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INVITED REVIEW

Bilateral deficit in maximal force production

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Abstract The bilateral deficit phenomenon, characterized by a reduction in the amount of force from a single limb during maximal bilateral actions, has been shown in various movement tasks, contraction types and different populations. However, bilateral deficit appears to be an inconsistent phenomenon, with high variability in magnitude and existence, and seems to be plastic, as bilateral facilitation has also been shown to occur. Furthermore, many mechanisms underlying this phenomenon have been proposed over the years, but still remain largely unknown. The purpose of this review was to clarify and critically discuss some of the important issues relevant to bilateral deficit. The main findings of this review were: (1) bilateral deficit does not seem to be contraction-type dependent; however, it is more consistent in dynamic compared to isometric contractions; (2) postural stabilization requirements and/or ability to use counterbalances during unilateral actions seem to influence the expression of bilateral deficit to a great extent; strong evidence has been provided for higher-order neural inhibition as a possible mechanism, but requires further exploration using a lower limb model; biomechanical mechanisms, such as differences in shortening velocity between contraction modes and displacement of the force–velocity curve, seem to underlie bilateral deficit in ballistic and explosive contractions; (3) task familiarity has a large influence on bilateral deficit and thus adequate testing specificity is warranted in training/cross-sectional experiments; (4) the literature investigating the relationship between bilateral deficit and athletic performance and injury remains scarce; hence, further research in this area is required.

Keywords Unilateral · Bilateral · Force · Interhemispheric inhibition · Interlimb · Motor control

Abbreviations

EMG	Electromyography
MU	Motor unit
MVC	Maximal voluntary contraction

Introduction

As early as 1961, Henry and Smith observed that the force produced during simultaneous *maximal* contraction of both limbs was lower than the sum of the forces produced by the left and right limbs separately (Fig. 1) (Henry and Smith 1961). Since the 1960s, this phenomenon, termed bilateral deficit, has been shown to be present in various movement tasks, contraction types and different populations, both male and female (see Tables 1, 2, 5). Since the last comprehensive review on the topic nearly 15 years ago (Jakobi and Chilibeck 2001), a large amount of literature has emerged and new methodological approaches have been introduced, which calls for the topic to be revisited.

In most studies, bilateral deficit has been determined through the calculation of bilateral index as presented by Howard and Enoka (1991):

$$\mathrm{BI}(\%) = \left(100 \times \frac{\text{bilateral}}{\text{right unilateral} + \text{left unilateral}}\right) - 100,$$

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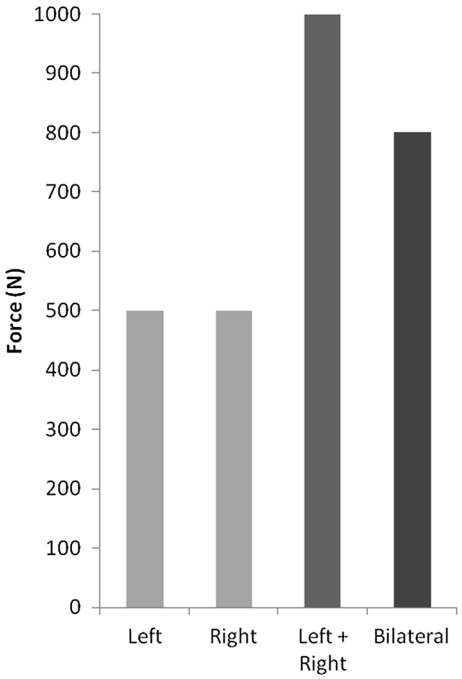

Fig. 1 Theoretical representation of the bilateral deficit (adapted from Nijem and Galpin 2014)

where 'bilateral' is the sum of forces produced by each leg separately during the bilateral action. A positive bilateral index is indicative of bilateral facilitation, while a negative value indicates bilateral deficit.

The phenomenon of bilateral deficit appears to be restricted to twin synchronous movements, e.g., simultaneous flexion, but not simultaneous flexion and extension (Ohtsuki 1983) and contraction of homonymous limbs (Schantz et al. 1989; Howard and Enoka 1991; Herbert and Gandevia 1996). There are some inconsistencies in the literature with regard to the existence of bilateral deficit, as some studies have observed this phenomenon while others have not (see Tables 1, 2, 4). In fact, some studies have shown the existence of bilateral facilitation (Secher 1975; Schantz et al. 1989; Howard and Enoka 1991), a phenomenon where maximal bilateral force production is greater than the sum of unilateral forces.

It has been suggested that determining the existence of bilateral deficit is important, as it may represent a control limitation of the neuromuscular system (Jakobi and Chilibeck 2001). Yet, the phenomenon appears to be plastic as shown by the existence of bilateral facilitation, which suggests that a control limitation, if there is one, may potentially be overridden. This may have applications to specific sports where a goal is to maximize either unilateral or bilateral force production. The existence of bilateral deficit may be of special concern to athletes who perform bilateral contractions exclusively (e.g., rowers, powerlifters, weightlifters, ski jumpers) and potentially athletes in sports where performance is ultimately limited by unilateral force production (e.g., high and long jumpers, throwing events in track and field, etc.). So far, the effect of bilateral deficit on athletic performance is largely unknown. The vast majority of sports include locomotion, a "reciprocal" movement pattern (Archontides and Fazey 1993), where forces are produced mostly unilaterally and this especially applies to ground-based sports. Thus, the question remains whether bilateral jumping and resistance exercises in training should better be replaced with their unilateral variations (Santana 2001). Elucidating the role of bilateral deficit in performance and the underlying mechanisms is thus the first step toward better individualization of training programs. While bilateral deficit is likely restricted to maximal contractions, its effect on the ability to perform bilateral activities in the elderly and a potential greater risk of injury as a result of it cannot be excluded.

The purpose of this review is to clarify and critically discuss some of the important issues relevant to the literature on bilateral deficit. Firstly, the review aims to explore whether bilateral deficit is contraction- and/or movement-type dependent, as well as its underlying mechanisms. Secondly, the effect of training on bilateral deficit and the relationship between bilateral deficit, athletic performance and injury are considered.

Search strategy

PubMed, Google Scholar and SPORT Discus were searched by the first author for relevant articles containing the words 'bilateral deficit', 'bilateral', 'unilateral' and 'force'. Abstracts of all articles were first reviewed. Full texts were retrieved when the primary criteria were satisfied. Additionally, reference lists of relevant articles were examined to identify any potential studies that might fit the criteria. The inclusion criteria for studies in this review were: (1) investigations comparing unilateral and bilateral force production of the limbs either acutely or before/after training interventions; (2) force production was maximal or a result of maximal expression of effort; (3) participants were healthy; (4) the full text was available in English. To make comparisons between studies easier, the average magnitude of bilateral deficit as referenced to the bilateral index (Howard and Enoka 1991) was calculated for isometric and dynamic contractions, both in total and separately for upper and lower body movements from all of the included studies. Not all studies reported the magnitude of bilateral deficit in percentages; therefore, the calculation was done by the authors if absolute means were available. For non-significant findings, bilateral index was considered to be zero.

Table 1 Summary of BLD literature using dynamic contractions

Reference	Movement	Contraction mode	BLD	BI (%)	EMG BLD	Subjects	R	LD
Botton et al. (2013)	Knee extension	Concentric	Yes	–9.6	–	Physically active ($n = 8$)—M—20 ± 4 years; 184 ± 9 cm; 74.2 ± 15.4 kg	UL and BL on separate days, but randomized	–
Botton et al. (2015)	Knee extension	Concentric	No	–	–	43 young women	BL followed by UL (randomized)	–
Brown et al. (1994)	Knee extension	Isokinetic	Yes (60°/s–240°/s); no (360°/s)	–1 to –12	–	12 F—34.9 ± 2.4 years; 160.7 ± 2.3 cm; 59.2 ± 3.3 kg	Yes	–
	Knee flexion	Isokinetic	Yes (60°/s–240°/s); no (360°/s)	–1 to –16	–			
Costa et al. (2015)	Knee extension	Concentric	Yes	–11	–	Healthy—12 M—24 ± 3.7 years	n/m	–
Cresswell and Overdal (2002)	Knee extension	Isokinetic - 60°/s	Yes	–17	Yes	Recreationally active—13 F, 15 M—24 ± 3 years; 177 ± 9 cm; 72.4 ± 12.2 kg	Yes	–
Dickin and Too (2006)	Knee extension	Isokinetic - −30 to 180°/s	Yes	–18 to –25	–	University-aged—18 F—23.5 ± 3.28 years; 168.4 ± 5.87 cm; 65.1 ± 15.2 kg	Yes	–
Häkkinen et al. (1996b)	Knee extension	Concentric	No	–	–	50 year-olds—12 M, 12 F—43–57 years 70-year-old—12 M, 12 F—59–75 years	No	–
Häkkinen et al. (1997)	Knee extension	Concentric	No (BLF)	–	No (BLF)	10 young men (29 ± 3 years) 12 middle-aged men (50 ± 4 years) and 12 women (48 ± 5 years) 12 elderly men (67 ± 4 years) and 12 women (68 ± 4 years)	n/m	No
Janzen et al. (2006)	Hip and knee extension	Concentric	Yes	–12.7	–	57 postmenopausal women	Yes	–
	Arm flexion		Yes	–8.8				
	Knee extension		No	–				
Kuruganti et al. (2005)	Knee extension	Isokinetic	Yes	–26.7	–	Older—10 M, 7 F—64 ± 6 years; 172 ± 11 cm; 82 ± 19 kg Younger—5 M, 11 F—28 ± 5 years, 171 ± 8 cm; 80 ± 7 kg	BL followed by UL (randomized)	–
	Knee flexion		Yes	–32.5				
Kuruganti and Seaman (2006)	Knee extension	Isokinetic	Yes	–25.4	No	Adolescent—8 F—15 ± 1 years; 167 ± 5 cm; 58 ± 6 kg Adult—8 F—31 ± 7 years; 166 ± 6 cm; 72 ± 12 kg Older—7 F—63 ± 6 years; 162 ± 6 cm; 70 ± 18 kg	BL followed by UL (randomized)	–
	Knee flexion		Yes	–27.8	No			
Magnus and Farthing (2008)	Hip and knee extension	Concentric	Yes	–12.1	No	Students—3 M, 5 F—22.9 ± 1.3 years; 174.7 ± 7.5 cm; 72.4 ± 11.6 kg	Yes	–
Owings and Grabiner (1998a)	Knee extension	Isokinetic (30°/s and 150°/s)	Yes	–13.7 to –14.0	–	Healthy men ($n = 20$)—25 ± 3 years; 178 ± 7 cm; 76.3 ± 8.9 kg	UL(R or L), BL, UL (L or R)	–
Roy et al. (1990)	Knee extension	Isokinetic	Yes	Not reported	–	Physically active male undergraduate students ($n = 42$)—21.1 ± 1.5 years; 173.9 ± 4.4 cm; 70.3 ± 6.3 kg	Yes	–
Taniguchi (1997)	Hip and knee extension	Isokinetic (80°/s)	Yes	– 6.5 to –18.6	–	Students—4 F, 17 M—20.3 ± 0.1 years; 1.69 ± 2 cm; 63.5 ± 2.0 kg	Yes	–
	Arm extension		Yes	– 7.2 to –9.6	–	Students—9 F, 9 M—21.2 ± 0.2 years; 167 ± 2 cm; 63.8 ± 2.9 kg	Yes	–
Taniguchi (1998)	Hip and knee extension	Isokinetic (80°/s)	Yes	– 0.5 to –15.3	–	Students—7 F, 32 M—20.5 ± 0.2 years; 171 ± 1 cm; 66.4 ± 2.2 kg	Yes	–
	Arm extension		Yes	– 3.7 to –11.8	–			

Table 1 continued

Reference	Movement	Contraction mode	BLD	BI (%)	EMG BLD	Subjects	R	LD
Vandervoort et al. (1984)	Hip and knee extension	Isokinetic	Yes	− 9 to −48.8		Students—9 M—20–24 years; 172–185 cm; 64–75 kg	No	–
Vandervoort et al. (1987)	Bench press	Isokinetic	No	–	–	Students—9 M—20–24 years; 172–185 cm; 64–75 kg	Yes	–
Weir et al. (1995)	Knee extension	Eccentric	Yes	Not reported	–	Physically active, young—17 M	UL (randomized), BL	No
Weir et al. (1997)	Knee extension	Concentric	Yes	Not reported	–	Physically active, young—16 M	UL (randomized), BL	Yes

BLD bilateral deficit in force (BI significantly different than 0), *BI (%)* bilateral index denoting the magnitude of bilateral deficit, *BLD EMG* bilateral deficit in electromyography, *R* randomization, *LD* limb domainance

Search result

The database searches yielded 77 relevant articles. 20 of those articles used a dynamic contraction model, of which 11 used isokinetic, 8 used concentric and 1 used eccentric contractions, respectively. Isometric contractions were used in 44 studies, and 13 investigated ballistic/explosive contractions. Concurrent bilateral deficit in force and EMG was reported in 33 of the relevant investigations, while 9 studies found no such coupling. 16 investigations did not randomize the order of contractions, 4 did not mention randomization, 2 performed unilateral and bilateral contractions on separate days, and 13 used a semi-fixed order of randomization (e.g., unilateral contractions performed first in a randomized fashion followed by bilateral contractions or vice versa). 32 articles also reported the effect of limb dominance on bilateral deficit.

