Exp Brain Res (2008) 187:129–138
DOI 10.1007/s00221-008-1288-x

RESEARCH ARTICLE

Lower limb force production and bilateral force asymmetries are based on sense of effort

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Received: 5 October 2007 / Accepted: 14 January 2008 / Published online: 5 February 2008

Abstract Previous research suggests that individuals use a sense of effort, more than proprioceptive feedback, to gauge force production in their upper limbs. We have adopted an isometric force matching task to determine if force asymmetry between lower limbs during bilateral force production results from a neural mechanism related to sense of effort. We hypothesized that subjects attempting to produce equal lower limb forces would generate equal percentages of their bilateral maximum voluntary strength rather than equal absolute limb forces. Ten subjects performed isometric lower limb extensions on an exercise machine. Subjects attempted to match forces in their lower limbs at three different submaximal levels (20, 40, and 60% of their weaker limb peak force during bilateral maximum voluntary contraction). Subjects received visual feedback of only the target and stronger limb force. Results showed that subjects consistently produced less force in their weaker limb during all force matching levels when normalized to their unilateral maximum voluntary contraction force (ANOVAs 20% $P = 0.0473$, 40% $P = 0.0012$, 60% $P = 0.0007$). As predicted by our hypothesis, normalizing force magnitudes by bilateral maximum voluntary contraction forces revealed no significant differences between limbs at all force levels (ANOVA $P = 0.8490$). Regardless of whether humans produce maximal or submaximal forces, limb force asymmetry appears to be related to neural factors rather than differences in mechanical capabilities between the limbs. Our findings have implications for bilateral asymmetries during movement in healthy and neurologically impaired populations.

Keywords Isometric contraction · Muscle · Strength

Introduction

Humans can control force production in their limbs via two main mechanisms. Muscle force sensation generated centrally from feedforward neural signals is generally termed sense of effort. It originates from an individual's perception of the descending motor command (McCloskey et al. 1974). This neural information has also been described as corollary discharge (Sperry 1950). An alternative mechanism generated peripherally from feedback neural signals (ascending sensory information) is generally termed sense of force or tension (Roland and Ladegaard-Pedersen 1977). The peripheral receptors, such as Golgi tendon organs and cutaneous receptors, can provide information about muscle tension and pressure in order to gauge the sense of force. Studies eliciting the tonic vibration reflex have provided evidence that the sense of force can operate in isolation without a sense of effort (McCloskey et al. 1974). Many studies have examined various upper limb motor tasks in

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an attempt to clarify when and how humans use these two mechanisms for activating their muscles.

Isometric force production is a simple motor task that has been previously used to examine how individuals estimate limb forces. In one variation, subjects first produce a target isometric force level in one of their two limbs (the reference limb), usually with visual force feedback. They are then asked to match the same force in the contralateral limb (the matching limb) without force feedback. Studies on healthy subjects have found that humans are able to match absolute forces between upper limbs fairly well (Carson et al. 2002). If the force capabilities of one limb are altered through unilateral fatigue of either the elbow extensors (Carson et al. 2002) or the elbow flexors (Jones and Hunter 1983; Proske et al. 2004), individuals produce less force in that limb during isometric force matching. Regardless of which limb (fatigued or unfatigued) was the reference limb, errors are consistently in this direction of the fatigued limb generating less force (Weerakkody et al. 2003; Proske et al. 2004). Carson et al. (2002) demonstrated that the end forces produced by each upper limb were equal percentages of each limb's maximum voluntary strength rather than equal absolute force levels. These studies suggest that humans use a sense of effort originating from a corollary discharge of the motor command to the muscles (Sperry 1950; McCloskey et al. 1974; Gandevia and McCloskey 1977), rather than absolute reliance on proprioceptive feedback, to gauge force production. Because the task of producing equal forces is prevalent in the upper limbs (i.e. holding a box or tray), researchers have focused their attention on the way individuals estimate force production in their upper limbs.

Symmetric lower limb forces are also necessary for many activities of daily living such as quiet standing, sitting and rising from a chair, or lifting a box from the floor to a shelf. In healthy individuals, a force asymmetry exists between limbs during a two-legged vertical jump (Bobbert et al. 2006; Newton et al. 2006). The bilateral asymmetry in vertical jumps is present even when there are no lower extremity anthropometric differences between limbs (Lawson et al. 2006). The prevalence of this asymmetry in healthy bilateral force production of the lower limbs in tasks other than the vertical jump is not reported in the literature. Several studies define the existence of a lower limb bilateral deficit, or a reduction in maximal voluntary strength during bilateral contractions compared with unilateral contracts, during bilateral tasks such as extensions at the knee and leg extensions (Schantz et al. 1989; Taniguchi 1997; Janzen et al. 2006). These studies do not report individual limb forces during bilateral trials. Comparing the individual limb forces between combinations of unilateral, bilateral, maximal and submaximal trials will provide insight into whether the resulting force asymmetries are more related to sense of effort or sense of force.

