

INTERLIMB COORDINATION DURING STEP-TO-STEP TRANSITION AND GAIT PERFORMANCE

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Abstract

Most energy spent in walking is due to step-to-step transitions. During this phase, the interlimb coordination assumes a crucial role to meet the demands of postural and movement control. This work reviews studies that have been carried out regarding the interlimb coordination during gait as well as the basic biomechanical and neurophysiological principles of the interlimb coordination. The knowledge gathered from these studies is useful for understanding step-to-step transition during gait from a motor control perspective and for interpreting walking impairments and inefficiency related to pathologies, like stroke. This review shows that unimpaired walking is characterised by a consistent and reciprocal interlimb influence that is supported by biomechanical models, and spinal and supraspinal mechanisms. This interlimb coordination is perturbed in subjects with stroke.

Keywords: Interlimb coordination, step-to-step transition, gait, energy expenditure, biomechanical, neurophysiology, spinal and supraspinal mechanisms, stroke

1. Introduction

The neural process in postural control is necessary for all motor actions that induce dynamic and inter-segmental forces and also shifts of the centre of mass (CoM) (Massion, 1998). Therefore, voluntary actions may be considered self-inflicted postural perturbations that may be predicted, to a certain degree, by the central nervous system (CNS), which adjusts the activity of postural muscles both prior to the actual movement and in response to it (Aruin, 2002). Two different views have been proposed to explain how the CNS manages both movement and postural control. The first considers two descending control pathways, one accounting for movement control and the other for balance maintenance (Massion, 1992). The second considers the existence of a common controller for focal and postural commands (Aruin & Latash, 1995a, 1995b; Latash, Aruin, & Shapiro, 1995). According to this second view, changes in the activity of postural muscles are not an addition to but an inherent part of a control process for an action (Latash, 1998).

Complex movements such as gait are a considerable challenge to our understanding, because a large number of body segments are involved and many tasks are taking place simultaneously, i.e., balance, body support and forward progression, some of which are collaborative and others competitive (Winter & Eng, 1995). Apart from these factors, walking in humans also requires a close coordination of muscle activation between the two legs (Dietz, 2002), which has been strongly associated with gait economy (Donelan, Kram, & Kuo, 2002a; Kuo, Donelan, & Ruina, 2007).

The understanding of interlimb coordination, i.e. the timing of motor cycles of the limbs in relation to one another (Swinnen & Carson, 2002), requires knowledge from the neurophysiological and biomechanical domains related to postural and movement control, as well as concepts related to gait efficiency. Neurophysiologists tend to focus on the principles of organisation of the central networks that generate muscle activity patterns. On the other hand, biomechanical researchers focus mainly on movement mechanics, including limb and body kinematics, kinetics and energy cost. Although complementary, these two approaches have not frequently been coupled to bring about interlimb coordination results. The conclusions obtained in each field combined could contribute more significantly to the construction of scientific knowledge about interlimb coordination. In fact, the importance of studying gait interlimb coordination is based on its impact on the metabolic cost of walking (Donelan, et al., 2002a; Donelan, Kram, & Kuo, 2002c; Kuo, Donelan, & Ruina, 2005; Kuo, et al., 2007), and is supported by biomechanical evidence (Donelan, et al., 2002a, 2002c; Kuo, et al., 2007; Winter & Eng, 1995), and neurophysiological factors at the spinal (Bajwa, Edgley, & Harrison, 1992; Corna, Galante, Grasso, Nardone, & Schieppati, 1996; Dietz, 1992) and supraspinal levels (Drew, Prentice, & Schepens, 2004; Matsuyama et al., 2004).

However, despite the importance of interlimb coordination in the metabolic cost of walking, the interlimb coordination has been poorly explored. This can probably be explained by the fact that walking is an energy-cheap activity for healthy subjects, because interlimb coordination is optimised and integrated. Yet, this interlimb coordination can be impaired directly or indirectly as a consequence of lesions in specific supraspinal neuronal structures (Fries, Danek, Scheidtmann, & Hamburger, 1993; Marque, Simonetta-Moreau, Maupas, & Roques, 2001; Maupas, Marque, Roques, & Simonetta-Moreau, 2004; Nardone & Schieppati, 2005). Also, the interlimb coordination is affected by gait symmetry (Krasovsky & Levin, 2009). Consequently, comprehension of interlimb coordination in individuals presenting asymmetric lower limb motor impairment, such as subjects with stroke, is necessary to

understand the atypical behaviour in the pathology. After unilateral stroke, interlimb coordination is often impaired (Dietz & Berger, 1984; Roerdink, Lamoth, Kwakkel, & van Wieringen, 2007; Wu et al., 2009) due to the primary brain lesion itself and/or resulting from adaptive changes (Crone, Johnsen, Biering-Sorensen, & Nielson, 2003; Lamy et al., 2009; Murase, Duque, Mazzocchio, & Cohen, 2004) in other connected central structures. Knowledge concerning interlimb coordination can provide a basis for answering clinical questions related to: how the movement control system changes for specific cases, how to look for alterations in performance, what changes to look for during movement analysis and most important, how outcomes of interventions may be quantified.