To support our assessment we have reported all the relevant articles, including their respective bilateral deficit magnitude values, movement and population studied, whether they performed randomization of contraction and whether or not limb dominance was noted. These studies are summarized in Table 1 (dynamic contractions), Table 2 (isometric contractions) and Table 5 (explosive/ballistic contractions).

Contraction- and/or movement-type dependency of bilateral deficit

The literature on bilateral deficit lacks consistency. While bilateral deficit is frequently reported in studies using a dynamic contraction model, the results of isometric contractions are more variable. Despite the variability of bilateral deficit in the literature, the results of Botton et al. (2013), who showed a similar magnitude of bilateral deficit between isometric and concentric knee extensions, suggest that the existence of the phenomenon is not contraction-type dependent. Furthermore, in a recent paper by the same research group, bilateral deficit was only observed in isometric, but not dynamic contractions (Botton et al. 2015). In an effort to establish consistency, the following discussion is separated into three parts based on the type of contraction.

Dynamic contractions

In dynamic contractions, whether concentric, eccentric and/or isokinetic, bilateral deficit is reported consistently. The average bilateral index in the gathered studies was -11.7 ± 9.7 % (Table 1). Upper body movements generally

Table 2 Summary of BLD literature using isometric contractions

Reference	Movement	BLD	BI (%)	EMG BLD	Subjects	R	LD
Aune et al. (2013)	Shoulder flexion	Yes	−20.4	–	Untrained (5 M, 5 F)—23 ± 1.3 years	Yes	–
	Index finger flexion	Yes	−5.1	–			
Behm et al. (2003)	Knee extension	No	–	Yes	Resistance trained ($n = 10$)—M—24.3 ± 6.7 years; 178.1 ± 6.1 cm; 82.3 ± 8.9 cm Untrained ($n = 6$)—M—23.1 ± 2.3 years; 177.3 ± 8.8 cm; 83.1 ± 13.6 kg	n/m	Yes (untrained)
Beurskens et al. (2015)	Hip and knee extension	Yes	−3.9 to −19.3	–	Old male adults ($n = 53$; 60–80 years) and young male adults ($n = 14$; 20–30 years)	BL followed by UL (randomized)	–
Botton et al. (2013)	Knee extension	Yes	−9.7	–	Healthy, untrained—11 M—20.6 ± 1 years; 174.4 ± 7 cm; 71.4 ± 6.4 kg	UL and BL on separate days, but randomized	–
Botton et al. (2015)	Knee extension	Yes	−10.5 to −13.8	Yes	43 young women	BL followed by UL (randomized)	–
Buckthorpe et al. (2013)	Knee extension	No	–	No	Physically active ($n = 12$)—M—23.9 ± 3.7 years; 168.8 ± 31.4 cm; 77.3 ± 6.9 kg	UL—BL—UL	–
Cengiz (2015)	Hand flexion	Yes	−9	Yes	Physically active—10 M—24.1 ± 2.38 years; 174.15 ± 0.8 cm; 79.48 ± 11.40 kg	Yes	Yes
Cornwell et al. (2012)	Hand flexion	Yes (left handed only)	−1.3	No	Untrained—31 M, 49 F	Yes	Yes (left hand)
Donath et al. (2014)	Hip and knee extension	Yes	−5.6 to −7.2	–	Athletes ($n = 20$)—M—24.5 ± 1.7 years; 181 ± 5 cm; 77.5 ± 7.1 kg	Yes	–
Drury et al. (2004)	Elbow flexion	Yes (45° and 90°); no (135°)	−11.4 to −20.1	–	Active—20 F—19 ± 1.2 years	Yes	–
Häkkinen et al. (1995)	Knee extension	No	–	No	33 M, 3 age groups—30 ($n = 11$), 50 ($n = 12$) and 70 ($n = 10$)	No	No
Häkkinen et al. (1996a)	Knee extension	No	–	No	Middle-aged—50-year-olds—12 M, 12 F Elderly—70-year-olds—12 M, 12 F	No	No
Häkkinen et al. (1997)	Knee extension	No (BLF)	–	No (BLF)	10 young men (29 ± 5 years) 10 older men (61 ± 4 years)	No	No
Henry and Smith (1961)	Hand flexion	Yes	−3	–	30 college-aged men	No	Yes
Herbert and Gandevia (1996)	Thumb adduction	No	–	No	5 M, 6 F—34 ± 10 years	Yes	No
Hernandez et al. (2003)	Elbow flexion	Yes	−11.1 to −11.9	Yes	Older—5 M, 12 F—73.3 ± 4.4 years Young—5 M, 16 F—22.4 ± 0.9	Yes	–
Howard and Enoka (1991)	Knee extension	Yes (untrained only); no (cyclists, facilitation—weightlifters)	−9.5 (untrained); −6.6 (cyclists); +6.2 (weightlifters)	No	Untrained ($n = 6$)—M—29 ± 3.2 years; 175.7 ± 4.9 cm Cyclists ($n = 6$)—M—33.1 ± 6.6 years; 178.2 ± 5.4 cm Weightlifters ($n = 6$)—M—22.7 ± 3.0 years; 177.6 ± 4.6 cm	No	–

Table 2 continued

Reference	Movement	BLD	BI (%)	EMG BLD	Subjects	R	LD
Jakobi and Cafarelli (1998)	Knee extension	No	–	No	Recreationally active—20 M—27.5 ± 1.78 years; 77.5 ± 2.0 kg	Yes	No
Kawakami et al. (1998)	Plantar flexion	Yes	−6.6 to 13.9	Yes (0° only)	6 M—23–30 years; 176.8 ± 5.4 cm; 76.8 ± 10.4 kg	Yes	–
Khodiguian et al. (2003)	Knee extension	No	–	No	Untrained—17 M—25.5 ± 6.7 years; 173.4 ± 7.6 cm; 71.0 ± 9.1 kg	Yes	No
Koh et al. (1993)	Knee extension	Yes	−17.0 to –24.6	Yes	Recreationally active—12 M	Yes	No
Kuruganti et al. (2011)	Knee extension	Yes (45°), No (0°, 90°)	−23.4 (45°)	No	Young, recreationally active—10 M—24.5 ± 2.7 years; 180 ± 4.71 cm; 82.5 ± 17.8 kg	BL followed by UL (randomized)	–
Kuruganti and Murphy (2008)	Knee extension	Yes	−18.5	Yes	Young, athletic—6 M—22.3 ± 2.9 years; 177.7 ± 6.4 cm; 72.4 ± 5.2 kg	BL followed by UL (randomized)	
MacDonald et al. (2014)	Hip and knee extension	Yes	−18.6 to –20.2	No	Swimmers—9 F—20.1 ± 1.3 years; 170 ± 4 cm; 68.3 ± 5.4 kg Untrained—9 F—21.7 ± 1.3 years; 170 ± 7 cm; 69.7 ± 4.5 kg	Yes	–
	Hand flexion	No	–	No			
Magnus and Farthing (2008)	Hand flexion	No	–	No	Students—3 M, 5 F—22.9 ± 1.3 years; 174.7 ± 7.5 cm; 72.4 ± 11.6 kg	Yes	–
Oda and Moritani (1994)	Elbow flexion	Yes	−3.4 to –7.9	Yes	11 males—27.5 ± 2.2 years; 174 ± 1 cm; 70.6 ± 2.6 kg	Yes	Yes
Oda and Moritani (1995)	Elbow flexion	Yes	−6 to –10	Yes	College oarsmen ($n = 25$)—19–22 years; 171–187 cm; 67.5–82.7 kg	Yes	Yes
Oda and Moritani (1995)	Hand flexion	Yes	−4.5 to –5.2	Yes	Untrained ($n = 8$)—M—26.6 ± 2.0 years; 176 ± 2 cm; 74.5 ± 2.4 kg	Yes	Yes
Oda and Moritani (1996)	Hand flexion	Yes	−3.9 to –4.9	Yes	Untrained ($n = 11$)—25.9 ± 1.5 years; 174 ± 1 cm; 71.2 ± 2.4 kg	No	Yes
Ohtsuki (1981)	Handgrip	Yes	−4 to –14	Yes	10 young women	Yes	Yes
Ohtsuki (1983)	Elbow flexion	Yes	−6.3 to –7.6	Yes	Healthy university students ($n = 10$)—F—20–23 years	Yes	No
	Elbow extension	Yes	−18.8 to –24.6	Yes			
Owings and Grabiner (1998b)	Knee extension	Yes	−6.5 to –12.9	–	Older—12 M, 23 F—72.1 ± 5.7 years; 163 ± 10 cm; 73.5 ± 13.1 kg	Yes	No
Post et al. (2007)	Finger abduction	Yes	−1.8 to –2.6	Yes	Healthy—10 M, 12 F—26.7 ± 6.1 years	Yes	No

Table 2 continued

Reference	Movement	BLD	BI (%)	EMG BLD	Subjects	R	LD
Schantz et al. (1989)	Knee extension	No	–	–	Physical education students—6 M, 8 F—23 ± 2 years; 171 ± 2 cm; 64 ± 2 kg	Yes	–
	Hip and knee extension	Yes	−10	No	Physical education students—9 M—28 ± 2 years; 182 ± 2 cm; 78 ± 3 kg Untrained—9 F—23 ± 1 years; 172 ± 3 cm; 59 ± 2 kg Untrained—5 M—26 ± 2 years; 179 ± 3 cm; 71 ± 1 kg Physical education students—5 F—24 ± 1 years; 170 ± 1 cm; 64 ± 2 kg Physical education students—5 M—25 ± 2 years; 184 ± 3 cm; 77 ± 3 kg Professional ballet dancers—5 F—27 ± 4 years; 165 ± 2 cm; 51 ± 2 kg Professional ballet dancers—5 M—26 ± 2 years; 181 ± 2 cm; 70 ± 2 kg Volleyball players—5 M—22 ± 1 years; 191 ± 3 cm; 84 ± 2 kg Resistance trained—5 M—28 ± 1 years; 176 ± 3 cm; 91 ± 5 kg		
Secher (1975)	Arm flexion	No (BLF)	–	–	40 oarsmen 26 ± 0.6 years		–
Secher et al. (1978)	Hip and knee extension	Yes	−25	–	6 males—23–26 years; 185 ± 2.3 cm; 80 ± 4.9 kg	No	–
Secher et al. (1988)	Hip and knee extension	Yes	−18	–	Untrained—90 F—30 ± 1.1 years	Yes	No
	Arm extension	No	–	–	Untrained—18 M—29 ± 1.1 years Weightlifters—38 M—20 ± 3.4 years Cyclists—8 M—23 ± 1.7 years Polio patient—1 W—30 years		–
Simoneau-Buessinger et al. (2015)	Plantar flexion	Yes (locked-unit); no (open-unit)	−9.3	No	Healthy adult males ($n = 20$)—22.7 ± 2.9 years; 176 ± 7 cm; 72.7 ± 15.1 kg	Yes	Yes
Taniguchi (1997)	Hand flexion	No	–	–	Students—23 M—20.6 ± 0.3 years; 169 ± 1 cm; 66.6 ± 2.1 kg	Yes	–
Teixeira et al. (2013)	Knee extension	Yes	−8.4	–	Resistance trained—27 M—25.1 ± 8.6 years	Yes	No
Vandervoort et al. (1984)	Hip and knee extension	Yes	−9	Yes	Students—9 M—20–24 years; 172–185 cm; 64–75 kg	No	–
Vandervoort et al. (1987)	Arm extension	No	–	–	Students—9 M—20–24 years; 172–185 cm; 64–75 kg	Yes	–
Van Dieën et al. (2003)	Finger flexion	Yes	−20 to –26.9	Yes	Untrained—5 M, 5 F—18–25 years	Yes	No
	Knee extension	Yes	−3.5 to –9.7	Yes	Untrained—6 M, 6 F—20–25 years	No	No
Vint and McLean (1999)	Elbow flexion	Yes	−11.4	No	College students ($n = 20$)—23.3 ± 3.9 years; 168.6 ± 9.5 cm; 71.9 ± 13.0 kg	No	Yes
Zijdewind and Kernell (2001)	Finger abduction	Yes	−5.1		Healthy—2 M, 3 F—20–25 years	No	No