We have adopted the isometric force matching task used by Carson et al. (2002) to study normal force asymmetry in the lower limbs of humans. The goal of this study was to determine if force asymmetry during bilateral force production results from a neural mechanism related to sense of effort. We hypothesized that subjects attempting to produce equal forces in their lower limbs would generate equal percentages of their bilateral maximum voluntary strength rather than equal absolute limb forces. If true, this could provide critical insight into the neural origins of lower limb force asymmetry during movement.

Methods

Subjects

Twelve neurologically intact subjects (seven males and five females; age: 25 ± 3.0 years, mean ± SD) gave written informed consent and participated in this study. The Institutional Review Board for Human Subject Research at the University of Michigan Medical School approved the protocol.

Experimental design

Subjects performed isometric lower limb extensions on a leg press exercise machine (Fig. 1). Subjects reclined on the exercise machine and placed their feet on a vertical dual force platform (Model Dual Accu-Gait, AMTI, Watertown, MA, USA) and their shoulders firmly braced. The device was locked with a mechanical stop such that each subjects' lower limbs were positioned in the middle of the range of motion used for a full lower limb extension (i.e. half-way between the sled position of 90° knee flexion and full knee extension). Subjects' feet were positioned hip width apart on the force platform and stabilized with foot straps to minimize movement during the experiment. For all trials, the subjects' lower limbs remained in the same posture (i.e. both feet are in the foot straps during unilateral as well as bilateral conditions). Therefore, regardless of the condition, all the data were collected with the same body position, same joint angles, and same muscle lengths.

All subjects performed a pre-test consisting of three bilateral isometric maximum voluntary contraction (MVC) trials. We verbally encouraged subjects to push as hard as they could with both feet and allowed them to rest 2–3 min between trials. Subjects were excluded from the study if there was less than 10% difference between the maximum forces recorded at their left and right feet during each trial

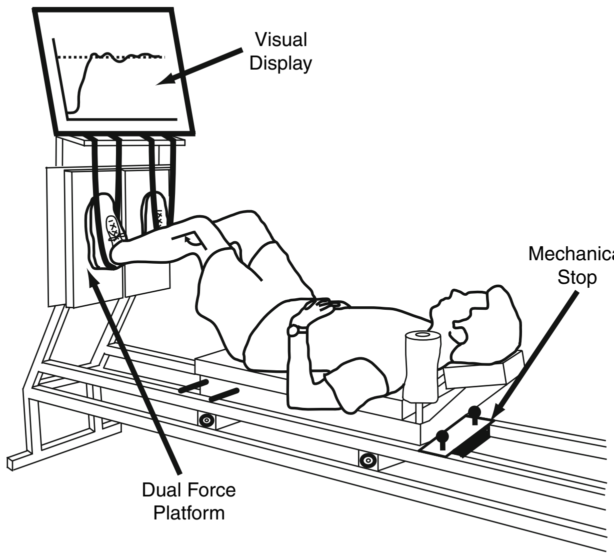

Fig. 1 Leg press exercise machine in use by a neurologically intact subject. A dual force platform measured individual lower limb forces. A mechanical stop prevented movement and allowed for isometric lower limb extensions. For the force matching conditions, subjects received visual feedback of the target force (*dashed line*) and the force produced by the stronger limb (*black line*)

(2 of 12 subjects, both males). This criterion was chosen because the purpose of the study was to determine if discrepancy between limbs during bilateral voluntary contractions could be explained by sense of effort. Ten subjects (five male, five female) possessed a greater than 10% force discrepancy in bilateral foot forces and completed the remainder of the study.

After completing the initial screening of MVC trials, we placed electromyography (EMG) electrodes on non-excluded subjects. Approximately 15 min later, subjects returned to the leg press machine for testing. We assessed subjects' isometric strength three trials each of bilateral, left limb, and right limb MVCs. The order of the nine trials was randomized. We verbally encouraged subjects to push as hard as possible with either one foot or both feet throughout each 5 s collection. During unilateral trials, subjects' resting limb remained in the same position as during bilateral trials (i.e. foot in the footstrap against the vertical force platform). Subjects rested 2–3 min between each MVC trial. When all nine trials were completed, we analyzed data from the bilateral MVC condition to identify the stronger limb. We determined the stronger limb as the limb that produced the higher peak force during the bilateral MVC condition.

After another 10 min rest period, we assessed subjects' ability to match forces in their lower limbs with nine trials of force matching tasks. Subjects exerted a force equal to 20, 40, and 60% of the peak force from the weaker limb during the bilateral MVC condition. Subjects received visual feedback of the target force level and the amount of force applied by the stronger limb throughout each trial. When subjects reached the target force level in the stronger limb, we instructed them to begin applying force with the weaker limb. No feedback was given to indicate the force applied by the weaker limb. We instructed subjects to verbally signal to the experimenter once they believed they had matched forces in both limbs. Upon this verbal cue, subjects held the isometric contractions for 3 s and then were told to relax. Subjects performed three trials at each of the three force levels in a randomized order with 2–3 min rest between each trial. Subjects were not told the study's purpose or which limb produced more force during the bilateral MVC condition. We instructed subjects using the identifiers "right limb" and "left limb" rather than "stronger limb" and "weaker limb" as described above.

