Neuromuscular drive and force production are not altered during bilateral contractions

Jakobi, J. M., and E. Cafarelli. Neuromuscular drive and force production are not altered during bilateral contractions. J. Appl. Physiol. 84(1): 200–206, 1998.—Several investigators have studied the deficit in maximal voluntary force that is said to occur when bilateral muscle groups contract simultaneously. A true bilateral deficit (BLD) would suggest a significant limitation of neuromuscular control; however, some of the data from studies in the literature are equivocal. Our purpose was to determine whether there is a BLD in the knee extensors of untrained young male subjects during isometric contractions and whether this deficit is associated with a decreased activation of the quadriceps, increased activation of the antagonist muscle, or an alteration in motor unit firing rates. Twenty subjects performed unilateral (UL) and bilateral (BL) isometric knee extensions at 25, 50, 75, and 100% maximal voluntary contraction. Total UL and BL force (±3%) and maximal rate of force generation (±2.5%) were not significantly different. Total UL and BL maximal vastus lateralis electromyographic activity (EMG; 2.7 ± 0.28 vs. 2.6 ± 0.24 mV) and coactivation (0.17 ± 0.02 vs. 0.20 ± 0.02 mV) were also not different. Similarly, the ratio of force to EMG during submaximal UL and BL contractions was not different. Analysis of force production by each leg in UL and BL conditions showed no differences in force, rate of force generation, EMG, motor unit firing rates, and coactivation. Finally, assessment of quadriceps activity with the twitch interpolation technique indicated no differences in the degree of voluntary muscle activation (UL: 93.6 ± 2.51 Hz, BL: 90.1 ± 2.43 Hz). These results provide no evidence of a significant limitation in neuromuscular control between BL and UL isometric contractions of the knee extensor muscles in young male subjects.

twitch interpolation; coactivation; average motor unit firing rate; bilateral deficit; maximal voluntary contraction

ALTHOUGH THE HUMAN NEUROMUSCULAR SYSTEM IS CAPABLE OF PERFORMING MOTOR TASKS OF GREAT COMPLEXITY, THERE ARE SEVERAL REPORTS IN THE LITERATURE DESCRIBING THE INABILITY OF HUMAN SUBJECTS TO GENERATE MAXIMAL FORCE WHEN CONTRALATERAL MUSCLE PAIRS OPERATE SIMULTANEOUSLY (13, 15–17, 23–27, 31, 33, 35, 38–40). FOR EXAMPLE, WHEN BOTH QUADRICEPS FEMORIS GROUPS CONTRACT SIMULTANEOUSLY DURING MAXIMAL ISOMETRIC KNEE EXTENSION, THE TOTAL FORCE FROM BOTH LEGS IS LESS THAN THE TOTAL FORCE IF EACH CONTRACTS INDEPENDENTLY (15, 17). THIS APPARENT FAILURE OF THE NEUROMUSCULAR SYSTEM, KNOWN AS THE BILATERAL DEFICIT (BLD), IS NOT PARTICULARLY ROBUST; DIFFERENT INVESTIGATORS USING SIMILAR PROTOCOLS IN NEAR-IDENTICAL SAMPLES HAVE FOUND A BLD IN SOME CASES (15, 38) BUT NOT IN OTHERS (6, 38). AT ONE TIME OR ANOTHER, IT HAS BEEN SUGGESTED THAT FACTORS SUCH AS TRAINING (15, 23, 31, 33, 34), AGE (9, 11), MOTOR DISORDERS (36), FATIGUE (18, 38, 39), FIBER TYPE (6, 17, 35, 38), AND RIGHT-LEFT DOMINANCE (13, 14, 22–25, 41) HAVE A ROLE IN THIS PHENOMENON.

