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Biomechanical and neurophysiological mechanisms related to postural control and efficiency of movement: a review

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Abstract

Understanding postural control requires considering various mechanisms underlying a person's ability to stand, to walk and to interact with the environment safely and efficiently. The purpose of this paper is to summarise the functional relation between biomechanical and neurophysiological perspectives related to postural control in both standing and walking based on movement efficiency. Evidence related to the biomechanical and neurophysiological mechanisms is explored as well as the role of proprioceptive input on postural and movement control.

Key words: postural control, upright standing, gait, efficiency

1. Introduction

Postural control has been defined as the control of the body's position in space for the purposes of balance and orientation (Horak, 2006; Massion, 1998; Shumway-Cook & Woolacott, 2000, 2007). Postural orientation involves the active control of body alignment and tonus in relation to gravity, base of support, environment and internal references (Horak, 2006; Kandel et al., 2000; Lundy-Ekman, 2002; Massion, 1998; Raine et al., 2009; Winter et al., 1990). Postural equilibrium involves the coordination of sensorimotor strategies to stabilise the body's centre of mass (CoM) during both self-initiated and externally triggered disturbances in postural stability (Horak, 2006). Postural stability has been defined as the ability to control the CoM in relation to the base of support (Shumway-Cook & Woolacott, 2000, 2007). The weight of each component (orientation and stability) varies according to the task and the environment. Indeed, the postural control system adjusts its goal under different circumstances, such as longitudinal alignment of the whole body to maintain a steady, erect stance; remodeling of stance in preparation for a voluntary movement; shaping of the body for display purposes, as in dance; maintenance of balance, as on the gymnast's beam; or conservation of energy in a demanding task (Kandel et al., 2000; Shumway-Cook & Woolacott, 2007).

Biomechanically, a postural control position is achieved when the CoM is within the base of support and is aligned with the centre of pressure (CoP) (Winter, 1995). Any external or internal perturbation that changes the projection

of the CoM to the limits of the base of support and the alignment between CoM and CoP may lead to postural challenge. The ability to maintain the body's CoM within a specific boundary is dictated by the efficiency of the individual's balance mechanisms (Raine et al., 2009) related to anticipatory postural adjustments (APA), triggered by feedforward mechanisms prior to the perturbation (Aruin & Latash, 1995; Belen'kii et al., 1967; Li & Aruin, 2007; Massion, 1992; Schepens & Drew, 2004), as well as to compensatory postural adjustments (CPA) that are initiated by sensory feedback signals (Alexandrov et al., 2005; Park et al., 2004). The process of generation of APA is likely to be affected by expected magnitude (Aruin & Latash, 1996; Bouisset et al., 2000) and direction (Aruin & Almeida, 1997; Santos & Aruin, 2008) of the perturbation, voluntary action associated to the perturbation (Arruin, 2003; Shiratori & Aruin, 2007), postural task and body configuration (Arruin, 2003; van der Fits et al., 1998). In conditions of high instability demands, the central nervous system (CNS) may suppress APA as a protection against their possible destabilising effects (Arruin et al., 1998). In fact, a relation between APA and CPA has been demonstrated (Santos et al., 2009), suggesting the existence of an optimal utilization of APA in postural control. The CPA response depends not only on the APA, but also on the direction and magnitude of the perturbation, the base of support dimension (Dimitrova et al., 2004; Henry et al., 1998; Horak & Nashner, 1986; Jones et al., 2008) and on the involvement in a secondary task (Bateni et al., 2004).

The main sensory systems involved in postural control are proprioception, the vestibular system and vision, and their afferent pathways within the CNS (Day & Cole, 2002; Shumway-Cook & Woolacott, 2007). Afferent and efferent pathways involve the spinal cord, the brain stem, the cerebellum, the midbrain, and the sensorimotor cortex. All of these contribute to the development of an internal representation of body posture that is continuously updated based on multisensory feedback and is used to forward commands to control body position in space (Massion, 1994; Mergner & Rosemeier, 1998). This provides a basis for all interactions involving perception and action with respect to the external world and is likely to be partly genetically determined and partly acquired through ongoing experiential learning. It is

therefore adaptable and vulnerable, is dependent on the ongoing information that it receives (Meadows & Williams, 2009) and is related to human movement variability, allowing for adaptable functional behavior (Van Emmerik & Van Wegen, 2000).

