Expression of the Bilateral Deficit During Reflexively Evoked Contractions

N. Khodiguian, A. Cornwell, E. Lares, P. A. DiCaprio, and S. A. Hawkins

Department of Kinesiology, California State University, Los Angeles

5151 State University Drive, Los Angeles, CA 90032

Nazareth Khodiguian, Ph.D.
Department of Kinesiology
California State University, Los Angeles
5151 State University Drive
Los Angeles, CA 90032

Tel: (323) 343-4676
Fax: (323) 343-6482
E-mail: nkhodig@calstatela.edu

Running head: Reflexive expression of the bilateral deficit
ABSTRACT

During maximal contractions, the sum of forces exerted by homonymous muscles unilaterally is typically larger than the sum of forces exerted by the same muscles bilaterally. This phenomenon is known as the bilateral deficit (BLD), and it is suggested that this deficit is due to neural inhibition. It remains unclear, however, if such inhibition is mediated by supraspinal mechanisms or by reflex pathways at the level of spinal cord. To further study the origin of likely neural influences, we tested for the presence of BLD under the condition of reflexive force generation. Force output and iEMG (quadriceps femoris) was measured in seventeen male participants after initiation of the myotatic patellar reflex under unilateral and bilateral conditions. A significant BLD of $9.26 \pm 1.19\%$ ($P = 0.004$) and $16.76 \pm 4.69\%$ ($P = 0.001$) was found for force and iEMG, respectively. However, since similar findings were not evident during maximal isometric knee extensions, it is difficult to predict the contribution of a spinal mechanism to the BLD under the condition of maximal voluntary activation.

Myotatic reflex; reflexive force generation; maximal voluntary contractions; cross-inhibition
INTRODUCTION

During maximal voluntary muscular actions, the sum of forces exerted by homonymous muscles when activated independently (unilaterally) is typically larger than the summated force produced when the same muscles contract simultaneously (bilaterally). Although not evident in all studies (e.g., 10-12, 18), this phenomenon has been demonstrated by the majority of investigations (e.g., 15, 17, 20-22, 24, 25, 27, 28, 30, 32, 33, 41) and has become known as the bilateral deficit (BLD). For example, a 7-25% reduction in bilateral force production compared to summed unilateral output has been reported for isometric knee extension and combined isometric hip and knee extension (17, 22, 33, 34, 37). Dynamic contractions also display this phenomenon (33, 39-45), and a similar effect has been found for the upper limbs, although the deficit is generally smaller compared to the lower limbs (for a review, see 19).

The BLD appears to be specific to homonymous muscles on each side of the body contracting simultaneously to produce a similar action. Howard and Enoka (17) found no bilateral force deficit when subjects performed maximal voluntary contractions with the left elbow flexors and right knee extensors. Similarly, no deficit was observed by Herbert and Gandevia (16) when testing the thumb adductors and elbow flexors. Furthermore, the phenomenon has not been demonstrated in simultaneous opposing motions of homonymous limbs such as elbow flexion/extension (31), and plantar flexion/dorsiflexion (20). Such findings suggest that the BLD is not the result of the central nervous system’s inability to maximally activate several muscle groups simultaneously. Evidence to corroborate this postulation was provided by Schantz et al. (34) who observed that the force deficit during bilateral isometric knee extension contractions was not increased when a bilateral isometric elbow flexion effort was added to the knee extension task.
At present, the underlying mechanism(s) responsible for the BLD is (are) not fully known. Nonetheless, it is generally accepted that some kind of neural inhibition prevails, even though the reduction in force in the bilateral condition has not always been paralleled by a reduction in the electromyographic (EMG) signal (19). The neural pathways responsible for such inhibition, however, remain unclear. One possibility is that the BLD is caused by mutual inhibition of the two cerebral cortices via transcollosal fibers (29). Oda and Moratani (29) investigated cortical involvement in the BLD by recording cortical activity via movement-related cortical potentials in subjects that performed maximal bilateral and unilateral handgrip contractions. In addition to lower force and EMG activity in the bilateral compared to unilateral conditions, cortical activity was also depressed lending support to the notion that neural inhibition is partly responsible for the BLD and that the origin of inhibition lies within the motor cortex. Cross-inhibitory interhemispheric interaction that impacts motor control is also demonstrated during various bilateral motor tasks in experiments involving commisurectomy patients (9, 46). Some studies (13, 26), however, have reported facilitation of the contralateral motor cortex as a result of transcranial magnetic stimulation of the ipsilateral side, and of the contralateral spinal cord (26) as a result of forceful voluntary activation of small hand muscles under specific conditions. In both of these studies, though, no direct measurements of force output from the contralateral test muscles were obtained.

