinsic muscle strength during lengthening, force is extra enhanced during and following lengthening compared to purely isometric contractions which is referred to as lengthening induced force enhancement (de Ruiter et al, 2000; Oskouei and Herzog, 2005; Oskouei and Herzog, 2006) and is possibly due to an enhanced force per attached cross bridge (Herzog, 1998). Thus in addition to the differences in intrinsic muscle strength between dynamic and isometric contractions,
the movement (i.e. the shortening or lengthening) itself may induce additional changes in neuromuscular activity.

A number of studies have investigated the effect of contraction mode on the regulation of torque production by studying motor unit firing behaviour at submaximal torque levels. Discharge rates were found to be lower during lengthening contractions compared to isometric and shortening contractions at similar absolute torque level (Del Valle and Thomas, 2005; Howell et al, 1995; Kossev and Christova, 1998; Linnamo et al, 2003; Søgaard et al, 1996). In contrast, during shortening contractions discharge rate was found to be higher (Pasquet et al, 2006; Søgaard et al, 1998; Tax et al, 1989), or similar (Del Valle and Thomas, 2005; Søgaard et al, 1996) compared to isometric contractions at similar absolute torque level. Moreover, additional motor units were found to be recruited during shortening contractions (Pasquet et al, 2006; Tax et al, 1989). This difference in the modulation of discharge rate between isometric, shortening and lengthening contractions was not accompanied by a difference in the order of recruitment of motor units. Although Linnamo et al (2003), Nardone et al (1989) and Howell et al (1995) reported a selective recruitment of fast twitch motor units during lengthening contractions, most studies found no reversal of the recruitment order during lengthening and shortening contractions (Beltman et al, 2004a; Kossev and Christova, 1998; Moritani et al, 1987; Pasquet et al, 2006; Søgaard et al, 1996; Stotz and Bawa, 2001; Tax et al, 1989).

In the studies mentioned the force – velocity related differences in intrinsic muscle strength between the contraction modes were not taken into account and therefore differences in relative contraction intensity (i.e. torque level as percentage of maximum) were present at the different contraction modes in these studies. The outcome of the studies mentioned above could thus at least partly be the result of differences in intrinsic muscle strength during shortening, lengthening and isometric contractions. Furthermore, although in some studies the shortening and lengthening contractions were compared with an isometric contraction, this isometric contraction was not performed at similar muscle length (Linnamo et al, 2003; Pasquet et al, 2006), which is the length of the muscle halfway the dynamic contraction. Moreover, there were only a few studies in which the same single motor unit was followed during the different contractions (Howell et al, 1995; Pasquet et al, 2006; Stotz and Bawa, 2001).

The purpose of this study was to establish whether differences in neuromuscular activity between isometric, shortening and lengthening contractions could be fully explained by differences in intrinsic muscle strength which were expected based upon the force – velocity relationship. Therefore, in the present study the
contractions in the different modes were performed at similar relative contraction intensity and comparable muscle length. We hypothesized that, even after correction for differences in intrinsic muscle strength expected from the force – velocity relationship, neuromuscular activity would be higher during shortening compared to isometric contractions, due to shortening induced force losses (de Ruiter and de Haan, 2003; de Ruiter et al., 1998; Lee et al., 1999) and the higher stimulation frequencies needed during shortening compared to isometric contractions in isolated rat muscle (de Haan, 1998). In contrast, we expected neuromuscular activity to be lower during lengthening compared to isometric contractions at similar relative torque and muscle length, due to the additional enhancement of force which may occur during lengthening (de Ruiter et al., 2000; Oskouei and Herzog, 2005; Oskouei and Herzog, 2006). In the present study neuromuscular activity during the different submaximal contractions was quantified based on the surface EMG of the quadriceps femoris muscle and discharge behaviour of single motor units of the vastus lateralis muscle.

**Methods**

Three experiments were performed with the approval of the ethics committee of the VU University Medical Centre in Amsterdam, The Netherlands and in accordance with the Declaration of Helsinki. After written and verbal explanations of the objectives and procedures of the experiments, subjects signed informed consent. All subjects refrained from heavy exercise 48 h prior to the experiments.

*Study design*

The first experiment was performed in order to determine the maximal voluntary activation (VA), and maximal voluntary contraction (MVC) torque of the knee extensor muscles at the different contraction modes: isometric, shortening and lengthening contractions, which was necessary to determine relative contraction intensities for Experiments 2 and 3.

In the second and third experiment, neuromuscular activity of the quadriceps muscles was investigated during submaximal voluntary isometric, shortening and lengthening submaximal contractions at a constant similar relative torque level; that is at the same percentage of the intrinsic muscle strength in each contraction mode. In the second experiment neuromuscular activity was measured using surface EMG during contractions at set torques (10 and 50 % MVC) and in the third experiment neuromuscular activity was studied by using surface and intramuscular wire EMG during contractions of which the torque was chosen approximately 20 % above the
recruitment threshold of the identified motor units.

**Torque recordings**
Isometric and isokinetic knee extension contractions were performed on a specially designed dynamometer, which recorded the exerted torque at its axis of rotation (Beltman *et al.*, 2004a; Beltman *et al.*, 2004b; Gerrits *et al.*, 2005). Subjects sat in an upright position with a hip angle of 85° (0° = full extension), straps restrained hip and shoulders. A cuff was fastened around the lower leg and was subsequently attached to the lever of the dynamometer. A shin guard ensured subjects could exert maximal forces without discomfort at the shin. The axis of rotation of the dynamometer was aligned with the lateral femoral condyle, while subjects delivered a torque of about 20% of their MVC (the expected average torque for motor unit recording) at a knee angle of 60° (0° = full extension). Contraction torques were AD-converted and stored on disk for off-line analysis. All recorded torques were corrected for the effect of gravity at all knee angles.

**Experiment 1**

**Subjects**
Eight healthy subjects, four men and four women, with a mean ± SD age of 28.4 ± 6.9 yr, height 178.4 ± 8.5 cm and mass 68.6 ± 10.6 kg volunteered to participate in this experiment.