The neural process involved on stability organisation and body orientation in space is necessary practically for all dynamic motor actions (Massion, 1998). Specifically, the control of balance during gait and while changing from one posture to another requires a complex control of a moving body CoM that is not within the base of foot support (Winter et al., 1993). In fact, human gait is influenced by a multifactorial interaction that results from neural and mechanical organisation, including musculoskeletal dynamics, a central pattern generator (CPG), based on a genetically determined spinal circuit, and peripheral and supraspinal inputs (Arechavaleta, 2008; Borghese et al., 1996; Horak & Macpherson, 1996; Mazzaro et al., 2005; McCollum et al., 1995; Segers, 2006). The CPG designs spinal networks than can generate patterns of rhythmic activity in the absence of external feedback or supraspinal control. However, these spinal networks are modulated by peripheral input and supraspinal control (Armstrong, 1986; Rossignol et al., 2006).

The present study aims to review the biomechanical and neurophysiological mechanisms related to postural control in both standing and walking based on movement efficiency. In the following sections, the neural mechanisms, the role of afferent information and biomechanical aspects will be considered to upright standing and human gait.

2. Postural and movement control

2.1 Neural mechanisms

Upright standing

The upright stance of the human is an unstable position (Peterka & Loughlin, 2004). Postural sway reflects noise and regulatory activity of the several control loops involved in maintenance of balance, which requires that the CoM never deviates beyond the support area. The control of the appropriate

level of neuromuscular activity to produce rapid postural control strategies involves medial descending systems (Raine et al., 2009). The role of these systems is fundamental to the organisation of postural tone appropriately according to environment demands, gravity and base of support. The vestibular system action is related to postural tone adjustments to body weight support (Matsuyama & Drew, 2000). This system plays a major role in the antigravity function (Latash, 1998; Siegel & Saprú, 2011) as it is responsible, through lateral vestibulospinal tract, for the activation of ipsilateral extensor motor neurons and their associated gamma motor neurons (Latash, 1998; Rothwell, 1994; Siegel & Saprú, 2011). The reticular formation has an important role on APA production (Schepens & Drew, 2004) as it receives afferent input from all the sensory system and also from the pre-motor cortex and supplementary motor area (Brodal, 1981; Kiernan, 2005; Rothwell, 1994). The possible role of the cortex in postural control has been discussed and there is reference in literature to the pre-motor cortex influence in APA production (Massion, 1992) and to the supplementary motor area as potential focus of control for APA generation (Jacobs et al., 2009).

Human gait

Appropriate mechanisms for controlling muscle tone are essential to maintain stable postural and locomotor synergies in bipedal gait performance. The dependency between postural control and movement may be justified by the connection between the cortex and the reticular formation. In fact, muscle tone and the locomotor system can be controlled, in parallel, by a combined input to the brain stem of net inhibition from the basal ganglia, and net excitation from the motor cortex (Takakusaki et al., 2004). Specifically, an important neuronal circuit that allows the coexistence of postural adjustments and execution of movement is the cortico-ponto-cerebellar pathway, which allows the connection of the cortex with the nucleus of the brain stem and cerebellum (Ito, 2006). With this circuit the postural control can be organised ipsilaterally to the activated side with respect to the control of movement in the contralateral side. This relationship between movement and postural control through the activation of ventro-medial and dorso-lateral systems, as well as the importance of the coactivation mechanism between the two lower limbs (Dietz et al., 2002)

to keep the body CoM over the feet (Dietz et al., 1992; Dietz et al., 1989), justify the study of mechanisms that occur in both sides of the body in relation to a unilateral movement like gait initiation as well as in relation to the gait cycle.

Basic structures involved in the control of locomotion and postural muscle tone are located in the midbrain (Takakusaki et al., 2004). Some circumscribed regions have been identified as relevant in activating and controlling the intensity of spinal locomotor CPG operation, maintaining equilibrium during locomotion, adapting limb movement to external conditions and coordinating locomotion to other motor acts (Armstrong, 1986; Jordan, 1986; Orlovsky, 1991). Among the main supraspinal centres involved are the sensorimotor cortex and the supplementary motor area (Kaprili et al., 2006; Mackay-Lyons, 2002; Miyai et al., 2002) the cerebellum, the basal ganglia (Garcia-Rill, 1986; Mackay-Lyons, 2002), the midbrain locomotor region (Kandel et al., 2000; Mileykovskiy et al., 2000) and the spinal cord (Dietz et al., 1992). The sensorimotor cortex is involved in the preparation for and execution of movement (Nelson, 1996). The cerebellum receives copies of CPG output to motoneurons via ventral spinocerebellar tract and spinoreticulocerebellar pathways, as well as information about the activity of the peripheral motor apparatus via the dorsal spinocerebellar tract (Orlovsky, 1991). Based on these, influences motoneurons indirectly via vestibulospinal, rubrospinal, reticulospinal and corticospinal pathways (Orlovsky, 1991). The cerebellum main role may be the timing of muscle activation, “fine-tuning” the output by adapting each step (Lansner & Ekeberg, 1994). Nevertheless, both the cerebellum and the basal ganglia seem to play an important role in timing of sequential muscle activation, with the basal ganglia operating at the level of planning, initiation, execution, and termination of motor programs as well motor learning (Mackay-Lyons, 2002; Wichmann & DeLong, 1996). The midbrain locomotor region activates “muscle tone excitatory system” and “rhythm generating system” (Takakusaki et al., 2004). Although not being relevant in gait, the motor cortex is involved in the modification of CPG activity in unstable surfaces or when gait needs a visual orientation (Mackay, 1999). The degree of supraspinal and spinal influences in movement generation is determined by context (Mackay-Lyons, 2002).