Tanaguchi (40) also purported a supraspinal mechanism after investigating the effect of training on the BLD. Bilateral training resulted in a reduction of BLD while unilateral training enhanced the BLD. Furthermore, in the unilaterally trained group, the untrained limbs also demonstrated an increase in BLD. The author interpreted these findings as evidence that the BLD is, at least in part, influenced by some neural mechanism at the supraspinal level.
Alternatively, the phenomenon might be related to inhibitory spinal reflexes (31). Afferent sensory input from one limb may inhibit the motor neurons controlling the contralateral limb at the level of the spinal cord. Cross inhibition at the spinal level has been demonstrated by measuring the magnitude of H-reflex in a selective muscle of one limb while simultaneously performing passive (4, 6) and active (6) motor tasks with the contralateral limb. Other investigations have demonstrated spinal level cross inhibition of the homonymous muscle motoneuronal pool (7) or muscle group (23). Cross inhibition of contralateral agonist and antagonist muscles at the spinal level was also shown in spinal cats (2) and in right hemispastic patients (7). These studies demonstrate the existence of interneurons that may provide intraspinal pathways that could transmit Ia impulses to the Ia inhibitory interneurons of the contralateral side (7).

Unfortunately, attempts to evaluate supraspinal versus spinal mediation of the BLD are few and additional research is necessary to elucidate the origin, in addition to the nature, of the underlying inhibitory mechanism. To further investigate the origin of likely neural influences, it was the purpose of the present study to test for the presence of the BLD under the condition of reflexive force generation. By studying the force responses to elicitation of the myotatic reflex under bilateral and unilateral conditions, it was possible to determine if the phenomenon still occurred in the absence of supraspinal influences. It was hypothesized that if the intraspinal neuronal circuitry were, even partially, responsible for the BLD, the sum of reflexive force output obtained by eliciting the myotatic reflex under bilateral conditions would be less than the summated force generated under unilateral conditions. Further, since a BLD under reflex conditions may arise because of reasons that are unrelated to those presiding under the condition of maximal voluntary activation, an additional purpose was to test for the presence of the BLD.
during maximal voluntary contractions. We also hypothesized that if a spinal mechanism was involved, BLDs would be found under both reflexive and maximal conditions and strong correlations between these deficits would surface.

METHODS AND PROCEDURES

Participants

Seventeen males (age 25.5 ± 6.7 years, height 173.4 ± 7.6 cm, mass 71.0 ± 9.1 kg; mean ± SD) volunteered as participants and provided informed consent prior to taking part in the study. The participants had not experienced any injury to the lower extremities in recent years and refrained from any intense exercise for three days prior to data collection. Furthermore, none of the participants were following a rigorous training schedule that might have influenced their potential to exhibit a BLD. Moreover, all participants were naive to the purpose of the study and the anticipated findings. Approval of the study was obtained from the appropriate institutional human subjects review committee.

Experimental protocol

Reflexive force output and associated EMG data from selected muscles of the quadriceps femoris muscle group were obtained after inducing the myotatic reflex with a patellar tendon strike. The reflex was induced in each leg either separately (unilaterally) or simultaneously (bilaterally). Since pilot testing revealed a large variability across trials in reflexive force output, twelve trials were conducted for each condition in a counterbalanced, random order yielding a total of 36 trials. Reliability of the BLD phenomenon was assessed by repeating the reflex test after 7 to 10 days.

In addition to reflex data, maximal unilateral and bilateral knee extension force and associated EMG data were also recorded for 11 of the participants. These procedures were added
to assess if our participant pool displayed a BLD when generating a maximal voluntary contraction. As pilot testing revealed that maximal force output was less variable than reflexive force generation, only three trials for each condition were performed. A smaller number of trials and relatively long rest intervals also negated the effect of fatigue.

