Role of the trunk in the regulation of upright posture and balance

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Dedication

This thesis is dedicated to my wife, Monica, and to my sons, Noah and Quinn. Thank you for your love and support during this long process.

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Thank you to my thesis supervisor, Dr. Joyce Fung, whose guidance and wisdom has been essential to the development and completion of this work. Thank you, as well, to all the members of the Jewish Rehabilitation Hospital Research Centre for your help, support, and patience in seeing me through this project. I look forward to our continued partnership.

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Contributions of Authors

The manuscripts contained in this thesis are primarily the work of Richard Preuss, including the conception of ideas, data collection and analysis, and the preparation of these manuscripts for publication. This entire process has been conducted under the direct supervision and guidance of Dr. Joyce Fung.

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1. Abstract

1.1 English Version

Research related to the control of upright posture and balance has historically focussed on the lower extremities, often treating the trunk as a single, rigid segment. The principal objective of this work, therefore, was to characterize the response of the multi-articular trunk, in healthy individuals, to unexpected support surface translations. Three dimensional trunk motions were captured, in both standing and sitting, during horizontal support surface translations in 8 directions. A 4-segment model, consisting of pelvic, lumbar, upper and lower thoracic segments, was used for all kinematic and kinetic analyses. Electromyographic (EMG) data was simultaneously acquired, bilaterally, from 7 trunk muscles and 1 hip muscle.

Complex, multi-segmental movement was observed in the trunk. Both the biomechanical and neuromuscular responses of the trunk were significantly affected by the direction of support surface translation and by the test posture, with an interaction effect between these variables. When the time-varying properties of these descriptive variables were studied, however, two independent profiles were found to explain the majority of the variability in the original data, for each test condition, suggesting a high degree of neuromuscular coupling. Despite this, the temporal relationships in the EMG data revealed a degree of variability and asymmetry that would not be expected if the observed neuromuscular coupling resulted from the activation of fixed motor programs, such as muscle synergies.

We conclude, therefore, that the trunk behaves as a highly coordinated multi-segmental body in response to a postural perturbation. This coordination, however,

appears to be related to the interaction between the actual perturbation experienced by the trunk and the biomechanical properties of the trunk, specifically its impedance, rather than to some fixed or pre-programmed postural response, such as direct synergic muscle activation.

1.2 Version Française

La recherche liée au maintien de l'équilibre s'est historiquement concentrée sur les membres inférieurs, traitant souvent le tronc comme un segment unique et rigide. L'objectif principal de ce travail était donc, de caractériser la réponse du tronc multi-articulaire chez les individus sains, suite à un mouvement inattendu de la surface de support. Le mouvement tridimensionnel du tronc a été capturé durant les mouvements horizontaux de la surface de support dans 8 directions, en position debout et assise. Un modèle du tronc comprenant le bassin, un segment lombaire, et des segments thoraciques inférieur et supérieur, a été utilisé pour les analyses cinématiques et cinétiques. Des données électromyographiques (EMG) bilatérales de 7 muscles du tronc et d'un muscle de la hanche ont été acquises simultanément.

Des mouvements complexes et multi-segmentaires ont été observés au niveau du tronc. Les aspects biomécaniques et neuromusculaires ont été affectés par la direction du mouvement de la surface de support et par la position initiale du sujet, avec un effet d'interaction entre ces variables. Cependant, quand la variabilité temporelle de ces mesures descriptives a été examinée, deux profils indépendants expliquaient la majorité de la variabilité dans les données originales, pour chaque condition d'essai, suggérant un degré élevé de coordination neuromusculaire. Malgré ceci, les rapports temporels dans les données d'EMG n'ont pas montré d'uniformité, ni de symétrie, qui serait anticipée suite à l'activation de synergies fixes.

En conclusion, le tronc répond d’une façon coordonnée et multi-segmentaire suite à une perturbation posturale. Cependant, cette coordination est le résultat d'une interaction entre les propriétés biomécaniques du tronc, spécifiquement l’impédance, et les caractéristiques de la perturbation réelle subie, et non le résultat d’activation de programmes moteur fixes, comme des synergies musculaires.

2. Introduction

The use of surface perturbation, as a means to study balance and postural control, has been a dominant paradigm for close to 30 years (Gurfinkel et al., 1974; Nashner, 1976), providing many important insights into neuromuscular control and coordination. In the past, however, the focus of this research has been on the lower limbs, often treating the trunk as a single, rigid segment (Bothner and Jensen, 2001; Henry et al., 1998b; Horak and Nashner, 1986; Hughes et al., 1995; Runge et al., 1999). In reality, the trunk represents a complex multi-articular body, whose flexibility and mobility are essential to most of our daily tasks. In fact, tests of the passive stiffness of the trunk have shown that important deviations in trunk alignment can be achieved with relatively small bending moments (McGill et al., 1994). Furthermore, modelling studies suggest that the muscles of trunk provide only limited stiffness to the spine, above these passive levels, when standing or sitting in a relaxed upright position (Cholewicki and McGill, 1996). As such, the treatment of the trunk as a rigid body represents an oversimplification that hinders the understanding of movement and postural control.

The compliance of the trunk, described above, suggests that a perturbation of the support surface, in upright standing or sitting, is likely to produce movement in the multi-segmental trunk. In order for this movement to be controlled, a finely tuned coordination must exist between the multiple kinematic degrees of freedom in the trunk. This can only be achieved via neuromuscular coupling (Hogan, 1985). In other words, functional movements in the trunk may only be achieved via the action of the multi-articular trunk musculature, which in turn must be coordinated via the central nervous system (CNS).

As such, any movement in the trunk resulting from a perturbation to its upright posture must be met by an appropriate and coordinated neuromuscular response.

The importance of the coordinated action of the trunk musculature is most evident in patient populations with impaired motor function in the trunk. A spinal cord injury at the thoracic level, for example, may result in paresis or paralysis of the paraspinal and abdominal musculature. Among the functional impairments experienced by these patients is a loss of balance control in the seated posture (Kukke and Triolo, 2004; Potten et al., 1999; Seelen et al., 1997). Similarly, trunk control appears to be an important factor in the functional recovery of patients following a stroke (Hsieh et al., 2002; Verheyden et al., 2006; Wang et al., 2005). Trunk muscle weakness in hemiplegic patients has been specifically related to impairments in balance and postural stability (Karatas et al., 2004). More subtle impairments in the coordinated action of the trunk musculature may also be related to certain forms of mechanical low back pain (Panjabi, 2006; Preuss and Fung, 2005). These impairments, however, are believed to result in a failure to maintain the clinical stability of the individual vertebral motion segments (Panjabi, 2003), as opposed to the overall postural stability of the trunk.

The above examples serve to illustrate the importance of a more comprehensive understanding of postural control in the trunk. Specifically, a better understanding of the role of the trunk in postural control, as well as a better understanding of the coordinated action of the trunk musculature, is essential to the development of appropriate, evidence based therapies for a wide range of neurological and musculoskeletal conditions. Due to the current lack of literature related to the role of the trunk in the regulation of upright posture and balance, it is important that we first understand the fundamental control mechanisms by studying healthy individuals.

2.1 Rationale

Surface perturbation has been well accepted as a paradigm for the study of postural reactions and balance. The conventional focus on investigating responses from only the lower extremities has, however, limited our knowledge of the role of the trunk in these processes. Three main issues have been identified that have contributed to this gap in the literature:

1) Most previous studies evaluating the maintenance of upright posture and balance have modelled the trunk as a single rigid segment, extending from the hips to the shoulders. This has precluded an evaluation of the kinematics and kinetics of the trunk during the postural response.
2) While several previous studies have included certain trunk muscles in their assessment of the postural response following surface perturbation, the number of trunk muscles assessed has typically been quite restricted.
3) Most previous studies have focussed on either the neuromuscular response or the mechanical response to surface perturbation. As neuromuscular control cannot function independently of the biomechanical properties of the system, however, myoelectric activity must be evaluated with respect to the coincident kinetics and kinematics of the system in order to be fully interpreted.

2.2 Objectives

Principal Objective

The principal objective of this work is to characterize the neuromuscular, kinematic and kinetic response of the trunk to unexpected, multi-directional support surface translations. We aim to provide a quantitative description of the individual activation patterns for the superficial trunk musculature, as well as the segmental and inter-segmental motion patterns in the trunk based on a multi-segmental linked segment model. Statistical pattern analyses will then be conducted in an effort to uncover the dimensionality of the neuromuscular coupling (inferred from the level of inter-muscular and inter-segmental coordination) underlying these postural responses, as well as the means by which this coordination might be achieved.

The body of this thesis work (Chapters 3-5) is presented in manuscript format, and is divided into three chapters; each representing a step toward realizing the principal objective above. The specific objectives of each chapter are as follows:

Chapter 3

Musculature and biomechanics of the trunk in the maintenance of upright posture.

The purpose of this first chapter is to provide a comprehensive description of the neuromuscular, kinematic and kinetic response in the trunk following support surface translation, using a multi-segmental model of the trunk. The focus will be on how the response is affected by the direction of support surface translation and the initial posture of the subject. For the latter, the specific focus will be on the effect of the inclusion or exclusion of limb dynamics, by testing subjects in both a standing and a sitting posture.

This manuscript is currently in press at the Journal of Electromyography and Kinesiology (Preuss and Fung, 2007), and with the exception of certain formatting changes (figure, table and section numbers), it is presented in the same format in which it will be published.

Chapter 4

Neuromuscular coupling in the control of trunk upright equilibrium.

The purpose of this second chapter is to determine the dimensionality of the neuromuscular and biomechanical descriptors of trunk motion following support surface translation. From the dimensionality of the EMG data, we can directly infer the degree of neuromuscular coupling imposed by the CNS. The dimensionality of the biomechanical data, on the other hand, can be interpreted as indirect evidence of the same neuromuscular coupling, as the mechanical behaviour of the system can only be coordinated by the combined action of the musculature and nervous system.

This manuscript is currently under review at the Journal of Physiology (London). With the exception of certain formatting changes (figure, table and section numbers), this chapter is presented in the same format in which it has been submitted for publication.

Chapter 5

Are fixed muscle synergies used in the control of upright trunk equilibrium?

The purpose of this third chapter is to determine if one or more fixed spatio-temporal relationships exists in the electromyographic (EMG) signals acquired from the muscles of the trunk following support surface translation. The existence of such a relationship could be used to infer the use of fixed, time-varying muscle synergies by the CNS to coordinate the muscular response in the trunk. These muscle synergies have been defined as fixed motor programs, which can be independently scaled in amplitude and shifted in time, resulting in the coordinated activation of groups of muscles with specific time-varying profiles (d'Avella et al., 2003).

It is our intention to submit this manuscript following the publication of the second manuscript in this thesis (Chapter 4). The submission of the article as been delayed only because the interpretation of these results relies heavily on the information provided in the previous two manuscripts, the second of which is not currently available to any potential reviewers. With the exception of certain formatting changes (figure, table and section numbers), however, this chapter is presented in the same format in which we intend to submit it for publication.

2.3 Background and Significance

2.3.1 Postural control following support surface perturbation

Support surface perturbations have been used as a means to study the control of upright balance and posture for over 30 years, with many of the early studies intended to determine the functional role of stretch reflexes at the ankle (Gurfinkel et al., 1974; Nashner, 1976). It quickly became evident, however, that the neuromuscular response following surface perturbation represents a much more complex combination of neurophysiological entities, influenced by a wide range of environmental and cognitive factors.

The role of higher centres in the central nervous system (CNS)

Central influences are most evident in the effect that variables which are not directly related to the perturbation itself may have on the resulting postural response (Horak, 1996). Prior experience with a specific task, or the expectation of a specific stimulus, will influence the postural response following perturbation. The intention of the subject (based, for example, on specific instructions on how to respond to the perturbation) may also influence the postural response to perturbation, although these effects typically become evident only after the postural response has been initiated.

One means by which higher centres in the CNS are thought to influence the control of upright posture is through descending synaptic modulation of spinal reflex pathways. The gain of the soleus stretch reflex (inferred from the amplitude of an electrically elicited H-reflex), for example, is known to be modulated by the CNS based on a change in subject posture or task. Examples include a shift from prone lying to standing (Koceja et al., 1995), and from standing to walking (Capaday and Stein, 1986).

The degree of disynaptic reciprocal inhibition between the soleus and tibialis anterior muscles also appears to be modulated by the postural condition, as well as by the level of voluntary co-activation of these muscles (Nielsen and Kagamihara, 1992), with the former based on observed differences between the sitting and standing postures, and between standing on a stable surface and an unstable surface. Such a coordinated modulation of reflex gain serves to illustrate the importance of neuromuscular coupling at even the most fundamental reflex level. This central modulation of length-dependent spinal pathways, for example, may aid to facilitate their role in increasing joint impedance above the level provided by voluntary co-activation of the musculature (Nichols, 2002).

Within the higher centres of the CNS, the cerebellum is known to play a role in the modulation of postural responses. Specifically, the cerebellum appears to be necessary for tuning the magnitude of the postural response based on experience. Patients with anterior cerebellar lobe lesions have been found to consistently demonstrate hypermetric responses to repeated support surface translation (Horak and Diener, 1994). Furthermore, when the perturbation amplitude was changed, these patients showed no adaptation in their postural response, even when this new perturbation condition was repeated multiple times. This inability to modulate the amplitude of the postural response may be related to the role of the cerebellum in modulating the gain of spinal reflex pathways, based on the postural condition. This has been demonstrated in patients with a general degeneration of the cerebellum and its connecting fibres (spino-cerebellar degeneration), with respect to the modulation of the soleus H-reflex (Tokuda et al., 1991).

The basal ganglia represent another centre in the CNS with a role in the modulation of postural control. Specifically, the basal ganglia are believed to play a role adapting postural strategies to changes in environmental conditions (Horak et al., 1996; Horak and Macpherson, 1996), prior to exposure to any perturbation. The ability to regulate tonic, background levels of postural tone, for example, may be impaired in Parkinsonian patients. This, in turn, may impair these patients' ability to rapidly generate appropriate levels of force in response to a postural perturbation (Horak et al., 1996).

Other higher centres may also be involved in postural control, but this role is somewhat less clear. The fact that the intended response of the subject may be able to shape the response to postural perturbation (Horak, 1996) implies an interaction between the descending commands related to voluntary movement and the reflex action initiated by peripheral stimuli (defined as coordinated, but involuntary muscle activation patterns: Pearson and Gordon, 2000, pg.735). Animal models have shown a role for the main corticospinal tract in the down-modulation of the H-reflex (Wolpaw, 1997). Some evidence also exists for changes in somatosensory evoked potentials, in the sensorimotor cortex, occurring with H-reflex conditioning (Wolpaw and Dowman, 1988).

Sensory integration for postural control

Evidence of a role for the sensorimotor cortex in postural control is supported by the fact that functional control of posture must occur within the context of the external environment. As such, sensory integration is essential, as it provides a means for the CNS to acquire the necessary information about the environment. This sensory information comes from at least three sources: vision, the vestibular system, and the somatosensory system (Horak et al., 1990). These multiple sensory inputs must then be integrated by the CNS to provide the information necessary to predict the effect of a given action (Bernstein, 1967), and to react in an appropriate manner to a given stimulus.

Visual input is known to have an impact on postural control and sway, by providing information related to position and motion within the environment (Horak and Macpherson, 1996). As the visual system has no direct communication with the descending tracts of the spinal cord (Hendelman, 2006), however, visual feedback must be integrated by the higher centres of the CNS. The impact of a loss of visual feedback is most evident when proprioceptive feedback is limited, as in lower limb amputees (Dornan et al., 1978), or altered, as with tendon vibration (Hay et al., 1996). As such, visual information may aid to reinforce any proprioceptive feedback that is available, and to correct (if only partially) any perceived inaccuracies in that feedback. It has therefore been suggested that visual information may be used to calibrate the spinal pathways mediated by proprioceptive feedback, particularly for novel tasks and conditions (Horak and Macpherson, 1996).

Vestibular feedback has a somewhat more direct impact on postural control, via the descending vestibulo-spinal tracts (Hendelman, 2006), and the vestibulo-spinal reflexes (Jones, 2000). The primary function of the vestibular response, however, is to stabilize the head in space (Jones, 2000). As such, while vestibular feedback has a role in modulating the postural response in the lower extremities and trunk following support surface perturbation, it does not appear to be a primary role (Horak et al., 1990; Horak et al., 1994). Differences between patients with vestibular loss and healthy subjects, following posterior support surface translations, were primarily related to the ongoing tonic muscle activation that followed the initial muscle bursts (Horak et al., 1994). As such, it cannot be said that these differences were not related to attempts to stabilize the head in space, rather than to maintain the postural equilibrium of the body as a whole.

Somatosensory feedback, and in particular proprioceptive feedback from muscles (Diener et al., 1984), appears to be the most important source of feedback related to postural control. Following support surface perturbation, proprioceptive feedback from multiple segmental levels is necessary to explain the timing of the combined neuromuscular response (Allum et al., 1995; Bloem et al., 2000; Henry et al., 1998a). Furthermore, the inter-muscular spinal pathways associated with muscles spindles and Golgi tendon organs provide the necessary neural architecture to support the functional neuromuscular coupling required for postural regulation and coordinated movement (Nichols, 1994). Proprioceptive feedback, therefore, is the main source of feedback mechanism through which the biomechanical and neuromuscular aspects of postural control and movement control may be directly linked (Hogan, 1985; Nichols, 1994).

The role of biomechanical factors

When using support surface translations to study postural control, it has been observed that factors related to the perturbation itself (such as direction, velocity, and amplitude), as well as factors affecting the subject's mechanical interaction with the support surface (such as the subject's initial posture and the surface configuration) all influence the postural response to perturbation (Brown et al., 2001; Diener et al., 1988; Henry et al., 1998a; Henry et al., 2001; Horak, 1996; Inglis et al., 1994; Runge et al., 1999). This serves to illustrate two points. The first is related to the importance of accurate and ongoing sensory feedback; a fact which has been widely recognized in the literature (Allum et al., 1998; Allum and Honegger, 1998; Bloem et al., 2002; Diener et al., 1988; Inglis et al., 1994). The second, and less acknowledged point, is that the postural response represents a mechanical interaction between an external perturbing force (movement of the support surface) and the biomechanical properties of the body.

Kuo and Zajac (1993) used a simple, 4-segment model of the body to demonstrate that biomechanical properties will greatly constrain the number of feasible kinematic patterns that may result from a postural perturbation. This analysis suggested that the "hip strategy" and "ankle strategy" (Horak and Nashner, 1986), often described following forward and backward support surface translations, may be determined largely by biomechanical constraints. Similarly, differences in the postural responses associated with the direction of support surface translation (Henry et al., 1998b), and stance width (Henry et al., 2001), are largely influenced by the biomechanical constraints of the body.

An analysis of the kinetics of the postural response also suggests that variables unrelated to muscular forces strongly influence the motion that follows a support surface translation (Bothner and Jensen, 2001). The neuromuscular response to postural perturbation may, in fact, be regarded as a means of dynamically regulating the biomechanical properties of the body (Hogan, 1985), as the concepts of stability and equilibrium are themselves related to the mechanics of the system.

Trunk kinematics and kinetics following support surface perturbation

The vast majority of studies evaluating postural control following support surface perturbation have modeled the trunk as a single, rigid segment (Bothner and Jensen, 2001; Henry et al., 1998b; Horak and Nashner, 1986; Hughes et al., 1995; Runge et al., 1999). Others have monitored trunk movement based on the position of a single reference point (Bloem et al., 2000; Carpenter et al., 1999; Huang et al., 2001). These data present obvious limitations, particularly with respect to the interpretation of the EMG activity of the trunk musculature.

Those few studies that have attempted to monitor the motion of the trunk as a multi-segmental body have found that this assumption of trunk rigidity is not valid. Forssberg and Hirschfeld (1994) monitored trunk motion in the sagittal plane, using reflective markers placed over the C7, T10 and L5 spinous processes, during support surface rotation and translation in long sitting. Although the results of this approach to modelling the kinematics of the trunk were limited, these authors observed that the trunk did not behave as a rigid body rotating about the hips.

Some attempts have been made to model the pelvis separately from the rest of the trunk during support surface translation (Jones et al., 2004), but the published results of these trials are, to date, quite limited. Similar models have also been used to study tasks such as lifting (Lariviere and Gagnon, 1998; 1999b) and gait (Callaghan et al., 1999). One series of studies was found in which the trunk was modelled as a multi-segmental body (Crosbie et al., 1997a; 1997b), for the purposes of assessing spine kinematic during gait. For each of these studies, the results imply that the treatment of the trunk as a single, rigid body is not valid.

Trunk EMG following support surface perturbation

Several previous studies have acquired EMG data from various trunk muscles following support surface perturbation (Henry et al., 1998a; Huang et al., 2001; Keshner et al., 1988; Runge et al., 1999). Although these data cannot be fully interpreted due to the lack of information regarding any coincident inter-segmental motion in the trunk, they do provide some insight into the neuromuscular behaviour of the trunk.

One consistent observation from these studies is that the onset of muscle activity in the trunk, following support surface perturbation in standing, tends to be very rapid (often <100ms) (Henry et al., 1998a; Keshner et al., 1988; Runge et al., 1999), even when proprioceptive information from the lower extremities is limited (Bloem et al., 2000). This suggests that the initial modulation of the neuromuscular activity in the trunk is in response to a local stimulus, and not simply a component of a pre-programmed response strategy initiated from below.

Studies of multi-directional perturbations in both standing (Henry et al., 1998a) and sitting (Zedka et al., 1998) have also found that trunk muscle activation will differ based on the direction of the support surface perturbation. Despite the lack of coincident kinematic data, the muscular activation in the trunk did not appear to be limited to only those muscles which might be stretched by the perturbation. Furthermore, the trunk muscles tested were often highly active for more than one direction of perturbation, and with different latencies of onset. This apparent neuromuscular coupling in the trunk is not surprising, given that muscle co-activation may be observed, in the upper extremity, even under isometric conditions (Flanders and Soechting, 1990). Achieving such coupling in the multi-articular trunk, however, represents a somewhat different challenge, due to the greater number of kinematic degrees of freedom, but the more constrained range of motion of the trunk relative to the upper limb. In addition to controlling the overall postural equilibrium of the trunk, the neuromuscular response must also modulate specific mechanical variables, such as impedance (Hogan, 1985), across all trunk levels (McGill and Cholewicki, 2001).

The postural response in the trunk also appears to be tied to external mechanical parameters other than perturbation direction. Specifically, with posterior support surface translations at different velocities, certain trunk muscles were only found to activate at the higher velocities (Runge et al., 1999). The authors of this study suggested that this threshold may mark the point at which trunk motion becomes important to the restoration of balance and equilibrium. Given that the "threshold" velocity for muscle activation differed between subjects, however, it is possible that this perturbation parameter simply marked the point at which the passive stiffness of the trunk was inadequate to account for the inter-segmental motion induced by the perturbation (i.e. indicative of an interaction between the internal and external mechanical parameters). It is important to note, however, that these two concepts are not mutually exclusive. Unfortunately, a complete interpretation of these findings is not possible, as the trunk was modelled as a single, rigid segment.

2.3.2 Theories of Motor Control and Neuromuscular Coupling

In order to produce functional movement in a multi-segmental system, a degree of coordination must exist between the individual kinematic degrees of freedom. The architecture of the musculoskeletal system, and in particular the presence of multi-articular muscles, provides the necessary mechanical coupling between the joints (Hogan, 1985). It is the extensive neural connections between those muscles, however, that provides a means to coordinate their actions (Nichols, 1994). This coordinated activation of the musculature, mediated by the CNS, may be referred to as neuromuscular coupling. The means by which this neuromuscular coupling is achieved is at the heart of most modern theories of motor control.

Motor control theories dealing with neuromuscular coupling can be divided into two general categories. The first category includes those theories which state that coordinated muscle activation is the direct result of CNS control. In other words, muscle activation is explicitly controlled by the CNS. The second category includes theories in which the CNS does not directly control muscle activation, but instead modifies certain specific parameters which completely define the desired state of the system. Muscle activation is then one of the implicit results of the difference between that desired state and the actual state of the system within its environment.

Although it is beyond the scope of this literature review to discuss the details of each specific theory, two widely debated versions of these two theories are outlined below.

Muscle synergies

Muscle synergies do not have a single, consistent definition in the literature. The general idea underlying this theory of motor control, however, is that movement and posture are controlled by the CNS through explicit activation of specific groups of muscles, or muscle synergies (Saltiel et al., 2001). The flexibility of the neuromuscular coupling achieved by this method stems from the assertion that a large variety of coordinated muscle activation patterns may be achieved by combining a much smaller number of functional synergies (d'Avella et al., 2003; Ting and Macpherson, 2005).