BLD bilateral deficit in force (BI significantly different than 0), *BI* (%) bilateral index denoting the magnitude of bilateral deficit, *BLD EMG* bilateral deficit in electromyography, *R* randomization, *LD* limb dominance

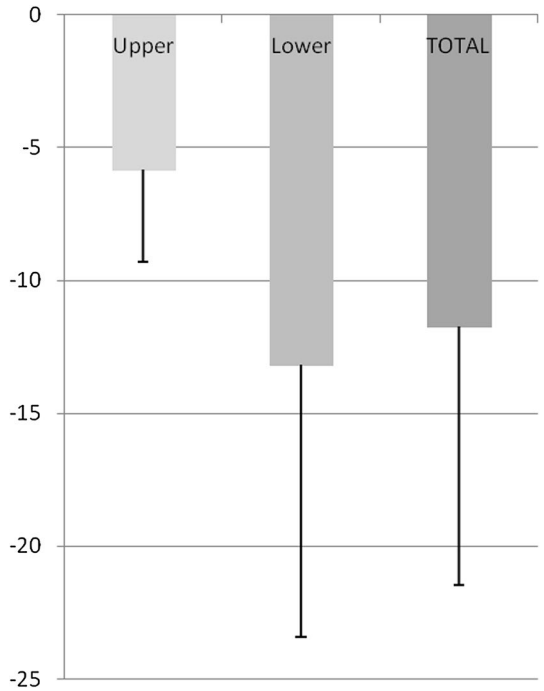

Fig. 2 Bilateral index of all studies using a dynamic contraction model (*Total*) compared with upper (*Upper*) and lower (*Lower*) body movements

exhibit lower bilateral index than lower body movements (bilateral index of -5.8 ± 3.5 vs. -13.2 ± 10.3 %, respectively; Fig. 2). The magnitude of bilateral deficit during concentric and/or eccentric contractions is about 10 % on average, while it has a bigger range during isokinetic contractions, usually increasing with increases in contraction velocity. For example, Vandervoort et al. (1984) performed a study using isokinetic combined hip and knee extension at ten different velocities and observed a linear increase in the magnitude of bilateral deficit ranging from 9 % during 0°/s up to 49 % during 424°/s.

Studies that were not able to show bilateral deficit during dynamic contractions are in the minority and include concentric knee extension (Häkkinen et al. 1996a; 1997; Janzen et al. 2006; Botton et al. 2015) and isokinetic bench press (Vandervoort et al. 1984). It is difficult to deduce the cause of such findings, as there are many confounding factors that can affect force production during dynamic contractions. Differences in subject characteristics are an unlikely contributor to this discrepancy in the literature, as bilateral deficit during dynamic contractions has been studied in younger and older male and female populations, respectively (Table 1). There have been some suggestions that the existence and magnitude of bilateral deficit may be caused by differences in postural stabilization requirements in different movements (Herbert and Gandevia 1996). For example, Magnus and Farthing (2008) investigated the relationship between the magnitude of bilateral deficit and postural stability requirements and showed the deficit for leg press, a task with greater postural stability requirements, while no deficit was observed for handgrip exercise. It is important to note, however, that the handgrip is an isometric task, while the leg press is dynamic and this could have been responsible for differences in the results. Furthermore, corticospinal and interhemispheric control of hand and leg musculature appears to be different, which may have affected the expression of bilateral deficit (Brouwer and Ashby 1990; Luft et al. 2002; Volz et al. 2015). It also appears that spinal cord circuits have a greater impact on the movement of the lower limbs (Danner et al. 2015). It is known that the quadriceps are larger (Miller et al. 1993), more difficult to fully activate (Behm et al. 2002) and produce greater force (Izquierdo et al. 1999) than hand muscles involved in handrip. Thus, it is possible that the mass of the quadriceps affects neural drive required to fully activate the muscle (Halperin et al. 2015), which may consequently affect the expression of bilateral deficit. There may also be differences in joint stability, which is closely related to postural stability requirements insofar as excursion of the hip and knee joints would require greater activity of synergists acting as joint stabilizers when compared with the carpo-phalangeal joints, which may have played a role in the expression of bilateral deficit. Recently, it has also been shown that the ability to use counterbalances to one's advantage can affect torque production during unilateral conditions and thus affect the expression of bilateral deficit (Simoneau-Buessinger et al. 2015). Based on the aforementioned findings, it seems plausible that the expression of bilateral deficit in knee extension is limited by low postural stability requirements and/or ability to use counterbalances (for more details, see "Mechanisms"). Future studies should try to control postural stabilization requirements and ability to use counterbalances. Furthermore, they should report the exact subject positioning during testing as this appears to affect the expression of bilateral deficit.

A possible confounding factor in the expression of bilateral deficit in dynamic actions is also randomization of unilateral and bilateral contractions. Not all studies have randomized the conditions (see Table 1) and therefore it is possible that fatigue and/or potentiation has affected the results (Jakobi and Chilibeck 2001). Furthermore, large variability between subjects is often observed, and this has been suggested to be due to inadequate reproducibility of dynamic tests, which only a few studies have reported (Vandervoort et al. 1984; 1987; Taniguchi 1997).

Overall, it is difficult to interpret the underlying mechanisms during dynamic actions, as many factors can affect the ability to produce force, including, but not limited to, interaction between actin and myosin filaments, whether the movement is single- or multi-joint, activation and

length of the muscles involved, as well as the velocity of contraction (Jakobi and Chilibeck 2001).

Isometric contractions

There are numerous studies that have investigated differences in unilateral and bilateral contractions during isometric conditions. This contraction model is the most suitable for investigation of the possible underlying mechanisms, as the mechanics of the movement are somewhat restricted (Jakobi and Chilibeck 2001).

Bilateral index of all the relevant articles using isometric contractions was 8.6 ± 8.5. Upper and lower body isometric contractions do not appear to differ in consistency of bilateral deficit (present in 70 and 71 % of all studies, respectively) or in magnitude, i.e., bilateral index (−9.0 ± 8.0 vs. −8.1 ± 9.2, respectively; Fig. 3).

With regard to isometric knee extension, the literature seems to be the most equivocal (Table 3), as some studies have shown the presence of bilateral deficit while others have not (Table 3). It is possible that the use of different populations has caused the discrepancy in the results as Howard and Enoka (1991) showed the deficit only for the untrained group, but not for cyclists, and even facilitation in weightlifters. However, Häkkinen et al. (1996b, 1997) and Owings and Grabiner (1998b) both used older populations and only the latter study showed bilateral deficit. The ambiguity of the literature on isometric knee extension could also be explained by differences in knee joint angles that were employed in different experiments. Kuruganti et al. (2011) were able to show bilateral deficit only for 45°, but not for 0° or 90°, respectively, possibly because maximal tension can be produced at intermediate muscle lengths (Lieber et al. 1994). However, their results contradict the findings of Owings and Grabiner (1998b), who showed bilateral deficit at both 45° and 90°. Matkowski et al. (2011), who found bilateral deficit during isometric knee extension, did so at 70° of knee flexion, a joint angle that was chosen because it is reportedly close to the optimal muscle length for maximal force production (Becker and Awiszus 2001; Kubo et al. 2004). On a related note, an investigation of bilateral deficit at different joint angles during elbow flexion also showed that the deficit was present at 45° and 90°, but not at 135° (Drury et al. 2004). From the reviewed literature, there seems to be a trend for a greater prevalence of bilateral deficit in knee extension at intermediate muscle lengths (Table 3). As mentioned above, it is also possible that postural stabilization requirements are too low to result in bilateral deficit and/or the ability to use counterbalances is limited in knee extension, or that they differ depending on the joint position.

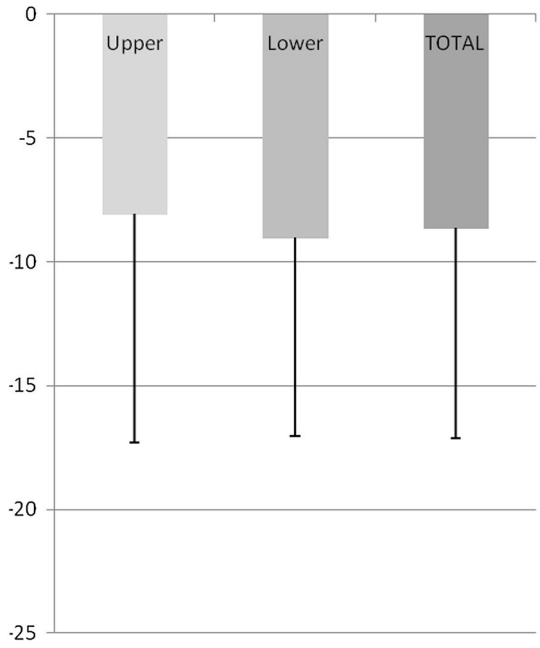

Fig. 3 BI of all studies using isometric contraction model (*Total*) compared with upper (*Upper*) and lower (*Lower*) body movements

Studies of isometric combined hip and knee extension show bilateral deficit consistently. All the studies were able to show the bilateral deficit phenomenon (Vandervoort et al. 1984; Schantz et al. 1989; MacDonald et al. 2014; Donath et al. 2014; Beurskens et al. 2015). More consistent results compared to knee extension cannot be explained solely by different populations used, as bilateral deficit has been studied both in young and old individuals for both movement types (Table 2). It is possible that greater consistency in terms of bilateral deficit is observed due to the greater postural stability requirements and ability to use counterbalances. Furthermore, differences in synergist contributions to combined hip and knee extension between unilateral and bilateral contractions could have been responsible for the consistency of the results (for further explanation, see "Mechanisms").

In the upper body, bilateral deficit has been shown in shoulder flexion, thumb adduction, finger abduction, and elbow flexion and extension, respectively (Table 2). Some ambiguity in the literature exists with regard to bilateral deficit in handgrip, as the majority of studies have reported bilateral deficit while some have not (Table 4). It is possible that high variability between the results stems from different subject positioning during testing between the studies, thereby causing differences in muscle length of hand flexors. For example, both Magnus and Farthing (2008) and Taniguchi (1997), who did not show bilateral deficit in handgrip, measured forces with extended elbows, while the majority of others measured strength with the elbows

Table 3 Summary of BLD literature using isometric knee extension with the respective joint angles

References	Joint angle (°)	BLD	BI (%)
Behm et al. (2003)	90	No	–
Botton et al. (2013)	60	Yes	−9.7
(Botton et al. 2015)	60	Yes	−10.5 to – 13.8
Häkkinen et al. (1995)	73	No	–
Häkkinen et al. (1996a)	73	No	–
Häkkinen et al. (1997)	73	No	–
Howard and Enoka (1991)	71	Yes/no[a]	−9.5[a]
Jakobi and Cafarelli (1998)	90	No	–
Khodiguian et al. (2003)	90	No	–
Koh et al. (1993)		Yes	−17.0 to – 24.6
Kuruganti et al. (2011)	0	No	0
	45	Yes	−23.4
	90	No	0
Kuruganti and Murphy (2008)	45	Yes	−18.5
Matkowski et al. (2011)	70	Yes	−7.8
Owings and Grabiner (1998a)	45	Yes	−11.1 to – 12.9
	90	Yes	−6.5 to – 8.9
Schantz et al. (1989)	90	No	0
Teixeira et al. (2013)	60	Yes	−8.4
Van Dieën et al. (2003)	90	Yes	−3.5 to – 9.7

Joint angle—0° full extension (all data have been transformed accordingly), *BLD* bilateral deficit in force, *BI* bilateral index

[a] Population-dependent—BLD was only observed for untrained group, but not for weightlifters and cyclists

flexed at 90° (Table 4). Furthermore, if stability requirements influence the expression of bilateral deficit, posture should be considered. While most of the studies performed testing while subjects were seated, Magnus and Farthing (2008) and MacDonald et al. (2014) recorded forces in a supine and standing position, respectively.