Reflexive force measurement

The participants were seated and secured by 4 nylon belts (at thigh, hip, chest and head) on a specially designed dynamometer as illustrated by Figure 1. A uniaxial force transducer, (Model 34, Sensotec, Columbus, OH) was placed against the distal end of each shin to measure reflexive force output. Each transducer was mounted on an adjustable bolt that was securely connected to a metal frame. In turn, the frame was cast in a block of concrete measuring 505 x 205 x 430 mm. To ensure the shin could press against the transducer without inducing any discomfort, the participant was fitted with a metal shin-plate designed to receive an iron rod that extended from the transducer. To standardize the initial conditions, each transducer was pressed against the shin by adjusting the mounting bolt so that a small force of 3 N was recorded while the subject was completely relaxed. The raw signal from each transducer was amplified by a transducer coupler (Type A, S72-25, Colbourn Instruments, Allentown, PA) with a gain of 266, and analyzed by an analog software package (Ariel Performance Analysis System (APAS), Ariel dynamics, Trabuco Canyon, CA). Data were sampled at 1000 Hz for a period of 2 seconds.

Two electromagnetically controlled reflex hammers were calibrated to strike the patellar tendon of each leg with a constant force across trials and with simultaneous contact in the bilateral condition. To achieve a constant impulse at impact, the hammers were released from a constant height by deactivating electromagnets that held the hammers in place. Since the
hammers were attached to a fixed axis of rotation via aluminum rods 30 cm in length, the hammers consistently struck the same place on the patellar tendon.

Insert Figure 1 about here

Before data collection commenced, 2-3 test trials were first performed in order to determine if the hammers struck each tendon simultaneously during the bilateral condition. This was accomplished by investigating the resulting force trace displayed by the APAS system. The initial sharp force displacement from the baseline was indicative of the time of hammer strike, since this was the result of passive force transfer (PFT) from the hammer impact rather than from reflexive force generation (Figure 2). The hammer strikes were considered simultaneous if the PFTs for both the right and left leg were within 1-2 ms of each other. If this were not the case, the hammers were slightly adjusted in height until synchronicity was obtained. Figure 2 illustrates a typical force trace. As mentioned, the initial portion of the curve (PFT) is caused by impact vibration, whereas the steep rise that follows (RFG: reflexive force generation) is a result of force generation via the myotatic reflex.

Insert Figure 2 about here

Throughout the testing session, the participants were prevented from seeing the hammer fall by a screen that was positioned approximately 0.5 m in front of them. This was to minimize any preparatory involvement from the central nervous system. Also, the hands remained placed on a pillow on the lap and this position remained constant for all trials; that is, the hand and arm posture was the same for both bilateral and unilateral conditions. Furthermore, the subjects were instructed to maintain a constant state of arousal and to not anticipate the hammer strike. The inter-trial interval was allowed to vary between 25 and 35 s to further protect against an anticipatory response.
Measurement of Maximal force Output

Unilateral and bilateral maximal isometric knee extensor force output (MVC) was measured for 11 participants. At the end of collecting reflexive force data on Day 1, the participants remained seated in the testing chair and an ankle strap was placed around each ankle after dismounting the force transducers and removing the shin plates. The straps were then connected to force transducers via cables (dashed lines in Figure 1) that were strung horizontally beneath the chair and securely fastened to the rear of the dynamometer framework. When the participant tried to forcefully extend the knee joints, the ankle straps and cable system maintained the quadriceps in isometric contraction and each force transducer monitored the force output. We did not measure torque output since we were only interested in relative differences between conditions within subjects and measuring the moment arms would have introduced another potential source of error. The moment arm from the knee joint center to the cable was kept constant by clamping each ankle strap in place and making sure no displacement occurred throughout the testing period.

Three MVCs were performed for each leg under unilateral and bilateral conditions after three warm-up sets. One set consisted of one right leg unilateral contraction, one left leg unilateral contraction, and one bilateral contraction, but not necessarily in that order. The order was predetermined for a particular subject and kept constant from set to set for both the warm-up sets and the maximal-effort sets. Across subjects, the test order was selected in a random, counterbalanced fashion.

For the first warm-up set, the participant was asked to produce what he perceived as 25% maximal effort, for the second set, 50% effort, and the third set, 90% effort (17). A 15 s rest interval was allowed between sets and conditions within each set. Maximal tests were conducted
90 s after the completion of the last warm-up trial, and the same (90 s) time interval was imposed between sets and conditions for the maximal effort contractions. Verbal encouragement was given during each MVC, which was maintained for approximately 3 s. Throughout the contractions, the hand and arm posture was the same for both bilateral and unilateral conditions, similar to that kept during the reflexive tests. Data were sampled at 1000 Hz for a period of 10 s.