Support for this theory comes from several sources, and from several experimental approaches. A recent series of studies, which has been used to advance the theory of muscle synergies, examined the EMG activity in the hind limb of the frog under a wide range of conditions (d'Avella et al., 2003; Saltiel et al., 2001; Tresch et al., 1999). Under each condition, statistical pattern analyses found that the observed muscle activation could be explained by a combination of a small number of discrete elements. The conclusion was that muscle activation results from the combined activation of one or more time-varying synergies. Furthermore, it was suggested that the activation of each synergy could be independently scaled in amplitude and shifted in time, in order to provide the flexibility required for each task.

Holdefer and Miller (2003) used a similar approach with primates during targeted reaching tasks of the upper limb, while simultaneously recording the neuronal activity in the primary motor cortex (arm area). Using cluster analysis and principal component analysis (PCA), these authors reached a similar conclusion regarding the correlation between the neuronal activation and the EMG patterns: "the system is organized around a relatively small number of synergistic groups of muscles" (pg. 242).

The concept of synergic muscle activation has also been implied in other theories related to the control of movement. Rhythmic movements such as locomotion, for example, have been hypothesized to originate from the activation of central pattern generators (CPG) in the spinal cord (Pearson, 2000). With respect to postural control, a theory that is still widely held in the clinical literature (e.g. Shumway-Cook and Woollacott, 1995) is that postural responses may result from a combination of two distinct strategies (the hip and ankle strategies) in different magnitudes and temporal relations (Horak and Nashner, 1986), thereby producing a continuum of potential responses. Statistical analyses have also been used to support the existence of muscle synergies in the maintenance of upright balance in both cats (Ting and Macpherson, 2005; Torres-Oviedo et al., 2006) and humans (Torres-Oviedo and Ting, 2006).

Variations on the equilibrium point hypothesis

The equilibrium point (EP) hypothesis has been expressed in many forms in the literature. In general, this hypothesis states that motor control can be achieved by specifying the point at which the system will be in a state of equilibrium within its environment, with movement achieved by moving that equilibrium point along specified virtual trajectories. One approach suggests that this control is achieved by explicitly setting muscle activations that define the equilibrium position (e.g. Otten, 2005). Another approach suggests that muscle activation is the implicit result of the mechanical interaction of the system about the specified equilibrium point.

A prominent theory within this second approach to the EP hypothesis is the lambda model of motor control (Adamovich et al., 1997; Feldman et al., 1998b; Tresilian, 1999). This model states that a limited number of specific parameters are needed to fully define the behaviour of any system within its environment (i.e. to set the EP of the system) (Feldman et al., 2004). Control of the system can then be achieved by modifying these system parameters. As such, these parameters (control variables) represent the only variables which must be explicitly controlled by the CNS, and are independent of the variables which describe the actual state of the system (the state variables), such as the kinematic and kinetic variables which describe motion. As such, any variable which cannot be changed independently of the state variables cannot be a control variable (Feldman et al., 2004). The relationship between muscle activation and muscle force, therefore, suggests that muscle activation is not a control variable, but is an implicit result of the interaction of the system with its environment, based on the difference between the EP of the system and its actual position.

The primary control variables in the lambda model are length-dependent muscle activation thresholds (λ^*), physiologically represented by the threshold potential of the α-motorneuron (Tresilian, 1999). The effective muscle threshold length (λ^*) is defined as: $\lambda - \mu\, dx/dt + \rho$, where only the λ component is centrally modulated. This centrally modulated λ depends on the influences of different descending systems projecting primarily (but not exclusively) to α-motorneurons. The time-dimensional parameter μ characterizes the dependency of the threshold on the velocity of muscle lengthening (effectively a damping parameter). The variable ρ reflects the influence on the muscle by the proprioceptive afferents of other muscles (i.e. inter-muscular feedback, including reciprocal inhibitory pathways), as well as other physiological systems, including Renshaw cells, γ-motorneurons, and descending central inputs to interneurons mediating mechanoreceptors in muscle, skin, etcetera (Adamovich et al., 1997). An increase in muscle activation is initiated when the difference between the actual (x) and the threshold (λ^*) length of the muscle becomes non-negative: $x - \lambda^* \geq 0$. This matching is hypothesized to occur at the level of the motorneuron membrane, when the postsynaptic potential exceeds the threshold potential of the motorneuron (Adamovich et al., 1997).

Muscle activation in the λ-model, therefore, depends on both central and peripheral/proprioceptive influences to determine the threshold length of each muscle, made possible by the convergence of descending and reflex pathways on common interneurons and motorneurons (Adamovich et al., 1997).

Globally, the configuration of the body at which all skeletal muscles may reach their individual activation thresholds has been described as the referent configuration of the body (St-Onge and Feldman, 2004). Global muscle activity is then determined by the comparison of this referent configuration with the actual configuration of the body.

Other models have taken a somewhat different approach to the EP hypothesis, focussing more closely on the biomechanical variables which must be controlled, rather than the physiological means by which this control may occur. Hogan (1985), for example, has suggested that the control of multi-joint posture and movement may be achieved by modulating the impedance (or inversely, the admittance) of the musculoskeletal system. The control of impedance (specifically stiffness and viscosity) is based around the observation that individual muscles, under most conditions, behave in a "spring-like" manner (i.e. there exists a relationship between displacement and force output) (Nichols, 2002), resulting in a spring-like behaviour for the multi-joint limb (Hogan, 1985). As this mechanical behaviour is due more to the action of spinal pathways than to the intrinsic properties of the muscle (Nichols, 2002), it can be controlled by the CNS. Furthermore, a degree of control over the net inertial properties of the system (another aspect of mechanical impedance) may also be achieved by modifying the geometry of the multi-articular system (Hogan, 1985). Together, the modulation of these mechanical properties can define an equilibrium position for the body.

Overlap between theories

Despite the debates that have brewed in the literature regarding the validity of these theories (Gottlieb, 1998; Ostry and Feldman, 2003; Tresilian, 1999), it is interesting to note how much of the experimental evidence for each could equally be interpreted as evidence for the other. Loeb et al. (2000) studied the force fields produced by individual muscles in the frog hind limb: i.e. the force vectors produced by contraction of each muscle at different points in the workspace. These force fields were then combined to predict the limb stabilization potential for different patterns of combined muscle activity. They found that specific muscle combinations existed which would stabilize the limb at predictable locations within the workspace, similar to those evoked by micro-stimulation of the inter-neuronal areas of the frog spinal cord. In other words, the synergic activity of specific groups of muscles (interpreted as muscle synergies) acted to stabilize the limb about a predictable equilibrium point. What remains unclear from this experiment, however, is if stimulation of the frog spinal cord leads to muscle activation, which in turn defines the EP; or if stimulation of the spinal cord defines the EP, which then results in the necessary muscle activation to move toward that EP.

Similarly, experimental correlates between cell activity in the CNS and specific variables describing the behaviour of the system, such as EMG activity (Holdefer and Miller, 2003) or movement direction (Georgopoulos, 1991), may also not represent an explicit link between the recorded CNS activity and the event being monitored (EMG, kinematics, etcetera). As such many of these experimental findings could equally be used to support both of the theories of motor control described above.

A similar potential for overlap can be seen in studies related to postural control. One example is the concept of "central set", which has been used to explain the influences of higher CNS centres on postural responses (outlined in section 2.3.1). Central set, as defined in the literature, refers to the feed-forward modulation of automatic postural reactions (i.e. triggered synergic activity, such as the ankle and hip strategy) based on an expectation of the stimulus and task characteristics (Horak et al., 1996; Horak, 1996; Horak and Diener, 1994; Horak and Macpherson, 1996). The observations on which the concept of central set is based, however, could be equally accounted for by a modulation of the reflex threshold parameters which determine the behaviour of the system about its equilibrium position (Adamovich et al., 1997), without the need for pre-programmed postural strategies.

2.3.3 Kinematic and muscular redundancy

Kinematic redundancy - Bernstein's problem

The problem of kinematic redundancy (often referred to as Bernstein's problem; e.g. Partridge, 1986) is frequently expressed in the perception that the multi-articulated nature of the body may provide more kinematic degrees of freedom than are necessary to complete a given task. This may be somewhat misleading. The problem, as stated by Bernstein (1967), is not related to the number of articular degrees of freedom, but to the manner in which the CNS masters (i.e. reduces) those potential degrees of freedom.

This problem is particularly relevant to the movement of the trunk and spine, as between the first cervical vertebra and the sacrum there are twenty-four motion segments, each with three potential degrees of freedom (more if inter-segmental translation is considered). This excess of potential degrees of freedom, however, applies only to the articular nature of the spine in isolation. This is because each degree of freedom, by definition, must be independent. The spine, however, is rarely thought of as a series of independent joints. As such, the true problem may lie more in our ability to count the actual (i.e. independent) degrees of freedom of the system than in the existence of excess, or redundant, degrees of freedom (Partridge, 1986).

This serves to illustrate a common assumption in describing Bernstein's problem: that the degrees of freedom of the isolated skeletal system can be independent of one another (Partridge, 1986), even when the neurological and musculoskeletal system is intact. For functional, goal directed movements to occur, this cannot be true, as problems of coordination, timing and interaction between different neural, muscular and skeletal structures must be addressed (Hogan, 1985). As such, even when a movement is isolated to a single joint, that movement cannot be said to be independent of the actual state of the other joints in the system. Similarly, the fact that two joints are capable of moving in isolation does not mean that they are independently controlled during movement. It is even reasonable to assume that, for certain movements, the number of independent degrees of freedom in the system may be fewer than the number of joints involved in the movement (Partridge, 1986), sacrificing the flexibility of the system to promote stable inter-joint (and inter-muscular) coordination (Nichols, 1994).

Although movement in a multi-articular system requires a degree of coordination between that system's articular degrees of freedom, the manner in which this occurs is unlikely to be fixed if the flexibility of movement that is available to humans is to be achieved. This flexibility of movement, however, must still be executed via the coordinated activation of the musculature, under the control of the CNS, which we describe as neuromuscular coupling. It is suggested, therefore, that neuromuscular coupling may be used to effectively limit the degrees of freedom of the body for most functional movements, but that this coupling will differ across the full range of functional behaviours. The two fundamental problems in the study of motor control, therefore, may be in counting the number of actual degrees of freedom of the system, and in determining the nature of the underlying neuromuscular coupling.

Kinematic degrees of freedom in eye movements

Eye movements present a relatively simple model to illustrate the difference between the potential kinematic degrees of freedom of a system, and the actual degrees of freedom. Examples also exist in this literature illustrating the potential for flexibility in the actual degrees of freedom of the system, based on neural control.

In theory, the eye can move vertically, horizontally, and torsionally; giving it 3 degrees of freedom. Despite this, when the head is immobilized, the torsional movement of the eye is largely determined by the vertical and horizontal orientation of the eye, effectively reducing the number of independent degrees of freedom to 2 (Listing’s Law) (Crawford et al., 2003). Simulation studies, based on the static architecture of the eye musculature, have suggested that the lines of pull of these muscles may predispose the eye to move in this manner. This, however, cannot represent a fixed constraint, as Listing’s law does not apply to every situation involving eye movement (examples are the rotational vestibulo-ocular reflex and optokinetic-nystagmus (Crawford et al., 2003)). This suggests a degree of flexibility in the biomechanical action of the eye musculature, and in the actual degrees of freedom of the system, based on the specific demands of the task.

Functional role for articular kinematic redundancy

When a task is evaluated from the simple point of view of attaining a desired end-point position (such as hand position in a reaching task), the available articular degrees of freedom may allow for more than one solution to the task; giving rise to the notion of redundancy. Those apparently redundant articular degrees of freedom, however, may serve a functional role beyond simply attaining the desired end-point position. Specifically, changing the configuration of the limb may provide a means to modulate the directional (i.e. asymmetrical) aspects of the limb impedance (Hogan, 1985), without altering the position of the end-point.

Control over the admittance (or mobility) of the system can be achieved by modifying the geometry of the multi-articular system, thus providing a degree of control over its net inertial properties (Hogan, 1985). This would not be possible in a rigid body. As such, the "kinematic redundancy" of the skeletal system may have a functional role in the control of the inertial behaviour of the system, and over its effective impedance (Hogan, 1985). Different limb configurations cannot, therefore, be considered equivalent, due to the interdependence between limb geometry and limb impedance.

Another functional role for the multi-articular nature of the body may be in the performance of ballistic movements such as jumping and throwing. Van Ingen Schenau (1989) suggests that one of the biomechanical requirements to effectively transfer joint rotations into ballistic, linear motions such as jumping and throwing, is a minimum of three segments per extremity (with distally decreasing inertial properties). The coordinated, proximal to distal sequence of joint rotations observed in such movements when performed by a system with at least 3 segments (e.g. the human lower limb) provides a significant mechanical advantage, in terms of maintaining the acceleration of the body's centre of mass, or of the mass of the object being thrown, despite the fact that a less articulated body might still be capable of following a similar movement trajectory (albeit with an altered acceleration profile). This may also provide some clues as to why animals that walk plantigrade, such as humans, are less efficient in generating ballistic movements such as running and jumping than animals who walk with a digitigrade stance, such as cats (Alexander, 1986); the latter effectively providing an extra functional segment for the transfer of energy.

Muscular redundancy

In addition to the concept of kinematic redundancy, it is often stated that a degree of redundancy exists in the musculature. This idea is based largely around two concepts. The first is that muscles can be described by their actions about a joint, and that there is generally more than one muscle at a given joint that performs the same action (often termed anatomical synergists). The second is that muscles have antagonists (i.e. muscles which produce opposite moments about the joint), and that a continuum of co-activation levels for these antagonists will result in the same net moment of force at the joint that they cross (with only the joint stiffness changing). Both of these notions, however, are oversimplifications of a complex system, as they examine muscular action across a single joint, without accounting for the necessary coupling that occurs across joints due to the architecture of the musculoskeletal system (Hogan, 1985; Nichols, 2002). Furthermore, when one takes into account the lines of action of the muscles that cross a given joint, and the number of joints spanned by each of those muscles, we must conclude that each muscle has a distinct action (Nichols, 1994). This is further supported by the observation that substantial changes in the mechanical action of muscles can occur with a change in the posture of the system (Flanders and Soechting, 1990).

As an example of these complexities, we can examine the three muscles often described as the principal elbow flexors: biceps brachii, brachialis, and brachioradialis. Not only does each of these muscles cross the elbow joint with a slightly different line of action, but each of these muscles differs in terms of the number of joints spanned. Both heads of the biceps attach to the scapula and to the radius, and therefore span the shoulder (glenohumeral), the elbow (humero-ulnar and humero-radial) and the proximal forearm (radio-ulnar) joints. Brachioradialis, on the other hand, attaches to the humerus and to the radius, and therefore spans only the elbow and proximal forearm. The action of Brachialis alone is limited to the elbow, attaching to the humerus and ulna. Due to the multi-articular nature of the first two muscles, their specific mechanical action at the elbow must change relative to the posture or action at the other joints spanned, as the force produced by skeletal muscle is both length and velocity dependent (van den Bogert et al., 1998). Even the action of the brachialis cannot be considered in isolation, as its role in elbow flexion must be coordinated with the action of the other muscles capable of imposing a flexion moment at the elbow (linked by various spinal pathways (Nichols, 1994)). As the action of these muscles is necessarily interdependent, and as none of these muscles performs exactly the same function, they cannot be considered redundant.

Next, consider the principal "antagonist" to the elbow flexors: the triceps brachii. This muscle has one head which spans the shoulder and elbow, and two more which span only the elbow. As such, even if the different lines of pull of the muscles crossing the elbow joint are ignored, only the brachialis and the mono-articular heads of the triceps can be properly considered antagonists. The other "prime movers" at the elbow (long head of triceps, biceps brachii, and brachioradialis) cannot be considered to have true anatomical antagonists, when their multi-articular nature is considered. Furthermore, when one considers that it may be functional to modulate the mechanical impedance of an individual joint without directly affecting the adjacent joints (Hogan, 1985), the presence of mono-articular antagonists cannot be used as an argument for muscular redundancy.

Experimental evidence against the notion of muscles as simple agonists and antagonists can be found in the coordinated muscle activation in the human arm. Even under isometric conditions, muscles are active over a wide range of force directions, with many muscles exhibiting a high degree of activation for distinctly different directions of isometric forces (Flanders and Soechting, 1990). As such, the description of muscles as "flexors" or "extensors" is certainly a misnomer (or at least an oversimplification). The same is true of the term "antagonist", as muscular co-activation, which occurs even during the most stable of isometric tasks (Flanders and Soechting, 1990), almost certainly represents a coordinated modulation of impedance, rather than an energetically inefficient expression of imperfect motor control.

Further arguments against the notion of muscular redundancy can be found when the lines of action of the muscles are taken into account. There are no muscles which can be considered equivalent in terms of direction of force production, with most muscles exerting moments about more than one axis of rotation (Nichols, 1994). The distinctiveness of each line of action may even extend to the different subdivisions within a muscle, which may be anatomically segregated to act upon specific divisions within the tendon, and may even receive different proprioceptive and cutaneous innervations (Nichols, 1994), thus providing an even greater degree of precision with respect to the generation of joint moments.

When all of this is taken into account, it is not surprising that Flanders and Soechting (1990) observed consistent changes in muscle activation at the wrist, as a function of upper limb posture, during various isometric tasks. The unique action of each muscle at a joint, and across the multi-articular skeleton, suggests that the number of possible solutions to the force requirements for each isometric task is likely much more limited than the theory of muscular redundancy would indicate.

These same limitations may be even greater during dynamic tasks, as additional constraints must be respected. One, which may be termed a geometrical constraint (van Ingen Shenau, 1989; van Ingen Shenau et al., 1987), stems from the fact that the ability to transfer the angular movement of a joint into translational movement between the distal ends of the articulated segments gradually decreases to zero as the joint angle approaches 180°. A second constraint may be termed an anatomical constraint (van Ingen Shenau, 1989; van Ingen Shenau et al., 1987), and stems from the fact that a joint's angular velocity must be decelerated to zero as the joint approaches its physiological end of range, in order to prevent injury. This is typically accomplished by muscular forces so as to prevent excessive stress on the articular capsule and ligaments.

When taken in the context of multi-articular movements, and in particular ballistic movements, these constraints suggest an "optimal" pattern of coordinated joint movement, and may therefore provide some insight into the unique action of each muscle within the coordinated movement pattern. During jumping, for example, three problems associated with the geometrical and anatomical constraints of the task must be addressed in order to optimize performance (for details, see van Ingen Shenau, 1989). First, a specific (and variable) ground reaction force must be produced at the distal segment, requiring a specific distribution of net joint moments at every stage throughout the task. Second, a proximal to distal sequence of joint rotations must be coordinated, in order to optimize the transfer of angular movement into translational movement. Third, the angular velocity of each joint must be brought to zero prior to its physiological end of range, in order to prevent joint injury. The muscular architecture of the lower limb, highlighted by the action of the bi-articular muscles (van Ingen Shenau et al., 1987), appears to have evolved to address these potential problems (similar issues exist during locomotion). Each muscle plays a unique role in the coordination of movement between the joints, in decelerating each joint prior to its end range, and in the transfer of energy, with minimal dissipation, from the proximal to the distal segments.

2.3.4 Three-dimensional linked segment modeling

Kinematics of movement

As outlined in previous sections, most studies dealing with the control of upright posture and balance have modelled the trunk as a single rigid segment. Although this simplification may have been largely due to an intentional focus on the lower extremities, it may also have stemmed from methodological limitations related to modelling the multi-segmental nature of the trunk. Many techniques have been used to capture the kinematics of trunk motion, including inertia-based gyroscopic transducers (Carpenter et al., 1999), electromagnetic transducers (Preuss et al., 2005a), an exoskeleton instrumented by potentiometers (Marras et al., 1992) and video-fluoroscopy (Cholewicki et al., 1991). Optical methods, however, using either passive or active marker systems, remain the benchmark for multi-segmental motion capture.

Reconstruction of the kinematics of the skeletal system, using external markers, has several limitations (Cappello et al., 1997; Cappozzo et al., 1997). In order to record motion in three-dimensions, a minimum of three markers must be associated with each segment (the underlying assumption of segment rigidity has its own limitations (Gruber et al., 1998)). As no measurement system is 100% accurate in the reconstruction of marker position, the distance between these markers must be sufficiently large, relative to this measurement inaccuracy, to minimize any error in segment orientation that may result (Cappello et al., 1997). Recent technological advances have reduced these measurement inaccuracies, allowing for smaller marker clusters. This issue, however, is unlikely to ever be fully eliminated.

The use of surface mounted markers also assures a degree of unwanted movement between the markers and the underlying skeletal structures, whose position the markers are intended to represent (Cappello et al., 1997; Cappozzo et al., 1997; Gruber et al., 1998). This presents another form of measurement error, and has similar implications for the accuracy of the reconstructed segment orientation. In the lower extremities, it has been suggested that the use of rigid marker clusters on the lateral portion of the thigh and tibia, far from the joints, may be preferable to individual markers placed over the bony prominences near the joints (Cappello et al., 1997). The actual degree of error for each marker setup, however, will vary based on the anthropometric and morphological characteristics of the subject, as well as on the movement being performed.

In the trunk, the fact that the spacing of the markers representing a given segment will affect the measurement error for that segment poses a greater problem than in the extremities. This is due to the size of the individual vertebrae relative to the length of the long bones of the legs and arms. As such, if a rigid-body, linked-segment model is to be used (a requirement for the traditional inverse dynamics approach to estimating the kinetics of motion, outlined below), it remains necessary to model several vertebral motion segments together as a single, rigid segment. A marker placement similar to that described by Crosbie et al. (1997a), dividing the trunk into as many as 4 segments, may therefore represent a reasonable compromise between the true multi-segmental nature of the trunk, and the traditional representation of the trunk as a single rigid body.

Kinetics of movement

Three dimensional linked-segment models can be used to estimate the net moment about a joint through inverse dynamics calculations (Kingma et al., 1996). This approach has been used extensively in the literature to estimate trunk moments, particularly in the lumbar spine (Callaghan et al., 1999; Lariviere and Gagnon, 1998; 1999b). In standing, two approaches have been suggested (Kingma et al., 1996): a bottom-up approach, using ground reaction forces under the feet, and proceeding upwards to the trunk; and a top-down approach, beginning at the hands and head, and proceeding downwards to the trunk. Unfortunately, due to limitations in the accuracy of kinematic and anthropometric measurements, both of these approaches are prone to some degree of absolute error in their estimates of joint moments.

Larivière and Gagnon (1998; 1999a; 1999b) have described both bottom-up and top-down approaches to estimate triaxial joint moments at the lumbo-sacral junction during lifting, reporting notable differences in the magnitude of the calculated joint moments between the two approaches. While potential errors in the recording and derivation of kinematic parameters may affect the calculated joint kinetics, errors in the estimated segment inertial parameters are likely to be of greater importance, particularly in the trunk

(Lariviere and Gagnon, 1998; 1999a). Unfortunately, attempts to determine the optimal method for estimating trunk segment parameters (Lariviere and Gagnon, 1999a) are unlikely to be generalizeable outside of the study population. As such, any calculation of absolute joint moment through linked-segment modelling must still represent an estimate that is prone to error from several different sources.

Patterns of joint kinetics obtained through inverse dynamics calculations may, however, be less prone to error than the magnitudes of the calculated moments. For example, while Larivière and Gagnon's (1998) comparison of the top-down and bottom-up calculation of absolute moment at L5/S1 showed differences in the absolute moments between the two methods, the patterns of the two joint moment estimates were virtually identical. As such, the analysis of spatiotemporal patterns in both kinematic (Stokes et al., 1999) and kinetic data may be an appropriate application of the data obtained through linked segment modelling.

2.3.5 Statistical pattern analysis

Bernstein (1967) has argued that the human motor system cannot attain any high degree of metric proficiency, but can be very sensitive to topological distinctions. Using handwriting as an example, he states that when movements are reproduced by an individual, the metrics of the movement may change, but the general topology does not (barring a change in the underlying motor program). As such, an evaluation of the patterns of human movement may be more appropriate when the goal is to reveal the nature of the motor control and coordination underlying the movement.

Evaluation of common and/or repeatable movements may provide the best opportunity to study the nature of neuromuscular coupling; representing the interaction between the musculoskeletal system and its underlying neural control. As suggested in section 2.3.3, one of the fundamental problems in the study of motor control may be to determine (i.e. count) the number of actual degrees of freedom of the system. This, in turn, may provide some insight in the nature of the underlying neuromuscular coupling. Statistical analysis of movement patterns may be valuable in this respect.