In Figure 1 are presented important structures involved in postural control as well the neural connection between postural control and movement control in functional tasks like walking and upright standing. The relevant role of afferent input, specifically the proprioceptive input, in postural and movement control justify the study of the role of Golgi tendon organ and muscle spindles and their afferences in standing and walking.

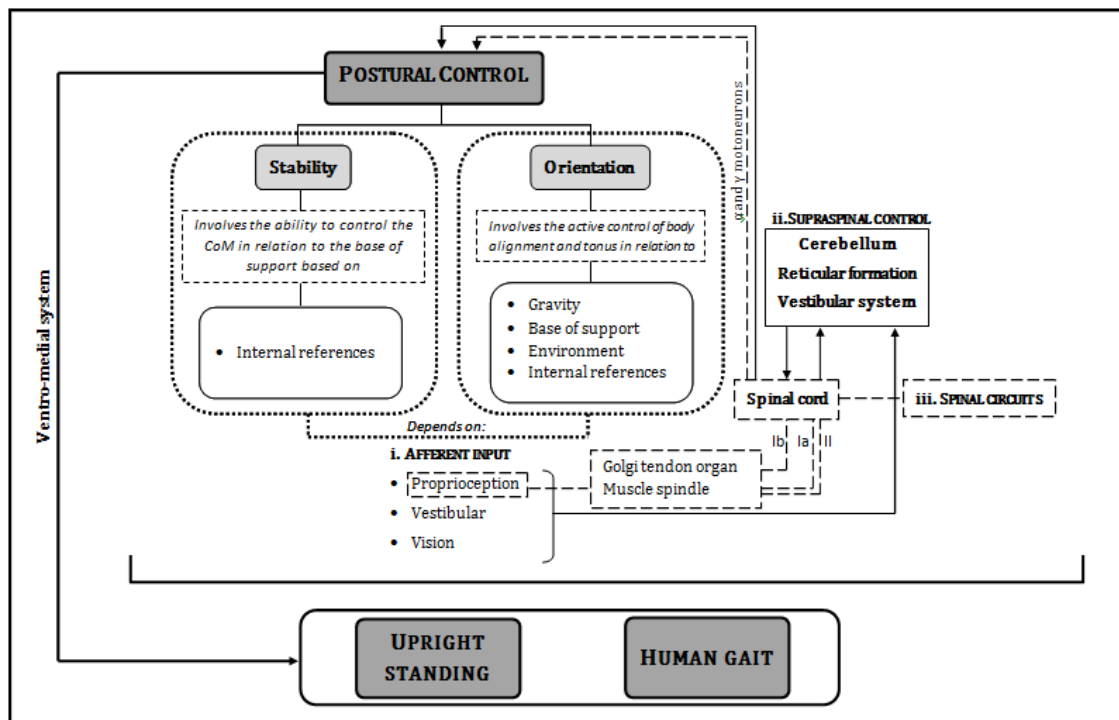


Figure 1: A conceptual schematic diagram illustrating the main structures involved postural control in both standing and walking.

2.2 The role of afferent information

Upright standing

The ability to reweight sensory information depending on the context is important to maintain stability when an individual moves from one context to another (Peterka, 2002). For instance, while vestibular information may not be a large contributor for the control of upright stance (Winter et al. 1998) and for triggering or coordinating muscle activation patterns associated to ankle strategy (Horak et al., 1990), it is likely to play a crucial role during moments of increased postural instability (Fitzpatrick and McCloskey 1994). As in normal conditions proprioceptive information assumes more relevance than other

sources, in this paper focus has been given to the role of proprioceptive information.