**Electrical stimulation**
The quadriceps femoris muscle was stimulated transcutaneously using a constant-current stimulator (DS7, Digitimer, Welwyn Garden City, UK) and self-adhesive surface electrodes (Schwa-Medica, Nieuw Leusden, Nederland). The cathode (5 x 5 cm) was placed in the trigonum femorale to stimulate the nervus femoralis; the anode (8 x 13 cm) was placed over the gluteal fold opposite the cathode. To determine VA during maximal attempts, three square wave pulses of 200 µs (triplet) were delivered to the muscle at a rate of 300 Hz, using supra-maximal current (Beltman *et al.*, 2004a). All subjects had experienced electrical stimulation before. Therefore, a familiarization session was not included.

**MVC and voluntary activation**
Firstly, subjects were asked to exert isometric forces maximally for about 3 – 4 s to determine MVC at a knee angle of 60°, which has shown to be about the optimum knee
angle for maximal torque production (Beltman et al, 2004). Two attempts were made, separated by 3 min rest to avoid fatigue. MVC torque was determined as the peak torque from the stable part of the torque signal. Real-time torque was visible on a computer monitor and subjects were encouraged to exceed their maximal value, which was also displayed. When the MVC torque of the two attempts differed more than 5 %, a third attempt was performed. Secondly, VA was determined for isometric contractions using superimposed stimulation. Triplets were applied to the fully relaxed muscle and superimposed during the MVC (Beltman et al, 2004a). Pilot studies have shown that triplet torque (300 Hz stimulation frequency) did not increase after an MVC, indicating that any potential post–activation potentiation does not affect the triplet torque. The torque enhancement due to the superimposed triplet was expressed as a percentage of the torque obtained when the triplet was applied on the resting muscle and subsequently subtracted from 100 %, resulting in a measure of VA. In formula: VA (%) = 100 – [(superimposed triplet torque / resting triplet torque) * 100].

Thirdly, maximal voluntary shortening and lengthening contractions were performed at an angular velocity of respectively 10°·s⁻¹ and -10°·s⁻¹. This relatively low speed was chosen because it was found to be the highest possible for the second experiment (see below). The range of motion for the dynamic contractions was between 50 and 70° knee flexion angle. A preload of 80 – 90 % of the maximal isometric torque at 60° had to be overcome to start the movement of the dynamometer lever arm. The preload ensured that muscle activation was already very high at the start of the movement. Shortening and lengthening MVC torque and VA values were established at a knee angle of 60° following the same protocol as the isometric MVC torque and VA determinations (see Figures 3.1B and C). Similar to the studies of Babault et al (2001; 2002), superimposed triplet torque enhancement was estimated by linear extrapolation of the slope of the prestimulus voluntary torque beyond the point of stimulation.

Due to the significantly lower VA during the dynamic MVCs compared to the isometric MVC (see Results) intrinsic muscle strength during shortening and lengthening contractions would be underestimated to a greater extent for the dynamic MVCs compared to the isometric MVC, if simply these MVC values were used. For example, in some subjects lengthening MVC was not higher or even lower than isometric MVC. Moreover, the greater the difference in VA was between the dynamic and the isometric contractions, the lower were the shortening and lengthening MVC relative to the isometric MVC (Figure 3.2). To determine intrinsic muscle strength during shortening and lengthening contractions relative to that during the isometric
contractions, we extrapolated the linear relation in Figure 3.2 to the point at which there would have been no differences in VA between either shortening and isometric or lengthening and isometric contractions. In this manner shortening and lengthening MVCs were respectively found to be 0.96 and 1.16 times the isometric MVC (Figure 3.2). These values were assumed to be the best representation of the contraction mode dependent differences in intrinsic muscle strength under conditions of similar near maximal muscle activation and were subsequently used to set the torques in the second and third experiment.

Figure 3.1. Example of knee angle (°) and torque signals (upper and lower traces respectively) of one subject during isometric (A), shortening (B) and lengthening (C) contractions. The vertical lines in the torque signals indicate the timing of the triplet on the relaxed (dotted line) and maximal contracting (solid line) muscle. Maximal isometric VA was 95.5 % for this subject.
Experiments 2 and 3

Subjects
Ten healthy subjects, five men and five women with a mean ± SD age of 26.7 ± 6.1 yr, height 178.2 ± 9.0 cm and mass 70.3 ± 8.1 kg voluntarily participated. Five of these subjects (2 men and 3 women) also participated in Experiment 1.

Figure 3.2. Shortening (A) and lengthening (B) MVCs (relative to isometric MVC) respectively as a function of the difference in shortening and isometric VA (VAsho – VAiso) and lengthening and isometric VA (VAlen – VAiso) for 8 different subjects (indicated by the different symbols). The positive linear relationships between VA differences and MVC for shortening (y = 1.40x – 0.44; $R^2 = 0.80$) and lengthening (y = 1.93x – 0.77; $R^2 = 0.70$) were significant. The 95% confidence intervals (dashed lines) are shown for both shortening (A) and lengthening (B) contractions. Maximal intrinsic muscle strength during shortening and lengthening were determined at the point at which there were no differences in VA between contractions (VAsho – VAiso and VAlen - VAiso = 0).
**Second experiment**

Preceding the second experiment, subjects were familiarized with tracking isometric and dynamic contractions in an additional practice session.

Because changes in absolute and relative torque levels during lengthening or shortening contractions could cause (de)recruitment of motor units, it was important that during each contraction the torque level would be constant and variations in the relative torque caused by the torque – knee angle relationship would be minimal. Therefore, optimum knee angle was determined for each subject individually in the second experiment and contractions were performed around this individual optimum. MVC of the knee extensors and flexors was determined at the individual optimum knee angle.

Subjects were asked to perform extension MVCs at different knee angles between 40 and 80° with 5° steps to determine optimum knee angle. Optimum knee angle was determined as the knee angle at which isometric torque was found to be maximal, by fitting a second order polynomial regression line. Thereafter, flexion MVC values were determined at optimum extension knee angle. EMG values during the flexion MVCs at optimum knee angle were used for normalization of the submaximal biceps femoris (BF) and semitendinosus (ST) EMG, which were used to quantify co-contraction during the knee extensions. The optimum knee angle as measured for each subject in the second experiment was also used for the third experiment.