**Measurement of electrical activity**

Bipolar surface EMG electrodes (Delsys, Boston, MA), consisting of two parallel silver bars, each 10 mm long, 1.0 mm wide, with a center-to-center interelectrode distance of 10 mm, were placed over the rectus femoris, vastus lateralis, and vastus medialis muscles of each leg. The bony prominence of the head of the left fibula was used to attach the ground electrode. Before placing the electrodes, the skin was shaved, cleansed with acetone, and abraded in order to reduce impedance between the skin and electrode. The raw signal was pre-amplified (1000 gain) at a fixed bandwidth of 20-450 Hz, full-wave rectified, and integrated (iEMG) to assess the activity of the quadriceps muscle group during the myotatic reflex and MVC tests. Data were sampled at 1000 Hz for a period of two seconds for reflexive force generation, and 10 seconds for maximal force generation using the APAS.

**Data reduction**

The APAS software was used to obtain the following variables. The procedures for determining each of these variables are outlined below:

- **Peak force**: Maximum recorded value on the force-time curve.
- **Time to peak force (TPF)**: Time from beginning of reflexive force generation to the peak force generated.
- **Rate of reflexive force generation (dF/dt)**: Peak force divided by the time to peak force.
• iEMG: The integrated area of EMG-time curve for each individual muscle monitored. The respective iEMGs for the vastus lateralis, vastus medialis, and rectus femoris were summed to obtain the total iEMG for each leg. For the reflexive force condition, the entire duration of the EMG response was integrated (from the onset to cessation of the EMG signal). For MVC condition, the EMG response corresponding to the last 250 ms of the plateau region of the force trace (signifying maximal force) was integrated.

• EMG duration (ED): Time from the onset to cessation of the EMG signal in the reflex condition.

• Pre-motor time (PT): Time from hammer strike (PFT) to onset of EMG in the reflex condition.

• Peak power frequency (PPF). Power spectral analysis was performed and the firing frequency at peak power output was noted.

**Bilateral Indices**

A Bilateral Index for force (BIF) (17) was calculated to express any relative difference in force output between unilateral and bilateral conditions for both the myotatic reflex tests and the MVC tests. The calculation performed was:

\[
BIF(\%) = \{100 \times \frac{(\text{right bilateral} + \text{left bilateral})}{(\text{right unilateral} + \text{left unilateral})}\}\} - 100
\]

Bilateral indices for each individual limb was calculated as:

\[
BI(\%) = [(\text{bilateral} ÷ \text{unilateral}) \times 100] - 100
\]

A negative BI indicated a bilateral deficit, and a positive BI, bilateral facilitation. Similar bilateral indices were also calculated for iEMG (BI_{EMG}), Peak Power Frequency (BI_{PPF}), pre-motor time (BI_{PMT}), and average rate of force development (BI_{dF/dt}).

**Analysis of results**
A paired sample t-test was used for the bilateral to unilateral comparison of means and a single sample t-test was used to test if the mean bilateral indices were significantly different from 0. A Pearson Product-Moment Correlation was employed to analyze the relationships between various parameters. Statistical significance was accepted at an alpha level of 0.05.

RESULTS

Reflexive contractions

There were no significant differences between Day 1 and Day 2 values of force or iEMG in bilateral and unilateral conditions for either right or left leg (Table 1). In addition, there were no significant differences in BI_F or BI_EMG between the two test days. Thus, all Day 1 and Day 2 values were pooled and further analysis of the data was performed using the combined data.

The coefficients of variation between the two days for BI_F and BI_EMG were 42 % and 73 %, respectively. Although these coefficients were relatively large, the BLDs were a consistent phenomenon and were significantly different from zero for both days (Table 1). All but one subject exhibited bilateral force deficit during both test days, but the individual not exhibiting BLD was not the same on each day. All but two individuals on Day 1 and three individuals on Day 2 demonstrated bilateral iEMG deficit; however, none of the individuals that did not demonstrate bilateral iEMG deficit in day 1 and day 2 were the same. A typical reflexive force and iEMG trace (right leg) for bilateral and unilateral conditions is shown in Figure 3.

Insert Figure 3 about here

The BI_F for combined right and left legs was -9.26 ± 1.19 % (P < 0.001) while the BI_EMG was –16.76 ± 4.69% (P < 0.005). Additionally, individual muscles of quadriceps muscle group, except the rectus femoris of right and left legs, also demonstrated significantly (P < 0.05) lower
iEMG in bilateral condition than in unilateral condition. The correlation between $BIF$ and $BI_{EMG}$ was 0.78 ($P < 0.002$) for combined right and left legs.