It is well known that the mechanoreceptors (i.e. specialised sensorial receptors responsible for transduction of mechanic events into neural signs (Grigg, 1994)) accounting for proprioceptive information are primarily founded on muscles, tendons, ligaments and capsule (Hogersvorst & Brand, 1998; Jami, 1992; Johansson et al., 1991). Receptors located in the deeper skin tissue and fascia are traditionally associated with touch receptors, being categorised as additional sources (Edin & Johansson, 1995; Grigg, 1994; Macefield et al., 1990). Support has been given to the role of the Golgi tendon organs in providing afferent input from “gravity-dependent” receptors required to indicate the projection of the body’s CoM within the base of support (Dietz, 1996; Dietz, 1998; Dietz & Colombo, 1996; Dietz et al., 1992). Also, the small magnitudes of sway observed during quiet standing may be enough to alter muscle lengths, resulting in changes of Ia-afferent input onto the motoneuron pool of the lower limbs. Recent studies by (Loram et al., 2005b) have suggested this possibility, whereby muscle length changes in the gastrocnemius and soleus muscles during quiet standing have been detected within the range at which muscle spindles are sensitive to movement (Proske et al., 2000). Support has been given to the role of medium latency responses from group II during standing (Corna et al., 1996; Nardone et al., 1996; Schieppati et al., 1995). Indeed there is evidence that muscle spindle type II fibres play a more relevant role than group Ia fibres in the control of bipedal stance (Marchand-Pauvert et al., 2005) as only medium latency responses have a stabilising effect during perturbations of stance, and also because these fibres are more influenced by the “postural set” (Nardone et al., 1990). Findings obtained by Grasso et al, 1996, demonstrate the existence of crossed neural pathways fed by these fibres, which explains the bilateral electromyographic responses to unilateral perturbations during standing. This finding is supported by (Dietz, 1996), as this author argues that a complex bilateral coordination of leg muscle activation (mediated by a spinal mechanism (Dietz & Berger, 1984)) is needed for upright postural control during locomotion.

All the receptors mentioned above and the corresponding afferents input may allow a modulation of postural activity in relation to muscle length and

tension variation, but only a combination of afferent inputs can provide the necessary information to control body equilibrium (Dietz, 1996). The role of proprioceptive information from ankle muscles has been highlighted in various studies (Fitzpatrick et al., 1994; Fitzpatrick et al., 1992a; Gatev et al., 1999; Loram et al., 2005a). Some authors go further, arguing that normal subjects can stand in a stable manner when receptors of the ankle muscles are the only source of information about postural sway (Fitzpatrick et al., 1994; Fitzpatrick et al., 1992a). The soleus and the gastrocnemius have traditionally been considered the source of muscle proprioceptive information signalling changes in body position (Fitzpatrick et al., 1992b; Loram & Lakie, 2002a; Loram et al., 2005b). These muscles act predominantly as active agonists and, because the foot is constrained on the ground, they prevent forward toppling of the body, whose centre of gravity is maintained in front of the ankle joint (Fitzpatrick et al., 1992a; Lakie et al., 2003; Loram & Lakie, 2002a; Loram et al., 2005a; Maki & Ostrovski, 1993). The problem with muscle spindles as position sensors is that they are able to generate impulses in response to muscle length changes as well as from fusimotor activity (Proske, 2006). According to (Di Giulio et al., 2009) the best proprioceptive information may come from un-modulated muscles crossing the joint in parallel with the active agonist. In fact earlier studies stated that, depending upon the stance conditions, muscle stretch does not necessarily result in a compensatory stretch reflex response but instead results in an antagonistic muscle activation (Gollhofer et al., 1989; Hansen et al., 1988). Based on this, it has been argued that reciprocal patterns of muscle activation are typically involved in postural control (Di Giulio et al., 2009; Latash, 1993). Neurophysiologically, reciprocal inhibition is mediated, at least in part, by a dysynaptic circuit in the spinal cord that is subject to several supraspinal as well as segmental modulator mechanisms (Jankowska, 1992) and varies according to the way in which antagonist muscles are activated (Lavoie et al., 1997). Synergies between antagonist muscles include simple patterns of reciprocal activation, co-contractions, and complex triphasic activation patterns (Lavoie et al., 1997). There is evidence that the strength of dysynaptic inhibition is reduced during co-contraction of antagonist muscles compared with reciprocal activation (Nielsen & Kagamihara, 1992). Another source of proprioceptive information may come from the cutaneous afferents of the feet

as there is a large distribution of cutaneous receptors at various locations on the sole of the foot (Kennedy & Inglis, 2002). It has been suggested that this source of proprioceptive information contributes to both the coding and spatial representation of body posture during standing (Roll et al., 2002) and that the architecture and physiology of the foot appear to contribute to the task of bipedal postural control with great sensitivity (Wright et al., 2012).