Despite the 26 studies on BLD that have appeared in the literature since 1961, no clear explanation for this phenomenon has emerged. It appears that BLD occurs more frequently in the upper body (13, 18, 22–27) and less frequently in contralateral muscle pairs that have undergone bilateral resistance training (15, 31, 34). There is no BLD when nonhomonymous muscles contract simultaneously, for example, during simultaneous flexion of one arm and extension of the other (14–16, 25). Perhaps the most perplexing finding has been the observation of BLD that have not been accompanied by proportional deficits in activation as measured with surface electromyography (EMG) (15, 16, 33), although this might be due, in part, to the potential insensitivity of the method. Furthermore, although some investigators have suggested that the BLD is the consequence of a disproportionate increase in antagonist coactivation (15, 17), no study has systematically addressed this possibility.

To accept the notion that the human neuromuscular system is incapable of solving the problem of generating maximal force when contracting bilaterally suggests limitations in the system that are not apparent in other, more complex, maneuvers. If maximal bilateral activation presents a problem for the neuromuscular system, one might expect to see differences in the way agonist and antagonist muscles are activated during submaximal contractions. This arises from the possibility of increased antagonist activity during submaximal bilateral contractions. More antagonist activity would require more agonist activation to achieve the same submaximal force. Similarly, altered agonist activation may be accompanied by changes in motor unit firing rates.

The purpose of the present experiment was to determine whether less force is produced during simultaneous contralateral knee extension compared with unilateral knee extensions. Our working hypothesis was that a BLD would result from decreased agonist activity, increased antagonist activity, or a combination of both. Furthermore, this neuromuscular alteration would be evident during submaximal contractions. If agonist activity or motor unit firing rate decreases, it could then be concluded that BLD occurs because of a reduction in excitatory drive or an increase in inhibitory input to the α-motoneurons. The results show that knee extensor force and agonist and antagonist electrical activation were not different between unilateral and bilateral maximal or submaximal contractions.

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METHODS

The extensors and flexors of both knees of 20 paid male volunteers (aged 27.5 ± 1.78 (SD) yr, weight 77.48 ± 2.00 kg) were used in this experiment. Subjects had not engaged in any systematic training during the 1 mo preceding the experiment, but they had been recreationally active, as determined by an activity questionnaire. The procedures were approved by the Human Participants Review Committee of York University, and all subjects signed a consent form after they were given an explanation of the experimental procedures.

Force measurements. Knee extensor force was measured in a dynamometer tilted backward 45° from a vertical position so that most of the subject's weight was supported on the buttocks. A complete description of the apparatus has been given previously (28). The subject's knees were flexed at 90°, his hips were restrained with a seat belt, and his ankles were secured to strain gauges that had been calibrated with known weights. All were instructed to generate maximal force as strongly and as quickly as possible, and visual feedback was provided. The maximal rate of force generation (dF/dtmax) was determined by calculating the first derivative of force as a function of time. Force signals were amplified, viewed on a 20-MHz digital storage oscilloscope, and stored on videocassette for subsequent analysis (model 500D, Sony; model 4000A digital pulse code modulator recording, Vet- ter). After analog-to-digital (A/D) conversion (A/D board DT 2801) at a sampling frequency of 1,000 Hz, force recordings were processed with sequences built in Easiest LX software (Keithley Asyst Technologies).

For the purpose of this experiment, a deficit was defined as a reduction in total force during bilateral contractions of the quadriceps femoris. We combined the absolute unilateral right and left forces for each subject to get a total unilateral force. These values were then pooled and used to determine whether there was a statistical difference in total force production between the two conditions. We also calculated whether there was a statistical difference in total force. These values were then pooled and used to determine right and left forces for each subject to get a total unilateral force. For the purpose of collecting AMUFRs, 10-s contractions of the quadriceps femoris were recorded. A/D conversion of the force signal at 20 KHz was time locked to a triggering pulse occurring 13 ms before the shock and proceeded for 150 ms. Estimates of the degree of activation were obtained by taking the ratio of the superimposed twitch (Twp) to the potentiated twitch (Twt) and expressing it as a percentage: [(1 − Twp/Twt) × 100] (%activation) (12).