**Insert table 1 about here**

Significant BLDs in force, iEMG and dF/dt were also observed in each individual limb separately, with no significant inter-limb differences (Table 2). The correlation between $BIF$ and $BI_{EMG}$ was $r = 0.64$ ($P < .01$) for the right leg and $r = 0.85$ ($P < .001$) for the left leg.

Pre-motor times were significantly shorter in unilateral than in bilateral conditions for each leg (Table 2). The bilateral index in pre-motor time ($BI_{PT}$) for combined right and left legs was $1.46 \pm 0.34 \%$ ($P < 0.003$).

**Insert table 2 about here**

Table 2 also shows the effect of bilateral contractions on the peak power frequency (PPF) of the EMG signal. Power spectral analysis of the EMG revealed significantly lower values for the PPF during bilateral condition for both the right and left leg.

The average rate of force development was significantly higher in the unilateral than in bilateral condition for both right and left legs (Table 2). However, the time to peak force for each leg did not differ between conditions. Also, there was no significant difference in iEMG duration between bilateral and unilateral conditions in the right leg ($78.5 \pm 10.0$ ms vs. $77.9 \pm 8.9$ ms, respectively) and in the left leg ($73.9 \pm 5.4$ vs. $75.8 \pm 5.2$ ms, respectively).

**Reliability of the BLD elicited by reflexive contractions**

Reliability of BLD in force and iEMG was established by testing the subjects twice, separated by a one-week interval. Since more than 93% of the subjects consistently exhibited bilateral force deficit and more than 80% bilateral iEMG deficit during both test days, the BLDs in force and iEMG are a consistent phenomenon. However, there were no significant correlations
in $B_{IF}$ or $B_{IEMG}$ between the two test days (large coefficients of variation). The lack of significant correlation was due to the large day-to-day variability of the BLD, rather than due to the presence or absence of it.

Maximal voluntary isometric muscular contractions

The data for the maximal voluntary isometric contractions is presented in Table 3. No significant differences were observed in any of the variables between bilateral and unilateral conditions. Consequently, no significant bilateral deficit or facilitation was displayed. Analysis of iEMGs and PPFs of individual muscles of the quadriceps muscle group also did not yield any significant differences between bilateral and unilateral conditions for either leg.

DISCUSSION

The primary goal of this investigation was to determine if the BLD phenomenon occurs during myotatic reflexes induced by a patellar tendon tap, and if the magnitude of any such BLD displays a relationship to the BLD that arises under the condition of maximal voluntary activation. It was reasoned that expression of a BLD under reflexive conditions could indicate the existence of cross-inhibitory neural pathways at the level of the spinal cord since evidence exists (3, 5) to suggest that the supraspinal centers would not have time to influence the force development under such conditions. Our results indicate that a BLD was indeed present when reflexive force output was measured after initiating the myotatic reflex in both legs simultaneously. Furthermore, the force decrement (9.3 %) in the bilateral condition as compared to the unilateral condition was in line with the findings (3-25 %) of previous work (1) that has typically employed maximal voluntary contractions. Moreover, the decline in force output was paralleled by a 16.8 % decrease in iEMG of the muscles tested, suggesting that the underlying mechanism was of a neural origin. Consequently, it is tempting to speculate that the presence of
the BLD under the condition of maximal activation may be, at least partially, mediated by the segmental neuronal circuitry of the spinal cord. However, similar findings were not evident when eleven of our participants performed maximal isometric knee extensions. No differences in force output or iEMG existed between bilateral and unilateral conditions. This is in agreement with some studies that used isometric knee extensions as a test modality (10, 18, 34) but not with others (22, 33, 41). It is difficult, therefore, to extrapolate the implications of the reflex data to the condition of maximal voluntary activation. We hypothesized that BLDs would be found under both reflexive and maximal conditions and that strong correlations between these deficits would surface if a spinal mechanism were also influential in the maximal condition. Because our data do not support this hypothesis, we cannot present any evidence to argue that the BLD demonstrated by previous investigations using maximal voluntary contractions might be accounted for by an inhibitory mechanism that resides at the level of the spinal cord.