Principal component analysis

Principal component analysis (PCA) is a technique that seeks to reduce the dimensionality of a data set while maximally preserving the variability in the data (Chau, 2001; Jolliffe, 1986). In essence, this technique identifies a reduced number of independent variables, or principal components (PCs), that can explain most of the variability present in the original data set. It has also been described as a data driven filter, used to separate the deterministic components of the data (the retained PCs) from the stochastic components (Daffertshofer et al., 2004).

While PCA provides a means to alert the investigator to the possible relationships hidden in the data (Hasan and Thomas, 1999), the interpretation of the retained PCs remains somewhat subjective. An example, given by Hasan and Thomas (1999), is that if a data set has eight variables (representing 8 potential degrees of freedom) that can be explained by a linear combination of only three (3 PCs, representing 3 actual degrees of freedom), then the remaining five relationships must somehow be imposed.

With EMG data, PCA can reveal a small number of profiles underlying the complex activation patterns of a large set of muscles (Ivanenko et al., 2004). Any relationship between the individual EMG signals may then be interpreted as a degree of neuromuscular coupling (i.e. a relationship between the activation profiles of the individual muscles due to their interconnectedness within the CNS).

For kinematic data, PCA can be used to uncover the spatiotemporal structure of joint and limb coordination (Courtine and Schieppati, 2004). As the PCs identified from this analysis are independent of one another, such a technique may provide a means to "count" the independent kinematic degrees of freedom of the system. Such a reduction in the actual degrees of freedom of the system can only result from a biomechanical interaction, likely involving neuromuscular forces. The PCs retained from the analysis of kinematic data, therefore, may also reflect the effects of neuromuscular coupling.

Previous studies have used PCA to reduce EMG profiles in walking (Merkle et al., 1998) and reaching (Sabatini, 2002), and to identify abnormal motor control strategies in elderly (Brach et al., 2001) and injured (Lariviere et al., 2000) subjects. Others have used PCA to evaluate kinematic data, such as elevation angles of limb and trunk segments (Courtine and Schieppati, 2004), and patterns in marker position during treadmill locomotion (Stokes et al., 1999). Only one study was found, however, which used PCA to evaluate the postural response following surface perturbation (Chong and Franklin, 2001). This study, however, limited its analysis to the latencies of muscle activations.

Independent component analysis

Independent component analysis is another statistical technique whose fundamental principle is to reduce a larger data set to a smaller set of independent components. Certain underlying assumptions (such as how the independence of the variables is determined), however, differentiate this technique from PCA (for a complete explanation see Hyvärinen and Oja, 2000). From a functional standpoint, there is some evidence to indicate that ICA may be better suited to the analysis of EMG data than PCA (Tresch et al., 2006), particularly in revealing the actual basis vectors underlying the larger data set. These differences, however, may be affected by the various statistical features of the actual data set (Tresch et al., 2006), and must also be weighed against various methodological considerations, such as how to determine the number of components to retain (Jolliffe, 1986) (i.e. the how to differentiate the true signal from the unwanted "noise" (Daffertshofer et al., 2004; Hyvärinen and Oja, 2000)).

Cluster analysis

Another means of assessing common patterns in a data set is hierarchical cluster analysis, which assesses the distance between variables in an n-dimensional space, where 'n' represents the number of criteria of interest. The position of each variable within the space is determined by its relationship (value) for each of the 'n' criteria. Clusters are then defined by a multi-step process, which culminates in the assignment of each variable to a specific cluster (membership), or the assignment of a probability of membership for each variable (Krishnapuram and Keller, 1993; Pal and Bezdek, 1995; Pal and Mitra, 1999).

White and McNair (2002) used this technique to identify patterns of trunk muscle activation during gait based on the normalized amplitude of muscle activation during successive epochs of the gait cycle. This technique has also been used to identify the way in which motor neuron discharge in the primary motor cortex relates to EMG activity in different muscle groups (Holdefer and Miller, 2003). This latter study also included different methods of validating the clusters found during the initial analysis, including repeating the cluster analysis after reducing the dimensionality of the original data through PCA.

2.3.6 Synthesis of Literature Review

As outlined in the previous sections, although a great deal is known about the control of upright posture and equilibrium, the conventional focus on the lower limbs had led to a critical gap in the literature with respect to the role of the trunk in balance control. The information that is available would suggest that the control of upright equilibrium in the trunk, following support surface translation, will be highly coordinated, and relatively stereotyped, in both the biomechanical and neuromuscular aspects of the response to perturbation. Given the conventional treatment of the multi-segmental trunk as a single rigid segment, however, the scale of the movement that will occur in the trunk under this experimental paradigm remains unclear. Furthermore, the means by which the behaviour of the trunk will be controlled, at both the mechanical and neural level, has yet to be explored.

3. Musculature and biomechanics of the trunk in the maintenance of upright posture.

Richard Preuss and Joyce Fung

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3.1 Preface

The first study in this series was motivated by a perceived gap in the literature stemming from three principal issues. The first was that most previous studies evaluating the maintenance of upright posture and balance had modelled the trunk as a single rigid segment, extending from the hips to the shoulders. As such, very little information was available related to the kinematics and kinetics of the trunk following support surface perturbation. The second issue was that, although previous studies using the support surface perturbation paradigm had included specific trunk muscles in their assessment of the neuromuscular response, the number of trunk muscles assessed was typically quite restricted. Finally, many previous studies using support surface perturbations had focussed on either the neuromuscular response or the mechanical response to surface perturbation. As the neuromuscular and biomechanical aspects of the response are, by necessity, interdependent, any evaluation of one without regards to the other must be viewed as incomplete. As such, the purpose of this first study was to provide a description of the neuromuscular, kinematic and kinetic response in the trunk following support surface translation, using a multi-segmental model of the trunk.

The methodology used in this study was similar to that used in previous studies focussing on the lower limbs (e.g. Henry et al., 1998a; 1998b). As many variables have been shown to affect the postural response following support surface perturbation, we chose to focus on the effect of two: the direction of support surface translation, and the initial posture of the subject (sitting vs. standing). The former was chosen as a means of comparing the findings in the trunk with previous findings from the lower limbs, in which the direction of support surface translation is known to have a significant impact on the postural response. The latter was chosen as a means of evaluating the effect of limb dynamics on the trunk postural response. Specifically, the sitting posture provided a means to deliver the postural perturbation directly to the trunk, as the pelvis was effectively constrained to move with the support surface. In the standing posture, however, the perturbation was conveyed to the trunk via the lower extremities, and as such was likely to be affected by the dynamics of the lower limbs.

3.2 Abstract

Surface perturbation has been used for decades to study balance and postural control; however the behavior of the trunk in these postural responses has been largely overlooked. Thirteen healthy males (18 to 23 yrs) were exposed to horizontal support surface translations delivered randomly in one of 8 different horizontal directions in both sitting and standing. A 4-segment model of the trunk was used to estimate the kinematics and kinetics associated with the postural response, while surface EMG was acquired, bilaterally, from 7 trunk muscles and 1 hip muscle. Multi-segmental movement was observed in the trunk in both test postures. Both the biomechanical and neuromuscular aspects of the trunk response were significantly affected by translation direction and test posture, with an interaction effect between these variables. The response in sitting was closely tied to the movement of the support surface, while the response in standing occurred in two phases: the first related to the dynamic response in the lower limbs, and the second tied to the movement of the support surface. As such, the observed postural responses could be largely explained by the biomechanical constraints of the system, such that the neural control of trunk equilibrium is simplified.

3.3 Introduction

Trunk control is essential to the maintenance of upright posture, and is of particular importance in patients whose motor control may be compromised by a neurological impairment, such as those with spinal cord injuries. Further, more subtle impairments in the muscular coordination and control of the trunk may be associated with lower back pain (Preuss and Fung, 2005; Radebold et al., 2001), as the muscles of the trunk must maintain the structural stability of the vertebral column (McGill et al., 2003), while at the same time maintaining equilibrium in the upright posture.

Surface perturbation, as a means to study balance and postural control, has provided many important insights into neuromuscular control and coordination. Previous studies using the surface perturbation paradigm have shown that, independent of the cognitive processes involved in the maintenance of posture, mechanical factors, such as the direction, velocity, and amplitude of the perturbation, the subject's initial posture, and the surface configuration, also influence the postural response to perturbation (Diener et al., 1988; Henry et al., 1998b; Horak, 1996; Horak and Macpherson, 1996; Inglis et al., 1994; Runge et al., 1999). The conventional focus on the lower extremities, however, has limited our knowledge of the behavior of the trunk in these processes. This stems, in part, from the fact that most previous studies evaluating the maintenance of upright posture and balance have modeled the trunk as a single rigid segment (Bothner and Jensen, 2001; Henry et al., 1998b; Horak and Nashner, 1986; Hughes et al., 1995; Runge et al., 1999). Important deviations in trunk posture, however, can be achieved with the application of relatively small moments of force (McGill et al., 1994). This, combined with the observation that the muscles of the trunk provide limited stiffness to the spine in a relaxed upright position (Cholewicki and McGill, 1996), suggests that a surface perturbation in upright standing or sitting is likely to produce movements in the multi-segmental trunk.

While the kinematics and kinetics of the trunk have been largely overlooked in this body of literature, previous studies have included certain trunk muscles in their assessment of the myoelectric response to surface perturbation. Although the number of trunk muscles assessed in these studies has often been quite restricted, the data that are available suggest that both the onset latency and the level of activation of the muscles of the trunk will vary based on the direction of perturbation, in both standing (Henry et al., 1998a) and sitting (Zedka et al., 1998). In order to fully understand the myoelectric behavior observed following support surface movement, however, these data must be examined along with the kinetics and kinematics of the response.

The purpose of this study is to provide a comprehensive description of the neuromuscular, kinematic and kinetic response in the trunk following horizontal translation of the support surface. Tests will be conducted in both standing and sitting, with support surface translations delivered in multiple directions, in order to assess both the effect of limb dynamics and perturbation direction on the postural response in the trunk. Kinematic and kinetic analyses will proceed using a multi-segmental trunk model.

3.4 Methods

3.4.1. Participants

Thirteen male volunteers, aged 18 – 23 yrs, participated in the study. Subjects were recruited from a convenient sample of the university student population, and were excluded from participation if they displayed any of the following: history of mechanical back pain or injury; history of any neurological, vestibular or other condition affecting balance; history of any significant lower extremity injury; previous diagnosis of spinal scoliosis. All subjects provided written, informed consent prior to participation. Ethics approval for this study was received from the ethics committee of the Montreal Centre de recherche interdisciplinaire en réadaptation (CRIR).

3.4.2. Data Acquisition

Test Postures

Subjects were tested in two different postures: standing and sitting. For the former, the subjects were asked to stand barefoot, with their feet at shoulder width, and their arms resting by their sides. Each subject's foot position was marked on the support surface to ensure a comparable starting position for each trial. In the sitting posture, the subjects were firmly strapped into a custom made chair, secured to the support surface. The chair was designed to maintain a spine posture similar to the standing condition, yet limiting the subject's ability to use the lower extremities during the postural response. Further, for the sitting trials, the subjects were also asked to cross their arms on their shoulders, thus minimizing the role of the upper extremities in the postural response. The standing and sitting test postures are shown in Figure 3.1A and 3.1B, respectively.

Two measures were used to ensure that the initial posture of the trunk was equivalent in the standing and sitting positions. The lumbar spine curvature in the sagittal plane was measured using a flexible rule, ensuring that the measures in the two postures were within a 5-degree window of intra-tester repeatability described by Youdas et al. (1995), using the trigonometric technique described by these authors. Iliac crest level, in the frontal plane, was also measured using an inclinometer, ensuring that the measures were within a 1-degree window of intra-tester repeatability, as described by Piva et al. (2003). Based on these criteria, no differences were noted in the starting trunk postures from the standing to the sitting condition.

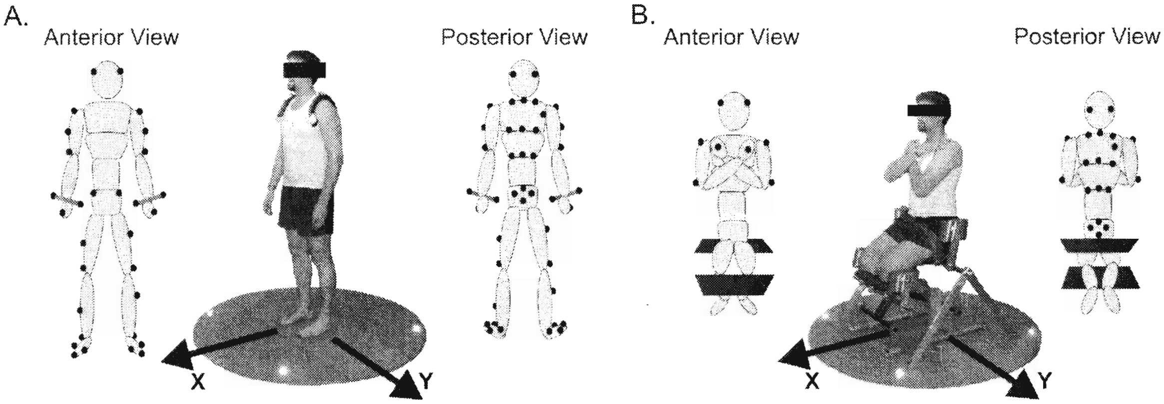


Figure 3.1 – Test postures
A. Standing test posture, with marker placement for the 17-segment linked-segment model used in this test posture. B. Sitting test posture, with the marker placement for the 5-segment linked-segment model used in this test posture.

Perturbation Protocol

Surface perturbations were delivered by a six-degree-of-freedom motion base, previously described by Fung et al. (1998; 2003). Each perturbation involved a horizontal support surface translation in one of 8 directions, at 45° intervals around the full circle, with each subject experiencing 4 perturbations for each of the 8 directions.

Data were first collected in the standing posture, followed by the sitting posture. For both postures, the trials were divided into 2 blocks, with each block consisting of 2 trials for each of the 8 translation directions, delivered in a random order. This method of randomization was used to minimize the potential for multiple consecutive trials in the same direction, and therefore decrease the potential for habituation. Further, by randomizing the order of the perturbations, the subjects were given no *a priori* knowledge of the perturbation direction, in order to minimize the likelihood of direction specific anticipatory actions, such as leaning in the expected direction of perturbation.

Each perturbation consisted of an acceleration phase lasting 250ms, followed by a period of 300ms at a relatively constant linear velocity of 0.45m/s, and finally a deceleration phase, such that the final support surface displacement was 150mm. Preliminary testing found this perturbation profile to be sufficient to consistently elicit an electromyographic response from the trunk musculature, while the subjects were generally able to maintain their balance in standing without stepping. Further, this profile provides a window of >500ms prior to the onset of platform deceleration, which has been shown to act as a second perturbation (Carpenter et al., 2005), able to alter the initial postural response.

Kinematic Data

Three-dimensional kinematic data were acquired using a 6-camera Vicon 512 motion analysis system (Vicon Motion Systems Ltd., Oxford, U.K.), with marker positions sampled at 120Hz. Two separate linked-segment models were used to calculate the kinematic variables for the standing and sitting paradigms, with the trunk divided into pelvic, lumbar, lower thoracic and upper thoracic segments, similar to a model used by Crosbie et al. (1997a) for the study of trunk contributions to gait.

The model in standing consisted of 46 reflective markers, dividing the body into 17 segments: head (to C7), bilateral upper arms (shoulder to elbow), bilateral forearms (elbow to wrist), bilateral hands (distal to wrist), upper thoracic trunk (T1-T6), lower thoracic trunk (T7-T12), lumbar trunk (L1-L5), pelvis, bilateral thighs (hip to knee), bilateral legs (knee to ankle) and bilateral feet. The model in sitting consisted of 24 markers, dividing the body into 5 segments: head (to C7), upper thoracic trunk including arms (T1-T6), lower thoracic trunk (T7-T12), lumbar trunk (L1-L5), and pelvis. The standing and sitting models are shown in Figure 3.1A and 3.1B, respectively. In addition, 4 reflective markers were affixed to the motion base surface in order to monitor the movement of the support surface.

For both models, the kinematic variables of interest were the position of the centers of mass (CoM) of each trunk segment, as well as the combined CoM of the head, arms and trunk (HAT), the orientation of each trunk segment, and the relative orientation of the adjacent trunk segments, representing the inter-segmental trunk angles at the mid-thoracic (MidTx), thoraco-lumbar (TxLx), and lumbo-sacral (LxSx) levels. Marker position was low-pass filtered at 8 Hz prior to modeling, using a dual-pass, 4th order digital Butterworth filter. After modeling, the kinematic variables of interest were filtered again, with a cut-off frequency of 3.5 Hz, in order to retain at least 95% of the frequency power spectrum based on Welch's averaged periodogram method (Welch, 1967). The kinematic variables of interest were determined using a representation of the above models created in Bodybuilder software (Vicon Motion Systems Ltd., Oxford, U.K.). Digital filtering was performed in Matlab (MathWorks, Massachusetts, U.S.A).

Kinetic Data

Estimates of the net moments of force at the MidTx, TxLx, and LxSx levels were derived from the same linked segment models described above. A 3-dimensional, top-down, inverse dynamics approach (Kingma et al., 1996) was used to estimate the net moments of force, using anthropometric variables adapted from deLeva (1996) and Pearsall et al. (1996). Trunk moments of inertia were approximated as cylinders with radius equal to half the anterior-posterior depth at the mid-point of the segment (measured for each subject). All inverse dynamics calculations were performed in Matlab (MathWorks, Massachusetts, U.S.A).

The top-down approach was used to ensure a degree of consistency between the standing and sitting models, the latter of which precluded simple measurement of contact forces for the lower extremities. Further, as this study's focus is the trunk, kinetic data from the lower extremities were not required. Finally, while contact forces could be acquired for the standing condition using the force plates embedded in the motion base, the inertial component of the force plate signals resulting from the movement of the platform could not be fully eliminated with a simple algorithm (Preuss and Fung, 2004b).

Electromyographic (EMG) Data

Surface EMG was acquired using a TeleMyo sEMG measurement system (Noraxon U.S.A. Inc.) with an operating bandwidth of 10-350Hz, an effective common mode rejection ratio of 130 dB DC, greater than 100 dB at 60 Hz, and a minimum of 85 dB throughout the operating bandwidth, and a fixed overall per-channel gain of 2000. EMG were digitally converted using a 12bit A/D board over a +/-5V range, sampled at 1080Hz, and stored for further analysis. All recordings were acquired using pre-gelled, disposable silver/silver chloride electrodes, with a 10mm diameter circular conductive area, in a bipolar configuration. Electrodes were positioned with a centre to centre distance of <4cm, parallel to the muscle fibers, and following careful skin preparation. Prior to analysis, all EMG signals were high-pass filtered using a dual-pass, 4th order Butterworth filter, with a cut-off of 40Hz, in order to minimize the appearance of electrocardiographic (ECG) artefact. The operating bandwidth of the EMG, and the sampling frequency of 1080Hz, was chosen based on a power spectrum analysis of previously acquired EMG data using a typical operating bandwidth of 10-500Hz (De Luca, 1997), sampled at 3000Hz. Analysis of 7 trunk muscles, following surface perturbation, found that 96.4 to 99.7% of the spectral power was below 300Hz.

EMG was acquired bilaterally from eight sites on the trunk and pelvis: Rectus Abdominis (RA), Internal Oblique (IO), External Oblique (EO), Upper Thoracic Paraspinals (TE4), Lower Thoracic Erector Spinae (TE9), Lumbar Erector Spinae (LE), Lumbar Multifidus (MF), and Tensor Fasciae Latae (TFL). Electrode placement is shown in Table 3.1 (refer also to McGill, 1992). Prefixes R and L are used to denote right and left (eg. RRA indicates Right Rectus Abdominis). During data acquisition, the activity of the RIO was visually assessed, using an oscilloscope, to ensure that the subject was fully relaxed prior to the onset of perturbation.

Table 3.1 - Electrode placement

Muscle	**Surface Electrode Placement***
Rectus Abdominis (RA)..........	3cm lateral to the Umbilicus (caudal bead of RA)
Internal Oblique (IO)...............	2cm medial and superior to the ASIS
External Oblique (EO)............	15cm lateral to the Umbilicus, anterior to axillary line
Upper Thoracic Paraspinals (TE4)	5cm lateral to T4 spinous process
Thoracic Erector Spinae (TE9)....	5cm lateral to T9 spinous process
Lumbar Erector Spinae (LE).....	3cm lateral to L3 spinous process
Lumbar Multifidus (MF)..........	2cm lateral to L4/5 interspace
Tensor Fasciae Latae (TFL)	Distal to the anterior iliac crest, lateral to the ASIS

*All measures are approximate, and take into account anthropometric differences between subjects

3.4.3. Data Analysis

Kinematic and Kinetic Data

Ensemble averages of the 4 trials in each perturbation direction, for each subject, were used for further analysis of the kinematic variables of interest (described above), and for the estimated inter-segmental moments of force, over the initial 500ms following perturbation onset. The moment-of-force data, at each trunk level, was then normalized to a percentage of body weight, for each subject, to allow for comparison across subjects. Based on these ensemble averages, the net inter-segmental power, at each trunk level, was calculated for each subject, using the method described by Winter (1990) to determine joint power.

Ensemble averages, as well as the standard errors for the ensemble averages, were then taken for the entire subject population, for each variable and for each direction of perturbation.

EMG Activation

Integrated EMG (IEMG) was used as an estimate of EMG activation level. The linear enveloped EMG, from each subject, muscle and trial, was taken using a low-pass, 2nd order Butterworth filter with a cut-off frequency of 2.5Hz (shown to approximate the tension profile of the muscle (Winter, 1990)). These linear envelopes were then ensemble-averaged for each subject and muscle, in the 8 directions of perturbation. The ensemble-averaged profile was then integrated over the initial 250ms (0-250ms) following onset of support surface movement, and over the subsequent 250ms period

(251-500ms), in order to provide a global estimate of the level of EMG activity over these two periods.

For each subject, and for each muscle, these values were then normalized to the maximum value obtained for that muscle in all testing conditions (2 postures, 8 directions, 2 time windows) in order to allow for comparison across subjects. Mean values were then taken for the entire subject population, for each of the 250ms windows, for each muscle and direction of perturbation. These mean values were then normalized once again for all test conditions.

EMG onset latencies, for each muscle, were determined automatically, for each individual subject and trial, using a fixed set of criteria. The EMG data were full-wave rectified, and a baseline EMG value was set from the mean and standard deviation of a 50ms window taken immediately prior to the onset of platform motion. This baseline was then compared with the mean of a moving 50ms-window beginning immediately following the onset of platform motion, and moving forward 1 frame until the mean of this window was found to exceed the mean of the baseline window by 2 standard deviations. Once this criterion was met, a moving 10ms-window was taken from the beginning of the final 50ms-window in the previous step, moving forward 1 frame at a time, until the mean in this 10ms window also exceeded the baseline mean by 2 standard deviations. EMG onset was then taken as the midpoint of the final 10ms window. If, however, during this process, a 50ms-window was found in which no point in the window exceeded the baseline mean, this window was then set as the new baseline.

For each subject, a muscle was considered to be active for a given direction of perturbation if the onset criteria described above were met for at least 2 of the 4 trials in that direction. Mean onset latencies were then taken for each subject, for those muscles which met this criterion, and these were used to determine the mean onset latencies for each of the 16 muscles tested, for each direction of perturbation, across the subject population.

3.4.4. Statistical Analysis

A two-way mixed-model analysis of variance (ANOVA) with repeated measures was used for all statistical analyses (Littell et al., 2002). This method was chosen as it takes into account any covariance that may result from the sequential nature of the data (Littell et al., 1998). Further, a least-squares method was used to estimate and compare means, thus accounting for the unbalanced structure that might result from any missing data (Littell et al., 2002). For each ANOVA, the subject posture (sitting vs standing) and the direction of perturbation were treated as the independent variables.

For the EMG data, three dependent variables were tested for each of the 16 muscles: IEMG over the initial 250ms, IEMG over the second 250ms, and EMG onset latency (ms). An alpha level of 0.003 was used for these measures, based on a Bonferroni adjustment for multiple comparisons, as the same dependent variable was being tested across 16 muscles.

For the kinematic and kinetic data, the only dependent variable tested was the net displacement of the HAT CoM at the end of the 500ms-window, using an alpha level of 0.05. This measure was chosen in order to provide an estimate of the actual perturbation experienced by the trunk in each test posture and direction. The metrics of the other kinematic and kinetic variables were not assessed statistically, as the temporal motion profiles were determined to be of greater interest.

3.5 Results

Missing Data

Following data acquisition, certain EMG channels were found to have been corrupted, and were thus excluded from analysis. These channels were the RTFL of one subject, RLE for one subject, and LLE for 2 subjects. Further, in the standing posture, two of the subjects tested were not able to maintain their balance without stepping following anterior (X) surface translation. As such the data for this test condition is based on the remaining 11 subjects. The statistical methods used were designed to take into account these missing data.

