Modular Organization of Motor Control during Dynamic Tasks

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Effects of Perturbation and Training

PhD Thesis by

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ABSTRACT

Human locomotion is characterized by an apparently complex control of many degrees of freedom. It has been suggested that the central nervous system optimizes muscle recruitment by using muscle synergies or motor modules, which are investigated by using non-negative matrix factorization of the EMG signals. Human bipedalism increases instability and the specific mechanisms involved in balance control during locomotion are well known, but the general control of human locomotion during perturbed conditions is only partially investigated.

This PhD thesis focuses on the modular control of locomotion and the effects of perturbations to balance on the neuromuscular control and biomechanics in different locomotor tasks. Moreover, it investigates the effects of balance training on the neural control of complex motor tasks under perturbed conditions. Using perturbations during walking, it was first investigated whether perturbations experienced among unperturbed trials would change motor control strategies during walking. The work demonstrated that the awareness of the possible perturbations did not affect motor behavior substantially. In terms of perturbations, it was found that the modular organization from unperturbed walking was preserved during perturbed walking and the most relevant changes were verified in the timing to activate motor modules, most likely as a response to strong afferent inputs caused by perturbations.

By using complex locomotor tasks (i.e., fast changes in direction while running), it was also verified that such tasks are also modular, showing impulsive burst-like activation signals to control motor modules that are similar to those found during walking and running. Perturbations elicited at initial contact during fast changes in direction evoked changes in the activation timing of the motor modules, which is consistent to the findings from the walking study of the PhD work. Observations on peripheral changes related to perturbations motivated the conduction of two additional studies involving balance training. It was observed that six weeks of unilateral balance training enhances postural responses to sudden perturbations during a single-limb standing position. A similar modular organization to perform fast changes in direction after training was found, however, specific changes in specific motor modules demonstrated an increased co-contraction at the hip and knee, upregulating joint stability during perturbations.

These results together indicate that perturbations to balance during locomotion may influence specific components within the modular organization. Balance training may be effective in improving inter-muscular coordination and with the mechanical stability in order to increase protection during unexpected slips.

ABSTRACT IN DANISH (DANSK RESUMÉ)

Menneskets bevægelser er karakteriseret ved kompleks kontrolleret med mange frihedsgrader.

Der menes, at central nervesystemet optimerer rekrutteringen af muskler ved at anvende muskel synergier eller motoriske moduler, som er blevet undersøgt ved hjælp af ikke-negative matrix faktorisering af EMG signalerne. Menneskets bipedalisme øger ustabilitet og de specifikke mekanismer, der er involveret i kontrol af balancen under bevægelse, er velkendte, men den generelle kontrol af menneskets bevægelser under perturberede betingelser, er stadig ukendt.

Denne Ph.d. afhandling fokuserer på den modulære kontrol af bevægelser samt effekten af perturbationer af balancen på den neuro-muskulære kontrol og biomekanik i forskellige bevægelsesmæssige opgaver. Ydermere undersøges effekten af balance træning af den neurale kontrol af komplekse motoriske opgaver under perturberede betingelser. Ved at anvende perturbationer under gang blev det først undersøgt, om det at anvende perturbationer under gang blandet med uperturberet gang, ville ændre de anvendte motoriske strategier for kontrol under gang. Dette viste, at opmærksomheden omkring muligheden for perturbationerne ikke ændrede motorikken væsentligt. Det viste sig også, at den modulære organisering af den uperturberede gang var bevaret under perturberet gang og de mest relevante ændringer blev verificeret i timingen af aktiveringen af motoriske moduler som et respons fra stærke afferente input forudsaget af perturbationerne.

Ved at anvende komplekse bevægelsesmæssige opgaver (for eksempel hurtige ændringer af retningen under løb) blev det bekræftet, at sådanne opgaver også er modulær, viser impulsive eksplosionsagtige aktiverings signaler til kontrol af motoriske moduler, som er ens med dem, der finder under gang/løb. Ydermere perturbationerne, der blev udløste ved indledende kontakt under hurtigt ændringer i retningen, fremkaldte ændringer hovedsageligt i aktiveringstimingen af de motoriske moduler, som stemmer over ens med fund fra forsøg under gang.

Observationerne af periferiske ændringer relateret til perturbationerne motiverede til udførsel af yderlige to studier, der involverede balance træning. Det var observeret, at 6

ugers af unilateralt balance træning øger den holdningsmæssig respons af pludselige perturbationer ved stående på et ben. Der ud over var ens modulære organisering fundet til at udføre hurtige ændringer i retningen, efter træning, men specifikke ændringer i de motoriske moduler øger co-kontraktionen i hoften og knæet hvormed led stabiliteten øges under perturbationerne.

Disse resultater indikerer at perturbationer af balancen under bevægelser, måske influerer specifikke komponenter af den modulære organisering. Som tilføjelse blev det fundet, at balance træning måske kan være effektivt til at forbedre intermuskulær koordinering for at øge beskyttelsen mod fald på glatte underlag.

ACKNOWLEDGEMENTS

I'd like to thank all my SMI colleagues for the nice time I had in the Department of Health Science and Technology. Also thanks to the colleagues from the Department of Neurorehabilitation Engineering (Georg-August University, Göttingen, Germany) for the nice time I spent in Germany with them! Especially Leonardo Gizzi, who was extremely patience and shared hours of his precious time teaching and discussing data throughout almost all this PhD period.

I'd like also to thank to Silvia Muceli and Shinishiro Shiozawa, who spent long time with me when I did not know how what to do in the Lab. Thanks to my two office mates Francesco and Thomas, they both were essential in helping me to deal with the data that I took from the Lab. The long and productive discussions were essential for my growing along the journey.

A special thanks goes to my supervisors. My co-supervisor Dario Darina by the support and guidance on the development of this Thesis. His advices were always very important. A special thanks to my friend and supervisor Uwe Kersting, who accepted the challenge of working with me. His serenity has always been a comfort when things were not as expected. I've certainly learned to be a better person and researcher by working with these two exceptional person.

I also would like to thank Priscila, most likely about everything I did since I decided to pursuit a PhD. Her wisdom took me from darkness thoughts and lead me to what I am now. The love we share is the most important treasure I have in life. Thanks for give me balance and for being the love of my life!

The greatest thanks goes to my parents, Maria da Graça and Sebastião. I dedicate this work to you, even though I know that nothing I can do will be enough to demonstrate my love and admiration for you. Amo vocês!

TABLE OF CONTENTS

CHAPTER 1 – LITERATURE REVIEW

1.1. Basics on human gait and balance control

Locomotion implies the translation of the center of gravity along a pathway requiring the least energy consumption (Vaughan 2003). It started to be investigated by Aristotle concerning animal locomotion (*De motu Animalium*), and nowadays it is still topic for deep discussion in terms of how gait is modulated. Human bipedalism may have been employed by the first hominids around 7 million years ago (Schmitt 2003), which drastically reduced the participation of the upper limbs on locomotion, enabling the development of new skills. In addition, bipedal locomotion has been proven to be four times less energy consuming in comparison to quadruped locomotion in chimpanzees (Sockol et al. 2007). There is a vast body of literature describing human gait in physiological and biomechanical contexts, therefore a summarized review on the human gait physiology and biomechanics is presented here.

1.1.1. Neural control of normal gait

The "theory of linking control and effect" states that locomotion is generated by a global entrainment of the neural system on one side, and the musculoskeletal system plus environment on the other side (Vaughan 2003). The two units initially seem not to be linked, but previous study has shown that the controller (i.e., the nervous system) and the effector (i.e., musculoskeletal system) can efficiently generate locomotion at different speeds and inclined surfaces by only altering one parameter of the model (Taga et al. 1991). Supraspinal commands that drive locomotion are delivered from the mesencephalic motor region (Garcia-Rill and Skinner 1987), while the motor cortex seems essential for refining and/or adapting locomotor movements to the environmental context, such as walking on a narrow beam (Armstrong 1988). New evidence also has shown important cortico-muscular coherence during walking, suggesting that the motor cortex has remarkable participation on modulation of locomotion (Petersen et al. 2012). However, the complexity involving human locomotion cannot be solved only by superior commands from the motor cortex, therefore there must be information from the periphery that requires new adjustments throughout the movement. The peripheral or

afferent information plays an essential role in human walking, by providing online feedback to the higher centers on the current status of the limbs (Duysens et al. 2008; Grillner 1985; Lacquaniti et al. 2012b).

It is believed that rhythmic movements, which include human locomotion, are generated by neuronal circuits in the spinal cord. These movements can be generated independently of supraspinal control by combining different motor components or modules called central pattern generators (CPGs) (Grillner 1985; Grillner 2006). Although polemic, the CPG theory has strong support from experiments dated more than 100 years ago (Graham Brown 1911; Graham Brown 1914). Despite other mammals, experiments in humans have shown rhythmic hind limb movements in partial and/or total spinal cord injured patients (Pinter and Dimitrijevic 1999). By investigating EMG activity during locomotion in high-decerebrate cats, Patla (1985) proposed a model of a few pattern generators that could modulate locomotion, which were flexible enough to accommodate changes in muscle activity at varying speeds. In the 1990's the same concept of few underlying motor patterns related to the generation of locomotion was firstly proposed for human gait (Davis and Vaughan 1993; Olree and Vaughan 1995), initiating some new trends in the investigation of neural control of locomotion. These concepts of motor patterns or motor modules on locomotion will be deeply explored later in this literature review.

1.1.2. *Posture and balance control during locomotion*

Loss of balance during locomotion can cause about 50% of falls even in people with good balance (Kirchhoff and Melin 2011; Winter 1995). Consequently, severe injuries, sick leave periods and even loss of lives (especially for elderly people) justify an enormous investment in research related to fall prevention (Cham and Redfern 2002; Duysens et al. 2008; Granacher et al. 2011; Winter 1995; You et al. 2001).

Differently from the quadrupeds, human bipedalism is very unstable. The erect posture raised the center of mass, which has its lowest position at heel strike, and highest position at midstance (Winter 1995). In addition, the use of only two segments to promote displacement has also reduced anterior-posterior stability, since the center of mass can easily be beyond the base of support, also called "controlled falling" (Perry

1992). Therefore, stability of human locomotion is continuously challenged, requiring mechanisms that integrate visual, vestibular and somatosensory inputs continuously (Cappellini et al. 2010; O'Connor and Kuo 2009; Winter 1995; You et al. 2001).

Human locomotion can be described basically by the CoM projection towards the leading limb by a controlled forward fall that ends in the initial contact (Winter 1995). The double support period is essential to transfer the load from the hind limb to the leading limb, during which the safe placement of the swing foot during initial contact is the major guarantee to prevent falls (O'Connor and Kuo 2009; Winter 1995; You et al. 2001). Since most of the body mass is located high above the bipedal support structure (i.e., in the head arms and trunk [HAT]), the dynamic balance while walking is mostly achieved by counterbalancing the moments generated in the hips. These moments accelerate or decelerate the trunk (consequently HAT) such that the inertial moments are constantly fluctuating around zero (Winter 1995).

Changes in the center of mass position during locomotion lead to postural responses, in a manner that the desired task can still be performed. Forward and backward lean while walking evokes kinematics changes in the lower limbs in order to achieve balance to maintain walking (Winter 1995). Concerning balance in the frontal plane (medial-lateral displacement), the strategies to maintain posture are based on keeping the center of mass inside the base of support by a more pronounced use of integrative visual feedback when compared to the sagittal plane (O'Connor and Kuo 2009; Oddsson et al. 2004). The lateral placement of the feet generates a mechanical moment, which is the main factor controlling stability in the frontal plane (Oddsson et al. 2004; Winter 1995). In addition, there is a medial hip acceleration every single support phase that is counterbalanced by the hip abductor moment, which also keeps the center of mass regularly within the base of support (Winter 1995).

The motion of the center of mass is controlled by proactive and reactive strategies. The proactive strategies involve predicted and anticipated needs for the forthcoming motor task (Maki and McIlroy 2007; Misiaszek 2006; Tang et al. 1998). When locomotion is perturbed, reactive strategies involving unpredictable postural changes are triggered. There are several mechanisms involved in regaining balance, which involve an automated control system that generates robust postural responses among different

individuals (Duysens et al. 2008; Misiaszek 2006; Tang et al. 1998). Moreover, walking is constantly modulated by the integration of many control systems, and the introduction of an external factor such as perturbation at the foot level implies altered constraint to the system (Misiaszek 2006; Tang et al. 1998). Even though, the nervous system is capable of selecting and executing the most appropriate response to the environmental change (Maki and McIlroy 2007).

1.1.3   Neural strategies for fall prevention while walking

The usual neuromechanical responses to perturbations require specific neural mechanisms (Figure 1). The immediate responses are the short-loop or short latency reflexes mediated by Ia afferent from muscle spindles, which are triggered just after the perturbation event and activate stretched muscles in the perturbed leg (Duysens et al. 2008). Subsequently, a late response (long latency reflexes) is mediated by long loop pathways from group II afferents. This control system involves supraspinal inputs, generating substantial activation of the supporting limb muscles and also the participation of other trunk and arms muscles. The evoked responses from this late control systems is not generic, instead is has specific goals in correcting posture to regain balance (Duysens et al. 2008; Maki and McIlroy 2007; Misiaszek 2006). In case of slips, however, the latency for the late responses might be slower (100-120ms) since the reflex onset depends on the mechanical changes on the periphery, such as slipping distance (Marigold and Patla 2002; Tang et al. 1998). The subsequent strategies related to postural control are voluntary and may vary in terms of magnitude and duration depending on the individual (Duysens et al. 2008).
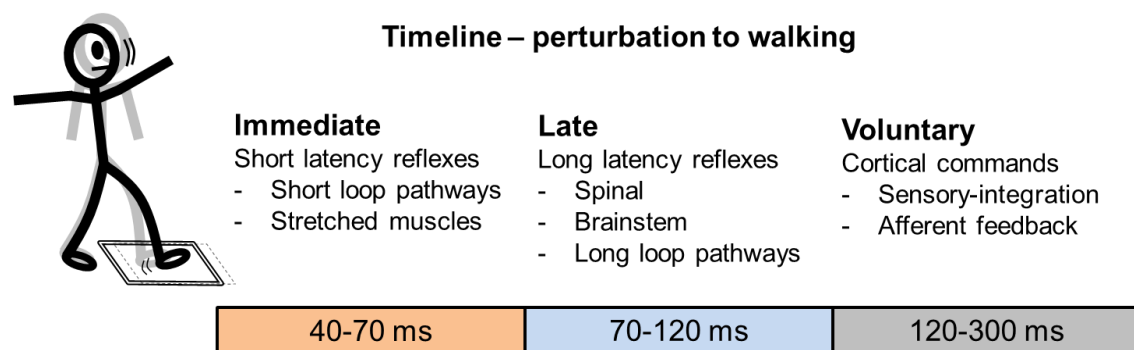
Figure 1. Timeline of the neuromechanical responses to perturbations while walking.

Specifically about perturbations involving foot displacement at (or shortly after) initial contact, there are many investigations describing postural responses while walking over slippery surfaces (Beschorner and Cham 2008; Cham and Redfern 2001; Chambers and Cham 2007; Cappellini et al. 2010; Parijat and Lockhart 2011; Redfern et al. 2001) and artificial platform translations (Ferber et al. 2002; Marigold and Patla 2002; Tang et al. 1998). Most of the outcomes show a similar mechanical strategy to reactively recover the balance, in which hip and knee joint movements are required in order to counteract changes in the center of mass position and speed (Cham and Redfern 2001; Duysens et al. 2008; Parijat and Lockhart 2011; Redfern et al. 2001; Tang et al. 1998; Yang et al. 2008; You et al. 2001).

Slips usually begin 50 ms after initial contact. In fact they are constantly occurring during human locomotion at a very small amplitude (< 2 cm), which does not elicit any major reactive response (Redfern et al. 2001). On the other hand, slip distances over 5 cm can compromise balance and result in falls if distances exceed 10 cm or the sliding velocity is greater than 50 cm/s (Cham and Redfern 2002; Redfern et al. 2001). In these cases the center of mass position cannot be counterbalanced by the previously described mechanisms and the collapse may result in a fall. The most critical phase of gait is shortly after initial contact, as the sustained body weight is being transferred to the potentially slipping foot and the center of mass moves from behind to ahead of the base of support (Grönqvist et al. 1989; You et al. 2001). Therefore, slips usually alter the position of the center of mass in relation to the base of support, and the postural response during slipping events aims to accelerate the center of mass towards the base of support (Yang et al. 2008; You et al. 2001).

Unexpected slips during walking also evoke contralateral lower limb reactions during slipping events, in response to polysynaptic long latency reflexes (Marigold and Patla 2002; Tang et al. 1998). The muscle onset latencies in the contralateral limb are comparable to the ipsilateral limb (Tang et al. 1998), generating an extensor strategy (ankle plantarflexion, knee extension, hip extension) that provides toe-touch. The contralateral toe-touch adds security to the individual and increases the base of support, consequently increasing stability (Marigold et al. 2003). In addition to the participation of the unperturbed limb, the elevation of the arms seems also important during unexpected slips, the displacement forward and outward assists in elevating the center

11

of mass and counterbalance its backward displacement (Marigold and Patla 2002; Marigold et al. 2003).

1.2. Locomotion described by a modular organization

Although locomotion seems to be an easy and automated task, there are several neurophysiological mechanisms acting constantly in order to control or modulate every unnoticeable action. Locomotion is usually learnt by humans in the first 12-24 months and the encyclopedia of motor tasks keeps updating/increasing throughout the whole life (Lacquaniti et al. 2012b). In terms of control, the human body has three main joints in the lower limbs (ankle, knee and hip), despite the pelvic complex that stabilizes HAT during gait. In order to control these joints, the central nervous system has to deal with approximately 100 muscles acting in the lower limbs and trunk simultaneously, therefore there are more actuators (i.e., muscles) than degrees of freedom (i.e. possible planar movements of a given joint) involved in the system (Lacquaniti et al. 2012b; Neptune et al. 2009; Olree and Vaughan 1995; Pandy and Andriacchi 2010). In the following chapter a literature review on the underlying modulation of human locomotion describes how CNS handles the complexity of the musculoskeletal system and can efficiently generate movements.

1.2.1. Theories on rhythmic motor acts

The first suggestions about the control of the muscles was given by Claudius Galenus in the 2nd century, who suggested that the brain was able to control individual muscles, so that every single contraction/relaxation has specific neural inputs driven from superior levels on the nervous system. However, the possible complexity involved in this model makes the computational tasks to be extremely fractioned, since the number of motor components that control movement matches the degrees of freedom (Bernstein 1967; Lacquaniti et al. 2012b; Pandy and Andriacchi 2010). Indeed, this is not the case. Studies on selective activation have demonstrated that the neural pathways in primates do not allow the activation of single muscles or motor units, and the CNS learns to control specific degrees of freedom with training (Fetz 2007; Kutch et al. 2008). If a fractioned motor control strategy is not possible, how does the CNS can control a large variety of muscles in order to generate such smooth and patterned movements during locomotion?

In the late 19th century it was first verified that spinal cord transected animals could generate locomotor-like movements (see Clarac 2008 and Guertin 2009 for historical context), therefore sensory information is not mandatory to initiate and keep rhythmic movements. Moreover, in the early 20th century, Sherrington (1910) first suggested that locomotion could be generated by basic motor patterns that integrate reflex actions from proprioceptors into specialized spinal centers. In addition, Sherrington suggested that specialized neurons in the spinal cord could use peripheral inputs in order to generate specific locomotor actions. Further investigations by a Sherrington's junior collaborator, Thomas Graham Brown, have first proposed that central pattern generators could evoke rhythmic movements in the lower limbs (Graham Brown 1914). This theory, as described in the Chapter 1.1, has been extensively studied in a large variety of species, including humans (Clarac 2008; Grillner 1985; Guertin 2009; Patla et al. 1985). The growing CPG theory raised the question whether the complexity in the control of locomotion was indeed a single-unit control, determining new trends on neurophysiology of locomotion and other rhythmic movements.

Grillner (1981) described a versatile organization of basic patterns that generate motor actions by studying lampreys' nervous system (unit-burst generators), which can recombine basic patterns in order to generate a variety of movements. Furthermore, (Grillner 1985) proposed that if descending commands can reach the correct neural circuits that compose unit CPGs, these unit-burst generators allow selective control of individual joints or muscle groups. Simultaneously, Patla and co-workers (1985) proposed a limb pattern generator model by applying a mathematical method (principal component analysis, PCA) consisting of (1) an oscillator that produces essential frequency of the output in response to tonic signals, (2) nonlinear shaping functions that molds the oscillator output to the respective pattern and (3) weighting functions that generate muscle activity patterns from basic waveforms. By using this model, Patla and co-workers (1985) claimed that basic patterns can modulate specific muscles with specific timing. From the first observations in the 1910's several models were proposed to explain the underlying mechanisms that controls CPGs (see Guertin 2009 for details), however, the ultimate explanation about the neuronal networks involved in the CPGs still remains to be shown (Clarac 2008; Guertin 2009).

1.2.2. Factorization analysis to describe motor behavior

In the mathematical field, several algorithms are available to group information that share similar characteristics, resulting in a reduced dimensionality of a dataset into a small set of basic vectors. Some examples of this type of algorithms are the principal component analysis (PCA), independent component analysis (ICA), vector quantization (VQ) and non-negative matrix factorization (NMF, Ivanenko et al. 2005; Lee and Seung 1999; Tresch et al. 2006). Each type of algorithm has special features and the focus in this literature review is upon NMF, which does not allow negative entries in the resultant base vectors. Lee and Seung (1999) have found that NMF provided the best results in image decomposition when compared to PCA and VQ. In addition, Brunet et al. (2004) have successfully used NMF to group a large amount of genes to a handful metagenes, allowing robust molecular pattern discovery. These are only a few examples on the use of NMF in the past, which have been largely used to describe motor patterns in animals and humans (Lacquaniti et al. 2012b; Tresch et al. 2006).

The basic idea of a factorization analysis for human locomotion involves the extractions of surface EMG from the main muscles involved in the task. An example of analysis is given by using three lower limb muscular groups during walking (Figure 2A, ankle plantarflexors, knee flexors and knee extensors muscles). It is evident that some muscles are acting in a synchronous pattern to other muscles, since they belong to the same muscular group (e.g., SOL, LG and MG are ankle plantarflexors), therefore showing a similar timing for the bursts of activation. The NMF algorithm basically groups similar information into basic patterns that can rebuild the original information (Figure 2B). Two parameters are extracted from NMF: the first is the gain factor/weighting coefficient or motor modules (M), which is responsible for rating the participation of the components from the original dataset (the different muscles in this case). The other parameter is the primitive or the activation signal (P), which determines the temporal property of the individual weightings. The product of P x M will generate a matrix containing reconstructed EMG for each muscle.

The reconstructed EMG has to successfully represent the original dataset. In this way, the reconstruction quality is obtained from the comparison of the original and the reconstructed datasets, by calculating the variation accounted for (VAF, Figure 2C). The

15

VAF is widely used to determine the number of required motor modules that can reliably describe the original dataset and the further conclusions on the dimensionality of the system. In this example, perfect reconstruction quality (i.e., VAF at 1) might be only achieved by using nine modules, which means that there is one neural controller per muscle. This assumption, however, is exactly what the factorization analysis aims to avoid, by determining that different muscles can be modulated by a common basic pattern. The explored example shows that neither one nor two motor modules were able to successfully reconstruct the original data when both original and reconstructed data are compared (Figure 2D). The use of less than three modules did not allow the visualization of the muscles of the same muscular group being gathered in the same motor module. The extraction of only one module accounts for the variability of the ankle plantarflexors muscles (PE, SO, LG, MG), which is determined by the higher weighting for these muscles and the temporal shaping of the activation signals (see figure 2B, green module). The inclusion of a second module introduces a more correct weighting for the knee extensor muscles, but the activation of the third muscular group (the knee flexors) is still not well defined. The extraction of three modules accounts for more than 90% of the variability in the original data and group the muscles in meaningful modules. Apart from three modules, the additional information might not result in relevant enhancement in the reconstruction quality, neither in the functionality of the muscles, not justifying increases in dimensionality.

1.2.3. *Muscles acting together - the muscle synergies theory*

The term "muscle synergies" has been recently used to express a group of muscles that are activated in a fixed balance (Tresch and Jarc 2009), or coordinated activations of groups of muscles with specific time-varying profiles (d'Avella et al. 2003). However, the nomenclature for synergies has also another connotation in which a synergy is related to how CNS modulates target movements. In this case synergies are task-specific groups of elements that modulate particular performance variables for a given movement (Krishnamoorthy et al. 2004; Latash et al. 2002) instead of modulating primarily muscular recruitment.
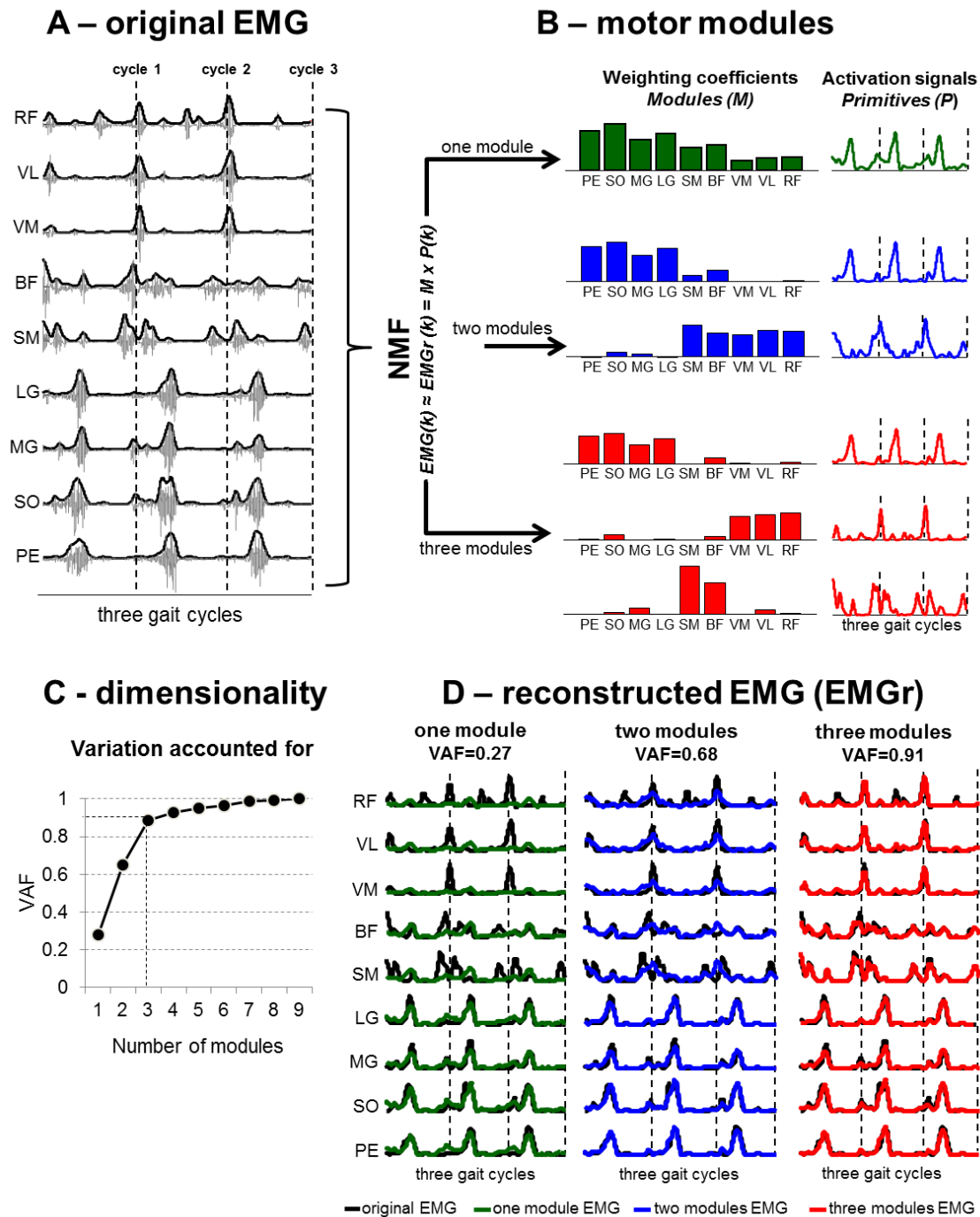
Figure 2. Non-negative matrix factorization (NMF) analysis to describe neural strategies to control motor actions. A) Original electromyography (EMG) from selected muscles during gait was rectified and low-pass filtered. NMF algorithm generates two parameters: the weighting coefficients (M) and the activation signals (P) for one, two or three motor modules that might describe successfully the original dataset (B). The reconstructed EMG (EMGr) results from the multiplication M x P, which is compared to EMG in order to determine the variation accounted for (VAF, C). The use of one or two motor modules does not reconstruct reliably the EMG data (D), therefore at least three modules are required. The final decision on the dimensionality for the dataset is defined by the verification that additional modules may not sufficiently enhance reconstruction quality. (PE: peroneus longus; SO: soleus; MG: medial gastrocnemius; LG: lateral gastrocnemius; SM: semimembranosus; BF: biceps femoris; VM: vastus medialis; VL: vastus lateralis; RF: rectus femoris.

The EMG signals collected from intramuscular or surface measurements may reflect the CNS input to the α-motorneurons (Davis and Vaughan 1993; Ivanenko et al. 2006; Lacquaniti et al. 2012a). Therefore, the recording of several EMG signals from the same limb during locomotion could provide information on how CNS regulates individual muscle activity, muscular groups or even different muscular groups that might be synergistically activated. However, back in 1980's, although the conceptual ideas of synergies were evident (Patla et al. 1985), the representation of the mechanism was not clear and required an optimal solution.

In the 1990's, investigations about human locomotion aimed to describe co-activity of muscles during the gait cycle and measured surface EMG from lower limb muscles. The differential procedure was the use of factor analysis in the matrices containing EMG envelopes from different muscles over time (Davis and Vaughan 1993; Olree and Vaughan 1995). The factor analysis grouped muscles with similar EMG envelopes in an objective manner, by identifying principal components that could represent a given amount of variability contained in the EMG dataset. Davis and Vaughan (1993) identified unilaterally two basic patterns related to the loading response and to the propulsion events during walking. Moreover, a third factor related to the transition from left to right stance (a coordination pattern) could also be identified when bilateral EMG signals were analyzed concomitantly (Olree and Vaughan 1995). The authors suggested that the CNS solves the problem of high dimensionality by generating a few basic patterns that control the main muscles involved in locomotion in both legs, forming the ground work to build a successful model of neural control of locomotion.

A series of studies on motor behavior has further explored the concepts proposed by Patla and co-workers (1985) and Olree and Vaughan (1995), also by enhancing the decomposition methods. Hind limbs of spinalized frogs were stimulated in different locations while EMG activity was recorded, and the resultant activations could be represented by a limited number of motor modules (Tresch et al. 1999). In addition, the motor behavior during kicking in intact frogs could be represented by three time varying motor modules, from which two of them had specific timing modulation related to the kicking kinematics (d'Avella et al. 2003). Furthermore, Motor modules extracted from kicks in frogs could also be identified in other motor behaviors such as walking, jumping and kicking (d'Avella et al. 2003; d'Avella and Bizzi 2005). This convincing

18

evidence of shared motor modules for different biomechanical contexts confirms the initial suggestions from Grillner (1981) concerning flexible output commands that are combined in order to generate a variety of movements. The quantification of behavior-independent motor modules suggested that basic biomechanical functions of the whole limb are possibly involved in the control of many tasks, whereas specific motor modules for a given behavior might be requested due to a unique biomechanical requirement (d'Avella and Bizzi 2005).

Specifically about human gait, recent studies have suggested a low-dimensional set of activation patterns waveforms that are consistent among different subjects, EMG datasets, walking speed and supported body weight (Cappellini et al. 2006; Ivanenko et al. 2004; Ivanenko et al. 2006; Ivanenko et al. 2008; Lacquaniti et al. 2012b; Neptune et al. 2009). It has been suggested that human locomotion is generated by a low-dimensional set of motor modules that provide the major input to the active motoneurons. These sequential inputs may involve the activation of one layer containing a rhythmic pattern generator and a second layer of CPGs located in the spinal cord. The specific CPG is therefore stimulated in order to recruit selected muscles for the respective biomechanical context on the gait cycle (Ivanenko et al. 2006; Lacquaniti et al. 2012b). Interestingly, the basic motor modules underlying the control human locomotion are not adequate for a co-ordinated voluntary task while walking (e.g., kicking a ball, grasping an object from the ground level), for which new motor modules have to superimpose a voluntary activation program onto the basic locomotor program (Ivanenko et al. 2005).

Locomotor skills in humans are developed throughout the different stages of the growing process. The most recent theory on the development of human gait suggest that it starts with two simple motor modules (related to leg extension and flexion) that provide body support during stance and drive the limb during swing. Two new motor modules related to touch-down and lift-off are added to the locomotion program at the first unsupported steps, which contribute to deceleration and acceleration of the body (Dominici et al. 2011). Over the following months the reduction in co-contraction plus more selective activation of the motor modules is observed in the activation signals, which begin to shift in time in relation to the step cycle. The adult characteristics of the motor modules, especially for the waveforms, are reached after the constant challenges

and experimentations evolved in learning a new task. From the moment that newborns initiate unsupported steps, the integration of supraspinal, spinal and sensory control require more sophisticated mechanisms, therefore a reorganization of the descending commands and interneuronal connectivity is required (Dominici et al. 2011; Lacquaniti et al. 2012a).

More recent investigations also revealed that motor modules are intrinsic components to human beings, since the two motor modules from neonates ensemble the load acceptance and the swing synergies usually found in adults (Dominici et al. 2011; Lacquaniti et al. 2012a). The characteristics of motor modules from human neonates and toddlers are also found in neonates and toddlers of other species (rats. Monkeys, cats and guinea fowls), suggesting that common inborn primitives may be involved in building the locomotor programs in various species. Moreover, CPGs coordinating muscle activity may have emerged during evolution from a common ancestral for legged vertebrates (Dominici et al. 2011).

The validity of the motor modules has also been an important question in neurophysiology, since the use of mathematical tools to describe the organization of biological systems might be purely noise extraction. In this way, Tresch et al. (2006) have demonstrated that the use of different factorization algorithms can reflect or represent basic patterns underlying the muscular activation of specific tasks. Moreover, the fact that surface EMG information might not fully represent the real descending commands from superior levels has also been discussed. Previous investigations have verified that sets of dedicated interneurons on the spinal cord may organize individual motor modules (Hart and Giszter 2010). In addition, motor modules related to arm and hand muscles are linked to specific projections from motor cortex to multiple neuronal pools (Holdefer and Miller 2002). This evidence suggests that outcomes from a factorization analysis on surface EMG signals may reliably describe the underlying organization of the central nervous system to perform motor actions.

1.2.4. *Postural control explained by modular organization*

Even though muscle synergies or motor modules can describe a possible CNS organization to control locomotion, they might not entirely account for the high complexity of sensory-motor integrations that may interfere in tens of muscles in each limb (Grillner 2006; Ivanenko et al. 2008 Lacquaniti et al. 2012b). Changes in the motor program might be elicited due to any alteration in lower levels of the CNS (cutaneous receptors and muscle spindles), such as during perturbations to the dynamic stability while walking (Cappellini et al. 2010).

The essential participation of afferent information in modulating postural responses was briefly described in Chapter 1.1.3. Additionally, recent investigations have hypothesized that aside from other motor gestures the control of posture is also possibly described by a modular organization. Postural responses to perturbations in different directions while cats remained standing can be resultant from the combination of four motor modules that specifies the endpoint force of a limb (Ting and Macpherson 2005). A specific motor module may therefore be activated as a function of the required biomechanical outcome across different postures (standing positions) and individuals, reflecting a global control mechanism that simplify the motor responses (Torres-Oviedo et al. 2006; Torres-Oviedo and Ting 2007; Torres-Oviedo and Ting 2010). Moreover, motor modules underlying postural responses while standing in humans may be responsible for the center of mass acceleration in order to recover balance (Chvatal et al. 2011).

Such evidence has contributed to the understanding of postural control while standing, but postural control during walking is also related to dynamic equilibrium (Minetti et al. 2011; Saibene and Minetti 2003). Changes in the environment such as the height of the landing surface at initial contact activate specific motor modules related to the surface height, which indicates that the absence of foot contact triggered short latency pathways (van der Linden et al. 2007). These authors suggested an internal model that is constantly comparing the expected sensory feedback and the actual sensory feedback generated an error signal, which is responsible for generating the fast postural responses. Moreover, the sensory feedback linked to the awareness of a slippery surface can change the overall muscle activation for the lower limbs and gait kinematics while walking (Cappellini et al. 2010). In addition, the increased motor-neuronal excitability

may correspond to a greater responsiveness to sensory inputs, as a strategy to increase awareness on the motor system to any possible postural request (Cappellini et al. 2010).

CHAPTER 2 – AIM OF THE THESIS

This chapter describes the motivation to perform the studies in this thesis and the objectives that have been addressed.

It is generally accepted that the control of locomotion relies on the integration of supraspinal and sensorial commands that drive the muscle actions. Taken together, these commands may be represented by a low-dimensional set of motor modules, which have been successfully recognized for unperturbed locomotor tasks in humans, such as walking and running. However, it remains unclear whether the modular organization to control locomotion is maintained when introducing perturbations to balance, since such perturbations alter muscle recruitment and evoke neural mechanisms to avoid falls (e.g., reflexes). Therefore, the aim of the thesis was to expand the concept of the modular control of different locomotor tasks in humans, while experiencing perturbations to balance. Additionally, it was aimed at verifying the effects of balance training on postural responses during perturbations to balance. To reach these aims, the first stage of the thesis involved the investigation of the effects of perturbations to balance during simple walking. A second stage involved the study of perturbations to balance during fast changes in direction while running. Finally, the third stage involved the implementation of a balance training in order to verify whether possibly enhanced balance control could be translated into improved postural responses during perturbations while changing direction.