It is suggested, however, that the notion of the segmental neuronal circuitry playing an inhibitory role not be discounted. Since the excitability of the neurons involved in the reflex arc can be modulated by supraspinal input (4), it is possible that such a mechanism might be overcome by commands from the higher centers, especially when the motor unit recruitment patterns are relatively simple as in isometric knee extensions. In other types of contractions, though, a spinal inhibitory mechanism may be of significance. Contrary to the work involving isometric contractions, studies involving more complex movement patterns such as dynamic, multi-joint tasks (34-39, 43), generally find a BLD rather than not. If a spinal inhibitory mechanism does have the potential to mediate the BLD, the intensity of such inhibition might be greater during dynamic movements as previous work (7, 23) indicates that afferent input from muscle spindles can elicit a cross-inhibitory effect on homonymous muscles. Since the nuclear
bag fibers of the spindle are primarily activated under dynamic conditions, one might speculate that spinal mediation of the BLD is more influential when maximum contractions are performed during dynamic, multi-joint movements. Consequently, if we had tested for the BLD under maximal conditions using a task such as a concentric leg press, some support for our hypotheses may have been obtained.

Regardless of the lack of support for our hypothesis, however, our finding that the BLD is expressed during reflexively evoked contractions expands the knowledge base pertaining to inter-limb interactions. Mutual inhibition of homonymous muscles under reflex conditions may be possible due to activation of reciprocal inhibitory circuitry similar to that responsible for the crossed-extensor reflex (23). Usually, this reflex is triggered by cutaneous receptors when a noxious stimulus is sensed. Typically, the response is to withdraw the affected limb from the stimulus site via flexion, whilst the contralateral limb is extended to provide postural support. This involves inhibiting the homonymous muscle groups and stimulating the antagonist muscle groups of the contralateral limb. Lagasse (23) provided evidence for a similar reflex to be elicited by afferent input from muscle spindles. Participants performed maximal bilateral isometric contractions of the quadriceps during which a sudden, unilateral stretch of the muscle group was imposed. Changes in force output of ipsilateral and contralateral legs were monitored. A significant increase in force for the ipsilateral leg resulted, whereas the contralateral side displayed a decrease. Although electromyographic data that might have supported a neural mechanism were not obtained, Lagasse (23) concluded that a superimposed muscle stretch upon already contracting muscles triggers a reflex similar to the crossed-extensor reflex. However, because the latencies of the ipsilateral and contralateral stretch reflexes were relatively long (500 and 1000 ms, respectively) the possibility of modulatory input from the supraspinal centers
Corroborating evidence, though, to support the existence of neural pathways that conduct afferent impulses from muscle spindles to the contralateral homonymous muscles has been provided by Delwaide and Pepin (7).

In the current study, subjects who demonstrated a strong reflex (as indicated by a large reflexive force output) displayed evidence to support the possibility that a crossed-reflex had been initiated. A withdrawal of the contralateral leg during the unilateral condition was indicated by a deflection of the force trace below the preset force of 3N. It is possible, however, that such an effect may have been simply artifact resulting from the body being pushed back by the reflexive force developed by the involved limb. Notwithstanding this possibility, the motoneuronal pools associated with quadriceps muscles may have received two opposing inputs in the bilateral condition: an excitatory input from the ipsilateral Ia afferents, and an indirect inhibitory input from the contralateral Ia afferents simultaneously reducing the force outputs of contralateral quadriceps muscles. The observed BLD might then be accounted for by mutual inhibitory inputs originating from the contralateral sides.

It may also be postulated that the expression of BLD is due to the larger involvement of antagonistic muscle groups during bilateral muscular action compared to unilateral muscular action (co-contraction of agonist and antagonist muscle groups). While we did not monitor the electrical activity of antagonistic muscles, our data do not support this notion since the iEMG/force ratios were similar during reflexive muscular action of right (0.59 ± 0.06 µVsec·N⁻¹ and 0.61 ± 0.05 µVsec·N⁻¹) and left (0.45 ± 0.04 µVsec·N⁻¹ and 0.52 ± 0.03 µVsec·N⁻¹) legs during bilateral and unilateral conditions, respectively. The same was also true for the MVC condition (0.36 ± 0.05 µVsec·N⁻¹ vs. 0.37 ± 0.04 µVsec·N⁻¹ for the right leg; 0.36 ± 0.05 µVsec·N⁻¹ vs. 0.38 ± 0.04 µVsec·N⁻¹ for the left leg). Similar iEMG/force ratios between the
conditions suggest that the co-contraction of the antagonistic muscle groups was either the same or was not present.