Explosive/ballistic contractions

Bilateral deficit has also been shown in ballistic actions (Table 5). For example, in human jumping, it has been shown that the sum of one-legged jumping heights is higher than the height of a bilateral jump. This is the case for the countermovement jump (van Soest et al. 1985; Bračič et al. 2010), drop jumps (Pain 2014)) as well as the squat jump (Challis 1998; Bobbert et al. 2006). However, it is important to note that jumping height may not be the best performance measure to determine bilateral deficit as it depends on whether it is normalized to height in upright standing (van Soest et al. 1985) or to height at takeoff (Bobbert et al. 1996). Despite these considerations, Hay et al. (2006) were still able to observe bilateral deficit of 13 % during leg press jumps by measuring the resultant ground reaction impulses. Pain (2014) was also able to observe bilateral deficit during drop jumps by measuring peak concentric force and peak power.

On the other hand, Ebben et al. (2009) observed bilateral facilitation in jumping when testing athletes from different track and field disciplines. The authors attributed the results to the fact that most of the subjects were participating in throwing events. However, their explanation is difficult to accept, as throwing events are not strictly bilateral in nature, in contrast to sports such as weightlifting or rowing, where bilateral facilitation in isometric force production has been shown (Secher 1975; Howard and Enoka 1991).

Bilateral deficit is also present during explosive dynamic contractions of the leg muscles and can be as high as 35 % (Rejc et al. 2010, 2015; Samozino et al. 2014). Furthermore, bilateral deficit has been shown to exist in the rate of

Table 4 Summary of BLD literature using isometric handgrip with respective joint angles and postures

References	Joint angle (°)	Posture	Hand position	BLD	BI (%)
Cengiz (2015)	90	Seated	n/m	Yes	−9
Cornwell et al. (2012)	90	Seated	Neutral	Yes[a]	−1.3[a]
MacDonald et al. (2014)	90	Standing	n/m	No	–
Magnus and Farthing (2008)	0	Supine	n/m	No	–
Ohtsuki (1981)	90	Seated	Supinated	Yes	−4.3 to –14.0
Oda and Moritani (1995)	90	Seated	Neutral	Yes	−4.5 to –5.2
Oda and Moritani (1996)	90	Seated	Neutral	Yes	−3.9 to –4.9
Taniguchi (1997)	0	n/m	n/m	No	–
Van Dieën et al. (2003)	90	Seated	Supinated	Yes	−20 to –26.9

Joint angle—0° full extension (all data have been transformed accordingly), *BLD* bilateral deficit in force, *BI* bilateral index, *neutral* semi-pronated/supinated position, *n/m* not mentioned

[a] Left-handed subjects only

Table 5 Summary of BLD literature using explosive contractions

References	Movement	BLD	BI (%)[a]	EMG BLD	Subjects	R	LD
Bobbert et al. (2006)	Squat jump	Yes	–	Yes	Physically active ($n = 8$)—M—20 ± 4 years; 184 ± 9 cm; 74.2 ± 15.4 kg	Alternating one- and two-leg jumps	Yes
Buckthorpe et al. (2013)	Explosive knee extension	Yes (explosive F, RFD); no (MVC)	−11.2 (explosive F) to – 14.9 (RFD)	No	Physically active ($n = 12$)—M—23.9 ± 3.7 years; 168.8 ± 31.4 cm; 77.3 ± 6.9 kg	UL-BL-UL	–
Bračič et al. (2010)	Countermovement jump	Yes	−19.1	–	Elite male sprinters ($n = 12$)—22.41 ± 3.39 years; 177.58 ± 6.86 cm; 74.92 ± 5.23 kg	Yes	Yes
Challis (1998)	Squat jump	Yes	–	–	College basketball players—7 F—168 ± 3 cm; 64.39 ± 6.93 kg	No	–
Dickin et al. (2011)	Hip and knee extension	Yes	–	–	University-aged—12 M—21.1 ± 3.2 years; 181 ± 7 cm; 87.1 ± 17.1 kg	Yes	Yes
Ebben et al. (2009)	Countermovement jump	No (BLF)	–		Athletes—13 M, 10 F—20.4 ± 2.4 years; 92.4 ± 17.2 kg	Yes	No
Hay et al. (2006)	Leg press jumps	Yes	−16.6	Yes	Healthy males ($n = 5$)—27.8 ± 3.5; 176 ± 3 cm; 72.2 ± 4.7 kg	Yes	No
Pain (2014)	Drop jumps	Yes	−16.8 to –35.5	–	Elite endurance and power athletes—7 + 7—175 ± 9 cm; 72.5 ± 10.2 kg	Yes	–
Rejc et al. (2010)	Hip and knee extension	Yes	−30.5	Yes	Healthy—10 M—23.1 ± 2.2 years; 178 ± 7 cm; 74.9 ± 9.4 kg	Yes	–
Rejc et al. (2015)	Hip and knee extension	Yes	−18.1	Yes	Healthy—10 M—23.1 ± 2.2 years; 179.0 ± 7.1 cm	No	–
Samozino et al. (2014)	Hip and knee extension	Yes	−36.7	–	Athletes ($n = 14$)—M—26.3 ± 4.5 years; 181 ± 7 cm; 83.9 ± 18.3 kg	No	–
van Soest et al. (1985)	Countermovement jump	Yes	–	Yes	Volleyball players—10 M—23 ± 4 years; 193 ± 6 cm; 83.5 ± 10.0 kg	n/m	–
Veligekas and Bogdanis (2013)	Countermovement jump	Yes (girls); no (boys)	–	–	10-year-olds (59 M, 55 F) and 12-year-olds (24 M, 34 F)	No	–

BLD bilateral deficit in force (BI significantly different than 0), *BI* (%) bilateral index denoting the magnitude of bilateral deficit, *BLD EMG* bilateral deficit in electromyography, *R* randomization, *LD* limb dominance

[a] BI in force not reported

force development during explosive isometric contractions (Van Dieën et al. 2003; Buckthorpe et al. 2013).

The mechanism of bilateral deficit during explosive and ballistic movements appears to be different from other contraction types, as it can be explained, at least to a certain degree, by changes in force–velocity relationship (Bobbert et al. 2006; Samozino et al. 2014) or by differences in muscle coordination (Rejc et al. 2010).

Summary

Bilateral deficit has been shown in different movements and contraction types. It appears to be a more consistent phenomenon in dynamic contractions, with the magnitude being greater in lower body compared to the upper body movements. The available evidence also suggests that the magnitude of bilateral deficit increases with the velocity of contraction. In isometric contractions, bilateral deficit is less consistent compared to dynamic contractions. Furthermore, the literature is the least consistent in knee extension, possibly due to smaller postural stabilization requirements and ability to use counterbalances. Bilateral deficit is also exhibited in explosive and ballistic movements and likely stems from a different mechanism.

Possible underlying mechanisms of bilateral deficit

The underlying mechanisms of bilateral deficit have been a subject of debate among researchers since the discovery of the phenomenon. The mechanisms appear to be largely unknown due to their complexity. It is likely that more than one mechanism is at play under a given set of circumstances. Many mechanisms have been proposed over the years and these will be discussed below. For better representation, the possible mechanisms have been split into four factors, namely psychological, task related, physiological and neurophysiological, as suggested earlier (Aune et al. 2013). Additionally, some methodological considerations have been taken into account.

Psychological factors

Perceived exertion

Jakobi and Chilibeck (2001) suggested that bilateral deficit may simply be caused by differences in the perceived exertion between unilateral and bilateral movements, especially during contractions of the lower limb muscles. Seki and Ohtsuki (1990) told subjects to exert 25, 50 and 75 % of perceived maximal voluntary contraction (MVC) during unilateral and bilateral contractions. The forces produced by subjects resulted in bilateral deficit, which led the authors to suggest that bilateral deficit may simply be due to the inability to exert oneself to the same capacity during bilateral as compared to unilateral contractions. Vint and McLean (1999) observed that bilateral deficit is larger in perceived submaximal contractions, possibly due to greater perceived exertion of bilateral actions during submaximal efforts. Their results were later also replicated by Hernandez et al. (2003). However, when subjects are told to produce maximal force, it is assumed that exertion was maximal regardless of the contraction mode, especially if proper methodological guidelines are followed (Gandevia 2001). Therefore, the extrapolation of the results from perceived submaximal efforts to maximal ones should be made with caution, as it may not necessarily reflect the mechanisms occurring during maximal contractions.

Subject naïveté

Secher et al. (1988) have shown a reduction of bilateral deficit when subjects are given incorrect pre-information (the subjects were told that bilateral force should be greater than the sum of unilateral forces). Their results suggest that bilateral deficit may simply be a result of awareness of the phenomenon, or lack of it. However, Koh et al. (1993) found no influence of the correct information on the existence of bilateral deficit. In the experiment of Donath et al. (2014), a population of athletes performed unilateral and bilateral contractions on an isometric leg press on three separate days. On the first day, they were not given any information about the existence of bilateral deficit, while on the remaining days they were given the standardized false and standardized correct information, respectively. They did not find any influence of information on bilateral deficit, as it was clearly present regardless of the instruction given to the subjects. In any case, due to the possibility that awareness of bilateral deficit may influence the results, researchers are encouraged not to disclose this information to the subjects before testing.

Division of attention

The theory of division of attention suggests that a reduction of force will occur when two remote parts of the body generate force simultaneously and is based on the dual task theory in the field of cognitive psychology, which suggests that attention is a limited resource and may put constraints on performance (Takebayashi et al. 2009). Vandervoort et al. (1984) speculated that there was a diffusion of concentration between the two legs during bilateral effort, which would result in a reduced excitation of the motoneuron pool. However, since bilateral deficit has been shown

to be restricted to twin synchronous movements (Ohtsuki 1983) and contraction of homonymous limbs (Schantz et al. 1989; Howard and Enoka 1991; Herbert and Gandevia 1996), the attention demands of the task are an unlikely contributors to the existence of bilateral deficit.

Task-related factors

Familiarity with the task

Vandervoort et al. (1987) stated that everyday activity (e.g., gait) is usually reciprocal. Since the performance of a maximal strength task improves with learning (Rutherford and Jones 1986), it is possible that bilateral deficit may be simply due to the fact that individuals are unaccustomed to performing maximal bilateral tasks. Secher et al. (1988) also noted that the magnitude of bilateral deficit significantly decreased after familiarization. Familiarity with the task may also be responsible for the results of Howard and Enoka (1991) and Secher (1975) who showed bilateral facilitation, as participants in their studies were used to performing bilateral actions.

Postural stability and ability to use counterbalances

It was first suggested by Herbert and Gandevia (1996) that the ability to contract the muscles bilaterally may be limited by the ability to make appropriate postural adjustments, and that this may be especially the case for large muscle groups. Janzen et al. (2006) showed bilateral deficit to be present only in multi-joint exercises, which should have greater postural stability requirements, but not in single-joint exercise. Magnus and Farthing (2008) tested the contribution of the postural stability requirements to bilateral deficit by comparing the magnitude of bilateral deficit in the leg press and handgrip, exercises with greater and smaller postural stability requirements, respectively. They found the presence of bilateral deficit only in the leg press, but not the handgrip, thereby supporting the hypothesis that postural stability influences the existence and/or magnitude of bilateral deficit.

Recently, Simoneau-Buessinger et al. (2015) provided evidence to support the notion that expression of bilateral deficit is a result of the ability to use counterbalances, i.e., when a dynamometer allows for trunk torsion to the contralateral side of the limb, greater net torque can be produced during unilateral conditions, which in turn affects the expression of bilateral deficit. Therefore, the question that arises is whether this makes postural stability requirements redundant in terms of the expression of bilateral deficit. That is—are there really differences in postural stabilization requirements that affect torque production during different test contractions (unilateral vs. bilateral), or are postural requirements merely another term to describe the ability to use counterbalances to ones advantage?

In any case, if the goal is to study the mechanisms of bilateral deficit, experimenters should try to control postural stability requirements and/or limit the ability to use counterbalances by conducting testing on appropriately designed dynamometers.