This thesis collected the work performed in six scientific studies:

I) Oliveira AS, Farina D, Kersting UG (2012)
Biomechanical strategies to accomodate expected slips in different directions during walking. *Gait & Posture* 36(2):301-306, doi: 10.1016/j.gaitpost.2012.03.016.

II) Oliveira AS, Gizzi L, Kersting UG, Farina D (2012)
Modular organization of balance control following perturbations during walking. *J Neurophysiol*. Epub ahead of print. doi: 10.1152/jn.00217.2012.

III) Oliveira AS, Silva PB, Lund ME, Kersting UG, Farina D (2012)
Fast changes in direction during human locomotion are executed by impulsive activation of motor modules. *Neuroscience*. In submission.

IV) Oliveira AS, Silva PB, Lund ME, Kersting UG, Farina D (2012)
Neuromechanics of cutting manoeuvres is maintained during perturbations to balance. *PLoS One*. In Submission.

V) Oliveira AS, Silva PB, Kersting UG, Farina D (2012)
Unilateral Balance training enhances reactive recovery to perturbations in trained and contralateral limbs. *Gait & Posture*. In submission.

VI) Oliveira AS, Silva PB, Lund ME, Kersting UG, Farina D (2012)
The effects of balance training on the neural strategies for balance recovery after perturbations. *In preparation to submission.*

CHAPTER 3 – STRUCTURE OF THE THESIS

This chapter describes the specific topics if the conducted studies and the main results achieved

Bipedal human locomotion is more instable than quadrupedal locomotion, which also requires mechanisms that can prevent and/or reduce the risk of falls – recognized as a major concern for public health. Rapid postural responses elicited by reflexes and automatic neural mechanisms are extremely important to assure safety when perturbations such as trips, stumbles and slips occur. Although specific strategies to reactively recover balance after perturbations are well described in the literature, the overall control of locomotion also includes the continuous outflow of neural commands that are integrated in order to generate the movements. However, It is still not known whether the postural responses to perturbations are integrated to the ongoing motor programs or whether it requires additional controllers to be elicited.

The neural control of locomotion has intrigued researchers for a long time. How can the central nervous system be capable of controlling so many muscles and degrees of freedom in the lower limb joints to coordinate walking? Theories dated from more than 100 years ago have suggested that the central nervous system somehow modulates the recruitment of combined muscles that act synergistically during motion. In this way, the complexity of the control could be drastically reduced. In the last 20 years the advances in biomechanics, signal processing and neurophysiology of locomotion allowed for more consistent evidence towards the simplified neural modulation of movements. Studies from humans and other species have been consistently shown that targeting as well as cyclic movements such as walking, running and cycling are modulated by only a few motor patterns or motor modules.

This PhD thesis focuses on the effects that perturbations may cause on the modular control of different locomotor tasks. Initially, it was determined whether perturbations experienced among unperturbed trials would change motor control strategies during walking, since the expectation of dangerous conditions might influence motor behavior. From the observations that awareness on the perturbation possibility did not affect motor behavior substantially in Study I, the modular control of perturbed walking was

25

investigated in Study II. The main results showed that modular organization was preserved and the most relevant changes were verified in the timing to activate motor modules as a response to strong afferent inputs caused by perturbations.

Further studies were carried out on fast changes in direction while running. A modular organization similar to those presented for walking/running was found, which are impulsively activated in time. Moreover, the performance of these movements might be dictated by the optimization in recruiting these motor modules to perform impact absorption and propulsion phases of the movement. The evidence that cutting manoeuvres could be represented in a modular organization inspired the inclusion of perturbations to balance during the task in Study IV. Similar to walking, perturbations during cutting manoeuvres elicited changes on the timing for the activation of the motor modules, which reduced hamstrings activation at the perturbation event and therefore might increase injury risks in the knee joint.

Many training protocols have been tested in order to reduce injury incidence, which have employed different strategies such as strength, agility, balance, mental activity among others. Especially balance training (also called proprioceptive or neuromuscular training) was consistently proven to be effective in reducing injury incidence for athletes, by improving neural mechanisms that subsequently improve joint stability. In study V it was investigated whether unilateral balance training could improve postural reactions during perturbations. It was found that neuromuscular responses to perturbations in unilateral standing position were faster and stronger for muscles of the trained limb after balance training. Additionally, cross-education effects for the untrained leg were verified, which improved instantaneous reactions to perturbation. These results suggested that balance recover is facilitated by balance training, which might indicate better postural reactions during dynamic perturbations. Therefore, in Study VI it was tested whether the neuromuscular enhancements from balance training could also benefit postural corrections during perturbed fast changes in direction. The results indicated that the motor modules related to trunk and hip stabilization during cutting manoeuvres were slightly altered and this adaptation may improve co-contractions and eventually improve postural reactions to perturbations. However, no relevant changes were found in the activation signals that drive the motor modules.

CHAPTER 4 – DISCUSSION

This chapter discusses the implications of the results of the preceding chapters and summarizes the main findings in the conclusion

The neural control of human locomotion has been described by a low dimensional set of motor modules, which are linked to specific biomechanical goals during gait cycle (Lacquaniti et al. 2012b). In Study III it was also verified that complex locomotor tasks such as fast changes in direction, could also be represented by a few motor modules, which are in fact similar to those found for walking and running (Cappellini et al. 2006). The presented results from Study II on walking and Studies IV and VI on fast changes in direction indicated that perturbations to balance during different locomotor task influence the neural control underlying its execution. These motor modules are preserved when walking is combined to other voluntary movements, such as kicking a ball or stepping over obstacles, which suggest that the modular control of locomotion is not affected by supplementary actions (Ivanenko et al. 2005). On the other hand, limb trajectory is influenced by the participation of afferent inputs to the motor program of wiping reflex in frogs (Kargo and Giszter 2000), which suggest that modulation of movements that rely on afferent information might not follow similar mechanisms as verified for voluntary actions while walking. Therefore, the participation of afferent components when locomotion is perturbed may require unique changes in the modular control of human walking.

In perturbed conditions, the most pronounced changes concerning the motor modules were verified in the activation signals, which contain the timing properties of individual motor modules. It has been reported that afferent responsiveness is altered when human balance is perturbed (Cappellini et al. 2010; Schillings et al. 2000; van der Linden et al. 2007), and that the overall control of human locomotion is susceptible to changes related to peripheral input (Lacquaniti et al 2012b; Rossignol 2006). The activation signals are representations of the integration of supraspinal and afferent signals that combine motor modules to produce a variety of motor actions (Lacquaniti et al. 2012b; d'Avella and Bizzi 2005), therefore changes in the periphery may influence the supraspinal commands that contribute during locomotion (Duysens et al. 2008; Lacquaniti et al. 2012b; Rossignol et al. 2006). In this way, the results from Study II, IV

and VI reinforce and progress the knowledge on the neural control of perturbed locomotion. It is suggested that during perturbations to balance the ongoing motor program receives maybe better and/or additional input from the periphery, which influences higher levels of the CNS.

The lack of major changes in the muscle weightings was somehow unexpected in the conducted studies, since previous investigations have described the weighting coefficients as the flexible component on the modular control of locomotion (Cappellini et al. 2006; Ivanenko et al. 2008; Lacquaniti et al. 2012b). In the case of a walking task (Study II), three out of four weighting coefficients were preserved, whereas no changes in the muscle weightings were found for the perturbed fast changes in directions in Study IV. The minor changes in the lower limb/trunk kinematics verified in Study IV might indicate that it would be difficult to find major changes in the weighting coefficients, since motion remains similar to the unperturbed condition. Literature is scarce on investigations comparing motor modules from unperturbed and perturbed conditions during any type of locomotion. Therefore, it is assumed that since the motor output is not drastically altered during perturbed changes in direction, the overall control of the task would be also similar to those from the unperturbed condition.

A balance training protocol was implemented to a specific population of healthy, young and active males in order to verify whether the acquired balance skills could be transferred to the postural responses during fast changes in direction. Since it was previously found in Study II and Study IV that perturbations influence the integration of supraspinal and afferent components to the motor program, the balance training might have the effect of reducing this influence on the modular organization. In recent studies it has been suggested that balance training may have predominant effects on supraspinal commands to the muscles (Perez et al. 2006; Taube et al. 2008; Taube et al. 2007), which result in improved inter-muscular coordination, faster reaction time and reduced reflex inhibition (Alentorn-Geli et al. 2009; Eils and Rosenbaum 2001; Linford et al. 2006; Osborne et al. 2001). In Study V, by using single-limb perturbations in a standing position it was verified that balance training improves postural responses to perturbations, which might be related to supraspinal adaptations as previously suggested above.

Interestingly, balance training influenced the modular organization of the task, predominantly on the muscle weightings related to trunk and hip stability when perturbations were delivered. This specific adaptation on the trunk and hip may be related to a better core stability, which improves balance and reduces injury risks (Alentorn-Geli et al. 2009; Leetun et al. 2004; Zazulak et al. 2007b; Zazulak et al. 2007a). Although the benefits from balance training are well known in the literature (Alentorn-Geli et al. 2009; Eils and Rosenbaum 2001), the specific effects on dynamic sports actions, such as fast changes in directions, are barely explored (Cochrane et al. 2010). The results of this last experiment (Study VI) suggest that balance training induces changes in the neural control of the task when perturbations occur.

CONCLUSION

Perturbations to balance elicited during the stance phase of walking and fast changes in direction while running are modulated by predominantly similar motor modules. However, the effects of perturbations on the afferent inputs that are integrated with supraspinal commands cause remarkable changes in the activation signals that drive these motor modules, even though the locomotor tasks are achieved successfully. Moreover, after a 6-week balance training protocol, despite positive adaptations to regain balance following static perturbations, there is a change of the neural control of core stability during perturbed changes in direction, which in practical terms might result in reduced injury risks while performing the motor action.

CHAPTER 5 – REFERENCES

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STUDY I

Published in Gait & Posture, 2012

Biomechanical strategies to accommodate expected slips in different directions during walking

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ARTICLE INFO

ABSTRACT

The aim of the study was to verify whether heel kinematics, ground reaction forces and electromyography (EMG) during walking are affected when anticipating slips in anterior–posterior (AP) and medial–lateral directions (ML). Eight healthy men walked through a 7-m walkway, stepping on a robotic force platform. Initially, baseline (BASE) gait mechanics were assessed with the platform at rest. Subsequently, two sets of randomized perturbations (10-cm translations with at different platform movement velocities) in the AP and ML direction were applied. Perturbations were interspersed with unperturbed walking (i.e., catch-trials C-AP and C-ML). Heel accelerations, ground reaction forces and activities from the perturbed leg and trunk muscles were analyzed. EMG was analysed in four epochs: PRE (-100 ms to heel strike [HS]), EARLY (HS to 150 ms after HS), MID (150–300 ms after HS) and LATE (300 ms to toe-off). Comparisons were made between BASE, C-AP and C-ML. The first peak of the vertical force component (Fz) was decreased for C-AP and C-ML ($p < 0.05$) but no changes were found for braking and propulsion impulses. EMG showed effects of expected slips on tibialis anterior, gastrocnemius lateralis, soleus and peroneus longus, especially for EARLY and MID epochs, with direction-specific increases in activity. In conclusion, expected slips in different directions determine only marginal changes in terms of kinetics and heel kinematics, but selective activation after HS indicates that direction-dependent strategies are adopted when anticipating perturbations.

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1. Introduction

Walking on a slippery and potentially dangerous surfaces changes overall muscular activation (electromyography [EMG]) and kinematics compared to normal walking [1]. These changes in motor control depend on learning processes triggered in order to avoid falls [2]. Usually, strategies to avoid falls are considered successful when heel velocity at heel strike is reduced [3]. This is achieved by reflex responses and voluntary activation of lower limbs and trunk muscles during the foot contact period, in order to reduce the distance between the slipping leg and the body's center of mass [4–6]. The most applied experimental perturbation during gait is the forward foot displacement, which requires regaining of balance in the anterior–posterior (A–P) direction. Conversely, only few studies have applied perturbations in medial–lateral (M–L) directions (e.g.,

Karayannidou et al. [7] in cats; Oddsson et al. [8] in humans). Nonetheless, although most slips may occur in a A–P direction we might experience lateral loss of balance by colliding with obstacles, walking along inclined surfaces or along uneven paths [8].

Changes in gait pattern may be related to the expectation of a perturbation even when perturbations are anticipated but not actually present (catch trials) [5,9]. Although not all investigators have reported changes in biomechanical parameters during catch trials [5,10], reduced vertical force peaks and the braking impulses in these trials due to a flatter foot position at heel strike were generally observed [2,9,11]. In addition, muscular activation patterns were altered when expecting slips [6,9,12] indicating that humans adopt a more cautious gait pattern [2].

Studies on postural adjustments in multi-directional perturbations revealed different strategies dependent on the direction of the perturbation during standing [13,14], being controlled by the same motor modules from superior levels of neural control [14]. Balance maintenance during walking when expecting slips may require conditioned motor learning and psychologically influenced postural adjustments, such as increased stiffness in the lower limb joints may be related to the fear of falling [15]. Thus it is indicated that

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neuromuscular adaptation strategies lead to a more cautious walking pattern after experiencing backward slips. However, M–L balance loss generates instability by moving the center of mass outside the base of support [8], which can be compensated for by adjusting the step length and width [16]. In the context of investigating the adaptational mechanisms involved it would be indicated to investigate both A–P and M–L perturbations which may also require distinct/direction dependent adaptations/strategies of cautious walking.

Thus, the aim of the present study was to compare different neuromuscular adaptation strategies of A–P and M–L perturbations by analysing kinematics, kinetics and EMG parameters during unperturbed gait and during catch trials interspersed with perturbations in the anterior–posterior (A–P, forward and backward slips) and medial–lateral directions (M–L, leftward and rightward slips). We hypothesized that catch trials are affected by perturbations during walking, by means of altered heel kinematics, ground reaction forces and muscular activity. Furthermore, direction-dependent mechanical and muscular adaptations will occur when expecting slips in the frontal or sagittal plane.

2. Methods

2.1. Subjects

Eight healthy men (age, 28 ± 4 yrs; body mass, 71 ± 10 kg; body height, 171 ± 7 cm) volunteered for the experiment. They had no known history of neurological or motor disorder. All subjects provided written informed consent before participation and the procedures were approved by the ethical committee of Northern Jutland (N-20100042).
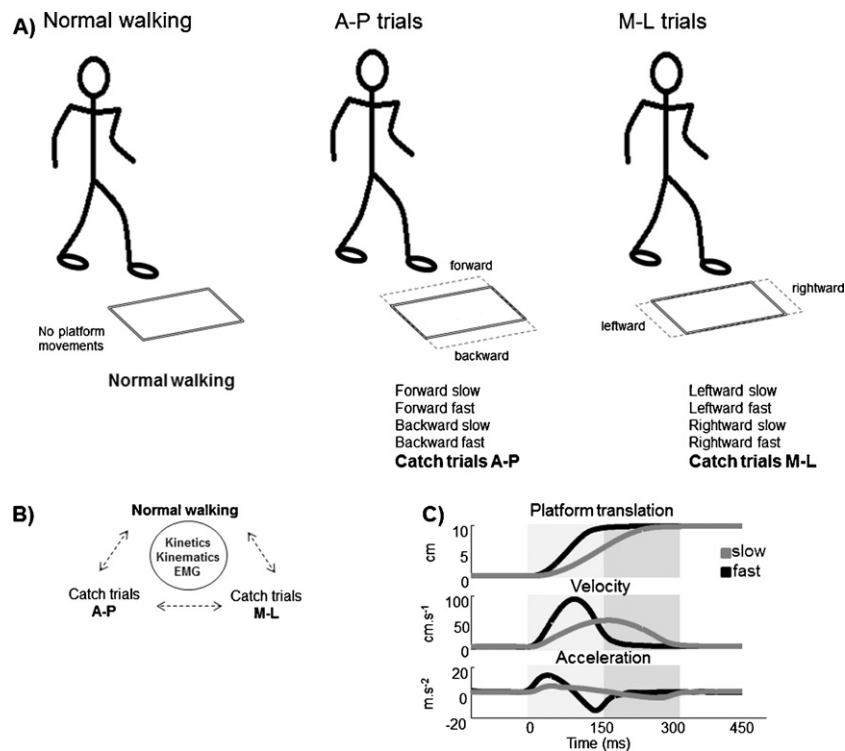
2.2. Experimental setup

Subjects were asked to walk at their preferred speed and step with the right foot on a robotic force platform positioned in the middle of a 7-m walkway. Lower limb and trunk muscle EMG and marker position were recorded from 500 ms before heel strike on the force platform until the next ipsilateral heel strike. Ground reaction forces were recorded during stance phase. Initially, a familiarization to the walkway was required, so that the subjects adjusted their step length to comfortably reach the force platform without targeting it. After familiarization, subjects performed 12 baseline trials without perturbations (BASE) to establish their normal walking pattern. Subsequently, two sets of trials were performed: A–P (with perturbations in the frontal plane, i.e., forward/backward) or M–L (with perturbations in the sagittal plane, i.e., left/right), including unperturbed (catch) trials in a randomized order. Each direction of perturbation (four directions: forward, backward, left and right) was delivered at two velocities (fast: averaged velocity = 41.2 cm s^{-1}, peak velocity = 88.7 cm s^{-1}; slow: averaged velocity = 27.8 cm s^{-1}, peak velocity = 49.4 cm s^{-1}). Therefore, for each set of perturbations (frontal and sagittal plane), subjects experienced five conditions: (1) direction-1 fast; (2) direction-1 slow; (3) direction-2 fast; (4) direction-2 slow and (5) catch trials (C-AP or C-ML) (Fig. 1), where direction 1 and 2 are forward/backward or left/right depending on the set. For each condition, 12 trials were performed, totalling 60 trials per set.

2.3. Kinematics

Retroreflective ball-shaped markers (14 mm diameter) were placed bilaterally on the posterior aspect of the calcaneus and tracked with a motion analysis system with eight infrared digital video cameras (Oqus 300 series, Qualisys, Gothenburg, Sweden). The kinematic data were recorded with a sampling frequency of 256 Hz and synchronized with the EMG and kinetic recordings. Subjects wore the same type of walking shoes, full stretch top and pants covering the EMG cables to avoid movement artefacts.

Fig. 1. Experimental setup. (A) Different walking tasks during the experimental session. Firstly subjects walked with no platform translations. After this, two blocks of walking trials including perturbations in the A–P or M–L directions and trials with no perturbation (catch trials) were administered in random order. (B) Comparisons were made among all unperturbed trials for ground reaction forces, heel kinematics and leg muscular activity. (C) Perturbed trials were 10 cm translations, administered in two velocities (slow and fast).

2.4. Kinetics

A three-dimensional force platform constructed over a hydraulic system [17] provided perturbation stimuli and simultaneous measures of vertical (Fz), anterior–posterior (Fy) and medial–lateral (Fx) ground reaction forces. Specific software (MrKick II, Aalborg University, Aalborg, Denmark) was used for recording (1024 Hz). Using an electric feedback circuit, the Fz force triggered force plate movements.

2.5. EMG recordings

Surface EMG signals were recorded in bipolar derivations with pairs of Ag/AgCl electrodes (Ambu Neuroline 720 01-K/12; Ambu, Ballerup, Denmark) with 22 mm of center-to-center spacing. The EMG signals were amplified with a gain of 2000 (EMG-USB, LISiN; OT Bioelettronica, Turin, Italy), sampled at 2048 Hz, and A/D converted on 12 bits and band-pass filtered (second-order Butterworth, 10–450 Hz). A reference electrode was placed at the right wrist. The EMG signals of the right limb were recorded from peroneus longus (PER), gastrocnemius lateralis (GL), soleus (SOL), tibialis anterior (TA), vastus lateralis (VL), rectus femoris (RF), biceps femoris (BF) and tensor fascia latae (TFL) according to Hermens et al. [18].

2.6. Data presentation and analysis

Data from BASE C-AP and C-ML were analyzed using MatLab (R2009B, The MathWorks, Mass.) and the results for a given subject are the result of an average of all trials in the condition. Kinematic data were low-pass filtered (6 Hz, second-order, zero lag Butterworth). The right heel positions in the A–P direction were used to determine the stride which contains the step over the platform. Horizontal heel acceleration (Hacc) and vertical heel acceleration
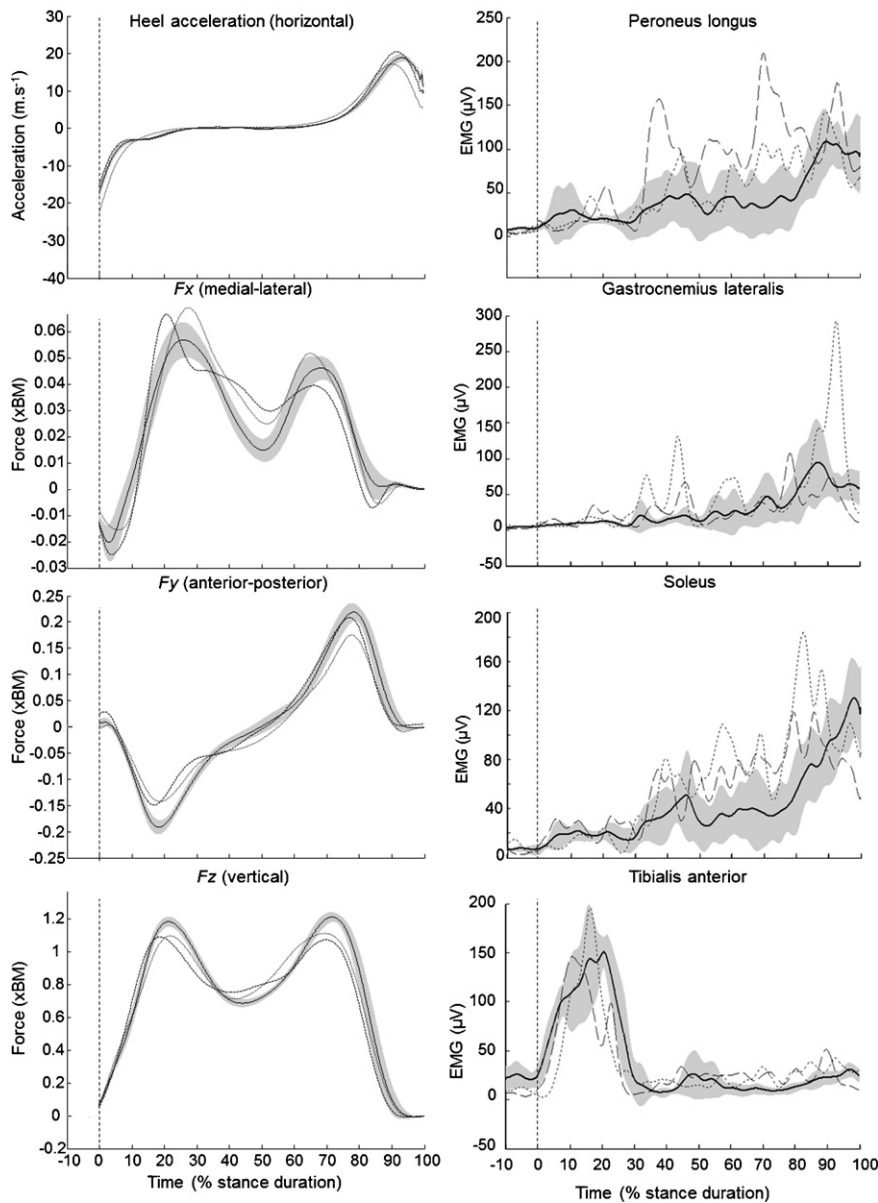
Fig. 2. (Left) Representative kinematics and kinetics data from one subject. Mean (thick black line) and standard deviation (grey surrounding area) of heel acceleration in the horizontal direction (Hacc), medial–lateral (Fx), anterior–posterior (Fy) and vertical (Fz) force components (represented as ratio of the body mass [xBM]) for all trials during BASE. Additionally, a single trial for C-AP (dotted lines) and for C-ML (dashed lines) were included for comparisons. (Right) Mean (thick black line) and standard deviation (grey surrounding area) representative leg muscles EMG of one subject. Additionally, a single trial for C-AP (dotted lines) and for C-ML (dashed lines) were included for comparisons.

(Vacc) were extracted by differentiating heel position using the central difference formulae [3].

Force data were initially low-pass filtered (55 Hz, second-order, zero lag Butterworth) and scaled with respect to body mass (N/kg). Fig. 2 shows representative force component data for one subject. The Fx component was used to determine the medial impulse (MED-imp, integral of medial component) and lateral impulse (LAT-imp, integral of lateral component). The Fy component was analyzed to determine breaking impulse (BRK-imp, integral of breaking phase), propulsion impulse (PRP-imp, integral of propulsion phase). In addition, the Fz component was analyzed to determine contact time (CTT), the first (PK1-Z) and second vertical peaks (PK2-Z) and minimum Fz (MIN-Z).

EMG activity was full-wave rectified and low-pass filtered (10 Hz, second order, zero lag Butterworth) and partitioned from 100 ms before the heel strike up to toe off (determined from Fz component). For each muscle, EMG signals for a single trial were scaled with respect to the maximal EMG found during all gait cycles from BASE condition [6]. EMG integrals from four epochs were analyzed: −100 ms to heel strike (PRE); heel strike to 150 ms (EARLY); 150–300 ms (MID), and 300 ms to toe-off (LATE). Intensities/amplitudes for each period were normalized (/ expressed as) with respect to the averaged BASE intensity (i.e., ratio C-AP/BASE or C-ML/BASE).

2.7. Statistical analysis

The effects of different conditions (BASE vs C-AP vs C-ML) on the dependent variables (iEMG in the different epochs, peak forces, impulses and kinematic measurements) were investigated using one-way ANOVA, followed by Tukey post hoc test if necessary. Especially for EMG measurements, the effects of epochs during stance phase (PRE vs EARLY vs MID vs LATE) on the iEMG for each muscle required a different analysis. Thus, the effects of different epochs during stance phase were verified by a one-way ANOVA. The significance level was set to $p < 0.05$. All data are presented as mean ± standard deviation.

3. Results

Fig. 2 (top left) shows representative data from one subject for Hacc as well as ground reaction forces as a function of body mass (xBM). There is an overall similarity for the curves of heel acceleration and ground reaction forces, but some minor discrepancies such as medial–lateral and vertical peaks can be found. Fig. 2 (right) shows representative data from one subject for right leg muscles for BASE, C-AP and C-ML. In this case, the most relevant changes are a greater EMG activity after heel strike during C-AP and C-ML when compared to BASE.

Table 1
Mean (SD) foot contact time on the force platform (CTT), heel acceleration in the anterior–posterior direction (Hacc) and in the vertical direction (Vacc). Fy braking (BRK-imp) and propulsion (BRK-imp) impulses and Fx medial (MED-imp) and lateral (LAT-imp) impulses during true baselines (BASE), catch trials among anterior–posterior perturbations (C-AP) and catch trials among medial lateral perturbations (C-ML).

	BASE	C-AP	C-ML
CTT (s)	0.665 ± 0.05	0.659 ± 0.05	0.655 ± 0.049
Hacc (m s^{-2})	−14.98 ± 3.91	−17.99 ± 3.32	−14.9 ± 4.13
Vacc (m s^{-2})	4.53 ± 0.57	3.94 ± 0.67	4.76 ± 0.75
BRK-imp (N s/kg)	1.23 ± 0.76	0.91 ± 0.55	1.27 ± 0.34
PRP-imp (N s/kg)	1.73 ± 0.26	1.87 ± 0.25	1.84 ± 0.19
MED-imp (N s/kg)	−0.25 ± 0.26	−0.22 ± 0.3	−0.29 ± 0.24
LAT-imp (N s/kg)	0.63 ± 0.29	0.65 ± 0.32	0.057 ± 0.36
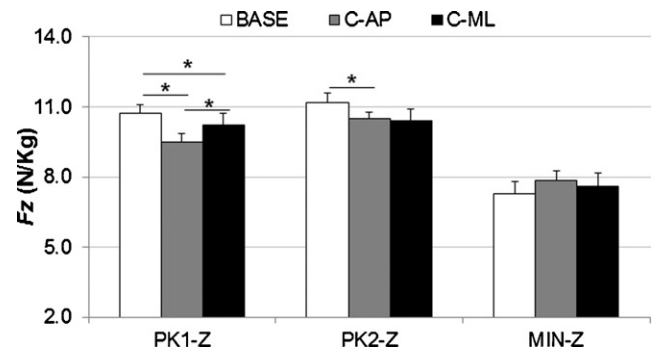
Fig. 3. Mean (SD) first vertical peak (PK1-Z), second vertical peak (PK2-Z), and minimum vertical force between peaks (MIN-Z) during true baselines (BASE), catch trials among anterior–posterior perturbations (C-AP) and catch trials among medial lateral perturbations (C-ML). * denotes significant difference between conditions ($p < 0.05$).

3.1. Heel kinematics

Foot contact time was similar among conditions ($p > 0.05$, Table 1). In addition, a higher deceleration for Hacc (~20%) was found accompanied by a lower acceleration for Vacc (~15%) in the C-AP when compared to the other conditions. However the statistical analyses did not reveal significance ($p = 0.09$ and $p = 0.1$, respectively).

3.2. Ground reaction forces

During ground contact, BASE showed a higher PK1-Z and PK2-Z compared to C-AP, and also an elevated PK1-Z when compared to C-ML ($F = 5.7$ and $F = 5.5$ respectively; $p < 0.05$, Fig. 3). In addition, PK1-Z during C-AP was significantly lower compared to C-ML ($F = 4.8$; $p < 0.05$). No significant differences were found for MIN-Z ($p > 0.05$, Table 1). For the horizontal force component, no significant changes were found for BRK-imp ($p = 0.38$) and PRP-imp impulses ($p = 0.43$). Similarly, no significant differences were found for the lateral force component for MED-imp and LAT-imp ($p > 0.05$).

3.3. Electromyography

C-AP elicited greater EMG for GL and SOL when compared to BASE during EARLY and MID ($F = 6.4$ and $F = 5.3$ respectively; $p < 0.01$, Fig. 4). In the same way, C-ML elicited similar increase for PER ($F = 4.3$; $p < 0.05$).

The development of muscle activity during catch trials was different from other conditions, being verified by an increased EMG amplitude during EARLY and MID in comparison to PRE for PER, GL and SOL ($p < 0.05$) for both C-AP and C-ML. Additionally, TA muscle presented greater EMG activity during LATE (C-AP) and MID (C-ML) in comparison to PRE ($F = 4.1$ and $F = 5.1$ respectively; $p < 0.05$). Further, the VL muscle presented higher EMG activity during LATE in comparison to PRE and EARLY ($F = 3.9$ and $F = 4.1$ respectively; $p < 0.05$). For all other muscles, no significant differences were found between walking conditions.

4. Discussion

The aim of the study was to compare different neuromuscular adaptation strategies for A–P and M–L perturbations during catch trials and we found no significant alterations in kinematics or kinetics. However, specific EMG responses indicated that different strategies may be required when experiencing slips in different directions, which affects muscular activation during stance phase.
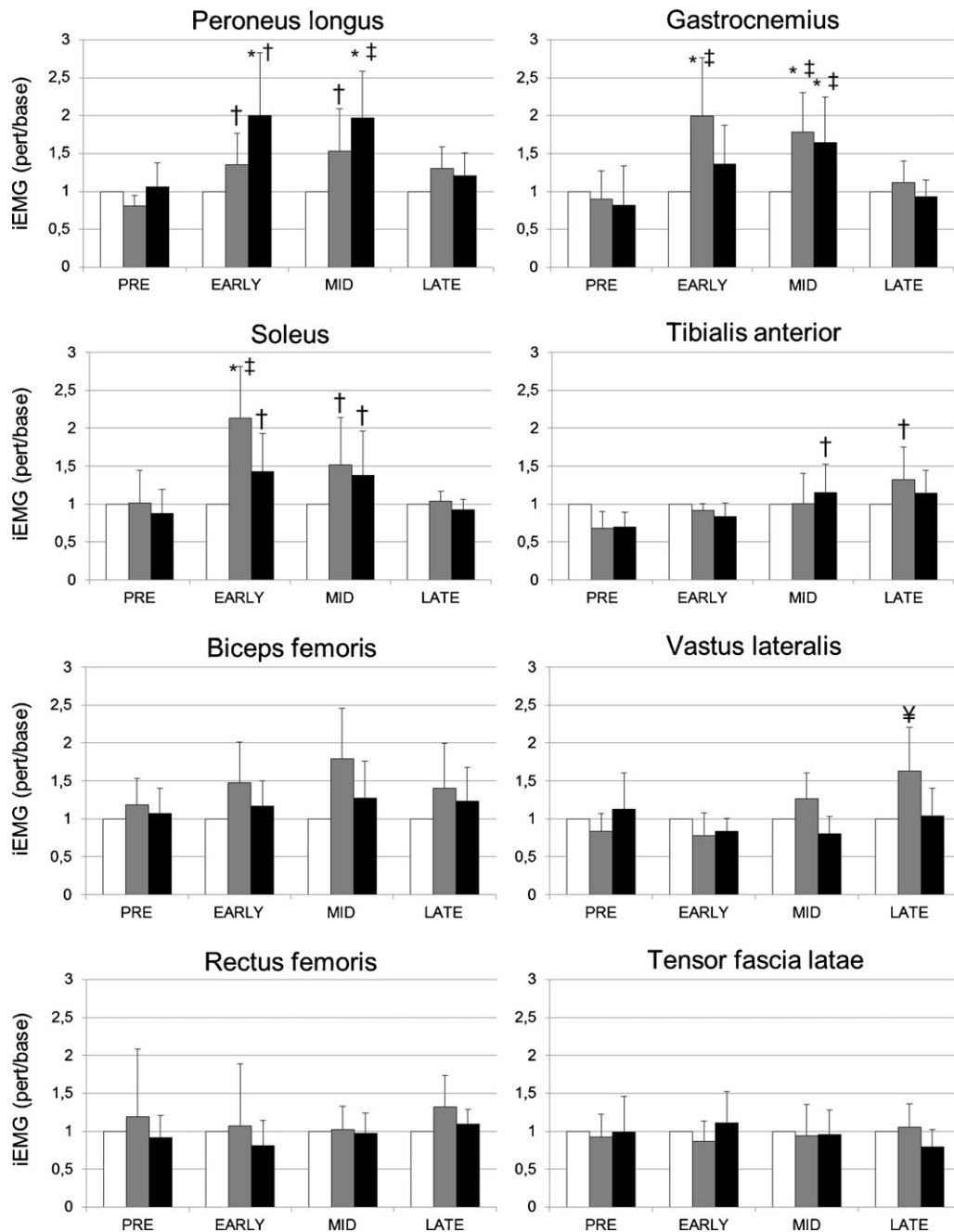
Fig. 4. Mean (SD) EMG activity (ratio iEMG perturbed trials/iEMG baselines [pert/base]) for leg, thigh and trunk muscles during true baselines (BASE, white bars), catch trials among anterior–posterior perturbations (C-AP, gray bars) and catch trials among medial lateral perturbations (C-ML, black bars). EMG signal was analyzed in sectors starting from 100 ms before heel strike to heel strike event (PRE), from heel strike to 150 ms after heel strike (EARLY), from 150 to 300 ms after heel strike (MID) and from 300 ms to toe-off event (LATE). * denotes significant difference in relation to BASE ($p < 0.05$); † denotes significant difference in relation to PRE ($p < 0.05$); ‡ denotes significant difference in relation to PRE and LATE ($p < 0.05$); ¥ denotes significant difference in relation to PRE and EARLY ($p < 0.05$).

It is known that ML imbalances require different strategies during standing [13,14] and also change step length and width [16]. Our results are adding some neuromuscular insights to elucidate motor control behaviour when gait is perturbed in the frontal plane.

Our results about Fz suggest that minor changes may occur especially for C-AP. Both the vertical peaks (PKZ-1 and PKZ-2) were reduced for C-AP, while only PK1-Z was affected during C-ML to a lesser extent. Previous studies have found no changes in vertical peaks [9,19], as well as changes for peaks and braking impulse component during slippery catch trials [9,11]. These changes may be related to increased caution in preparation for heel strike during walking after experiencing slips [9]. Beschorner and Cham [3] have

shown that Hacc during A–P slips may be reduced (i.e., increased deceleration) as an essential strategy to prevent slips. However only a trend for Hacc reduction was found in this study, most likely due to the accommodation period given in this experiment allowing for development of a strategy to cope with the applied slips [9]. C-AP showed specific effects of perturbations on force measurements, which were less pronounced for C-ML.

More relevant direction-dependent changes were observed for leg muscles activity, which increased by 1.5 or 2 times in the catch trials with respect to BASE, although previous studies may not consider these changes sufficient to change the characteristics of gait [6]. For GL and SOL a greater activation during C-AP was found,

while for PER there was higher activation for C-ML. The plantar flexors (GL and SOL) act in movements in the sagittal plane, while ankle everters (PER) present function in the frontal plane movements. Thus these muscles were selectively recruited during the stance phase depending on the direction of the perturbation. Especially, PER might play an important role in the stability during perturbations in different directions. However the specific reason to these changes needs further investigations. As responses to forward perturbations, TA, VL, BF and RF present higher activation and GL presents lower initial activation during slip events [2,5,6,9]. These strategies are elicited to reactively recover the balance and avoid falls.

In contrast with our expectation and previous results [9], no changes in EMG were found before heel strike for any lower limb or trunk muscle. Muscular activation started to be pronounced in relation to BASE only after heel strike, and it lasted ~150–300 ms depending on the muscle and the direction of the possible perturbations. This fact (concomitant to kinematics analysis) demonstrates no anticipatory strategy before heel strike. An altered EMG before heel strike may be interpreted as an attempt to increase joint stiffness [20], caution and feed-forward control to anticipate threats shortly before and after heel strike [9]. On the other hand, a limitation to this study is that the subjects were not performing continuous walking, and the gait cycles had to be adjusted in such way that subjects could step onto the platform. Therefore our results have to be carefully interpreted.