Human gait

During gait afferent feedback adapts dynamically, through a reciprocal relationship, the response of the CPG to environmental requirements and assumes multiple roles in regulating the production of motor patterns, such as: (1) the production of detail in the temporal pattern of muscle activation sequence (Ivanenko et al., 2006; Pearson, 1993), (2) the reinforce of ongoing motor activity, particularly those involving load-bearing muscles, such as the extensor muscles during the stance phase of gait (Pearson, 1993; Sinkjær et al., 2000; Stephens & Yang, 1996), and (3) the control of transition from one phase of movement to another (Lacquaniti et al., 1999; Pearson, 1993). Swing is initiated when the leg is extended (stretching the flexor muscles) and unloaded (reduced force in extensor muscles sensed by the Golgi tendon organ of the extensor muscles) (Zehr & Duysens, 2004). Consequently gait cycles depend on the afferent input from peripheral receptors as the muscle force production at a given level of motor unit recruitment can change according to length (velocity) and tension variations (Frigo et al., 1996)

The monosynaptic excitation of spinal motoneurons from the large diameter group Ia afferent fibres related to short latency response (Matthews, 1991) has been demonstrated when an expected stretch of the ankle extensors is imposed during gait (Sinkjaer et al., 1996; Yang et al., 1991). Also a phasic modulation of Ia input has been demonstrated by changes in the magnitude of H-reflex over the course of the gait cycle, with the greatest attenuation occurring during flexion (Schneider et al., 2000; Yang & Whelan, 1993). This modulation is consistent with the fact that the maximum soleus length occurs during foot off, when maximum plantar flexion of the foot occurs, which is coincident with its maximum force production (Orendurff et al., 2005). The modulation of the H-

reflex is a reflection of: (1) the background excitability of the motoneuron pool, (2) the modulation associated to the activation of the antagonist muscle, and (3) presynaptic inhibition of the primary afferents (Yang & Whelan, 1993) that seems to be related partially to Ia afferents from the hip and knee extensor muscles (Brooke et al., 1997). Medium latency response from group II has been demonstrated during gait (Dietz et al., 1985) and some authors argue that this group is more important to feedback in the stance phase than group Ia (Grey et al., 2001; Grey et al., 2002; Nielsen & Sinkjaer, 2002; Sinkjær et al., 2000). Earlier studies have suggested that strong central effects of group II muscle afferents are mediated via a complex neural pathway influenced by supraspinal input and peripheral input during walking (Dietz et al., 1987; Yang et al., 1991). Specifically, there is evidence for the role of vestibulo- and reticulo-spinal pathway (Davies & Edgley, 1994) which supports the hypothesis that the facilitation of the relevant lumbar propriospinal neurons by descending tracts neurons would be stronger over group II during maintenance of posture than during voluntary contractions (Marchand-Pauvert et al., 2005). Also, the role of group Ib load-sensitive afferences related to medium latency response has been reported to contribute to the regulation stance phase of gait (Stephens & Yang, 1999) associated to a disynaptic Ib reflex-reversal (Stephens & Yang, 1996). Findings obtained in (Grey et al., 2007) suggest that tendon organ feedback via an excitatory group Ib pathway contributes to the late stance phase enhancement of the soleus muscle activity. The combination of the different afferent inputs plays an important role on gait dynamics related to the ipsilateral limb but also on the contralateral limb, as it has been demonstrated that unilateral leg displacement during gait evokes a bilateral response pattern, with a similar onset on both sides (Dietz & Berger, 1984). From a functional point of view, this interlimb coordination is necessary to keep the body's CoM over the feet (Dietz, 1996).

Figure 2 summarizes the role of proprioceptive receptors and respective afferences in standing and walking. Important networks related to integration of proprioceptive information (cerebellum) and to the modulation of afferent information at spinal cord (reticulospinal and vestibulospinal tracts) are represented.