This review aims to describe the role of interlimb coordination on forward progression and postural control of walking and its impact on gait efficiency, as well the neurophysiological and biomechanical mechanisms that are involved. This overall review of interlimb coordination adds to the pool of knowledge for research in the field of motor control. This study not only brings together the neurophysiological and biomechanical perspectives that have more frequently been discussed independently, but also it provides important insights into post-stroke rehabilitation, taking into account that walking ability becomes impaired in more than 80% of subjects with stroke (Duncan et al., 2005; Wevers, van de Port, Vermue, Mead, & Kwakkel, 2009). The interlimb coordination process which is reviewed here takes into account healthy subjects and subjects with stroke.

2. Gait asymmetry and interlimb coordination impairment in subjects with stroke: postural and movement control requirements

Walking efficiently does require bilateral symmetry; however, symmetry and coordination are often compromised, especially in post-stroke gait (Brandstater, de Bruin, Gowland, & Clark, 1983; Olney & Richards, 1996; Wall & Turnbull, 1986). Following stroke, typical motor impairments include impaired balance (Mizrahi, Solzi, Ring, & Nisell, 1989; Olney & Richards, 1996), disorganised postural control synergies and excessive muscle co-contraction, weight shift toward the ipsilesional side, and compensatory movement patterns such as excessive hip and knee movements during gait (Chen, Patten, Kothari, & Zajac, 2005; Olney & Richards, 1996; Paillex & So, 2003). All these generate an asymmetric walking pattern associated to impaired interlimb coordination. In fact, gait energy expenditure may be increased in subjects with stroke due to the reduction in strength (force generation capacity) and impaired coordination of the affected leg or legs (Kuo & Donelan, 2010). Interlimb coordination, especially the maintenance of reciprocal, out of phase motions of the limbs, is particularly critical for stable human

(bipedal) walking, predominantly during step-to-step transition, because the transition from one stance limb inverted pendulum to the next appears to be a major determinant of the mechanical work of walking (Donelan, et al., 2002c; Kuo, et al., 2007).

In terms of postural control, the support base, during the double support periods, is not very stable since one foot is carrying the weight on the small area of the heel while the other is pushing off on the forepart of the foot (Winter, 1995; Yang, Winter, & Wells, 1990). During double support, stability depends not only on the activity of each limb, but also on the relation between them to keep the CoM within the safe limits of the support base (Freitas, Freitas, Duarte, Latash, & Zatsiorsky, 2009; Jacobs, 1997; Kiemel, Elahi, & Jeka, 2008; Morasso & Schieppati, 1999; Nicholas, Doxey-Gasway, & Paloski, 1998; van der Kooij, Jacobs, Koopman, & Grootenboer, 1999). Stability also depends on controlling the CoM in terms of the environment conditions, including the gravitational forces, reaction forces from the supporting surfaces, imposed accelerations and obstacles (Dietz, Gollhofer, Kleiber, & Trippel, 1992; Latash, 1998). According to motor control theories, the system adjusts muscle activation thresholds of the trailing limb to guarantee dynamic gait stability (Feldman, Krasovsky, Baniña, Lamontagne, & Levin, 2011). Consistent with mathematical models, the energy dissipation due to non-elastic foot-ground interaction during the heel strike may be an essential element of legged locomotion rather than an accidental imperfection (Ahn & Hogan, 2012). It may not only provide indispensable sensory cues from foot contact of the leading leg (reflecting cutaneous input or load –related afferents) to coordinate locomotor patterns, but may also be a key mechanical factor that determines the stability of locomotion (Ahn & Hogan, 2012) as medio-lateral stability is mainly ensured by foot placement (‘stepping strategy’) (Hof, Vermerris, & Gjaltema, 2010). The importance of double support phase is also linked to the relation between postural stability, interlimb coordination and the metabolic cost of walking (Donelan, Shipman, Kram, & Kuo, 2004; Holt, Jeng, Ratchliffe, & Hamill, 1995; Krasovsky et al., 2012).