Subsequently, subjects were asked to track three different trapezoidal torque trajectories that were displayed on the computer monitor (Figure 3.3). A slow isometric ramp up (5 s duration) contraction was performed to a constant absolute torque level (either 10 or 50 % MVC), followed by a torque plateau of 10 s and a 5 s ramp down. These torque trajectories were performed at optimum knee angle during the isometric contractions and ± 10° around optimum knee angle during the shortening and lengthening contractions. Torque should be kept constant throughout the 10 s torque plateau, even while the knee angle was changing during the dynamic part of the torque plateau. The torque plateau during the dynamic contractions consisted of an isometric hold phase of 3 s, followed by a dynamic phase (shortening or lengthening, 10°s⁻¹) of 2 s and a second isometric hold phase of 5 s (Figure 3.3). The range of motion during the dynamic phase was set ± 10° around optimum knee angle for each subject to minimize the influence of the torque – knee angle relation on the relative torque produced during the movement. Indeed the torque – angle relationship was very flat between 50 and 70° (see Results). Moreover, EMG was analyzed only over the mid range (55 – 65°) during which maximal isometric torque changes were < 2 %. To enable comparing the
different contraction modes at similar relative torque levels, two additional isometric contractions were performed at 1.04 (= 1/0.96) and 0.86 (= 1/1.16) times the isometric (Iso) torque at optimum knee angle.

Five contractions were performed in random order (see Table 3.1). These five contractions were performed twice at both 10 and 50 % MVC. During all contractions, torque traces were visible on a computer screen and subjects were verbally encouraged to follow the trapezoidal traces as closely as possible. At the end of the second experiment, subjects were asked to perform again extension MVCs at optimum knee angle and optimum ± 10° and flexion MVCs at optimum knee angle.

![Figure 3.3](image-url)

**Figure 3.3.** Torque trajectory of 50-70°. In the lower part of the figure the ramp up, the constant torque level and the ramp down are shown. In the upper part of the figure the changes in knee angle for the dynamic contractions are shown, from 70 to 50° for the shortening (sho) contraction (dotted line) and from 50 to 70° for the lengthening (len) contraction (dashed line). Note that EMG was analyzed from t = 8.5 to 9.5 s (shaded rectangle).
Table 3.1. Overview of the different submaximal contractions which were performed in random order.

<table>
<thead>
<tr>
<th>No.</th>
<th>Contraction mode</th>
<th>Torque (Nm)</th>
<th>Relative torque (% MTC in the different modes)</th>
<th>Knee angle</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Isometric</td>
<td>50</td>
<td>20</td>
<td>60°</td>
</tr>
<tr>
<td>2.</td>
<td>Shortening</td>
<td>50</td>
<td>21</td>
<td>70-50°</td>
</tr>
<tr>
<td>3.</td>
<td>Lengthening</td>
<td>50</td>
<td>17</td>
<td>50-70°</td>
</tr>
<tr>
<td>4.</td>
<td>1.04Iso</td>
<td>52.5</td>
<td>21</td>
<td>60°</td>
</tr>
<tr>
<td>5.</td>
<td>0.86Iso</td>
<td>42.5</td>
<td>17</td>
<td>60°</td>
</tr>
</tbody>
</table>

For this example torque trajectory was set at 50-70° (optimum knee angle at 60°) and torque level was set as 50 Nm (20% MVC). Note that the relative torque levels of isometric contractions 4 and 5 were respectively similar to that of the dynamic contractions 2 and 3 (fourth column).

Third experiment

In the third experiment subjects were asked to perform submaximal isometric, shortening and lengthening contractions in random order, following a similar trapezoidal torque trajectory as during the second experiment. Firstly, a submaximal isometric contraction was performed and repeated until stable selective recordings of single motor unit action potentials (SMUAPs) were obtained (see Intramuscular electromyography). Torque level was set approximately 20% higher than torque at which the motor unit was recruited, thereafter the five contractions were performed (Table 3.1). A motor unit was successfully tracked when the unit could be followed twice during all five contractions. After successfully tracking a motor unit, all contractions were performed at a different submaximal torque level to track another motor unit. At the end of the third experiment flexion and extension MVCs were determined as described in the second experiment.

Surface electromyography

Surface EMG data of 5 muscles, vastus lateralis (VL), vastus medialis (VM), rectus femoris (RF), BF and ST, was obtained during the second experiment. Electrical activity of the BF and ST were recorded to determine co-contraction. For the VL muscle two electrode pairs were placed at the part of the muscle from which in the third experiment motor unit EMG would be obtained (referred to as mid VL position). The second electrode pair was placed more distally on the VL muscle (referred to as distal VL position). This was done to determine if possible effects of knee angle and contraction mode on EMG were similar in the mid VL position compared to the more distal VL position we usually record from. During the third experiment surface EMG
was only obtained from the mid position of the VL muscle, and the electrodes were placed on both sides of the intramuscular wire electrodes (see Intramuscular electromyography). Furthermore, during the third experiment only surface EMG from the BF was obtained to monitor co-contraction.

EMG was recorded using surface electrodes (Blue Sensor, Ambu, Ølstykke, Denmark, lead-off area: 1.0 cm\(^2\)). After shaving and cleaning the skin with 70 % ethanol two electrodes were placed on the belly of each muscle in a bipolar configuration, in line with the muscle fibre direction and with an inter-electrode distance of 25 mm. For the mid VL muscle the inter-electrode distance was 30 mm, as they were placed on both sides of the intramuscular wire electrodes in the third experiment. Reference electrodes were put on the right patella and on the lateral epicondyle of the femur of the right leg. The location of each electrode was accurately marked with a waterproof felt tip pen for precise electrode re-application in subsequent experiments. Surface EMG signals were amplified (x1000) with a biosignal amplifier (g.tec, Austria, 10-500 Hz, input impedance 110 MOhm), AD-converted with a Simultaneous-Sampling AtoD board (PCI-6143, National Instruments, America), digitized (10 kHz), band-pass filtered (4\(^{th}\) order Butterworth, bi-directional, 10-400 Hz) and stored with the torque signal on computer disk.