Walking on a potentially "moving" or unstable surface area may lead to motor adaptation/learning, which can possibly increase leg EMG during catch trials [15]. Possible explanations for changes in EMG activity after heel strike are (1) postural conditioned reflex, triggered by foot contact with a moving surface segment; (2) our weak ability of switching to a "natural" gait pattern after been exposed to perturbations [15], altering H-reflex conditioning throughout a single session [21]; and (3) the fear of falling which triggers involuntary strategies to increase stability during the stance phase [22]. Thus, there are strategies triggered during stance phase, which can be specifically modulated depending on the direction of expected slips. As no perturbation occurs in catch trials, the threat is not confirmed and the EMG activity during LATE becomes similar to the normal walking level. Walking velocity during this experiment could affect the interpretation of results, but contact time was similar. This may be supported by previous results where no differences in walking velocity, stride duration and length were shown for these different conditions [23].

TA and VL showed altered activation patterns when comparing catch trials vs. BASE, where both muscles exhibited increased EMG the end of stance phase. TA presents decreased activation during the early phase of foot contact [5,9], which may be qualitatively identified (Fig. 2, right) but was not statistically confirmed. Thus, the significant differences verified for C-AP and C-ML during MID and especially LATE may be highlighted by this initial depression before and just after heel strike. In the case of VL muscle, previous investigations about forward slips verified delayed responses (Chambers and Cham [24], >230 ms after the event), which also can be related to the unconscious muscular activity across slipping trials.

5. Conclusion

In conclusion, the expectation of slipping in anterior–posterior or medial–lateral directions determines only marginal differences in terms of kinetics and kinematics, for which instantaneous vertical forces are lower for catch trials in the anterior–posterior direction. On the other hand, selective activation especially for ankle joint muscles indicates that modular strategies may be utilized in case of a possible/expected perturbation. These modulations are specifically triggered after heel strike, but as soon as the perturbation does not occur, the additional recruitment is terminated during the late stance phase of gait.

Conflict of interest statement

The authors declare that they have no conflict of interest.

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STUDY II

Modular organization of balance control following perturbations during walking

AQ: 1

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AQ: 2

Oliveira AS, Gizzi L, Kersting UG, Farina D. Modular organization of balance control following perturbations during walking. *J Neurophysiol* 108: 000–000, 2012. First published July 5, 2012; doi:10.1152/jn.00217.2012.—Balance recovery during walking requires complex sensory-motor integration. Mechanisms to avoid falls are active concomitantly with human locomotion motor patterns. It has been suggested that gait can be described by a set of motor modules (synergies), but little is known on the modularity of gait during recovery of balance due to unexpected slips. Our hypothesis was that muscular activation during reactive recovery of balance during gait has a modular organization. The aim of the study was to verify this hypothesis when perturbations were delivered in different directions. Eight healthy men walked on a 7-m walkway, which had a moveable force platform embedded in the middle. Subjects experienced unperturbed walking as well as perturbations delivered in the sagittal (forward and backward) and frontal (leftward and rightward) planes. Bilateral full-body kinematics and surface electromyography (EMG) from lower limbs, trunk, and neck were recorded during walking. Synergies and activation signals were extracted from surface EMG signals. Four modules were sufficient to explain the unperturbed gait and the gait perturbed in any of the perturbation directions. Moreover, three of four modules extracted from the unperturbed gait were the same for gait perturbed forward, leftward, and rightward (similarity in synergies = 0.94 ± 0.03). On the other hand, the activation signals were different between unperturbed and perturbed gait (average correlation coefficient = 0.55 ± 0.16). These strategies to recover balance were robust across subjects. In conclusion, changes in lower limb and trunk kinematics provoked by perturbations were reflected in minimal adjustments in the muscular modular organization of walking, with three of four modules preserved from normal walking. Conversely, the activation signals were all substantially influenced by the perturbations, being the result of integration of afferent information and supraspinal control.

balance; EMG; gait; synergies

AQ: 3

IT HAS BEEN SUGGESTED that the central nervous system (CNS) may simplify the control of complex movements by activating a limited number of motor modules, also called muscle synergies (Ivanenko et al. 2004, 2005; Muceli et al. 2010; Ting and McKay 2007; Torres-Oviedo and Ting 2007). Motor modules have been identified in the control of natural motor behaviors, such as swimming and kicking in frogs (d'Avella et al. 2003)

as well as during human locomotion (Cappellini et al. 2006; Gizzi et al. 2011; Ivanenko et al. 2004, 2005, 2006; Monaco et al. 2010). In these studies, human walking could be described by a set of four to six modules associated with locomotion at different speeds (Ivanenko et al. 2004, 2005). Interestingly, the inclusion of a voluntary action during walking, such as kicking, could be described by adding one motor module, which was interpreted as a superposition of a task-specific module with the locomotion modules (Ivanenko et al. 2005).

Walking is substantially altered when balance is compromised. For example, Cappellini et al. (2010) observed increased overall muscular activity during walking on a slippery surface. Indeed, maintenance of posture and balance for humans involves complex sensory-motor integration (Torres-Oviedo and Ting 2007, 2010). Similar to walking, postural adjustments during quiet standing have been described by few motor modules, which are consistent across different directions of perturbation (see Torres-Oviedo and Ting 2007, 2010 for details). However, little is known on the motor control strate- AQ: 4 gies associated with maintenance of balance following an unexpected perturbation during walking.

Perturbations to walking such as those due to stumbling or to the effect of tilting support surfaces require muscular reactions in different phases of the gait cycle (Pijnappels et al. 2005; Schillings et al. 2000) and might also require more than five steps until a complete recovery (Oddsson et al. 2004). The interlimb coordination in this case has to sequentially provide time and clearance for the positioning of the recovery limb (Pijnappels et al. 2004), which might not be essential in other perturbation conditions such as slipping. Slippery surfaces lead individuals to assume a more cautious gait pattern, which has different body kinematics and muscular activity throughout the gait cycle (Cappellini et al. 2010; Chambers and Cham 2007). Usually natural slips forward begin 50 ms after a heel strike at high velocity, which induces sliding (Chambers and Cham 2007; Redfern et al. 2001). These perturbations to balance are likely to result in falls if the slip distance exceeds 10 cm (Cham and Redfern 2002; Redfern et al. 2001) or if the sliding velocity is greater than ~50 cm/s (Redfern et al. 2001). These parameters (slipping onset, distance, and velocity) observed during natural slips can be controlled by using moving surfaces to induce forward perturbations (Ferber et al. 2002; Tang et al. 1998). It has been shown that strategies to avoid falls with perturbations or when walking on slippery surfaces involve hip and knee movements in order to counteract changes in the center of mass position and speed (Duysens et al. 2008; Redfern et al. 2001; AQ: 9

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AQ: 9

You et al. 2001). These relevant mechanisms to avoid falls have been described only for forward perturbations, in the sagittal plane.

Previous evidence suggests participation of afferent information to modulate limb movements (Kargo and Giszter 2000b). Furthermore, limb trajectory might be dependent on the afferent participation for the wiping reflex in frogs, even though the target movement is accomplished, since the combination of spinal motor programs ensures limb motion in deafferented animals (Kargo and Giszter 2000a). In humans, sensory information during walking tunes the muscular activation in order to optimize descending commands (Lacquaniti et al. 2012). Therefore, the modulation of gait in a slippery event might be influenced by the sensory inputs from perturbations, but the original task (gait) might still be maintained since the addition of biomechanical components during walking does not necessarily influence the overall locomotor program (Ivanenko et al. 2005). Therefore, in this study it was hypothesized that the motor modules related to normal locomotion would not be influenced by perturbations, but additional motor modules would be superimposed on the current motor programs in order to assist balance recovery. To test the hypothesis, we analyzed the reaction to recover balance during walking after perturbations in different planes. Slips in the anterior-posterior (AP) and medial-lateral (ML) directions were induced by a moveable force platform embedded in a walkway, and surface electromyography (EMG) was recorded from the lower limb, trunk, and neck muscles.

METHODS

Subjects

Eight healthy men (age 28 ± 4 yr; body mass 71 ± 10 kg; stature 171 ± 7 cm) volunteered for the experiment. They had no known history of neurological or motor disorder at the time of testing that may have affected their ability to perform the experiment. All subjects provided written informed consent before participation, and the procedures were approved by the ethical committee of Northern Jutland (N-20100042).

Walking Conditions

The experiment consisted of repeated walking trials along a 7-m walkway. A force platform was positioned in the middle of the walkway, embedded in the floor. Subjects were asked to step with the right foot on the force platform and to continue walking. The force platform could be activated for translational movements (10-cm translation in 150 ms) at an average velocity of 66.67 cm/s and peak velocity of 88.7 cm/s, in different directions during walking. Lower limb and trunk muscle EMG, joint kinematics, and ground reaction forces were recorded from the full gait cycle preceding heel strike on the platform and from the full gait cycle following heel strike while the subjects walked along the walkway.

Normal (unperturbed) walking. After familiarization, the subjects performed 10 unperturbed trials to establish a normal walking pattern. They were asked to walk at their natural speed along the walkway, at a constant velocity (on average 1.3 ± 0.11 m/s). During these trials they were not informed that the platform could translate but were asked to step on the platform.

Perturbed walking. After the unperturbed gait trials, two sets of trials were performed for the AP (forward/backward) and ML (leftward/rightward) perturbations. The subjects experienced three types of stimuli: *1)* catch trials; *2)* direction-1 (forward for AP and leftward for ML); and *3)* direction-2 (backward for AP and rightward for ML). Forward, leftward, and rightward perturbations were delivered 35 ms after the initial contact, whereas backward perturbations were delayed

by 250–350 ms, as determined by the timing of the stance phase in the prior unperturbed trials. This delay served to deliver the backward perturbations during the late stance phase. During the catch trials, no perturbation was delivered, although the subjects were not informed as to which trials were of this type. For each direction, 12 trials were performed, totaling 30 fully randomized trials for each set (24 perturbed trials and 6 catch trials). A rest interval was provided after each 15 trials in order to avoid fatigue effects. Catch trials were included in the protocol in order to reduce predictability of the perturbations. Figure 1 illustrates the walking tasks performed.   **F1**

Data Recording

Kinematics. Retroreflective ball-shaped markers were placed bilaterally on each side of the subject on the skin overlying the following landmarks: heel, first and fifth metatarso-phalangeal joint, lateral malleolus, lateral condyle, greater trochanter, anterior superior iliac spine, posterior superior iliac spine, and gleno-humeral joint. Additional markers were also placed in the bilateral segments (foot, shank, thigh, and arms), serving as tracking markers to define the three-dimensional (3D) motion. In addition, markers were placed on the seventh cervical vertebra and upper and bottom ends of the sternum. The marker positions were tracked with a motion analysis system with eight infrared digital video cameras (Oqus 300 series, Qualisys, Gothenburg, Sweden). Kinematic data were recorded with a sampling frequency of 256 Hz and synchronized with the EMG and kinetic recordings. All subjects wore the same type of walking shoes, provided during the experiment, and full-stretch top and pants covering the EMG cables to avoid movement artifacts.

Kinetics. Ground reaction forces were recorded at 1,024 Hz by a 3D force platform (AMTI, OR6-5, Watertown, MA) mounted to a hydraulic actuator (van Doornik and Sinkjaer 2007). Software based on the LabVIEW platform (MrKick II, Aalborg University, Aalborg, Denmark) was used for recording. With an electric feedback circuit, the vertical force (Fz) served as trigger signal to initiate the force plate movement.

Electromyography. Surface EMG signals were recorded in bipolar configuration with Ag/AgCl electrodes (Ambu Neuroline 720 01-K/12; Ambu, Ballerup, Denmark) with 22-mm center-to-center spacing. A reference electrode was placed on the right wrist. Prior to electrode placement the skin was shaved and lightly abraded. The EMG signals were amplified with a gain of 2,000 (EMG-USB, LISiN; OT Bioelettronica, Turin, Italy), band-pass filtered (second-order, zero-lag Butterworth, bandwidth 10–450 Hz), sampled at 2,048 Hz, and A/D converted on 12 bits per sample. The EMG signals were recorded bilaterally from the following muscles according to the SENIAM recommendations (Hermens et al. 2002), except for those explicitly described: peroneus longus (PER), gastrocnemius lateralis (GL), soleus (SOL), tibialis anterior (TA), vastus lateralis (VL), rectus femoris (RF), biceps femoris (BF), tensor fascia latae (TFL), gluteus maximus (GLU), rectus abdominis (RAB, ~3 cm lateral of the umbilicus; Ivanenko et al. 2006), external oblique (EOB, right above the midpoint between the top of the iliac spine and the anterior superior iliac spine; Kaneda et al. 2009), and erector spinae at L1 (ESP, 2 cm lateral to the spinous process; Ivanenko et al. 2006), medial deltoideus (MD), upper trapezius (TRA), splenius capitis (SPL), and sternocleidomastoideus (SCM).

Data Analysis

For the kinematic analysis, the body was modeled as an interconnected chain of rigid segments: foot, shank, thigh, pelvis, and trunk were investigated, with joint angles between segments being analyzed in Visual 3-D (v. 3.79, C-motion). The ipsilateral and contralateral gait cycles under consideration were defined with respect to the right heel strike on the force platform to the subsequent right heel strike. The first heel strike and stance phase were determined from the force plate recordings (when the vertical ground reaction force exceeded 20 N). The platform movement was activated by the trigger signal linked to the force threshold
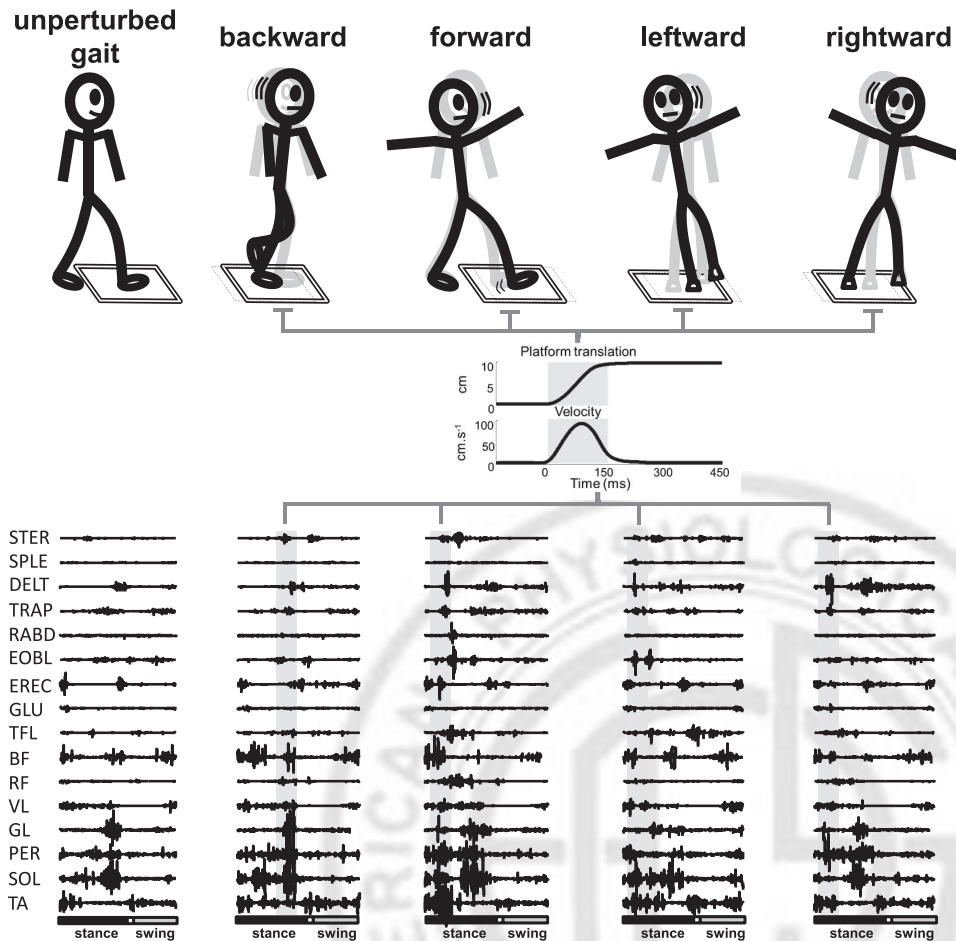
Fig. 1. Representative illustration of walking tasks with raw EMG signals from 1 representative subject. Subjects initially performed unperturbed gait, followed by forward, backward, leftward, and rightward perturbations (in random order). The perturbations were triggered by contact with the ground. Forward, leftward, and rightward perturbations were delivered at the heel contact, while backward perturbations were delayed by 250–350 ms with respect to heel contact in order to coincide with the late stance phase. Perturbations were 10-cm translation and lasted 150 ms.

($>$20 N) to deliver perturbations. The subsequent heel strike was defined by assessing the next minimum value for the Z component of the heel marker.

Signal processing. After segmentation, the surface EMG signals from the 32 muscles were full-wave rectified, low-pass filtered (10 Hz), and time-normalized in order to obtain 200 data points for one gait cycle (d'Avella et al. 2003; Ivanenko et al. 2004). For each subject, all trials for a given condition were averaged, followed by the application of nonnegative matrix factorization (NMF) (d'Avella et al. 2003; Gizzi et al. 2011; Lee and Seung 2001; Muceli et al. 2010) in order to identify motor modules and activation signals. Similarly to other multivariate analysis tools (Tresch et al. 2006), NMF is used to factorize the matrix representing the muscular activation pattern into the product of two matrixes that represent the motor modules (synergy matrix) and the activation signals. The factorization is performed by minimizing a cost function under specific updating rules (see Lee and Seung 2001), with the only constraint that the synergy matrix and the activation signals are nonnegative.

Motor module model. The EMG signals recorded from M muscles were indicated as

$$X(k) = \left[x_1(k), x_2(k), \cdots, x_M(k)\right]^T \qquad (1)$$

where $x_m(k)$ is the activity of the mth muscle at time instant k. The activation signals $P(k)$ were indicated as ($N < M$)

$$P(k) = \left[p_1(k), p_2(k), \cdots, p_N(k)\right]^T \qquad (2)$$

The relation between $X(k)$ and $P(k)$ is described as follows:

$$X(k) \approx X_r(k) = S \cdot P(k) \qquad (3)$$

where $X_r(k)$ is the muscle activity vector reconstructed by the factorization. In *Eq. 3*, the EMG $X(k)$ are obtained by linear transformation

of the activation signals $P(k)$ with gain factors s_{mn}. The matrix whose columns are the weights of each activation signal for each muscle is denoted as S in *Eq. 3* and will be referred to as the motor module (or synergy) matrix (Lee and Seung 1999).

Dimensionality. The number of motor modules N needed for accurate description of the movement was assessed by the dimensionality analysis proposed by d'Avella et al. (2003). According to this procedure, the quality of reconstruction of the muscle activation pattern is analyzed as a function of the number of modules and the minimum number of modules is identified as the point in which this curve pronouncedly changes its slope (d'Avella et al. 2003). In addition to this criterion, a minimum threshold for reconstruction quality was set at 80%. For quantifying the quality of reconstruction, the estimated muscular activation pattern was compared with the recorded pattern by means of the variation accounted for (VAF) value, defined as the variation that can be explained by the model VAF = 1 − SSE/SST, where SSE (sum of squared errors) is the unexplained variation and SST (total sum of squares) is the pooled variation of the data.

Similarities were investigated for motor modules and activation signals for both the perturbed and unperturbed legs. The motor module matrices were compared by computing the scalar product between pairs of columns, normalized by the product of the norms of each column (Muceli et al. 2010). Similarities between activation signals were quantified by the value of the cross-correlation function at zero time lag (Gizzi et al. 2011). The presence of shared modules among different perturbation directions was analyzed by computing the similarities between one module from a given condition and each of the modules from another condition until the best match was found.

After computation of the reconstruction quality, the motor modules for each subject were extracted from the concatenation of all trials in a given

perturbation direction for both the perturbed and unperturbed legs. Similarities among subjects and the presence of shared modules among conditions were assessed from this data set. In addition, the EMG activities from all subjects were concatenated for a given condition, from which motor modules were extracted to represent the whole group of subjects. In this way, all the variability in the data set was taken into account and the presence of shared modules among conditions was analyzed.

Kinematic data were low-pass filtered (6 Hz, second-order, zero-lag Butterworth). The right heel positions in the AP direction were used to determine the stride that contains the step over the platform. Stride duration, stride length, scaled to leg length for each subject, and walking velocity were obtained for each trial. Joint angles for each gait cycle were extracted for ankle, knee, and hip (bilaterally) and trunk and were compared qualitatively with the joint angles from unperturbed gait in order to describe the kinematic changes during perturbations. In addition, the stance duration and double support duration were calculated. To verify the effects of the perturbation direction on the kinematic variables, a one-way ANOVA was used, followed by the Tukey post hoc test when necessary (SPSS 19, SPSS, Chicago, IL). An intertrial analysis was performed in order to verify the effect of accommodation to the task on the EMG signals. For this analysis, the EMG envelopes were normalized by the respective maximum value for each perturbation direction. The EMG envelopes were then averaged over three intervals: the first 50% of the stance phase, from 50% to 100% of the stance phase, and during the full swing phase. The values of averaged EMG envelopes in the three intervals were further averaged over the first three and last three trials for each subject. The resulting EMG activity for the first and last three trials were compared by a paired Student's t-test to identify potential differences due to the time at which the trials were performed (beginning or end of the experiment). The significance level was set to $P < 0.05$.

RESULTS

F2   Figure 2 shows the stride duration and stride length for both the perturbed (PRT) and unperturbed (UPRT) limbs. The perturbations had a significant effect on stride duration ($P = 0.025$). Backward perturbations showed shorter stride duration compared with forward perturbations for PRT and UPRT ($P < 0.05$). Stride length was shorter for leftward and rightward compared with forward perturbations for both limbs ($P < 0.05$). The stride duration for any of the perturbation directions was different from baseline. Walking velocities among tasks were not different from each other (1-way ANOVA, $P > 0.05$; Fig. 2). In particular for PRT, the time of initial double support and perturbed stance phase duration were similar among the perturbations ($P > 0.05$).

Kinematics

Figure 3 shows the joint angles for the perturbed and F3 unperturbed legs, and Fig. 4 shows the trunk kinematics. F4 Changes for a given perturbation direction are associated to the plane of motion, e.g., forward perturbations show changes in the sagittal plane (flexion/extension). Backward perturbations induced pronounced ankle dorsiflexion and trunk flexion during the second part of the stance phase, which were corrected before the swing phase. Forward perturbations elicited immediate knee extension, which was corrected before midstance. Furthermore, hip external rotation and trunk extension were increased during stance. Leftward perturbations provoked immediate changes in the ankle, knee, and hip, especially in the sagittal plane. However, the most pronounced changes in this case were associated to the trunk, which was more extended, bent to the left, and externally rotated during most of the swing phase. Rightward perturbations elicited ankle inversion and hip abduction during the stance phase, as well as trunk extension, mostly during the swing phase.

The unperturbed side was less influenced by perturbations, as expected. There were no relevant changes after the sagittal plane perturbations (forward/backward), whereas perturbations in the frontal plane elicited alterations at the ankle (eversion/inversion, depending on the direction) and hip (adduction/abduction, depending on the direction). The trunk kinematics
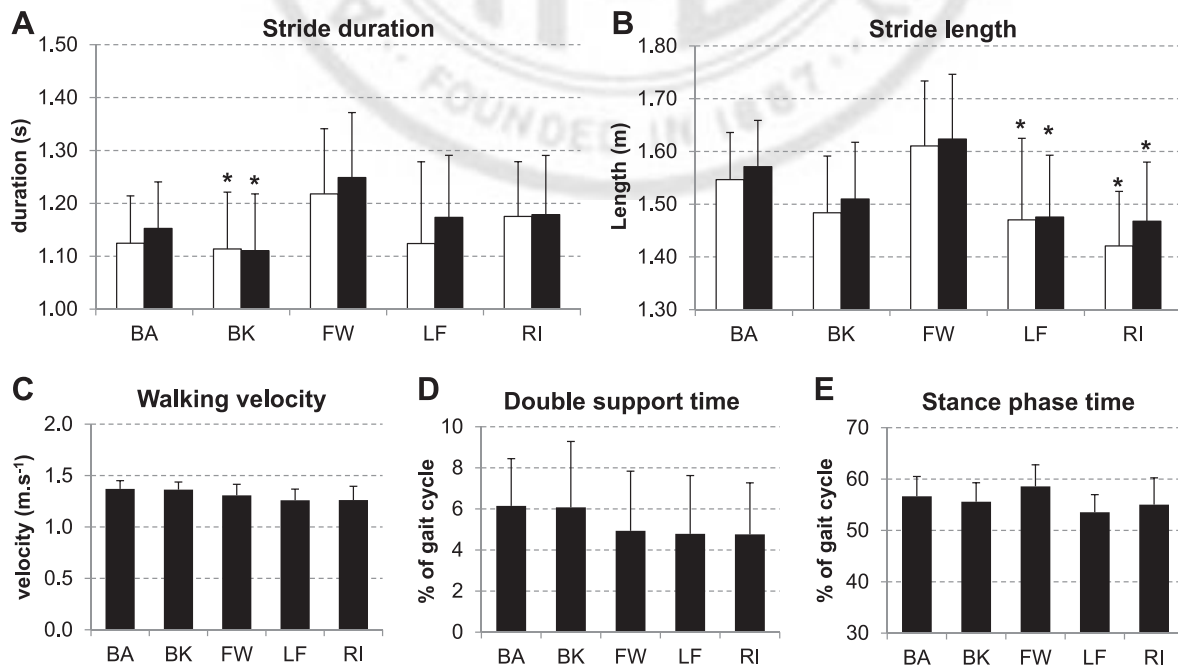

Fig. 2. *A* and *B*: mean (SD) stride duration (*A*) and stride length (*B*) for both perturbed and unperturbed legs during unperturbed gait (BA) and backward (BK), forward (FW), leftward (LF), and rightward (RI) perturbations. *C–E*: walking velocity (*C*), double support duration (*D*), and stance phase duration (*E*) for the perturbed leg. *Significant difference with respect to forward perturbation ($P < 0.05$).
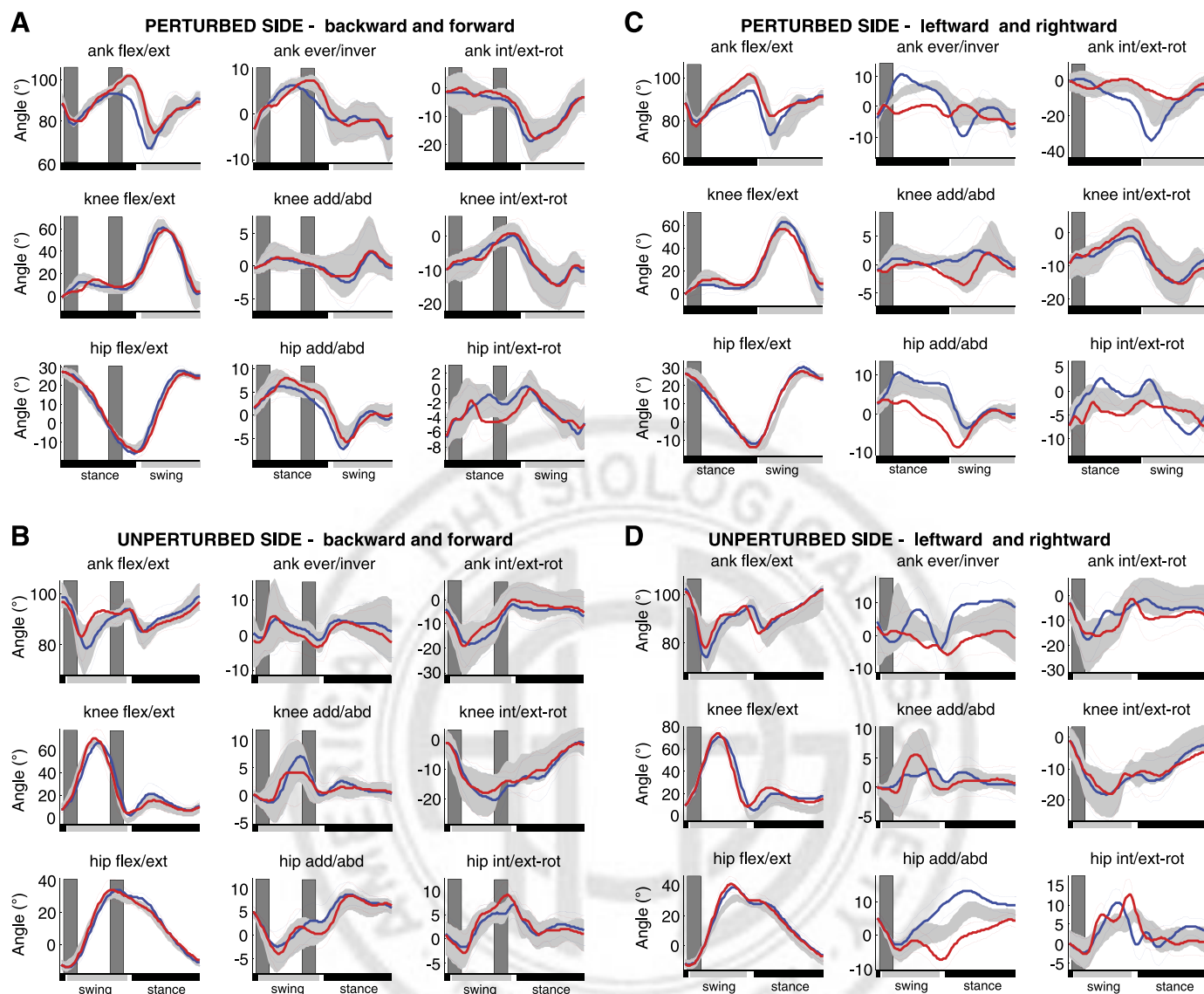
Fig. 3. Averaged perturbed and unperturbed limb kinematics (8 subjects). *Left*: normal walk (light gray area), backward perturbations (blue thick line ± SD as blue dotted lines), and forward perturbations (red thick line ± SD as red thin lines) are summarized for perturbed (*A*) and unperturbed (*B*) sides. *Right*: normal walk (light gray area), leftward (blue thick line ± SD as blue dotted lines) and rightward (red thick line ± SD as red thin lines) perturbations are shown for perturbed (*C*) and unperturbed (*D*) sides. Dark gray vertical bars indicate the average perturbation period during the gait cycle. For backward perturbations there is a second dark gray area in *A* and *B*, indicating that this perturbation was delivered late during stance phase. Stance and swing phases are indicated as the black and gray areas at *bottom*, and the white region between these areas indicates the amount of variability of the durations.

AQ: 8

COLOR

was also influenced differently depending on the perturbation direction, being usually displaced in the opposite way of the perturbation direction (i.e., trunk moving forward when the perturbation was backward).

F5 Figure 5 shows the center of mass displacement. Forward perturbations elicited changes in the vertical and anterior-posterior component (i.e., lower and forward center of mass) in the early stance phase. Perturbations in the frontal plane (leftward/rightward) induced a change in walking direction. The center of mass was usually in a lower vertical position at the transition from stance to the swing phase (i.e., the minimum value of the curves in Fig. 5*A*) when sagittal perturbations were compared to unperturbed walking, even though most of the kinematic changes from the sagittal perturbations were counteracted before the swing phase. This means that small changes in the lower limb joints and trunk might still influence the center of

mass positioning, which aids in maintaining safety once the subjects are experiencing perturbations. In the same way, a lower vertical center of mass position at the transition from stance to the swing phase was observed when frontal perturbations were compared to unperturbed walking (Fig. 5*B*).

Intertrial Variability During Perturbations

Figure 6 shows the comparison between the EMG activity **F6** (computed as described in METHODS) from the first three and the last three trials. For most muscles and perturbations, there was no significant effect of the set of trials. There were significant effects only in few cases, especially for the calf muscles, VL and BF, and in these cases the absolute differences were very limited anyway. These results indicate that the learning effect caused by repeated exposure to specific perturbations was only marginal.
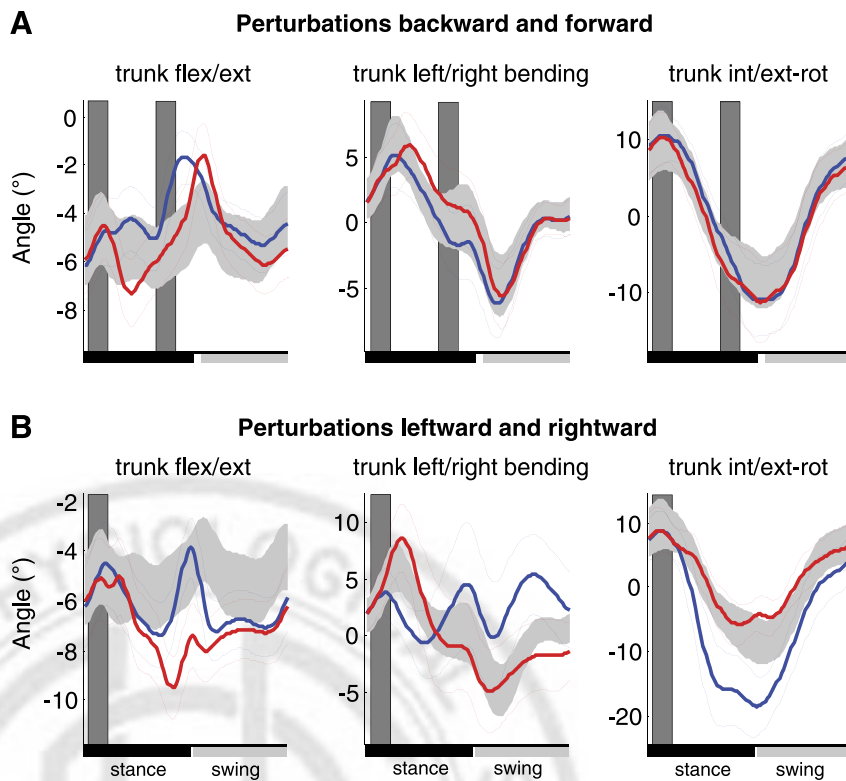
Fig. 4. Averaged perturbed and unperturbed trunk kinematics. *A*: normal walk (light gray area), backward perturbations (blue thick line ± SD as blue dotted lines), and forward perturbations (red thick line ± SD as red thin lines). *B*: normal walk (light gray area), leftward perturbations (blue thick line ± SD as blue dotted lines), and rightward perturbations (red thick line ± SD as red thin lines). Dark gray vertical bars indicate the average perturbation period during the gait cycle. For backward perturbations there is a second dark gray area in *A*, indicating that this perturbation was delivered late during stance phase. Stance and swing phases are indicated as the black and gray areas at *bottom*, and the white region between these areas indicates the amount of variability of the durations.

Number of Motor Modules

The analysis of dimensionality determined that four motor modules were required to reconstruct unilateral muscular activation for both normal and perturbed gait tasks. On average, VAF reached values >90% (the range of values was 0.82–0.94%) with four modules, and the addition of a fifth module only increased VAF by 5.0 ± 0.3% (average over all conditions). These results indicate that normal walking and perturbed walking can be expressed by the same number of motor modules.

Description of Perturbed Walking from Motor Modules of Unperturbed Walking

When the four modules obtained from baseline were used to reconstruct the muscular patterns of the perturbed walking, the VAF was on average below 0.8 (VAF backward perturbations = 0.79 ± 0.02, forward = 0.67 ± 0.1, leftward = 0.66 ± 0.07, rightward = 0.75 ± 0.1). This indicated that the modules of normal walking could not explain the perturbed walking. Conversely, the unperturbed leg showed acceptable reconstruction quality with baseline modules, with VAF above 0.8 for all conditions (VAF backward = 0.82 ± 0.1, forward = 0.82 ± 0.06, leftward = 0.83 ± 0.14, rightward = 0.83 ± 0.02).

Intersubject Similarities

The motor modules and activation signals extracted from concatenated trials for different subjects in the different perturbation directions showed a mean similarity among subjects of 0.82 and 0.83, respectively, considering both the perturbed and unperturbed sides. Table 1 shows similarities for motor modules, averaged across the four modules in each perturbation direction. Table 1 also shows similarities between the activation signals associated to the four modules in each perturbation direction. A high mean similarity (≥0.8) was verified among subjects for both the unperturbed and perturbed gait, for both limbs.

Motor Modules

Since the similarity among subjects was high for all conditions for both legs, we extracted motor modules from a concatenation of signals from all subjects in order to take into account all the variability in the data set. Figure 7*A* shows the muscle weightings for motor modules, and Fig. 8*A* shows the activation signals for the unperturbed gait and the perturbed gait for each of the perturbation directions (perturbed leg). The four modules found for unperturbed gait (BASE) could be related to the main gait phases. The first module (M1) mainly consisted of the activation of TA and knee extensors and flexor activation during early stance and late swing of normal walking, likely to support the body during load acceptance. The second module (M2) consisted mainly of TFL, EOB, ESP, SPL, and SCM, predominantly active during midstance but also moderately active throughout the swing phase. The third module (M3) consisted mainly of calf muscles (GL and SOL, PER) for body support and forward propulsion. Finally, the fourth module (M4) consisted of TA, RF, and trunk/neck muscles stabilizing the upper body and contributing during the swing phase.

The overall similarity of motor modules from different perturbation directions in comparison to unperturbed gait is shown in Fig. 7*A*. Walking with backward perturbations was described by similar modules as baseline walking, but the activation signals for M2 (midstance) and especially M4 (swing) were influenced (Fig. 8*A*), since the perturbation occurred at late stance.