In terms of movement control, the double support phase has been described as one of the most determinant in the metabolic cost of walking (Donelan, et al., 2002a). The generation of energy at one joint and the absorption at another joint that occurs mainly during the double support phase of gait is associated with increased energy expenditure. Indeed, the energy increase of the push-off leg takes place as the weight-accepting leg absorbs energy (Winter, 2005). Also, to redirect and accelerate the CoM through step-to-step transition, the amount of energy spent on each collision between the foot and the ground at heel-strike must be replaced by contralateral limb propulsion (Donelan, et al., 2002a; Kuo, et

al., 2005, 2007; Neptune, Kautz, & Zajac, 2004) to redirect the CoM upward and forward (Donelan, et al., 2002a). In fact, it has been demonstrated that the work performed to propel the CoM forward during final stance constitutes a significant portion of the net metabolic cost of normal walking (Donelan, et al., 2002a; Gottschall & Kram, 2003; Grabowski, Farley, & Kram, 2005).

Considering the aforementioned, lower limb asymmetry in subjects with stroke involving movement and postural control dysfunction (Olney, Griffin, Monga, & McBride, 1991; Olney & Richards, 1996; Ryerson, Byl, Brown, Wong, & Hidler, 2008; Silva, Sousa, Tavares, et al., 2012) is associated with interlimb coordination impairments (Sousa, Silva, Santos, Sousa, & Tavares, 2013). In fact, few correlations were observed in electromyographic and kinematic variables between lower limbs in subjects with stroke (Sousa, Silva, Santos, et al., 2013) comparing to healthy subjects (Sousa, Silva, & Tavares, 2013).

3. The impact of decreased interlimb coordination on gait efficiency in subjects with stroke

In patients recovering from stroke, mechanical work measurements suggest that the contralesional leg performs much less push-off work and that both legs perform more total mechanical work than speed-matched healthy individuals (Kim & Eng, 2004; Olney & Richards, 1996). This increase in work suggests that patients recovering from stroke experience an elevated metabolic cost because step-to-step transitions require more mechanical work (Kuo & Donelan, 2010). According to the double-inverted pendulum model (Donelan, et al., 2002a; Kuo, et al., 2007), a major energy expenditure in walking is due to step-to-step transitions (Donelan, et al., 2002a), as the forces of the two legs need to redirect the CoM velocity from a downward and forward direction, to an upward and forward direction. The leading leg strikes the ground, performing negative work on the CoM and the energy spent may be restored through positive work by the trailing leg. The double-inverted pendulum model predicts that the trailing leg restores mechanical work through a powerful plantar flexion at the time of the initial contact and loading response of the contra-lateral limb (Kuo, 2002; Kuo, et al., 2005). The larger the heel strike cost in the leading leg during the initial contact, the higher the metabolic cost of walking, i.e. the energy dissipated during step-to-step transition explains 29% of the variance in the metabolic energy cost of walking (Doets, Vergouw, Veeger, & Houdijk, 2009). Transition between steps reaches an optimum level when the propulsion and the initial contact-loading response have the same magnitude and a short duration (Kuo, et al., 2007).

A lower push off work by the contralesional limb of subjects with stroke (Kim & Eng, 2004; Olney & Richards, 1996; Sousa, Silva, Santos, et al., 2013) is associated with higher energy expenditure since higher push-off work must be performed by the ipsilesional limb in the next step (Sousa, Silva, Santos, et al., 2013). Besides this, a higher negative work performed by the leading limb during initial contact and loading response (Sousa, Silva, Santos, et al., 2013) also leads to a higher need of push-off work. This is probably related to increased plantar flexion at initial contact (Olney & Richards, 1996) caused not only by weakness in the contralesional limb muscles (Richards, Malouin, Dumas, & Lamontagne, 1998), but also due to postural control dysfunction (Ikai, Kamikubo, Takehara, Nishi, & Miyano, 2003). The similarities in ankle postural control strategies between the first half of stance and standing (Yang, et al., 1990) highlight the impact of ankle postural control dysfunction on the negative work performed during initial contact. This makes sense when the importance of the role of ankle plantar flexors in upright standing is taken into account (Fitzpatrick, Douglas, & McCloskey, 1994; Loram, Maganaris, & Lakie, 2005). Finally, a decrease in the ability of the trailing limb to adjust its activity according to the actions of the leading limb can also decrease step-to-step transition efficiency. Therefore, the importance of exploring interlimb coordination in stroke patients relies not only on understanding the impact of the limb contralateral to the affected hemisphere (contralesional limb) on the ipsilateral limb (ipsilesional limb), but also the impact of the ipsilesional limb on the actions of the contralesional limb. This happens because, depending on the location of the lesion (Matsuyama, et al., 2004), the performance of the contralesional limb can be affected by neural pathways responsible for movement control while the performance of the ipsilesional limb can be affected by the ipsilaterally distributed neural pathways responsible for postural control (Latash, 1998; Matsuyama, et al., 2004). Also, changes in the motor function have been demonstrated in the contralesional limb (Olney & Richards, 1996) and in the ipsilesional limb (Cramer et al., 1997; Genthon et al., 2008).