Kinematics and Kinetics

The kinematic and kinetic motion patterns were found to be largely symmetrical, with the motion patterns following diagonal surface translation representative of a combination of the patterns observed following translations along the X and Y axes. As such, only the motion patterns for perturbations in the anterior-rightward (AR) and posterior-leftward (PL) directions will be described in detail. Further, as no perturbation was delivered in the transverse plane, or in the vertical (Z) axis, any movement occurring in this plane, or along this axis, will not be described.

CoM Kinematics

Figure 3.2 (A and B) illustrates the mean linear displacement of the HAT CoM along the X and Y axes, following AR and PL translations respectively. In the sitting posture, the onset of HAT motion was closely tied to that of the support surface. For support surface translations with an anterior (X) component, the mean (+/-2SE) delay for the onset of HAT motion in the anterior direction was 6ms (+/-8ms); for translations with a posterior (-X) component, the delay for posterior HAT movement was 1ms (+/-3ms); and for translations with a lateral (Y or –Y) component, the delay for lateral HAT movement was 0ms (+/-2ms). In standing, however, there was a remarkable delay in the onset of HAT CoM motion in the direction of support surface movement for all perturbation directions. For support surface translations with an anterior (X) component, the mean delay in standing was 279ms (+/-45ms); for those with a posterior (-X) component, the delay was 351ms (+/-46ms); and for translations with a lateral (Y or –Y) component, the delay was 178ms (+/-26ms).

Test posture was also found to have a significant effect ($p<0.0001$) on the net displacement of the HAT CoM 500ms after the onset of support surface movement. The displacement of the HAT CoM was also significantly affected by the direction of the perturbation ($p<0.0001$), with the smallest HAT displacements occurring following anterior (X) and posterior (-X) translations; although no interaction effect was noted between direction and posture for this kinematic variable. The net displacement of the HAT CoM, 500ms following support surface translation, is illustrated in Figure 3.2C.

The delay observed in the onset of HAT CoM motion in the direction of support surface movement, in the standing posture, was also evident in the motion patterns of the trunk segment CoM (Figure 3.3). Onset of pelvis motion, in sitting, was virtually synchronized with support surface motion, while a marked delay was evident in the standing posture in both the X and Y axes, for both the AR and PL translation directions. Further to this delay in pelvis motion, the initial motion of the more rostral trunk segments, in standing, tended to be opposite to that of the support surface, particularly in the X-axis.

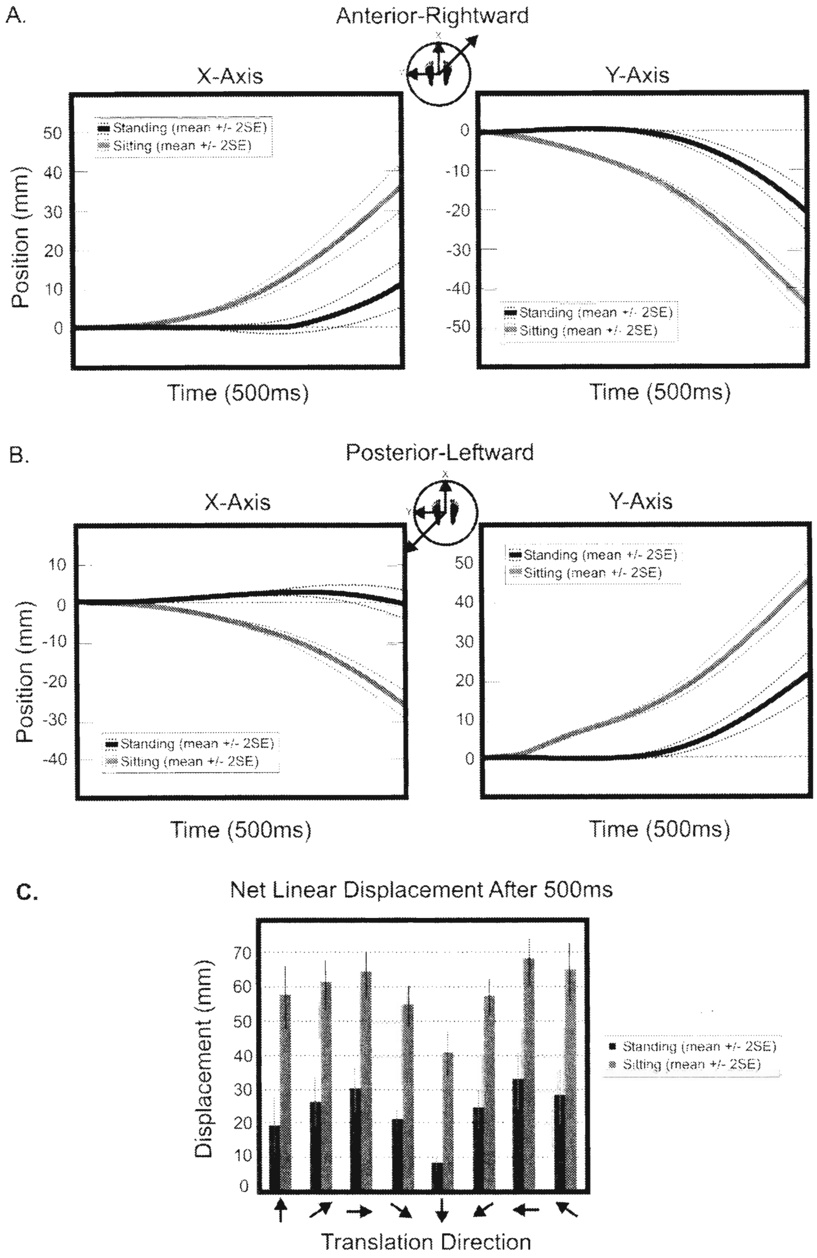


Figure 3.2 – Linear kinematics of the HAT CoM

A. Linear displacement of the HAT CoM following surface translation in the anterior-rightward direction over the initial 500ms following onset of support surface movement. B. Linear displacement of the HAT CoM following surface translation in the posterior-leftward direction over the initial 500ms following onset of support surface movement. C. Net linear displacement (vectorial sum of the relative position along the X and Y axes) of the HAT CoM 500ms following the onset of support surface translation.

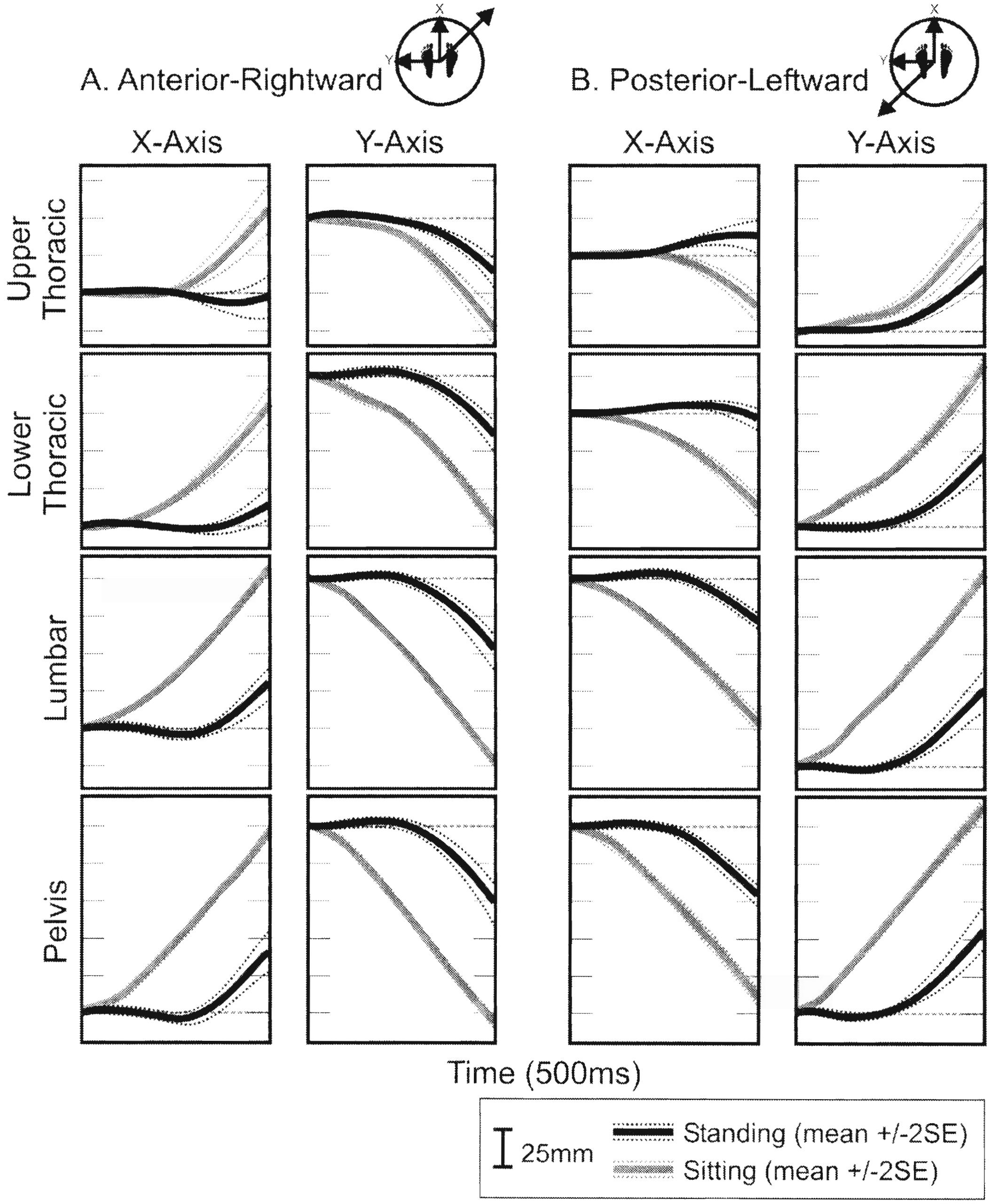


Figure 3.3 – Linear segmental kinematics
Linear displacement of the trunk segment CoM over the initial 500ms following onset of support surface movement following: A. anterior-rightward translation. B. posterior-leftward translation.

Following the onset of pelvis motion in the direction of support surface translation, a caudo-rostral delay in the progression of trunk segment CoM motion was evident in both test postures, and this delay was more evident in the anterior-posterior (X-axis) motion than the lateral (Y-axis) motion.

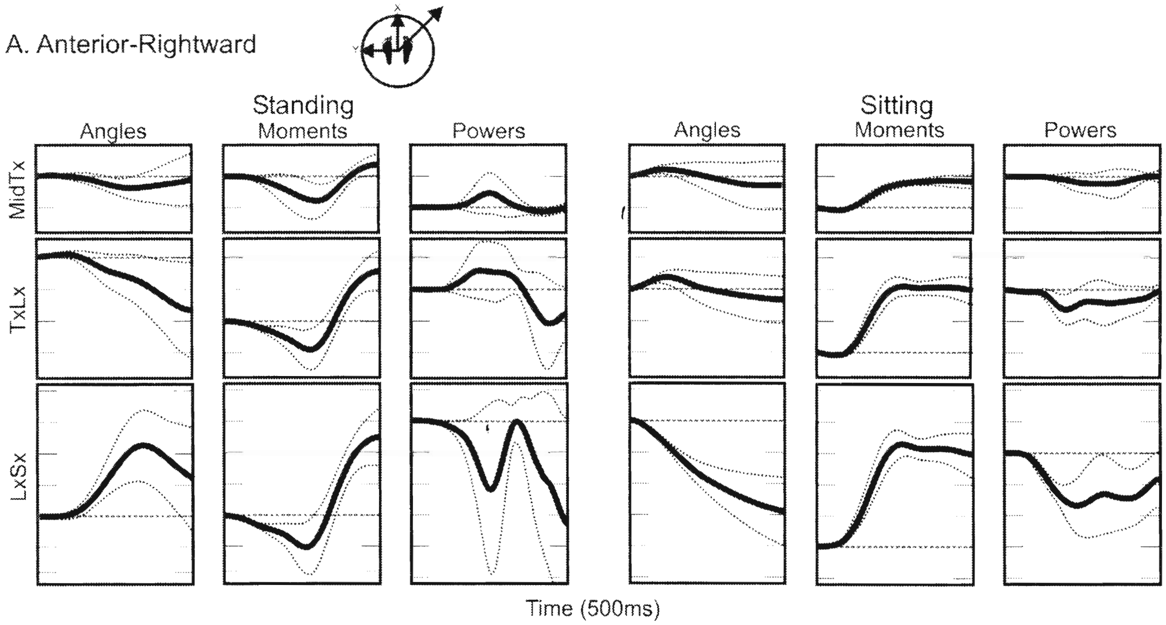
Inter-segmental Kinematics and Kinetics

Inter-segmental movement patterns for the AR and PL translation directions are shown in Figure 3.4 (sagittal plane) and Figure 3.5 (frontal plane), with the patterns contrasted between standing (left) and sitting (right). Non-negligible inter-segmental movement was observed in the first 500ms following the onset of surface translation, in both the standing and sitting postures, although the magnitude of that movement tended to be larger at the more caudal levels, and in the sagittal plane more than the frontal plane.

In the sagittal plane (Figure 3.4), the trunk inter-segmental kinematic and kinetic patterns in sitting were somewhat less complex than in standing. In sitting, for both the AR and PL translation directions, the inter-segmental moment-of-force profiles were mono-phasic, and oriented towards the direction of perturbation. Further, these profiles were similar in shape at all trunk levels, but tended to decrease in amplitude from the caudal to the rostral levels. The largest inter-segmental angular movements were seen at the LxSx level, also becoming progressively smaller rostrally, although more variability was observed in the inter-segmental angular movement than in the moment-of-force patterns. In the AR translation direction, the dominant movement was an eccentrically controlled extension, despite an initial flexion of the trunk at the TxLx and MidTx levels. In the PL translation direction, however, the movement was eccentric at only the LxSx level, where trunk flexion was observed, while at the more rostral levels concentric extension occurred.

In standing, the inter-segmental moment-of-force profiles in the sagittal plane were biphasic (Figure 3.4), with the transition between phases occurring shortly after the onset of linear motion of the inferior segment in the direction of platform motion (Figure 3.3). For example, following AR translation, the mean time between the onset of platform motion and onset of pelvis motion in the X-axis was roughly 270ms, corresponding closely with the first apex in the mean LxSx moment-of-force curve, while reversal of that curve (from an extension moment to a flexion moment) occurred after roughly 330ms (a similar delay of ~60-70ms was also observed at the other trunk levels). As in sitting, however, the moment-of-force curves in standing were similar in shape at all trunk levels (with the exception of the MidTx level following PL translation), and of decreasing amplitude from the caudal to the rostral levels. The magnitude of the inter-segmental motion was also quite variable in standing, with the largest movements occurring at the LxSx and TxLx levels. The mean power profiles indicate that the sagittal plane movement in standing was generally eccentric, although concentric motion was seen in the first phase of movement following AR translation at the two more rostral levels. The inter-subject variability in both the kinematic and kinetic profiles, however, were such that the mean trends in the power profiles did not always hold across the 95% confidence intervals shown in Figure 3.4, for either test posture.

A. Anterior-Rightward



B. Posterior-Leftward

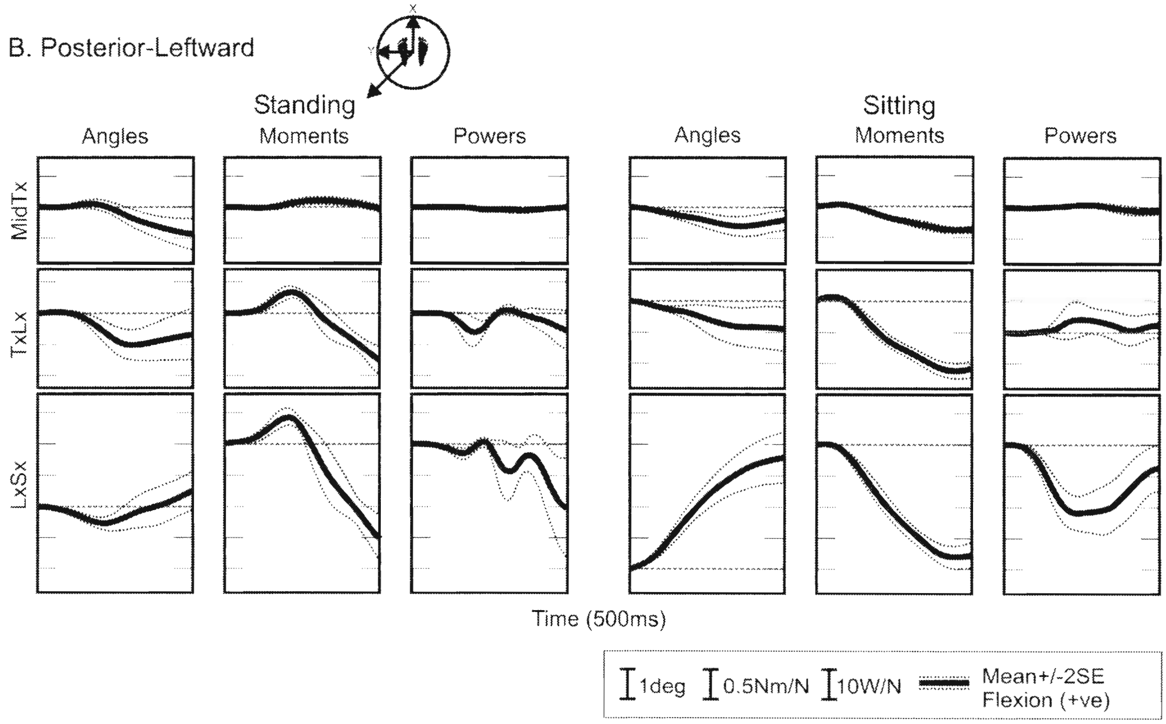


Figure 3.4 – Angular inter-segemental kinematics: sagittal plane
Sagittal plane inter-segmental motion patterns in the trunk over the initial 500ms following onset of support surface movement following: A. anterior-rightward translation. B. posterior-leftward translation.

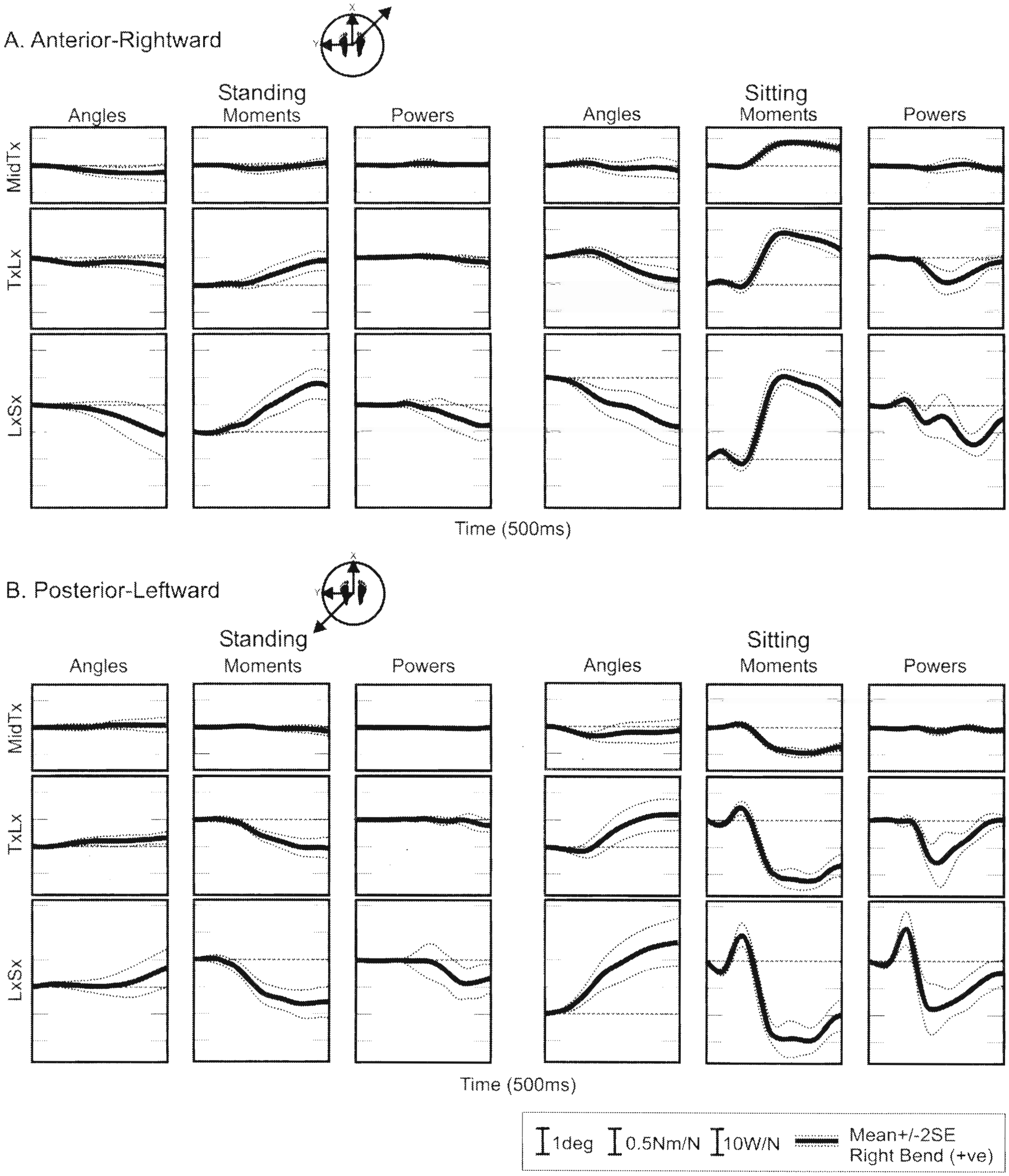


Figure 3.5 – Angular inter-segemental kinematics: frontal plane
Frontal plane inter-segmental motion patterns in the trunk over the initial 500ms following onset of support surface movement following: A. anterior-rightward translation. B. posterior-leftward translation.

Trunk motion in the frontal plane (Figure 3.5) was less complex than in the sagittal plane, with generally mono-phasic moment-of-force profiles, oriented towards the direction of translation, in both the standing and sitting postures. Further, in both test postures, these moment-of-force profiles tended to correspond to an eccentrically controlled movement, away from the direction of translation, although at the MidTx level, and at the TxLx level in standing, the motion profiles were effectively isometric. Two primary differences, however, can be noted between the standing and the sitting conditions. First, inter-segmental movement in the frontal plane in standing tended to be delayed compared to the sitting condition, similar to the delay observed prior to the onset of linear segmental motion in this test posture. Second, in the sitting condition, a moment-of-force of short duration, away from the direction of perturbation, was observed at the LxSx and TxLx levels shortly after the onset of platform motion (more evident in the PL condition). This moment-of-force was observed for most trials with a lateral translation component, but did not correspond to any observed trunk EMG (reported below). As such, this short-lived moment-of-force possibly originated at a level below the trunk, as a means to maintain contact of the ischium with the chair, due to compliance in the strap used to secure the subjects' thighs.

EMG Activation

Figure 3.6 illustrates the tuning curves for the normalized IEMG (see section 2.3.2) over the first two 250ms intervals following onset of support surface movement, as well as those muscles for which significant differences were found based on the direction of support surface translation and the test posture.

For both 250ms periods, the bilateral TFL, the only hip muscle tested, displayed strongly mono-polar tuning curves in both test postures, although the activation level and the orientation of the tuning curve, differed between the two test postures. Specifically, the activation levels in standing tended to be greater, and oriented towards the contralateral translation directions, while the curves in sitting had much lower amplitudes, and were oriented more ipsilaterally.