A – CENTER OF MASS – SAGITTAL PLANE PERTURBATIONS

B – CENTER OF MASS – FRONTAL PLANE PERTURBATIONS

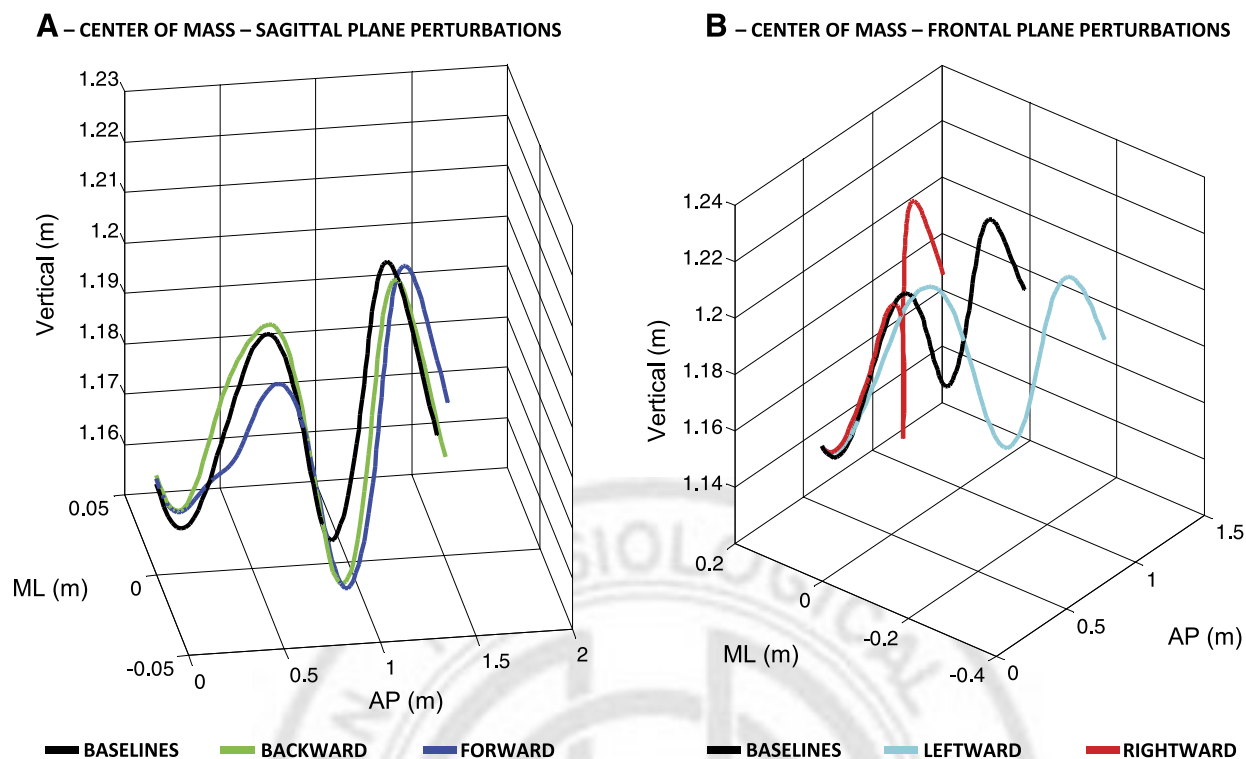■ BASELINES   ■ BACKWARD   ■ FORWARD   ■ BASELINES   ■ LEFTWARD   ■ RIGHTWARD

Fig. 5. Three-dimensional illustration of the averaged center of mass displacement for perturbations in the sagittal plane (*A*) and in the frontal plane (*B*). All curves start at the same point on *left*. Forward perturbations (blue line in *A*) show a different pattern in the vertical axis, whereas leftward and rightward perturbations (light blue and red in *B*) show medial lateral displacements in opposite directions (i.e., perturbations leftward induce walking rightward). ML, medial-lateral; AP, anterior-posterior.

For the other perturbation directions, three of four motor modules were preserved with respect to unperturbed gait (averaged similarity = 0.90 ± 0.07). Depending on the perturbation, one module differed. For forward perturbations, the M1 module (contact) changed, which is explained by a forced knee extension at heel strike, which influences quadriceps activation (VL weighting is reduced) and also elicits reflex components on the ankle muscles in order to increase stiffness. Additionally, this type of perturbation induced a center of mass forward displacement (You et al. 2001), which increased the activation for TA and trunk/neck muscles. In addition to changes in M1, the activation signals for the other motor modules (which were unchanged) were influenced by forward perturbations.

The leftward and rightward perturbations elicited the most substantial changes during swing, where all joints were influenced, together with the trunk. For these perturbations, modules M1, M2, and M3 were preserved but their activation signals changed to fit the new mechanical constraints from a medial or lateral foot displacement. The hip joint was adducted or abducted for leftward and rightward perturbations, respectively, and for both cases there was internal rotation. Similar to the events from forward perturbations, the changes in segment positions during stance required adjustments only to the activation signals. However, the swing phase was compromised by a new walking direction that frontal plane perturbations provoked (see Fig. 5). Thus both module M4 and its activation signal changed in order to move the leg from an unexpected position to perform the swing. Frontal plane perturbations provoked a different swing phase, most likely aiming at preventing a fall instead of maintaining a normal walking pattern.

This could explain the absence of evident activation signals for the swing phase.

The unperturbed leg showed essentially the same modular organization found for normal walking, with no changes in motor modules (average similarity 0.97 ± 0.03) (Fig. 7*B*). However, the activation signals exhibited differences with respect to unperturbed gait, especially for the initial contact and the swing phase (Fig. 8*B*).

DISCUSSION

When gait was perturbed in different directions, the modularity of the muscular pattern was maintained and three of four motor modules were common between unperturbed and perturbed gait. These changes were robust across individuals; therefore the neural control of human balance may solve immediate threats during gait by activating specific modules at the most adequate timing. Furthermore, the unperturbed side, which has to perform the crucial next step, showed the same muscle modules for unperturbed and perturbed conditions, even though the planned direction could have changed.

Recent investigations suggested that human locomotion may be controlled by just a few inborn motor modules implemented in a neural network or central pattern generator at the spinal level, which provides the major input to motoneuron activity (Dominici et al. 2011; Ivanenko et al. 2004; Rossignol et al. 2006). The modulation of timing is distributed through the gait cycle in a task-dependent manner, which is determined by the combination of supraspinal and sensory information (Cappellini et al. 2010; Rossignol et al. 2006). Our results are in agreement with these hypotheses, since the perturbed gait
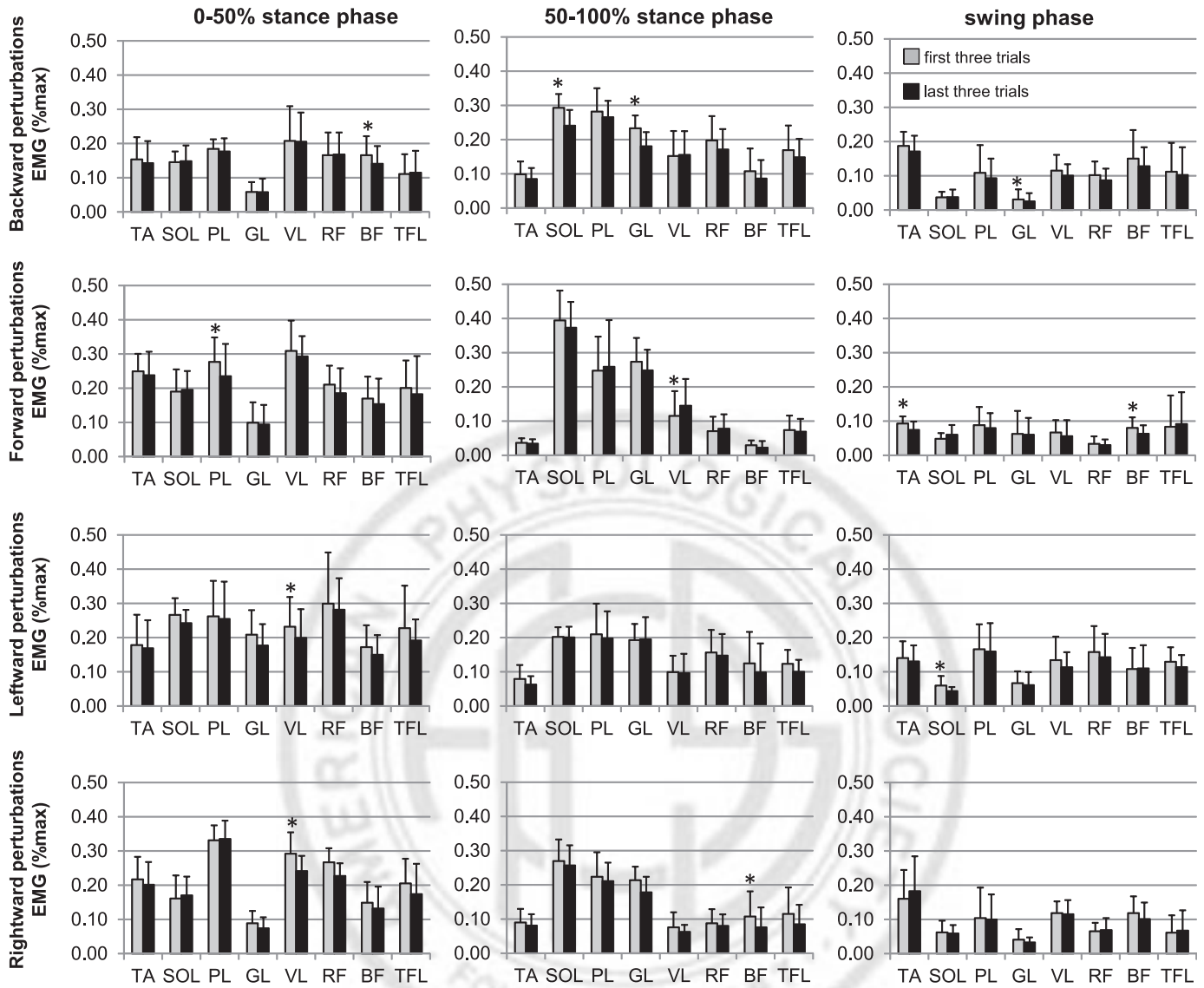
Fig. 6. Mean (SD) EMG activity (see text for details on how this is computed) in 3 time intervals for the 4 perturbation directions [backward (*top*), forward (2nd row), leftward (3rd row), rightward (*bottom*)] for the first 3 perturbed trials (gray bars) and the last 3 perturbed trials (black bars). EMG activity was averaged for the first 50% of the stance phase (*left*), from 50% to 100% of the stance phase (*center*), and during the swing phase (*right*). *Significant difference between the 2 sets of trials ($P < 0.05$).

could be explained by most of the motor modules observed during the unperturbed gait, with adjustments in the activation signals. However, postural responses from perturbations may have a more complex interaction, in which brain stem (Macpherson et al. 1997) and cortical (Beloozerova et al. 2003; Mihara et al. 2008) participation are possible. Bhatt and Pa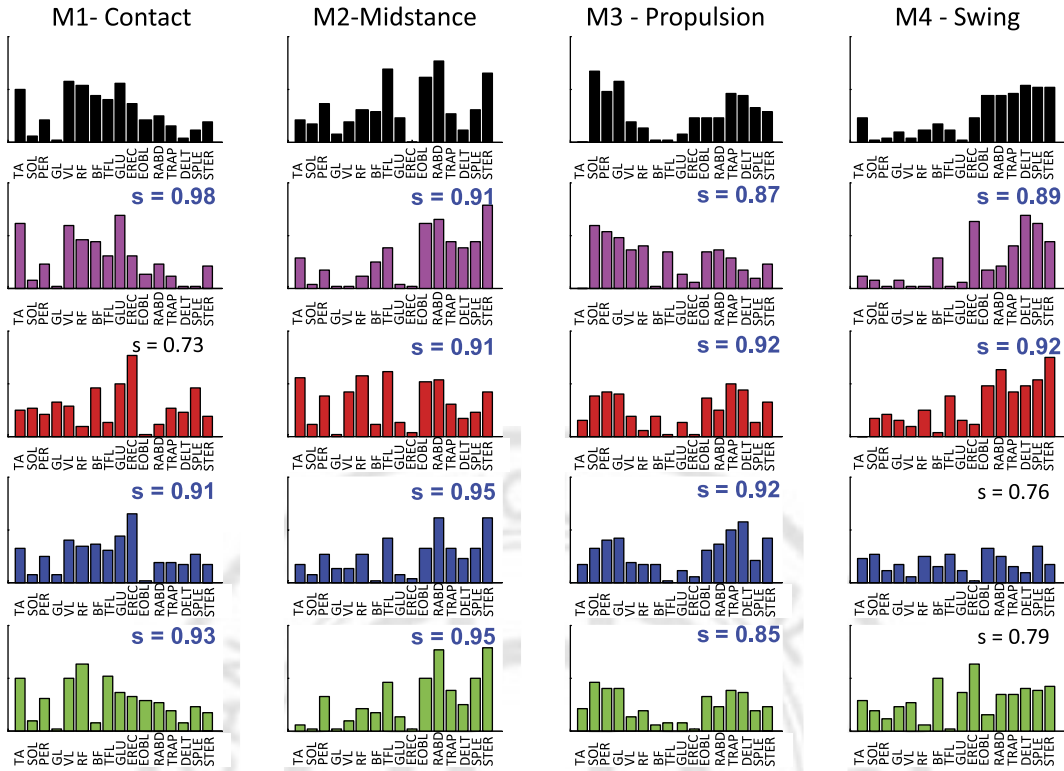i (2009) found that the successful recovery of balance after experiencing slips requires task-related experience, such that the CNS can continuously modify motor plans. Our results corroborate these findings by indicating that innate locomotion characteristics (motor modules) cannot be drastically changed because of a perturbation, whereas timing patterns are influenced by essential afferent information that updates the slipping lower limb status at the spinal level.

AQ: 6

Table 1. *Intersubject similarity for motor modules and activation signals of perturbed and unperturbed legs for different perturbation directions and for unperturbed walking*
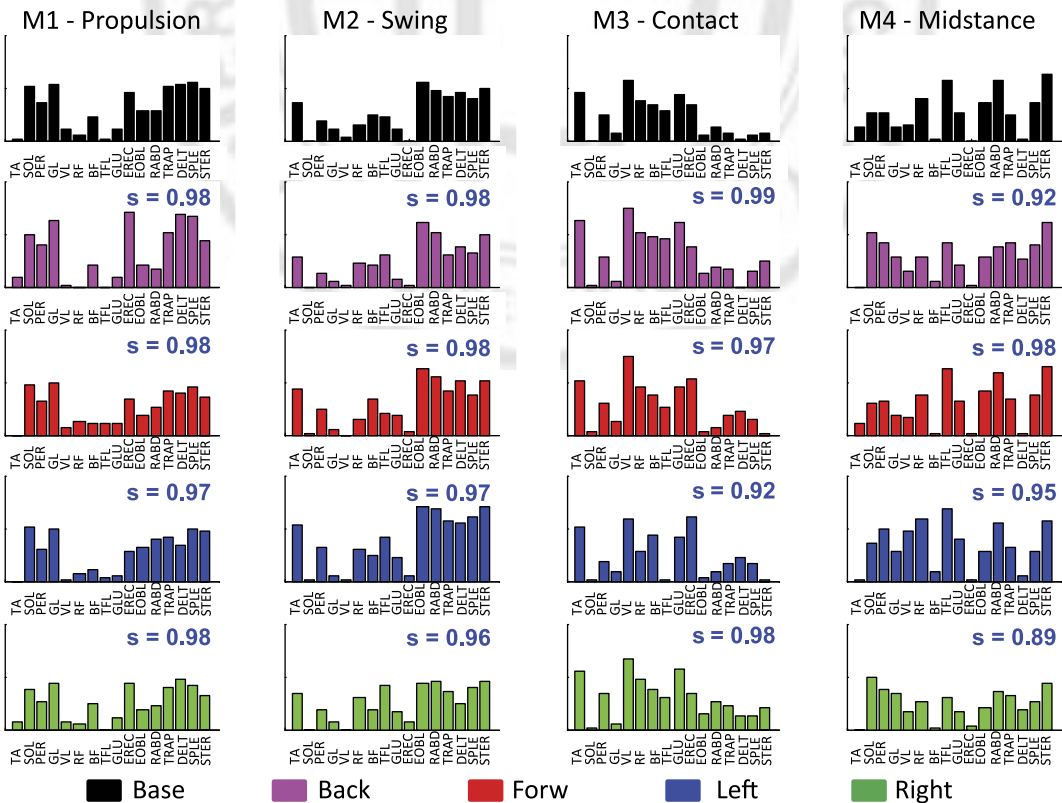
| | BASE | | BACK | | FORW | | LEFT | | RIGHT | |
	PERT	UNP	PERT	UNP	PERT	UNP	PERT	UNP	PERT	UNP
MOD	0.84 ± 0.12	0.80 ± 0.16	0.85 ± 0.1	0.84 ± 0.11	0.84 ± 0.09	0.84 ± 0.21	0.83 ± 0.14	0.80 ± 0.13	0.87 ± 0.09	0.79 ± 0.14
ACT	0.83 ± 0.09	0.76 ± 0.14	0.87 ± 0.08	0.83 ± 0.09	0.83 ± 0.07	0.80 ± 0.1	0.83 ± 0.09	0.80 ± 0.09	0.86 ± 0.05	0.80 ± 0.124

Values are mean ± SE intersubject similarity for the motor modules (MOD) and activation signals (ACT) of the perturbed (PERT) and unperturbed (UNP) legs for different perturbation directions and for unperturbed walking (BASE). BACK, backward; FORW, forward; LEFT, leftward; RIGHT, rightward.

Fig. 7. Motor modules for the perturbed (*A*) and unperturbed (*B*) sides. *Top* to *bottom*: baseline, backward, forward, leftward, and rightward conditions. Modules from different conditions are ordered by the events from baseline (*top*, black), except for M4 of leftward perturbations, which has no homologous module in the analysis for the perturbed side. Similarities (s) were inserted for each motor module compared to the corresponding module of baseline. Similarities above 0.80 are highlighted in blue.
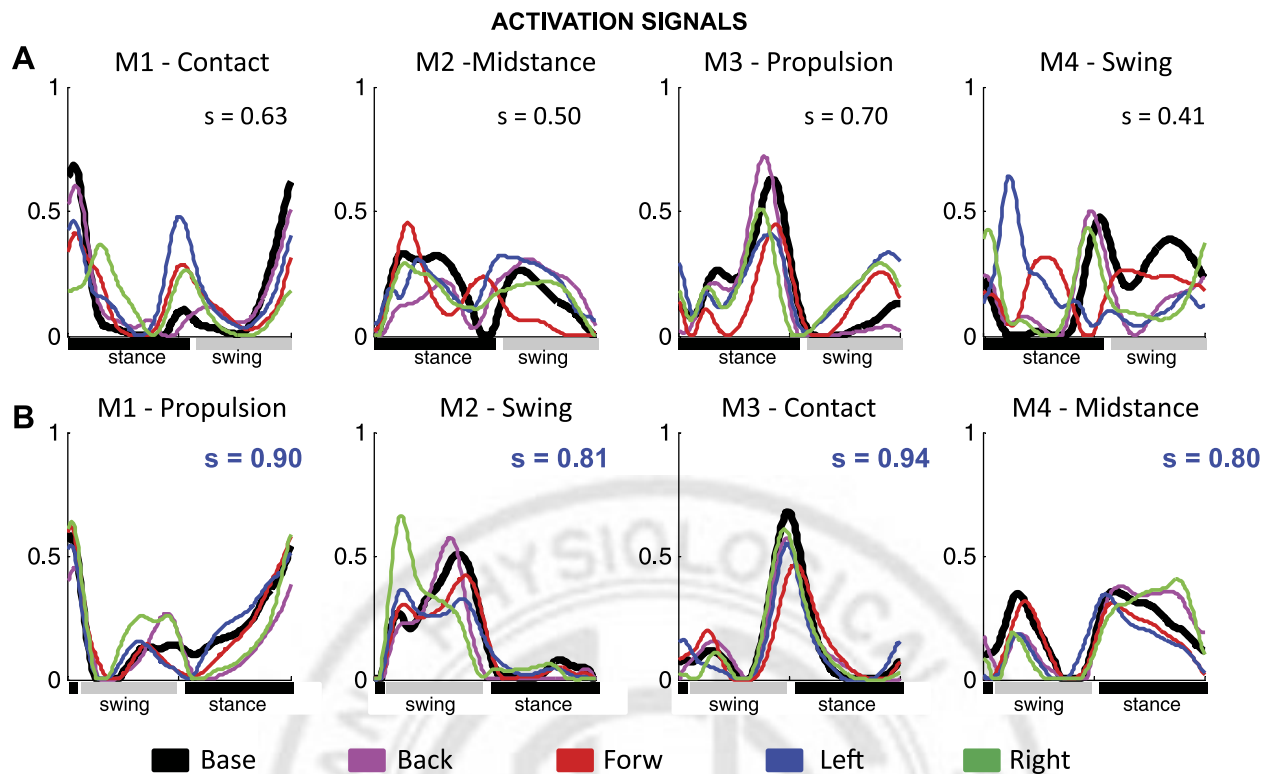
ACTIVATION SIGNALS

Fig. 8. Activation signals for the perturbed (*A*) and unperturbed (*B*) sides associated to the 4 motor modules reported in Fig. 7. Average similarities (s) were inserted for each activation signal compared to the signal of baseline. Similarities above 0.80 are highlighted in blue.

The reduced amount of changes in the unperturbed limb may be due to the reduced afferent information from subcutaneous receptors, muscle spindles, and other structures throughout the perturbed task (Rossignol et al. 2006). There might exist a marginal effect from interlimb neural network pathways, which may elicit contralateral reflex activities (Bhatt and Pai 2009), but our results suggest that changes in the activation signals for the unperturbed leg are under voluntary control rather than an automatic response.

Four modules were sufficient to reconstruct a locomotion task with sufficient quality (VAF > 0.88). This result is in agreement with previous studies on cyclic locomotion, which have successfully represented locomotion tasks by using four (Gizzi et al. 2011; McGowan et al. 2010; Monaco et al. 2010;) or five (Ivanenko et al. 2005, 2006) modules. Differences among studies may relate to the specific sets of muscles investigated. Studies conducted by using up to 16 muscles per body side describe gait by four modules, whereas using 32 muscles produced a greater dimensionality (Ivanenko et al. 2004, 2005). In the present study the perturbed walking could also be explained by the same dimensionality as the normal walking. This result suggests that maintenance of balance during perturbed walking may be attained with a similar modular organization as unperturbed walking by preserving most of the motor modules used for unperturbed walking.

Three of the four motor modules used in unperturbed gait were still present when perturbations occurred in different directions. A previous study investigated the control of voluntary tasks during walking (Ivanenko et al. 2005) and verified that additional modules were needed to explain the task. However, our protocol induced changes in locomotion by a perturbation on the foot, rather than a previously planned

motion. The activation of a single different motor module in case of forward, leftward, and rightward perturbations may be compared to the results from multidirectional perturbations while standing investigated by Torres-Oviedo and Ting (2007). The authors verified that balance recovery could be achieved by using a few motor modules (6 or less), which were differently combined to generate postural responses depending on the perturbation direction. In the same way, our results suggest that neural control of human balance during walking is achievable by a low-dimensional set of motor modules that are predominantly similar, regardless of the perturbation direction. The present investigation shows similar conclusions but in a different context in which gait tasks also contain inertial components from the center of mass displacement. Moreover, the center of mass displacement is also combined with a constant modulation for the muscular activation, whereas standing requires equilibrium maintenance until the perturbation occurs.

Postural control during AP perturbations may be described by an "ankle" strategy, which consists of recruiting distal lower limb muscles, whereas a "hip" strategy related to ML perturbations involves more proximal muscles (Horak et al. 1997; Tang et al. 1998; Torres-Oviedo and Ting 2007). Our findings also corroborate previous findings of AP postural responses occurring predominantly more distal. ML perturbations were delivered at heel strike, causing changes especially in the modulation of hip muscles during the stance phase. It remains possible that the overall modulation of the swing is preserved when perturbations do not induce limb dislocation in the sagittal plane, whereas the stance phase becomes compromised by unusual positioning of body segments. Muscles controlled by modules associated with specific biomechanical tasks have

altered mechanical output if the mechanics of the task is changed in simulations (McGowan et al. 2010). For instance, the muscles related to body support modules are sensitive to changes in body weight; therefore it was suggested that motor modules can be modulated independently to produce a coordinated movement to maintain forward progression (McGowan et al. 2010). Moreover, perturbations to balance in different directions might elicit the recruitment of motor modules that allow center of mass acceleration in order to recover balance (Chvatal et al. 2011). The results of the present investigation corroborate these findings, since there were specific changes in the motor modules related to the biomechanical adjustment necessary to keep the forward progression after perturbation, which also may require repositioning of the center of mass. Our results also suggest some flexibility in the muscle weightings, so that the biomechanical task could be achieved (McGowan et al. 2010).

Perturbations forward induce anterior foot displacement, which requires immediate activation of anterior leg muscles and both the anterior and posterior thigh muscles (Tang et al. 1998). Previous studies have shown that the most relevant strategies to regain balance after slipping include knee and hip movements, in order to counteract the center of mass displacement (Cham and Redfern 2001; Duysens et al. 2008). The results of the present study showed that the activation signal related to heel strike is prolonged until the perturbation is finished, which may be an important strategy to maintain balance. The analysis performed in this study does not allow the identification of reflex components, since the filtering used for extracting the EMG envelopes has a relatively low cutoff frequency. Nonetheless, these components are important for the recovery strategy since the increased activation of the anterior leg and thigh muscles in the M2 module occurs at the moment of perturbation, as verified previously when humans are perturbed forward while walking (Duysens et al. 2008).

Leftward perturbations induced more extensive kinematic changes throughout the gait cycle. The activation signals for the M4 module (see Fig. 8A, blue line) suggest that it could be inserted between the contact and midstance modules. As previously explained, it may only modulate global stiffness given the difficulty in finding a solution that provides the transition from the load acceptance to midstance. Results on perturbations in the frontal plane during walking are very scarce (O'Connor and Kuo 2009; Oddsson et al. 2004), with no reference to EMG or 3D kinematics. Therefore it is difficult to compare our findings to previous work. Perturbations in the frontal plane during standing require different strategies to maintain balance compared with the sagittal plane (Jones et al. 2008; Matjacic et al. 2001; Torres-Oviedo and Ting 2007). Our results replenish this information by suggesting similar phenomena for perturbed walking.

A limitation of this study was that subjects were repeatedly exposed to perturbations, which may reduce the initial responses that monosynaptic and polysynaptic reflexes represent to postural corrections (Rossignol et al. 2006). In addition, our elicited perturbations cannot be classified as fully unexpected, since subjects were experiencing these perturbations throughout the experimental protocol. The repeated exposure might also have influenced the activation timing, such as during the first half of the stance phase for backward perturbations, which was expected to be similar to the normal walking since the perturbation was delayed. This effect may have contributed to the minor changes over time observed in the EMG envelopes (Fig. 6). Nonetheless, the subjects experienced randomized perturbations in different directions interspaced with unperturbed or catch trials without perturbations, and they did not have knowledge on which situation would occur at each trial. In this way, the possibility of anticipation was minimal. The catch trials were previously investigated, and they do not present any changes in kinematics/kinetics and only minor effects on the EMG activity during the stance phase (Oliveira et al. 2012). Another issue might be the fact that subjects were targeting to step onto the platform, even though there was a sufficient familiarization procedure in order to minimize environmental effects. This fact might influence EMG activity, which may not mimic a fully natural gait pattern. However, we found consistent motor modules, which are in line with previous results in the literature from overground walking where no targeting was required.

In conclusion, the muscular activation during walking with perturbations elicited in different directions can be described by a small set of motor modules, which is similar to the set used during normal walking (all modules but one). The strategies to recover balance in the different directions were similar across subjects. Contrary to the initial hypothesis that additional motor modules would be required to assist balance recovery, the results showed that the CNS adapts existing motor modules to achieve the biomechanical goal rather than including new modules. Despite the similarity in motor modules, the activation signals were all substantially influenced by the perturbations, being presumably the result of the integration of afferent information and supraspinal control.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s). **AQ: 7**

AUTHOR CONTRIBUTIONS

Author contributions: A.S.C.O., L.G., U.G.K., and D.F. conception and design of research; A.S.C.O., L.G., U.G.K., and D.F. performed experiments; A.S.C.O., L.G., U.G.K., and D.F. analyzed data; A.S.C.O., L.G., U.G.K., and D.F. interpreted results of experiments; A.S.C.O., L.G., U.G.K., and D.F. prepared figures; A.S.C.O., L.G., U.G.K., and D.F. drafted manuscript; A.S.C.O., L.G., U.G.K., and D.F. edited and revised manuscript; A.S.C.O., L.G., U.G.K., and D.F. approved final version of manuscript.

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STUDY III

FAST CHANGES IN DIRECTION DURING HUMAN LOCOMOTION ARE EXECUTED BY IMPULSIVE ACTIVATION OF MOTOR MODULES

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ABSTRACT

This study investigated the modular control of complex locomotor tasks that require fast changes in direction, i.e., cutting manoeuvres. It was hypothesized that such tasks are accomplished by an impulsive (burst-like) activation of few motor modules, as observed during walking. It was further hypothesized that the performance in cutting manoeuvres would be associated to the relative timing of the activation impulses. Twenty-two healthy men performed 90° side-step cutting manoeuvres while EMG activity from 16 muscles of the supporting limb and trunk, kinematics, and ground reaction forces were recorded. Motor modules and their respective temporal activations were extracted from the EMG signals by non-negative matrix factorization. The kinematic analysis provided the velocity of the center of mass and the external work absorbed during the load acceptance (negative work, W-Abs) and propulsion phases (positive work, W-Prp) of the cutting manoeuvres. Five motor modules explained the EMG activity of all muscles and were driven in an impulsive way, with timing related to the initial contact (M2), load acceptance (M3), and propulsion (M4). The variability in timing between impulses across subjects was greater for cutting manoeuvres than for running. The timing difference between M2 and M3 in the cutting manoeuvres was significantly associated to W-Abs ($r^2=0.45$) whereas the timing between M3 and M4 was associated to W-Prp ($r^2=0.43$). These results suggest that complex locomotor tasks can be achieved by impulsive activation of muscle groups, and that performance is associated to the specific timing of the activation impulses.

Keywords: side-step cutting, motor modules, EMG, motor performance.

1. INTRODUCTION

It has been suggested that the many mechanical degrees of freedom to be controlled during locomotion are modulated by the central nervous system (CNS) at a low-dimensional level, by activating sets of relative intensities or weightings (motor modules) of muscleactivation that are recruited in a specific sequence. Such motor modules are believed to represent neural structures in the spinal cord, activated by descending neurons and central pattern generators, combined to afferent input, to produce a wide range of movements (d'Avella et al, 2003; Ivanenko et al, 2005; Muceli et al, 2010; Lacquaniti et al, 2012b). A consistent observation in human locomotion is that four to six motor modules are activated by sequential impulses of activity that provide the timing for synchronous activation of muscles over time (Ivanenko et al, 2004; 2006; Cappellini et al, 2006; Gizzi et al, 2011; Lacquaniti et al, 2012b). The specific timing of activity of motor modules allows the precise association to gait events, such as the initial contact, load acceptance, and push off (Ivanenko et al. 2008).

Although the muscle weightings are flexible and may change across tasks (Lacquaniti et al, 2012b), the timing of sequential impulsive control of locomotion is consistent across tasks and subjects (d'Avella et al, 2003; Ivanenko et al, 2004; d'Avella and Bizzi, 2005; Cappellini et al, 2006; Ivanenko et al, 2006). For example, walking and running show similar patterned control of neural commands (Cappellini et al, 2006, Lacquaniti et al, 2012b) and become automatized motor gestures by experience, with primitive basic motor patterns which are innate (Lacquaniti et al, 2012a). When other tasks are added to a locomotion motor pattern, such as kicking during walking, additional modules and timing activation signals are added in a linear way, maintaining the basic structure of impulsive control (Ivanenko et al, 2005).

In this study we analyse the neuromuscular organization of more complex locomotor tasks than those previously analysed. In these tasks, the subjects are requested to suddenly change the direction of running by 90°. These tasks, also called cutting manoeuvres, are characterized by a change in the original momentum 105 of straight running, which may require changes in the motor patterns to perform negative work, discontinuing the forward displacement, followed by the generation of additional laterally directed impulse against the ground (Rand and Ohtsuki, 2000). We hypothesised that such complex tasks are still controlled by the same burst-like impulses of activations, as in walking and running, with timings related to the main events during the change in direction. Verification of this

hypothesis would show that the sequential impulsive control observed during walking/running is a general control strategy for locomotion, valid also for more complex locomotor tasks. Given the need for precise timing in complex tasks, it was further hypothesized that cutting manoeuvres, which are less natural tasks than walking and running, would show a greater timing variability in activation impulses across subjects and that this variability would explain the differences in task performance across subjects. Verification of this hypothesis would associate a precise functional meaning to the timing of the neural commands to activate muscle groups, in order to accelerate or decelerate the body center of mass.

The aim of the study was to verify the two hypotheses of sequential burst activation of a low number of motor modules in the complex task analysed and association of the activation timing to the biomechanical goals during the motion. We provide this analysis for a large number of subjects to identify subject-specific differences in the performance of the analysed task and association of these differences with the timing of neural control.

2. EXPERIMENTAL PROCEDURES

2.1. Subjects

Twenty-two healthy men (age, 28±4 yrs; body mass, 71±10 kg; body height, 171±7 cm) volunteered for the experiment. All subjects were recreational practitioners of team sports (soccer, basketball, handball, ice hockey). They had no known history of neurological or motor disorder. All subjects provided written informed consent before participation and the procedures were approved by the ethical committee of Northern Jutland (N-20100042).

2.2. Experimental Setup

The subjects were asked to perform repeated 90° cutting movements during a single session. The task consisted of running from 6-7 meters away of a force platform, aiming to step with the right foot over the platform, turn 90° to the left and continue running (Figure 1). Each subject performed 10-15 cutting trials for familiarization, when they were instructed to accelerate in a straight path towards the force platform and turn as fast as possible to the left. Adjustments on approaching running speed were necessary in order to ensure that subjects were performing the correct cutting trials as fast as possible. Subsequently, 10 cutting movements were recorded with a 40-60 s rest interval between trials to reduce the effects of fatigue. All subjects wore the same type of court shoes (FZ 2600W, FORZA®, Brønderslev,

Denmark) in order to keep consistent conditions for all subjects. Additionally, 10 of the subjects were asked to perform jogging on an 8 m walkway. Subjects performed 10 trials with a 30-s rest interval between each trial.
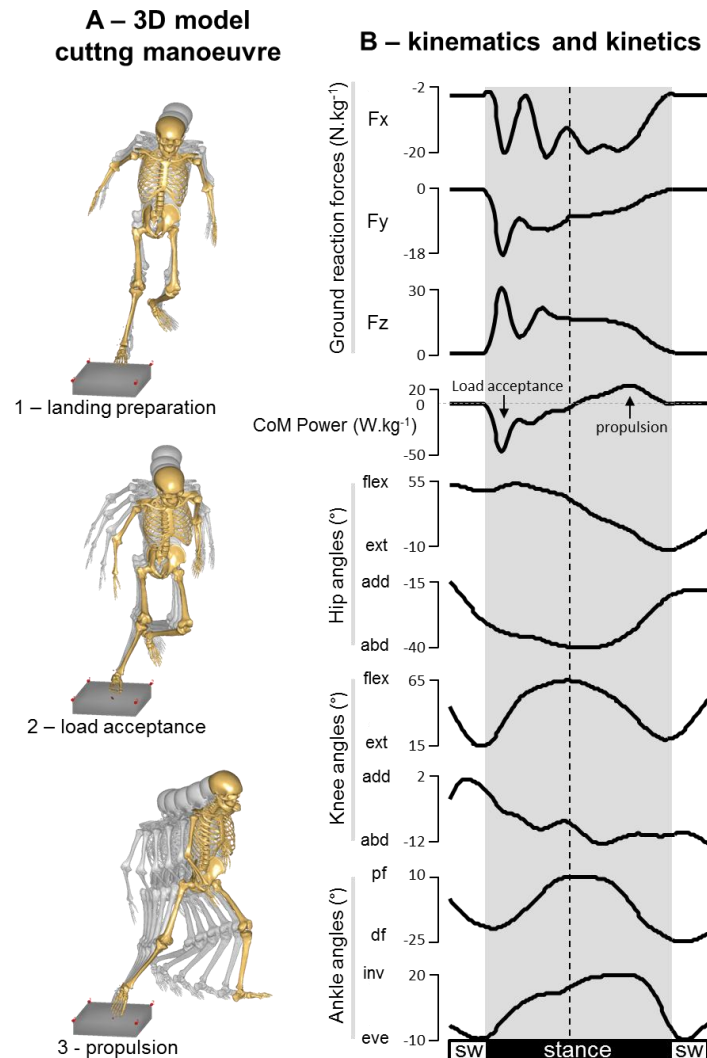
FIGURE 1. Representative data from one subject performing a cutting movement. A) 3D model describing the approach to initial contact (A1), load acceptance (A2) and propulsion (A3). On the right (B) ground reaction forces (*Fx*, *Fy* and *Fz*), center of mass (CoM), power and joint angles for the hip knee and ankle are illustrated in a period before, during (*gray area*) and after the stance phase. The dashed vertical line indicates the transition from the absorption period to the propulsion period of the cutting.

2.3. Data collection

Kinematics: Retroreflective ball-shaped markers were placed bilaterally each side of the subject to the skin overlying the following landmarks bilaterally: calcaneous, first and fifth metatarso-phalangeal joint, lateral malleolus, lateral condyle; greater trochanter, anterior superior iliac spine, posterior superior iliac spine and gleno-humeral joint. In addition, one

marker was placed in the seventh cervical vertebrae, upper and lower endpoint (suprasternal notch and xyphoid process of the sternum). Further markers were placed bilaterally on lower extremity segments: one on thighs, four on the legs and one on each arm, serving as tracking markers to define the 3D motion. The positions of the markers were tracked with a motion analysis system with eight infrared digital video cameras (Oqus 300 series, Qualisys, Gothenburg, Sweden). The kinematic data were recorded with a sampling frequency of 256 Hz and synchronized with the EMG and kinetic recordings. Subjects wore full stretch pants covering the EMG cables to avoid movement artefacts.