Although biomechanical characteristics of stroke walking have been widely explored and described (Chen, et al., 2005; Goldie, Matyas, & Evans, 2001; Kim & Eng, 2004; Lamontagne, Malouin, Richards, & Dumas, 2002; Lamontagne, Richards, & Malouin, 2000; Lamontagne, Stephenson, & Fung, 2007; Lin, Yang, Cheng, & Wang, 2006; Olney, Griffin, & McBride, 1994; Olney & Richards, 1996; Shiavi, Bugle, & Limbird, 1987; Verma, Arya, Sharma, & Garg, 2012; Woolley, 2001), only recently has the interlimb coordination been a subject for study.

4. Neurophysiological mechanisms involved in interlimb coordination impairment in subjects with stroke

The territory of the middle cerebral artery is the most frequently affected arterial territory in stroke (Mohr, Lazar, & Marshall, 2004). This artery supplies either the cortical and the sub-cortical structures (Crafton, Mark, & Cramer, 2003; Schiemanck, Kwakkel, Post, Kappelle, & Prevo, 2006), particularly the internal capsule. Lesions at the internal capsule level have the potential to affect the contralesional disposed dorsolateral system and the ipsilesional disposed ventromedial system highlighted in Figure 1. The role of the cortico-ponto-reticulospinal-spinal interneuronal system in controlling interlimb relations has been highlighted (Figure 1) (Jankowska, Hammar, Slawinska, Maleszak, & Edgley, 2003; Matsuyama, et al., 2004). The corticoreticular axons originate primarily from regions of the sensorimotor cortex (mostly area 6), and descend with the corticospinal axons through the internal capsule and cerebral peduncle (subcortical level). These corticoreticular axons, some of which arise as collaterals of corticospinal axons, terminate bilaterally in the pontomedullary reticular formation from which the long-descending reticulospinal axons originate. The pontine and medullary reticulospinal axons descend mostly ipsilaterally throughout the spinal cord influencing spinal motoneurons and interneurons and are related to postural control. The corticospinal tract is responsible for movement in the contralateral side (Matsuyama, et al., 2004).

Studies involving healthy subjects demonstrated that neural circuits controlling each leg are coupled. When both limbs have a supportive role, the perturbation of one limb evokes a purposeful bilateral response pattern, with similar muscular onset latency on both limbs (Bajwa, et al., 1992; Nardone, Grasso, Giordano, & Schieppati, 1996). This response is thought to be mediated at the spinal level but under supraspinal control (Berger, Dietz, & Quintern, 1984; Dietz, 1992). In fact, experiments have demonstrated the existence of a group of interneurons (Edgley, Jankowska, Krutki, & Hammar, 2003; Jankowska & Noga, 1990) that receive supraspinal inputs from the vestibulo- and reticulo-spinal pathways and the corticospinal tract (Davies & Edgley, 1994; Jankowska, Edgley, Krutki, & Hammar, 2005; Jankowska, Stecina, Cabaj, Pettersson, & Edgley, 2006) and they also receive bilateral peripheral inputs from group Ia, group II afferents (Jankowska, et al., 2005) and cutaneous afferents (Edgley & Aggelopoulos, 2006). A contribution from the cerebellum to this spinal interlimb coordination via reticulospinal neurons has been suggested for both cats (ItoBonnet, Gurfinkel, Lipchits, & Popov,

1984;1976) and humans (Dietz, Zijlstra, & Duysens, 1994; Stubbs & Mrachacz-Kersting, 2009). Also, there is evidence of bilateral interlimb coordination in the homonymous muscle groups in the human, as each limb affects the strength of muscle activation and the time-space behaviour of the other (Dietz, et al., 1994; Stubbs & Mrachacz-Kersting, 2009).