Surface EMG. Bipolar silver-silver chloride recording electrodes (EQ), 0.75 cm in diameter with a fixed 2-cm interelectrode distance, were placed on both the right and left legs over the belly of the vastus lateralis −10–12 cm proximal to the superior border of the patella. Although we only recorded from one of the components of the quadriceps femoris, the activation of the vastus lateralis is known to parallel that of the vastus medialis and rectus femoris during static contractions (10). Another set of recording electrodes was placed over the long head of the biceps femoris, one-half of the distance between the ischial tuberosity and the popliteal fossa. EMG signals were preamplified ×35 at the electrode, amplified again downstream, and stored on videocassette for off-line analysis. After A/D conversion at a rate of 1,000 Hz, the interference pattern was rectified and integrated according to the following procedure by using sequences in Easiest LX. A 1-s epoch beginning 500 ms before maximal force was used in the assessment of maximal agonist and antagonist drive. Submaximal EMG was determined from a 1-s segment of signal obtained when force was held constant for 3 s. The submaximal integrated EMG data are presented in millivolts or are normalized to the EMG obtained during maximal contractions.

Single-motor unit recordings. Average motor unit firing rates (AMUFRs) were collected to determine whether there was a difference in the rate at which motor units fired during bilateral contractions at the same absolute force. Tungsten microelectrodes (Howarth Instruments) were used to record action potentials from single motor units. The skin over the vastus lateralis was prepared by shaving and cleansing the area with a 70% ethyl alcohol solution. A small puncture was made in the skin and underlying fascia with a 25-gauge hypodermic needle, and the micro electrode was then inserted perpendicularly into the belly of the vastus lateralis. Once the needle was completely inserted, it was withdrawn and reinserted in an adjacent location in the muscle. The needle was reinserted into the muscle 2–3 times per experiment but never in the same site. A reference needle was inserted at a shallow angle into the subcutaneous tissue immediately proximal to the patella. A wet wrap surrounded the upper thigh served as a ground. The signal from the tungsten microelectrode was preamplified near the source, passed through a second amplifier (×60), and stored on videocassette for off-line analysis. The signal was also sent to a third amplifier (Neurolog NL 106 alternating current-direct current amplifier, ×1 to ×40) and filtered on-line (Neurolog NL 120 filter, band pass 1–5 kHz); this filtered signal was delayed 5–10 ms and (Neurolog NL 202 AC signal delay) and then displayed on an oscilloscope (Gould 0S300) set at a sweep speed of 10 ms/sweep. The rate of action potential discharge was analyzed off-line by using a software routine (Easiest LX). Spike trains were considered to be from the same motor unit if a minimum of four successive spikes had the same shape, a comparable amplitude, and a similar interspike interval. Under these experimental conditions, the probability of counting the same unit twice as the needle was advanced through the vastus lateralis is <0.15 (29). For the purpose of collecting AMUFRs, 10-s contractions of 25, 50, and 75% MVC were each performed twice. Maximal contractions were performed four times and held for 5 s to
prevent fatigue. Target forces of 25, 50, and 75% were maintained with visual feedback and verbal encouragement.

Protocol. Twenty subjects were randomly divided into two groups of 10; each subject visited the laboratory twice (Table 1). On day 1 we evoked the maximal twitches necessary to verify MVC, determined unilateral and bilateral MVC, and recorded force and EMG from maximal flexion contractions (28). Group 1 performed unilateral and bilateral submaximal contractions of 25, 50, 75, and 100% MVC while surface EMG was recorded. Group 2 performed unilateral and bilateral knee extensions of 25, 50, 75, and 100% MVC on day 1 while we recorded from single units. On day 2 the protocols were reversed. These arrangements are shown in Table 1.

On day 1 at least three brief (3- to 5-s) maximal unilateral and bilateral contractions were practiced before verification of maximal force was undertaken. The greatest unilateral MVC amplitude was used to normalize all force data. The EMG values used for analyses were recorded during the three greatest MVCs that were within 10% of each other. Extensor force and agonist and antagonist electrical activity of the noncontracting leg were monitored during unilateral contractions if there was activity in these tracings, the trial was discarded (~5%) and the contraction was performed again. To avoid an experimental-order effect, unilateral and bilateral contractions were performed in an irregular sequence on both days.