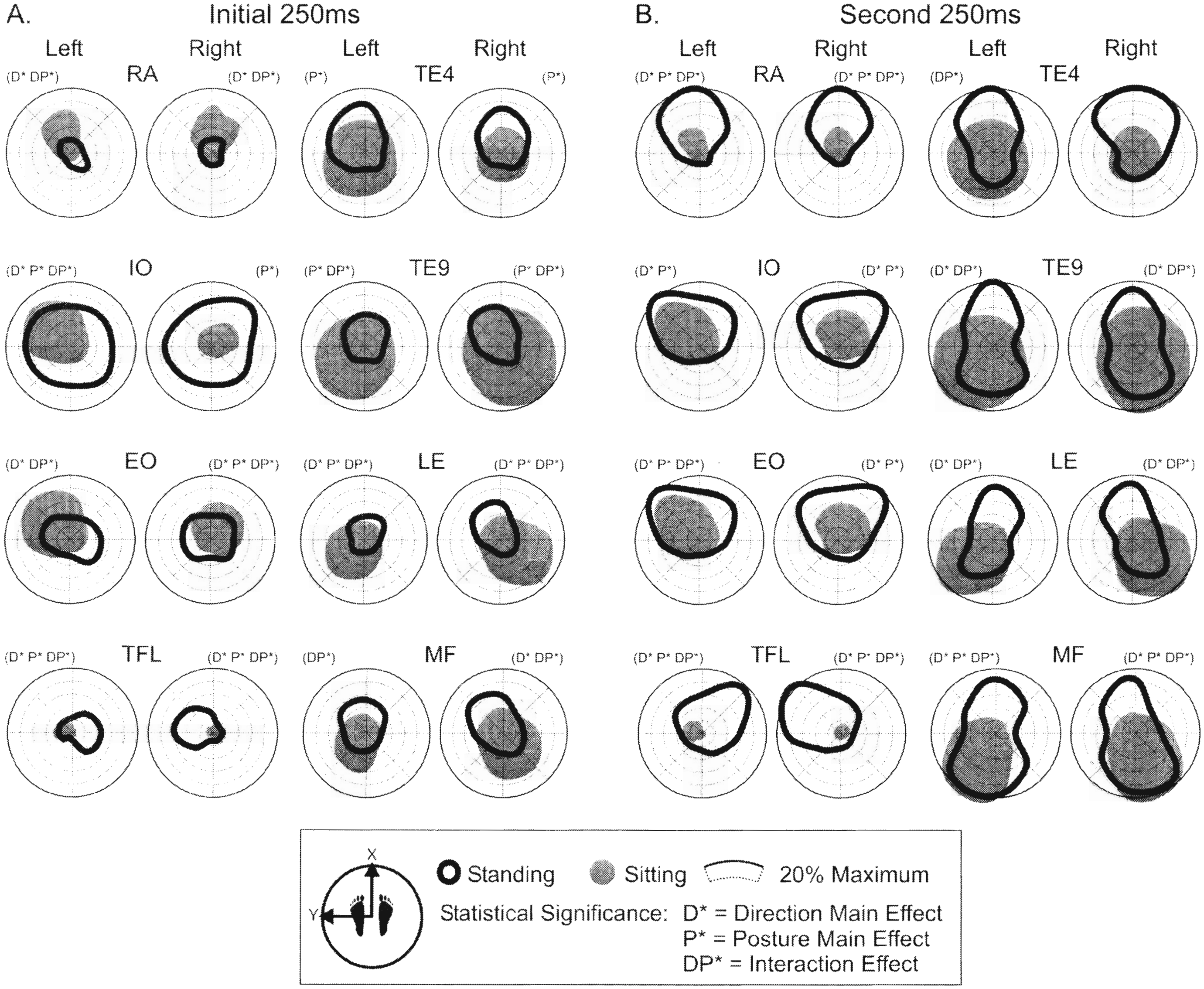
For the muscles of the trunk, over the initial 250ms period, the tuning curves in both the standing and the sitting conditions tended to be largely mono-polar, and oriented in opposite directions for the two test postures. The most notable exception was the IO in standing, for which no specific orientation was evident for the tuning curve, despite the relatively high activation levels.

Over the second 250ms period, the tuning curves in sitting tended to remain fairly consistent with those observed over the initial 250ms, while notable changes occurred in the tuning curves for the standing posture. The tuning curves for the abdominal musculature (RA, IO, EO), in standing, tended to be oriented towards the anterior translation directions, while for the muscles of the back, the tuning curves became largely bipolar, oriented anteriorly and posteriorly, with a tendency for higher activation levels in the contralateral-anterior and ipsilateral-posterior directions for LE and MF.

The mean EMG onset latencies for all muscles tested, in both the standing and sitting postures, are shown in Figure 3.7, along with the results of the statistical analysis. In standing, the mean onset latencies for the bilateral TFL tended to be shorter than those of the trunk muscles, generally falling between 50ms and 150ms, with the variability between subjects tending to be low. Further, the bilateral TFL met the criteria for onset for all subjects and for all directions of perturbation, with the exception of the anterior (X) direction for which the criteria were met for all but 2 subjects. In sitting, however, the onset latencies for these muscles tended to be somewhat longer, with fewer subjects meeting the onset criteria in several directions. For those subjects in whom the criteria were met, however, the latencies for the TFL in sitting were still comparable to those for the muscles of the trunk. In both test postures, the shortest latencies tended to coincide with the directions of perturbation for which the TFL displayed the highest EMG activation levels over the initial 250ms period (Figure 3.6A).

For the muscles of the trunk, the mean onset latencies in standing were typically longer than those for the TFL, falling between 100ms and 200ms, with a few exceptions. In sitting, a somewhat larger range of onset latencies was observed, typically between 70ms and 250ms, again with a few exceptions. The muscles of the trunk were also found to meet the criteria for onset more reliably in standing than in sitting, with the abdominal muscles often failing to reach the onset criteria following perturbations in the posterior and contralateral directions in the seated posture. For those cases in which the muscles did reach the criteria set for onset, the shortest latencies tended to coincide with the directions of perturbation for which the muscle in question displayed the highest EMG activation levels over the initial 250ms period (Figure 3.6A). For example, in sitting, the onset latencies for the abdominal muscles tended to be shortest following surface translations in the ipsilateral-anterior directions, while the muscles of back tended to have their shortest onset latencies following ipsilateral-posterior translations.

Figure 3.6 – IEMG tuning curves



Tuning curves for the IEMG, based on the 8 directions of surface translation. A. Initial 250ms period following the onset of support surface movement. B. Second 250ms period following onset of support surface movement. The intersections of the curves along the 8 radii represent the mean of the normalized IEMG values, as described in section 2.3.2 EMG, for the subject population. For the purposes of illustration, each graph has been smoothed between these points using a spline function to produce a tuning curve.

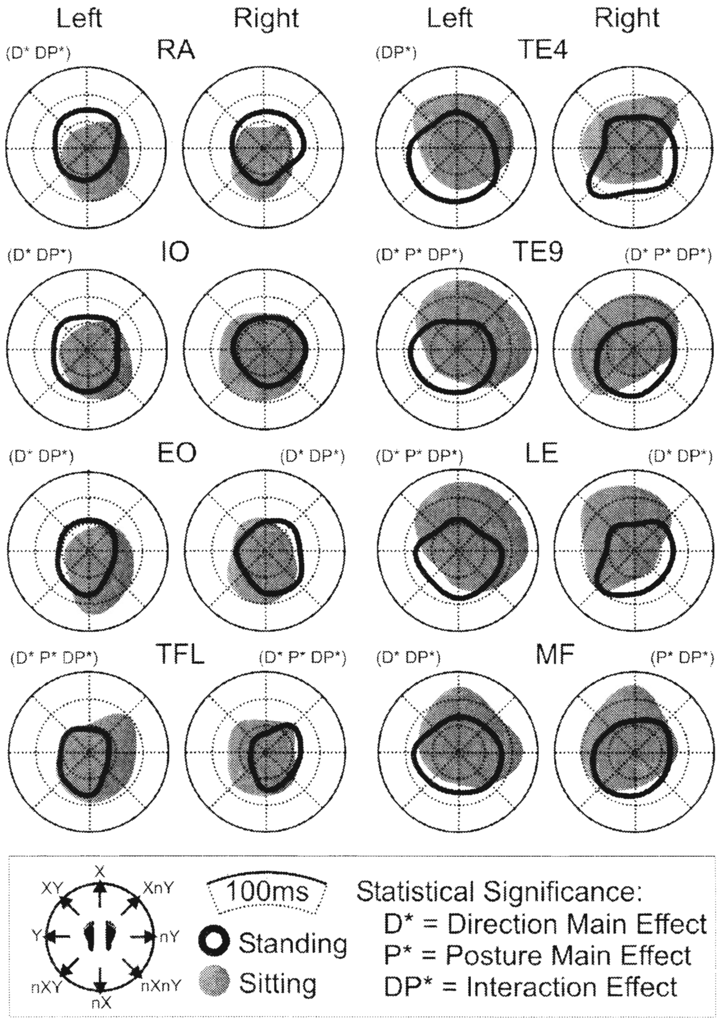


Figure 3.7 – EMG onset latency tuning curves
Mean EMG onset latencies for the 8 directions of surface translation.

3.6 Discussion

The purpose of this study was to provide a comprehensive description of the postural response in the trunk following support surface translation, with a focus on the effect of two variables: the direction of support surface translation, and the test posture. Our findings indicate that both the direction of the surface translation and the initial subject posture have a significant effect on both the biomechanical and neuromuscular response in the trunk to horizontal surface translation.

Effect of Limb Dynamics

The purpose of comparing the standing and sitting postures was to gain insight into the effect of limb dynamics on the trunk postural response. This effect was most evident in the displacement of the HAT CoM. Over the 500ms window of interest, the HAT CoM was subjected to a significantly smaller displacement in standing than in sitting (main effect of posture), regardless of the direction of translation (no interaction effect) (Figure 3.2C). This difference appears to result primarily from a delay in the onset of movement of the trunk in the direction of the support surface translation in standing, due to the initial dynamic response in the lower limbs. Following this delay, however, the displacement curves for the two test conditions appear to run more or less in parallel (Figures 3.2A & 3.2B). Bothner and Jensen (2001) have made a similar observation, indicating that the acceleration of the support surface may not be a major contributor to the initial destabilization of the HAT segment in standing.

The delay described above was also found to be directionally specific, with the HAT CoM following platform motion more quickly in the lateral (Y or –Y) directions that in the anterior (X) or posterior (-X) directions. This fits well with previous observations in the literature that the dynamic response in the lower limbs will differ based on the direction of translation, reflecting the biomechanical constraints of the body (Henry et al., 1998b).

The dynamic response of the lower limbs, however, did more than simply introduce a delay in the perturbation experienced by the trunk. In standing, the initial linear motion of the trunk segments was often opposite to the direction of support surface translation, particularly in the X-axis (Figure 3.3), while inter-segmental motion was observed prior to the onset of linear motion of the trunk in the direction of the support surface movement, particularly in the sagittal plane (Figure 3.4). This implies that the dynamic response of the lower limb in standing provided an initial perturbation to the trunk, prior to the perturbation delivered by the movement of the support surface. This is most evident in the inter-segmental moment-of-force profiles in the sagittal plane (Figure 3.4), where a biphasic response pattern was observed in standing, with the transition between phases temporally linked to the onset of trunk segment motion in the direction of the support surface translation. The lack of this initial response phase in the frontal plane is likely explained by the different biomechanical constraints of the lower limbs in this plane, which allow for less rotation than in the sagittal plane (wider based of support, parallel hip and ankle axes, etc.).

Biomechanical Constraints in the Trunk

Limb dynamics alone, however, cannot fully explain why the HAT CoM was less perturbed in the X-axis than in the Y-axis, as this pattern was clearly present in both the standing and sitting postures (Figure 3.2C – no significant interaction effect of translation direction and test posture). The significant effect of translation direction on the displacement of the HAT CoM, therefore, is likely related to the caudo-rostral delay in the progression of trunk segment CoM motion (Figure 3.3), which was more evident in the anterior-posterior (X-axis) motion of the trunk segments than in the lateral (Y-axis) motion. This suggests that the trunk may be more compliant in the sagittal plane than in the frontal plane - a finding also corroborated by McGill et al. (1994).

The inter-segmental motion patterns observed in this study can also be largely explained by biomechanical constraints. The moment-of-force patterns at the LxSx and TxLx levels were, without exception, similar in shape, but of greater magnitude at the more caudal level. As these patterns were estimated by an inverse dynamics analysis, it follows that they can be largely explained by inertial properties. The similarity in shape, however, can also be explained to a certain extent by the muscular architecture of the trunk, in which those muscles best able to generate high moments-of-force also span several vertebral levels. As such, the moment-of-force patterns at the LxSx and TxLx trunk levels must be generated, at least in part, by the same muscles. This implies that the neural control at these two levels of the trunk is unlikely to be independent, baring independent segmental control within the same muscle and the ability to generate tension within an isolated portion of that muscle. Further, the fact that the moment-of-force patterns at the MidTx level also tended to be similar in shape to those at the more caudal levels suggests that the neural control required to produce the observed postural responses in the trunk need not be as complex as the multi-segmental nature of the movement patterns might otherwise imply.

The postural responses observed in the trunk were also generally eccentric, suggesting that the observed motion patterns resulted directly from the specific perturbations experienced by the trunk. Two notable exceptions to this rule, however, were observed: at the TxLx and MidTx levels following AR translation in standing, and at the TxLx level following PL translation in sitting. The moment-of-force patterns at the different trunk levels for these perturbation conditions, however, remained similar in shape. These concentric movement patterns, therefore, are likely explained by the action of the multi-segmental trunk architecture, and the caudo-rostral progression of movement in the trunk.

Specifically, it is likely that the initial muscular response occurred as a result of the perturbation at the LxSx level, resulting in eccentric movement at this level. Due to the action of multi-segmental muscles, however, this moment of force would then have been transmitted to the more rostal levels, either prior to the onset of movement at these levels, or at a greater magnitude that was necessary to control this movement, leading to concentric motion. This concentric motion was only observed in the sagittal plane, however. As such, it is possible that other factors may have been involved in producing these deviations from the otherwise eccentric movement patterns. The curvature of the spine in the sagittal plane may provide some predisposition to this pattern of motion, as this phenomenon was noted in both conditions in which the LxSx level was initially brought into flexion. It is also possible that a specific control strategy was used in these two conditions, unrelated to the biomechanical constraints described above, such as that needed to stabilize the head in space. Given that independent neural control at these two trunk levels is unlikely, however, a biomechanical explanation is more plausible. Further study, using a more detailed model of the trunk, taking into account factors such as the spinal curvature and the stiffness provided by the rib cage, would be required to fully understanding the role of biomechanical constraints in these observations.

EMG Activation

The EMG activation levels for the muscles of the trunk, and the TFL, were significantly affected by the direction of surface translation. This directional specificity, however, was different between the standing and sitting conditions (interaction effect), and for many of the muscles tested the activation levels were different for the two test postures (main effect of posture) (Figure 3.6).

Similar data has been previously reported in cats, where the direction of horizontal support surface translation was found to affect the EMG response from the thoracic and lumbar epaxial extensors (Macpherson and Fung, 1998). Furthermore, a change in quadrupedal stance distance was also found to affect this response, particularly at the lumbar level, suggesting a similar effect of limb dynamics on the trunk response to perturbation.

An effect of translation direction on the neuromuscular response in the trunk has also been observed in human bipedal stance, by Henry et al. (1998a). While this previous study focused on the response in the lower limbs, the TFL, as well as the RA and erector spinae (left side only) were also assessed. Despite a somewhat different perturbation protocol (90mm translation over 200ms, peak velocity 0.35m/s), the tuning curves reported by these authors for the EMG activity over the 70-270ms window following perturbation were similar to our results over the initial 250ms, with the onset latencies reported by these authors also similar to our findings.

Trunk muscle activation has also been previously assessed in sitting. Zedka et al. (1998) used a rapid tilt of the support surface, on which the subjects were directly seated with the legs extended. These authors reported a direction-specific activation of the trunk muscles, reflecting their anatomical placement in relation to the direction of perturbation. Our data confirm this finding, with the mono-polar activation patterns for the trunk muscles in sitting (Figure 3.6) coinciding closely with the directions of translation in which those muscles would be lengthened during the mono-phasic, largely eccentric movement patterns observed in this posture (Figures 3.4 & 3.5).

In the current study, the trunk muscle activity in standing was also found to reflect their anatomical placement relative the direction of perturbation, although this was somewhat less evident due to the dual nature of the perturbation experienced by the trunk in this posture. For the dorsal muscles (TE4, TE9, LE, MF), over the initial 250ms period, a direction specific response was observed which can be linked to the initial phase of the sagittal plane response following translations with an anterior component (mono-polar distribution seen in Figure 3.6A). Over the second 250ms, these muscles had an even higher level of activation for these anteriorly directed surface translations (Figure 3.6B), reflecting two factors. The first is that the second phase of the trunk response in standing began more than 250ms following the onset of platform motion (Figure 3.4), and as such the second 250ms window overlaps the two phases of the trunk response. The second is that the reversal of trunk motion that occurred between these two phases is likely accompanied by a degree of co-activation between the dorsal and ventral muscles, such that the dorsal musculature would remain active well past the onset of the second phase of the trunk response, even for perturbations with an anterior component. Conversely, the activation of the dorsal muscles over the second 250ms window, following translations with a posterior component, and the activation of the ventral muscles (RA, IO, EO) following translations with an anterior component (Figure 3.6B), can be linked directly to the second phase of the trunk response in the sagittal plane, which followed the onset of trunk motion in the direction of support surface motion. The fact that the ventral muscles showed very little direction specific tuning over the first 250ms (Figure 3.6A) is explained by the observation that there was much less trunk motion over the first 250ms following posterior (-X) translation of the motion base (Figure 3.4B) as compared to anterior (-X) translation (Figure 3.4A); likely explained by the anatomical constraints of the trunk (eg. the spinal curvature).

The TFL, unlike the muscles of the trunk, had mono-polar tuning curves for both test postures, and for both the initial and second 250ms-windows. Thus, TFL activation is more closely linked with the dynamic response of the lower limbs than with the motion of the trunk. This direction-specificity is likely related to stretch, in that the TFL response is most active for the directions of perturbation in which the movement at the hip causes this muscle to lengthen, with its shortest onset latencies also occurring in these directions.

The onset latencies of the trunk EMG were affected in a similar manner to the IEMG levels, with the shortest onset latencies occurring in the translation directions with the largest IEMG levels for the initial 250ms period (Figures 3.6A & 3.7). Of note, however, was the asymmetry that was evident in the onset latencies for the abdominal musculature (RA, IO, EO). The latencies for the left sided abdominals were significantly affected by the direction of perturbation (main effect of direction), although this direction effect was differently distributed between the two test postures (interaction effect). Of the right-sided abdominal muscles, however, this was true only for the REO. Although the handedness of the subjects in this study was not recorded, this asymmetrical behavior might be related to the fact that most individuals are right-handed. Given the symmetrical nature of the kinematic and kinetic motion patterns observed in the trunk, these asymmetrical onset latencies are unlikely to reflect different neural control strategies in the bilateral abdominal musculature, and are more likely due to differences in the passive mechanical properties of these muscles. As the observed movement patterns were largely eccentric, a smaller, more compliant muscle might be expected to have shorter onset latencies than larger, stiffer muscles. As such, these onset latencies are likely a poor indicator of the neural control required under these test conditions.

3.7 Conclusions

The biomechanical and neuromuscular responses in the trunk, following support surface translation, are significantly affected by both the direction of the translation and the initial subject posture, with an interaction effect between these variables. Further, these responses can be largely explained by the actual perturbation experienced by the trunk, and by its biomechanical constraints. As such, the actual neural control required to maintain or restore the upright posture of the trunk may be much simpler than would be suggested by the complex multi-segmental motion patterns that follow translation of the support surface.

4. Neuromuscular coupling in the control of trunk upright equilibrium.

Richard Preuss and Joyce Fung

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4.1 Preface

The second study in this series follows directly from the conclusions of the first. In describing the kinematic, kinetic and neuromuscular response in the trunk following support surface perturbation, a degree of interdependence was noted at all trunk levels. The purpose of this second study, therefore, was to determine the dimensionality (i.e. the degree of interdependence) of the neuromuscular and biomechanical descriptors of trunk motion following support surface translation.

Principal component analysis and independent component analysis were used as a means of uncovering the underlying relationships between the descriptive variables. Any such relationships in the EMG data must result, to a large degree, from the action of the nervous system, and as such may be viewed as relatively direct evidence of neuromuscular coupling (i.e. the coordination of the musculature by the CNS). Coordination within the biomechanical descriptors of trunk motion, on the other hand, must result in part from the coordinated response of the musculature, and may therefore be interpreted as indirect evidence of this same neuromuscular coupling.

4.2 Abstract

Previous findings have suggested that the postural response in the trunk following support surface translation is determined largely by the impedance of the system. Based on this, we hypothesized that a high degree of neuromuscular coupling would be present in the trunk, and that the degree of this coupling will be relatively unchanged between the standing and sitting postures. Principal component analysis was used to determine the dimensionality of specific biomechanical and neuromuscular descriptors of trunk motion,

while independent component analysis was used to determine the time-varying patterns underlying that dimensionality. For each data set, two independent components were found to explain the majority of the variance, suggesting a high degree of neuromuscular coupling in the trunk. Analysis of the EMG data revealed similar dimensionality, along with similar underlying basis vectors, for all directions of perturbation, in both the standing and sitting conditions, supporting the above hypotheses. Only the results from the kinematic data, however, fit closely enough with those of the EMG data to suggest that the control of these variables may be an explicit goal of the observed neuromuscular coupling. These findings fit well with the postulation that neuromuscular coupling may be the implicit result of a preset impedance of the trunk in controlling upright posture, rather than the expression of preset muscle activation patterns.

4.3 Introduction

The trunk represents a complex multi-articular body, and as such requires a degree of coordination between its multiple kinematic degrees of freedom (DoF) (Stokes and Gardner-Morse, 1994). Mechanically, the necessary coupling between joints is achieved through the action of multi-articular muscles (Hogan, 1985), which make up the majority of the trunk musculature. For this mechanical coupling to be functional, however, a degree of coordination must also exist between muscles, which can only be achieved via neural control. The coordinated action of multiple muscles may therefore be described as neuromuscular coupling.

The central nervous system (CNS) must ultimately be responsible for the neuromuscular coupling necessary to achieve coordinated movement. This may occur, at least in part, at the higher levels of the CNS, although whether descending commands from these higher centres encode explicit (Holdefer and Miller, 2003) or implicit (St-Onge and Feldman, 2004) coordinated muscle activity remains an active topic of debate (e.g. Gottlieb, 1998; Ostry and Feldman, 2003; Tresilian, 1999). The coupling that occurs at the spinal cord level, however, is better understood. Inter-muscular reflex pathways allow for both inhibitory (e.g. reciprocal inhibition) and excitatory (e.g. length-dependent reflex pathways) influences between muscles crossing the same joint, and may even extend to multiple segmental levels (Nichols, 1994). Due to the presence of these spinal and proprio-spinal connections, any given muscle's action cannot be independent of the action of the other muscles to which it is linked. The full extent of these anatomical connections, however, remains to be determined. Furthermore, the functional interdependence of those muscles connected via reflex pathways is variable, depending on both the context and the task (e.g. Nielsen and Kagamihara, 1992).

Statistical techniques, such as principal component analysis (PCA), are powerful tools for the identification of neuromuscular coupling, for two primary reasons. The first is that PCA acts as a "data-driven filter" (Daffertshofer et al., 2004), allowing the user to tease apart the deterministic and stochastic components of the data. The second is that PCA provides a means to uncover hidden relationships within the data (Hasan and Thomas, 1999). Specifically, if a data set with N original variables can be explained by a linear combination of M principal components (PCs), then the remaining N-M relationships represent imposed constraints between the original N variables within the data set. For biomechanical and neuromuscular data, such relationships are indirectly (in the case of biomechanical variables) and directly (in the case of EMG data) indicative of neuromuscular coupling. In other words, the underlying dimensionality of a set of biomechanical or neuromuscular variables infers the degree of neuromuscular coupling that was present in the observed movement or task (the lower the dimensionality, the greater the degree of neuromuscular coupling).

A potential weakness of PCA, however, was revealed in a recent comparison of matrix factorization algorithms, using both simulated and experimental data sets (Tresch et al., 2006). For the simulated data, for which the original basis vectors were known, PCA was weaker than several other methods at identifying those vectors. The best performing algorithms, and those recommended by these authors, were two variations of independent component analysis (ICA); one applied to the PCA reduced-dimension data (ICAPCA), and the second using a predetermined number of bases (i.e. a pre-determined dimensionality for the data set). The strong performance of the ICAPCA algorithm, however, implies that PCA remains a computationally efficient means of revealing the underlying dimensionality of a data set. It may, however, best be used in conjunction with other algorithms, such as ICA, for better identification of the basis vectors underlying the original data.

Another potential weakness of these matrix factorization algorithms is that, although they may separate the stochastic elements of the data set from the deterministic elements, they are not capable of determining whether the organization underlying the data is a result of some active process, such as neuromuscular coupling, or simply the result of inherent structural similarities between individual variables. For example, if multiple signals from independent sources have similar frequency spectra, a few harmonics would be capable of reproducing each signal with great accuracy (Bracewell, 1989). Such structural similarities cannot, however, be interpreted as interdependence. The potential for structure arising by random chance must, therefore, be accounted for when using techniques such as PCA.