In pilot experiments twitch stimulation was applied to the femoral nerve and the M-wave shapes were studied to confirm that the EMG electrodes remained distal to the motor end plate zone following a change in knee angle during the dynamic contractions: M-wave amplitude was found to be constant for the range of knee angles used in the present study and there was no change in the order of occurrence of the positive and negative phase of the M-wave.

Intramuscular electromyography
The method to record and analyze SMUAPs has been described in more detail before (de Ruiter et al, 2005; de Ruiter et al, 2004). Custom-made, fine-wire electrodes were constructed from four polyterefaltate-butylene-coated wires (0.044 mm diameter, stainless steel core, Capable, The Netherlands) to record SMUAPs. The four wires with a length of 10 cm were glued together at the tip and cut transversely, passed through a hypodermic needle (0.75 x 40 mm) and bent backwards over the needle tip for the last 2 mm. The needles including the electrodes were sterilized for 30 min at 150°C. A new needle-electrode was used for each measurement. Before insertion, the skin at the electrode site was shaved and cleaned with 70 % ethanol. The needle-electrode-combination was inserted 40 mm deep in the middle part of the belly of the vastus
lateralis muscle and the needle was subsequently withdrawn, leaving the quadrifil lar tip of the electrode in the muscle. After insertion the subjects were asked to perform a few maximal (brisk) voluntary contractions to stabilize the position of the electrode in the muscle. Six bipolar EMG signals were led off from the four free ends of the electrode which were connected to 50-cm-long isolated cables. The signals were amplified (x1000) with a biosignal amplifier (g.tec, Austria, 0.01-10 kHz, input impedance 110 MOhm), AD-converted with a Simultaneous-Sampling AtoD board (PCI-6143, National Instruments, America), digitized (44.1 kHz), played through loud-speakers online and saved on computer disk. A ground electrode was placed on the patella of the right knee. Following band-pass filtering (1-10 kHz) the six bipolar signals were displayed immediately on-screen.

Intramuscular EMG was considered stable and selective, when one or two motor units had a distinctive amplitude and shape on at least one of the six EMG channels throughout a complete submaximal isometric contraction. If there was no unit which could selectively be recorded after insertion of the wire electrode, the electrode was slightly re-positioned by gentle pulling until selective recording became possible.

**EMG analysis**

For the surface EMG data, rectified surface EMG (rsEMG) during the maximal isometric, shortening and lengthening contractions in the first experiment were calculated during 500 ms before the superimposed stimulation. For the submaximal contractions in the second and third experiment, rsEMG was calculated at t = 8.5 – 9.5 s, which was halfway the shortening and lengthening phase of the torque plateau for the dynamic contractions (see Figure 3.3). RsEMG of the two attempts of each contraction were averaged. Subsequently, rsEMG during shortening, lengthening, 0.86Iso and 1.04Iso submaximal contractions were normalized to the rsEMG during the submaximal isometric (Iso) contractions. Antagonist (ST and BF) rsEMG was normalized to the rsEMG (500 ms) obtained at maximal torque during maximal flexion contractions.

For the intramuscular EMG data of the third experiment, SMUAPs were identified on the basis of their amplitude and shape using custom-written Matlab software (de Ruiter et al., 2005; de Ruiter et al., 2004). Figure 3.4A illustrates the firings of two motor units on two different channels during a shortening contraction for subject 1, the second motor unit only fires during the dynamic part of the contraction. Figure 3.4B shows the firings of two motor units during a lengthening contraction for subject 2, in this example the second recruited motor unit stops firing during the lengthening
phase of the contraction. The lower panels in Figures 3.4A and 3.4B show consecutive superimposed SMUAPs of the motor units firing, each the average of 1 s of firing. Small changes in SMUAP amplitude and/or shape occurred gradually during the different contractions, due to small and unavoidable changes in position. Therefore, in the analysis, motor unit templates were made and updated within and also between contractions. Motor unit discharge rates, the inverse of the inter-SMUAP intervals, were calculated at $t = 8.5 – 9.5$ s. Motor unit discharge rates of two attempts of each contraction were averaged and were subsequently normalized to their isometric values.

**Statistical analysis**

Data are presented as mean values ± SD. Repeated measures analyses of variance (ANOVA, SPSS version 12.0) were used to compare MVC, VA and rsEMG during maximal contractions between the three contraction modes of the first experiment. Furthermore, ANOVA (3 x 2) for repeated measures was performed on the normalized torque and rsEMG of the submaximal isometric contractions to test between 0.86Iso, 1.04Iso and Iso contractions at 10 and 50 % MVC. Moreover, to test between respectively shortening vs. 1.04Iso at 10 and 50 % MVC and between lengthening vs. 0.86Iso at 10 and 50 % MVC ANOVA (2 x 2) repeated measures was performed on normalized torque and rsEMG.

For the normalized rsEMG and discharge rate data of the third experiment, for each subject the averaged value of the normalized rsEMG and discharge rates of the different motor units were calculated ($n = 10$) and subsequent ANOVAs for repeated measures were performed to test between the 0.86Iso, 1.04Iso and isometric (Iso) contractions. Paired-samples t-tests were used to compare shortening vs. 1.04Iso and lengthening vs. 0.86Iso contractions. If significant main effects were observed, Bonferroni tests were performed for post hoc analysis. Coefficients of variation (CV) values were calculated to test for reliability between two attempts. The level of significance of all statistical analyses was set at $P < 0.05$. 
Figure 3.4. Single motor unit action potentials (SMUAPs) for subject 1 during a shortening contraction (A) and for subject 2 during a lengthening contraction (B). In (a) the change in knee angle is shown, in (b) the torque produced, in (c) the intramuscular EMG at one (B) and two (A) channels, in (d) the time axis and in (e) for each unit the consecutive superimposed SMUAPs, each SMUAP is the average waveform of 1 s. Note that in A unit 2 is recruited during the shortening phase of the contraction and in B unit 2 is derecruited during the lengthening phase of the contraction. Actual recruitment of unit 2 (A) and derecruitment of unit 2 (B) occurs slightly before the movement due to anticipation of the subjects.