Data acquisition and analysis

We recorded individual foot forces at 1,000 Hz from the dual force platform mounted to the vertical footplate (Fig. 1). Each limb's MVC, both unilateral and bilateral, were determined as the maximum force measured within the three trials of each condition (Jones and Hunter 1983; Proske et al. 2004). For the three different levels of force matching, we calculated the average force applied by each limb for 3 s after the verbal cue was signaled. We normalized foot forces to each limbs' unilateral MVC force. In other words, the force recorded during each condition was divided by the force recorded during that limbs' unilateral MVC force. This analysis can provide insight into whether or not the lower limb force asymmetry might be due to musculoskeletal differences (e.g. a fundamental difference in muscle strength between limbs). In a separate analysis, we normalized force to each limbs' bilateral MVC force to detect any bilateral facilitation or deficit in the subjects.

We recorded surface electromyography (EMG) at 1,000 Hz (Delsys Inc., Boston, MA, USA) from four lower limb muscles on each limb (vastus lateralis: VL, vastus medialis: VM, medial hamstrings: MH, and gluteus maximus: GM) using bipolar surface electrodes. To examine changes in EMG amplitude between trials, we calculated root mean squared (RMS) EMG values for each subject during a 1 s period in the middle of each trial (Tracy and Enoka 2006). EMG data were high pass filtered (second-order Butterworth filter, cutoff frequency 20 Hz) and rectified before RMS EMG values were computed. For each muscle, RMS EMG values were normalized to the highest RMS EMG value recorded during any of the unilateral MVC trials.

From the unilateral and bilateral MVC force values, we calculated a bilateral index for each subject using the following equation (Koh et al. 1993; Taniguchi 1998; McLean et al. 2006):

$$\mathrm{BI}\ (\%\ ) = 100\left(\frac{\text{Left Bilateral} + \text{Right Bilateral}}{\text{Left Unilateral} + \text{Right Unilateral}}\right) - 100 \quad (1)$$

where left and right bilateral indicate the respective MVC forces during the isometric bilateral MVC condition, and left and right unilateral indicate the respective MVC forces during the unilateral MVC condition for each limb. A bilateral index less than zero indicated that the total bilateral force was less than the sum of the unilateral forces (i.e. bilateral deficit), whereas a bilateral index of greater than zero indicated that the total bilateral force was greater than the sum of the unilateral forces (i.e. bilateral facilitation).

For MVC trials, we used a repeated measures two-way ANOVA (limb by condition) to test for differences between peak force measured during the bilateral and unilateral MVC conditions, as well for interaction effects (JMP IN software, SAS Institute, Inc., Cary, NC, USA). For submaximal force matching trials, we used separate repeated measures two-way ANOVAs (limb by force level) to test for differences in force normalized to unilateral MVC, force normalized to bilateral MVC, and RMS EMG, as well as interaction effects. When interaction effects were significant, we ran separate ANOVAs on each limb, condition, and force level. When ANOVAs indicated significance ($P < 0.05$), we used Tukey–Kramer Honestly Significant Difference (THSD) post hoc tests to determine differences between limbs and force levels ($P < 0.05$). Post hoc power analyses were carried out where appropriate.

Results

MVC trials showed significant differences in force magnitude between limbs and conditions (ANOVA $P < 0.0001$, limbs $P = 0.0043$, conditions $P < 0.0001$) (Table 1; Fig. 2). There was also a significant interaction effect between limbs and conditions (ANOVA $P = 0.0394$). During the bilateral MVC condition, subjects produced an average peak force of 1143 N ± 130 N (mean ± SEM) in the stronger limb and 904 N ± 111 N in the weaker limb. Peak forces produced in the weaker limb were significantly lower than in the stronger limb (separate ANOVA $P < 0.0001$). A difference in peak forces between limbs for the bilateral MVC condition was expected because this was the criteria for selection into the study. Peak force averages produced during the unilateral MVC trials of 1625 N ± 180 N and 1582 N ± 157 N, respectively, for the stronger and weaker limb, showed no significant differences (separate ANOVA $P = 0.3832$). All subjects demonstrated less peak force during the bilateral MVC condition when compared to the unilateral MVC condition for each limb (separate ANOVA $P < 0.0001$). These data resulted in a bilateral index of −35.3% ± 7.1%, indicating a bilateral deficit.

Example data from one subject attempting to produce equal forces in her lower limbs show the general trend for

Table 1 Summary of main and interaction effects of repeated measures ANOVA of peak force recorded during unilateral and bilateral MVC trials

	df	*F*	*P*
Two-way ANOVA (limb by condition)			
Effect of limb	(1, 27)	9.73	0.0043
Effect of condition	(1, 27)	164.39	<0.0001
Limb × condition	(1, 27)	4.69	0.0394
Separate ANOVAs			
Effect of limb			
Unilateral MVC	(1, 9)	0.84	0.3832
Bilateral MVC	(1, 9)	72.98	<0.0001
Effect of condition			
Weaker limb	(1, 9)	97.37	<0.0001
Stronger limb	(1, 9)	43.81	<0.0001

Limb: weaker/stronger, condition: unilateral/bilateral MVC, *df* degrees of freedom