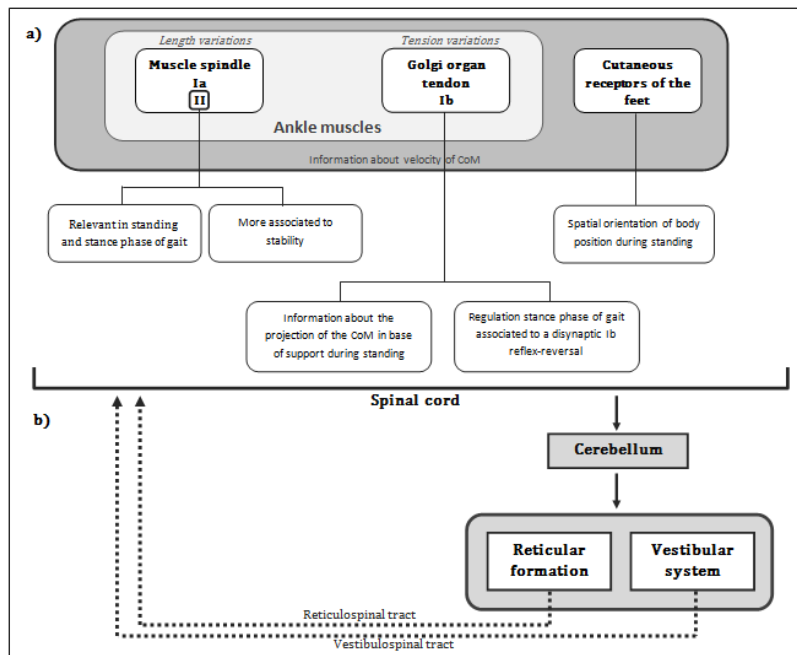


Figure 2: Representation of the most important proprioceptive receptors and afferences and their role in standing and stance phase of gait (a). There are also represented important networks related to proprioceptive information (b). In this part of illustration (b), dotted lines represent efferent pathways and solid lines represent afferent pathways.

2.3 Biomechanical aspects

Upright standing

Upright stance is associated with small deviations from an upright body position, which results in a gravity-induced torque acting on the body, causing it to accelerate further away from the upright position. Corrective torque must be generated to counter the destabilizing torque due to gravity. This process of continuous small body deviations countered by corrective torques creates a pattern known as spontaneous sway. The mechanisms underlying spontaneous sway are not fully understood, and controversy remains regarding the organisation of sensory and motor systems contributing to spontaneous sway. Numerous authors have suggested that active feedback control mechanisms contribute to the maintenance of upright stance (Fitzpatrick et al., 1996; Johanson & Magnusson, 1991; Peterka & Loughlin, 2004; Peterka & Benolken, 1995; van der Kooij et al., 2001). Recent studies have shown that a model based primarily on a feedback mechanism with a 150- to 200-ms time delay can

account for postural control during a broad variety of perturbations (Peterka, 2002; Peterka & Loughlin, 2004; Peterka & Benolken, 1995) and can yield a spontaneous sway pattern that resembles normal (Peterka, 2000) or pathological spontaneous sway (Parkinson's disease; (Maurer et al., 2003)). However, the relevance of feedback mechanisms for postural control is still debated. Some authors concluded from their experiments that corrective torque originating from feedback control is insufficient for stabilizing the body (Fitzpatrick et al., 1996). Others suggested additional sources for corrective torque, like prediction (Morasso et al., 1999; van der Kooij et al., 2001), or have proposed more complex concepts (Baratto et al., 2002; Collins & De Luca, 1993; Loram & Lakie, 2002b). Postural sway has been viewed as a result of a correlated random-walk process (Collins & De Luca, 1993), a result of computational noise (Kiemel et al., 2002), and/or a moving reference point (Zatsiorsky & Duarte, 1999). The possible importance of postural sway as a reflection of a hypothetical search process within the system of postural stabilization has been emphasised (Mochizuki et al., 2006; Riley et al., 1997).

From a functional point of view, the control of human upright posture stability is commonly viewed as a continuous stabilization process of a multilink inverted pendulum, where the main controlled parameter is the CoM position within the limits of the supporting base (Maurer & Peterka, 2005). This aspect has been described as biomechanical constraints that determines patterns of postural coordination (Buchanan & Horak, 2003). In stance, the limits of stability - that is, the area over which individuals can move their CoM and maintain equilibrium without changing the base of support - are shaped like a cone (McCollum & Leen, 1989a). Thus, equilibrium is not a particular position but a space determined by the size of the support base and the limitations on joint range, muscle strength and sensory information available to detect limits. The CNS has an internal representation of this cone of stability that it uses to determine how to move to maintain equilibrium (Horak, 2006). Gatev et al., 1999, reported a significant correlation between spontaneous body sway and the activity of the gastrocnemius muscle. They also discovered that gastrocnemius activity preceded temporally CoM displacement, suggesting a central program of control of the ankle joint stiffness working to predict the

loading pattern. More recent studies proposed that the actual postural control system during quiet standing adopts a control strategy that relies notably on velocity information of CoM and that such a controller can modulate muscle activity in an anticipatory manner without using feedforward mechanisms (Masani et al., 2003). According to this view, velocity feedback can play a significant role in anticipating body position changes because it carries information about the subsequent state of the body, i.e., a change in CoM velocity indicates the direction and intensity with which the current CoM displacement will be changed in the following time instant. It has been hypothesised that the integration of proprioceptive and plantar cutaneous sensations would play a significant role in the velocity feedback mechanism (Masani et al., 2003). Another biomechanical constraint is related to frequency of postural sway (Nashner et al., 1989), as when postural sway is lower than 0.5 Hz the body can be compared to a simple inverted pendulum (McCollum & Leen, 1989b), and when it is higher than this value the body can be compared to a double inverted pendulum with the fulcrum at the hip level (Yang et al., 1990).