Our previous work has shown that the kinematic, kinetic and neuromuscular responses in the trunk, following perturbation of the support surface, are dependent on both the direction of perturbation and on the subject's initial posture (sitting vs. standing) (Chapter 3). Despite the significant variations in the postural response in the trunk between perturbation conditions, it was noted that each variable could be largely explained by the interaction of the movement of the support surface and the biomechanical constraints of the body: specifically its mechanical impedance (inertia, stiffness, and damping).

As the passive stiffness of the trunk is low (Cholewicki and McGill, 1996), and as the stiffness provided by the musculature is due more to the action of spinal pathways than to the intrinsic properties of skeletal muscle (Nichols, 2002), the stiffness of the trunk is largely under the control of the CNS. The inertial properties of the trunk may even be subject to a degree of CNS control, as the inertia of a multi-articular system may be determined in part by its geometry or posture (Hogan, 1985). The impedance of the trunk, at any given posture, may therefore be set by the coordinated action of the trunk musculature.

We hypothesize that a high degree of neuromuscular coupling is present in the trunk, in the control of upright equilibrium following postural perturbation. Furthermore, based on the postulation that the goal of this neuromuscular coupling is to regulate the impedance of the trunk, we hypothesize that the degree of neuromuscular coupling will be relatively unchanged between the standing and sitting postures, despite our previously observed differences in the response to perturbation (Chapter 3). PCA will be used to determine the underlying dimensionality of the kinematic, kinetic and neuromuscular variables previously used to describe these postural responses in the trunk (Chapter 3).

The results of these analyses will then be compared with an analysis of similarly structured, but randomly generated data, in order to determine if the variability explained in the biomechanical and neuromuscular data is greater than that attributable to random chance alone. Finally, the fastICA algorithm described by Hyvärinen and Oja (2000), will be used as an additional tool to better illustrate the vectors represented within the identified dimensionality.

4.4 Methods

4.4.1. Data Acquisition

Subjects

Data were collected from 13 male volunteers, aged 18 – 23 yrs, recruited from a university student population. Exclusion criteria were: a history of any mechanical back pain or injury; history of any neurological, vestibular or other condition affecting balance; history of any significant lower extremity injury; previous diagnosis of spinal scoliosis. All subjects provided written, informed consent prior to participation. Ethics approval for this study was received from the ethics committee of the Montreal Centre for Interdisciplinary Research in Rehabilitation (CRIR). The kinematic, kinetic and neuromuscular aspects of the postural response in the trunk for these subjects have been previously described in detail (Chapter 3).

Test Postures

Data was acquired in two postures: standing and sitting. In standing, the subjects were barefoot, and were instructed to stand with their feet at shoulder width, with their arms resting by their sides (Figure 4.1A). The initial foot position was marked on the support surface in order to ensure that the same foot position was adopted for each trial. In sitting, the subjects were firmly strapped into a custom made chair, secured to the support surface, with the lower extremities constrained to move with the chair, and the arms crossed over the chest in order to minimize the role of the upper extremities (Figure 4.1B).

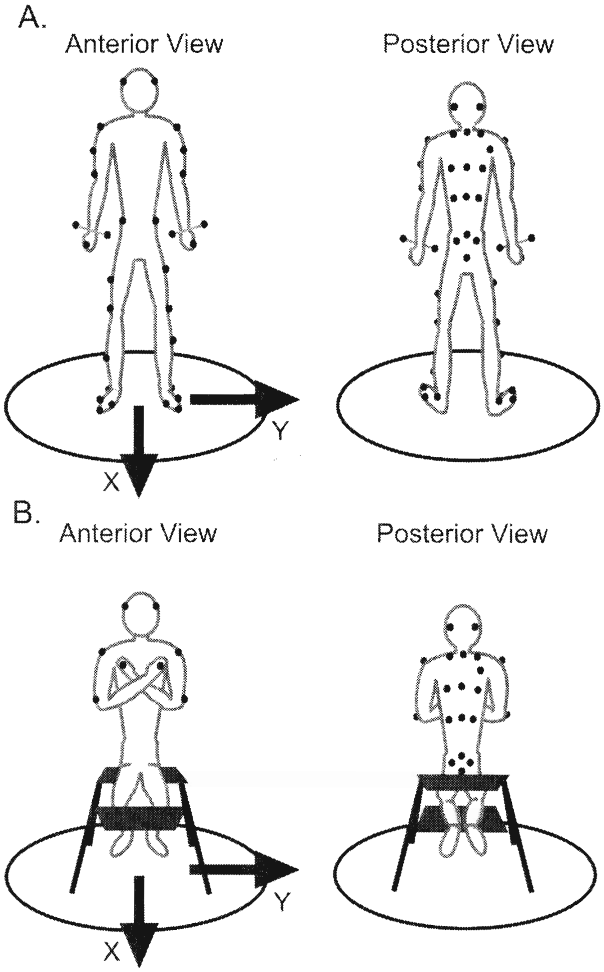


Figure 4.1 – Test postures and marker placements
A. Standing and B. Sitting.

In order to ensure that the subjects' initial trunk position was similar in the two test postures, two measures were used. In the sagittal plane, the lumbar lordosis was measured using a flexible rule, ensuring that the measures in standing and sitting were within the 5o window of intra-tester repeatability described by Youdas et al. (1995), using the trigonometric technique described by these authors. In the frontal plane, iliac crest height was measured using an iliac crest level instrumented with an inclinometer, ensuring that the measures were within the 1o window of intra-tester repeatability described by Piva et al. (2003). Based on these criteria, no differences were noted in the starting trunk postures from the standing to the sitting condition.

Surface Translation Parameters

Surface translations were delivered by a six-degrees-of-freedom motion base (MB) (Fung et al., 1998; 2003). The total amplitude of each perturbation was 15cm, delivered using a ramp profile of 700ms duration. The initial 500ms following perturbation onset were used for further analysis, consisting of the initial MB acceleration, lasting 250ms, and a period of motion at a constant linear velocity of ~0.45m/s. The final deceleration phase of the MB movement was purposely excluded from analysis, as this constitutes a second perturbation that may aid in the recovery of balance (Carpenter et al., 2005).

Test Protocol

Each subject experienced 4 horizontal surface translations in 8 different directions, at 450 intervals around the full circle, for each test posture. The 32 trials for each test posture were divided into 2 blocks of 16, with each block containing 2 trials per direction, delivered in a random order. This block randomization was used to minimize the potential for habituation, by decreasing the likelihood of multiple consecutive trials in the same translation direction. Further, this method minimizes the subjects' ability to predict the direction of the upcoming perturbation, thus minimizing the likelihood of direction specific anticipatory actions, such as leaning in the direction of the expected perturbation. For all subjects, testing was first done in the standing posture, followed by the sitting posture.

Kinematic Data

Kinematic data was acquired using a 6-camera Vicon 512 motion analysis system (Vicon Motion Systems Ltd.), with three dimensional marker position sampled at 120Hz. Two linked-segment models were used, with the trunk divided into pelvic, lumbar (L1-L5), lower thoracic (T7-T12) and upper thoracic (T1-T6) segments (Crosbie et al., 1997a). The standing model consisted of 46 reflective markers, with the body divided into 17 segments, including the 4 trunk segments (Figure 4.1A). The model in sitting consisted of 24 markers, with a total of 5 segments (the lower limbs were not modelled; the arms were included in the upper thoracic segment) (Figure 4.1B). An additional 4 reflective markers were affixed to the MB surface in order to monitor the movement of the support surface.

Two kinematic variables of interest were calculated: the orientation of each trunk segment in 3-dimensional space (relative to a fixed, external axis system), and the relative orientation of the adjacent trunk segments, representing the inter-segmental trunk angles at the mid-thoracic (MidTx), thoraco-lumbar (TxLx), and lumbo-sacral (LxSx) levels (inter-segmental angles were based on the relative orientation of an axis system fixed to move with the rostral segment within an axis system fixed to move with the caudal segment). Prior to inclusion in the kinematic models, individual marker position was low-pass filtered at 8Hz using a dual-pass, 4th order digital Butterworth filter. After modelling, the kinematic variables of interest were filtered again, with a cut-off frequency of 3.5Hz, based on a power spectral analysis of these data. Kinematic modelling was performed in Bodybuilder software (Vicon Motion Systems Ltd.). Digital filtering was performed in Matlab (The MathWorks, Massachusetts, U.S.A).

Inter-Segmental Moments-of-Force

Estimates of the net inter-segmental moments-of-force at the three inter-segmental trunk levels described above were calculated using a 3-dimensional, top-down, inverse dynamics approach (Kingma et al., 1996). All anthropometric variables were adapted from deLeva (1996) and Pearsall et al. (1996), except the moments of inertia on the trunk segments, which were approximated as cylinders with radius equal to half the anterior-posterior depth at the mid-point of the segment (taken from individual subject measurements). Calculations were performed in Matlab (The MathWorks, Massachusetts, U.S.A). After modelling, these data were filtered, as above, at a cut-off frequency of 3.5Hz.

Inter-Segmental Powers

Inter-segmental powers were calculated as the product of the inter-segmental moment-of-force and the first derivative of the inter-segmental trunk angle (Winter, 1990), for the 3 inter-segmental trunk levels.

Electromyographic Data (EMG)

Surface EMG was acquired using a TeleMyo surface EMG measurement system (Noraxon U.S.A. Inc.): operating bandwidth 10-350Hz; effective common mode rejection ratio (CMRR) 130 dB DC, >100 dB at 60 Hz, minimum 85 dB; fixed overall per-channel gain 2000. Signals were acquired using pre-gelled, disposable Ag/AgCl electrodes (10mm diameter circular conductive area) in a bipolar configuration, with a centre to centre distance of <4cm, parallel to the muscle fibres, following careful skin preparation. EMG were digitally converted using a 12bit A/D board over a +/-5V range, sampled at 1080Hz, and stored for further analysis. Prior to analysis, all EMG signals were high-pass filtered using a dual-pass, 4th order Butterworth filter, with a cut-off of 40Hz, in order to minimize the appearance of electrocardiographic artifact (ECG).

EMG activities were acquired bilaterally from eight sites on the trunk and pelvis: Rectus Abdominis (RA), Internal Oblique (IO), External Oblique (EO), Upper Thoracic Paraspinals (TE4), Lower Thoracic Erector Spinae (TE9), Lumbar Erector Spinae (LE), Lumbar Multifidus (MF) (McGill, 1992), and Tensor Fasciae Latae (TFL). Precise electrode placement has been previously described (Chapter 3, Table 3.1). During testing, the activity of the right IO was visually assessed, using an oscilloscope, to ensure that the subject was fully relaxed prior to the onset of perturbation.

The linear envelope of each EMG signal (LEMG) was used for all further analyses, as the LEMG has been shown to approximate the tension profile of the muscle in question (Winter, 1990). The LEMG was produced by full-wave rectifying (FWR), and low-pass filtering each EMG signal using a 2nd order digital Butterworth filter, with a cut-off of 3Hz (Kavcic et al., 2004).

4.4.2. Data Analysis

Five principal variables were analyzed: inter-segmental angular movement for the 3 trunk levels; segment orientation for the 4 trunk segments; inter-segmental moments-of-force for the 3 trunk levels; inter-segmental powers for the 3 trunk levels; LEMG profiles for the 16 muscles of the trunk and pelvis. All data were analyzed over the first 500ms following perturbation onset.

The first 4 variables above (i.e. inter-segmental angular movement, segment orientation, inter-segmental moments-of-force, and inter-segmental powers) were normalized as a proportion of the largest value for each subject in a given perturbation direction, in order to better compare across subjects. For example, if the largest angular movement in the trunk, for a given trial, was at the lumbo-sacral level in the sagittal plane, then the remaining inter-segmental angular movements, in all 3 planes, would be normalized as a proportion of this movement. This technique of normalization was chosen for two reasons. First, these data are subject to a degree of measurement error, potentially resulting in poor signal to noise ratios in the off-axis planes of motion, which might bias the analysis if these were to be magnified in the normalization process. Second, Scholtz and Schoner (1999) have suggested that not all degrees of freedom are controlled to the same extent during movement, such that only the movements in the plane of the perturbation may be closely controlled by the CNS. As such, it was not considered desirable to remove the effect of the relative amplitude from these data.

Each LEMG profile, however, was normalized to its own amplitude over the duration of the 500ms window, by subtracting the minimum value and dividing by the adjusted maximum value, effectively giving each muscle profile a range from zero to one. The

EMG was normalized in this manner for two reasons. First, the recorded amplitude of each surface EMG signal is affected by factors which are independent of the actual level of electrical activity within the muscle, but which may not be equal for each recording site (De Luca, 1997). Second, the amplitude of the acquired EMG signal is affected by factors such as the size of the recorded muscle (De Luca, 1997), and is therefore not necessarily indicative of the strength of the neural command to the muscle, but more of the anthropometric and physiological properties of the muscle itself. As such, the normalization technique chosen effectively removes the influence of amplitude, while maintaining the time-varying properties of each EMG activation profile.

This method of normalization for the LEMG data, however, has a potential drawback, in that the activation level for all 16 of the muscles studied may not increase above baseline levels for every trial. In an inactive muscle, any variation about the baseline would therefore be amplified by the normalization procedure, potentially allowing inactive muscles to contribute to the statistical variability of the overall data set. As such, a second series of EMG data was created in which the normalized activation level for any muscle found to be inactive during the 500ms following the onset of MB movement was set to zero. A muscle was considered inactive if no 50ms interval was found, over the 500ms window of interest, for which the mean amplitude of the FWR EMG exceeded baseline levels by at least 2 standard deviations. The baseline EMG was set from the mean and standard deviation of the FWR EMG over the 50ms window immediately preceding the onset of support surface movement.

Following normalization, the data representing each of the 5 principal variables described above, including both series of EMG data, were organized in 3 ways for analysis. First, the data from the 4 individual trials for each subject, for each combination of perturbation direction and test posture, was organized in matrix form in order to analyze any within subject variability (e.g. EMG subject data matrices = 540 frames x 64 muscle profiles; inter-segmental angular movement data matrices = 60 frames x 36 angle profiles; etc.). Second, the ensemble average (EA) of these 4 individual trials per subject, for each combination of perturbation direction and test posture, was calculated for each individual variable (e.g. LxSx flexion/extension; LxSx side-bending; etc.). The ensemble averages for all 13 subjects were then grouped into matrix form for each perturbation condition, and for each of the 5 principal variables, in order to analyze any between subject variability (e.g. EMG EA data matrices = 540 frames x 208 muscle profiles; inter-segmental angular movement data matrices = 60 frames x 117 angle profiles; etc.). Finally, the EA data for each of the two test postures were combined into a single matrix, including all subjects and perturbation directions, for each of the 5 principal variables (e.g. EMG data matrices = 540 frames x 1664 muscle profiles; inter-segmental angular movement data matrices = 60 frames x 936 angle profiles; etc.).

The dimensionality of each data matrix was then assessed, using principle component analysis (PCA), by determining the minimum number of principal components (PCs) required to produce the observed movement patterns. Singular value decomposition (SVD) was used as a computationally efficient means of finding the PCs, along with the eigenvalues reflecting the variance explained by the PCs (and hence the explained variance of the original data) (Jolliffe, 1986). PCs were initially extracted and retained based on the a priori guideline that the underlying PCs should explain a cumulative percentage of the total variation of ≥90%. This value was chosen as it provides a means of reducing the number of variables, while preserving most of the information contained in the original data. The final step was an independent component analysis (ICA) of the data matrices containing the ensemble averaged data (the 2nd and 3rd organization methods described above), using the fastICA algorithm described by Hyvärinen and Oja (2000), with the number of initial bases based on the dimensionality of the data revealed by PCA (as opposed to the ICAPCA algorithm described by Tresch et al. (2006) in which the ICA was run on the PCA reduced-dimension data). Both the PCA and fastICA algorithms were performed in Matlab (The MathWorks, Massachusetts, U.S.A).

Simulated, Pseudo-Random Data

Data sets containing pseudo-randomly generated signals were produced for comparison with each of the data sets above. Each individual variable within these sets was produced as the sum of 9 sine waves of random amplitude, random phase shift within the 500ms window, and a random frequency between 1Hz and 3Hz (3.5Hz for the simulated kinematic and kinetic data). The randomization of each component was performed using the "rand" function in Matlab (The MathWorks, Massachusetts, U.S.A).

For the simulated kinematic / kinetic data sets, 104 [60 x 36] matrices were generated for comparison with the individual subject data (13 subjects x 8 directions = 104). Another group of 8 [60 x 117] matrices were generated for comparison with the ensemble averaged data matrices. These 8 matrices were then combined into a single [60 x 936] matrix for comparison with the combined data matrix described above. A similar procedure was used for the simulated EMG data sets. These included 104 [540 x 64] matrices; 8 [540 x 208] matrices; and a single [540 x 1664] matrix.

PCA was performed on each generated matrix, as described above, with ICA also performed on the 2nd and 3rd organization methods. Two-sample, two-tailed t-tests, assuming equal variance, were performed on the percent variability explained by the first two PCs for the 1st and 2nd organization method, for each of the 5 principal variables with their pseudo-random counterparts, in order to determine if the variability explained by the first 2 PCs in these data was greater than that attributable to random chance. Due to the number of statistical comparisons, an α-level of 0.001 was set for all comparisons.

4.5 Results

Missing Data

In the standing posture, two of the subjects tested were not able to maintain their balance without stepping following anterior (X) surface translation. Further, EMG data from the right TFL of one subject, right LE for one subject, and left LE for 2 subjects were found to have been corrupted. The matrix components representing these missing data were set to zero, so as not to affect the variability of the overall data set. Further, these data were excluded when determining the ensemble averages for those analyses.

Principal Component Analysis

PCA results indicated that the majority of the variability in each of the principal variables could be accounted for by 2 components, in both test postures. Table 4.1 provides a summary of the percent variance explained by the first 2 principal components for each of the 5 principal variables, as well as their pseudo-random counterparts, and the results of the statistical comparisons (t-tests) for these data.

Table 4.1 - Percent variance explained by 2 principal components

Data Sets	Posture	Value	IS Angles	Segment Orient.	IS Moments	IS Powers	EMG	EMG No Inact.	Rand Kin	Rand EMG
A.	Standing	Mean	*97.5%	*98.9%	*98.6%	*96.8%	*94.2%	*94.5%	83.8%	88.8%
		Min.	89.1%	95.2%	90.1%	85.5%	82.2%	90.0%	76.6%	85.9%
		Max.	99.7%	>99.9%	>99.9%	>99.9%	99.0%	97.8%	90.2%	91.5%
	Sitting	Mean	*99.0%	*99.7%	*99.8%	*97.7%	*91.6%	*94.9%		
		Min.	93.7%	98.6%	99.4%	86.4%	83.7%	89.7%		
		Max.	99.9%	>99.9%	>99.9%	>99.9%	97.8%	98.5%		
B.	Standing	Mean	*96.0%	*98.5%	*93.3%	82.1%	90.6%	*95.4%	83.6%	87.9%
		Min.	94.7%	97.5%	89.8%	75.2%	87.7%	94.2%	81.5%	87.5%
		Max.	96.8%	99.3%	96.3%	87.2%	92.8%	96.4%	85.4%	88.5%
	Sitting	Mean	*98.3%	*99.5%	*97.1%	88.8%	84.9%	*95.8%		
		Min.	97.6%	99.2%	94.1%	82.0%	83.2%	94.7%		
		Max.	99.2%	99.8%	99.2%	95.9%	87.3%	97.3%		
C.	Standing		95.8%	98.3%	91.9%	80.2%	89.4%	94.9%	83.3%	87.8%
	Sitting		98.1%	99.4%	96.0%	86.0%	84.0%	95.2%		

Table Legend

A. Data sets including individual trial data for each subject, and each perturbation direction. Means are reported across all subjects and perturbation directions. Minimum and maximum are reported for any single subject and perturbation direction.

B. Data sets including ensemble averaged data for each subject, combined for each of the 8 directions of perturbation. Mean, minimum and maximum values are reported across all perturbation directions.

C. Single data set for each test posture, including ensemble averaged data for each subject for all 8 directions of perturbation (no statistical comparisons).

IS: inter-segmental

EMG No Inact.: analysis with inactive muscles removed

Rand Kin: Pseudo-random data sets simulating the kinematic / kinetic data

Rand EMG: Pseudo-random data sets simulating the EMG data

* indicates that the variance explained is significantly greater than for a data matrix of random variables ($p<0.001$)

Pseudo-Randomly Generated Data

PCA of the pseudo-randomly generated data sets found that the first 2 principal components explained ~84% of the variance in the simulated kinematic / kinetic data sets, and ~88% of the variance in the simulated EMG data sets (Table 4.1). For both the simulated kinematic / kinetic data and EMG data, the variance explained by these first 2 PCs showed a slight decrease as the size of the data sets increased.

The results of the ICA found the underlying patterns to be highly consistent for all of the simulated data sets. Figure 4.2 illustrates the patterns revealed by ICA for these pseudo-random data sets, for the 2nd and 3rd organization methods described above, along with polar plots illustrating the variability explained by the first 2 PCs. Although no directionality was present in these pseudo-random data sets, they have been presented in the same manner as the acquired data sets (Figures 4.3-4.6) to facilitate comparison. It is also important to note that the time-varying patterns revealed by the fastICA algorithm are not extracted in a hierarchical manner (Hyvärinen and Oja, 2000), and are therefore not necessarily illustrated in the order in which they were extracted.

Inter-Segmental Angles

The variability explained by the first 2 PCs, for the inter-segmental angle data, was found to be significantly greater than for the pseudo-random simulated kinematic / kinetic data, at all levels of data organization, and for both test postures (Table 4.1).

ICA of the combined subject data (13 subjects, for each perturbation direction; set B in Table 4.1), based on 2 independent components, found 2 similar patterns underlying the inter-segmental angle data for all perturbation directions, for both test postures. Temporal differences were, however, noted between the patterns in the standing and sitting postures. Figure 4.3 illustrates the patterns revealed by ICA for the inter-segmental angle data, for the standing and sitting postures, along with polar plots illustrating the variability explained by the first 2 PCs for each perturbation direction.

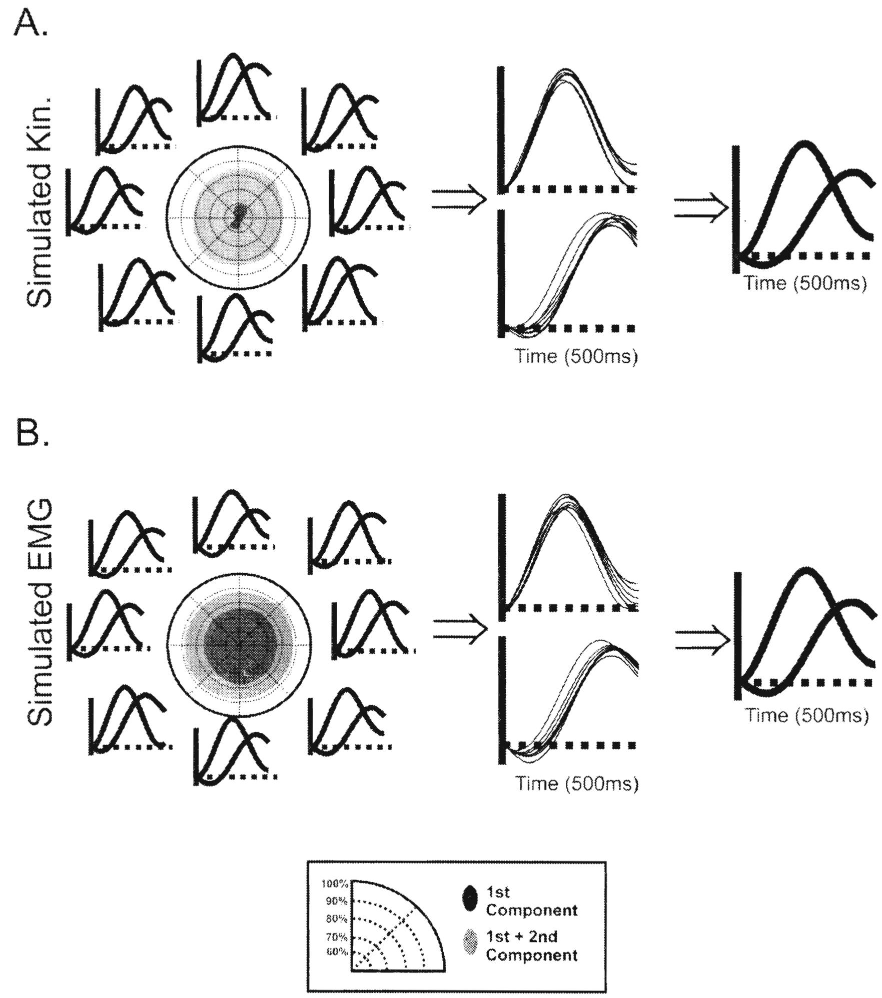


Figure 4.2 – PCA and ICA results: Pseudo-random data sets
Patterns underlying the pseudo-random data sets, for the simulated ensemble averaged data. A) Simulated kinematic & kinetic data. B) Simulated EMG data. For each variable: Left-Centre: Tuning curve representing the variance explained by the first 2 principal components for the 8 data sets simulating the ensemble averaged data for each perturbation direction (sets were arbitrarily assigned a direction to facilitate comparison with the acquired data). Left-Periphery: Patterns revealed by independent component analysis for each direction of translation, based on 2 independent components: x-axis = time(500ms). Centre: The two patterns revealed by ICA, for all 8 data sets. Right: Patterns revealed by independent component analysis for the data set simulating the combined ensemble averaged subject data, based on 2 independent components.