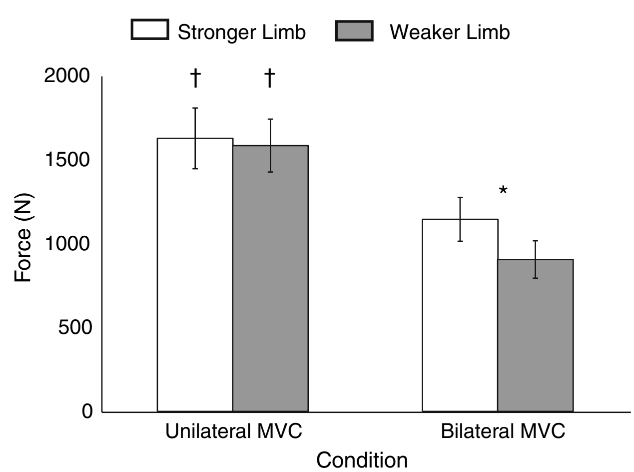

Fig. 2 Average peak force recorded during the bilateral and unilateral MVC conditions for all subjects. *White columns* represent average peak forces recorded in the stronger limb and *gray columns* represent average peak forces recorded in the weaker limb. The stronger limb produced significantly more force than the weaker limb during the bilateral MVC condition (ANOVA *: $P < 0.0001$). Forces during the unilateral MVC conditions were significantly higher than the bilateral MVC condition for each limb (ANOVA †: $P < 0.0001$). *Error bars* are the standard error of the mean

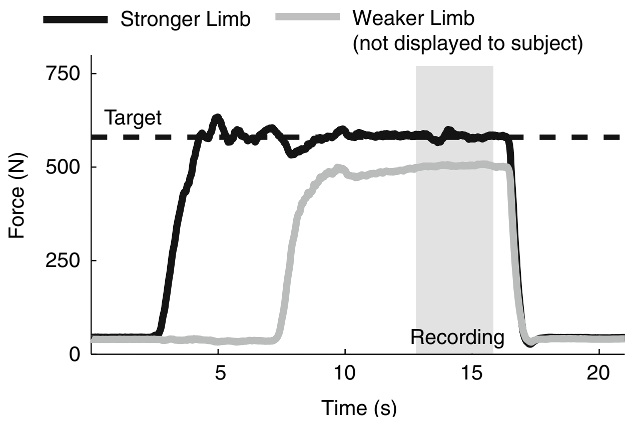

Fig. 3 Example plot of foot forces as a function of time during a 60% force matching trial for one subject. The *dashed line* represents force level target. The *black trace* represents stronger limb force and the *gray trace* represents weaker limb force. Weaker limb force profiles were not displayed to subjects at any time. *Gray shading* indicates the period over which data was recorded and analyzed. The start of recording was determined by a verbal cue from the subject indicating that they believed the forces in both limbs were equal

all subjects during the submaximal force matching task (Fig. 3). During this trial the target force equaled 60% of the maximum force recorded on the weaker limb during the bilateral MVC condition. The subject was able to match the force of her stronger limb to the target force with visual feedback but was not able to accurately produce equal forces between limbs. The subject produced significantly less force in her weaker limb. When normalizing average force magnitude by unilateral MVC force, there were significant differences between limbs and force level (ANOVA $P < 0.0001$, limbs $P < 0.0001$, force level $P < 0.0001$). There was also a significant interaction effect between limbs and force level (ANOVA $P = 0.0059$). When normalizing average force magnitude by unilateral MVC force, subjects consistently produced less force in their weaker limb at all force levels (separate ANOVAs 20% $P = 0.0473$, 40% $P = 0.0012$, 60% $P = 0.0007$) (Table 2; Fig. 4a). When normalizing average force magnitude by bilateral MVC force, there were significant differences between force levels but not between limbs at any of the three force levels (ANOVA $P < 0.0001$, force levels $P < 0.0001$, limbs $P = 0.8490$). There was no significant interaction effect when average force magnitude was normalized to bilateral MVC force ($P = 0.2263$) (Fig. 4b).

Lower limb EMG analysis during MVC trials revealed significant differences in normalized RMS EMG between conditions and limbs for vastus medialis (ANOVA $P < 0.0001$, conditions $P < 0.0001$, limbs $P = 0.0455$) (Table 3). EMG analysis showed significant differences between conditions but not limbs for vastus lateralis (ANOVA $P = 0.0013$, conditions $P < 0.0001$, limbs $P = 0.2468$), medial hamstrings (ANOVA $P < 0.0001$, conditions $P < 0.0001$, limbs $P = 0.1649$), and gluteus maximus (ANOVA $P < 0.0001$, conditions $P < 0.0001$, limbs $P = 0.1129$) (Fig. 5). There was a significant interaction effect for vastus medialis ($P = 0.0269$) and gluteus maximus ($P = 0.0251$) but not for vastus lateralis ($P = 0.1136$) or medial hamstrings ($P = 0.3166$). Comparing muscle activation of the stronger limb between the unilateral and bilateral MVC conditions showed significantly lower normalized RMS EMG in the bilateral condition for vastus lateralis (THSD $P < 0.05$), vastus medialis (separate ANOVA $P = 0.0135$), and medial hamstrings (THSD $P < 0.05$). Comparing muscle activation of the weaker limb during the unilateral MVC condition to the bilateral MVC condition showed significantly lower normalized RMS EMG in the bilateral condition for vastus lateralis (THSD $P < 0.05$), vastus medialis (separate ANOVA $P < 0.0001$) medial hamstrings (THSD $P < 0.05$), and gluteus maximus (separate ANOVA $P < 0.0001$). When comparing RMS EMG of the stronger leg to the weaker leg during the bilateral MVC condition, there was a significant decrease in RMS EMG of the weaker leg in the vastus medialis (separate ANOVA