Human gait

The coordination between posture and movement involves the dynamic control of the CoM in the base of support (Stapley et al., 1999). Consequently, to access the simplified concept of locomotion it is necessary to consider the behavior of the CoM during gait cycles. The trajectory described by the CoM in the plan of progression is a sinusoidal curve that moves vertically twice during one cycle and laterally in the horizontal plan and that is similar in form to that found in the vertical displacement (Gard et al., 2004; Norkin & Levangie, 1992). Peak-to-peak amplitude is described as being about 4-5 cm for adults at freely chosen speed and has been used to estimate exchanges of mechanical energy, efficiency, work, and to describe the symmetry as an indicator of the quality of gait (for more information see (Gard et al., 2004)).

The human gait results from a complex interaction of muscle forces, joint movements and neural commands. Variables including electromyographic activity, muscle torque, ground reaction forces, kinematics and metabolic-

energy costs have been measured and quantified. This data set requires an interpretation and organisation of the fundamental principles that elucidate the mechanisms of gait. Several models have been suggested to describe human gait mechanisms (Cavagna & Kaneko, 1977; Cavagna & Margaria, 1966; Donelan et al., 2002b; Kuo et al., 2005; Kuo et al., 2007; Saunders et al., 1953; Waters & Mulroy, 1999). The six determinants of gait theory (Saunders et al., 1953), based on the premise that vertical and horizontal CoM displacements are energetically costly, proposes a set of kinematic features that help to reduce CoM displacement. However, there is evidence that some determinants have a non-significant role on the CoM vertical displacement and that there is higher metabolic expenditure when subjects voluntarily reduce vertical displacement of CoM (for review see (Kuo et al., 2007)). The inverted pendulum model proposes that most of the work during gait is performed by a passive mechanism of exchange of gravitational potential and kinetic energies (60-70%)(Cavagna et al., 1977; Griffin et al., 2003). However this model cannot reproduce the existence of two peaks in vertical ground reaction force (Pandy, 2003; Zajac et al., 2003) and does not account for the costs which are not considered responsible for work, like isometric force stabilisation and body weight support (Kuo et al., 2005). The difference in the percentage of energy recovery in relation to an ideal inverted pendulum has been related mostly to double support phase (McGeer, 1990). Indeed, it has been demonstrated a low percentage of energy recovery in the double support phase (Geyer et al., 2006) related to the interruption of the energy-conserving motion of single support by an inelastic collision of the swing leg with the ground, leading to changes in velocities of the legs and the CoM (Kuo et al., 2007). This energy loss can be reduced by 75% through the application of a propulsion impulse in the trailing leg immediately before collision of the leading leg (Kuo, 2002). Simulations suggest that the ankle plantar flexor (soleus, gastrocnemius) and the uni- and bi-articular hip extensors (gluteus maximus, hamstrings) dominate work output over the gait cycle (Neptune et al., 2004). These muscles, being active in the late stance and in the beginning of stance, are therefore restoring energy to the body near double-support (Zajac et al., 2003).

Ankle plantar flexors are the primary contributors for forward progression and vertical support (Kepple et al., 1997), before midstance they hinder progression (Neptune et al., 2001) and during midstance they maintain body support and the forward motion of the trunk and leg, which is consistent with inverted-pendulum-like ballistic walking as the synergy of these muscles in this subphase occurs with minimal metabolic energy expenditure, as expected in ballistic-like walking (Zajac et al., 2003). Biarticular hip extensors generate forward acceleration during the first half of stance, while uniarticular quadriceps muscles and the uniarticular hip extensors decelerate the body mass centre and provide body support (Liu et al., 2006; Neptune et al., 2004). The biarticular quadriceps muscle is a significant contributor to forward progression in late stance (Neptune et al., 2004).

According to Donelan, 2004, lateral stabilisation exacts a modest metabolic cost as walking requires active lateral stabilisation. It has been demonstrated that the gluteus medius, although acting primarily outside the sagittal plane in walking, contributes to support and slows progression (less than the other muscles) in the first half of stance and contributes to support in the second half (Liu et al., 2006). Also, it has been demonstrated that the body lateral motion is partially stabilised via medio-lateral foot placement (Donelan, 2004; Kuo, 1999).