Results

Verification of the data

The behaviour of surface EMG among the three measured quadriceps muscle components (VM, VL and RF) and among the two measured hamstring muscles (BF and ST) was similar during the different maximal and submaximal contractions in the three experiments. Therefore, following normalization mean quadriceps and hamstring rsEMG are presented. Moreover, since in the second experiment the rsEMG at the distal VL position was not significantly different from the mid VL position, the rsEMG from the distal VL position will not be presented separately.

For the second experiment, CV values of the rsEMG between two attempts did not differ (P > 0.05) between modes and contraction levels, and ranged from 4.2 – 8.5 % among subjects. Furthermore, CV of respectively the discharge rate and the rsEMG values between the two attempts in the third experiment respectively ranged from 6.3 – 8.4 % and from 5.9 – 8.6 % and did not differ between contraction modes. These
results indicate that reliability of the intramuscular and surface EMG measurements was acceptable in all contraction modes.

First experiment
Isometric, shortening and lengthening VA and MVC
There were significant main effects of contraction mode for MVC ($F_{2, 14} = 16.5$, $P < 0.001$), VA ($F_{2, 14} = 16.4$, $P < 0.001$) and rsEMG ($F_{2, 14} = 13.5$, $P < 0.001$). Mean MVC during shortening (224.7 ± 61.2 Nm) was significantly lower than the mean MVC during lengthening (274.7 ± 79.1 Nm) and isometric (269.4 ± 63.1 Nm) contractions. Mean MVC during lengthening was not significantly different from the isometric MVC (Figure 3.5A). VA during shortening (87.9 ± 6.7 %) and lengthening (90.2 ± 5.8 %) contractions was significantly lower than VA during isometric contractions (97.1 ± 1.9 %). Shortening and lengthening VA did not differ significantly from each other (Figure 3.5B). Furthermore and in line with the results for VA, quadriceps rsEMG during shortening (547 ± 232 µV) and lengthening (542 ± 248 µV) was significantly lower compared to rsEMG during isometric (660 ± 229 µV) contractions. Shortening and lengthening quadriceps rsEMG were not different (Figure 3.5C).

Maximal VA during dynamic contractions was lower than maximal isometric VA but the latter was > 94 % in all subjects. There were significant positive linear relationships between the differences in dynamic and isometric VA on the one hand and shortening/isometric MVC (Figure 3.2A, $R^2 = 0.80$, $P < 0.05$) and lengthening/isometric MVC (Figure 3.2B, $R^2 = 0.70$, $P < 0.05$) on the other hand. Thus subjects with a more similar VA between contraction modes (e.g. subject 5) had higher dynamic/isometric MVCs than subjects (e.g. subject 7) with a large difference in maximal VA between contraction modes. Extrapolation of the relationships in Figure 3.2 to the point where dynamic and isometric VA became the same showed that maximal intrinsic muscle strength for shortening and lengthening contractions respectively was 0.96 and 1.16 times that of the maximal isometric strength. The value of 1.16 was significantly higher than 1.0 ($P < 0.05$) and although 0.96 was not significantly lower than 1.0 ($P = 0.10$), we assumed that intrinsic muscle strength during lengthening and shortening contractions were respectively 16 % higher and 4 % lower than maximal isometric strength. Therefore, during the submaximal contractions of the second and third experiment, two additional submaximal isometric contractions were performed at respectively 1/1.16 (= 0.86) and at 1/0.96 (= 1.04) times the submaximal isometric torque (Iso).
Second experiment

Maximal isometric torques

During the second experiment there was a main effect of knee angle on MVC ($F_{2,18} = 8.2$, $P = 0.003$). MVC at optimum knee angle ($62.5 \pm 4.2^\circ$) was on average $271.9 \pm 74.8$ Nm. MVCs at the ends of the range of motion of the dynamic contractions ($52.5 \pm 4.2^\circ$ and $72.5 \pm 4.2^\circ$) were significantly lower than at optimum knee angle, but not significantly different from each other (respectively $258.1 \pm 69.2$ and $259.5 \pm 62.9$ Nm at $52.5 \pm 4.2^\circ$ and $72.5 \pm 4.2^\circ$). Consequently submaximal isometric contractions at the extremes of the range of motion were always performed at the same absolute and relative torque. Furthermore, at none of the knee angles maximal voluntary torque at
the end of the experiment differed from the values at the beginning, indicating that no significant fatigue had developed and that optimum knee angle was not shifted during the experiment (Table 3.2, $F_{1,9} = 18.2$, $P = 0.13$). In addition, for all knee angles, maximal torques at the end of the third experiment were not significantly different from the torques measured in the second experiment (Table 3.2, $F_{2,18} = 0.07$, $P = 0.94$).

Table 3.2. Maximal voluntary isometric knee extensor torques (Nm, mean ± SD) at the beginning (pre) and at the end (post) of the second experiment and at the end of the third experiment.

<table>
<thead>
<tr>
<th>Knee Angle</th>
<th>Second experiment Pre</th>
<th>Post</th>
<th>Third experiment Post</th>
</tr>
</thead>
<tbody>
<tr>
<td>52.5°</td>
<td>258.1 ± 69.2*</td>
<td>258.9 ± 60.4*</td>
<td>246.7 ± 62.6*</td>
</tr>
<tr>
<td>62.5°</td>
<td>271.9 ± 74.8</td>
<td>273.2 ± 58.9</td>
<td>271.2 ± 63.8</td>
</tr>
<tr>
<td>72.5°</td>
<td>259.5 ± 62.9*</td>
<td>254.0 ± 66.0*</td>
<td>252.7 ± 68.0*</td>
</tr>
</tbody>
</table>

*Indicates significantly lower compared to torque at 62.5° ($P < 0.05$).