Kinetics: The vertical (*Fz*), anterior-posterior (*Fy*) and medial-lateral (*Fx*) ground reaction forces were recorded at 1024Hz by a three-dimensional force platform (AMTI, OR6-5, Watertown, MA) constructed over a hydraulic system (van Doornik and Sinkjaer, 2007). Software developed in Labview platform (MrKick II, Aalborg University, Aalborg, Denmark) was used for recording. Using a feedback electric circuit, the *Fz* force also served as trigger signal to initiate the force plate movement.

Electromyography: Surface EMG signals were recorded in bipolar derivations with pairs of Ag/AgCl electrodes (Ambu Neuroline 720 01-K/12; Ambu, Ballerup, Denmark) with 22 mm of center-to-center spacing. Prior to electrode placement the skin was shaved and lightly abraded. The EMG signals were amplified with a gain of 2,000 (EMG-USB, LISiN; OT Bioelettronica, Turin, Italy), sampled at 2,048 Hz, band-pass filtered (second-order, zero lag Butterworth, bandwidth 10–500 Hz) and 12 bits per sample A/D converted. A reference electrode was placed on the right wrist. The EMG signals were recorded from the following muscles of the right side according to the SENIAM recommendations (Hermens et al, 2002) and previous literature (Ivanenko et al, 2006): tibialis anterior (TA), peroneus longus (PER), soleus (SOL), gastrocnemius medialis (GM), vastus medialis (VM), vastus lateralis (VL), rectus femoris (RF), biceps femoris (BF), semitendinosus (ST), adductor muscles (ADD), gluteus medius (GME), gluteus maximus (GMA), tensor fascia latae (TFL), erector spinae at L1 (ESP), rectus abdominis (RAB) and external oblique (EOB).

2.4. Data Analysis

For the kinematic analysis, the body was modeled as an interconnected chain of rigid segments: foot, shank, thigh, pelvis, trunk and arms. The trunk center of mass, joint angles and angular velocities between segments were analyzed in the AnyBody Modelling System

5.1 (Anybody Technology, Aalborg, Denmark). The segmentation for EMG factorization was defined from the left initial contact prior the right foot step on the force platform to the end of the stance phase on the force platform. The left initial contact was defined from the foot kinematic data, whereas the end of the stance phase for the right leg was determined by the force plate recordings (when the vertical ground reaction force exceeded 20N). The body center of mass (CoM), CoM power (CoMp: sum of forces * CoM velocity [watts/body weight]), and joint angles were calculated during the period of contact to the force platform. The external work (Saibene and Minetti, 2003) was calculated by the integration of CoMp during the absorption period (W-Abs, defined as the integral of the negative power) and during the early propulsion period (W-Prp, defined from the zero crossing of CoMp to end of ground contact. CoMp, see Figure 1 for illustration). The external work has been used as a reliable estimation of the work done to raise and accelerate the center of mass during locomotion tasks (Saibene and Minetti, 2003). The CoM acceleration directly reflects the body displacement generated by the forces applied on ground (Cavagna, 1975; Saibene and Minetti, 2003; Hamner et al, 2010), therefore enhanced performance requires more work to be generated/less work to be absorbed within a fixed time. This concept was used in the present investigation to justify the use of external work to describe performance during cutting manoeuvres.

Signal processing. After segmentation, the surface EMG signals from the 16 muscles were full-wave rectified, low-pass filtered (10 Hz) and time-normalized in order to obtain 200 data points for one gait cycle (d'Avella et al, 2003, Ivanenko et al, 2004). For each subject, all trials for a given condition were averaged, followed by the application of non-negative matrix factorization (NMF) (d'Avella et al, 2003, Gizzi et al, 2011) in order to identify motor modules and activation signals (Figure 2).

Motor module model. The EMG signals recorded from *M* muscles were indicated as:

$$X(k) = \left[x_1(k), x_2(k), \cdots, x_M(k) \right]^T \qquad (1)$$

where $x_M(k)$ is the activity of the *m*th muscle at the time instant *k*. The activation signals $P(k)$ were indicated as ($N < M$):

$$P(k) = \left[p_1(k), p_2(k), \cdots, p_N(k) \right]^T \qquad (2)$$

The relation between $X(k)$ and $P(k)$ is described as follows:

$$X(k) \approx X_r(k) = S \cdot P(k) \qquad (3)$$

where $X_r(k)$ is the muscle activity vector reconstructed by the factorization. In Eq. (3), the EMG $X(k)$ are obtained by linear transformation of the activation signals $P(k)$ with gain factors s_{mn}. The matrix whose columns were the weights of each activation signal for each muscle is denoted as S in Eq. (3) and will be referred to as the motor module matrix (Lee and Seung, 1999).
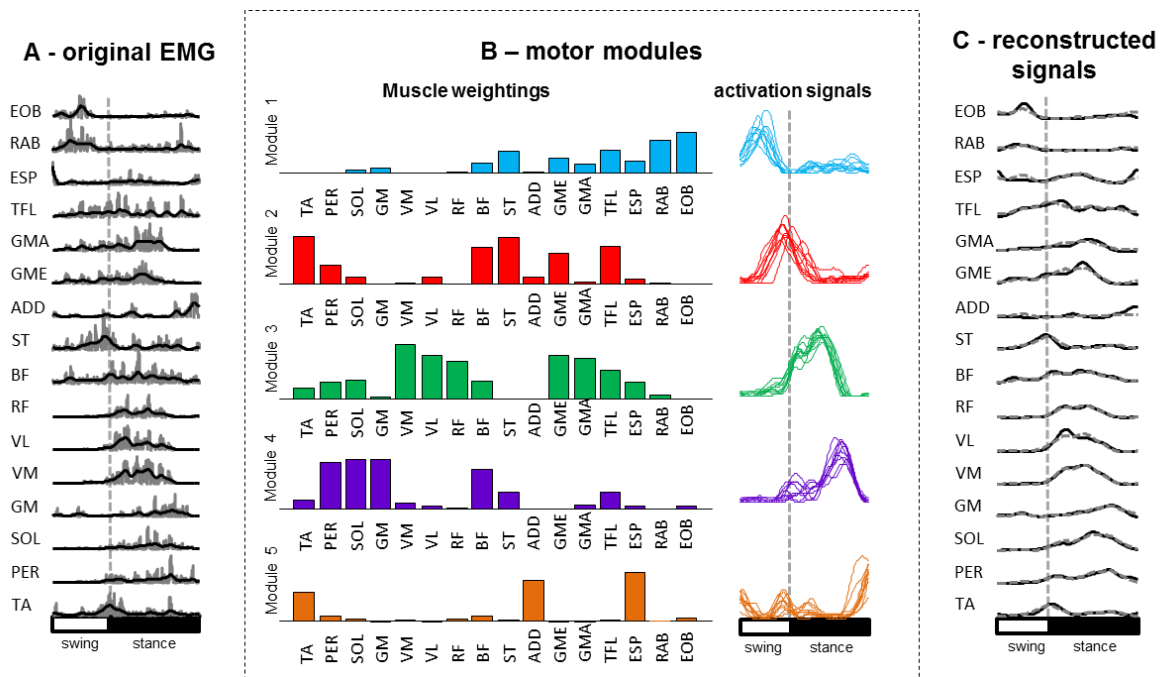
FIGURE 2. Reconstruction of EMG signals by non-negative matrix factorization (NMF) for a representative subject in 10 cutting manoeuvres. A) Raw rectified muscle activation (*grey lines*) and low-pass filtered envelopes (*black lines*), throughout one cutting cycle. B) Muscle activity was processed by a NMF algorithm, which reconstructs the original EMG using a small set of modules. C) Original (*black solid lines*) and reconstructed EMG from the multiplication of muscle weightings and activation signals (*grey dashed lines on top of black lines*).

Dimensionality. The number of motor modules N needed for accurate description of the movement was assessed by the dimensionality analysis proposed by (d'Avella et al, 2003). According to this procedure, the quality of reconstruction of the muscle activation pattern is

analyzed as a function of the number of modules and the minimum number of modules is identified as the point in which this curve pronouncedly changes its slope (d'Avella et al, 2003). In addition to this criterion, a minimum threshold for reconstruction quality was set at 80%. For quantifying the quality of reconstruction, the estimated muscular activation pattern was compared with the recorded pattern by means of the variation accounted for (VAF) value, defined as the variation that can be explained by the model: $VAF = 1 - SSE/SST$, where SSE (sum of squared errors) is the unexplained variation and SST (total sum of squares) is the pooled variation of the data.

After computation of the reconstruction quality, the motor modules for each subject were extracted from the concatenation of all trials. Similarities among the different subjects were investigated for motor modules and activation signals. The motor module matrices were compared by computing the scalar product between pairs of columns, normalized by the product of the norms of each column (d'Avella et al, 2003; Torres-Oviedo and Ting, 2007; Muceli et al, 2010). Similarities between activation signals were quantified by the value of the cross-correlation function at zero time lag (Clark et al, 2010; Gizzi et al, 2011). In addition, the EMG activities from all subjects were concatenated for a given condition, from which motor modules were extracted to represent the whole group of subjects. In this manner, all the variability in the dataset was taken into account. The timing of each activation signal was defined as the time instant of maximum value of the activation signal as a percentage of the running/cutting cycle.

Kinematic data were low-pass filtered (10 Hz, second-order, zero lag Butterworth) CoM mass speed was computed from 200 ms to 100 ms before right foot contact to the force platform. Joint angles/angular velocities were analysed qualitatively from the averaged data across all trials and subsequently averaged across subjects. For each activation signal respective to the motor modules from running and cutting, the peak timing of the curves (% of cutting cycle) was defined as the maximum value of the bursts. The bursts were automatically selected by specific algorithms and manually checked by the researchers for consistency. Coefficients of variations (CoV) were calculated for the kinematics and ground reaction force variables, as well as for the timing of the activation signals from running and cutting. The Pearson coefficient of determination was used to explain the relation between 1) the external work generated during the absorption period (W-Abs) in relation to the timing of M3 (propulsion) and the external work generated during the propulsion period (W-Prp) in relation to the net

change in time from M2-M3 (ΔProp); 2) the external work absorbed during the initial phase of the propulsion in relation to the timing of M4 (push-off) and to the net change in time from M3-M4 (ΔPush-off); and 3) the total external work generated/absorbed during stance phase in relation to the net change in time from M2-M4 (ΔStance). The significance level for the linear regressions was set to $p<0.05$.

3. RESULTS

The running task was performed at approximately 9 km.h^{-1} (min 8.67 km.h^{-1}, max 9.3 km.h^{-1}). The stance duration, peak ground reaction forces and trunk CoM speed 100 ms before initial contact had low variability among subjects (Table 1). The trunk center of mass speed was on average 2.6 m.s^{-1} (9.6 km.h^{-1}) and also showed low variability (CoV<20%). On the other hand, the distance of the left foot in the step prior to the cutting manoeuvre showed high variability among the subjects (CoV > 50%; Table 1).

Table 1. Mean(SD) and coefficient of variation (CoV) of stance duration (stc_dur), vertical peak force during absorption phase (pk_abs), propulsion phase (pk_prp), lateral peak force to push-off (pk_lat), distance of left foot to the force platform previous to right initial contact (left_dist) and center of mass speed 100 ms before right initial contact to the platform (CoM_speed) for all measured subjects (n=22).

	stc_dur (ms)	pk_abs (N.kg^{-1})	pk prp (N.kg^{-1})	pk_lat (N.kg^{-1})	left_dist (cm)	CoM_speed (m.s^{-1})
Mean±SD	327±50	27.9±7	18±2.4	7.3±1.9	55.7±30	2.67±0.4
CoV(%)	15.49	26.32	13.41	25.63	54.39	19.12

3.1. Kinematics of cutting movements

The stance phase for the cutting manoeuvre started with hip flexed (25±2.3°), knee abducted (20±1.1°) near extension (17±2.4°), and ankle dorsiflexed (-16±3.7°) (Figure 3). During the first half of the stance phase, the hip and knee flexion were combined with progressively increased external rotation and ankle plantar flexion. Subsequently, there was a general extension for the hip, knee and ankle in order to generate propulsion. The change in direction in the last 25% of the stance period involved hip adduction and external rotation, in addition to ankle eversion towards the push-off event.

Joint angles for cutting manoeuvres
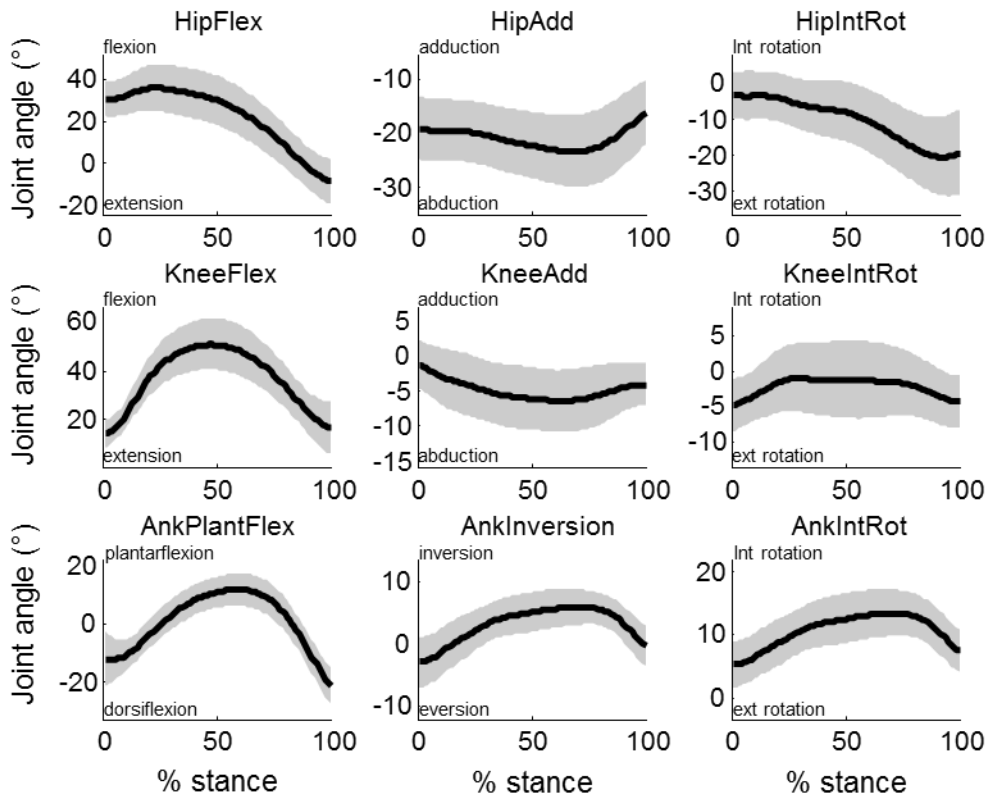
FIGURE 3. Mean (*black lines*) and 1 SD range (*grey area*) of the right limb joint angles during the stance period of cutting maneouvres.

3.2. Dimensionality

The analysis of dimensionality from single trials determined that five motor modules were required to reconstruct unilateral muscular activation for both running (average VAF = 0.93±0.02) and cutting manoeuvres (average VAF = 0.91±0.02). On average, VAF reached 90% (range from 0.89-0.97) with five modules, and the addition of a sixth module only increased VAF by 2.0±0.6% (average over all subjects from the running and cutting tasks). The dimensionality from the concatenation of all trials for each subject also indicated that five modules were sufficient to reconstruct the muscular activation pattern of running with VAF> 90% (0.92± 0.03; 10 subjects), but cutting movements showed lower quality for the concatenations (average = 0.81±0.04; 22 subjects).

3.3. Motor modules in running and cutting manoeuvres

Running motor modules (Figure 4A) showed modular organization that resembled previously reported data (Cappellini et al. 2006). The first module was related to heel strike and load

acceptance, consisting of TA, quadriceps and hip extensors. The second module was related to push-off that ends the stance phase, by the recruitment of plantar flexor muscles. The third module consisted of trunk muscles during the transition from stance to swing phase. The fourth module consisted of the activation of TA, RF, ADD, TFL and ESP, in order to perform swing. The fifth module had predominant activation of hamstrings and hip extensors, together with ESP and EOB, responsible for hip and trunk stabilization prior to landing.

Figure 2 shows the motor modules obtained during cutting manoeuvres for a representative subject, ordered by the timing of the activation signals. Module 1 (M1) consisted in the activation of hip and trunk muscles prior to the initial contact to the force platform. BF and ST decelerate the knee joint flexion and GME, TFL, RAB and EOB stabilize the hip and trunk prior to landing. Module 2 (M2) was related to the foot strike event, which consisted of the synchronous activation of foot stabilizers (TA and PER), hamstrings, and lateral hip stabilizers in the frontal plane (GME, TFL). The third module (M3) was related to the impact, absorption and propulsion, where the predominant muscles are the quadriceps muscles (VL, VM and RF) and hip extensors (GME, GMA). The fourth module (M4) was related to the push-off in the final phase of the contact to the force platform. This module consisted in the activation of plantar flexors and hamstrings. The fifth module (M5) consisted in the activation of TA, ADD and ESP, during swing, initial contact and predominantly at the end of stance. This module may be responsible for modulating ankle and hip stability while turning to the left, as well as for maintaining the trunk erect posture.

3.4. Comparison between running and cutting tasks
For both running (Figure 4A) and cutting tasks (Figure 4B), temporally ordered impulses of activity modulated the weightings of the muscle set. Running was segmented from initial contact to initial contact, whereas cutting movements were segmented from maximal right knee flexion to right toe-off from the platform. The concatenation of all subjects for cutting manoeuvres also revealed similar functionality for the motor modules shown in Figure 2, as well as a similar timing pattern in relation to the cycle (swing or stance phase) for its activation.

The similarity analysis revealed that weighting coefficients from running were similar to those of cutting movements (similarities >0.80; Figure 4B). Moreover, it was possible to qualitatively identify similarities for the timing of the peaks with respect to the cutting phase

(stance or swing). For instance, both M2 from running task and M4 from cutting task showed peak activation timing towards the end of the stance phase. Although high similarity was found, there were also differences in motor modules between the two tasks. For instance, weighting for M2 during cutting did not include trunk muscles (ESP, EOB), which were recruited in M5 instead in order to assist the trunk rotation to the left. These results suggest that running and cutting tasks show similar modular organization, which has specific timing modulation to recruit the necessary muscles to accomplish the motor gesture. However, the apparently complex change in direction is accomplished by slight changes in few muscle weightings, together with temporal adjustments of the activation signals.
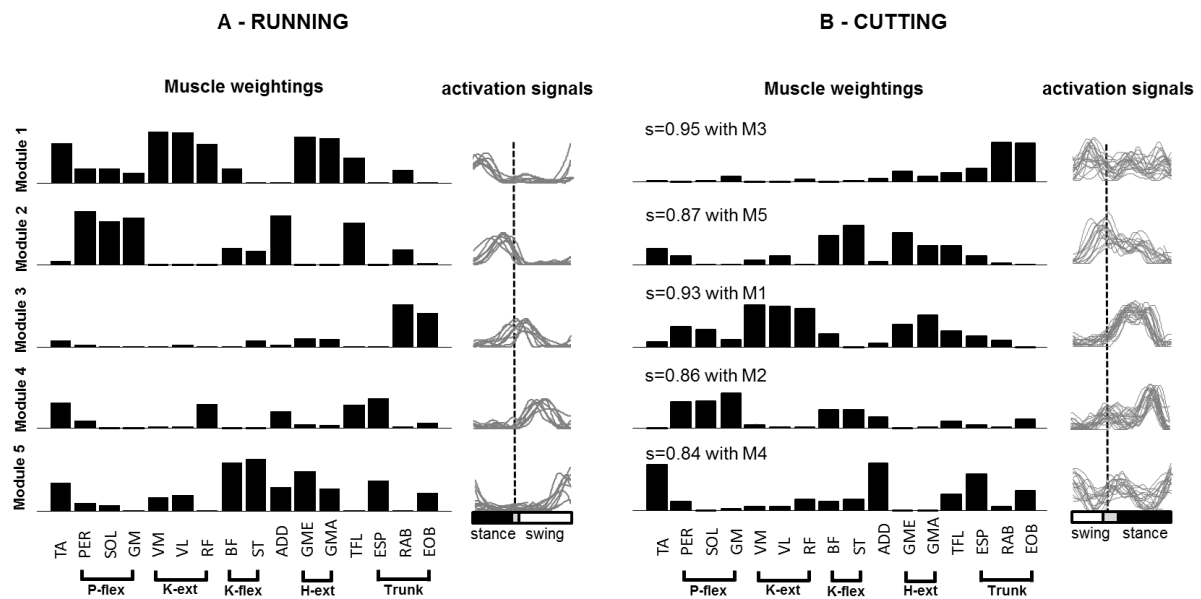
FIGURE 4. Motor modules that represent running (A, n=10) and cutting (B, n=22). "s" on top of weighting coefficients for cutting correspond to similarities with respect to weighting coefficients from running. Abbreviations of the muscle nomenclature is described in the Methods (Section 2.3). P-flex: plantar flexors; K-ext: knee extensors; K-flex: knee flexors; H-ext: Hip extensors.

3.5. Intra- and inter-subject similarity

Similarity was computed for each individual separately, by comparing muscle weightings and activation signals from one cutting manoeuvre to all the others (Table 2). The muscle weighting coefficients showed a mean inter-trial similarity of 0.84 and low inter-subject variability. Motor modules extracted from cutting manoeuvres of different subjects showed an average similarity of 0.75. When the different motor modules were analysed separately, the greater similarities were found for M2, M3 and M4 (Table 3).

Table 2. Mean (SD) and range of inter-trials similarity for weighting coefficients (motor modules) of each individual during cutting manoeuvres.

	Similarity – Motor modules	
	Mean±SD	**Range**
Sub-1	0.84±0.06	0.75-0.92
Sub-2	0.83±0.06	0.65-0.95
Sub-3	0.86±0.06	0.77-0.94
Sub-4	0.85±0.06	0.73-0.90
Sub-5	0.86±0.05	0.75-0.94
Sub-6	0.81±0.07	0.72-0.91
Sub-7	0.86±0.05	0.77-0.95
Sub-8	0.82±0.06	0.74-0.94
Sub-9	0.84±0.05	0.77-0.94
Sub-10	0.86±0.05	0.78-0.96
Sub-11	0.86±0.05	0.75-0.95
Sub-12	0.81±0.07	0.71-0.92
Sub-13	0.79±0.07	0.71-0.88
Sub-14	0.82±0.07	0.70-0.94
Sub-15	0.84±0.07	0.76-0.96
Sub-16	0.87±0.06	0.77-0.96
Sub-17	0.87±0.04	0.80-0.95
Sub-18	0.91±0.04	0.84-0.97
Sub-19	0.83±0.07	0.76-0.88
Sub-20	0.82±0.06	0.73-0.93
Sub-21	0.83±0.06	0.76-0.91
Sub-22	0.86±0.05	0.81-0.91
Total	**0.84±0.03**	**0.75-0.93**

Table 3. Mean (SD) and range of similarities among subjects for the muscle weightings and activation signals of the five motor modules extracted from the cutting manoeuvres.

	muscle weightings		activation signals	
	Mean±SD	**range**	**Mean±SD**	**range**
M1	0.74±0.11	0.52-0.96	0.51±0.11	0.32-0.96
M2	0.71±0.09	0.43-0.94	0.71±0.12	0.50-0.96
M3	0.82±0.07	0.51-0.98	0.77±0.12	0.45-0.99
M4	0.76±0.10	0.51-0.95	0.76±0.13	0.47-0.98
M5	0.72±0.10	0.50-0.94	0.52±0.10	0.24-0.88

3.6. Activation signals

The variability in activation signal timing, as measured by CoV, was smaller for running (range ~3-8%; Table 4), than cutting monoeuvres (especially for M1 and M5, with CoV

~28%). The motor modules related to forward/lateral propulsion by the plantarflexors showed the lowest CoV for both running (M2) and cutting tasks (M4).

Table 4. Mean (SD) peak activation timing for the five motor modules that describe running and cutting manoeuvres. Coefficient of variation (CoV) was also calculated (standard deviation / mean).

	running		cutting	
	mean±SD	CoV(%)	mean±SD	CoV(%)
M1	8.2±0.6	8.1	15.4±4.6	29.8
M2	34.8±1.9	5.7	37.2±6.1	16.4
M3	49.7±3.5	7.0	63.7±10.6	16.8
M4	75.7±1.94	2.6	82.3±9.4	11.4
M5	92.4±3.3	3.6	81.4±23.4	28.6

The difference in variability of timing between the two tasks is evidenced in Figure 5, which shows the five motor modules and their respective activation signals for running (Figure 5A and 5B) and cutting manoeuvres (Figures 5C and 5D). Colormaps that represent the activation signals from running show robust inter-subject peak timing position (*vertical dashed traces*), with low variation in time *(the grey area around the traces represents* ±SD*)*. The timing for cutting manoeuvres had greater variability, especially for M1 and M5.

3.7. Activation timing and task performance

There were significant associations between W-Abs and ΔProp (r^2 =0.45, 95% confidence interval =-26.2 to -18,1, $p<0.001$; Figure 6A), between W-Prp and ΔPush-off (r^2 =0.43, $p<0.001$; Figure 6B), and between the total external work during the stance phase and ΔStance (r^2 =0.35, $p<0.001$; Figure 6C).

1. DISCUSSION

The neural control of cutting manoeuvres is determined by a sequence of activation impulses that act on a small set of muscle weightings, in a similar fashion as during running. Since the cutting tasks are less common than running, the timing of the activation signals was more variable in these tasks than in running. This higher variability in timing for cutting manoeuvres could be partly explained by inter-subject variability in absorbing external work during the stance phase. Changes in direction indeed require optimization of the external

work conversion during the impact absorption and the following propulsion. Therefore, the amount of external work conversion was associated to the relative timing or switching between motor modules.
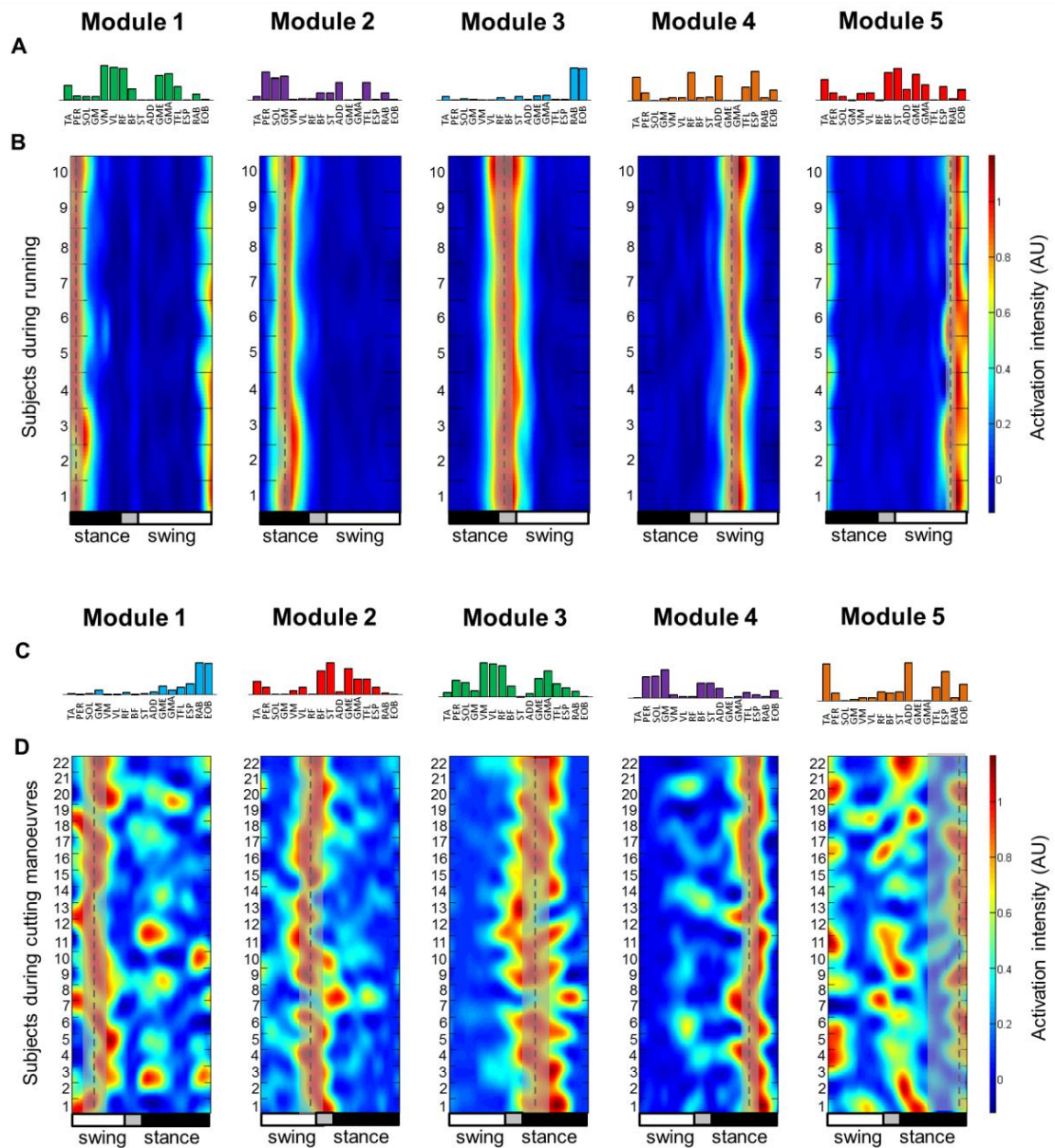
FIGURE 5. Motor modules that describe running and cutting manoeuvres. At the top, running weighting coecfficients (A) and activation signals from all subjects represented in a colourmap (A). In the same way, at the bottom, weighting coecfficients (C) and activation signals from all subjects represented in a colormap (D) for cutting manoeuvres. Homologous motor modules in running and cutting manoeuvres are represented by the same colorbars. The vertical traces indicate the position of mean timing for the main peak throughout the cycles. The grey area surrounding the mean values represent the standard deviation for the peak timing. The running and cutting cycles are represented at the bottom of the colorbars. The grey area represents the standard deviation of the transition from stance to swing (running) or swing to stance (cutting). The order of the muscles in the motor modules is the same as in Figure 4.
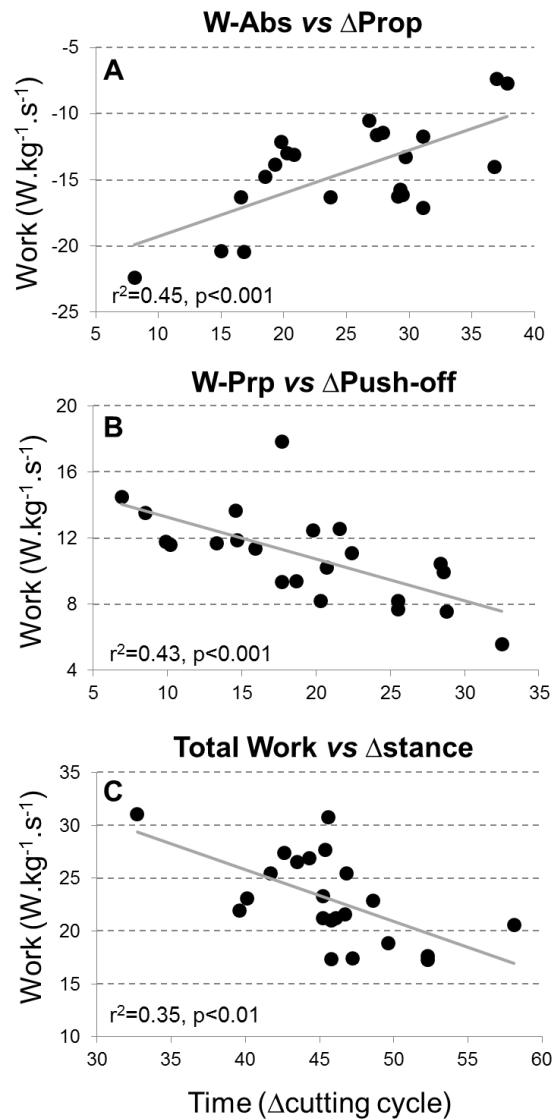
FIGURE 6. Coefficient of determination (r^2) and significance level (p) for the relationship between A) external work for the absorption phase (W-Abs) and the time window between the peaks of activation signals of M2 to M3 (ΔProp); and B) external work for the propulsion phase (W-Prp) and the time window between the peaks of activation signals of M3 to M4 (ΔPush-off). C) total external work generated during stance phase and the time window between peaks of activation signals of M2 to M4.

Previous literature has shown that running can be represented by the same motor modules found during walking, with differences in timing of the activation signals to determine the biomechanical goals throughout the gait cycle (Cappellini et al, 2006; Ivanenko et al, 2006). Moreover, cyclic movements, such as walking, running and swimming may have the same modular organization (d'Avella et al, 2003). Therefore, there is strong evidence suggesting that muscular coordination for a given movement rely on intrinsic motor patterns that are activated in the most adequate timing. Our results complement this evidence by suggesting that discrete complex locomotor movements can also be described by a few motor modules

that may be intrinsic to individuals with different previous exercise experience and anthropometric characteristics. The motor modules and activation signals that control running in the present investigation are comparable to previous literature (Cappellini et al, 2006; Ivanenko et al, 2008). Despite slight differences in the selection of muscles, the functionality of the described motor modules and especially the activation timing are in agreement with previously reported motor patterns for running (Cappellini et al, 2006).

The values for muscle weightings in cutting manoeuvres were similar to those of running. Cutting tasks involve essentially similar biomechanical goals as running, that accordingly require the activation of similar muscles. For instance, the recruitment of knee and hip extensors during load acceptance and propulsion, or the activation of plantar flexors and hamstrings (acting as hip extensors) to perform push-off were found in the present study and also in previous investigations concerning human walking and running (Ivanenko et al, 2004; 2005; Cappellini et al, 2006; Clark et al, 2010; Gizzi et al, 2011). These similarities suggest that the locomotor events in cutting tasks and running are explained by similar motor modules, even though cutting manoeuvres are non-cyclical and require a fast change in direction. Despite predominant similarities between modules from running and cutting manoeuvres, there were specific changes that determined the differences between the two tasks. The motor module related to landing during cutting manoeuvres (M2) showed reduced weighting for ADD and increased weighting for TFL when compared to the homologous module during running (M5). These slight changes are essential to allow the optimal motor performance during the task and reinforce previous concepts that the flexibility of motor modules allows for performance of many different motor behaviours (Ivanenko et al, 2004; d'Avella and Bizzi, 2005; Lacquaniti et al, 2012b). It is also important to highlight that the change in direction during cutting manoeuvres may also be related to the recruitment of contralateral muscles especially in the trunk, which were not included in the present analysis.

Previous investigations have described the muscular coordination for cutting manoeuvres (Neptune et al, 1999), and most of the functional roles for each muscle/muscular group were confirmed in the present experiment by using EMG factorization instead of individual timing profiles. A more recent investigation has used computer-based modelling of running in order to describe individual muscle contributions to the CoM displacement (Hamner et al, 2010). The authors suggested that during the braking phase of stance there is predominant activation of the quadriceps muscles, whereas ankle plantarflexors are the main contributors to the

propulsion phase. The present description of muscular patterns of activation for running and cutting manoeuvres corroborates the results from Hamner and co-workers (2010) in a neurophysiological perspective, by suggesting that neural control of such locomotor tasks might be partitioned in motor modules linked to biomechanical goals, such as landing, braking and propulsion.

A pulsative pattern for muscle recruitment was found for both running and cutting manoeuvres in the present investigation, which is in agreement with previous investigations of human locomotion (Ivanenko et al, 2005; 2006; Lacquaniti et al, 2012b). The activation impulses for running task had smaller overlapping in time and lower variability in timing across subjects than those of cutting tasks. These differences may be explained by the fact that humans have a well-established motion pattern for walking and running (Lacquaniti et al., 2012). Cutting manoeuvres are tasks of greater complexity and less frequent with respect to walking/running and can be performed with different degrees of efficiency.

The present results suggest that differences in activation timing across individuals can alter performance, allowing individuals with faster transitions between motor modules to generate more external work,. The absorption period of a cutting cycle is defined by a negative power generation that decelerates the CoM. The energy is mostly absorbed by the eccentric knee and hip flexion, which start the propulsion subsequently. The propulsion period is characterized by a positive external work to perform the sideward displacement by knee and hip extension and subsequent push-off. The amount of external work generated during sports gestures varies with experience, since the motor gesture can be optimized to become faster and/or more precise (Sigward and Powers, 2006). Enhancements related to motor learning or practice are the facilitation of agonist and reduced antagonist activity, generating a smoother movement (Gabriel et al, 2006). The faster the transition from M2 to M3, the higher the En-ABS, which indicates that individuals more adapted to switch modules can optimize (i.e., increase) the impact absorption to perform a faster movement. In the same way, greater En-PRP indicates that subjects can perform the propulsion and push-off more effectively, by generating higher muscular power, likely on the basis of a faster transition from M3 to M4.

Our results revealed that the ability to perform the sub-phases of cutting movements is strictly linked to an overall coordination that controls the movement. This coordination involves the activation of subsets of muscles in the adequate timing that slightly varies among individuals.

Therefore, the sensory-motor integration of muscular actions and reaction forces has to be solved to perform the manoeuvre, and the transitions between the modules may be modulated by sensory feedback (Lacquaniti et al, 2012b), dictating the "pace" of the movement. The present results are the first to date that correlates the modular organization of a locomotor task to its global performance. The timing for activation patterns during locomotion may define the type of task (walking, running, cutting etc.) and also its efficiency while the lower limb is interacting with the surface.