Table 2 Summary of main and interaction effects of repeated measures ANOVA of normalized average force during three submaximal force matching conditions

	df	Force as % unilateral MVC		Force as % bilateral MVC	
		F	*P*	*F*	*P*
Two-way ANOVA (limb by force level)					
Effect of limb	(1, 45)	35.04	<0.0001	0.037	0.8490
Effect of force level	(2, 45)	214.71	<0.0001	476.33	<0.0001
Limb × force level	(2, 45)	5.78	0.0059	1.53	0.2263
Separate ANOVA					
Effect of limb					
20% Force level	(1, 9)	5.27	0.0473		
40% Force level	(1, 9)	21.58	0.0012		
60% Force level	(1, 9)	25.65	0.0007		

Limb: weaker/stronger, force level: 20/40/60% force matching level, *df* degrees of freedom

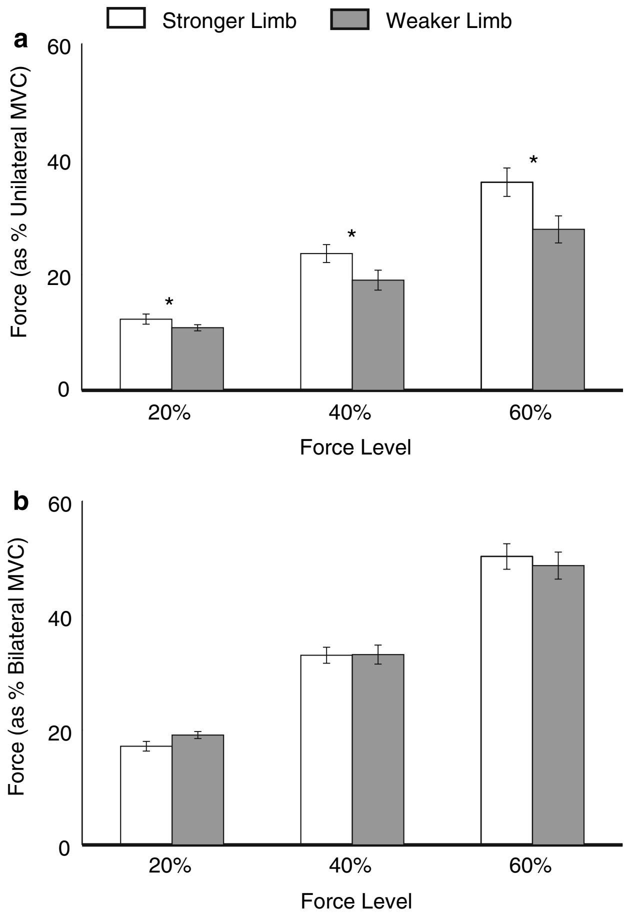

Fig. 4 Average forces for all subjects during three submaximal force matching conditions. Target forces were equal to 20, 40, and 60% of the weaker limb peak force during the bilateral MVC condition. *White columns* represent forces recorded in the stronger limb and *gray columns* represent forces recorded in the weaker limb. **a** Forces normalized to unilateral MVC for each limb show significant differences between limbs (ANOVAs *: 20% $P = 0.0473$; 40% $P = 0.0012$; 60% $P = 0.0007$). **b** Forces normalized to bilateral MVC shows no differences between limbs (ANOVA $P = 0.8490$). *Error bars* are standard error of the mean

$P = 0.0111$). Power analyses indicated power was less than 0.62 for RMS EMG data across all these tests.

When comparing RMS EMG during the force matching trials, there were significant differences between limbs and force levels for vastus lateralis (ANOVA $P < 0.0001$, limbs $P = 0.0145$, force levels $P < 0.0001$) (Table 4). There were significant differences between force levels but not limbs for vastus medialis (ANOVA $P < 0.0001$, force levels $P < 0.0001$, limbs $P = 0.0809$) and medial hamstrings (ANOVA $P < 0.0001$, force levels $P = 0.0302$, limbs $P = 0.0611$). There were no significant differences between limbs or force levels for gluteus maximus (ANOVA $P < 0.0001$, force levels $P = 0.0914$, limbs $P = 0.3932$). No significant interaction effects were found (VM: $P = 0.6973$, VL: $P = 0.6057$, MH: $P = 0.2274$, GM: $P = 0.6307$).