Surface EMG during submaximal isometric, shortening and lengthening contractions

Absolute isometric torques during contractions at 10 and 50 % MVC were on average 28.1 ± 6.9 and 139.8 ± 34.8 Nm. Overall, there were no differences between the torques which were actually produced and the intended torques ($F_{1,9} = 0.1$, $P = 0.73$). The torques which were actually produced during the additional 1.04Iso and 0.86Iso contractions, were respectively 1.05 ± 0.01 and 0.85 ± 0.01 of the isometric torque levels for both 10 and 50 % MVC ($P > 0.05$). Furthermore, for contractions at 10 and 50 % MVC the actual shortening torques were on average respectively 0.98 ± 0.03 and 0.97 ± 0.03 times the target torques ($P > 0.05$) and for the lengthening torques the respective values were on average 1.05 ± 0.06 and 1.01 ± 0.03 times the target torques ($P > 0.05$) for the 10 and 50 % MVC respectively.

Normalized quadriceps rsEMG for the 1.04Iso, isometric (Iso) and 0.86Iso contractions at 10 and 50 % MVC are shown in Figure 3.6. There was a significant effect of torque level between the 1.04Iso, Iso and 0.86Iso contractions on normalized rsEMG ($F_{2,18} = 143.6$, $P < 0.001$). Normalized rsEMG for the 1.04Iso contraction at 10 and 50 % MVC was on average 1.05 ± 0.05 which was significantly higher than that for the isometric contraction (1.0). Normalized rsEMG for the 0.86Iso contractions at 10 and 50 % MVC was on average 0.76 ± 0.04 and was significantly lower than 1.0. These results indicate that a 4 % higher and a 16 % lower torque were accompanied by respectively about 5 % higher and 24 % lower rsEMG during isometric contractions.

Normalized quadriceps rsEMG during the shortening contractions at 10 and 50
% MVC was on average 1.30 ± 0.11, which was, as expected, significantly higher than the rsEMG during the 1.04Iso contractions (which was 1.05) at both torque levels (Figure 3.7A; $F_{1, 9} = 44.4, P < 0.001$). However, and in contrast to our hypothesis, during lengthening contractions normalized rsEMG of the knee extensors at 10 and 50 % MVC (on average 1.05 ± 0.12) was significantly higher (instead of lower) compared to the 0.86Iso contraction (during which normalized rsEMG was on average 0.76 ± 0.04; Figure 3.7B; $F_{1, 9} = 56.0, P < 0.001$).

Figure 3.6. Normalized (isometric contraction = 1.0) quadriceps rectified surface EMG for 0.86Iso, isometric (Iso) and 1.04Iso contractions at 10 % (closed squares) and 50 % MVC (open circles). * Indicates significantly different from the isometric contraction (P < 0.05).

Normalized hamstring rsEMG for the five different contractions at 10 and 50 % MVC are shown in Table 3.3. There was a significant effect of torque level between the 1.04Iso, Iso and 0.86Iso contractions on normalized hamstring rsEMG ($F_{2, 18} = 23.4, P < 0.001$). Normalized hamstring rsEMG was significantly higher during the isometric quadriceps contraction at 1.04Iso and lower during the isometric quadriceps contraction at 0.86Iso compared to the isometric (Iso) contraction. Moreover, normalized hamstring rsEMG was significantly higher during the shortening compared to the isometric quadriceps contraction at 1.04Iso, both for contractions at 10 and 50 % MVC ($F_{1, 9} = 3.2, P = 0.03$). Normalized hamstring rsEMG was not different during the lengthening compared to the isometric quadriceps contraction at 0.86Iso at 10% MVC ($t = 0.016, P = 0.98$); however at 50 % MVC, normalized hamstring rsEMG during lengthening contraction of the quadriceps was significantly higher than the hamstring
rsEMG during isometric quadriceps contraction at 0.86Iso (t = -6.4, P < 0.001). The significant differences in antagonist hamstring rsEMG between the 1.04Iso and isometric quadriceps contractions at 10 and 50 % MVC were on average only 0.28 ± 0.28 %, and between the 0.86Iso and isometric quadriceps contractions the average value was 0.79 ± 0.54 %. Furthermore, differences in antagonist hamstring rsEMG between shortening and 1.04Iso quadriceps contractions at 10 and 50 % MVC was on average only 0.57 ± 0.71 %. The difference in antagonist hamstring rsEMG between lengthening and 0.86Iso quadriceps contractions at 50 % MVC was only 1.06 ± 0.52 %. Thus, although co-contraction of the knee flexors differed significantly among contraction modes, these differences were very subtle and probably of little influence on our main results.

Third experiment

Intramuscular EMG during shortening, isometric and lengthening contractions

Contraction mode dependent changes in normalized rsEMG for VL and BF in the third experiment were similar to the changes in normalized rsEMG in the second experiment (Figures 3.6 and 3.7, Table 3.3), therefore these results were not repeated.

In total 46 motor units were followed twice during isometric (3 torque levels), shortening and lengthening contractions. Relative torque levels (as percentage of MVC) during the contractions varied from 4 up to 76 % MVC (with recruitment torques from 0.5 up to 61.1 % MVC), and were on average 20.9 ± 17.6 % MVC. Overall, there were no differences between the torques which were actually produced and the intended torques ($F_{1.9} = 3.8, P = 0.08$). Actual torque levels, expressed as percentage of the isometric contraction, were for the 1.04Iso and 0.86Iso contractions respectively 1.05 ± 0.02 and 0.86 ± 0.02 and, as this was not significantly different from the target torque values (1.04 and 0.86), this indicates that similar to the second experiment (with torques of 10 and 50 % MVC) subjects were able to perform the isometric contractions at the required torque level over a broad torque range (4 – 76 % MVC). For the shortening and lengthening contractions the actual torque ratios respectively were 0.99 ± 0.03 and 1.06 ± 0.06 times the isometric torque, and did not significantly differ from the target values of 1.0.
Figure 3.7. Normalized (isometric contraction = 1.0) quadriceps rectified surface EMG for shortening and 1.04Iso contractions (A) and lengthening and 0.86Iso contractions (B) at 10 % (closed squares) and 50 % MVC (open circles). * and † indicate significantly different from respectively the 1.04Iso and the 0.86Iso contractions (P < 0.05).

Table 3.3. Normalized (% MVC) hamstring rsEMG (mean ± SD) during shortening, 1.04Iso, isometric, 0.86Iso and lengthening contractions at 10 and 50 % MVC.