In conclusion, the neural control of complex locomotion tasks, such as cutting manoeuvres, can be described by a low-dimensional set of motor modules, similar across subjects. These modules are controlled in an impulsive way, in relation to the biomechanical goals of the task (impact absorption, propulsion). The relative timing for switching between modules determines the external work production to move the CoM. Thus, the optimal progression during locomotor tasks is related to the correct timing to activate muscle weightings. Complex and fast movements can be better performed by refining the relative timing of the activation of motor modules related to specific biomechanical goals.

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STUDY IV

Submitted to PLoS ONE Journal

EFFECTS OF PERTURBATIONS TO BALANCE ON NEUROMECHANICS OF FAST CHANGES IN DIRECTION DURING LOCOMOTION

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ABSTRACT

This study investigated whether the modular control of complex locomotor tasks can be influenced by perturbations to balance. Twenty-two healthy men performed 90° side-step unperturbed cutting manoeuvres while running (UPT) as well as manoeuvres perturbed at initial contact (PTB, 10 cm translation of a moveable force platform). Surface EMG activity from 16 muscles of the supporting limb and trunk, kinematics, and ground reaction forces were recorded. Motor modules and their respective temporal activations were extracted from the EMG signals by non-negative matrix factorization. Knee joint moments, co-contraction ratios (CCR) and co-contraction indexes (CCI, hamstrings/quadriceps) and motor modules were compared between UPT and PTB. Five motor modules were enough to reconstruct UPT and PTB EMG activity (variation accounted for [VAF]=0.91±0.05). Moreover, no changes were found in the motor modules responsible for the modulation of UPT and PTB (similarity=0.83±0.08), but the activation signals that drive the temporal properties of the modulation were influenced by perturbations (similarity=0.71±0.18). Although similar modules were found between UPT and PTB, there was a poor reconstruction quality for the reconstruction of PTB by using activation signals from the UPT condition (VAF=0.59±0.11). Perturbations at initial contact reduced knee abduction moments (7%), as well as CCR (11%) and CCI (12%) shortly after the perturbation onset. These changes in CCI and CCR were caused by a reduced activation of hamstrings that was also verified in the activation signals of the specific motor module related to initial contact. Our results suggested that perturbations to balance influence afferent inputs to the motor pattern and consequently alter temporal properties of muscle recruitment. Consequently, the protection from neural mechanisms is reduced and injury risk might be increased in more severe perturbations.

Key words: cutting, motor modules, perturbations, EMG

INTRODUCTION

Stability during human locomotion is continuously challenged, requiring mechanisms that integrate visual, vestibular and somatosensory inputs [1-3]. In intense sport activities, such as running and sudden changes in directions (i.e., cutting manoeuvres), the attention is not essentially focused on balance control since there are other relevant aspects concerning motor performance and there may be unpredictable changes in the environment (i.e., the interaction between the practitioner and the opponents/surfaces). It is known that there are direct connections between hamstring muscles and the anterior cruciate ligament [4] and that hamstrings muscles contribute to knee joint stability while running/cutting [5,6]. Nonetheless, changes in the environment are risk factors for lower limb injuries [7-10] since changes in the muscular activation may reduce the above mentioned protective mechanisms [5,6,11-14]. Perturbations such as slips usually occur shortly after initial contact of cutting manoeuvres, and may expose the lower limb joints to injury risks [15]. Knowing the central nervous system (CNS) strategies elicited during perturbations to balance, based on experimental data directly related to the motor gesture, may be relevant to advance injury prevention.

Muscular coordination for changes in direction during running has been considered a crucial factor for injury prevention [16,17]. In addition to the study of the activity of each muscle, muscle coordination can also be investigated by a reduction of dimensionality, focusing on less primitive signals than the active muscles [18]. Motor modules (also called muscle synergies) are defined as sets of muscles recruited in specific time-varying profiles [18-20]. With this approach, recently, Oliveira and co-workers described the modular organization of neural inputs to the muscles during changes in direction [21]. Perturbations to balance while walking elicit specific and rapid neural strategies to avoid falls [22,23], but the modulation of walking is predominantly preserved [20,24]. On the other hand, the activation signals that dictate the timing for the recruitment of motor modules are substantially altered by perturbations [20], suggesting that the afferent input must play essential role during perturbations.

Therefore, the reduced protection caused by altered muscular activation during changes in direction might be linked to changes in the afferent participation on the task performance. In the present investigation we aimed to verify whether perturbations

delivered at initial contact could influence the modular control and stability of the lower limb joints. We hypothesized that motor modules extracted during changes in direction could be influenced by small perturbations to balance, especially by the altered afferent components evoked by perturbations. Motion analysis and factorization analysis were used in order to understand the perturbation effects and suggest further strategies to improve training strategies for improving safety/reduce injury risk.

METHODS

2.1. Subjects

Twenty-two healthy men (age: 28±4 yrs; body mass: 71±10 kg; body height: 171±7 cm) volunteered for the experiment. All subjects were recreational practitioners of team sports (soccer, basketball, handball, ice hockey). They had no known history of neurological or motor disorder. All subjects provided written informed consent before participation and the procedures were approved by the ethical committee of Northern Jutland (N-20100042).

2.2. Experimental Setup

Subjects were asked to perform repeated running trials with a 90° change in direction (cutting manoeuvres) during a single session. The task consisted in running from 6-7 meters away of a moveable force platform, aiming to step with the right foot onto the plate, turn 90° to the left and continue running (see Figure 1 for illustration). Initially, 10-15 familiarization trials were required and instructions to accelerate in a straight path towards the force platform and turn as fast as possible to the left were provided. Subsequently, 11 cutting manoeuvres were recorded with 40-60 s rest intervals within each trial to reduce the effects of fatigue. Without any previous warning, there was a perturbation elicited at the initial contact to the moveable force platform during the 11th trial. The perturbation consisted of a 10-cm translation lasting 150 ms (average speed 66.6 cm/s) in the original running direction. Subjects wore the same type of court shoes (FZ 2600W, FORZA®, Brønderslev, DK) in order to reduce the effects of different footwear on the measurements.
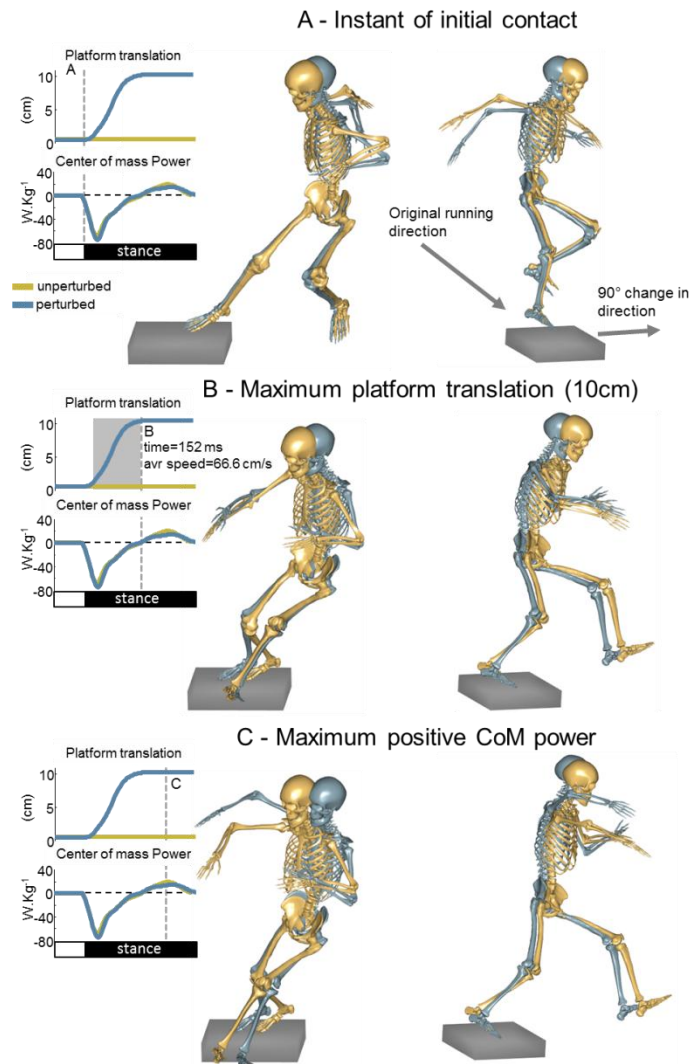
Figure 1. Three dimensional models from a representative subject performing unperturbed (*yellow*) and perturbed (*blue*) cutting manoeuvres. The comparison between the two conditions was emphasized in three events. A) The time of initial contact, note that there is no difference in the lower limbs kinematics, indicating consistent inter-trial behavior. B) The time 152 ms (*grey area in the translation plot*) after initial contact. This time corresponds to 10 cm translation of the platform in the perturbed trial. Note the perturbed model shows the right foot forwarded in relation to the unperturbed model, as well as a more abducted hip position. C) The time of maximum power output. The maximum power generated during the stance phase is slightly lower for the perturbed condition. At this instant, the trunk position is influenced by the perturbations as well as the contralateral leg.

2.3. Data collection

Kinematics: Retroreflective ball-shaped markers were placed bilaterally each side of the subject to the skin overlying the following landmarks bilaterally: calcaneus, first and fifth metatarso-phalangeal joint, lateral malleolus, lateral condyle; greater trochanter, anterior superior iliac spine, posterior superior iliac spine and acromion. In addition, one marker was placed on the seventh cervical vertebrae, upper and lower endpoint of sternum (suprasternal notch and xyphoid process).

Extra markers were placed bilaterally on lower extremity segments: one on the thigh, four on the shank and one on the upper arm, serving as tracking markers to define the 3D motion. Marker positions were tracked with a motion analysis system with eight infrared digital video cameras (Oqus 300 series, Qualisys, Gothenburg, Sweden). The kinematic data were recorded with a sampling frequency of 256 Hz and synchronized with the EMG and kinetic recordings. Subjects wore full stretch pants covering the EMG cables to avoid movement artifacts.

Kinetics: The vertical (*Fz*), anterior-posterior (*Fy*) and medial-lateral (*Fx*) ground reaction forces and the corresponding reaction moments (Mx, My, Mz) were recorded at 1024 Hz by a force platform (AMTI, OR6-5, Watertown, MA) constructed over a hydraulic system [25] Software developed on the Labview platform (MrKick II, Aalborg University, Aalborg, Denmark) was used for data recording. Using a feedback electric circuit, the *Fz* force also served as trigger to initiate the force plate movement.

Electromyography: Surface EMG signals were recorded in bipolar derivations with pairs of Ag/AgCl electrodes (Ambu Neuroline 720 01-K/12; Ambu, Ballerup, Denmark) with 22 mm of center-to-center spacing. Prior to electrode placement the skin was shaved and lightly abraded. The EMG signals were amplified with a gain of 2,000 (EMG-USB, LISiN; OT Bioelettronica, Turin, Italy), sampled at 2,048 Hz (12 bits per sample), band-pass filtered (second-order, zero lag Butterworth, bandwidth 10–500 Hz). A reference electrode was placed on the right wrist. The EMG signals were recorded from the following muscles of the right side according to the SENIAM recommendations [26] and previous literature [20,21,27]: tibialis anterior (TA), peroneus longus (PER), soleus (SOL), gastrocnemius medialis (GM), vastus medialis (VM), vastus lateralis (VL), rectus femoris (RF), biceps femoris (BF), semitendinosus (ST), adductor muscles (ADD), gluteus medius (GME), gluteus maximus (GMA), tensor fascia latae (TFL), erector spinae at L1 (ESP), rectus abdominis (RAB) and external oblique (EOB).

2.4. Data Analysis

The body of the subjects was modeled as an interconnected chain of rigid segments: foot, shank, thigh, pelvis, trunk and arms. The trunk center of mass, joint angles and angular velocities between segments were analyzed in the AnyBody Modeling System

5.1 (Anybody Technology, Aalborg, Denmark). The left initial contact was defined from the foot kinematic data, whereas the end of the stance phase for the right leg was determined by the force plate recordings (when the vertical ground reaction force exceeded 20 N). The body center of mass (CoM), CoM power (CoMp: sum of ground reaction forces times CoM velocity [watts/body weight]), joint angles and joint moments were calculated during the period of contact to the force platform.

Signal processing. The segmentation for EMG factorization was defined from the left initial contact prior the right foot step on the force platform to the end of the stance phase on the force platform. After segmentation, the surface EMG signals from the 16 muscles were full-wave rectified, low-pass filtered (10 Hz) and time-normalized in order to obtain 200 data points for one gait cycle [19,28]. For each subject, non-negative matrix factorization (NMF) [19,29] was applied for each trial in order to identify motor modules and activation signals (Figure 2).

Motor module model. The EMG signals recorded from *M* muscles were indicated as:

$$X(k) = \left[x_1(k), x_2(k), \cdots, x_M(k)\right]^T \qquad (1)$$

where $x_M(k)$ is the activity of the *m*th muscle at the time instant *k*. The activation signals $P(k)$ were indicated as ($N<M$):

$$P(k) = \left[p_1(k), p_2(k), \cdots, p_N(k)\right]^T \qquad (2)$$

The relation between *X(k)* and *P(k)* is described as follows:

$$X(k) \approx X_r(k) = S \cdot P(k) \qquad (3)$$

where $X_r(k)$ is the muscle activity vector reconstructed by the factorization. In Eq. (3), the EMG *X(k)* are obtained by linear transformation of the activation signals *P(k)* with gain factors s_{mn}. The matrix whose columns were the weights of each activation signal

for each muscle is denoted as S in Eq. (3) and will be referred to as the motor module matrix [30].

Dimensionality. The number of motor modules N needed for accurate description of the movement was assessed by the dimensionality analysis proposed by [19] separately for the perturbed and unperturbed cutting manoeuvres. According to this procedure, the quality of reconstruction of the muscle activation pattern is analyzed as a function of the number of modules and the minimum number of modules is identified as the point in which this curve pronouncedly changes its slope [19]. In addition to this criterion, a minimum threshold for reconstruction quality was set at 80%. For quantifying the quality of reconstruction, the estimated muscular activation pattern was compared with the recorded pattern by means of the variation accounted for (VAF) value, defined as the variation that can be explained by the model: $VAF = 1 - SSE/SST$, where SSE (sum of squared errors) is the unexplained variation and SST (total sum of squares) is the pooled variation of the data.

After computation of the reconstruction quality, the motor modules for each subject were extracted from the concatenation of all unperturbed trials, as well as from all perturbed trials. Similarities among the different subjects were investigated for motor modules and activation signals for both unperturbed and perturbed conditions. The motor module matrices were compared by computing the scalar product between pairs of columns, normalized by the product of the norms of each column [19,31,32]. Similarities between activation signals were quantified by the value of the cross-correlation function at zero time lag [29,33]. In addition, the EMG activities from all subjects were concatenated for a given condition, from which motor modules were extracted to represent the whole group of subjects. In this manner, all the variability in the dataset was taken into account. The timing of each activation signal was defined as the time instant of the maximum of the activation signal as a percentage of the cutting cycle.

Kinematic data were low-pass filtered (10 Hz, second-order, zero lag Butterworth) and CoM mass speed (CoM_{SPD}) was computed between 200 ms and 100 ms prior to right foot contact to the force platform. Joint angles and joint moments from the hip, knee and ankle were calculated and the peak angles and moments during the load acceptance

stance period (defined as period in which the CoM power is negative), and the propulsion period (defined as the period in which the CoM power is positive) were computed for each trial. In addition, the external work (integration of the CoM power) was calculated for the load acceptance (W_{LAC}) and propulsion (W_{PRP}) period of cutting manoeuvres.

Additional EMG analysis were conducted by using the same EMG envelopes used for NMF, in order to extract the co-contraction ratio (CCR) and co-contraction index (CCI) for the relationship between knee flexors and extensors [34]. The CCR was defined as the average knee flexors EMG activity ((BF+ST)/2) divided by the knee extensors activity ((VM+VL+RF)/3). The CCI was defined as the product of the averaged EMG activation of from all knee flexors and extensors and the CCR. CCI and CCR were calculated in three time-epochs: 1) 10 ms before initial contact (i-pre10); 2) from initial contact until negative peak CoM power during load acceptance (i-abs); 3) a 50-ms time window around the peak CoM power during the propulsion phase of cutting manoeuvres (i-prop). The effects of perturbation on the dependent variables (stance duration, CoM_{SPD}, W_{LAC}, W_{PRP}, peak joint angles, peak moments, CCI, CCR and peak timing of the activation signals) were investigated using Student's t-test. The significance level was set to $p < 0.05$.

RESULTS

The comparison between perturbed and unperturbed performance of cutting manoeuvres (Figure 1) showed that subjects did not change the approach to perform the perturbed cutting manoeuvre (Figure 1A), since they had no previous warning on the perturbation event. The platform translation in the direction of the original running increased knee extension and hip and knee abduction (Figure 1B), but no changes in the contralateral limb or trunk position were observed. The most pronounced effects of the perturbation were observed at the instant of peak CoM power generation (Figure 1C), where the trunk position is compromised, causing this subject to raise the arms in order to facilitate balance recovery. In addition, there is a greater knee external rotation in the perturbed knee at this moment. Perturbations to balance during cutting manoeuvres did not influence stance duration and CoM_{SPD} ($P > 0.05$, Table 1). On the other hand, W_{LAC} and W_{PRP} were reduced for the perturbed condition ($p < 0.05$).

Table 1. Mean(SD) stance duration (stc_sur), , CoM speed 100ms before initial contact (CoM$_{SPD}$), external work during load acceptance (W$_{LAC}$) and propulsion period (W$_{PRP}$) for the unperturbed and perturbed cutting manoeuvres. * indicates significant difference in relation to unperturbed cutting.

	Unperturbed	Perturbed
stc_dur (ms)	327.90±5	324.7±5
CoM_speed (m.s^{-1})	2.67±0.4	2.62±0.5
W$_{LAC}$ (W.kg^{-1})	-14.3±3.9	-15.5±5.2*
W$_{PRP}$(W_kg^{-1})	9.9±3.2	7.9±3.3*

No effects of perturbation were found for CCI and CCR before initial contact (i-pre10, Figure 2). On the other hand, during i-Abs, both CCI and CCR were reduced when perturbations were elicited ($p<0.05$). Moreover, both CCI and CCR showed significant increases during i-prop for the perturbed condition ($p<0.05$).
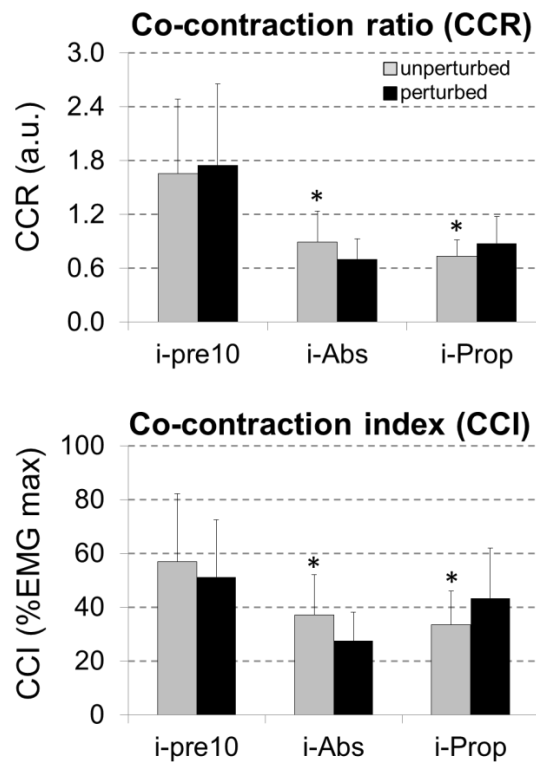

Figure 2. Mean (SD) co-contraction ratios (top) and co-contraction indexed (bottom) 10ms before initial contact (i-pre10), during absorption phase (i-abs) and propulsion phase (i-prop) of unperturbed (grey) and perturbed cutting manoeuvres (black). * denotes significant difference in relation to the perturbed condition ($p<0.05$).

The effects of perturbation on joint kinematics

Figure 3A shows the average joint angles for the perturbed and unperturbed cutting manoeuvres throughout the stance period. It was observed that joint angles are very similar for the hip joint. On the other hand, knee showed reduced peak flexion

86

(6.1±1.2°), and increased peak external rotation (0.04±3.1 and -0.61±4.0, respectively, $p<0.05$, Figure 3B). The ankle joint showed reduced peak dorsiflexion (7.2±1.9°, $p<0.05$). Towards the end of the perturbed stance period, it was observed that the knee was more externally rotated, and the ankle was more everted and externally rotated in relation to the unperturbed condition. Concerning the timing of the peaks, there was a verifiable delay in the peak of hip adduction and ankle dorsiflexion due to perturbations (~4%, Figure 3C, $p<0.05$). The ankle joint showed earlier peaks for inversion and internal rotation, whereas the knee showed earlier peaks for all directions for the perturbed condition. (6-12%, $p<0.05$).
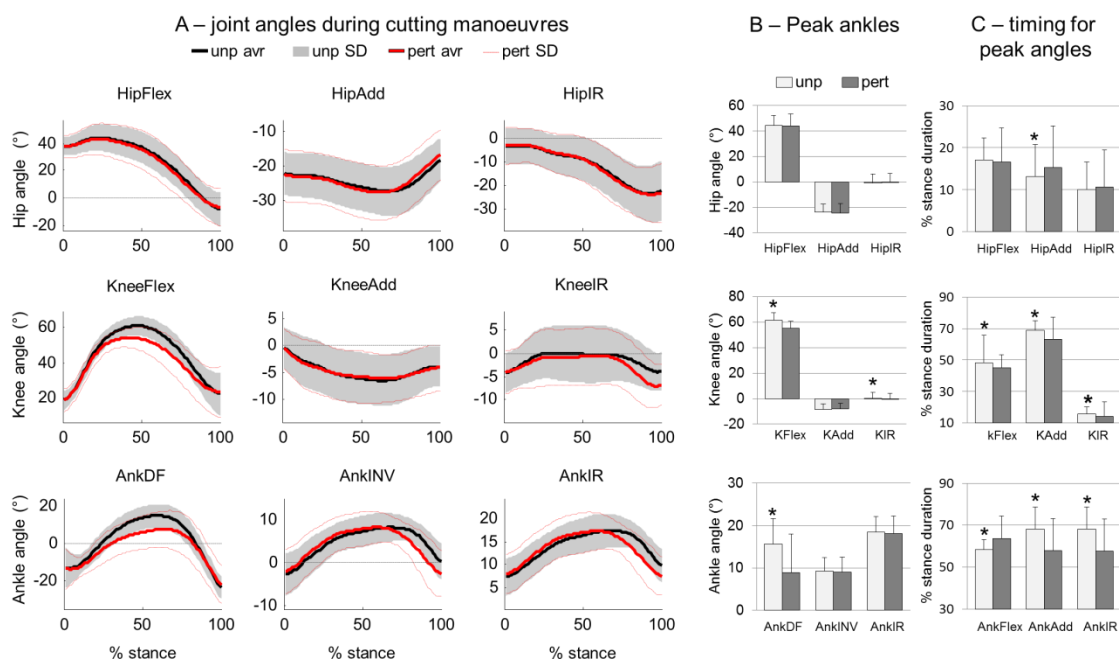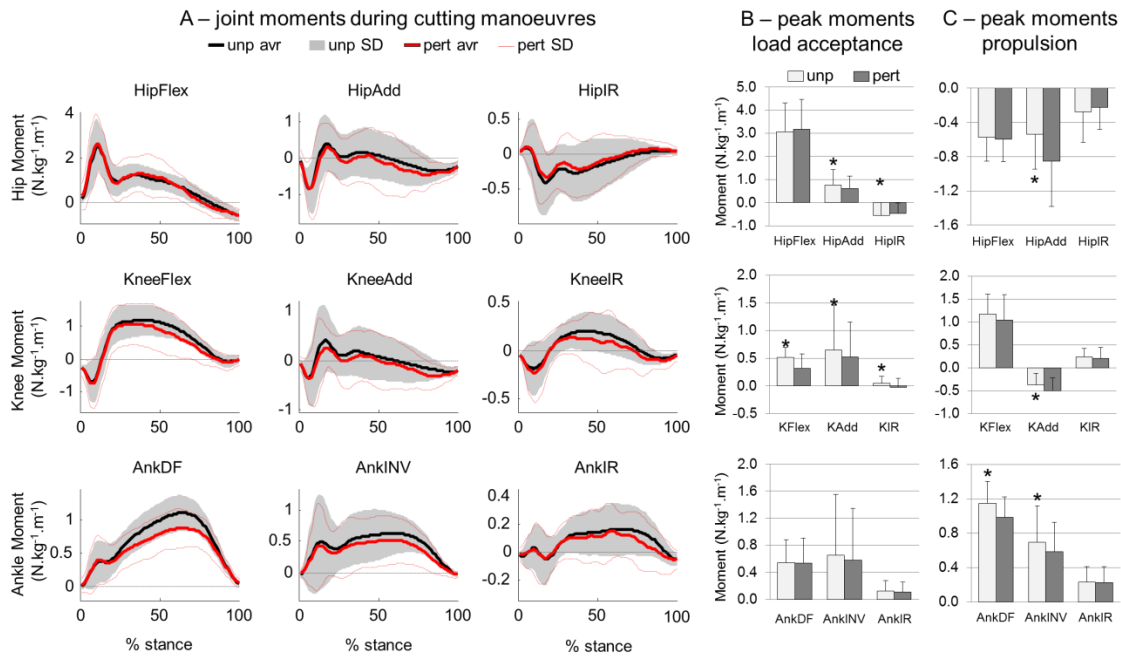

Figure 3. Kinematics of unperturbed (unp) and perturbed (pert) cutting manoeuvres. A) Three dimensional joint angles were extracted from the hip, knee (K) and ankle (Ank). Statistical analysis compared the peak angles (B) and the timing for the peak angles (C). Flex = flexion; Add = adduction; IR = internal rotation; DF = dorsiflexion; IN V= inversion. * denotes significant differences in relation to PERT.

The effects of perturbation on joint moments

Changes in joint moments were found predominantly in the medial-lateral and flexion-extension directions (Figure 4A). With respect to the load acceptance period (approximately the first 20-25% of the stance period), the peak hip adduction and external rotation moments were reduced ($p<0.05$, Figure 4B). In the same way, the peak knee flexion, adduction and internal rotation momentswere reduced ($p<0.05$) during the load acceptance period, with no changes in ankle moments. Increases in hip and knee peak abduction moments during the propulsion period (Figure 4C, $p<0.05$) were

87

demonstrated. In addition, peak ankle dorsiflexor and invertor moments were reduced during the propulsion period.

Figure 4. Joint moments of unperturbed (unp) and perturbed (pert) cutting manoeuvres. A) Three dimensional joint moments were extracted from the hip, knee (K) and ankle (Ank). Statistical analysis compared the peak moments during load acceptance period (B) and during propulsion period (C). Flex= flexion; Add = adduction; IR = internal rotation; DF = dorsiflexion; INV = inversion. * denotes significant differences in relation to PERT.

Dimensionality

The analysis of dimensionality from single trials revealed that five motor modules were required to reconstruct unilateral muscular activation for both unperturbed (average VAF = 0.92±0.05) and perturbed cutting manoeuvres (average VAF = 0.90±0.06). On average, VAF reached 90% (range from 0.87-0.96) with five modules, and the addition of a sixth module only increased VAF by 4±0.6% (average over all subjects from the unperturbed and perturbed cutting tasks). The dimensionality from the concatenation of all trials for each subject also indicated that five modules are sufficient to reconstruct cutting at reconstruction quality above 80% (0.86± 0.03, averaged from all perturbed and unperturbed conditions).

Motor modules that describe unperturbed and perturbed cutting

Aside from the observation that the number of modules was similar for perturbed and unperturbed cutting manoeuvres, the five extracted motor modules for

perturbed cuttings were also similar to those from the unperturbed condition. By comparing motor modules from unperturbed and perturbed cutting manoeuvres (Figure 5) it can be seen that EMG signals are influenced by perturbations (*panel A*). However, there were minor changes in the weighting coefficients accompanied by more substantial changes in the activation timing (*panel B*). Both perturbed and unperturbed cutting manoeuvres were successfully reconstructed by these five motor modules (*panel C*).
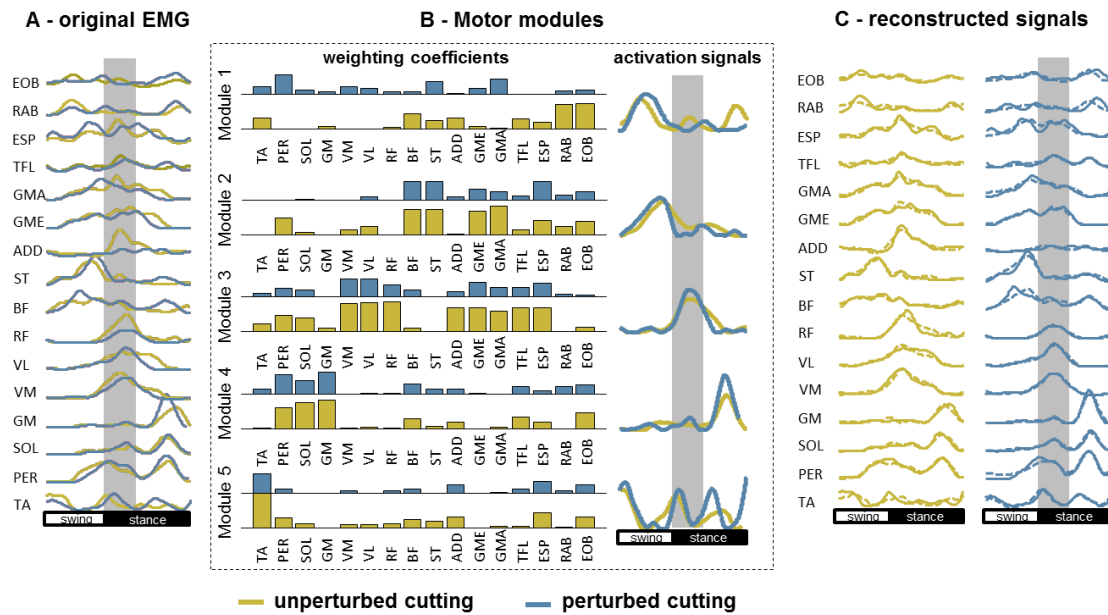
Figure 5. Representative modular organization for perturbed and unperturbed cutting manoeuvres. A) EMG envelopes for unperturbed (*yellow*) and perturbed cutting manoeuvres (*blue*) throughout the cutting cycle. B) muscle activity was processed by a NMF algorithm, which reconstruct the original EMG using a small set of motor modules for both conditions in a similar way. C) original (*solid lines*) and reconstructed EMG from the multiplication of muscle weightings and activation signals (*dashed lines on top of solid lines*).

Similarity between normal and perturbed cutting maneuvers

Similarity was verified for muscle weightings of all motor modules (r>0.7, Table 2), but activation signals showed reduced similarity for motor module 1 (M1), motor module 2 (M2) and motor module 5 (M5). These results suggest that the perturbation event affects activation signals responsible for the modulation of hip/trunk stabilizer and hamstring muscles.

Table 2. Mean (SD) and range of similarities between unperturbed and perturbed cuttings for the muscle weightings and activation signals of the five extracted motor modules from all subjects.

	muscle weightings		activation signals	
	Mean±SD	**range**	**Mean±SD**	**range**
M1	0.81±0.17	0.33-0.98	0.66±0.22	0.23-0.92
M2	0.84±0.13	0.46-0.98	0.68±0.24	0.15-0.93
M3	0.86±0.11	0.51-0.98	0.81±0.17	0.22-0.98
M4	0.80±0.16	0.33-0.95	0.74±0.20	0.20-0.95
M5	0.85±0.11	0.51-0.96	0.68±0.19	0.20-0.91

Inter-subject similarity for perturbed cutting manoeuvres

The delivered perturbations to cutting manoeuvres reduced the similarities among subjects for the muscle weightings, whereas activation signals showed no similarities for all motor modules (Table 3).

Table 3. Mean (SD) and range of similarities among subjects for the muscle weightings and activation signals of the five motor modules extracted from the perturbed cutting manoeuvres.

	muscle weightings		activation signals	
	Mean±SD	**range**	**Mean±SD**	**range**
M1	0.72±0.13	0.24-0.97	0.50±0.15	0.23-0.92
M2	0.73±0.13	0.33-0.98	0.49±0.14	0.21-0.93
M3	0.74±0.15	0.23-0.98	0.52±0.16	0.22-0.98
M4	0.79±0.13	0.33-0.95	0.50±0.15	0.20-0.90
M5	0.72±0.14	0.30-0.96	0.51±0.15	0.27-0.88

*Concatenated motor modules to explain strategies to postural reactions*

Figure 6 shows the concatenation of all subjects for the unperturbed (Figure 6A) and perturbed cutting manoeuvres (Figure 6B). In line with the averaged motor modules from Figure 4, the concatenation also shows similar weighting coefficients when comparing unperturbed and perturbed cutting manoeuvres. The lowest similarity among weighting coefficients was found for M2 (0.89) for which hip extensors, ESP and EOB were also activated in this module in response to the perturbation event. The activation signals showed similarity only for M3 and M4, whereas the other three modules were influenced by the perturbation event.

A – normal cutting   **B – perturbed cutting**
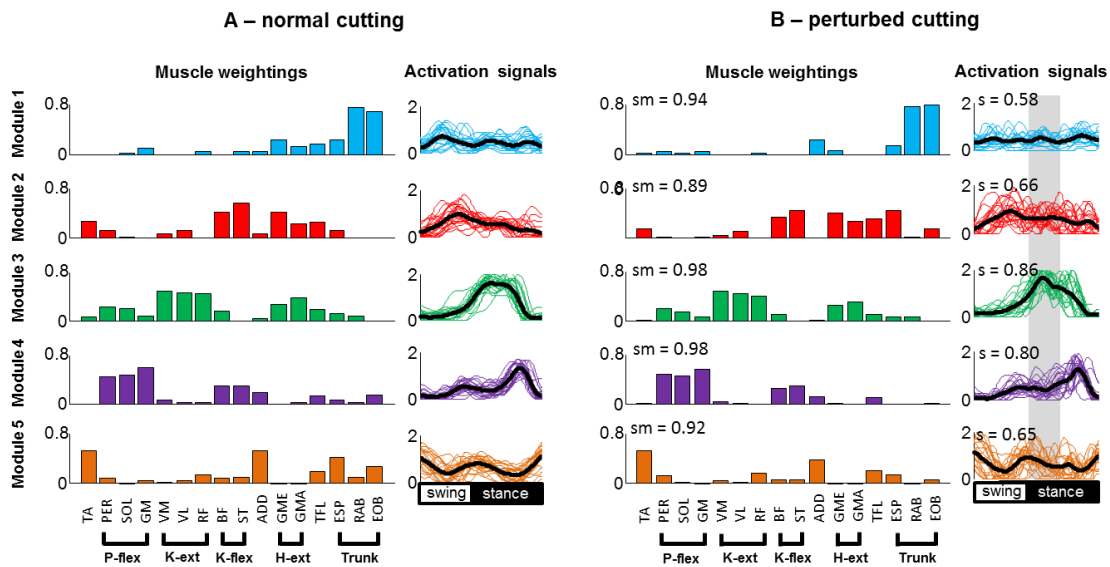
Figure 6. Motor modules that describe cutting manoeuvres without perturbations (A) and with perturbation (B) . Abbreviations of the muscle nomenclature are described in the Methods (Section 2.3). The 'sm' is the similarity computed between the motor modules from unperturbed and perturbed cuttings. The 's' is the similarity computed between the activation signals from unperturbed and perturbed cuttings.P-flex: plantar flexors; K-ext: knee extensors; K-flex: knee flexors; H-ext: Hip extensors.

Reconstruction of perturbations from the unperturbed cuttings

The reconstruction of perturbations from unperturbed cuttings showed an overall VAF at 0.59±0.11, indicating that perturbations cannot be reconstructed from motor modules of unperturbed cutting manoeuvres. Analysis of the VAF showed consistent values among muscles (Figure 7).
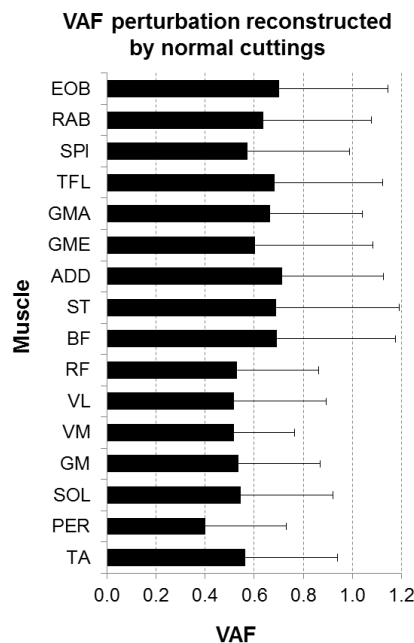
Figure 7. Mean (SD) variation accounted for (VAF) based on the reconstruction of EMG signals of perturbed cutting manoeuvres for each subject from the respective unperturbed EMG signals.

91

Perturbation effects on the activation signals

The peak timing of the activation signals related to the stance phase of cutting were not different when comparing unperturbed and perturbed cuttings (p>0.05, Table 4). In addition, the time duration between the peak timing from M2 to M3 and from M3 to M4 of unperturbed cutting task were also not statistically different when compared to perturbed cutting task (p>0.05).

Table 4. Peak timing for the activation signals (% of cutting cycle) of the three motor modules related to the stance phase of unperturbed (UNP) and perturbed (PERT) cutting manoeuvres . M2-M3: time period from the peak activation of M2 to the peak activation of M3; M3-M4: time period from the peak activation of M3 to the peak activation of M4.