Discussion

Our results clearly demonstrated that force imbalance persisted at both maximal and submaximal force levels. This suggests that the mechanisms involved in the deficit are likely the same for maximal and submaximal contractions. Interpreting these results in light of past studies on sense of effort (Gandevia and McCloskey 1977; Carson et al. 2002; Proske et al. 2004) suggests that force production in the lower limbs is based on sense of effort during submaximal contractions. Results of the current study should have been different if subjects were relying on their sense of force or tension rather than their sense of effort in lower limbs during the submaximal force matching tasks. If this were the case, subjects should have been able to match absolute forces between limbs because their unilateral MVC forces (and therefore individual limb strengths) were not significantly different from each other. Their lower limbs had the capacity to produce equal forces, but during the submaximal force matching trials they did not generate equal forces.

Although the peak force produced by subjects during bilateral isometric maximum voluntary contractions was significantly different between limbs, the peak force during unilateral isometric maximum voluntary contractions was not. Biomechanical factors that determine muscle force include muscle length, shortening velocity, activation history, and current activation (Huijing 2000). During both unilateral and bilateral maximum contraction trials, we have controlled for three of the four factors. Subjects are lying down in the same position with the shoulders firmly braced. With the same posture and joint angles, muscle lengths remain the same. Shortening velocity remains the same at ~ 0 cm/s as this is a maximum isometric contraction, and before both trials subjects have rested and therefore have the same activation history. The only variable influencing a change in muscle force therefore is current activation neural drive (i.e. unilateral or bilateral maximum contraction). Similar peak forces between limbs during unilateral isometric maximum voluntary contractions demonstrate that the mechanical capabilities of each limb are equal. It is activating the legs at the same time (i.e. bilateral movement) that results in asymmetric limb forces. Regardless of whether humans produce maximal or submaximal forces, limb force asymmetry appears to be related to neural factors rather than differences in mechanical capabilities between the limbs.

Lower limb EMG results from the vastus medialis, vastus lateralis, medial hamstrings, and gluteus maximus muscles did not explain this force asymmetry. This is likely a result of the inherent high variability in EMG amplitudes compared to force measures. Muscles act as low pass filters so that relatively large variations in EMG are not seen in

Table 3 Summary of main effects and interaction effects of repeated measures ANOVA of RMS EMG during unilateral and bilateral MVC trials

	df	VL		VM		MH		GM	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Two-way ANOVA (limb by condition)									
Effect of limb	(1, 27)	1.4	0.2468	4.40	0.0455	2.04	0.1649	2.69	0.1129
Effect of condition	(1, 27)	34.59	<0.0001	49.71	<0.0001	42.56	<0.0001	34.57	<0.0001
Limb × condition	(1, 27)	2.67	0.1136	5.48	0.0269	1.04	0.3166	5.62	0.0251
Separate ANOVAs									
Effect of limb									
Unilateral MVC	(1, 9)			0.047	0.8332			1.66	0.2296
Bilateral MVC	(1, 9)			10.13	0.0111			3.68	0.0874
Effect of condition									
Weaker limb	(1, 9)			54.19	<0.0001			444.82	<0.0001
Stronger limb	(1, 9)			9.37	0.0135			4.48	0.0636

Limb: weaker/stronger, condition: unilateral/bilateral MVC, *df* degrees of freedom, *VL* vastus lateralis, *VM* vastus medialis, *MH* medial hamstrings, *GM* gluteus maximus

muscle force (Winter 2004). As a result, our EMG measures provided low statistical power (power < 0.62). On average, more than 40 subjects would have been required to achieve statistical power greater than 0.8 for the EMG data. As a result, determining a correlating change in EMG activity is beyond the scope of our study.

The bilateral index of −35.3 ± 7.1% measured during isometric lower limb extensions reveals large bilateral deficits in our subjects. Comparisons of bilateral index to previous studies measurements are difficult due to a shortage in reported values for isometric whole lower limb extensions. Many more studies have reported bilateral indices for isometric knee extension, ranging from −24% (bilateral deficit) to +4% (bilateral facilitation) (Schantz et al. 1989; Koh et al. 1993; Jakobi and Cafarelli 1998). The large bilateral deficit demonstrated in our subjects results from several factors. First, isometric lower limb extensions involve contractions across multiple joints compared to knee extensions that only involve contractions across a single joint. When individuals have performed both isometric MVC trials of lower limb extensions (i.e. multi-joint) and isolated knee extensions (single-joint) their bilateral index changes from a bilateral deficit to a bilateral facilitation, respectively (Schantz et al. 1989). Another reason for an increase in bilateral deficit may be due to the fast rate of lower limb force development. Subjects possess a larger bilateral deficit when they are instructed to generate force as quickly as possible (BI = −24.6%) rather than generate force gradually (BI = −17.0%) (Koh et al. 1993). The bilateral index also depends upon training, such that with bilateral training the bilateral deficit is reduced (Taniguchi 1997, 1998; Janzen et al. 2006). Our subjects were typical university students and not specifically trained in bilateral movements.