In addition to the standard BLD calculated by combining the force output from both legs, each leg also independently demonstrated a similar BI_F (10%) supporting the possibility of equal mutual inhibition. Since all subjects displayed right leg dominance (determined by leg preference for ball kicking), no difference in inhibition existed between the dominant and non-dominant legs. This is in line with the work of Owings and Grabiner (33) who investigated the BLD in relation to the lower limbs, but in contrast to most studies that focused upon the upper limbs (15, 27-30). Generally, there has been a greater reduction in force on the dominant side when maximal bilateral contractions were performed with the upper limbs. Perhaps this is the result of an attempt to equate the absolute force output of each limb for the purpose of motor control.

Numerous investigators have reported a concomitant, but not necessarily parallel, reduction in force and iEMG during maximal bilateral, as compared to unilateral, contractions (22, 27, 29, 41, 43) while others (17, 34,) could not demonstrate any such relationship. Ohtsuki (30, 31), on the other hand, demonstrated a parallel reduction in force and EMG with a moderately strong direct linear relationship between them. In the present study, as well as obtaining a strong relationship between force and iEMG during reflexive muscular contractions for the right (r = 0.83) and left (r = 0.94) legs, a moderately strong relationship was observed between BI_F and BI_{EMG} for each leg (r = .64, right; r = .85, left; P < 0.01). Such a finding bolsters the postulation that a neural inhibitory mechanism was responsible for the depression of reflexive force output under bilateral conditions. Moreover, it is likely that the origin of this inhibition resides at the level of the spinal cord since the force developed was associated with the stretch reflex. The latency for this reflex is much shorter than any voluntary activity (3, 5);
hence, the force developed should have been minimally, if at all, influenced by the supraspinal centers.

Regardless of the origin of inhibition, several researchers have suggested that the higher threshold or fast motor units are preferentially inhibited when a BLD has been demonstrated in maximal voluntary contractions (21, 22, 27, 41), while others suggested that the BLD is due to the selective inhibition of slow twitch motor units (35, 36). One technique that has been used to indirectly estimate the relative involvement of fast versus slow twitch motor units between different conditions is subjecting EMG data to a power spectral analysis. Recent studies (22, 27, 34) suggest that a shift in the mean power frequency to lower values is indicative of a greater relative contribution of slow twitch fibers to the force output. We compared the peak power frequency between the bilateral and unilateral conditions for each leg and found a significantly lower value in the bilateral condition for both limbs (Table 2). Consequently, under reflexive conditions, fast twitch motor unit inhibition might contribute more to the BLD than inhibition of the slow twitch motor units. Such a postulation is congruent with Henneman’s size principle, which argues that motor units are recruited and de-recruited in order of their size (14). Specifically, motor unit recruitment occurs in the order of small (slow) to large (fast) motor units and de-recruitment takes place in the reverse order. This recruitment pattern also prevails during reflexive muscular contractions (3, 8, 38).

Further support of the notion that the faster motor units might be preferentially inhibited is provided by the difference in pre-motor time (time from the hammer strike to the first sign of electrical activity) between the two conditions. Since faster motor units are innervated by larger diameter axons that conduct impulses at higher velocities, it is reasonable to expect an increase in pre-motor time if these motor units are selectively inhibited. In the present study, pre-motor
times were significantly longer for both limbs in bilateral condition compared to unilateral condition (Table 2) providing additional support for preferential inhibition of fast twitch motor units during reflexive bilateral contractions. Furthermore, the rate of change in force was significantly lower during bilateral than during unilateral reflexive contractions (Table 2), also indicating that fast twitch motor units may have been preferentially inhibited.

In summary, our findings show that the BLD is also expressed during reflexively evoked contractions and might be accounted for by inhibitory neural circuitry that operates at the level of the spinal cord. It is also feasible that afferent impulses from muscle spindles are the source of potential inhibitory pathways that enable mutual inhibition of homonymous muscles during reflexive bilateral muscular actions. However, our data do not reveal that such a mechanism might account for the BLD that can occur under the condition of maximal voluntary activation.
REFERENCES


Figure legends:

Figure 1. Dynamometer arrangement for the measurement of reflexive force output.

Figure 2. Typical force and EMG (vastus medialis) records resulting from a patellar tendon strike of the right leg. PT = Premotor time; TPF = Time to peak force; ED = EMG duration; PFT = Passive force transfer; RFG = Reflexive force generation.