	UNP	PERT
M2 (% cycle)	37.2±6	38.5±14
M3 (% cycle)	64.1±9	65.7±10
M4 (% cycle)	82.9±4	81.6±9
M2-M3 (% cycle)	27.6±8	27.2±14
M3-M4 (% cycle)	16.7±10	17.0±12

Selected activation signals for M1, M2 and M5 from unperturbed and perturbed conditions were compared for six individuals (Figure 8). The predominance of changes in the timing occurred during/after the perturbation period, with minor changes during swing. The M1 showed a second peak activation during the perturbation period when perturbations were elicited. In addition, M2 (related to initial contact modulation) showed reduced activation from initial contact (*the grey in the figure area limits the perturbed period*), which might reduce the activation of hamstring muscles in the early period of stance. M5 showed no constant pattern between subjects, for both perturbed and unperturbed conditions.

DISCUSSION

The main findings of this study were that small perturbations to balance delivered during fast changes in direction have no influence in the modular organization of the task, since the motor modules were essentially preserved. On the other hand, the activation signals were influenced, most likely, by potentiated afferent input, which may for a short period reduce muscular activation during load acceptance for specific motor modules. These results suggest that perturbations to balance during changes in direction

92

reduce knee stability, and that the CNS might not be able to counteract instantaneously to threats occurring at the periphery by means of muscular recruitment in non-trained subjects.
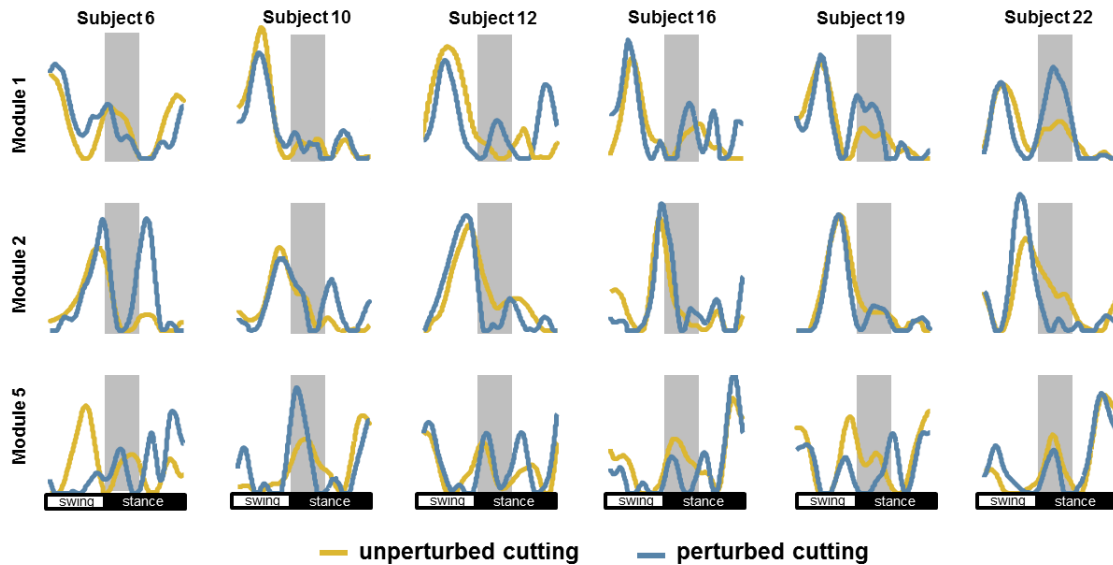
Figure 8. Activation signals of modules 1, module 2 and module 5 for unperturbed cutting (*yellow*) and perturbed cutting task (*blue*) are shown for six subjects. Grey vertical area denotes the perturbation period for the perturbed cutting manoeuvres.

The neural control of locomotion tasks such as walking and running has been described by a modular organization, in which a low-dimensional set of motor modules account for the activation of the main lower limb/trunk muscles [18,35]. However, only a few investigations were conducted concerning changes in CNS strategies to control locomotion under perturbed conditions [3,20,36]. Afferent input to the modulation of gait is considered essential, and its role is even more remarkable when balance is challenged. Previous studies have reported increased afferent responsiveness and consequent altered muscular activation during locomotion over slippery surfaces [3] or perturbations such as stumbling [36] and absent support surface [37]. In addition, afferent contributions during walking have also been recently suggested as the main cause for the changes in lower limb activity throughout translational perturbations such as slips [20]. The present results are in line with these previous reports, since changes in the activation timing of the motor modules were imposed by strong afferent inputs that are most likely integrated with supraspinal descending commands. These commands are subsequently directed to apparently fixed muscles weightings involved in specific biomechanical goals related to changing direction while running. Although similar

motor modules were found between conditions, the reconstruction accuracy of motor modules from the perturbed condition based on fixed motor modules from the unperturbed condition does not allow for acceptable reconstruction (Figure 7). Thus, it is suggested that the activation signals are indeed the relevant parameters altered by perturbations.

Only activation signals related to M3 and M4 were preserved, which modulate limb extension and forward propulsion by the calf muscles, suggesting that the motor patterns that drive these biomechanical goals during fast changes in direction are robust and may resist perturbation events. The changes in the activation signals for M2 (hamstrings/gluteus activity) reduced the hamstrings activation while the perturbation was occurring, which was eventually reflected in reduced CCI and CCR calculated shortly after initial contact during perturbed trials. On the other hand, there was increased excitation in M5 (TA, ADD, TFL, ESP) immediately following the perturbation (Figure 8). For both cases, these changes may be linked to the fact that the supporting limb is unloaded, which leads to a reduced co-contraction of trunk and lower limb muscles [38]. Subsequently, a greater co-activation occurred, possibly attributable to monosynaptic stretch reflexes after unexpected perturbations [2,22,23,39], which may have induced/increased the stiffness in the hip and knee joints, allowing a safe completion of the movement [10,37,40]. However it is difficult to clearly separate reflex components from the voluntary actions in factorization analysis such as NMF [20], and assumptions concerning the specific participation of reflex components must be carefully interpreted.

The modularity found in the present investigation is in agreement with previous reports on running [35] and cutting manoeuvres [21], in which five modules were sufficient to describe the neural control of fast changes in direction during running and a more detailed discussion concerning the neurophysiological meaning of the motor modules has been provided in the respective papers. The perturbation event in the present investigation, however, did not change the modularity of the task, suggesting that the CNS can solve the unpredictable event without increasing the complexity of the control strategy. This result corroborates those reported in our recent investigation [20], in which the number of modules remained unchanged during perturbations, but one module was reorganized for perturbations forward, leftward and rightward in order to

regain balance and continue walking. In addition to the changes in one motor module, the activation signals were substantially altered for most motor modules, most likely caused by afferent input received throughout the perturbation event.

Perturbations to balance in the present investigation did not cause substantial changes in hip and knee kinematics. Even though, a reduction in hamstrings EMG activity while sliding, as well as increased knee extension and abduction moments were found. These biomechanical alterations have been previously related to knee injuries in recreational sports practitioners and athletes, and verified in different experimental protocols [41-43]. It is believed that reduced hamstrings activation during knee extension may expose the ligamentous structures to higher anterior shear forces, increasing risk of sustaining injuries such as ACL ruptures [6,12]. Cutting manoeuvres require a high level of stability in the knee joint that might be compromised by reductions in muscle activations during a perturbation event (Figure 2). Despite the fact that perturbations reduced joint moments during load acceptance, the joint moments in the frontal plane were increased for the hip and knee (adduction moment for both joints), concomitant to increased CCI and CCR. These results suggest that small slips while cutting can change the overall joint mechanics and influence the neural control of the lower limb muscles just after the perturbation [38].

Methodological limitations in eliciting perturbations during high speed movements with a change in direction might be the reason to the lack of investigations in this topic. Being aware about these limitations and risks, we elicited harmless 10 cm translations to assure safety with no falls and/or related injuries being reported during the whole experiment. Slips while performing running or cutting manoeuvres might easily overcome 10 cm, requiring stronger postural reactions that may differ from the described reactions in the present results. Such a small translation must be considered as a methodological limitation in order to assure safety. In this way, computer-based simulations may be the best approach in order to understand the possible underlying mechanisms related to postural reactions in such delicate conditions. Even though, our results reinforce the knowledge on the importance of neural commands to the muscles during hazardous events by suggesting that slips strongly influence the neural control of dynamic tasks.

In summary, small perturbations to changes in direction while running elicited mild biomechanical changes during the stance phase. Although there is most likely a remarkable influence of afferent commands on the activation signals that drive the motor modules during perturbations, no substantial changes occur in the motor module organization itself. Moreover, reductions in co-contraction ratio for the knee joint muscles, and increased knee abduction moments suggest reduced protection from the neural mechanisms and consequently that the risk for injury might be increased in more severe perturbations.

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STUDY V

UNILATERAL BALANCE TRAINING ENHANCES NEUROMUSCULAR REACTIONS TO PERTURBATIONS IN THE TRAINED AND CONTRALATERAL LIMB

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ABSTRACT

The aim of this study was to investigate the effect of unilateral balance training on the reactive recovery of balance for both trained and untrained limbs. Twenty-three subjects were randomly assigned to either a control group (CG) or a training group (TG). The latter performed 6 weeks of balance training for the right leg. The pre- and post-training measurements were based on single leg standing posture on a moveable force platform which moved 6 cm anteriorly. TG subjects were tested on the trained (TR) and untrained leg (UTR), whereas CG subjects were tested on the right leg (CTR). The center of pressure trajectory length (CP_{LEN}) and average speed (CP_{SPD}) as well as onsets of muscular activation and time to peak (EMG_{T2PK}) from lower limb muscles were calculated and compared by a 2-way ANOVA (3 legs x 2 training status). Muscular onsets were reduced after training for TR (~ 19 ms, $p<0.05$) and UTR (~17 ms, $p<0.05$) with no significant changes for CTR. No effects of training for CP_{LEN} and medial-lateral CP_{SPD} was found. Furthermore, the EMG_{T2PK} of UTR was predominantly greater before training (~17 ms, $p<0.05$). However, after training the EMG_{T2PK} was similar among limbs. These results suggest that concomitant with improved balance recovery and neuromuscular reactions in TR, there is also a cross-education effect in UTR, which might be predominantly related to supraspinal adaptations shared between interconnected structures in the brain.

Key words: balance training, cross-education, perturbations, standing

INTRODUCTION

The ability of reacting to unexpected perturbations to balance relies on the interaction between reflexes (modulated by spinal and supraspinal pathways), automatic responses and voluntary responses [1, 2]. These mechanisms have essential implications for avoiding falls and assuring safe locomotion during daily life. Inefficient balance recovery strategies after perturbations during standing/walking are directly related to fall incidence [3]. Therefore, the use of perturbations in order to challenge balance skills and train postural control has been proposed [4-6].Balance training (also called neuromuscular training) has been proven to reduce lower limb injury incidence and falls incidence. The use of simple devices such as wobble boards (also called ankle discs) for training purposes may reduce the injury incidence in athletes by over 50% [7-9]. Balance training has been effective in altering muscular reaction time (or muscle/electromyographic (EMG) onsets) to perturbations [8, 10-13], improved joint positioning sense, hamstring/quadriceps ratio and joint stiffness [10, 11], as well as postural sway while standing on a force platform [8, 14]. In addition, recent investigations have shown that short-term balance training is effective in enhancing neuromuscular coordination of postural muscles, as well as neural adaptations on spinal and cortical levels [6].

Despite the fact that balance can be trained for both lower extremities, it remains to be shown whether adaptations to unilateral balance training can be transferred to the untrained limb by a cross-education effect [15]. This phenomenon has been extensively described in the literature concerning strength and resistance training [16, 17], in which the untrained limb also shows positive gains in strength elicited by training stimuli. Possible explanations to the cross-education effect range from peripheral to supraspinal levels (see Carrol and co-workers [15] for a detailed review). Recent investigations suggested that supraspinal commands play an important role for adaptations to balance training [18, 19], therefore, neural adaptations from unilateral balance training may be transferred to the untrained limb via superior levels of the CNS. However cross-education after balance training has been poorly addressed in the literature [8].

Understanding cross-education from balance training may have significant implications in neurophysiology and sports medicine. Therefore, the aim of the present study was to verify whether 6 weeks of unilateral balance training could enhance reactive recovery of balance during single-leg stance perturbations for the trained leg and also for the untrained leg. To achieve this aim, surface EMG and ground reaction forces were measured to determine

muscle onsets and center of pressure (CoP) displacement during single leg standing perturbations. The main hypothesis was that balance training could enhance balance recovery from unexpected perturbations for the trained leg and also for the untrained leg. The optimized balance control provided by balance training could improve neuromuscular properties (muscle onsets, burst durations and magnitudes) and also be reflected in altered reactive CoP displacements, reducing its length and average speed).

METHODS

Subjects

Twenty-three healthy men volunteered for the experiment. These subjects were randomly assigned to a training group (TG, n=13, age, 28±4 yrs; body mass, 69±8 kg; body height, 173±5 cm) or a control group (CG, n=10, age, 25±3 yrs; body mass, 72±8 kg; body height, 172±3 cm). All subjects were right-dominant as determined by a kicking test. Exclusion criteria included history of knee or ankle ligament injury, current lower-extremity injury, recent (within 6 months) low back injury, or vestibular dysfunction. All subjects provided written informed consent before participation and the procedures were approved by the ethical committee of Northern Jutland (N-20100042).

Experimental Setup

Pre-training and post-training measurements consisted of single-leg stance perturbations to balance. Both left and right limbs were tested in a random order in TG, in one single session while for CG only the right limb was tested (Figure 1).

The subjects were asked to stand still on a moveable force platform with their knee slightly flexed while looking straight forward at a fixed target located on a wall 4 m away. The free leg had to be elevated at least 5 cm above the platform while the hands were kept akimbo. The platform delivered forward and backward sudden perturbations to balance (6 cm length, 80 ms duration, average speed 75 cm/s). The target perturbation was the forward displacement, however, perturbations backward were included to assure unpredictability but were not analysed. Lower limb and trunk muscle EMG and CoP displacement were recorded from 500 ms before the perturbation onset until 1 s after. A few practice trials were allowed for each direction before measurements. After habituation, 12 perturbations forward and 12 perturbations backwards were delivered in random order, with a rest interval of 10-15

seconds between them. A longer rest interval (2 minutes) was provided after 12 perturbations to avoid fatigue effects.
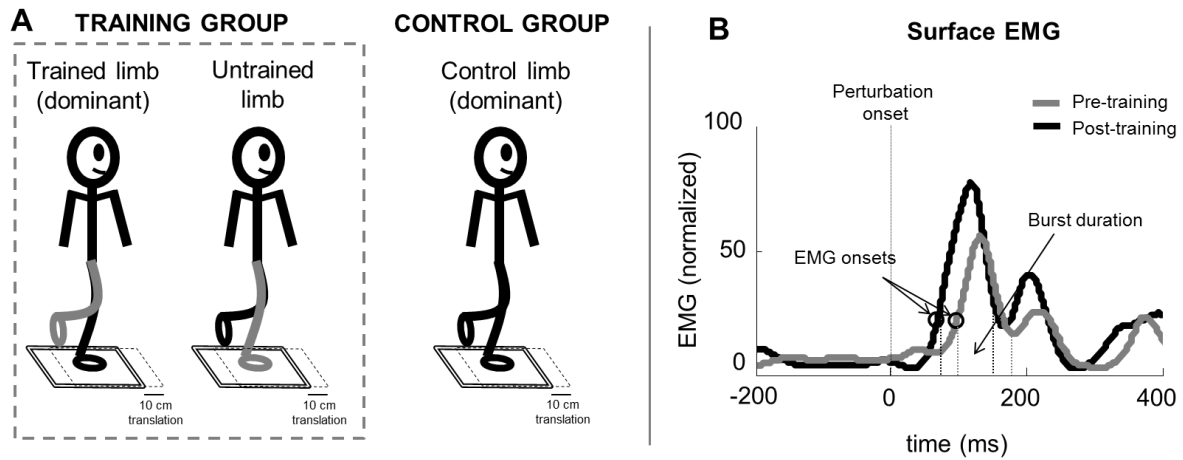
Figure 1. Illustrative experimental design. A) Subjects from the training group were tested on both trained (dominant) and untrained legs, whereas subjects from the control group were tested only in the dominant leg. The test consisted in perturbations to balance that elicited backward displacement of the center of mass (10 cm translation). B) Surface electromyography was recorded from the perturbations and the perturbation onset, as well as burst duration and other variables were calculated before (*grey*) and after balance training (*black*).

The training protocol consisted of 6 weeks of balance exercises for the right limb. There were four sessions/week (24 sessions of training of 25 minutes duration each). The exercises were based on single leg stance performed initially on the floor and progressively increasing difficulty for balance maintenance by using foam pads, dyna discs and wobble boards (see Table 1 for exercise progression). No training stimuli were allowed for the left leg during the whole training period. Subjects of the control group were asked to maintain normal daily life activities during the 6-week training program in between the two measurements.

Kinetics

A three-dimensional force platform (AMTI, OR6-5, Watertown, MA) mounted to a hydraulic system [20] provided perturbation stimuli and simultaneous measures of vertical (Fz), anterior-posterior (Fy) and medial-lateral (Fx) ground reaction forces and moments (Mx, My and Mz). Custom-made software (MrKick II, Aalborg University, Aalborg, Denmark) was used for force recordings (1024Hz). Using an electronic feedback circuit, the software triggered force plate movements. Ground reaction forces and moments were recorded and sampled by a kinematic tracking system (Qualisys Track Manager, Qualisys, Gothenburg, Sweden) at 256 Hz. Signals were digitally low-pass filtered with a 4th order

zero-lag Butterworth filter (8 Hz cut-off). Displacement of the center of pressure (CoP) was calculated as $(x,y) = (x0 + My/Fz, y0 + Mx/Fz)$, where $(x0, y0)$ was the geometrical center of the force plate. The effects of platform movements during perturbations on the forces and moments were taken into account. A series of identical platform movements (the same delivered during the experiment) were recorded with no loads over it, in order to determine the forces and moments generated only by moving the device. Subsequently, these inertial forces and moments were subtracted from the real forces and moments used to determine the CoP.

Table 1. Balance training protocol and progression. EO: eyes open, EC: eyes closed, reps: repetition, Low difficulty: a ball was caught only in front of the subject, high difficulty: a ball was caught closely or far away from the trunk, on the sides, below knee height or above head height.

Week 1 – normal floor	Week 2-3 Foam and Dyna-discs	Week 4-6 wobble board
Quiet single leg stance	*Quiet single leg stance*	*Quiet single leg stance*
3x1 min (EO)	3x1 min (EO)	3x1 min (EO)
3x1 min (EC)	3x1 min (EC)	3x1min (EC)
Single leg stance (3x1 min)	*Single leg stance (3x1 min)*	*Single leg stance (3x1 min)*
Moving head and trunk (EO)	Moving head and trunk (EO)	Moving head and trunk (EO)
Moving head and trunk (EC)	Moving head and trunk (EC)	Ankle movements (AP and ML)
Single squats	*Single squats*	*Single squats*
Eyes open (2x10 reps)	EO (3x10 reps)	EO (3x10 reps)
Eyes closed (2x10 reps)	EC (3x10 reps)	Moving head (3x10 reps)
Catching a ball while standing	*Catching a ball while standing*	*Catching a ball while standing*
Low difficulty (2x90 sec)	Low difficulty (3x90 sec)	Low difficulty (3x90 sec)
High difficulty (2x60 sec)	High difficulty (3x60 sec)	High difficulty (3x60 sec)

Electromyography

Surface EMG signals were recorded in bipolar configuration with pairs of Ag/AgCl electrodes (Ambu Neuroline 720 01-K/12; Ambu, Ballerup, Denmark) with 22 mm of center-to-center spacing. The EMG signals were amplified with a gain of 2,000 (EMG-USB, LISiN; OT Bioelettronica, Turin, Italy), A/D converted (12 bit), sampled at 2048 Hz and band-pass filtered (second-order Butterworth, 10–500 Hz). A reference electrode was placed at the right wrist. The EMG signals of the right limb were recorded from tibialis anterior (TA), rectus femoris (RF), vastus lateralis (VL) and biceps femoris (BF) according to Hermens et al.[21]. EMG signals were synchronized to the ground reaction force by the trigger signal to the perturbation onset.

CoP analysis

CoP data were analysed for each trial from the perturbation onset to 1000 ms after it, a period in which it is possible to regain stability after a similar perturbation according to Hirata et al. [22]. The following variables were analysed to evaluate postural balance: CoP maximal excursion length (CP_{LEN}) defined as the distance covered within 1000 ms. CoP speed (CP_{SPD}) defined as the average speed of the CP during the recovery period. CP_{LEN} and CP_{SPD} were calculated for both AP and ML directions.

EMG analysis

EMG signals were band-pass filtered (2nd order, zero-phase-lag Butterworth, 20 to 500 Hz), full-wave rectified, and smoothed (15Hz low-pass, 4th order, zero-phase-lag Butterworth). EMG envelopes were normalized to baseline EMG defined from a 200 ms interval preceding the perturbation for each individual trial.

Temporal aspects of EMG responses to the postural perturbation were assessed by the EMG onset (EMG_{ONS}), burst duration (EMG_{DUR}), burst magnitude (EMG_{MAG}) and time to peak EMG (EMG_{T2P}). The EMG_{ON} for each muscle was determined as the instant in time where the amplitude surpassed two standard deviations from baseline [23]. EMG_{DU} was defined as the time where EMG activity remained above the onset level within the first second after perturbations. EMG_{MA} was determined as the integrated activity during the burst divided by the burst duration, normalized by the integral from the baseline interval. EMG_{TP} was defined as the time from the EMG_{ON} to the EMG maximum level of activation. In addition, EMG approximate entropy (EMG_{ENT}) was defined as the complexity or predictability of the temporal series [24, 25] from the perturbation onset to 1000 ms after it for each muscle separately.

Statistical analysis

A 2-way repeated measures analysis of variance (RM-ANOVA) was used to analyse all CoP and EMG parameters. The first factor was the tested leg with three levels (TG right leg [trained leg, TR], TG left leg [untrained leg, UTR] and CG right leg [control leg, CTR]). The second factor was time with 2 levels (Pre-training and Post-training). The Tukey LSD test was used for post-hoc analysis when necessary. The data are presented as mean and standard deviation (SD). The significance level was set to $p < 0.05$.

RESULTS

Center of Pressure

No legs x time interaction was observed for any CoP measurements ($p>0.05$). In addition, no training effects for CP_{LEN} on both anterior-posterior and medial-lateral components were found as well as the medial-lateral CP_{SPD} for TR, UTR and CTR legs (Figure 2). On the other hand, anterior-posterior CP_{SPD} was reduced after training for TR (~35%, training effect $p<0.01$), whereas for UTR and CTR the percental changes were ~6% and ~8% respectively.
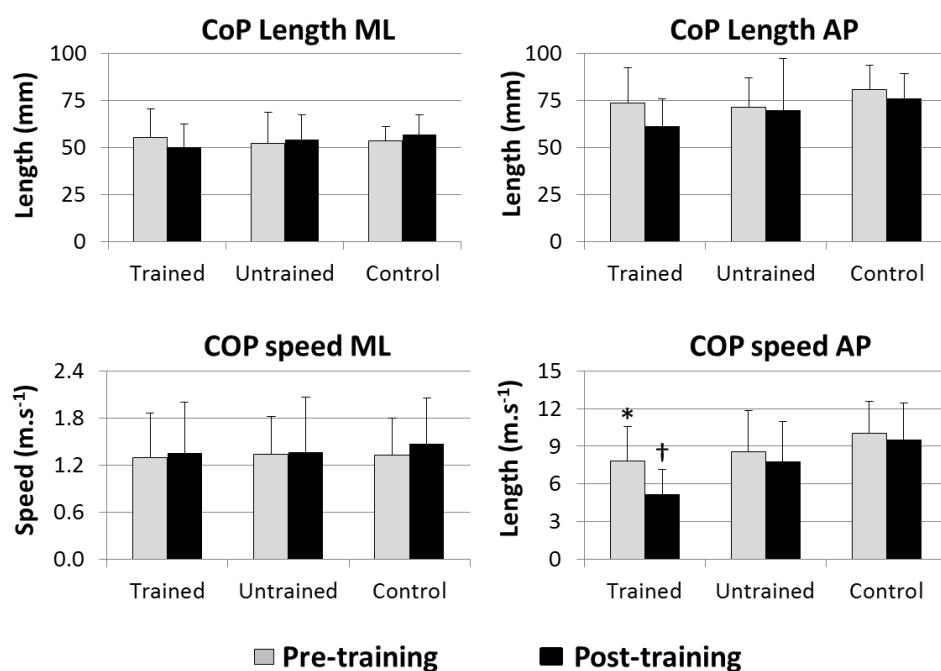

Figure 2. Mean (SD) Center of pressure (CoP) total length and average speed in the anterior-posterior (AP) and medial-lateral (ML) directions. CoP measurements were conducted for the trained and untrained leg for the trained subjects, whereas the control group was tested only the right leg (control) before training (*gray bars*) and after training (*black bars*). * denotes a significant difference in relation to post-training ($p<0.05$). † denotes significant difference in relation to untrained and control legs ($p<0.05$).

Electromyography

No main interactions (legs x time) were observed for any of the EMG variables ($p>0.05$), except for EMG_{T2P} and EMG_{ENT} ($p<0.05$). However, activity onsets (Figure 3, *left side*) were also reduced after training for all muscles in TR (~19 ms or 16%, $p<0.05$) and UTR (~17 ms or 14%, $p<0.05$) with no significant changes for CTR (percental change ~3%). EMG_{DUR} (Figure 3, *right side*) was increased for all muscles in TR (~15%, $p<0.05$) with no changes in UTR and CTR (percental change ~4%).

Burst magnitude was increased for TA and reduced for BF after training only for TR ($p<0.05$, Table 2), with no changes for UTR and CTR legs. Time to peak activity demonstrated specific changes depending on the muscle with TA and BF showing reductions (~17 ms, $p<0.01$), and RF showing an increase (~16%, $p<0.05$). In addition, TA, RF and BF muscles had a reduced EMG_{T2P} before training for the UTR ($p<0.05$). After training, EMG_{T2P} was similar among limbs (Table 2) and EMG_{ENT} showed no training effects for TR, UTR and CTR. Opposedly, UTR showed higher EMG_{ENT} in comparison to TR and CTR before and after training ($p<0.05$, Table 2).
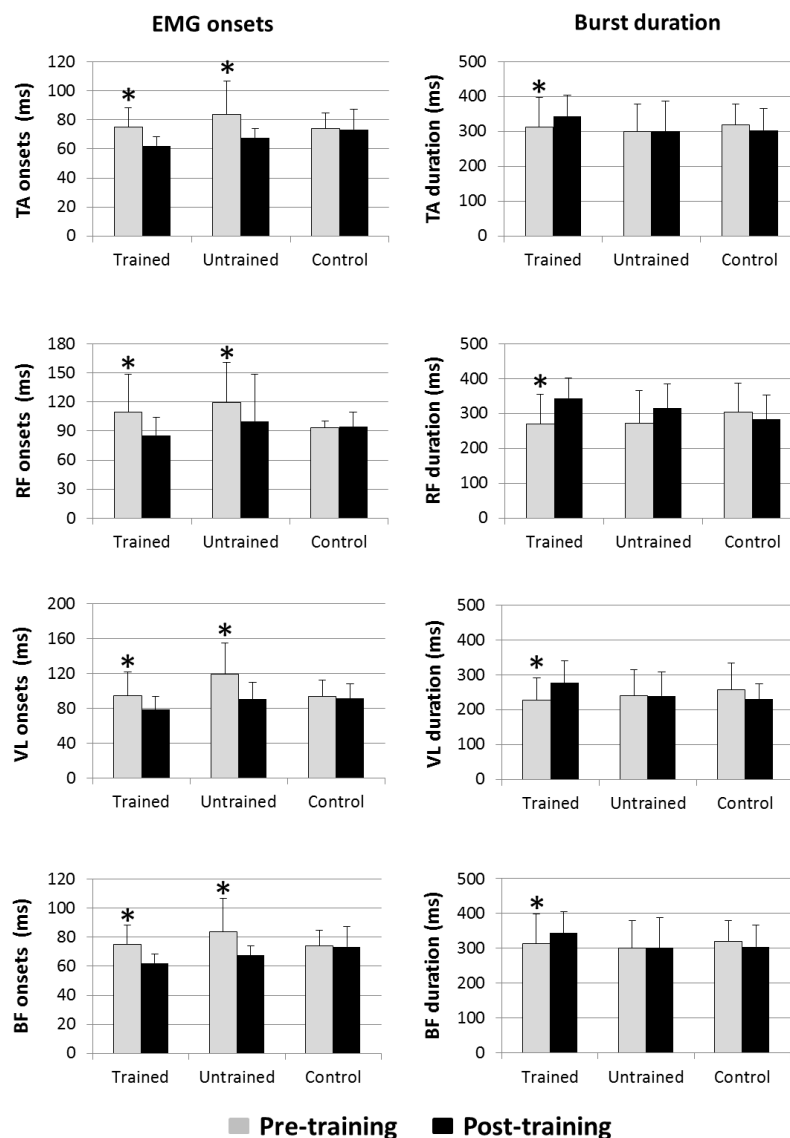
Figure 3. Mean (SD) EMG onsets and EMG burst magnitude for tibialis anterior (TA), rectus femoris (RF), vastus lateralis (VL) and biceps femoris (BF) muscles. EMG measurements were conducted for the trained leg (TR) and untrained leg (UTR) for the trained subjects, whereas the control group was tested only the right leg (CTR) before training (Pre) and after training (Post). * denotes a significant difference in relation to post-training ($p<0.05$). † denotes significant difference in relation to untrained and control legs ($p<0.05$).

108

Table 2. Mean (SD) Burst magnitude, EMG time to peak and approximate entropy extracted from tibialis anterior (TA), rectus femoris (RF), vastus lateralis (VL) and biceps femoris (BF) muscles. EMG measurements were conducted for the trained leg (TR) and untrained leg (UTR) for the trained subjects, whereas the control group was tested only the right leg (CTR) before training (Pre) and after training (Post). * denotes significant difference in relation to post-training ($p<0.05$). † denotes significant difference in relation to untrained and control legs ($p<0.05$).

	Magnitude (% baseline)			Time to Peak (ms)			Entropy (a.u)		
	TR	UTR	CTR	TR	UTR	CTR	TR	UTR	CTR
TA-Pre	993±443	879.4±446	831.4±352	88.5±16	120.3±33†	101.9±20	0.54±13	0.78±28†	0.61±12
TA-Post	1421.5±404*	1002.8±320	822±255	88.7±16	79.8±17*	89.5±18	0.54±10	0.86±22†	0.59±10
RF-Pre	349±128	367±125	349.3±135	129.8±42	143.1±50†	127.6±38	0.58±0.05	0.93±0.3†	0.57±0.07
RF-Post	310.3±72	359.1±97	324.7±79	154.7±46	109.5±64*	118±32	0.64±0.03	0.94±0.3†	0.59±0.07
VL-Pre	280.6±95	328.363	320.3±73	94.7±33	94.8±26	103.6±23	0.6±0.1	0.93±0.2†	0.55±0.1
VL-Post	305.3±76	312.7±117	302.8±61	113.1±47	100.1±26	99.2±25	0.55±0.05	0.90±0.2†	0.55±0.06
BF-Pre	761.9±415*	783.3±447	569.7±328	104.2±28	114.3±55†	110.1±41	0.55±0.1	0.77±0.2†	0.56±0.1
BF-Post	607.3±401	509.9±182	469.5±169	91.9±34	89.3±40*	96.1±36	0.57±0.2	0.66±0.1†	0.6±0.1

DISCUSSION

This study aimed at verifying whether unilateral balance training would improve balance recovery after forward perturbations in the trained limb (TR), and also on the contralateral side (UTR). Our main findings were that neuromuscular responses to perturbations were enhanced after training for both legs, while the most pronounced changes were found for TR. The UTR showed faster EMG_{ON} for all muscles and significantly reduced EMG_{T2P} for TA and BF compared to CTR. Therefore, unilateral balance training improved postural control for TR and improved initial neuromuscular responses to perturbations. These results have practical implications by demonstrating that unilateral balance training enhances recovery of balance. Moreover, these balance skills might be stimulated by a cross-education effect, leading to reduced balance loss in cases of unilateral lower limb injury. Although no interaction effects were found in the statistical analysis in some cases the relative change achieved by the training program evidently indicates adaptations for both TR and UTR legs.

Changes in CoP_{LEN} have been related to better postural control after balance training [10, 14], but no changes in this parameter were verified in the present results. However, we proposed a perturbation protocol in which the perturbation and recovery times summed were about one second, much shorter than the standing task proposed in these previous studies (30 seconds). Moreover, the proposed balance training protocol induced reduction in the CoP_{SPD} in the

anterior-posterior direction, which indicates an enhanced ability to recover balance. These improvements on CoP variables may be related to the specific constraints imposed by different surfaces (foam, dyna discs and wobble boards). The sway patterns became less complex over time, possibly improving the efficiency of postural corrections [14].

Shorter muscular onsets and longer burst duration for TR may be interpreted as positive adaptations in terms of balance recovery allowing for rapid and prolonged muscular actions to counteract balance loss. Balance training has previously been shown to be successful in enhancing muscular onsets [6, 8, 12], which may be related to the selection of appropriate postural reflexes, initiated by ankle proprioceptors [26]. An evident involvement of supraspinal pathways on postural responses has been demonstrated previously [18, 19, 26] which were reflected in increased corticospinal excitability and EEG-EMG coherence [27], and increased muscular cortical representation areas [28]. Moreover, stance stability following balance training was well correlated to decreased cortical stability, but not with spinal excitability, suggesting that the most relevant adaptations to balance training are achieved at supraspinal levels [29]. In addition, strengthening of muscles, tendons, ligaments and other connective tissues are also possible [30]. Our results for TR may be the result of the sum of all these adaptations, however literature is scarce on the effect of balance training. Therefore, further investigations are needed in order to explain neurophysiologic mechanisms of cross-education following balance training.

Reduced EMG amplitude are generally found after balance training [4, 6], which might be related to the simplification of the motor task by learning it [6]. However, it may also be caused by adaptations of cerebellar nuclei structures [26]. In the present investigation we found reduced EMG amplitude for BF muscle, but increased EMG for TA muscle in TR. This discrepancy might be related to the respective function for these muscles while recovering balance. Especially reduced EMG amplitude for BF may indicate adaptations in the agonist/antagonist relationship since there was a reduction in RF EMG (not significant).

The absence of training-related changes in EMG_{ENT} reveals that this training protocol may not be sufficient to adapt the neuromuscular system throughout automatic and voluntary phases of balance recovery. Recent investigations on balance training have found neuromuscular adaptations predominantly during early and late automatic responses (from 0 to 350ms) [5]. However, inhibition of spinal reflexes in balance tasks has also been described

as adaptation to balance training protocols, due to a higher co-activation of antagonist muscles. Therefore, it may be that adaptations related to the applied balance training are predominantly achieved by automatic responses, rather than voluntary/stabilizing strategies. Cross-education effects have been extensively studied in strength/resistance training protocols. Despite marginal contributions from peripheral/physiologic adaptation, strength training shows cross-effects by increased neural drive to the muscles, altered participation of commissural interneurons on the spinal cord, which act on the excitation/inhibition of contralateral motorneurons [15-17]. In addition, cortical adaptations mediated by interhemispheric connections via the corpus callosum might induce contralateral adaptation [15]. It is not possible to directly extrapolate adaptations from resistance training to balance training, even though, supraspinal adaptations to balance training have been reported in the literature [5, 27, 29]. In fact, a reduction in corticospinal excitability might be the main adaptation to balance training, rather than spinal adaptations, which are accompanied by improved motor performance during perturbations to balance [6, 29]. Since interhemispheric connections might induce contralateral adaptations [15], we may suggest that supraspinal adaptation could be the primary mechanism to elicit cross-education following balance training. Other adaptations such as improved attention and confidence due to training might also elicit adaptations to UTR, therefore further studies must be conducted in order to clarify the underlying mechanisms related to cross-education on balance training.

In the present investigation, cross-education effects were predominantly limited to neuromuscular properties (muscular onsets, magnitudes). The slight trends to reduced CoP_{LEN} and CoP_{SPD} may indicate limited enhancement on performance for the untrained leg. Therefore, cross-education effects occur predominantly at a neural level without requiring the execution of exercise by the limb itself for its achievement. In practical terms, the results of the present investigation suggest that neuromuscular properties of postural responses can be enhanced by a cross-education mechanism. It is not possible yet to determine whether injured patients can benefit from this cross-education effect, which could be confirmed by further studies involving injured patients.

In summary, unilateral balance training over six weeks was effective in improving neuromuscular reactions to perturbations during single-leg stance for the trained leg and to a lesser extent for the untrained leg. This suggests that balance training facilitates postural reactions when perturbations occur. The main adaptations from the trained limb about

muscular onsets were also observed in the untrained limb, accompanied by reduced EMG$_{T2P}$, which may have been acquired most likely by cortical interconnections that transfer adaptations between limbs.

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CHAPTER 6

STUDY VI

In preparation to submission

THE EFFECTS OF BALANCE TRAINING ON NEURAL STRATEGIES FOR

BALANCE RECOVERY AFTER PERTURBATIONS

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INTRODUCTION

External loading is a potential factor for injuries during sports activities. The knee joint is at high risk during landing and cutting manoeuvres. Increased loading in varus-valgus and rotational direction have been linked to knee injuries, particularly ACL ruptures since the external loading must be counteracted by internal structures (Besier et al. 2001; Cochrane et al. 2010; Lloyd 2001). The rate of lower limb injury incidence is reduced following balance training protocols, which improve dynamic stability on the knee and ankle joints (Alentorn-Geli et al. 2009; Hübscher et al. 2010; Myer et al. 2005). Balance training also enhances intermuscular co-ordination and facilitates neural drive (Aagaard 2003; Schubert et al. 2008; Oliveira et al., 2012b; Taube et al. 2007), which may be related to earlier muscle onsets and peak activations during unexpected actions (Oliveira 2012; training; (Lloyd 2001; Osborne et al. 2001). In addition, balance training may enhance hamstrings/quadriceps co-contraction by supressing stretch reflexes and stimulating the knee joint ligament and capsular receptors (Lloyd 2001).