Statistical analysis. A 2 × 4 (condition [UL, BL] × force [25, 50, 75, and 100% MVC]) repeated-measures analysis of variance was used to analyze the dependent variables of force, AMUFR, and vastus lateralis and biceps femoris EMG. Statistical significance for all analyses was accepted at P ≤ 0.05, and post hoc assessment of statistical power assumed a beta level of 0.2 (power = 1 – β). All statistical procedures were run with Statistica software (Statistica for Windows, ver. 5.1, Statsoft, Tulsa, OK).

RESULTS

Maximal voluntary force. The individual subject data for maximal contractions during unilateral and bilateral contractions are shown in Fig. 1. Figure 1 is arranged so that one can compare the force produced by either leg during unilateral and bilateral contractions. In the case of the right leg, four subjects showed a BLD > 10%, and only one had a bilateral facilitation >10%. Similarly, five subjects had a deficit in the left leg that exceeded 10%, and one showed a facilitation.

Table 1. Illustration of protocol for both subject groups on both experimental days

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<tr>
<th></th>
<th>Day 1</th>
<th>Day 2</th>
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<tr>
<td></td>
<td>Group 1 (n = 10)</td>
<td>Group 2 (n = 10)</td>
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<tr>
<td>Maximal twitch</td>
<td>UL and BL MVC</td>
<td>Maximal twitch</td>
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<tr>
<td>Flexion MVC</td>
<td></td>
<td>UL and BL MVC</td>
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<tr>
<td>Maximal and submaximal contractions with surface EMG</td>
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<td>Maximal and submaximal contractions with needle EMG</td>
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We chose 10% to illustrate the magnitude of any differences observed and to acknowledge the variability of maximal contractions. Out of 20 subjects, only one had a deficit and one had a potentiation in both legs. Statistically, there was no significant difference between the right MVC between the unilateral and the bilateral conditions; this was also true of the force produced by the left leg. In this sample of subjects, the mean force in the left extensors was slightly greater than that produced by the right extensors (P < 0.05). Comparison of the forces on a relative basis showed that the BI = 3.2 ± 6.1 (SD)%, which was not different from zero.

In Fig. 2 the left-right forces are totaled and arranged in descending order by condition. This figure illustrates that the ability of the knee extensor muscles to generate force about the joint was not compromised when the limbs contracted bilaterally. Out of 20 subjects, two showed a total deficit of >10% and two a potentiation of >10%. Statistically, there was no significant difference in the unilateral and bilateral peak forces or in the total peak force when the values were averaged and compared between conditions (Table 2). In addition to the peak forces being unaffected during bilateral contractions, we also found that dF/dtmax and the time at which it occurred did not vary across conditions (Table 2).

Muscle activation. Activation of the right quadriceps in both conditions was assessed in 10 of the subjects with the modified twitch interpolation technique described by Allen et al. (1), Hales and Gandevia (12), and Herbert and Gandevia (14). Table 2 shows that ~90% activation (UL: 93.6 ± 2.51, BL: 90.1 ± 2.43) was possible in both conditions and that there was no difference in right quadriceps activation between bilateral and unilateral contractions. Four of the ten subjects attained 100% maximal activation, and one of these attained maximal bilateral activation. Three of the subjects who were unable to attain maximal activa-
tion in either condition attained a higher level of activation in the bilateral condition. These differences were not significant.

In parallel with the pooled force data, there was no significant difference between the mean maximal integrated EMG (iEMG) in the bilateral and unilateral conditions (Table 2). The statistical power of this analysis to reveal a 10% difference in iEMG (e.g., Ref. 17) was 0.99. When submaximal force is plotted as a function of iEMG (Fig. 3), there is no difference in the amount of muscle activation required to attain similar unilateral and bilateral forces.