Based on the neuroanatomic fundamentals previous mentioned, it can be expected that lesions at the subcortical level are associated with the dysfunction of the bilateral limb response (Dietz, Quintern, Boos, & Berger, 1986), when both limbs are performing a supportive role (Dietz & Berger, 1984; Marchand-Pauvert, Nicolas, Marque, Iglesias, & Pierrot-Deseilligny, 2005). The deregulation of the group II pathways demonstrated in the contralesional limb of subjects with stroke (Marque, et al., 2001; Nardone & Schieppati, 2005) can also explain their interlimb coordination problems. The information provided by spindle group II fibres has an important role in postural control circuits (Morasso, Baratto, Capra, & Spada, 1999; Nardone, Corrà, & Schieppati, 1990; Nardone, Giordano, Corrà, & Schieppati, 1990; Schieppati, Nardone, Siliotto, & Grasso, 1995). Some authors go further arguing that both legs and foot muscles are the site of postural control segmental reflexes (Schieppati, et al., 1995), mainly because of spindle group II fibres (Grey, Ladouceur, Andersen, Nielsen, & Sinkjær, 2001; Grey, Van Doornik, & Sinkjær, 2002; Nielsen & Sinkjær, 2002; Schieppati & Nardone, 1997; Sinkjær, Andersen, Ladouceur, Christensen, & Nielsen, 2000).

The control of interlimb coordination during the antiphase pattern for locomotion has been interpreted as evidence that existing spinal circuits controlling the predominant antiphase pattern are either selectively recruited or disinhibited. However, the additional muscle activation associated with moving the nonparetic ankle in an antiphase mode strongly degraded paretic ankle movements compared with a unilateral performance (Kautz & Brown, 1998; Kautz & Patten, 2005; Tseng & Morton, 2010). These findings cannot be explained by the central pattern generator dysfunction in subjects with stroke.

5. Interlimb coordination between ipsilesional and contralesional lower limbs in subjects with stroke during gait

While interlimb coordination between the terminal stance propulsion and the initial contact and loading response is perfectly integrated in healthy subjects (Sousa, Santos, Oliveira, Carvalho, & Tavares, 2012; Sousa, Silva, & Tavares, 2013), in subjects with stroke at the subcortical level (internal capsule),

limited evidence indicates that only the activity of the contralesional limb is influenced by the activity of the ipsilesional limb (Sousa, Silva, Santos, et al., 2013).

Results obtained in healthy subjects indicate that the activity of the major muscles acting on terminal stance propulsion (Liu, Anderson, Pandy, & Delp, 2006; Neptune, et al., 2004; Zajac, Neptune, & Kautz, 2003) of the trailing limb is positively correlated to the anteroposterior and vertical ground reaction forces during initial contact and loading response (Sousa, et al., 2012) to replace energy spent during the heel strike by the contralateral limb (Donelan, Kram, & Kuo, 2002b; Donelan, et al., 2002c; Kuo, et al., 2005). Mathematical models argue that the energy expenditure can be reduced through the application of a propulsion impulse in the trailing limb immediately before collision of the leading limb (Kuo, 2002; Kuo, et al., 2007). This out-of-phase interlimb relation is also perfectly justifiable from a postural control perspective, as the onset of anticipatory postural adjustments may be time-locked with certain events within the locomotor cycle rather than the onset of the prime mover (Nashner & Forssberg, 1986). Also, the activity of the main muscles responsible for impact reduction during heel strike (tibialis anterior, biceps femoris and vastus) (Liu, et al., 2006; Neptune, et al., 2004; Perry, 1992; Sadeghi et al., 2002; Wakeling & Nigg, 2001a, 2001b; Whittle, 2007) is inversely related to the activity of the same muscles and positively related to the soleus activity during contralateral terminal propulsion (Sousa, Silva, & Tavares, 2013). In healthy subjects, there is a reciprocal influence between the leading limb during double support and the trailing limb during terminal stance propulsion, as proprioceptive information related to ground reaction force can be used to create feedforward commands to regulate contralateral plantar flexor activity in the preceding subphase of walking, and also because the main responsible muscles for impact reduction during heel strike are influenced by the homologous activity and by the soleus of the contralateral limb during terminal stance propulsion (Sousa, et al., 2012; Sousa, Silva, & Tavares, 2013).