Even though an evident reduction in injury incidence following balance training was consistently shown, there is a lack of experiments that investigate the effects of interventions on the sports gesture (Hübscher et al. 2010). Few studies have shown reduced knee loading after balance/neuromuscular training, which has been considered a positive adaptation that may reduce injury risks (Cochrane et al. 2010; Myer et al. 2005). Lower limb injuries may also be related to unpredictable changes in the environment, such as perturbations to balance and altered shoe-surface interface (Althoff et al. 2009; Hewett et al. 2006). During locomotion, perturbations to balance induce postural responses that are integrated to the ongoing motor patterns (Oliveira et al. 2012a; Oliveira et al., 2012d; van der Linden et al. 2007). Moreover, perturbations during cutting manoeuvres reduce electromyographic (EMG) activity of selected muscles on the hip and knee immediately after the perturbation event, altering joint moments and consequently it might reduce joint stability (Oliveira et al., 2012d) in the early loading phase (Zebis et al. 2009).

It has recently been suggested that complex motor gestures such as cutting manoeuvres are controlled by a few motor patterns or motor modules (Oliveira et al., 2012c), which are flexible structures in the spinal cord that generate appropriated modulation for

specific muscles when combined (Lacquaniti et al. 2012). Perturbations to locomotion have minor effects on the motor modules related to the task ((Oliveira et al. 2012) Oliveira et al., 2012d). On the other hand, the activation signals that recruit these motor modules throughout the locomotor task are substantially changed due to perturbations to walking and/or cutting manoeuvres (Oliveira et al. 2012a; Oliveira et al., 2012d; Cappellini et al. 2010). Such evidence may suggest that descending commands controlling specific muscles are influenced by the perturbation event, thus compromising the control of joint stability) during unpredictable conditions. The fact that balance training reduces injury incidence may indicate that the activation of specific muscles (i.e., pairs of antagonist muscles) during such activities is enhanced, and therefore enhanced joint stability may add protection to lower limb joints when perturbations to balance are experienced in functional tasks, such as cutting manoeuvres.

In this study, perturbations to balance while performing cutting manoeuvres were delivered before and after a 6-week balance training protocol. The main hypothesis was that balance training could be effective in enhancing postural responses to perturbations, therefore balance recovery from perturbations after training would be facilitated. The confirmation of these two hypotheses have strong practical implications about the underlying mechanisms that justify the use of balance training for injury prevention in recreational and high level athletes.

METHODS

Subjects

Twenty-three healthy men volunteered for the experiment. These subjects were randomly assigned to a training group (TG, n=13, age: 28±4 yrs; body mass: 69±8 kg; body height: 173±5 cm) or a control group (CG, n=10, age: 25±3 yrs; body mass: 72±8 kg; body height: 172±3 cm). All subjects were right-dominant as determined by a kicking test. Exclusion criteria included history of knee or ankle ligament injury, current lower-extremity injury, recent (within 6 months) low back injury, or vestibular dysfunction. All subjects provided written informed consent before participation and the procedures were approved by the ethical committee of Northern Jutland (N-20100042).
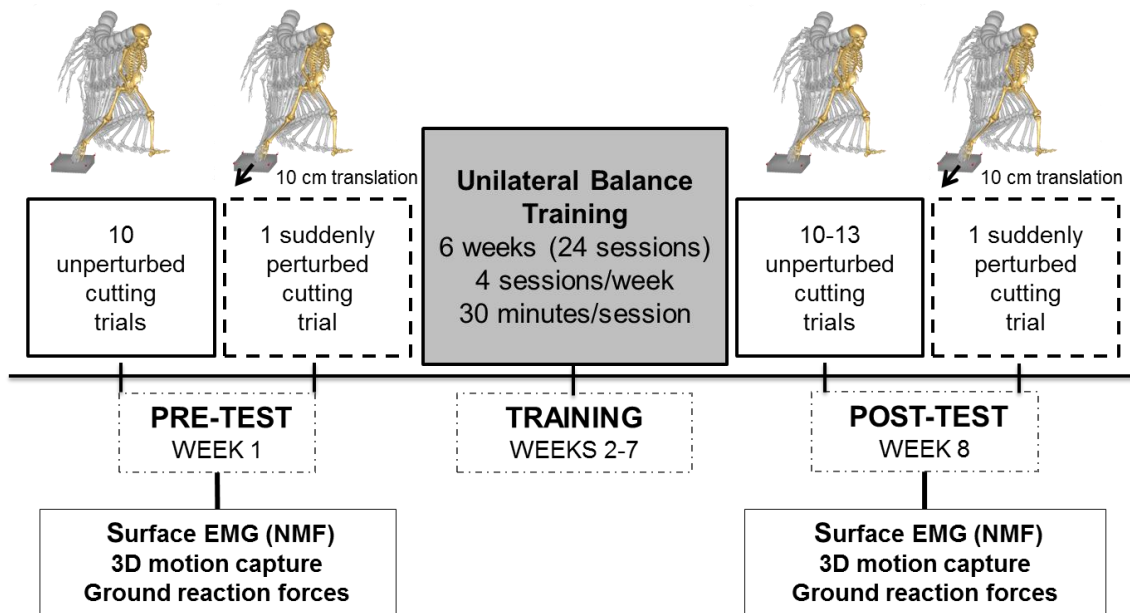
Experimental Setup

Pre-training and post-training measurements consisted in a single session, during which the subjects were asked to perform repeated 90° cutting manoeuvres. Initially, 10-15 familiarization trials were required and instructions to accelerate in a straight path towards the force platform and turn as fast as possible to the left were provided. Subsequently, 11 cutting trials were recorded with 40-60 s rest intervals between trials to exclude fatigue effects. Without any warning, a perturbation to the moveable force platform was elicited at initial contact during the 11th trial in the pre-training session. For post-training, as the subjects had already experienced the perturbation at the 11th trial, the perturbation was elicited between the 11th and the 14th trial in order to avoid anticipation. The perturbation consisted of 10 cm translation lasting 150 ms (average speed 66.6 cm/s) in the original running direction.

The training protocol consisted of six weeks of balance exercises for the right limb exclusively. A detailed description of the training protocol is provided elsewhere (Oliveira et al., 2012b). There were four sessions/week (24 sessions of training of 25 minutes duration each). The exercises were based on single leg stance performed initially on the floor and, with progressively increasing difficulty, using foam pads, dyna discs and wobble boards. Subjects of the control group were asked to maintain normal daily life activities during the 6-week training program in between the two measurements (Figure 1).

Data collection

Kinematics: Retroreflective ball-shaped markers were placed bilaterally on each side of the subject to the skin overlying the following anatomical landmarks: calcaneus, first and fifth metatarso-phalangeal joint, lateral malleolus, lateral femoral condyle; greater trochanter, anterior superior iliac spine, posterior superior iliac spine and acromion. In addition, one marker was placed on the seventh cervical vertebrae, upper and lower endpoint of sternum (suprasternal notch and xyphoid process). Extra markers were placed bilaterally on lower extremity segments: one on the thigh, four on the shank and one on the upper arm, serving as tracking markers to define the 3D motion. Marker positions were tracked with a motion analysis system with eight infrared digital video cameras (Oqus 300 series, Qualisys, Gothenburg, Sweden). The kinematic data were

117

recorded with a sampling frequency of 256 Hz and synchronized with the EMG and kinetic recordings. Subjects wore full stretch pants covering the EMG cables to avoid movement artifacts.

Figure 1. Experimental setup: Subjects first performed 10 unperturbed cutting trials, immediately followed by a perturbed cutting movement (10 cm translation in the direction of the original running). For each cutting manoeuvre, surface EMG was recorded in order to apply non-negative matrix factorization (NMF). Subsequently, subjects of the training group (TG) were assigned to a 6-week balance training, whereas subjects of the control group were asked to keep their normal activities throughout the six following weeks. Both groups were re-tested after 6 weeks.

Kinetics: The vertical (Fz), anterior-posterior (Fy) and medial-lateral (Fx) ground reaction forces and the corresponding reaction moments (Mx, My, Mz) were recorded at 1024 Hz by a force platform (AMTI, OR6-5, Watertown, MA) constructed over a hydraulic system (van Doornik and Sinkjaer 2007) Software developed on the Labview platform (MrKick II, Aalborg University, Aalborg, Denmark) was used for data recording. Using a feedback electric circuit, the Fz force also served as trigger to initiate the force plate movement.

Electromyography: Pre- and post-training surface EMG signals were recorded in bipolar derivations with pairs of Ag/AgCl electrodes (Ambu Neuroline 720 01-K/12; Ambu, Ballerup, Denmark) with 22 mm of center-to-center spacing. Prior to electrode placement the skin was shaved and lightly abraded. The EMG signals were amplified with a gain of 2,000 (EMG-USB, LISiN; OT Bioelettronica, Turin, Italy), sampled at

2,048 Hz (12 bits per sample), band-pass filtered (second-order, zero lag Butterworth, bandwidth 10–500 Hz). A reference electrode was placed on the right wrist. The EMG signals were recorded from the following muscles of the right side according to the SENIAM recommendations (Hermens et al. 2002) and previous literature (Oliveira et al. 2012a; Ivanenko et al. 2006; Aagaard et al. 2002): tibialis anterior (TA), peroneus longus (PER), soleus (SOL), gastrocnemius medialis (GM), vastus medialis (VM), vastus lateralis (VL), rectus femoris (RF), biceps femoris (BF), semitendinosus (ST), adductor muscles (ADD), gluteus medius (GME), gluteus maximus (GMA), tensor fascia latae (TFL), erector spinae at L1 (ESP), rectus abdominis (RAB) and external oblique (EOB).

3D kinematics: The body of the subjects was modeled as an interconnected chain of rigid segments: foot, shank, thigh, pelvis, trunk and arms. The trunk center of mass, joint angles and angular velocities between segments were analyzed in the AnyBody Modeling System 5.1 (Anybody Technology, Aalborg, Denmark). The left initial contact was defined from the foot kinematic data, whereas the end of the stance phase for the right leg was determined by the force plate recordings (when the vertical ground reaction force exceeded 20 N). Joint angles were calculated throughout the whole stance period for knee flexion (KA_{FL}), and abduction (KA_{AB}), as well as for hip flexion (HA_{FL}) and abduction (HA_{AB}), whereas joint moments were calculated during the weight acceptance period (Besier et al. 2003) for knee flexion (KM_{FL}), and abduction (KM_{AB}), as well as for hip flexion (HM_{FL}) and abduction ($HM_{AB)}$

Data analysis

The segmentation for EMG factorization was defined from the left initial contact prior the right foot step onto the force platform to the end of the stance phase on the force platform. After segmentation, the surface EMG signals from the 16 muscles were full-wave rectified, low-pass filtered (10 Hz) and time-normalized in order to obtain 200 data points for one gait cycle (d'Avella et al. 2003; Ivanenko et al. 2004). For each subject, non-negative matrix factorization (NMF) (d'Avella et al. 2003; Gizzi et al. 2011) was applied for each trial in order to identify motor modules and activation signals. A detailed description of the motor modules model used, calculation of dimensionality and motor modules similarities were described elsewhere (Oliveira et al. 2012a; Oliveira et al., 2012d). Briefly, after extracting the motor modules, the estimated

muscular activation pattern was compared with the recorded pattern by means of the variation accounted for (VAF) value, defined as the variation that can be explained by the model: $VAF = 1 - SSE/SST$, where SSE (sum of squared errors) is the unexplained variation and SST (total sum of squares) is the pooled variation of the data. The reconstruction quality is analyzed by plotting the VAF as a function of the number of modules, and the minimum number of modules is identified as the point in which this curve pronouncedly changes its slope (d'Avella et al. 2003). In addition to this criterion, a minimum threshold for reconstruction quality was set at VAF>0.8.

After computation of the reconstruction quality, the motor modules for each subject were extracted from the concatenation of all unperturbed trials, as well as from all perturbed trials pre- and post-training. Similarities among the different subjects were investigated for motor modules and activation signals for both unperturbed and perturbed conditions. The motor module matrices were compared by computing the scalar product between pairs of columns, normalized by the product of the norms of each column (d'Avella et al. 2003; Muceli et al. 2010; Torres-Oviedo and Ting 2007). Similarities between activation signals were quantified by the value of the cross-correlation function at zero time lag (Gizzi et al. 2011; Clark et al. 2010). In addition, the EMG activities from all subjects were concatenated for a given condition, from which motor modules were extracted to represent the whole group of subjects. In this manner, all the variability in the dataset was taken into account. From the activation signals, the peak timing (PK_{TIM}, i.e., the maximum value of the curve throughout the cutting cycle) and the burst duration (BST_{DUR}, i.e., the period in which the amplitude around the peak was higher than 50% of its peak) were also calculated.

In order to verify the effects of training on the motor modules and activation signals, similarities were computed between pre- and post- training conditions for TG and CG separately, for both single trials (for each subject separately) and concatenated signals (comprising all subjects). The effects of training and perturbations were investigated by using a 2-way repeated measures ANOVA on the following dependent variables: KA_{FL}, KA_{AB}, HA_{FL}, HA_{AB}, KM_{FL}, KM_{AB}, HM_{FL}, HM_{AB}, PK_{TIM} and BST_{DUR}. The significance level was set to $p<0.05$.

RESULTS

In general, no substantial changes were identified when comparing knee and hip joint angles (Figure 2A) and joint moments (Figure 2B) for the stance phase of perturbed and unperturbed cutting manoeuvres. The most pronounced changes on the curves are revealed for the knee flexion angles and moments. Moreover, both CG and TG essentially showed a similar pattern for the joint angle and moment curves for both perturbed and unperturbed cutting manoeuvres.
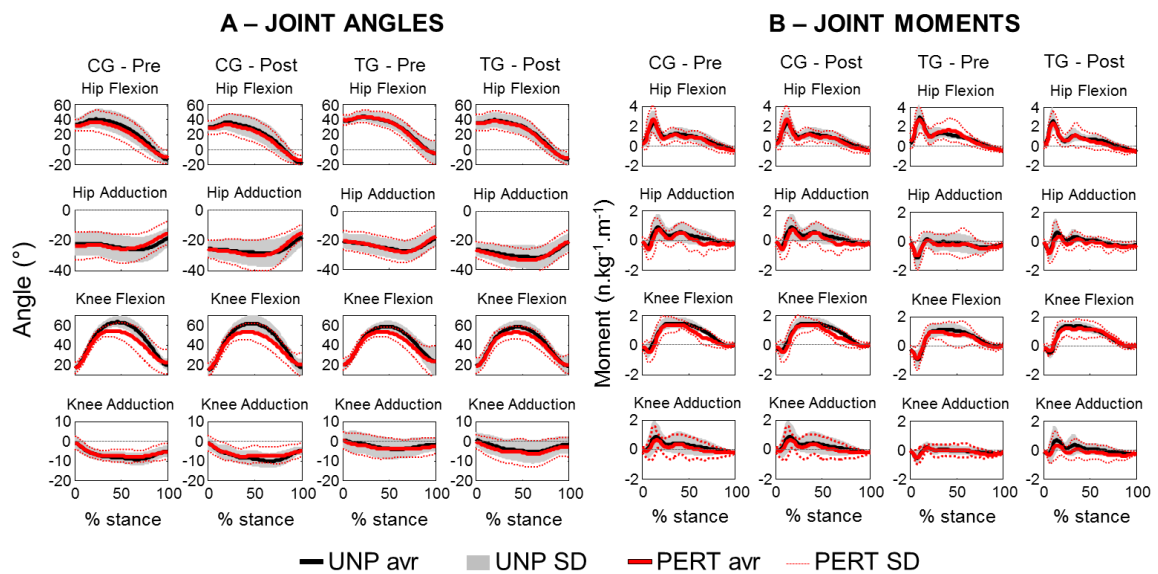

Figure 2. Joint moments of unperturbed (UNP) and perturbed (PERT) cutting movements. A) Three dimensional joint moments were extracted from the hip, knee (K) and ankle (Ank). Statistical analysis compared the peak moments during load acceptance period (B) and during propulsion period (C). avr = average; SD = ± one standard deviation.

No significant training x perturbation interaction was found for joint angles and joint moments (p>0.05). Perturbations delivered at initial contact did not influence peak hip flexion and hip adduction for both CG and TG before and after the intervention period (Figure 3, *first row*). On the other hand, perturbations reduced peak knee flexion for both CG and TG (10-20%, p<0.05), but no effects of balance training were found.

Concerning peak moments during load acceptance (Figure 3, *second row*), perturbations to balance increased hip abduction moments before training (13-21%, p<0.05), with no significant effects for hip flexion, knee flexion and knee adduction moments before training. Balance training increased knee flexion moments for both unperturbed (~53%,

p<0.05) and perturbed conditions (~36%, p<0.05) for TG, and reduced knee abduction moments under perturbed conditions (~42%, p<0.05) whereas CG varied 22% (p>0.05), with a higher variability. Furthermore, after training hip abduction moments for perturbed cutting trials were reduced in comparison to perturbations before training for TG (~32%, p<0.05), whereas CG varied ~7%.
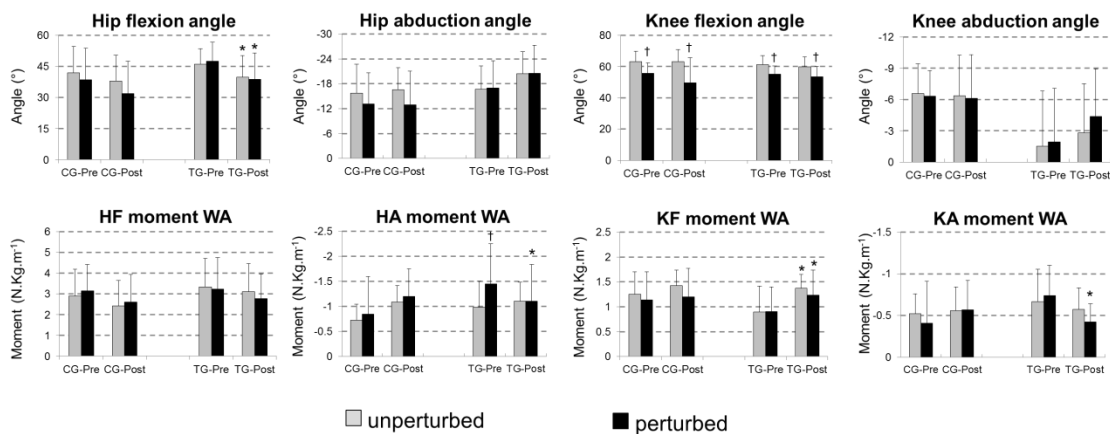
Figure 3. Mean (SD) peak angles (*first row*) and peak moments during weight acceptance (WA, *second row*). For angles and moments, flexion and adduction are shown as positive values. Angles and moments were extracted for the control group (CG) and training group (TG) before (Pre) and after 6-weeks balance training (Post) for the unperturbed (*grey bars*) and perturbed cutting manoeuvres (*black bars*). HF = hip flexion; HA = hip adduction; KF = knee flexion; KA = knee adduction. * denotes significant difference in relation to Pre (p<0.05); † denotes significant difference in relation to unperturbed cutting manoeuvres (p<0.05)

3.1. Dimensionality

The analysis of dimensionality from single trials determined that five motor modules were required to reconstruct unilateral muscular activation for both CG and TG (Figure 1). The addition of a sixth module only increased VAF by 3.9±1.0% for the unperturbed cutting task (average over all subjects from all conditions) and only by 4.7±1.8% for the perturbed cutting task. Balance training did not influence dimensionality. On the other hand, perturbations to balance slightly reduced the VAF for both groups before and after training. The dimensionality from the concatenation of all trials for each subject also indicated that five modules are sufficient to reconstruct cutting manoeuvres at reconstruction quality 0.79± 0.1 and 0.73±0.1 for perturbed and unperturbed conditions respectively.
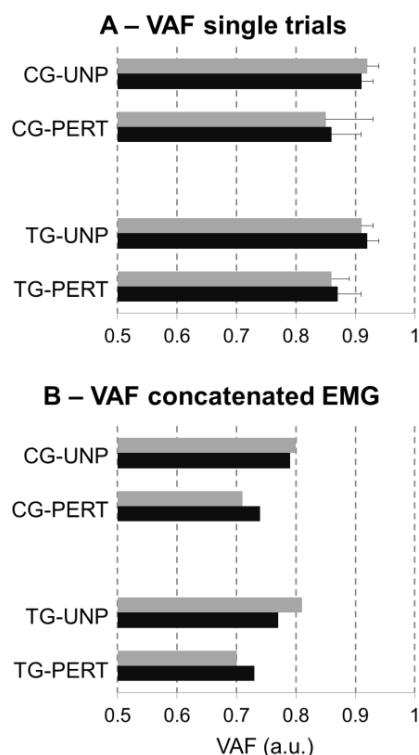
Figure 4. Variation accounted for (VAF) extracted from the factorization analysis of single trials (A) and from the concatenation of all subjects (B) of the control group (CG) and training group (TG) during unperturbed (UNP) and perturbed (PERT) cutting manoeuvres before (*grey bars*) and after 6-weeks balance training (*black bars*).

The effect of balance training on the motor modules

The five motor modules extracted before training period were compared to motor modules extracted after training by analysis of similarity for each subject (Figure 5). Unperturbed cutting tasks showed similar modules in both pre- and post-training conditions for CG (averaged similarity= 0.81±0.13 for all subjects and motor modules) and slightly lower similarity for TG (averaged similarity= 0.76±0.14). Similarities computed from the perturbed cutting task were lower in comparison to the unperturbed cutting task for CG (averaged similarity= 0.73±0.15), and TG (averaged similarity= 0.71±0.12) especially for M3 and M4 in both groups.

Concerning the motor modules extracted from the concatenation of all subjects, the control group showed averaged similarity between pre- and post-training period at 0.92±0.04 (average from all five motor modules) and 0.90±0.06 for unperturbed (Figure 3A) and perturbed trials (Figure 3B). For the TG, similarity pre- to post-training for unperturbed trials was 0.93±0.02 (Figure 3C), whereas for perturbed trials the similarity was 0.82±0.09 (Figure 3D). The reduced similarity for the motor modules was related to

the following changes in the muscle weightings: In M1, there was a reduced activation of RAB after training; In M2, there were increased weightings for the gluteus muscles (GME and GMA) and RAB after training. In M4, there were increased weightings for ADD and ESP muscles, whereas the weighting for EOB was reduced after training. The missing activation of RAB was included in M5 after training, together with an increased weighting for EOB muscle.
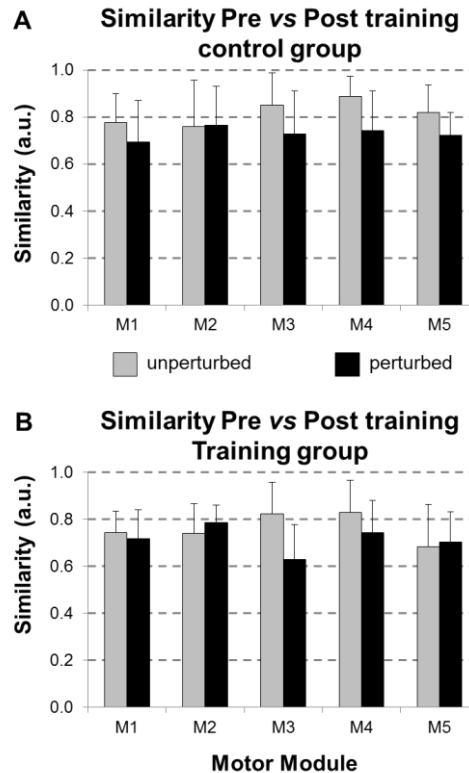
Figure 5. Mean (SD) Pre- and Post-training similarities for motor modules of the control group (A) and training group (B) from unperturbed (*grey bars*) and perturbed cutting manoeuvres (*black bars*).
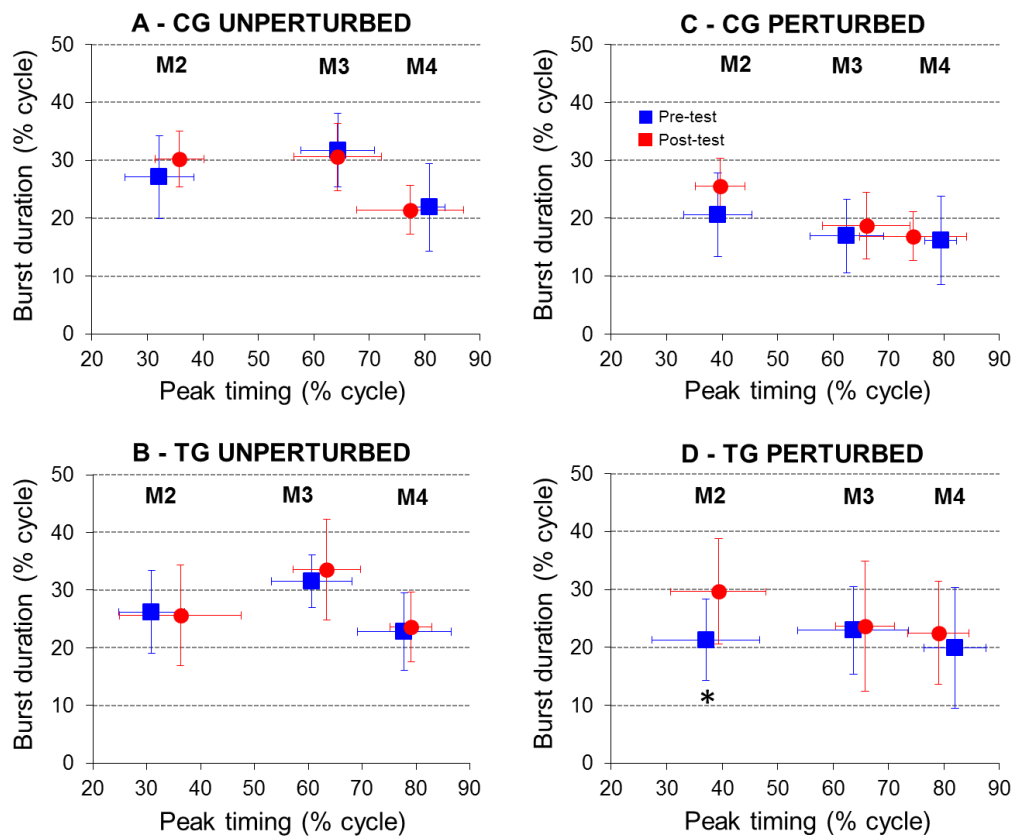
Activation signals

Analysis of variance did not reveal a significant effect of balance training on the moment of the peak activation for M2, M3 and M4 ($p > 0.05$, Figure 4), as well on the burst duration for M3 and M4 ($p > 0.05$). On the other hand, increased burst duration for M2 was found after training (~8%, $p < 0.05$), while CG did not show any significant difference.
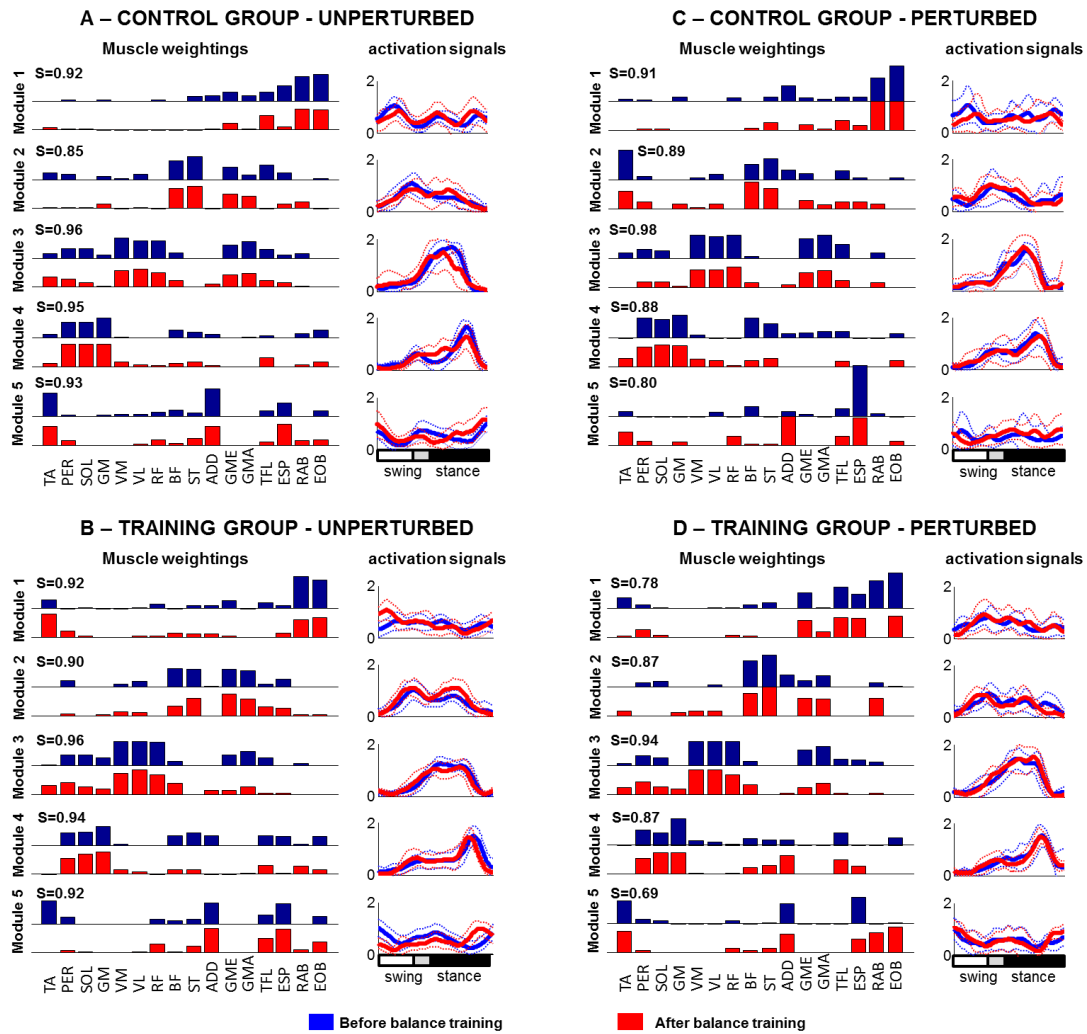
Figure 6. Motor modules (weighting coefficients) and activation signals from the concatenated EMG of control group in the unperturbed (A) and perturbed conditions (B), and for the training group in the perturbed (C) and unperturbed conditions (D). Muscle weightings from cutting manoeuvres performed before (*blue bars*) and after 6-weeks balance training (*red bars*) were compared by computing similarities ('S'value on top of each couple of muscle weightings). Mean activation signals (*thick lines*) and ± one standard deviation (*dashed lines*) respective to each motor module were plotted for the conditions before before (*blue lines*) and after 6-weeks balance training (*red lines*) throughout the entire cutting cycle.

DISCUSSION

The main findings in the present investigation were that balance training reduces external load on the hip and knee during cutting manoeuvres for both perturbed and unperturbed conditions. Moreover, balance training enhanced the activation of muscles that stabilize the trunk and hip joint during landing and propulsion when perturbations were elicited. These results suggest that balance training is effective in altering specific muscle weightings in order to improve stability under hazardous conditions such as slips while cutting.

Figure 7. Mean (SD) burst duration (Y axis) and moment of peak timing (X axis) of the activation signals from motor modules of unperturbed cutting manoeuvres for the CG (A) and the TG (B), and from the perturbed cutting manoeuvres for the CG (C) and TG (D) before (*blue*) and after 6-weeks balance training (*red*).

Prevention programs focusing on reducing injury incidence apply combinations of different exercises such as balance, plyometric, strength and trunk/core control (Alentorn-Geli et al. 2009). Therefore, it is difficult to isolate the specific effects of each modality. Previous investigations have demonstrated that balance training is more effective in reducing knee loading during cutting manoeuvres than strength-based training protocols (Cochrane et al. 2010). An appropriated knee joint stability may require strengthening of hamstrings muscles and therefore strength training program targeting this muscular group is recommended(Alentorn-Geli et al. 2009). Our results are in line with previous investigations that described reductions in knee abduction (or valgus) moment following balance training, interpreted as beneficial for joint loading.

Previous investigations have suggested that locomotion can be described by a low-dimensional set of motor modules or muscles synergies (Lacquaniti et al. 2012;

Ivanenko et al. 2004). For humans, locomotion tasks such as walking, running and also cutting manoeuvres may be controlled in a similar manner (Lacquaniti et al. 2012; Oliveira et al., 2012c), since specific biomechanical goals to perform locomotion are similar, such as initial contact and propulsion.. A recent study has shown that perturbations delivered at initial contact during cutting manoeuvres influence the activation signals related to the motor modules, but not the motor modules itself (Oliveira et al., 2012d). The authors concluded that afferent information influences the modulation of trunk/leg muscles during perturbations, as previously verified in perturbed walking (Oliveira et al. 2012a). The present investigation showed that balance training may not alter modulation of balance control during unperturbed cutting manoeuvres, suggesting that the specificity of the training is not adequate to improve the motor action. One previous investigation has shown a reduction in joint loading for cutting manoeuvres and landing following balance training (Cochrane et al. 2010). The performance of cutting manoeuvres may depend on previous experience, adequate shoes and training status (Sigward and Powers 2006; Stacoff et al. 1996). Moreover, postural stability in athletes is improved when balance training is combined with plyometrics, strength and resistance training (Alentorn-Geli et al. 2009; Paterno et al. 2004). Improvements in balance and postural stability are relevant to recreational and high-level athletes, and our results suggested that balance training may enhance postural responses to perturbations, which may occur in the practice and induce injuries even for high-level athletes.

Back and lower limb injuries are also associated with poor core stability, which is usually related to lack of optimization of the kinetic chains for upper and lower limb functions (Borghuis et al. 2008; Leetun et al. 2004; Zazulak et al. 2007b; Zazulak et al. 2007a). In addition, proprioceptive deficits in the body's core may be related to reduced neuromuscular control of the lower limbs, which may lead also to knee injuries (Leetun et al. 2004; Borg 1990). Zazulak and co-workers (Zazulak et al. 2007b) recommended that improvements in core stability may reduce injury risks on the knee for both male and female athletes. It is known that core stability precedes lower limb muscle activity in temporal sequence of athletic tasks (Hodges and Richardson 1997), therefore improvement on stability before landing may be essential to reduce injury incidence. In this way, the presented results showed that balance training have altered motor modules in order to provide better trunk/hip stability in perturbed conditions. It may be suggested

127

that the neural strategies to recruit the trunk/hip muscles during perturbations can be optmized. There was an earlier activation of RAB and a more constant activation of EOB along the perturbed period, which may assure better core stability in the perturbed conditions. Moreover, M2 showed an increased activation for hip extensors, accompanied by a longer period of activation for this module. These changes may reveal that balance training may optimize muscle activation to better accommodate the slip. In addition, the increased weighting for ADD and ESP concomitant to the reduced activation of EOB for M4 may indicate that balance training optimized trunk/hip coordination to perform propulsion after the perturbation event and therefore assuring a safer performance. The reduction in the knee abduction moment for the perturbed cutting manoeuvres for TG support these results, suggesting that balance training enhances the postural responses under unexpected conditions.

Many investigations have used balance training in order to verify whether this intervention may reduce injury risks (Caraffa et al. 1996; Osborne et al. 2001 ;Wedderkopp et al. 1999). Although valuable information is available and certainly states that these training interventions are relevant, the underlying mechanisms that explain the improvement are poorly addressed. For instance, previous investigations have concluded that balance training facilitates neural drive by investigating the H-reflex in the leg muscles before and after training (Schubert et al. 2008; Taube et al. 2007). It seems evident that balance exercises may enhance core stability, muscle onsets, inter-muscular coordination and also facilitates descending neural drive to muscles according to the literature cited previously. However, the evaluation of balance training rarely includes the practical situation. Studies on ankle sprains have been successfully imitating the injury mechanism and showed that balance training improves muscle reaction time, and therefore the joint has an improved mechanism to avoid the sprain (Dias et al. 2011; Eils and Rosenbaum 2001; Hupperets et al. 2009). In terms of cutting manoeuvres, the only intervention study that tested the motor gesture was Cochrane and co-workers (Cochrane et al. 2010), which showed reduced knee abduction moments following training. The authors speculated that after balance training the practitioners had better control of the upper body. Our results corroborate this assumption, by showing that the modular control of trunk muscles (RAB, EOB and ESP) and proximal hip muscles originated in the pelvic region (ADD, GME and GMA)

is altered. The results of this altered modular control may explain the benefits of balance training in unexpected slips while performing cutting manoeuvres.

The perturbations to balance in the present investigation were within safe margins. Therefore, a limitation of this study may be the 10 cm translation, which might not elicit substantial postural responses as it could be expected from real slips. Moreover, the cutting manoeuvres executed were not aiming to mimic ACL injury mechanisms, the results from the present investigation showed positive effects for a possible loading that is usually verified for the ACL injury mechanism, however the present results did not aimed to be linked exclusively to ACL injuries. The likelihood of muscle strains, meniscus ruptures and other non-contact injuries may also be reduced by balance training using the hypothesized mechanism. Nonetheless, future studies on modular control of complex sports activities are necessary in order to better understand the neurophysiology involved in injury mechanisms.

In conclusion, balance training is effective in reducing knee joint loads when perturbations to balance are elicited during the stance phase of cutting manoeuvres. Moreover, balance training alters the modular organization for specific motor modules related to landing and propulsion during perturbed cutting manoeuvres, enhancing postural responses for trunk/hip stability on the basis of spinal adaptations rather than supraspinal changes on descending commands.

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