<table>
<thead>
<tr>
<th>Contraction</th>
<th>10 % MVC</th>
<th>50 % MVC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shortening</td>
<td>2.29 ± 0.99†</td>
<td>6.99 ± 2.84†</td>
</tr>
<tr>
<td>1.04Iso</td>
<td>1.95 ± 0.73*</td>
<td>6.20 ± 2.61*</td>
</tr>
<tr>
<td>Isometric</td>
<td>1.80 ± 0.69</td>
<td>5.78 ± 2.40</td>
</tr>
<tr>
<td>0.86Iso</td>
<td>1.62 ± 0.71*</td>
<td>4.38 ± 1.46*</td>
</tr>
<tr>
<td>Lengthening</td>
<td>1.62 ± 0.65</td>
<td>5.44 ± 1.73‡</td>
</tr>
</tbody>
</table>

*Significantly different compared to isometric contractions; †significantly higher compared to 1.04Iso contractions; ‡significantly higher compared to 0.86Iso contraction (P < 0.05).
Motor unit discharge rates during the 1.04Iso and 0.86Iso contractions were on average 12.3 ± 2.3 and 10.9 ± 2.1 Hz compared to 12.0 ± 2.1 Hz for the isometric contraction. There was a significant effect on normalized discharge rate between the 1.04Iso, Iso and 0.86Iso contractions ($F_{2, 18} = 18.2$, $P < 0.001$). However, the normalized discharge rate for the 1.04Iso contraction was 1.03 ± 0.04 which was not significantly different from 1.0 (the isometric value): a 4 % higher torque level was not accompanied by a significantly higher discharge rate. Normalized discharge rate for the 0.86Iso contraction was significantly lower (0.91 ± 0.07) than that of the isometric contraction, indicating that a 14 % lower torque was accompanied by about 9 % lower discharge rates (Figure 3.8).

Average discharge rates during the shortening and lengthening contractions respectively were 14.3 ± 1.8 Hz and 10.6 ± 1.5 Hz. As expected and in line with the results of the second experiment, normalized discharge rate for the shortening contraction (1.22 ± 0.13) was significantly higher compared to the 1.03 ± 0.04 obtained during the 1.04Iso contraction (Figure 3.9A; $t = 4.9$, $P < 0.001$). In contrast to our expectations, but in line with the rsEMG (Figure 3.7B) normalized discharge rate for the lengthening contraction (0.90 ± 0.08) was not significantly lower than the 0.91 ± 0.07 obtained during the 0.86Iso contraction (Figure 3.9B; $t = 0.30$, $P = 0.77$).

**Figure 3.8.** Normalized discharge rates for 0.86Iso, isometric (Iso) and 1.04Iso (isometric contraction = 1.0) at an average 20.9 ± 17.6 % MVC. * Indicates significantly lower compared to the isometric contraction ($P < 0.05$).
Ten motor units studied at the highest torque level (47.8 ± 15.5 % MVC) showed similar discharge rate behaviour compared to motor units studied at low torque levels (4.8 ± 0.9 % MVC, n = 10), indicating that torque level did not influence the effects of contraction mode on motor unit discharge rate (F$_{1,9}$ = 0.10, P = 0.78).

**Discussion**

The present study was the first study to investigate neuromuscular activity during shortening, lengthening and isometric contractions, corrected for the differences in intrinsic muscle strength and at comparable muscle lengths. The main finding was that both discharge rate and rsEMG were greater during shortening compared to isometric contractions and in contrast to our expectations, neuromuscular activity was not lower during lengthening compared to isometric contractions performed at a similar relative torque level.

**Figure 3.9.** Normalized discharge rates for shortening and 1.04Iso contractions (A) and lengthening and 0.86Iso contractions (B) at an average 20.9 ± 17.6 % MVC. * Indicates significantly higher compared to the 1.04Iso contraction (P < 0.05).
Mode dependent strength differences

In accordance with the literature voluntary activation (VA) was lower during maximal shortening and lengthening compared to maximal isometric contractions and as a consequence maximal voluntary lengthening torque did not exceed the maximal isometric torque (Babault et al., 2001; Babault et al., 2002; Babault et al., 2003; Beltman et al., 2004a; Pinniger et al., 2000; Westing et al., 1988; Westing et al., 1990). However, during maximal activation lengthening torque is higher than isometric torque (de Ruiter et al., 2000). We therefore linearly extrapolated the shortening and lengthening MVC relative to the isometric MVC to conditions of maximal voluntary activation, and found that the intrinsic muscle strength for shortening and lengthening contractions respectively was 0.96 and 1.16 times the isometric muscle strength (Figure 3.2). These values are comparable with those which can be estimated from the data of de Ruiter et al (2000) during maximal stimulated contractions of the adductor pollicis muscle at the same angular velocities (10°·s⁻¹), assuming, of course, that the lever ratios of the adductor pollicis and quadriceps are the same. Additional isometric contractions were therefore performed at respectively 1.04 and 0.86 times the isometric torque for comparison with respectively shortening and lengthening. Neuromuscular activity was higher during the 1.04Iso contraction, albeit not significant for the discharge rate data, and lower during the 0.86Iso contraction compared to the isometric contraction (Figures 3.6 and 3.8), indicating that contraction mode dependent differences in muscle strength significantly contribute to the differences in neuromuscular activity between shortening, lengthening and isometric contractions found in previous studies (Del Valle and Thomas, 2005; Howell et al., 1995; Kossev and Christova, 1998; Linnamo et al., 2003; Pasquet et al., 2006; Søgaard et al., 1998; Søgaard et al., 1996; Tax et al., 1989).

To determine the contraction mode dependent differences in intrinsic muscle strength, it is important that VA is maximal or at least similar between shortening, lengthening and isometric MVCs. Since this is usually not the case (present study, (Babault et al., 2001; Babault et al., 2002; Babault et al., 2003; Beltman et al., 2004a)) we had to use linear regression and extrapolation as shown in Figure 3.2. Although this is a limitation there is no better alternative. At least all our subjects had a very high VA during isometric MVCs (range 94 – 100 %) and we consider the intercepts of 0.96 and 1.16 to be the best representation of the differences in intrinsic muscle strength between respectively shortening and lengthening contractions compared to isometric contractions.