Limb dominance

In the pioneering study of Henry and Smith (1961), it was proposed that bilateral deficit is due to force reduction in the dominant limb. The effect of limb dominance on bilateral deficit has been shown in several studies examining unilateral and bilateral contractions, yet not in others (Tables 1, 2, 4). However, it seems to be more prevalent in the upper than the lower body. This may be due to differences in the physical activity level between the upper and lower limbs in the activities of daily living, as lifetime assessments of physical activity have shown differences in activity level between dominant and non-dominant limbs in the upper, but not the lower body (Jakobi and Chilibeck 2001). Since left-handed individuals show less discrepancy between the strength of the dominant and non-dominant limbs (Crosby et al. 1994; Armstrong and Oldham 1999), it is also possible that the limb dominance effect on bilateral deficit is limited to right-handed individuals. However, this is not supported by Cornwell et al. (2012) who performed the only direct investigation of the effect of limb dominance on bilateral deficit. The subjects performed unilateral and bilateral handgrip contractions and were separated into groups based on handedness. Bilateral deficit was evident only in the left-handed group, and only the left hand of the left-handed group showed a significant reduction in force during bilateral contractions, despite the fact that the discrepancy between hand strength was smaller than in the right-handed group. Since some of the participants were stronger in their non-dominant hand, they later rearranged the groups based on strength dominance. A greater significance of force reduction of the left hand was observed for the left-hand-strength-dominant group, but only a trend for the same reduction was observed for the right-hand group. These results suggest that the effect of limb dominance on bilateral deficit may be restricted to left-handed individuals. However, the results may have been different had the right-handed subjects exhibited bilateral deficit. Furthermore, the degree of bilateral deficit was relatively small, only 1.3 %, compared to other studies investigating unilateral and bilateral handgrip contractions, where deficits between 5 and 22 % have been shown (Ohtsuki 1981; Oda and Moritani 1995; Van Dieën et al. 2003; Post et al. 2007).

In this light, it is interesting to note that Oda and Moritani (1995) observed a greater deficit in cortical activity in the non-dominant arm, while a greater deficit in force and EMG was observed for the dominant arm during bilateral handgrip contractions.

Physiological factors

Contribution of synergists, core muscles and antagonists

Antagonist activation has been shown not to be different during bilateral and unilateral contractions, and thus it appears not to have an effect on the existence of bilateral deficit (Howard and Enoka 1991; Koh et al. 1993; Jakobi and Cafarelli 1998; Cresswell and Overdal 2002; Van Dieën et al. 2003; Behm et al. 2003; Kuruganti et al. 2011; Buckthorpe et al. 2013). Moreover, Koh et al. (1993) and Simoneau-Buessinger et al. (2015) were able to show an even greater antagonist activation during unilateral compared to bilateral contractions, thus supporting the hypothesis of antagonist activation having no effect on bilateral deficit.

An interesting observation regarding antagonist activation came from the study of Cresswell and Overdal (2002) who investigated bilateral deficit during knee extension. During the unilateral performance, subjects were not given specific instructions with regard to the non-active leg and that limb was also not specifically fixed. They noticed a burst of hamstring EMG activity in the contralateral leg, which had also previously been shown by Howard and Enoka (1991). Furthermore, the subjects who activated the hamstrings in the contralateral leg during unilateral actions exhibited greater bilateral deficit compared to the subjects who did not (bilateral deficit of 21 vs. 14 %, respectively). They suggested that "afferent feedback produced by the contralateral hamstrings activation may interact in a facilitatory manner with the descending command to the quadriceps muscle performing unilateral extension", thereby increasing the force production of the agonist (Cresswell and Overdal 2002). However, this kind of crossed facilitation would usually be expected to result from the original action, i.e., extensors in this case, and not flexors, which questions their interpretation. Another possibility is that the contralateral hamstring activation contributed to increased stability, thereby increasing the torque of unilateral actions (Howard and Enoka 1991).

In terms of antagonist activation, it is also important to consider the actual mechanical contribution of the antagonist to net joint moment. Although EMG may provide an indication of antagonist activity, the extent to which it can be taken as an indicator of muscle force, and therefore joint mechanics, is limited (Kellis 1998). For example, in the case of knee extension, it is unlikely that countermoments associated with antagonist activity mathematically cancel out across sides (Krishnan and Williams 2010), especially due to significant variability in antagonist activity between the legs during isometric testing (Krishnan and Williams 2009). Therefore, even if differences in antagonist activation between unilateral and bilateral contractions were observed, whether this has a meaningful impact on torque production and/or a difference in torque production with different contraction modes and thus any effect on bilateral deficit is questionable.

Magnus and Farthing (2008) were the only investigators who assessed the contribution of core muscles to the bilateral deficit. They showed that the activity of core musculature was greater in leg press than in handgrip exercises, which corresponded to bilateral deficit in the leg press, but not the handgrip exercise. Differences in the activation of core muscles between unilateral and bilateral contractions were not noted between the exercises. However, Magnus and Farthing (2008) speculated that similar core activation may have created a disadvantage for bilateral conditions by providing smaller input to postural stability, since the ground reaction forces were likely higher in bilateral conditions. Exploring the potential lateral difference in the activity of the core muscles may also be worth considering in future research, as it may have an effect on net force production of the kinetic chain.

Co-activation of synergist muscles has often not been taken into consideration as a possible underlying mechanism of bilateral deficit. McCurdy et al. (2010) showed that activation of the gluteus medius was greater in modified single-leg squat compared to bilateral squat exercise. Since greater synergist contribution leads to greater net torque about a joint, this may explain the deficit observed during bilateral conditions. Further research in this area is warranted and researchers should try to include recordings of the synergist muscles. Considering that the ability to use counterbalances likely affects bilateral deficit, it seems plausible to hypothesize that synergist contributions would differ between contraction modes should a dynamometer allow for trunk torsion to the contralateral side of the limb. From this perspective, recording activity of the synergist muscles would provide a way to control or monitor counterbalances during the experiment.

Biomechanical mechanisms

Based on the available evidence, it seems possible that during ballistic actions such as human jumping or during explosive dynamic contractions, bilateral deficit may be simply explained by differences in force–velocity curves between unilateral and bilateral actions. This has been

suggested to be the case despite a tendency for EMG activity to be coupled with bilateral deficit in force (Bobbert et al. 2006).

A comparison of one-legged and two-legged countermovement jumps by van Soest et al. (1985) showed the presence of bilateral deficit during human jumping. They noted many differences in performance of one-legged and two-legged jumps. The main one was that the work production per leg in a two-legged jump was less than in one-legged jumps. This finding led the authors to believe that the force–velocity relationship may contribute to the existence of bilateral deficit. However, after observing that differences in length and contraction velocities were relatively small, they discarded this hypothesis.

Bobbert et al. (2006) found that during squat jumps there is a large bilateral deficit in peak joint moments (20–30 %) and suggested that differences in the contractile conditions of the muscles could explain their results. Since the velocity of the center of mass was greater in two-leg compared to one-leg jumps, the extensor muscles will have shortened at higher velocities in the two-leg jump and therefore produced less force and consequently less work. Also, it is important to consider that the body weight is equally distributed between two legs during the two-legged jump, which results in the muscles of individual legs having a reduced active state in the initial equilibrium position. Therefore, it seems plausible that in the initial part of the range of motion, the muscles in the two-legged jump are submaximally active (Bobbert et al. 2006). As stated by Bobbert et al. (2006), this consideration is especially important in squat jumps, since they do not involve a preparatory countermovement that allows for a development of the active state of the extensor muscles (Bobbert and Casius 2005). Furthermore, Bobbert et al. (2006) performed a musculoskeletal model simulation and showed that as much as 75 % of the bilateral deficits can be explained by higher shortening velocities in the two-legged jump, which suggests that differences in the force–velocity relationship may be a possible underlying mechanism of the phenomenon.

It has to be noted that the body position differs between one- and two-legged jumps, which could have had an effect on the differences reported by Bobbert et al. (2006). Furthermore, the average push-off time appears to be longer in unilateral compared to bilateral jumps (Bobbert et al. 2006), but this is likely the result of differences in the amount of load between conditions, that is–the load is larger during unilateral jumps.

Rejc et al. (2010) investigated explosive combined hip and knee extensions against different loads and showed that bilateral actions are characterized by a displacement of the force–velocity curve to a lower level compared to unilateral actions (Fig. 4). It is also important to note that

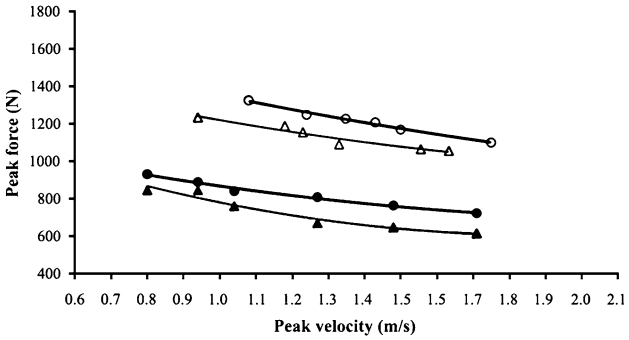

Fig. 4 *F–V* relationships for UL and BL contractions during explosive hip and knee extension. *Thick curves* right limb, *thin curves* left limb, *filled circles and triangles* right and left bilateral actions, respectively; *open circles and triangles* right and left unilateral actions, respectively (Rejc et al. 2010)

mean pushing times and shortening velocities did not differ between unilateral and bilateral contractions, suggesting that bilateral deficit is due to different force outputs in the bilateral versus unilateral condition. Subsequent work performed by the same research group included modeling the external dynamic mechanical capabilities of the lower limb via force–velocity relationship during unilateral and bilateral explosive combined hip and knee extension (Samozino et al. 2014). They showed that about 43 % of bilateral deficit in ballistic actions could be explained by a shift in force–velocity relationship due to a change in movement velocity, with the remaining part attributed to a shift in force–velocity relationship due to neural factors. Furthermore, the non-neural mechanism of bilateral deficit appears to be highly individual, as lower bilateral deficits were observed in subjects with force–velocity relations oriented toward velocity capabilities.

Recruitment pattern of motor units and inhibition of types of muscle fibers

One of the objectives of older research about the mechanisms of bilateral deficit was the investigation of inhibition of motor units during bilateral actions (Archontides and Fazey 1993). The first investigations used pharmacological agents to block a certain muscle fiber type and concluded that bilateral deficit may be caused by selective inhibition of type I muscle fibers (Secher 1976; Secher et al. 1978). The problem with this conclusion is that it violates the principle of orderly recruitment of MUs (Henneman 1957). Furthermore, as pointed out by Archontides and Fazey (1993), when Secher et al. (1976, 1978) blocked type I fibers, bilateral deficit was still present, albeit to a lesser extent.

Many studies have found that bilateral deficit increases in magnitude with increasing speed of contraction

(Vandervoort et al. 1984; Koh et al. 1993; Dickin and Too 2006; Buckthorpe et al. 2013). Since it has been shown that type II fibers contribute more to force production at high velocities (Thorstensson et al. 1976; Coyle et al. 1979; Tihanyi et al. 1982; Moritani et al. 1991), it has been suggested by many researchers that bilateral deficit may be due to the inhibition of type II muscle fibers during bilateral contractions. Koh et al. (1993) investigated differences in bilateral deficit during step and ramp contractions. They found that the deficit was greater when force was produced rapidly compared to when the force was increased linearly. Therefore, they suggested that bilateral deficit could be explained by inhibition of type II muscle fibers (Koh et al. 1993). Interestingly, Buckthorpe et al. (2013) investigated bilateral deficit using explosive force, rate of force development and maximal voluntary contraction (MVC). The existence of bilateral deficit was limited to explosive force (force in the first 100 ms) and rate of force development. However, no changes in the EMG activity were noted. On the other hand, Owings and Grabiner (1998a) showed that the magnitude of bilateral deficit was the same when isokinetic knee extensions were performed at 30°/s and 150°/s, respectively, which is in contrast to investigations using similar velocities (Vandervoort et al. 1984; Dickin and Too 2006). Furthermore, Brown et al. (1994) showed that the magnitude of bilateral deficit decreased with increasing speed of isokinetic contractions from 60°/s to 240°/s, and was actually absent at 360°/s thereby contradicting the findings of other studies. However, it should be noted that the above-mentioned velocities are still considered slow, when compared with maximal human movement angular velocities (e.g., sprinting), and are thus unlikely to be accompanied by significant differences in recruitment patterns.

Kawakami et al. (1998) tested the hypothesis that the magnitude of bilateral deficit would be greater in muscles consisting of predominantly type II muscle fibers by investigating bilateral deficit during plantar flexion. By manipulating knee joint angle, they were able to distinguish between the contribution of gastrocnemius, a muscle with a greater percentage of type II muscle fibers (Johnson et al. 1973), and soleus to the plantar flexion. They found that bilateral deficit was greater when the knee was extended, i.e., at the point of greater gastrocnemius contribution to the movement, supporting the hypothesis of inhibition of type II fibers.