The lack of correlation between the propulsive impulse of the ipsilesional limb and the braking impulse of the contralesional limb (Sousa, Silva, Santos, et al., 2013) leads to a lower efficiency in interlimb coordination in subjects with stroke since the CNS does not seem to consider proprioceptive information from the contralesional limb to adjust the ipsilesional propulsive activity. Sensory dysfunction is estimated to be present in more than half of stroke survivors (Carey, 1995; Carey, Oke, & Matyas, 1996; Tyson, Hanley, Chillala, Selley, & Tallis, 2008). A deregulation of the group II pathways demonstrated in the contralesional limb of subjects with stroke can be the origin of unilateral interlimb

coordination (Marque, et al., 2001; Nardone & Schieppati, 2005). In fact, the alteration of muscle tone in a paretic limb (Eng, Kim, & MacIntyre, 2002; Olney & Richards, 1996) may have an impact on proprioceptors in muscles and tendons even if the fibre tracts of the proprioceptive system itself have not been affected by the brain lesion (Thiel, Aleksic, LKlein, Rudolf, & Heiss, 2007). A possible dysfunctional information provided by plantar cutaneous receptors during initial contact and loading response of the contralesional limb could also explain the unilateral interlimb coordination (Edgley & Aggelopoulos, 2006). This afferent was demonstrated to be related to the parameters of the ground reaction forces (Kavounoudias, Roll, & Roll, 1998; Zehr, Komiyama, & Stein, 1997), to assist placing and weight acceptance at the beginning of stance (Zehr & Stein, 1999), and it also has an important role in balance maintenance during walking (Van Wezel, Ottenhoff, & Duysens, 1997; Zehr, et al., 1997; Zehr & Stein, 1999). However, a tactile sensation deficit of the plantar cutaneous receptors was not related to the incidence of falls (Marigold & Eng, 2006) neither to standing instability in subjects with stroke (Marigold, Eng, Tokuno, & Donnelly, 2004). Besides, load perception during initial contact and loading response is likely to be easier than on the other stance subphases in subjects with stroke (Chu, Hornby, & Schmit, 2014). While the perception of an impact force is primarily sensory in nature, the perception of a self-generated force also involves the motor system, thus complicating perception (Shergill, Bays, C.D., & Wolpert, 2003). The higher deficit in load perception during terminal stance and pre swing (Chu, et al., 2014) emphasises the role of proprioceptive impairment on interlimb deficit in subjects with stroke. On the other hand, the growing body of evidence suggesting that load information provided by group 1b afferents contributes substantially to ongoing unilateral muscle activity in late stance (Grey, Nielsen, Mazzaro, & Sinkjaer, 2007; Pearson & Collins, 1993), highlights the importance of information provided by type II fibres in adjusting trailing limb muscle activity during late stance according to leading limb muscle activity during initial contact and loading response. Impairment of the reticular system in the subcortical stroke may also explain interlimb coordination impairment in subjects with stroke considering its relevance during the moment of touchdown in matching the muscle activity of both legs with the ground surface (Sousa, Silva, & Tavares, 2013) and the strong influence of this system over interneurons that mediate information by the group II afferents of both lower limbs during walking (Davies & Edgley, 1994; Jankowska, et al., 2003; Matsuyama, et al., 2004).

Although motor control deficits have been described in the contralesional limb when promoting forward propulsion (Olney & Richards, 1996), there is evidence that the contralesional propulsive

impulse is adaptable due to the braking impulse of the ipsilesional limb during initial contact and loading response (Sousa, Silva, Santos, et al., 2013). These findings indicate that the neural control of contralesional limb motor patterns may be substantially influenced by the ipsilesional leg sensorimotor state during the bilateral lower limb function. Based on this, more “appropriate” sensorimotor information from the ipsilesional limb, i.e. from the less affected limb, would be integrated by the nervous system and would contribute to a more appropriate contralesional pattern. During the push-off phase of the gait cycle, the increase in sensory gating associated with volition may contribute to the poorer performance in load perception of the contralesional limb (Chu, et al.). In fact, subjects with stroke (Sousa, Silva, Santos, et al., 2013), like healthy subjects (Sousa, Silva, & Tavares, 2013), present an inverse relation between the activity of muscles responsible for impact reduction during leading initial contact (Liu, et al., 2006; Neptune, et al., 2004; Perry, 1992; Sadeghi, et al., 2002; Wakeling & Nigg, 2001a, 2001b; Whittle, 2007) and the main agonists during pre-swing (Neptune, Kautz, & Zajac, 2001; Neptune, et al., 2004). The results obtained in healthy subjects indicate that despite being the primary cause for the leg energy absorption and consequent negative work (Winter, 2005), the higher activity of the vastus medialis, biceps femoris and tibialis anterior can reduce the leading limb heel strike impact (Liu, et al., 2006; Neptune, et al., 2004; Perry, 1992; Sadeghi, et al., 2002; Wakeling & Nigg, 2001a, 2001b; Whittle, 2007), decreasing the positive work needed by the trailing limb. This was demonstrated through a decreased muscle activity of the main responsible muscles for forward propulsion (Neptune, et al., 2001; Neptune, et al., 2004; Sousa, Silva, & Tavares, 2013; Winter, 2005). The positive work for forward progression of the trailing limb depends strongly on the negative work performed by the leading limb, and these components have a significant impact in the metabolic cost of walking (Sousa, Silva, & Tavares, 2013). These findings are in accordance with the biomechanical models proposed for step-to-step transition (Kuo, et al., 2007) since the energy dissipated is related to an inelastic collision of the swing leg with the ground, leading to changes in velocities of the legs and the CoM that need to be compensated for active work of the trailing limb. The importance of the role of the plantar flexors in restoring energy expenditure during step-to-step transition is highlighted by the higher magnitude of positive mechanical work compared to the magnitude of the negative work (DeVita, Helseth, & Hortobagyi, 2007; Sousa, Silva, & Tavares, 2013).