3. Movement efficiency

The relationship between muscle activity and whole body mechanics is too variable and complex to allow direct control of the latter without an intermediate kinematic representation (Lacquaniti et al., 1999). There is evidence that supports the idea that global kinematic gait is controlled (Ivanenko et al., 2004). Kinematics is relatively invariant in various modes of locomotion, while the electromyographic activity patterns to produce the required kinematic patterns can vary considerably (Grasso et al., 1998; Ivanenko et al., 2004). These findings suggest that neural circuitry can somehow specify limb kinematics and the appropriate muscle synergies would be determined in a subordinate and flexible manner to adapt to the current mechanical constraints (Lacquaniti et al., 1999; Lacquaniti et al., 2002). The basic biomechanical control signal may exert

its action through an appropriate model of inverse dynamics and feedback device that determines the muscle torque necessary to achieve kinematic patterns (Ivanenko et al., 2004). The significance of muscle redundancy would then be to allow the same movement to be carried out by means of different combinations of muscle activity under different environmental circumstances, for instance, to cope with fatigue or changes in load (Lacquaniti et al., 1999).

The major function of muscles in gait is to generate and absorb energy; such function is largely ignored in neurophysiological research (Winter & Eng, 1995). The body has the capacity of transferring energy between segments across the joint centres and can store and recover energy in the passive elastic tissues in the tendon and muscles. However, this last energy conserving mechanism is quite small in walking (Winter & Eng, 1995). The CNS has learnt how to create motor patterns to conserve much of the energy that was generated earlier in the gait cycle. It has been estimated that of the total energy changes of all body segments over the gait cycle only 33% are caused by active muscle generation and absorption, while 67% are due to the passive transfers between segments (Pierrynowski et al., 1980). Considering this it is important to quantify the movement also on the criterion of efficiency (Fetters & Holt, 1990; Sparrow & Newell, 1998).

In biomechanical and physiological research, efficiency of movement is normally defined as the ratio of the mechanical work performed and the metabolic cost of performing the work (Stainsby et al., 1980). Typically an efficiency formula will take the form:

$$Efficiency (\%) = \frac{Mechanical\ work}{Energy\ work} \times 100$$

Energy expenditure during walking can be characterised through mechanical energy estimations (Cavagna et al., 1963; Saibene & Minetti, 2003; Willems et al., 1995) or metabolic energy measurements (Waters, 1999). Mechanical energy is generally estimated by one of three approaches: (1) analysis of energy changes of the CoM relative to the surroundings (external work) and of the body segments relative to the CoM (internal work) (Cavagna & Margaria, 1966; Cavagna et al., 1963; Willems et al., 1995); (2) analysis of the

energy changes of moving body segments (sum of segmental energies) or (3) measurement of muscle power around the joints (net joint work) (Winter, 2005). In all mechanical energy estimations the actual amount of work performed is underestimated as additional metabolic work resulting from isometric muscle contractions or antagonist co-contractions is not taken into account (Fetters & Holt, 1990; Winter, 2005). This problem is overcome when assessing metabolic energy i.e. measuring oxygen consumption during walking (Fetters & Holt, 1990; Vandewalle, 2004). The relation between metabolic cost and the mechanical work performed by stance limb muscles to lift and accelerate the CoM during walking has been already demonstrated (Donelan et al., 2001; Donelan et al., 2002a) and has been considered a valid predictor of walking performance (Anderson & Pandy, 2001). Metabolic energy expenditure can be accessed through indirect calorimetry, where oxygen consumption and/or carbon dioxide production is measured and converted into energy expenditure using formulae (Cunningham, 1990; Garby & Astrup, 1987) which have been reported as a valid method (Levine, 2005). Mechanical and metabolic energy analyses allow monitoring how the CNS takes advantage of energy conserving mechanisms in order to achieve a more efficient movement.

Summary/Concluding remarks

Postural control has been vastly explored in the scientific community. However, the complexity of the interrelations between neural and mechanical aspects and environment leads to the need of studying postural control in a holistic way. In addition, the study of postural control needs to reflect the dynamic inter-relation of the different components of human movement on the basis of movement efficiency. The adaptability, vulnerability and continuous dependency of afferent information on the postural control system turns this area a focus of clinical interest. Considering that the postural control system has the capacity of reorganization for higher movement performance, it is important to understand in detail the static and dynamic postural control mechanisms and strategies and how these mechanisms influence other systems and are influenced by changes in afferent and efferent information.

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