It is well known that during knee extension in the position assumed by our subjects the antagonist muscle on the posterior thigh is also active (4, 5, 28). Although it is not possible to measure the opposing force generated by these muscles, it may be estimated from the biceps femoris EMG. If the level of coactivation increased, especially during submaximal contractions, the opposing force could have contributed to any BLD. Bilateral and unilateral biceps femoris iEMG corresponded to ~12 and 14%, respectively, of that recorded during maximal flexion (Fig. 4). Coactivation increased as extension force increased but showed no differences between bilateral and unilateral contractions. At an extension force of 225 N, a force that corresponded to ~25% of maximum knee extension, the hamstrings were ~5% active.

Even though there were no differences between bilateral and unilateral vastus lateralis iEMG, there may have been offsetting differences in recruitment or rate coding between bilateral and unilateral contractions. The tracings at the top of Fig. 5 show examples of single-unit recordings obtained from the right vastus lateralis. The AMUFR was 15 ± 0.46 (SE) Hz at 25% MVC and increased approximately linearly to an average of 27 ± 0.85 Hz at maximum (Fig. 6). There were no significant differences in firing rate at any of these levels in either condition. The statistical power of this analysis to reveal a significant 10% difference in AMUFR between conditions was 0.99.

**DISCUSSION**

For there to be a true BLD, there must be an alteration in the neuromuscular control system. A force deficit during a bilateral contraction would only occur if central drive decreased or antagonist coactivation increased. Normally, force and EMG are coupled; if total bilateral force decreases there should also be a proportional decrease in EMG. The most likely candidates to cause the acute uncoupling of this relationship in unfatigued muscle would be a change in synergistic or antagonist muscle activity.

The purpose of the present experiment was to determine whether the knee extensors of young male subjects are capable of generating the same amount of

**Table 2. Electrical and mechanical characteristics of maximal UL and BL contractions**

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<tr>
<th></th>
<th>UL</th>
<th>BL</th>
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<tbody>
<tr>
<td></td>
<td>Right leg</td>
<td>Left leg</td>
</tr>
<tr>
<td>Force, N</td>
<td>430 ± 20</td>
<td>534 ± 21</td>
</tr>
<tr>
<td>dF/dt, N/s</td>
<td>1.703 ± 196</td>
<td>1.602 ± 247</td>
</tr>
<tr>
<td>EMG, mV/s</td>
<td>0.92 ± 0.11</td>
<td>1.14 ± 0.16</td>
</tr>
<tr>
<td>Act, %</td>
<td>93.52 ± 2.42</td>
<td>90.12 ± 2.28</td>
</tr>
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Values are means ± SE. dF/dt, rate of force generation; Act, muscle activation (not measured in left leg).
force in a bilateral isometric knee extension MVC as in a unilateral isometric MVC. We found no differences in bilateral and unilateral maximal force or in the ability of these subjects to activate their quadriceps at high force levels. Furthermore, dF/dt\text{max}, maximal EMG, maximal AMUFR, electrical activity of vastus lateralis, and AMUFR during submaximal contractions of 25, 50, and 75% MVC were all not different between bilateral and unilateral contractions. Along the continuum of submaximal to maximal knee extension forces, biceps femoris coactivity increased linearly, and the increase was the same for bilateral and unilateral contractions. The data from this experiment therefore provide no evidence of alterations in activity of the agonists and antagonists during bilateral and unilateral contractions.

Investigations that have not shown a clear force-EMG relationship or explained its uncoupling are difficult to interpret. For example, Kawakami et al. (16) and Schantz et al. (33) each found a decrease in total bilateral force but not a proportional decrease in neuromuscular activation as shown by the EMG. Koh et al. (17) found a BLD with a corresponding decrease in EMG, as well as a decrease in coactivation. The decrease in bilateral force was paralleled by changes in agonist activation, but during the bilateral contractions coactivation decreased nearly threefold more than agonist activation. Although these changes were not statistically significant, they could imply that less of the agonist activity during a bilateral contraction was being used to overcome antagonist activity. Similarly, Howard and Enoka (15) reported an experiment in which the untrained subject’s total bilateral force was \(\sim 9.5\%\) less than total unilateral force but the EMG was \(\sim 1.2\%\) greater. In this case, it is unclear what role coactivation played in the force deficit because it was not always present in unilateral trials and was not reported for bilateral contractions. In contrast, several papers from our laboratory (4, 5, 28, 31) have shown that biceps femoris is 12–16% activated during extension MVC.