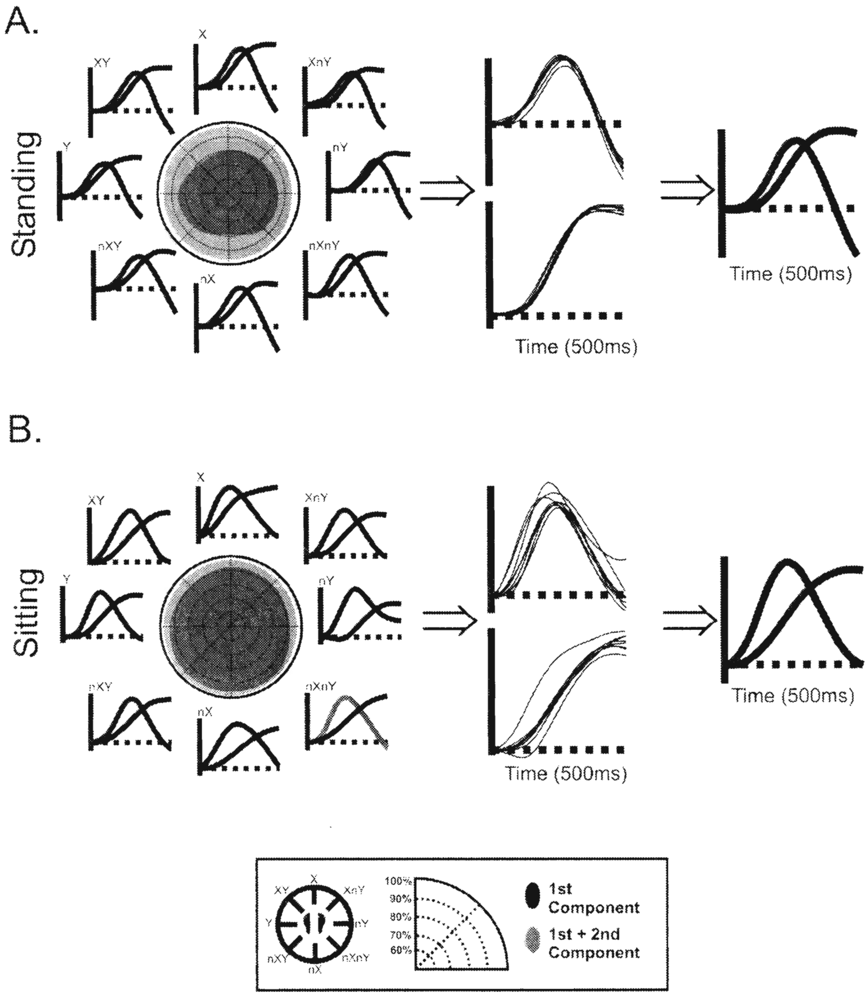


Figure 4.3 – PCA and ICA results: Inter-segmental angles

Patterns underlying the postural response to surface translation for the ensemble averaged inter-segmental angle data, for the A) standing and B) sitting test postures. For each variable: Left-Centre: Tuning curve representing the variance explained by the first 2 principal components for each of the 8 directions of translation. Left-Periphery: Patterns revealed by independent component analysis for each direction of translation, based on 2 independent components: x-axis = time(500ms). Centre: The two patterns revealed by ICA, for all 8 directions of perturbation. Right: Patterns revealed by independent component analysis for the combined ensemble averaged subject data (all directions), based on 2 independent components.

Segment Orientation

Similar to the inter-segmental angle data, the variability explained by the first 2 PCs, for the trunk segment orientation data, was found to be significantly greater than for the pseudo-random simulated kinematic / kinetic data, at all levels of data organization, and for both test postures (Table 4.1).

ICA of the combined subject data, based on 2 independent components, also found 2 similar patterns underlying the segment orientation data for all perturbation directions, for both test postures. As for the inter-segmental angular data, however, temporal differences were noted between the patterns in the standing and sitting postures for the segment orientation data. Figure 4.4 illustrates the patterns revealed by ICA for these data, for the standing and sitting postures, along with polar plots illustrating the variability explained by the first 2 PCs for each perturbation direction.

Inter-Segmental Moments

As for the kinematic variables, the first 2 PCs for the inter-segmental moment data were found to explain significantly more variability than for the pseudo-random simulated kinematic / kinetic data, at all levels of data organization, for both test postures (Table 4.1).

The time-varying patterns underlying the combined subject inter-segmental moment data, as revealed by ICA, were found to be more variable across perturbation directions than the patterns underlying the kinematic data. This was most evident in the standing posture, but also noted for these data in sitting. Figure 4.5 illustrates the patterns revealed by ICA for the inter-segmental moment data, for the standing and sitting postures, along with polar plots illustrating the variability explained by the first 2 PCs for each perturbation direction.

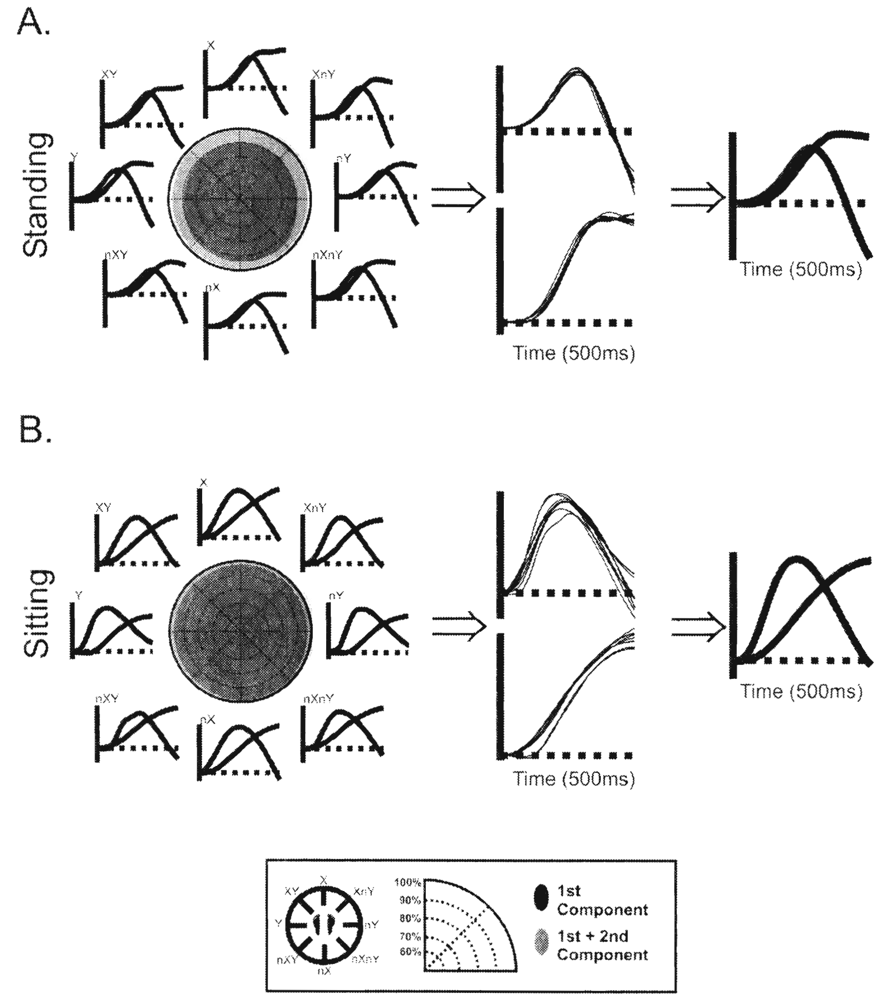


Figure 4.4 – PCA and ICA results: Segment orientation
Patterns underlying the postural response to surface translation for the ensemble averaged trunk segment orientation data, for the A) standing and B) sitting test postures. For each variable: Left-Centre: Tuning curve representing the variance explained by the first 2 principal components for each of the 8 directions of translation. Left-Periphery: Patterns revealed by independent component analysis for each direction of translation, based on 2 independent components: x-axis = time(500ms). Centre: The two patterns revealed by ICA, for all 8 directions of perturbation. Right: Patterns revealed by independent component analysis for the combined ensemble averaged subject data (all directions), based on 2 independent components.

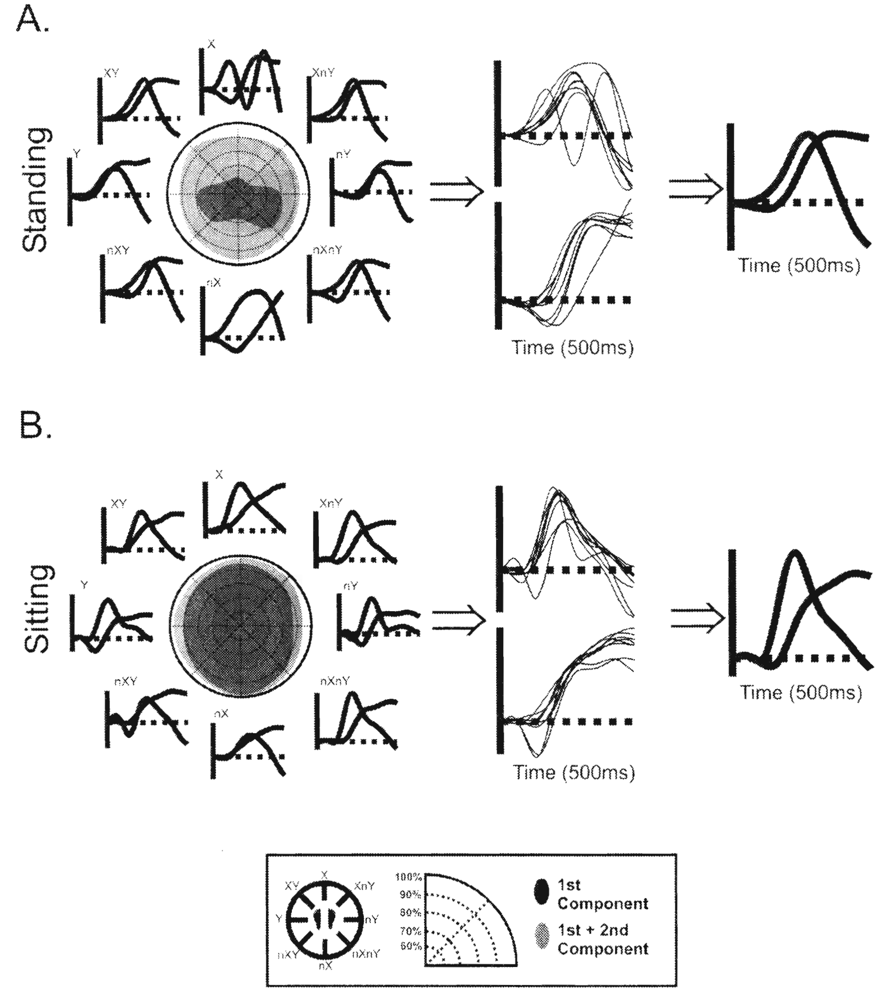


Figure 4.5 – PCA and ICA results: Inter-segmental moments
Patterns underlying the postural response to surface translation for the ensemble averaged inter-segmental moment-of-force data, for the A) standing and B) sitting test postures. For each variable: Left-Centre: Tuning curve representing the variance explained by the first 2 principal components for each of the 8 directions of translation. Left-Periphery: Patterns revealed by independent component analysis for each direction of translation, based on 2 independent components: x-axis = time(500ms). Centre: The two patterns revealed by ICA, for all 8 directions of perturbation. Right: Patterns revealed by independent component analysis for the combined ensemble averaged subject data (all directions), based on 2 independent components.

Inter-Segmental Powers

For the inter-segmental power data, a significant difference in the variability explained by the first 2 PCs, compared with the variance explained in the pseudo-randomly generated kinematic / kinetic data, was found only for the individual trial data.

When the ensemble averaged data was combined for all subjects, for each of the 8 directions, the variability explained by the first 2 PCs did not differ significantly from the pseudo-randomly generated data sets. This was true for both the standing and sitting conditions. As such, no further analysis was performed for the power data.

EMG

At the individual subject level, the variability explained by the first 2 PCs for the EMG data sets, both with and without the inactive muscles included, was significantly greater than for the pseudo-random simulated data sets. When ensemble averaged data was combined for all subjects, for each of the 8 perturbation directions, however, the variability explained by the first 2 PCs for the EMG data differed significantly from that explained in the pseudo-random data sets only when the inactive muscles were excluded from the analysis (Table 4.1). As such, further analysis was performed only on the EMG data sets with the inactive muscles removed.

ICA of the combined subject data (13 subjects, for each perturbation direction; set B in Table 4.1), based on 2 independent components, found 2 similar patterns underlying the EMG data (inactive muscles removed) for each of the 8 directions of perturbation, in both the standing and sitting postures. Figure 4.6 illustrates the patterns revealed by ICA for the EMG data, for the standing and sitting postures, along with polar plots illustrating the variability explained by the first 2 PCs for each perturbation direction.

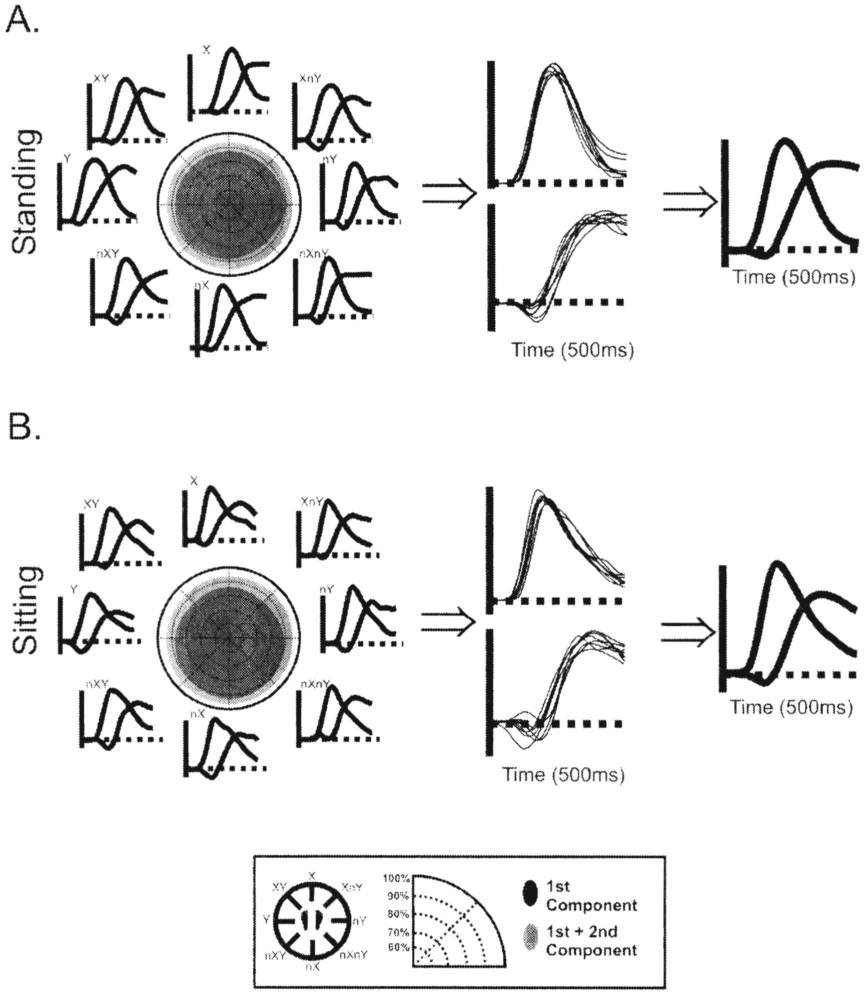


Figure 4.6 – PCA and ICA results: EMG with inactive muscles removed

Patterns underlying the postural response to surface translation for the EMG data, with inactive muscles removed, for the standing and sitting test postures. For each variable: Left-Centre: Tuning curve representing the variance explained by the first 2 principal components for each of the 8 directions of translation. Left-Periphery: Patterns revealed by independent component analysis for each direction of translation, based on 2 independent components: x-axis = time(500ms). Centre: The two patterns revealed by ICA, for all 8 directions of perturbation. Right: Patterns revealed by independent component analysis for the combined ensemble averaged subject data (all directions), based on 2 independent components.

4.6 Discussion

The findings of this study support the hypothesis that a high degree of neuromuscular coupling is present in the trunk in the maintenance of upright equilibrium following support surface translation. Specifically, 2 independent basis vectors were found to be sufficient to explain the majority of the variability in both the neuromuscular and biomechanical descriptors of trunk motion following multi-directional horizontal support surface translation. This interdependence was not the simple the result of structural similarities (such as frequency content) within the data, but reflects an imposed organization within these data sets from which we can infer an active neuromuscular coupling by the CNS.

The basis vectors revealed by ICA also provide important insight into the organization of these data across perturbation directions. The time-varying patterns of the basis vectors underlying the pseudo-random data were found to be highly consistent: more so than those underlying any of the other data sets analyzed (Figure 4.2). As each pseudo-random variable was generated independently of the others, but using a similar process, the consistency in time-varying patterns for the basis vectors underlying each of these data sets is most likely reflective of the similar structural aspects of these data. Within the biomechanical and neuromuscular data sets, more consistency was noted in the basis vectors for the kinematic (Figure 4.3 & 4.4) and EMG (Figure 4.6) data than for the moment-of-force data (Figure 4.5), across perturbation directions. This suggests that the variables describing the kinematic and neuromuscular response in the trunk are more structurally consistent than the resulting kinetics.

The reduced dimensionality in the EMG data (inactive muscles removed), regardless of the direction of support surface translation or initial test posture, and regardless of how that data was organized prior to analysis (Table 4.1), provides statistically robust evidence for the presence of a relatively fixed level of neuromuscular coupling within the trunk, under the current experimental paradigm (i.e. horizontal translation of the support surface translation, with an initially upright trunk posture). This, in fact, constitutes relatively direct evidence for neuromuscular coupling as, despite the myriad of factors which influence the signal acquired through surface electromyography (De Luca, 1997), the primary influence on this signal is the actual electrical activity within the underlying muscle. Under normal physiological conditions, this myoelectrical activity can be interpreted as the net influence of the CNS on that muscle. The results of the PCA on the EMG data, which were very similar for the two test postures (Figure 4.6 and Table 4.1), therefore serve to support our second hypothesis: that the degree of neuromuscular coupling would be relatively unchanged between the standing and sitting postures. The similarity in the basis vectors underlying the EMG data for the two test postures (Figure 4.6) further serves to support this hypothesis, providing evidence for a similar structure within these data.

The degree of coupling between the kinematic variables was also relatively fixed, and statistically robust. Unlike the EMG data, however, the coordination between the kinematic variables can only be seen as indirect evidence for neuromuscular coupling. As briefly outlined in the introduction, however, the kinematic and neuromuscular components of movement are inextricably linked (Hogan, 1985), as functional coordination in the multi-segmental trunk can only occur if the actions of the multi-segmental musculature are also well coordinated. As such the results of the PCA on the kinematic data provide further support for the existence of a high degree of neuromuscular coupling within the trunk.

The dimensionality of the inter-segmental moment-of-force data was also found to be somewhat consistent with that of the kinematic and EMG data. This is likely explained, at least in part, by the link between muscle force and EMG activation (Cholewicki and McGill, 1995). It has also been postulated that the specification of forces, through inverse dynamics calculations similar to those used to estimate the moment-of-force data in the current study, may be inherent in neuromuscular control (Hollerbach, 1982; Ostry and Feldman, 2003). Two factors from the results of the current study, however, cast some doubt as to the intrinsic relationship between the neuromuscular coupling described by the EMG data, and the coordination within the moment-of-force data. The first is that the results of the ICA, which can be said to be representative of the basis vectors underlying the original data (Tresch et al., 2006), were more structurally consistent for the EMG data (Figure 4.6), across perturbation directions, than for the moment-of-force data (Figure 4.5). Second, the actual variability explained by each individual component (PC) was much more variable across perturbation directions for the moment-of-force data (Figure 4.5) than for the EMG data (Figure 4.6), particularly in the standing posture.

Inter-segmental power was also analyzed, as this variable provides a degree of insight into the interaction between the kinetics and kinematics of movement. Specifically, this variable may be used to determine if the net muscular action at a joint serves to generate a movement (positive power = concentric muscle action) or to control a movement generated by some external force (negative power = eccentric muscle action). Although a reduced dimensionality was observed in these data, the degree of consistency was much less than in the kinematic and EMG data. Furthermore, when the ensemble averaged data for each subject was combined for each perturbation direction, the variability explained in these data did not differ from that which might be attributed to random chance. As such, these data provide no evidence for active coordination of inter-segmental powers within the trunk, following postural perturbation.

The invariance in the time-varying profiles revealed by ICA, for both the EMG (Figure 4.6) and kinematic (Figure 4.3 & 4.4) data, suggests that the neuromuscular coupling in the trunk may be related to some invariant aspect of the study paradigm, which might provide a common structure to these data. While much of this can be attributed to the methods used in pre-processing these data, such as filtering and normalization, the time varying aspects of the basis vectors underlying these data differed somewhat from those of the pseudo-random data (Figures 4.2). Furthermore, the variability explained by these first two vectors was greater for the EMG and kinematic data than for the pseudo-random data, suggesting that the underlying structure was not simply the result of common frequency spectra or the normalization methods used. The most likely explanation is that the invariability in these basis vectors is related to the movement profile of the support surface, as this was the only invariant factor across perturbation directions. This may also serve to explain the temporal difference between the two basis vectors underlying the kinematic data in the standing and sitting postures (Figure 4.3 & 4.4), as differences existed in the actual perturbation experienced by the trunk in these two conditions (Chapter 3), due to the presence or absence of a dynamic response from the lower limbs. This also fits very well with the previous observation that the postural response in the trunk can be largely explained by the biomechanical constraints of the system (Chapter 3), or more specifically its impedance. Impedance control would serve to limit the frequency response of the trunk following perturbation (the cut-off frequency of 3.5Hz for our biomechanical data was set based on a power spectral analysis of these data), as well as the amplitude of that response, thereby imposing a certain structure on the variables used to describe this response. As the impedance of the system is largely regulated via length-dependent spinal pathways (Nichols, 1994; Nichols, 2002), this method of motor control could further serve to explain the similarity in the patterns underlying the kinematic and EMG signals observed in the current study. The observed postural responses may therefore have been achieved by setting the impedance of the system about a specific geometrical configuration (Hogan, 1985), such as the initial upright posture. This method of CNS control would link the neuromuscular coupling in the trunk to the perturbation, independent of its direction, while still allowing for the emergence of direction specific kinematic and EMG patterns (Chapter 3).

The findings of the current study also fit well with previous findings which indicate that the actual movement patterns in the standing posture are somewhat more complex than those in sitting, following support surface translation (Chapter 3). Although the variance explained by 2 PCs for the kinematic and kinetic data were found to be similar for both test postures, the 1st PC accounted for a much larger proportion of that variability in the sitting posture than in the standing posture. This was not true, however, for the EMG data, in which the proportion of the variance explained by the first two PCs was similar for both test postures (but still larger than for the pseudo-random data). This suggests that, despite the increased complexity in the actual movement that occurs in the trunk in standing, the complexity of the neuromuscular coupling in the trunk required to coordinate the biomechanical response may be similar for both test postures.