Since Pinniger et al (2000) found that both maximal and submaximal voluntary lengthening torques did not exceed the isometric torques, indicating that the higher
torque capacity during lengthening could not be utilized during voluntary contractions, it could be argued that our correction for a greater intrinsic muscle strength during lengthening would be unnecessary or even incorrect. However, the incomplete VA during maximal lengthening contractions was suggested to be related to the inhibition of motoneurones via Golgi tendon organs at high torque levels (Aagaard et al., 2000; Westing et al., 1990) and may not be present during submaximal contractions. Indeed, during the submaximal lengthening contractions in the present study neuromuscular activity was lower than during isometric contractions performed at the same absolute torque (see below) indicating that intrinsic muscle strength was increased during submaximal lengthening contractions.

Effect of contraction mode on neuromuscular activity

During the lengthening part of the constant torque contraction neuromuscular activity of the quadriceps muscles was lower, as seen in the lower discharge rate compared to the isometric contraction (see also the derecruitment of the motor unit in Figure 3.4B). However, and in contrast to our expectations, at similar relative contraction intensity neuromuscular activity was not lower in lengthening compared to the isometric contractions. It seems therefore likely that the higher intrinsic muscle strength during lengthening can fully account for the reduced level of neuromuscular activity (motor unit discharge rate, rsEMG).

It may be argued that surface EMG is not a very good measure of neuromuscular activity, particularly during dynamic contractions where electrodes may shift relative to the muscle fibres (Farina, 2006; Farina et al., 2001), however, the change in knee angle was limited in the present study (20°) and performed at slow speed (10°·s⁻¹). Moreover, the similarities in changes in the behaviour of surface and motor unit discharge rates are striking (see also (Pasquet et al., 2006)). The only exception in this respect was seen during lengthening contractions. Whereas discharge rates were similar during lengthening compared to 0.86Is0 contractions, normalized lengthening rsEMG was higher at similar relative contraction intensity. There are several possible explanations for the higher normalized lengthening rsEMG in absence of a higher lengthening motor unit discharge rate. The first possible explanation is that additional motor units would be recruited during lengthening compared to isometric contractions, while discharge rates of already recruited units remained constant. However, this would necessitate a change in the input - output relation of the motor unit activation model of De Luca & Erim (1994), which is not very likely and not in accordance with the occasional finding of the derecruitment of a motor unit during
lengthening (Figure 3.4B). A second explanation could be an increase in the synchronization of the motor units firing during lengthening (Semmler et al, 2002). At submaximal excitation levels, Yao et al (2000) found, using a computer model of muscle contraction, moderate synchronization could increase the surface EMG amplitude by ~50%. Therefore a limited synchronization can in theory fully account for the ~30% higher rsEMG during lengthening compared to 0.86Iso contractions.

In line with our hypothesis, the neuromuscular activity of the quadriceps muscle during shortening was higher than during isometric contractions at similar relative contraction intensity and muscle lengths, which was reflected by a higher discharge rate and rsEMG and probably also by the recruitment of additional motor units during the shortening phase of the contraction (Figure 3.4A). One explanation for the higher muscle activity during shortening could be that the torque level of the 1.04Iso contraction was underestimated (that is an overestimation of the extrapolated shortening capacity relative to the isometric capacity, see Figure 3.2). However, uncertainty about this value may be small since de Ruiter et al (2000) measured a similar shortening relative to isometric capacity (~1.06) using maximal electrically evoked contractions of the adductor pollicis muscle. A second explanation for the increased neuromuscular activity during shortening contractions compared to isometric contractions at similar relative torque level, the lower intrinsic muscle strength during shortening could not be the sole cause. Possibly neuromuscular activity during shortening contractions was also increased due to shortening induced force depression, probably as a consequence of a stress-induced inhibition of cross bridge attachment within the new zone of overlap between the thick and the thin filaments, due to a distortion of the thin filaments (Daniel et al, 1998; Granzier and Pollack, 1989; Herzog, 2004; Marechal and Plaghki, 1979). In addition de Haan (1998) showed that higher stimulation frequencies were needed to obtain maximal torque during shortening contractions than during isometric contractions, suggesting that higher calcium concentrations and therefore increased neuromuscular activity would be required during shortening contractions.

Although a number of studies have investigated the effect of contraction mode on neuromuscular activity, a comparison between isometric, shortening and lengthening contractions at similar relative torques and a comparable muscle length was never made. Some studies did compare the shortening and lengthening contractions with isometric contractions, however, not at muscle lengths halfway the dynamic contraction (Linnamo et al, 2003; Pasquet et al, 2006). Moreover, differences in intrinsic muscle strength were only once taken into account (Del Valle and Thomas,
Therefore, the present study is the first in which the same single motor units were studied during isometric and dynamic contractions at similar muscle length and at similar relative torque (% maximal capacity). A lower neuromuscular activity has often been found during lengthening, when lengthening contractions were compared to shortening contractions (Del Valle and Thomas, 2005; Kossev and Christova, 1998; Pasquet et al, 2006; Søgaard et al, 1996; Tax et al, 1989). In the explanation of the results the authors usually focused on the different behaviour of lengthening contractions. The findings were usually attributed to a higher intrinsic muscle strength during lengthening (Del Valle and Thomas, 2005; Howell et al, 1995; Kossev and Christova, 1998; Søgaard et al, 1996) or to a reduced excitation of the motoneuron pool (Pasquet et al, 2006), as indicated by a lower MEP induced by magnetic and electrical stimulation and a lower H-reflex, during lengthening compared to shortening contractions (Abbruzzese et al, 1994; Romanò and Schieppati, 1987; Sekiguchi et al, 2003). Although an enhanced motoneuron excitability during shortening and a lower excitability during lengthening would be useful adaptations to the respectively lower and higher intrinsic muscle strength during shortening and lengthening contractions, the present study shows that the larger adaptations in neuromuscular activity occur during shortening contractions. We conclude that force – velocity related strength differences can fully account for the lower neuromuscular activity during submaximal lengthening contractions, but can not completely explain the higher neuromuscular activity during submaximal shortening contractions.
References