Most of the evidence that BLD is a result of neuromuscular alterations has come from EMG activity recorded during maximal contractions (22–27). Force and EMG in vastus lateralis normally have a linear relationship (8). Any alteration in this relationship during maximal bilateral contractions should also be apparent during submaximal contractions. For example, if BLD is a result of decreased neuromuscular drive, the same amount of agonist activation in submaximal unilateral and bilateral contractions would result in less force in the bilateral condition. Alternatively, if the neuromuscular system requires a greater degree of activation to perform a bilateral MVC, the EMG at submaximal forces would be greater for the bilateral contraction; that is, the amount of activation per unit force would have to increase. The present results show that there was no difference in bilateral and unilateral EMG during maximal and submaximal contractions and the same level of activation (EMG) produced the same amount of submaximal force.

It is possible that subtle differences in agonist activation were not apparent from surface EMG, especially if these changes took the form of reciprocal changes in rate coding and recruitment. A difference in firing rate between bilateral and unilateral contractions would imply that descending drive to the motoneurons is organized differently or that the responsiveness of the motoneuron pool differs between one- and two-leg contractions (3). At 25% MVC in both conditions, the AMUFR was 15 Hz and increased to \(\sim 26\) Hz at MVC. Our data are therefore the first to show that there is no difference in vastus lateralis AMUFR between bilateral and unilateral contractions and that it is unlikely that alterations in rate coding would contribute to a force deficit.

The twitch interpolation technique provides an objective measure of maximal voluntary muscle activation. It has been determined that, on most occasions, subjects are capable of nearly complete, but not always full, activation of the involved musculature during MVC (1, 2, 7, 12, 14). On average, only 22–25% of all MVC attempts attain full activation (1, 14). We have shown that the ability to voluntarily activate the quadriceps is not altered in a bilateral contraction compared with a unilateral contraction. In the present experiment, an average of \(\sim 90\%\) activation of the right quadriceps was possible in both bilateral and unilateral contractions. This is somewhat less than the level of activation that
has been reported for other muscles (1, 14) but similar to the only other data on the knee extensors we know of that was recently reported by Roos and Rice (30). Furthermore, Herbert and Gandevia (14) found that median maximal voluntary activation scores differed by 1.7% and MVC force by ~2% in bilateral and unilateral thumb adduction. Similarly, we found small differences between unilateral and bilateral contractions of 2.5% for activation and 3% for force in the knee extensors.

We have no satisfying explanation for the disparate findings on BLD in various muscle groups and in different subject populations found in the literature, although the different methodologies employed have certainly contributed to the assortment of findings that have been reported. One point seems clear: the inability to generate maximal force during bilateral contractions would represent a significant departure from the level of competence expected of the human neuromuscular system. Any observation of such an acute failure of force generation would require corroborating evidence.

Fig. 5. Examples of single-unit recordings obtained from right vastus lateralis during contractions of 25% (A; 12 Hz) and 100% MVC (B; 28 Hz) are shown at left. Each recording is ~1 s long. Right traces represent dotted spikes on longer record (left) that are repetitive firings of a single cell overlaid on a faster time base. Right middle tracing has been inverted so that it fits in figure. Time and voltage scales apply to high-speed traces.

Fig. 6. Relationship between average motor unit firing rate (AMUFR) and absolute pooled force from all 20 subjects. There was no difference in average firing rate between UL (○) and BL (●) contractions. Symbols are at 25, 50, 75, and 100% MVC. There are ~200 counts in each data point.
from other measurements of the control properties of muscle. Our data provide no evidence that is consistent with a force deficit during bilateral isometric contractions of the knee extensors in healthy young male subjects.

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