Subjects' posture during the experiment may also contribute to the large bilateral deficit. Subjects were supine with their feet on a vertical force platform. As described in the Methods section, the lower limbs were positioned in the middle of the range of motion used for a full lower limb extension, leading to knee angles ranging from 110° to 120° (180° defined as full knee extension). Therefore, subjects had increased knee and hip extension compared to previous studies that reported knee and hip angles of 90° for knee extension trials.

Regardless of the reasons for the difference in magnitude of the bilateral deficit, an important comparison in the current study was to determine if force matching experiments in the lower limbs show similar results to upper limb force matching studies. Our results relate to a multi-joint lower limb bilateral task, whereas other studies have involved single joints of the upper limb including either the finger (distal interphalangeal joint) (Li and Leonard 2006; Park et al. 2007) or the elbow (Gandevia and McCloskey 1977; Carson et al. 2002; Weerakkody et al. 2003; Proske et al. 2004). In several elbow joint studies, force asymmetry was induced by weakening agonist muscles through unilateral fatigue of the elbow extensors (Carson et al. 2002) or the flexors (Weerakkody et al. 2003; Proske et al. 2004). Similar to the results of the current study, subjects attempting to produce equal forces between limbs actually produced equal relative forces when individual limb forces were scaled to the instantaneous maximum strength of the muscle groups (i.e. the post-fatigued maximum strength). Different results, however, were seen in experiments involving force matching between ipsilateral fingers. When reference and matching finger forces were normalized to individual finger strength, the weaker finger produced a higher relative force (Li and Leonard 2006). Absolute

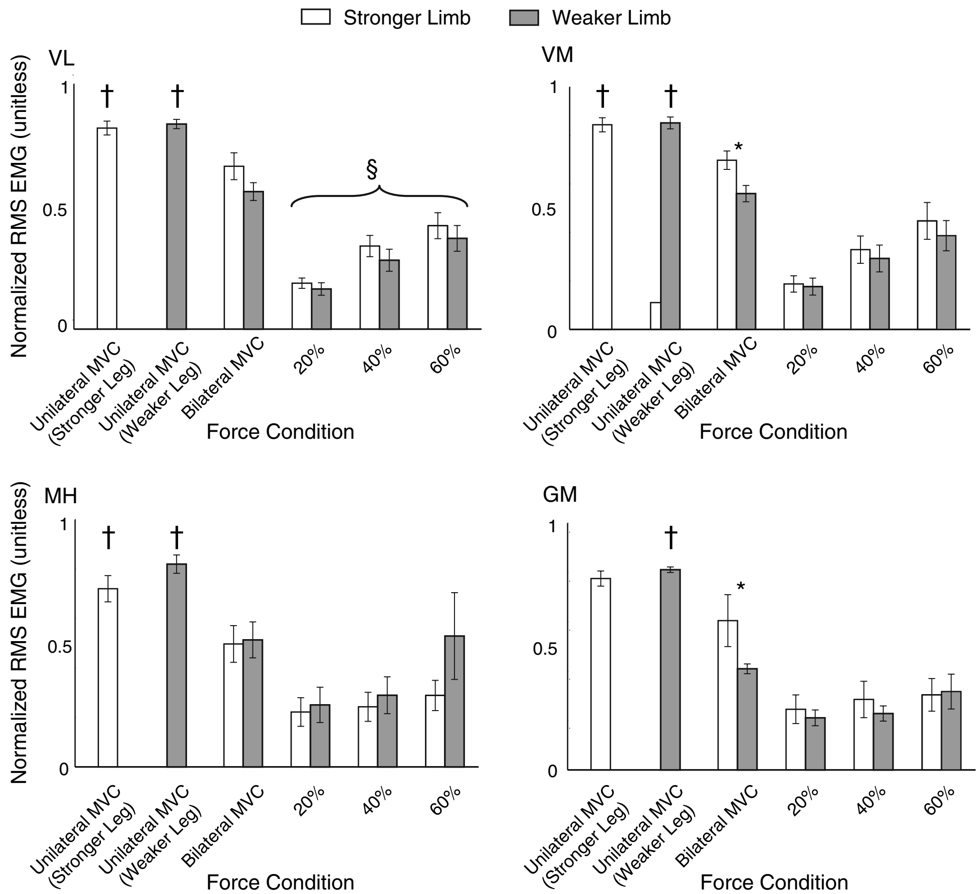

Fig. 5 Average normalized RMS EMG for all subjects. Force conditions included unilateral MVCs on each limb, bilateral MVC, and three submaximal force matching levels. Force matching target levels were 20, 40, and 60% of the weaker limb peak force during the bilateral MVC condition. *White columns* represent forces recorded in the stronger limb and *gray columns* represent forces recorded in the weaker limb. Reported muscle data is for the vastus lateralis (*VL*), vastus medialis (*VM*), medial hamstrings (*MH*), and gluteus maximus (*GM*) on each side. For each muscle, RMS EMG values were normalized to the highest RMS EMG value recorded during any of the unilateral MVC trials. † indicates significant difference between EMG during unilateral and bilateral MVC conditions within each limb. * indicates significant difference between stronger and weaker limb EMG during the bilateral MVC condition. § indicates significant difference between stronger and weaker limb EMG across force levels. *Error bars* are standard error of the mean