Research by Burke et al. (1973) showed that MUs exhibiting sag in response to electrical stimulation, which were classified as fast twitch, were also the ones to exhibit a substantial decrease in force in response to repeated electrical stimulation and were thus classified as fatigue sensitive. Based on these findings, many researchers have investigated the effects of fatigue on bilateral deficit to elucidate the role of fiber type and/or recruitment of MUs in bilateral deficit. Vandervoort et al. (1984) showed that there was a smaller decline in bilateral as compared to unilateral force over the duration of a concentric combined hip and knee extension fatigue test. Based on the hypothesis that high-threshold MUs are more fatigable, a smaller decline in bilateral force led the authors to suggest that there was a reduction in recruitment of high-threshold MUs during bilateral contractions. However, during the bench press exercise fatigue test, the bilateral actions were more susceptible to fatigue (Vandervoort et al. 1987). Vandervoort et al. (1987) tried to explain these results by differences in the training level of the muscles, familiarity of the movement patterns used in both investigations and/or differences in the fiber-type distribution between different muscles, respectively. However, regarding repeated unilateral and bilateral contractions, there are also other confounding factors that need to be considered. Specifically, there are systemic influences associated with fatigue, such as the so-called non-local muscle fatigue (Halperin et al. 2015), which are difficult to account for and are likely both neurological and biochemical in nature (Halperin et al. 2015). There is also some ambiguity as to whether unilateral or bilateral contractions are more susceptible to these systemic influences associated with fatigue (Halperin et al. 2015). Furthermore, there may be differences associated with the contribution of synergist muscles between unilateral and bilateral tasks that may be potentiated when repeated contractions are performed. It is also unclear whether there are related differences between unilateral and bilateral contractions during closed (e.g., combined hip and knee extension) versus open kinetic chain exercise (e.g., bench press). In a similar line of research, Owings and Grabiner (1998a) only showed an increase in the magnitude of bilateral deficit after a fatiguing leg extension protocol performed at 30°/s, but not at 150°/s. Their results suggest a speed-dependent influence on bilateral deficit following fatigue, but, as stated by the authors, contradict the hypothesis that bilateral deficit may be caused by inhibition of type II muscle fibers. However, as mentioned before, the velocities used in the experiment may be considered slow and may not be accompanied by significant differences in recruitment patterns. Furthermore, it is difficult to account for systemic influences of a fatigue protocol and how much they confound the post-measures and subsequently the expression of bilateral deficit. Thus, drawing conclusions about inhibition of any type of muscle fiber and/or MU needs to be done with caution. In this context, it has to be noted that the scheme proposed by Burke et al. (1973) has failed to identify discrete types of MUs in human muscles, and the properties of MUs are likely distributed continuously within an MU population (Heckman and Enoka 2012; Enoka and Duchateau 2015). Furthermore, fatigability of MUs is classified based on electrical stimulation of MUs and cannot be so easily extrapolated to

voluntary contractions, where many impairments that cause fatigue are at play (Heckman and Enoka 2012). Hence, the basis for this line of research appears to be weak and should be interpreted with a degree of caution.

An indirect way to assess the recruitment of MUs during a contraction is to perform EMG power spectrum analysis. It is based on the idea that muscle fiber diameters and their corresponding conduction velocities are related to MU type, with discharge rate having a negligible effect on the power density spectrum (Lago and Jones 1977). Oda and Moritani (1994) showed a shift to lower values of median power frequency during bilateral compared to unilateral contractions, albeit only in the dominant arm, and therefore suggested that bilateral deficit in neural activation may be due to decreased activation of high-threshold MUs. Khodiguian et al. (2003) measured force output during reflexively evoked contraction, i.e., after induction of patellar myotatic reflex with a patellar tendon strike, as well as during the MVC. They were also able to show a decrease in peak power frequency of the EMG signal during reflexively evoked bilateral compared to unilateral contractions, which suggests inhibition of the high-threshold MUs. They further supported this hypothesis by showing that during reflexively evoked contractions, the premotor time was longer in the bilateral condition. However, they were not able to replicate this during MVC; thus, their findings should be interpreted with a degree of caution. Other studies that have analyzed the EMG power spectrum (Schantz et al. 1989; Koh et al. 1993) have not been able to show any differences between unilateral and bilateral actions. Koh et al. (1993) suggested that median frequency may not be sensitive enough to indicate differences in the relative contribution of low- and high-threshold MUs between unilateral and bilateral conditions. Overall, interpretation of the power density spectrum needs to be made with caution. As pointed out by Farina et al. (2014), there are four factors that confound the extrapolation of findings from power density spectrum analysis: two main fiber types may differ in diameter, but not have distinct conduction velocities; the average conduction velocity may be confounded by skewed distribution of the number of muscle fibers innervated by a MU; the contribution of a MU to average conduction velocity varies with discharge rate; and the discharge rate varies with shortening of muscle fibers during dynamic contractions.

Neurophysiological factors

Muscle activity (EMG)

Surface EMG has been applied concurrently with force recordings in many investigations concerning the differences between unilateral and bilateral contractions. There is some ambiguity in the literature with regard to the parallelism between force and EMG, as some studies have shown that bilateral deficit in force follows the same trend in EMG activity, while others did not show such coupling (see Tables 1, 2, 4). If bilateral deficit in EMG activity is present, it may be attributable to changes within muscles fibers, changes in motoneuron excitability and/or cortical excitability (Post et al. 2007).

The equivocal nature of this particular line of research is a topic of debate. Howard and Enoka (1991) suggested that since the magnitude of force change is relatively small between bilateral and unilateral contractions, it is less likely to be detected with surface EMG. An important consideration is also the force–EMG relationship, which tends to be curvilinear and may only exhibit linearity at high force values (Lawrence and De Luca 1983). Hence, small changes in maximum force are unlikely to be detected with EMG. The force–EMG relationship also seems to be muscle dependent and is influenced by factors such as motor unit recruitment and rate coding properties, relative amounts and location of motor unit types, viscoelastic properties and cross talk from adjacent muscles (Lawrence and De Luca 1983). Furthermore, it has also been suggested that different contributions of antagonists and/or synergists could have an effect on EMG activity of the agonist, thereby causing this discrepancy (Herbert and Gandevia 1996; Post et al. 2007).

Solomonow et al. (1990) warned against using EMG to predict force, since different muscles use different recruitment strategies to produce force. Therefore, it could be argued that investigating different muscles could be responsible for the discrepancy in the literature. However, Howard and Enoka (1991) did not show coupling between force and EMG during knee extension, while Van Dieën et al. (2003) did, despite the fact that they both investigated the vastus lateralis muscle. It is also possible that differences in electrode locations are responsible for this discrepancy, as surface EMG recordings are largely dependent on it. It should also be noted that when typical surface EMG recordings are performed using mono- or bipolar electrode configurations, activity is only recorded from a small portion of MUs in the muscle investigated. This issue can be circumvented by using multichannel surface EMG with array electrodes that allow activity to be recorded from a larger area of the muscle (Zwarts and Stegeman 2003). This technique has not been applied to date in relation to bilateral deficit and may be worth considering for future investigations.

Howard and Enoka (1991) also showed that the EMG–force relationship varies greatly between subjects and between unilateral and bilateral contractions. For example, they showed that the parallelism between EMG and force was observed only for highly trained weightlifters, but no such trend was observed for cyclists or untrained

individuals. Therefore, differences between studies could be explained by the variability of EMG and force recordings.

Interpretation of EMG signals is also greatly influenced by the methodological approach, i.e., quantification of EMG amplitude, the time period of integration and normalization procedure. Additionally, EMG amplitude cancelation can vary and therefore underestimate the amount of MU activity (Keenan et al. 2005). Siegler et al. (1985) also indicated that different signal processing may lead to slight variations in the EMG–force relationship. It is also noteworthy that small fluctuations in MU activity are not detectable with EMG (Farina et al. 2014). It is possible that differences between unilateral and bilateral contractions in terms of MU activity were too small in some studies to detect any significant difference.

It is important to note that the amplitude of the EMG signal is not a direct indicator of muscle activation (Farina et al. 2010). Therefore, if the parallelism between force and EMG recordings with regard to bilateral deficit is not observed, the possible effect of neural factors should not be discounted. This is especially the case with dynamic contractions, where changes in muscle length occur (Farina 2006), which may be the reason for greater consistency of coupling between force and EMG bilateral indices in isometric compared to dynamic contractions (81 vs. 40 %, respectively; see Tables 1, 2).

The only study that investigated the discharge rate of MUs during unilateral and bilateral contractions was that of Jakobi and Cafarelli (1998). A difference in MU recruitment and firing rates between unilateral and bilateral contractions would indicate that the motoneuron pool modulates unilateral and bilateral contractions differently. They showed that average MU firing rates did not differ between contractions performed with one limb or two limbs concurrently, irrespective of the intensity of the contraction. However, these recordings were obtained during submaximal, but not maximal, contractions. Furthermore, they did not observe bilateral deficit in force. Therefore, it remains unclear whether discharge rate would have differed between unilateral and bilateral actions had bilateral deficit been observed and/or had recordings been performed during maximal efforts.

Rejc et al. (2010) also investigated intermuscular coordination with the use of integrated EMG of rectus femoris, vastus lateralis, biceps femoris and gastrocnemius, during explosive bilateral and unilateral contractions of combined hip and knee extension against different loads (based on percentage of body mass). They calculated the dispersion index from the algebraic sum of integrated EMG values of each pair of muscles, and plotted values at different time windows, thereby obtaining an index of the time course of muscle coordination (Fig. 5). They showed that the muscles

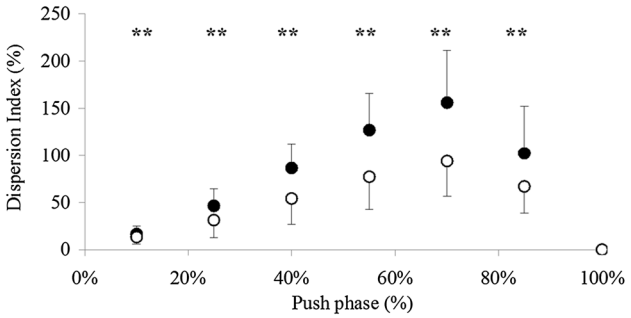

Fig. 5 Differences in dispersion index between bilateral (*filled circle*) and unilateral (*open circle*) contractions at different time points during the concentric (push) phase of explosive hip and knee extension; $^{**}p < 0.001$ (Rejc et al. 2010)

investigated followed a different time course in bilateral and unilateral contractions, suggesting that intermuscular coordination may play a role in bilateral deficit. Whether the same principle applies to one-joint, non-explosive and/or isometric contractions remains unclear.

Spinal mechanisms

There appears to be a shared neural network between contralateral limbs as evidenced by cross-extensor reflexes (Sherrington 1910) and the cross-education phenomenon (Carroll et al. 2006). Furthermore, this shared neural network may play a role in non-local effects of fatigue (Halperin et al. 2015) and stretching (da Silva et al. 2015; Behm et al. 2016). Therefore, it has also been proposed that peripheral reflex systems may contribute to the existence of bilateral deficit (Ohtsuki 1983). Delwaide et al. (1988) showed that activation of the contralateral arm increases the degree of reciprocal inhibition, suggesting an effect of Ia afferents on the contralateral limb. Kawakami et al. (1998) measured H-reflexes from one leg, while the contralateral leg was relaxed or maximally contracting. They showed that H-reflex amplitude was smaller in the MVC condition, which led them to suggest that motoneuron excitability was reduced in the bilateral condition. Furthermore, they speculated that contraction of one leg would result in sensory input to the spinal cord, thereby inducing inhibition of motoneurons in the contralateral leg. However, Howard and Enoka (1991) contradicted the theory of spinal reflexes, as electrical stimulation of one limb caused facilitation in the contralateral limb. As suggested by Kawakami et al. (1998), the stimulation may have also resulted in the withdrawal reflex, thereby facilitating the crossed-extensor reflex in the contralateral limb.

Khodiguian et al. (2003) found bilateral deficit in force and EMG activity for reflexively evoked contractions, but could not replicate the existence of bilateral deficit during

MVC, which makes the contribution of spinal reflexes to the phenomenon difficult to interpret. It may very well be that modulation of reflexively evoked and maximal voluntary contractions are different, which would make comparisons redundant. Khodiguian et al. (2003) observed that subjects who exhibited the strongest reflex were also those who showed the greatest withdrawal of the contralateral leg. Furthermore, they suggested that during bilateral actions, it is possible that two opposing inputs were at play, namely an excitatory input of ipsilateral Ia afferents and indirect inhibitory input from the contralateral Ia afferents, which would mean that bilateral deficit may be caused by mutual contralateral inhibitory inputs.