Despite subjects with stroke present functional interlimb coordination synergies between ipsilesional heel strike and loading response and contralesional propulsion similar to that observed in

healthy subjects (Sousa, et al., 2012; Sousa, Silva, Santos, et al., 2013; Sousa, Silva, & Tavares, 2013), only the ipsilesional limb afferents from the BF muscle during initial contact and loading response in related to the forward propulsion activity of contralesional limb during pre-swing. The afferents from ipsilesional ankle plantar flexor during initial contact impair contralesional propulsive activity during pre-swing (Sousa, Silva, Santos, et al., 2013). Although the ipsilesional limb has been frequently defined as the non-affected limb, motor impairments have been reported in both the upper (Colebatch & Gandevia, 1989; Desrosiers, Bourbonnais, Bravo, Roy, & Guay, 1996; Jones, Donaldson, & Parkin, 1989) and lower extremities (Adams, Gandevia, & Skuse, 1990; Genthon, et al., 2008; Lindmark & Hamrin, 1995). These motor impairments are considered to be the result of adaptations to function deficits of the contralateral limb (contralesional limb) (Aruin, 2006), caused by disuse, as well as from neuronal damage depending on the anatomical region of vascular disruption (Matsuyama, et al., 2004). According to some authors, ipsilesional disorders related to lower soleus activity levels, higher ankle coactivation values, changes in feedforward mechanisms and increased centre of pressure dispersion under the ipsilesional limb are related to a dysfunction of the ventral-medial system in sub-cortical injuries located at the internal capsule level (Genthon, et al., 2008; Silva, Sousa, Pinheiro, Ferraz, et al., 2012; Silva, Sousa, Pinheiro, Tavares, et al., 2012; Silva, Sousa, Tavares, et al., 2012). Based on studies involving subjects with stroke (Silva, Sousa, Pinheiro, Ferraz, et al., 2012; Silva, Sousa, Pinheiro, Tavares, et al., 2012; Silva, Sousa, Tavares, et al., 2012; Sousa, Silva, Santos, et al., 2013), it can be argued that the negative influence of the ipsilesional limb over the contralesional limb can be attributed to postural control deficits of the ipsilesional limb. These findings support the argument for the dysfunction of the ventral-medial system over the ipsilesional limb as one of the causes for the impaired interlimb relation in subjects with stroke.

6. Clinical implications

Rehabilitation of subjects with stroke in a chronic stage is associated with elevated costs (Gorelick, 1994). However, there is a lack of scientific knowledge supporting rehabilitation guidelines to promote interlimb coordination, enhancing the gait economy. The importance of studying subjects with stroke in a chronic stage is also sustained by the evidence of functional improvement beyond the acute phase after stroke (6 months) (Ferrucci et al., 1993), which can be explained by knowledge about neuroplasticity physiology (Hallett, 2001).