Table 4 Summary of main effects and interaction effects of repeated measures ANOVA of RMS EMG during three submaximal force matching conditions

	df	VL		VM		MH		GM	
		F	*P*	*F*	*P*	*F*	*P*	*F*	P
Two-way ANOVA (limb by force level)									
Effect of limb	(1, 45)	6.47	0.0145	3.19	0.0809	3.69	0.0611	0.74	0.3932
Effect of force level	(2, 45)	53.99	<0.0001	44.95	<0.0001	3.79	0.0302	2.52	0.0914
Limb × force level	(2, 45)	0.36	0.6973	0.51	0.6057	1.53	0.2274	0.47	0.6307

Limb: weaker/stronger, force level: 20/40/60% force matching level, *df* degrees of freedom, *VL* vastus lateralis, *VM* vastus medialis, *MH* medial hamstrings, *GM* gluteus maximus

forces were not significantly different when total force (instructed and uninstructed) was considered. Uninstructed fingers may produce force resulting from enslaving effects, or involuntary force production of one or more fingers when another finger is activated (Zatsiorsky et al. 1998). These findings led to conclusions that the central nervous system perceives absolute force from all fingers (Li and Leonard 2006) rather than a relative force as concluded in the current study. The contrasting results also may be due to the function of the muscles involved. Lower limb muscles are typically involved in gross motor function, whether it is producing large forces or in controlling posture, whereas smaller muscles are involved in fine motor control in order to perform accurate movements. The central nervous system may perceive absolute force when the muscles involved are used for fine motor control, such as in the finger, and relative force when the muscles involved are for gross motor function, such as in the lower limbs.

There are several neural mechanisms that could account for the changes in force observed during bilateral activation. Mechanisms proposed for causing the bilateral deficit include reduced motor neuron excitability (Vandervoort et al. 1984; Kawakami et al. 1998), interhemispheric inhibition (Gazzaniga and Sperry 1966), and limitation of the central neural drive (i.e. ceiling effect) (Li et al. 1998, 2001). Although these mechanisms could account for the drop in total maximum strength when a task is performed bilaterally as compared with unilaterally, they could not explain the bilateral force asymmetry described in this study.

There is another neural mechanism called common drive that may account for the neural origin of force asymmetry during bilateral activation (De Luca et al. 1982a, b; De Luca 1985). Common drive describes the unison behavior of the firing rates of motor units and might indicate that when homologous muscle groups are bilaterally activated, the nervous system treats them as one unit. This mechanism has been proposed to exist for both maximal and submaximal contractions (Oda and Moritani 1996). Alternatively, there could be a chronic asymmetric neural drive to the dominant and non-dominant lower limbs. Long-term potentiation could have created the asymmetry because of greater use by the dominant lower limb. Future studies relying on functional magnetic resonance or other types of brain imaging may provide more insight into the mechanisms.

The current results may have implications for other tasks and/or other populations. We examined static lower limb extensions in healthy individuals attempting to match forces between their lower limbs. Subjects with neurological disabilities typically have a mismatch between their sense of effort and force production (Bertrand et al. 2004; Mercier et al. 2004). Individuals with post-stroke hemiparesis have increased limb force asymmetry partially due to reduced strength capacity in the involved muscles of one side of the body. During upper limb submaximal matching tasks, these subjects consistently overestimate forces produced in the paretic upper limb, even though maximum voluntary force trials reveal that they have the ability to produce forces of equal magnitude (Bertrand et al. 2004; Mercier et al. 2004). These results suggest that subjects rely on their sense of effort to predict upper limb forces. More recently, Milot et al. (2006) found that normalizing joint moments during gait to the maximum joint moment capabilities led to similar effort levels in the paretic and non-paretic limbs. Thus, it seems that sense of effort is an important factor in determining lower limb muscle activation in hemiparetic individuals.

The field of rehabilitation can benefit from knowing that post-stroke individuals use sense of effort in predicting force output. Current rehabilitation therapies focus on strengthening the paretic limb of these individuals. Although this is a necessary component, force matching studies would suggest that therapy also needs to address improving patients' impaired force scaling abilities. Improved results may occur with designing training techniques to address both of these components. One new strategy, symmetry-based resistance (Simon et al. 2007), has the potential to improve both the patients' force scaling abilities and limb strength. With symmetry-based resistance, task resistance increases with increasing limb force asymmetry. Lower limb extension training with symmetry-based resistance is a potential means for training subjects to recalibrate their effort to force relationship. Subjects can learn to scale muscle activation more appropriately to achieve a desired force outcome. This would enable stroke subjects to better match paretic limb forces to task requirements during activities of daily living. The results from this study demonstrate that there is a lower limb asymmetry existing even in healthy neurologically intact subjects. Therefore, future studies using symmetry-based resistance for patient populations need to consider this asymmetry as a potential factor in the study design and results.

Acknowledgments The authors would like to thank the members of the University of Michigan Human Neuromechanics Laboratory for their assistance during data collections and for helpful comments on revisions of the manuscript. This research was supported in part by National Institutes of Health R01 NS045486 and the National Science Foundation GRFP.

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