Perez et al. (2014) performed transcranial magnetic stimulation during unilateral and bilateral contractions, concurrently with cervicomedullary stimulation, a stimulation of the descending tracts at the cervicomedullary junction, which evokes a short-latency response termed cervicomedullary motor evoked potential (Taylor 2006). Cervicomedullary motor evoked potentials are not affected by changes in cortical excitability and presynaptic inhibition and can therefore be used to measure changes in spinal motor neuronal excitability (Taylor 2006). Perez et al. (2014) showed that cervicomedullary motor evoked potentials remained unchanged during bilateral compared to unilateral actions, suggesting that the spinal mechanisms are not different during unilateral and bilateral contractions. It is important to note, however, that they performed the measurements during low-force contractions (10–30 % of MVC). It is therefore unclear whether they would have observed similar results had they performed maximal contractions. As already mentioned, modulation of unilateral and bilateral actions may not necessarily be the same between submaximal and maximal contractions.

Voluntary activation level

The assessment of voluntary activation level of a muscle can be performed using the interpolated twitch technique first described by Merton (1954). This technique involves applying supramaximal electrical stimuli either to the nerve trunk or intramuscular nerve branches during maximal voluntary contraction. Those MUs that have not been recruited or fired at submaximal rates respond with a twitch-like force increment, suggesting that the agonist was not activated to its fullest capacity (Belanger and McComas 1981). Studies that investigated the extent of voluntary activation during unilateral and bilateral actions show somewhat conflicting results. Although they all show near-complete muscle activation during both bilateral and unilateral contractions, not all of them have shown differences between contractions performed with one or two limbs concurrently. Herbert and Gandevia (1996) showed that voluntary activation level is greater during unilateral than bilateral thumb contractions (90.3 vs. 88.6 %, respectively). Similarly, Van Dieën et al. (2003) reported significantly greater activation level during unilateral compared to bilateral isometric knee extensions (94 vs. 89 %, respectively; voluntary activation level deficit of 3.5 %) and a strong relationship between bilateral deficit and voluntary activation level ($r = 0.80$), suggesting that reduced neural drive may underlie the phenomenon. Conversely, Behm et al. (2003) reported significantly smaller voluntary activation measured with the interpolated twitch technique during unilateral compared to bilateral knee extensions in both resistance-trained and untrained individuals. In contrast, Jakobi and Cafarelli (1998) were not able to show a difference in activation level between unilateral and bilateral contractions. However, despite not reaching statistical significance, the relative level of voluntary activation during unilateral and bilateral contractions was similar to other studies (93.6 vs. 90.1 % for unilateral and bilateral contractions, respectively). Matkowski et al. (2011) were also not able to find any differences in voluntary activation between unilateral and bilateral contractions (roughly 91 % for both). Their methodology was unique compared to other studies insofar as they applied the interpolated twitch technique in both legs simultaneously during bilateral actions. It is important to note that the majority of the above-mentioned studies reported large variability between subjects. As suggested by Jakobi and Chilibeck (2001), it is possible that this variability between subjects may account for general differences between studies with regard to the existence of bilateral deficit.

Higher-order neural inhibition

According to Beaulé et al. (2012), execution of strictly unilateral movement is a result of complex interhemispheric interactions between comprehensive cortical areas. Gazzaniga and Sperry (1966) observed that reaction time was longer for bilateral than unilateral contractions, while there was no difference if the subjects had had the two hemispheres surgically sectioned. Based on their findings, Ohtsuki (1983) was the first to suggest that the force deficit observed during bilateral actions may be due to interhemispheric inhibition. The latter is mediated by transcallosal fibers passing through the corpus callosum, as it has been shown to be absent or have a delayed onset latency in patients with radiographical abnormalities in the corpus callosum (Meyer et al. 1995, 1998).

In the classic study of Ferbert et al. (1992), it was observed that the amount of interhemispheric inhibition, quantified using paired-pulse transcranial magnetic stimulation, increased in the relaxed right first dorsal interosseous muscle when the left was active at the same time, suggesting

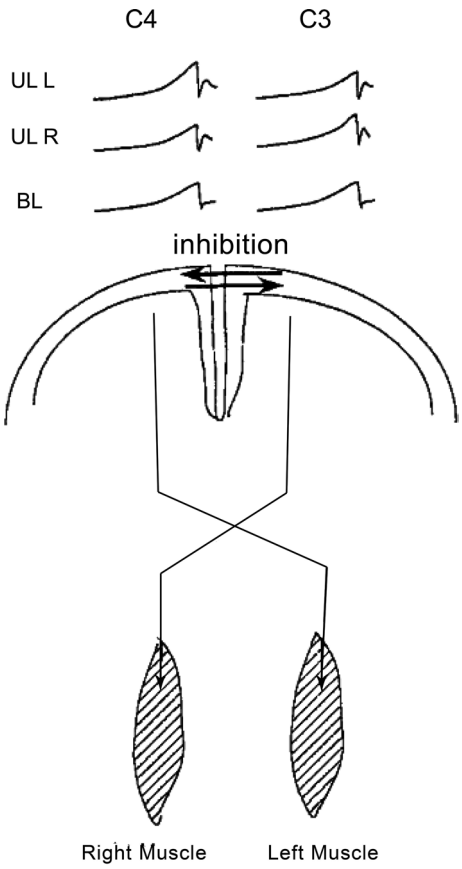

Fig. 6 Interhemispheric inhibition and corresponding movement-related cortical potentials during unilateral and bilateral handgrip contractions (Oda and Moritani 1995)

that there is a difference in voluntary control of bilateral versus unilateral contractions. They proposed that transcallosal connections could inhibit the activity on one hand and thus ensure strictly unilateral movement. Oda and Moritani (1995) recorded movement-related cortical potentials with electroencephalography during unilateral and bilateral maximal handgrip contractions. They showed that during unilateral contractions movement-related cortical potentials were most prominent in the contralateral hemisphere. However, during bilateral contractions, symmetrical movement-related cortical potentials of lower amplitude were evident (Fig. 6). This was later confirmed in another study done by the the same researchers (Oda and Moritani 1996). In that study, they also showed that a common drive exists between the motor cortices in the modulation of maximal bilateral contractions. They suggested that this common drive may be associated with interhemispheric interactions, possibly suppressing the potentials of opposite hemispheres so that the amplitude of both movement-related cortical potentials becomes very similar (Oda and Moritani 1996). These results suggest that the underlying mechanism of bilateral deficit is inhibition of the primary motor cortex. In theory, this should reflect lower voluntary activation level in bilateral actions, compared to unilateral ones, but this has not always been shown to be the case (see previous section).

As already mentioned, an interesting finding from the study of Oda and Moritani (1995) was that a greater deficit was shown in cortical activity in the non-dominant (left) arm, whereas a greater deficit in force and EMG was shown for the dominant (right) arm during bilateral handgrip contractions. As postulated by Oda (1997), this discrepancy indicates that the effect of changes in cortical activity in the right hemisphere is smaller than the effect of changes in the left hemisphere. Oda (1997) also stated that a possible contribution of decreased neural input to both motor cortices and/or inhibitory mechanisms in other brain stem pathways should be considered as possible underlying mechanisms of bilateral deficit.

Post et al. (2007) recorded brain activity with functional magnetic resonance imaging along with force and EMG recordings during unilateral and bilateral abductions of the index finger. They observed a significant decline in the blood oxygen-dependent response in the precentral gyrus during bilateral actions, thereby decreasing the input to the primary motor cortex. This expands on the observation of Oda and Moritani (1995) that the underlying mechanism of bilateral deficit is supraspinal, but its origin may be located upstream of the primary motor cortex.

A recent study by Perez et al. (2014) examined ipsilateral silent period after transcranial magnetic stimulation during unilateral and bilateral elbow flexion and extension. Ipsilateral silent period is a pause in the ongoing EMG activity in the ipsilateral muscles after the application of transcranial magnetic stimulation, and is, similarly to the paired-pulse paradigm described by Ferbert et al. (1992), a way of assessing interhemispheric inhibition (Wassermann et al. 1991; Ferbert et al. 1992; Giovannelli et al. 2009). Perez et al. (2014) showed that in both movements, the depth and area of ipsilateral silent period, indices of interhemispheric inhibition, were increased during bilateral compared to unilateral contractions. Their study was also in line with investigations of bilateral and unilateral contractions of the finger muscles, which have shown that interhemispheric inhibition is more pronounced during bilateral compared to unilateral contractions (Yedimenko and Perez 2010; Soteropoulos and Perez 2011). However, caution needs to be exercised when interpreting their findings as the measurements were performed during low-force contractions, i.e., 10–30 % of MVC (Perez et al. 2014), and may not necessarily reflect motor control during MVC.

Archontides and Fazey (1993) also provided a cortical explanation as to why bilateral deficit is limited to twin synchronous movement of homonymous limbs. They suggested that this is due to the fact that the area controlling the flexor on one side of the body is not interconnected

with the area that controls the extensor on the contralateral side of the body.

The existence of higher-order neural inhibition is also supported by different magnitudes of bilateral deficit in proximal compared to distal muscles (Aune et al. 2013). Aune et al. (2013) tested the theory that different levels of bilateral deficit will be observed in muscles with different anatomical and physiological characteristics. It has been shown in primates that the number of transcallosal projections is greater in proximal compared to distal muscles (Pandya and Vignolo 1971; Gould et al. 1986; Rouiller et al. 1994), while the number of corticospinal projections is greater in distal compared to more proximal arm muscles (Kuypers 1978; Palmer and Ashby 1992). Based on these findings, Aune et al. (2013) suggested that the more direct connection between the cortex and distal muscles could potentially result in smaller interhemispheric inhibition. They were able to show that bilateral index was greater in shoulder flexion (proximal) compared to index finger flexion (distal), thereby supporting the contribution of higher-order neural inhibition to the bilateral index. Since they restricted movement so that only one degree of freedom could be performed, their results suggest that the differences in bilateral deficit could not have been due to different postural stability requirements as suggested before (Herbert and Gandevia 1996; Magnus and Farthing 2008). However, they did not perform any direct measures of interhemispheric inhibition (e.g., via electroencephalography or transcranial magnetic stimulation). Future studies should try to replicate their hypothesis with the inclusion of interhemispheric inhibition measures to confirm the cortical mechanism.

It should be noted that all the aforementioned findings are based on contraction of the upper limbs. However, neuronal control has been shown to differ between the upper and lower limbs (Luft et al. 2002; Volz et al. 2015). Recently, our research group employed transcranial magnetic stimulation and peripheral nerve stimulation during maximal unilateral and bilateral knee extensions (Škarabot et al., manuscript in preparation). Based on unaltered silent periods, we could not support the concept of inhibition at the cortical level in relation to bilateral deficit. On the other hand, higher amplitudes of motor evoked potentials and voluntary activation level during bilateral compared to unilateral contractions suggest the involvement of facilitatory mechanisms. Therefore, more research is needed; specifically, upper and lower limbs should be treated separately and later compared.

Summary

Many psychological, task-related and physiological mechanisms have been proposed over the years to try to explain the occurrence of bilateral deficit. Perceived exertion, subject naïveté and division of attention are unlikely contributors to the phenomenon. Familiarity of the task may, at least to a degree, explain bilateral deficit or influence its magnitude. Postural stability requirements and/or the ability to use counterbalances likely have an effect on the expression of bilateral deficit, and their control in experiments appears to be of paramount importance. The effect of limb dominance on bilateral deficit is highly variable across studies and some evidence suggests that it may be restricted to left-handed individuals only. Ipsilateral activation of antagonists has largely been discounted as the mechanism of bilateral deficit. However, some evidence suggests that antagonist activation of the contralateral leg can influence bilateral deficit, which warrants its control in experiments. Co-activation of synergists has not been studied, but it may potentially influence the net torque about the kinetic chain and may be different between unilateral and bilateral actions. In terms of biomechanical mechanisms, differences in shortening velocities between unilateral and bilateral actions, and displacement of the force–velocity curve during bilateral actions have been observed, but these mechanisms are likely restricted to ballistic and explosive contractions. Differences in recruitment patterns of MUs between unilateral and bilateral contractions and inhibition of type II fibers during bilateral actions have been extensively studied to try to explain the bilateral deficit. However, the results of these studies are largely contaminated by methodological limitations.