Paresis of ankle plantar flexor muscles have been demonstrated to be the main cause of the reduced forward propulsion of the contralesional limb during the stance phase of gait (Knarr, Kesar,

Reisman, Binder-Macleod, & Higginson, 2013; Lamontagne, et al., 2002; Neptune, et al., 2001; Olney, et al., 1991; Olney & Richards, 1996). Based on interlimb coordination knowledge, it can be argued that the lower performance of contralesional propulsion in subjects with stroke in a chronic stage is not only explained by the neuronal damage but also by the influence of the ipsilesional limb. This recent evidence is of significant relevance for clinical rehabilitation of subjects with stroke. Specifically, in subjects with stroke in the middle anterior cerebral artery involving subcortical areas such as the internal capsule and the corona radiata. Strategies to improve postural control in the ipsilesional limb should be adopted not only to decrease the ipsilesional postural control deficit, but also to decrease its negative impact on controlling the movements of the contralesional limb. Rehabilitation approaches should focus on proprioceptive facilitation techniques (Nudo, 1999; Taub, Uswatte, & Elbert, 2002; Ward & Cohen, 2004). Rehabilitation of sensorimotor integration deficits has been shown to improve postural control in subjects with stroke (Bayouk, Boucher, & Leroux, 2006; Smania, Picelli, Gandolfi, Fiaschi, & Tinazzi, 2008). While performance advantages associated with bilateral arm movements after stroke have been reported (Cunningham, Stoykov, & Walter, 2002; Harris-Love, Waller, & Whittall, 2005; Rose & Winstein, 2005), supporting bimanual upper extremity training protocols for recovery of arm movements after stroke (Luft, McCombe-Waller, Whittall, & et al., 2004; Mudie & Matyas, 1996, 2000; Whittall, McCombe, Silver, & Macko, 2000), studies of lower limb coordination do not seem to support bilateral protocols to improve interlimb coordination during locomotion (Kautz & Brown, 1998; Kautz & Patten, 2005; Sousa, Silva, Santos, et al., 2013; Tseng & Morton, 2010).

Walking after stroke is characterised by slow gait speed (Olney & Richards, 1996; Sousa, Silva, Santos, et al., 2013; von Schroeder, Coutts, Lyden, Billings, & Nickel, 1995), poor endurance (Dean, Richards, & Malouin, 2001) and a reduced ability to adapt to the task and to environment constraints (Said, Goldie, Patla, Sparrow, & Martin, 1999). Motor impairments are believed to be the primary cause for this poor walking ability as suggested by the association between muscle weakness of specific muscle groups, such as the plantar flexors on the contralesional side, and the slow speed (Nadeau, Gravel, Arsenault, & Bourbonnais, 1999; Olney, et al., 1994). Whereas studies using correlation analysis have revealed that some electromyographic abnormalities such as spasticity (Lamontagne, Malouin, & Richards, 2001), altered coactivation (Lamontagne, et al., 2000), and muscle paresis (Lamontagne, et al., 2002) are more pronounced in subjects with low gait speed, a cause-effect relationship of some of these abnormalities with poor locomotor performance (Detrembleur, Dierick, Stoquart, Chantraine, & Lejeune,

2003) remains difficult to establish. The study of the interlimb relation during the stance phase of gait in subjects with stroke can give significant insights into the understanding of the low performance of stroke gait, considering the importance of step-to-step transition performance in global gait efficiency.

7. Concluding remarks

The role of the interlimb coordination on the forward progression and postural control of walking and its impact on gait efficiency has been clearly demonstrated in biomechanical studies. Its importance is sustained not only by biomechanical models but also by neuroanatomy and neurophysiology studies, as well as by experimental studies involving animals but also humans. Unimpaired walking is characterised by a consistent and reciprocal interlimb coordination which is not observed in subjects with stroke. In addition to decreased interlimb coordination, a dysfunctional influence of the ipsilesional limb over the contralesional forward propulsion was observed. This suggests that the lower performance of contralesional forward propulsion is not only related to the contralateral supraspinal damage, but also to a negative influence of the ipsilesional limb. The knowledge gathered from this review as to the interlimb coordination is useful to promote understanding about gait step-to-step transition from a motor control perspective and for interpreting the walking impairments and inefficiency related to pathologies involving unilateral or bilateral asymmetric impairment of lower limbs. Taking into account that stroke is a prevalent disorder, the study of this pathological condition is important to gain a better understanding about the performance deficits and the potential for functional recovery, as well as to develop intervention strategies that maximise recovery.

This study presents an overview about the interlimb coordination and its impact in gait performance; however, it is not a systematic review. Taking into account that a systematic review gives a clear and consistent overview about a particular research topic, including information that allows to draw relevant conclusions and stress the demand for more research, systematic reviews regarding the interlimb coordination and its impact in gait performance are suggested as they can lead to important insights into this topic.

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FIGURE CAPTIONS

Figure 1: Illustration of part of the neuronal systems related to postural control and movement.