Figure 3. Typical force and EMG records resulting from patellar tendon strike of the right leg in bilateral and unilateral conditions. BL = Bilateral; UL = Unilateral.
Table 1. Day 1 to day 2 variation of force output, iEMG, and bilateral indices for force (BIF) and iEMG (BIEMG) during reflex unilateral and bilateral isometric extension of right leg (RL) and left leg (LL).

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<td>Bilateral</td>
<td>Unilateral</td>
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<td>RL force, (N)</td>
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<td>± 4.4 ± 4.6</td>
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<td>19.1 25.9</td>
<td>18.9† 22.2</td>
</tr>
<tr>
<td></td>
<td>± 4.3 ± 5.6</td>
<td>± 3.4 ± 3.4</td>
</tr>
<tr>
<td>BIF, %</td>
<td>-8.89 ± 1.4*</td>
<td>-9.65 ± 1.7*</td>
</tr>
<tr>
<td>BIEMG, %</td>
<td>-15.7 ± 7.7*</td>
<td>-14.0 ± 6.8*</td>
</tr>
</tbody>
</table>

Values are Means ± standard error of the mean.
† Value in bilateral condition is significantly smaller (P < 0.05) than the value in unilateral condition.
* Value is significantly smaller than 0 (P < 0.05).
Table 2. Force, iEMG, peak power frequency (PPF), premotor time (PT), average rate of force development (dF/dt) and bilateral index (BI) during bilateral and unilateral leg extensions induced by myotatic stretch reflex in individual limbs. Two-day combined data for each individual limb.

<table>
<thead>
<tr>
<th></th>
<th>Right leg</th>
<th></th>
<th>Left leg</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Unilateral</td>
<td>Bilateral</td>
<td>BI, %</td>
<td>Unilateral</td>
</tr>
<tr>
<td>Force, N</td>
<td>36.1 ± 4.6</td>
<td>33.0 ± 4.4†</td>
<td>-10.0 ± 1.8*</td>
<td>34.3 ± 4.7</td>
</tr>
<tr>
<td>iEMG, µV·sec</td>
<td>23.2 ± 2.8</td>
<td>20.5 ± 2.7†</td>
<td>-11.7 ± 4.2*</td>
<td>20.0 ± 3.4</td>
</tr>
<tr>
<td>PPF, Hz</td>
<td>47.9 ± 1.6</td>
<td>46.5 ± 1.6†</td>
<td>-2.7 ± 1.1*</td>
<td>49.6 ± 1.8</td>
</tr>
<tr>
<td>PT, ms</td>
<td>17.4 ± 0.4</td>
<td>17.7 ± 0.4†</td>
<td>1.28 ± 0.5*</td>
<td>18.8 ± 0.5</td>
</tr>
<tr>
<td>dF/dt, N·sec⁻¹</td>
<td>0.38 ± 0.05</td>
<td>0.35 ± 0.05†</td>
<td>-9.1 ± 1.9*</td>
<td>0.37 ± 0.05</td>
</tr>
</tbody>
</table>

Values are Means ± standard error of the mean.

† Value in bilateral condition is significantly different (P < 0.05) from the value in unilateral condition.

* Value is significantly different from 0 (P < 0.05).
Table 3. Force, iEMG and peak power frequency (PPF) values for maximal voluntary isometric bilateral and unilateral leg extensions.

<table>
<thead>
<tr>
<th></th>
<th>Right leg</th>
<th>Left leg</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Unilateral</td>
<td>Bilateral</td>
</tr>
<tr>
<td>Force, N</td>
<td>549.4 ± 48.5</td>
<td>558.3 ± 54.7</td>
</tr>
<tr>
<td>iEMG, µV·sec</td>
<td>217.5 ± 26.7</td>
<td>211.3 ± 31.8</td>
</tr>
<tr>
<td>PPF, Hz</td>
<td>56.9 ± 4.2</td>
<td>55.9 ± 3.8</td>
</tr>
</tbody>
</table>

Values are Means ± standard error of the mean.
Fig 1. Dynamometer arrangement for the measurement of reflexive force output.
Fig 2. Typical force and EMG (vastus medialis) records resulting from a patellar tendon strike of the right leg. PT = Premotor time; TPF = Time to peak force; ED = EMG duration; PFT = Passive force transfer; RFG = Reflexive force generation.
Figure 3. Typical force and EMG records resulting from patellar tendon strike of the right leg in unilateral and bilateral conditions. BL = Bilateral; UL = Unilateral.