With regard to neurophysiological mechanisms, bilateral deficits in force and EMG have not always been shown in parallel. This may be due to variability of EMG recordings, differences in data analysis and signal processing methods between studies, EMG amplitude cancelation and other factors. Furthermore, it seems plausible that differences in EMG activity between bilateral and unilateral actions are too small to be detected. Despite this variability of the results, possible neural factors should not be discounted. Studies employing the interpolated twitch technique have been able to show near-complete muscle activation in both unilateral and bilateral contractions, but not all studies have noted differences between contraction modes. They have, however, consistently observed large variability between subjects. The potential inhibition of spinal reflexes during bilateral actions remains equivocal, largely due to lack of data from maximal contractions. A strong case has been made for interhemispheric inhibition through a transcallosal pathway as the mechanism of bilateral deficit based on recordings of brain activity. Additional evidence from functional magnetic resonance imaging suggests that the mechanism is supraspinal, but it may be upstream of the motor cortex. However, these findings are based solely on upper limb muscles, and considering the literature

suggesting differences in neuronal control of upper and lower limbs, more research is warranted that includes lower limb muscles.

Methodological considerations

There are also some methodological factors that could contribute, at least to a certain degree, to the existence and/or magnitude of bilateral deficit. Firstly, since only a small number of unilateral and bilateral contractions are usually performed during experiments and the comparison is usually performed between the peak values, the results could potentially favor unilateral performance (Buckthorpe et al. 2013). Therefore, it is suggested that future research also considers calculation of bilateral index by taking the average value of all trials as a representative of bilateral and unilateral forces, respectively.

Secondly, it has been suggested that since bilateral actions rely on performance of two limbs at the same time, it seems unlikely that both limbs operate at their highest force-producing capacity, which could contribute to bilateral deficit irrespective of physiology (Buckthorpe et al. 2013). Buckthorpe et al. (2013) tested this hypothesis by recording forces from each limb separately during bilateral actions and found no differences in force between the limbs. Similarly to Matkowski et al. (2011), they also found only a small onset of force discrepancy between the limbs, suggesting that the neuromuscular system is capable of almost simultaneous activation of both limbs during bilateral actions.

Thirdly, Simoneau-Buessinger et al. (2015) hypothesized that the type of dynamometer used in studies may influence the expression of bilateral deficit. If a dynamometer allows for counterbalances, torques in other parts of the body could potentially influence the net torque of the examined body part (Simoneau-Buessinger et al. 2015). By using a special dynamometer with two settings, one that allowed the body adjustments to take place (locked-unit) and one which did not (open-unit), they were able to show that mechanical configuration of the dynamometer may be responsible for differences between unilateral and bilateral contraction torques. The principles of this study should be replicated in other muscles, and possibly coupled with other methodological tools to discount the influence of other mechanisms.

Lastly, experiments often use a design where one limb, i.e., unilateral condition, acts as a control. However, the decision as to what constitutes a control condition seems to be random. Considering that physiology acts in a systemic manner (e.g., neurological cross talk), the bilateral condition may be a more suitable control. From this perspective, the issue that presents itself is whether we are still considering this phenomenon as bilateral deficit, or whether a more suitable term would be unilateral facilitation. Moreover, when training influences this phenomenon, bilateral facilitation has been shown to occur. However, let us consider a hypothetical situation where training also causes greater neural drive (measured via EMG, interpolated twitch or some other technique) during bilateral conditions, with minimal or no change in unilateral conditions. In this case, bilateral facilitation should actually be regarded as unilateral deficit.

Effect of training on bilateral deficit

Physiological alterations as a result of strength training have been shown to be very specific (Sale and MacDougall 1981). Therefore, it is to be expected that the type of training performed has an effect on bilateral deficit. Available literature consistently shows that bilateral training reduces bilateral deficit, while unilateral training increases it (Weir et al. 1995; Häkkinen et al. 1996a; Taniguchi 1997, 1998; Kuruganti et al. 2005; Janzen et al. 2006; Beurskens et al. 2015). The mechanism of change in magnitude of bilateral deficit due to training has not been explored specifically, but, based on the existing literature in strength training, is likely of spinal origin (Aagaard et al. 2002). Interestingly, 35 days of bed rest did not affect the existence or magnitude of bilateral deficit (Rejc et al. 2015), despite previous findings suggesting that prolonged disuse alters MU recruitment patterns and muscle activation strategy, as evidenced by decreased voluntary activation levels and reductions in EMG activity (Duchateau 1995; Shinohara et al. 2003; Narici and De Boer 2011).

However, what is generally not accounted for in longitudinal studies is the cross talk that likely occurs in the process. The phenomenon of cross-education, whereby unilateral strength training increases the strength of the contralateral, untrained limb (Carroll et al. 2006) may potentially mask and/or confound the effects of a training intervention on bilateral deficit, especially when unilateral training is employed. While so-called cross talk does not represent a problem in acute studies of maximal contractions, as even familiarization produces only a small bias in within-subject designs (Carroll et al. 2006), the contralateral effect of strength training is very much real, albeit small (Carroll et al. 2006). Muscular adaptations are likely not a significant confounding factor, as both cross-education and bilateral deficit phenomena seem to be limited to homologous limbs, and systemic influences driven by hormonal mediators, changes in enzyme concentrations and contractile protein composition should have affected the nonhomologous limbs similarly (Carroll et al. 2006). However, muscular adaptation could potentially be driven by a

small degree of activity in the contralateral leg during unilateral training and similar activity between the limbs during bilateral training. On the other hand, neural adaptations (Carroll et al. 2006), both spinal and supraspinal (Kidgell et al. 2015), likely play a role, and it is unknown whether these are similar between unilateral and bilateral strength training. Thus, it is difficult to establish a true control condition when examining alterations in bilateral deficit before and after a training intervention.

Cross-sectional studies of specific populations of athletes remain equivocal. Based on longitudinal studies, it should be expected that athletes involved in sports that regularly include bilateral movements should exhibit reduced bilateral deficit. Furthermore, even bilateral facilitation has been found in weightlifters (Howard and Enoka 1991) and rowers (Secher 1975). However, the existence of bilateral facilitation in the latter study was limited to the highly experienced group, which consisted of Olympic medalists. The results of weightlifters in the study of Howard and Enoka (1991) could not be replicated by Secher et al. (1988), who found this specific group of athletes not to be different from untrained individuals. Schantz et al. (1989) were also not able to show any difference in bilateral deficit between trained and untrained people. A recent study compared female swimmers with untrained controls and showed that bilateral deficit was evident in both groups during the performance of dynamic leg press exercise with no differences between groups (MacDonald et al. 2014). Since swimmers are involved in "reciprocal" activity and since everyday activity (e.g., gait) is also reciprocal (Vandervoort et al. 1987), their results should have been expected. Interestingly, during drop jumps from different heights, Pain (2014) observed bilateral deficit in peak force and peak power in elite endurance and power athletes, but the former exhibited bilateral facilitation in jumping height, while the latter showed bilateral deficit. Since endurance athletes are not involved in specific bilateral activities, the author speculated that the results may be due to the protocol, in particular due to controlled single leg jumps and the choice of specific drop jumping heights (Pain 2014).

The ambiguity of cross-sectional studies is possibly due to the specificity of testing. It has been suggested that adaptations to training may be masked if the movement pattern of testing does not match the movement pattern used in training (Sale and MacDougall 1981). This could explain why Howard and Enoka (1991) showed bilateral facilitation, while Secher et al. (1988) did not, as the subjects comprising the weightlifting group in the former study had been performing maximal bilateral knee extension exercises 1 year prior to the experiment. Secher et al. (1988) did, however, note a decrease in bilateral deficit after familiarization with the experimental apparatus, further supporting the need for testing specificity. In terms of the latter, the movement pattern itself, including contraction type and joint angle, will likely influence the results, as shown in our recent experiment (Škarabot et al., manuscript in preparation). As also noted above, it is difficult to determine the true control condition, as training adaptations in cross-sectional studies of athletes may have been confounded by different factors, including systemic influences and neurological cross talk.

Relationship between bilateral deficit, athletic performance and injury

It is currently still unclear what role the magnitude of bilateral deficit plays in a given sport. To the authors' knowledge, the only investigation that tried to answer this question was conducted by Bračič et al. (2010), who investigated the relationship between bilateral deficit in countermovement jump and sprint-start performance in elite sprinters. They showed that lower bilateral deficit values in the countermovement jump were associated with higher peak force production of the rear leg during the double sprint start and higher total force impulse on the blocks. More studies are needed in different athlete populations to determine the relationship between bilateral deficit and performance. These studies would also help to clear up the debate about whether certain athletes should train using predominantly bilateral or unilateral contractions. If specificity and transfer are the main concerns of strength training for an individual sport, then it would seem prudent that most sports involving reciprocal movement patterns, where force is produced mostly unilaterally at a given point in time and/or where weight distribution is unilaterally biased (Santana 2001), should include predominantly unilateral actions into their training regimen.

To the authors' knowledge, the relationship between injury and/or injury prediction and bilateral deficit has not been studied to date. It has been speculated before that in older adults, bilateral deficit could have a profound effect on the ability to perform bilateral activities and possibly increase the risk of injury (Hernandez et al. 2003). However, daily activities are rarely maximal and since bilateral deficit is likely limited to maximal force production, this issue seems redundant regardless of the study population. Furthermore, as maximal contractions are being seldom used and the degree of bilateral deficit is only roughly 6–13 % during dynamic contractions, the degree of the deficit may not be considered practically problematic for the general population. Nonetheless, considering that the absolute maximal capacity of a single limb may differ between unilateral and bilateral conditions, with predominance depending on whether one exhibits bilateral deficit or facilitation, potential risk of injury cannot be excluded,

especially when performing bilateral or unilateral dominant activities. Hence, this relationship certainly seems worth exploring in future investigations.

Conclusions and future directions

Bilateral deficit is a phenomenon that has been shown to be present in different movement and contraction types. Some variability in the existence of the phenomenon has been mainly shown in single-joint isometric contractions, possibly due to smaller postural stabilization requirements and the ability to use counterbalances.

Many mechanisms underlying bilateral deficit have been proposed over the years ranging from psychological, task-related, physiological and neurophysiological factors. Postural stability requirements and/or the ability to use counterbalances likely have a profound effect on the expression of bilateral deficit, and their control in experiments appears to be of paramount importance. A lot of investigators agree that bilateral deficit is a result of alteration in the nervous system, but the literature concerning EMG and voluntary activation measures remains equivocal. Based on recordings of brain activity, a strong case has been made for higher-order neural inhibition. Future research is warranted, however, as these findings are largely based on upper limb models and the evidence suggests that neuronal control of upper and lower limbs may differ. Strong evidence has also been presented for differences in shortening velocities between unilateral and bilateral actions and displacement of the force–velocity curve during bilateral actions, but these mechanisms are likely restricted to ballistic and explosive contractions. When attempting to elucidate mechanisms, some methodological issues need to be considered, mainly the design of the dynamometer and whether it allows one to use counterbalances. Furthermore, whether a unilateral or bilateral condition is regarded as a control requires further consideration. Future studies should therefore consider employing a design where the ability to use counterbalances is restricted, with the addition of measuring the activity of synergist muscles, and the action of the contralateral, non-active leg during unilateral contraction is constrained and monitored. Furthermore, if neurophysiological measures are performed (e.g., via electroencephalography, transcranial magnetic stimulation, functional magnetic resonance imaging, etc.), upper and lower limb models should be treated separately and then possibly compared. Investigations should use maximal contractions, control for velocity of contraction carefully (if dynamic contractions are used) and provide enough rest between contractions as to limit the systemic influences that may occur with fatigue, which would likely confound the effects.

The literature consistently shows that bilateral and unilateral resistance training seems to reduce and increase bilateral deficit, respectively. However, in this type of study the neurological cross talk that has likely occurred in the process of training would have ideally been controlled for. Cross-sectional studies suggest that task familiarity has a large influence on bilateral deficit as even bilateral facilitation has been shown in athletes who perform predominantly bilateral activities. However, these findings are likely constrained by the adequacy of testing specificity, which should be controlled for in future designs.

Currently, the literature investigating the relationship between bilateral deficit and athletic performance remains scarce. Further exploration is warranted, which would allow for better individualization of training programs, as well as answering questions about the relevance of unilateral or bilateral exercises to the physical preparation of an athlete. Likewise, the relationship between bilateral deficit and injury, and the connection between bilateral deficit and injury prediction have not been explored to date and require further investigation.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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