Despite the numerous parallels between the results of the kinematic and EMG data in the current study, it is important to account for the fact that, even with the inactive muscles removed, the variance in the EMG data explained by 2 PCs was somewhat less than that for the kinematic data. This difference is likely attributable, at least in part, to the differences in how these data were normalized. The EMG data was normalized in such a way as to remove the effect of amplitude from the analysis, for all 16 channels of EMG, thus amplifying any stochastic components in the data. For the kinematic data, however, the normalization procedure effectively removed the effect of amplitude for comparison across subjects, but not between the different kinematic variables, so as to minimize the amplification of any stochastic components in the data. As such, it was somewhat foreseeable that a greater percentage of the variability of the EMG data would be excluded from the retained PCs (Daffertshofer et al., 2004). For the pseudo-random data, however, the opposite was true. As each variable was constructed using a randomization function, only the structural aspects of the data should have been non-stochastic. The differences in amplitudes between variables for the simulated kinematic / kinetic data would be expected to be smaller than in the actual data sets (in which off-axis movements were often quite small), thus making them more similar to the pseudo-random EMG data, despite the different normalization procedures. The frequency content of the simulated kinematic / kinetic data, however, was between 1 and 3.5Hz, while the simulated EMG was between 1 and 3Hz, this allowing somewhat more structural variability in the former.

Several previous studies have used similar matrix factorization techniques to analyze both kinematic and EMG data. While each of these studies used a slightly different protocol for both the pre-processing and analysis of the data, and each group of authors provided their own unique interpretation of the results, the common finding across these studies was that a reduced number of variables could account for the majority of the variance in the original data. Courtine and Schieppati (2004) used PCA to examine the spatio-temporal coordination in the segment orientation of the lower limbs during gait, when walking along both a straight and a curved path. Both gait patterns were found to have a low dimensionality, with 3 PCs accounting for more than 90% of the variance. Ivanenko et al. (2004) also studied gait, but used factor analysis (FA) to examine EMG data at different walking speeds and gravitational loads. Once again, a reduced dimensionality was found, such that 5 factors could account for about 90% of the total waveform variance across different muscles during normal gait, with little change in these factors at different walking speeds and gravitational loads. Ting and Macpherson (2005) and Torres-Oviedo et al. (2006) used nonnegative matrix factorization (NMF) to examine, respectively, EMG data and a combination of EMG and force data during the postural response to support surface translations in cats. Once again, a high percentage of the variability (>95% and >80% respectively) in the original data matrices was accounted for by a reduced number of variables (4 and 5 respectively).

As illustrated in the differing methodology of the examples above, the use and interpretation of statistical pattern analyses for biomechanical and EMG data remains somewhat subjective, and therefore constitutes a limitation of the current study. There is no universally agreed upon matrix factorization technique to use in these analyses, no universally agreed upon method to organize the data prior to analysis and no single method for determining the number of components to retain. Pre-processing of data may also pose a limitation, as illustrated by the high percentage of the variability accounted for by 2 PCs for our pseudo-random data sets. The use of linear enveloped EMG data may also remove certain aspects of the neuromuscular response, such as short-latency stretch reflex responses of brief duration. The linear envelope, however, provides an estimate of the muscular force profile (Winter, 1990), which is desirable for the analysis of mechanical coupling between joints. The interpretation of the results of this study, as well as of those described above, however, rely quite strongly on each of these factors. As noted by Hasan and Thomas (1999), the results of such analyses are seldom easy to interpret, although they remain valuable in uncovering the existence of hidden relationships within data.

4.7 Summary

The findings of this study suggest a high degree of neuromuscular coupling in the trunk following support surface translation. Two independent basis vectors were capable of explaining the majority of the variability in the acquired EMG data, in both standing and sitting, providing statistically robust evidence to support the presence of neuromuscular coupling. The dimensionality of this neuromuscular coupling was similar in the standing and sitting conditions, as were the basis vectors underlying that dimensionality. This was also true across perturbation directions. Two independent components were also sufficient to explain the majority of the variability in the biomechanical variables of the trunk, although only the results from the kinematic data fit closely enough with those of the EMG data to suggest that the control of these variables may be an explicit goal of this neuromuscular coupling. Each of these findings fits well with the postulation that neuromuscular coupling may be the implicit result of a preset impedance of the trunk, set to maintain an upright posture, rather than the expression of preset muscle activation patterns.

5. Are fixed muscle synergies used in the control of upright trunk equilibrium?

Richard Preuss and Joyce Fung

5.1 Preface

The final study in this series followed from the findings of the two previous studies, which implied a high degree of neuromuscular coupling in the trunk following support surface translation. As outlined in section 2.3.2, one of the leading theories on how this coupling may be achieved is through the activation of muscle synergies; defined as "the coordinated activation of groups of muscles with specific time-varying profiles" (d'Avella et al., 2003, pg. 300). The purpose of this third study, therefore, was to determine if one or more fixed spatio-temporal relationships was present in the electromyographic (EMG) signals acquired from the muscles of the trunk following support surface translation. The existence of such relationships could then be used to infer the presence of muscle synergies in the trunk.

5.2 Abstract

The control of upright equilibrium, following postural perturbation, requires a coordinated response from the musculature, which has been postulated to occur through the combined action of a limited number of fixed, universal, time-varying muscle synergies. Three criteria would need to be fulfilled if such fixed motor programs were responsible for the EMG activity observed following postural perturbation: 1) the overall EMG response must be characterized by groups of muscles with similar time-varying patterns of activation; 2) these groupings must be consistent across trials, for a given perturbation condition; 3) these groupings must be consistent across subjects, and symmetrical for perturbations with opposite lateral components. The EMG activation from 8 muscles of the trunk and pelvis was acquired, bilaterally, from 13 healthy subjects,

following multi-directional horizontal support surface translations, in 2 test postures: standing and sitting. A 2-step process, involving principal component analysis and cluster analysis, was used to identify those muscles with similar time-varying EMG profiles. Of the three criteria above, only the first was found to be satisfied, with muscle groups identified for each data set based on similarities in their spatio-temporal activation patterns. For individual subjects, however, more than half of the muscles tested were unaccounted for in the groupings consistently identified for any given perturbation condition. Futhermore, no significant consistency was identified in these grouping across subjects, with only limited symmetry observed, particularly in the standing posture. These data, therefore, do not support the use of fixed muscle synergies in the control of upright trunk equilibrium.

5.3 Introduction

It has been well established that individual muscles are not independently controlled during movement (d'Avella et al., 2003; Feldman et al., 1998a; Hogan, 1985). The question remains, however, as to how the coordinated muscle activity that is essential for goal directed movement is organized by the central nervous system (CNS). One means by which motor control may be achieved is through the explicit control of muscle activation (and therefore muscle force, stiffness, damping, etc.) by the CNS. This theory states that commands from the motor cortex to the muscles, via motor neurons, are distributed in hierarchically interconnected areas of the spinal cord, brainstem and forebrain, with the integration of sensory information into this system being processed in parallel systems. Each level, through their input and output connections, is then capable of organizing and regulating complex motor responses and actions (Ghez and Krakauer, 2000). Within this theory exists the notion of muscle synergies: groups of muscles activated together by a fixed motor program within the CNS (d'Avella et al., 2003; Saltiel et al., 2001; Ting and Macpherson, 2005). This theory states that functional muscle activation results from the combined action of a limited number of fixed, time-varying synergies (d'Avella et al., 2003), thus reducing the complexity of the motor control required to produce the coordinated muscle activity that occurs during movement.

Bernstein (1967), however, stated that when producing or controlling movement, mechanical factors and muscle excitation cannot be independent from one another, as the same pattern of muscle excitation may produce different kinematic results based on the actual internal and external mechanical forces acting on the system. As such, a one-to-one relationship between muscle excitation and movement does not, and cannot, exist. Under this reasoning, the use of fixed muscle synergies by the CNS may be impractical, given the scope of movement available to biological systems. As such, it is of particular importance to our understanding of motor control to determine if the muscle activity that coordinates movement does, in fact, result from the explicit activation of fixed, time-varying muscles synergies by the CNS.

Statistical pattern analysis techniques, and more specifically matrix factorization algorithms (Tresch et al., 2006), have recently gained popularity for the analysis of biomechanical and electromyographic data. One application of such algorithms is to tease apart the deterministic and stochastic components of movement, thereby acting as a data-driven filter (Daffertshofer et al., 2004). The usual interpretation of these results is that, despite the inherent variability present in movement, the deterministic components of movement may represent the underlying control structure. Furthermore, the number of deterministic variables identified in the movement data may represent the underlying dimensionality of that control structure. This dimensionality has been interpreted by several authors (e.g. d'Avella et al., 2003; Ting and Macpherson, 2005; Torres-Oviedo et al., 2006; Tresch et al., 2006) as the number of active muscle synergies.

One potential pitfall in using statistical pattern analysis techniques to identify muscles synergies from time-varying EMG profiles is that these techniques assume a degree of independence in the underlying control signals (Hyvärinen and Oja, 2000; Jolliffe, 1986). While, by definition, muscle synergies may be independently shifted in time (d'Avella et al., 2003), two or more synergies activated simultaneously might not be identified as independent. The number of deterministic factors identified, therefore, may not correspond with the number of active muscle synergies.

Despite this, if synergic activation is, in fact, the control strategy used by the CNS, then groups of muscles with common time-varying activation patterns should still be identifiable. For example, if two synergies are active, then as few as one, and as many as three, muscle groups with similar time-varying activation patterns may be present, depending on the degree of temporal overlap in the activation of each synergy. These groups include those muscles affected only by the first synergy, those muscles affected only by the second synergy, and those muscles affected by both synergies. As such, while the number of deterministic factors underlying the time-varying EMG signals may not necessarily correspond with the number of active muscles synergies, the presence of specific groups of muscles with shared spatio-temporal activation characteristics would provide a degree of support for the theory of synergic muscle activation by the CNS.

In a previous study (Chapter 4 of this thesis) we used a combination of principal component analysis (PCA) and independent component analysis (ICA) to demonstrate that 2 deterministic factors were sufficient to explain the majority of the variability in the trunk EMG following multi-directional surface translation; implying a high degree of coordination between the muscles of the trunk in the maintenance of upright posture (described as neuromuscular coupling). One means by which this coupling might be achieved would be through the action of two or more fixed muscle synergies. The observed EMG response, however, was closely tied to the trunk kinematics, suggesting that control of the spatial aspects of movement by the CNS, rather than explicit synergistic muscular activation, might also explain the motor control underlying the observed neuromuscular coupling.

The purpose of this paper is to test the hypothesis that the explicit activation of fixed, time-varying muscle synergies by the CNS is responsible for the high degree of neuromuscular coupling observed in the trunk following support surface translation. We postulate that if the upright posture of the trunk is regulated by a limited number of muscle synergies, then the time-varying EMG patterns of those muscles involved in the postural response following support surface translations should be characterized by groups of muscles with similar time-varying patterns of EMG activity. Furthermore, if these muscle synergies represent fixed motor programs, then once the stochastic aspect of the EMG signals has been removed, the muscle groupings identified for a given perturbation direction should be consistent across trials. Finally, if these fixed muscle synergies represent universal motor programs, then a degree of consistency should be present in the identified muscle groupings across all subjects, and a degree of symmetry should be evident with respect to the groupings identified for perturbations with opposite lateral components.

5.4 Methods

5.4.1. Data Acquisition

The subjects and data acquisition methods for this study have been previously described in detail (Preuss and Fung, 2007). Briefly, thirteen healthy male subjects experienced multidirectional horizontal support surface translations in 8 directions, at 45° intervals about the full circle. The total amplitude of each perturbation was 15cm, with a window of >500ms prior to the onset of platform deceleration. Each subject experienced 4 randomly ordered trials, in each perturbation direction, in 2 test postures: standing and sitting.

Electromyographic (EMG) activity was recorded, using surface electrodes, from 7 trunk muscles, and 1 hip muscle, bilaterally: Rectus Abdominis (RA), Internal Oblique (IO), External Oblique (EO), Upper Thoracic Paraspinals (TE4), Lower Thoracic Erector Spinae (TE9), Lumbar Erector Spinae (LE), Lumbar Multifidus (MF) and Tensor Fasciae Latae (TFL). Electrode placement has been previously described (Chapter 3, Table 3.1). Prior to analysis, each EMG signal was high-pass filtered using a dual-pass, 4th order Butterworth filter, with a cut-off frequency of 40Hz, in order to minimize the appearance of electrocardiographic artifact (ECG). A linear envelope of each EMG signal was then produced by low-pass filtering each full-wave rectified EMG signal using a 2nd order digital Butterworth filter, with a cut-off frequency of 3Hz. Finally, the linear enveloped EMG, for each subject and trial, was normalized to its own amplitude over the 500ms window immediately following the onset of support surface movement, by subtracting the minimum value and dividing by the adjusted maximum value, effectively giving each muscle profile a range from zero to one. This normalization was intended to remove the effect of amplitude from the EMG signals, while preserving the spatio-temporal characteristics of each signal.

5.4.2. Data Analysis

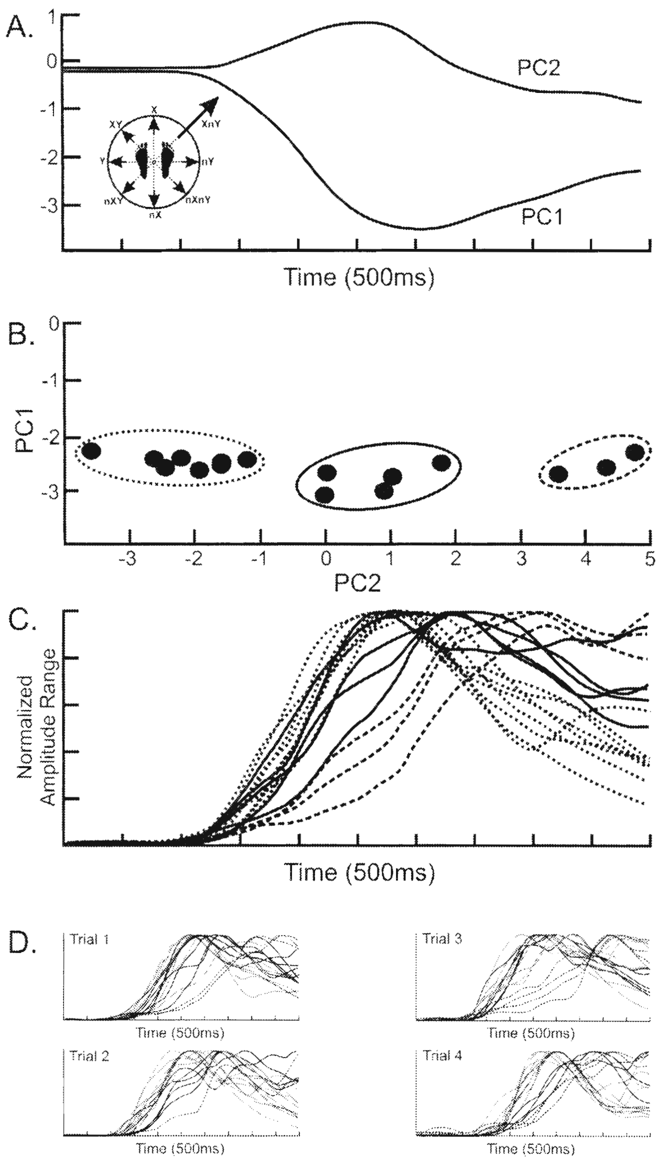
The statistical analysis of the pre-processed EMG data was done in 2 steps. The first step was a principal component analysis (PCA) of the EMG signals from the 16 muscles of the trunk and hip, over the 500ms window of interest. Singular value decomposition (SVD) was used as a computationally efficient means of finding the PCs (Daffertshofer et al., 2004; Jolliffe, 1986), along with the eigenvalues explaining the variance of the PCs (and hence the variance of the data), and the muscle loadings for each PC: namely the degree to which the variability of each of the original 16 EMG signals was represented by each PC. Based on our previous findings with respect to the dimensionality of these data (chapter 4 of this thesis), the first 2 PCs were retained for further analysis (Figure 5.1A). PCA was therefore used, as suggested by Daffertshofer et al. (2004), as a data driven filter, to separate the deterministic components of the data (the retained PCs) from the stochastic components.

The second step was a cluster analysis (Figure 5.1B), to identify common time-varying patterns in the muscle profiles based on individual muscle loadings for the identified PCs. As the 16 original EMG signals, minus their stochastic components, can be reproduced as the linear sum of the products of the PCs and their muscle loadings, those muscles with similar time-varying signals must share similar loadings for the 2 PCs (Preuss and Fung, 2004a). Cluster analysis was done using a fuzzy c-means approach. A 2-dimensional space was created, with the 2 dimensions representing the 2 PCs. Each muscle was then assigned a position in that space based on its loading onto each PC. The initial step in the analysis involved choosing "c" initial points from which to begin, where "c" represents the number of clusters to be found. The first 2 points were chosen as those muscles with the greatest distance between one another in the PC space, with additional points chosen, as necessary, at even intervals between the initial 2 points. These initial points represent an original estimate for the centre of the "c" clusters. The subsequent analysis involved improving upon this original estimate through the minimizing of an objective function representing the distance for each point to a given cluster centre (Pal and Mitra, 1999). By using a fuzzy approach, each muscle was not assigned to a single cluster, but rather was assigned a probability that it belonged to any one of the clusters in the PC space, referred to as membership, with the probabilistic constraint that the memberships of any one muscle across all clusters must sum to 1 (Krishnapuram and Keller, 1993; Pal and Bezdek, 1995). The weighting exponent "m" of the model (also called the "degree of fuzziness"), which represents how closely the model should approximate a "crisp" set (a set with binary membership of 0 or 1), was chosen as 2, based on the recommendation by Pal and Bezdek (1995) that "m" should be between 1.5 and 2.5. Further, the maximum number of clusters to be sought was limited to 4, as these authors also suggest a value of "c" no larger than the square-root of the number of variables in the set. As such, the cluster analysis began by initially seeking 2 clusters, adding one cluster as necessary until each variable had a membership of ≥ 0.75 in any one cluster, or the number of clusters was equal to 4. This cut-off of 4 possible clusters was deemed acceptable for these data, as 2 independent time-varying synergies should produce between 1 and 3 identifiable muscle groups with common activation patterns, depending on the degree of temporal overlap in the activation of those synergies.

Initially, the EMG data for each individual trial, for each subject, was analyzed as described above. The groupings identified for the individual trials, for each perturbation direction, in both test postures, were then analyzed to identify any groups of muscles found to cluster together in more than one trial, for each subject. Fixed groupings were defined, for each individual subject, as two or more muscles clustering together in 4 out of 4 trials for a given perturbation direction and posture. For the subject population, a power analysis for a chi-squared analysis of pairs at an α-level of 0.95 and a β-level of 0.80, found that the same fixed grouping would have to be identified in >75% of the subjects (i.e. 10 of 13) to be considered statistically significant evidence of that fixed grouping existing across the population. A slightly more relaxed criteria was also employed, defined as repeated groupings, for which two or more muscles had to cluster together in only 3 of the 4 trials for a given perturbation direction and posture. The same criterion of 10 of 13 subjects was then employed to define repeated groupings across the subject population.

Finally, ensemble averages of each EMG signal were taken for the 4 trials in each of the 8 perturbation directions, for each subject, in both test postures, and analyzed as above. An averaged grouping was then defined, for the subject population, as two or more of the ensemble averaged muscles patterns in a given perturbation direction and posture clustering together for 10 of the 13 subjects.

Figure 5.1 – Two-step statistical identification of muscle groupings



A. Time-varying principal components identified from a set of linear enveloped EMG data for the 16 muscles of the trunk, for a single subject, following anterior-rightward (see inset) support surface translation in standing.

B. Three clusters identified within the individual muscle loadings, in PC space, based on the individual muscle loadings for the PCs shown in (A). Membership of each muscle was ≥0.75 for their respective cluster.

C. The ensemble averaged EMG data (used in the analysis for (A) and (B)), coded to match the results of the cluster analysis in (B). Dotted –bilateral TE9, LE, and MF, LTE4, LIO. Dashed – bilateral RA, RIO. Solid – bilateral EO and TFL, RTE4.

D. EMG data from the individual trials (T1-4) following anterior-rightward support surface translation in standing, for the same subject.

T1: Dotted – bilateral TE9, RLE, RMF, LIO, LTE4; Dashed – bilateral RA; Solid – bilateral EO and TFL, RTE4, LLE, LMF; Grey - RIO.

T2: Dotted – bilateral TE9 and MF, RLE, LIO, LTFL; Dashed – LRA; Solid – RRA, RIO, REO, RTFL, RTE4; Grey – LEO, LTE4, LLE.

T3: Dotted – bilateral TE9, RMF; Dashed – bilateral RA, RIO, REO; Solid – bilateral LE, RTFL, LIO, LMF; Grey – bilateral TE4, LEO, LTFL.

T4: Dotted – bilateral TE4, TE9, LE, and MF, LIO; Dashed – bilateral RA, RIO; Solid – bilateral TFL, REO; Grey – LEO.

5.5 Results

An example of the 2-step statistical analysis is given in Figure 5.1. Figure 5.1A illustrates the two time-varying PCs extracted from the ensemble averaged data set of a representative subject, for the anterior-rightward surface translation direction in standing. Figure 5.1B illustrates the muscle loadings for those two PCs, clustered using the method described above. For this data set, only three clusters were required to provide each muscle with a membership of ≥ 0.75. Figure 5.1C illustrates the 16 ensemble averaged EMG traces, making up the original data set, colour-coded as in Figure 5.1B. Figure 5.1D illustrates the 16 EMG traces for the same subject, for the four individual trials under the same perturbation condition (i.e. the trial data from which the ensemble averaged data in Figure 5.1C were derived). For these individual trial data sets, 4 clusters were required to establish membership for all 16 muscles.

Missing Data

Two of the 13 subjects failed to maintain their balance, without stepping, following anterior translation of the support surface in standing. As such, the data for the anterior perturbation direction, in standing, are based on the remaining 11 subjects. EMG data from the right TFL (RTFL) of one subject, right LE (RLE) for one subject, and left LE (LLE) for 2 subjects were also found to be compromised. Population groupings, therefore, for the anterior perturbation direction in standing, and for any grouping involving the LLE, are based on two or more muscles grouping together for at least 9 of 11 subjects. The criteria for a population grouping involving the RTFL or RLE were, however, maintained as at least 10 of 12 subjects in order to maintain the statistical criteria of >75%.

Fixed Muscle Groupings

For the standing and sitting postures respectively, the number of fixed groupings identified for each subject × direction combination, as well as the number of muscles accounted for by those groupings, is shown in Tables 5.1 and 5.2. On average, 2 or 3 fixed muscle groupings were identified, for the individual subjects, in each of the directions of perturbation, in both test postures. These numbers, however, were quite variable between subjects and directions. In standing, as many as 6 fixed groupings were identified for a single subject, while no fixed groupings were identified for 4 of the subject × direction combinations. In sitting, the highest number of identified fixed groupings was 5, with no fixed groupings identified for 7 of the subject × direction combinations.

More importantly, however, not all of the muscles studied were accounted for by these fixed groupings. In standing, the mean number of muscles accounted for was between 4 and 8, for each direction of perturbation: i.e. only 25-50% of the muscles studied. In sitting, these numbers were slightly higher, averaging between 5 and 10 for the different perturbation directions.

Those fixed groupings that were identified for the individual subjects were not found to be common across the subject population, with no pairing of muscles meeting the *a priori* criteria described above. The most consistent pairings in standing were LE bilaterally, and MF bilaterally, each of which met the criteria for a fixed grouping for 7 of the 13 subjects following posterior (nX) surface translations. In sitting, the most consistent pairings were RRA with RIO in the anterior (X) direction, RRA with LRA in the anterior (X) direction, and LRA with LIO in the anterior-left (XY) direction, each of which met the criteria for a fixed grouping in 9 of the 13 subjects.

Table 5.1 – Fixed muscle groups in standing

	X	XnY	nY	nXnY	nX	nXY	Y	XY
Subject 1	3(7)	2(5)	3(6)	6(15)	4(11)	4(9)	3(6)	4(8)
Subject 2	3(6)	1(3)	2(4)	4(10)	4(11)	2(5)	4(14)	5(13)
Subject 3	2(6)	1(2)	3(6)	3(7)	2(7)	5(12)	1(2)	2(5)
Subject 4	2(4)	3(7)	1(2)	3(8)	3(6)	2(6)	2(4)	1(2)
Subject 5	3(6)	3(3)	2(4)	3(10)	3(6)	1(2)	4(10)	1(3)
Subject 6	1(3)	3(9)	1(2)	2(4)	2(5)	1(2)	2(4)	2(4)
Subject 7	0(0)	2(4)	1(2)	1(5)	4(12)	3(8)	4(8)	5(10)
Subject 8	n/a	5(12)	4(10)	2(4)	2(4)	2(4)	3(6)	4(8)
Subject 9*	3(6)	1(2)	1(3)	2(5)	3(7)	0(0)	1(2)	0(0)
Subject 10	4(8)	2(7)	1(2)	2(5)	4(9)	0(0)	5(14)	5(11)
Subject 11	2(5)	2(4)	1(2)	3(6)	2(5)	2(7)	2(4)	2(4)
Subject 12	n/a	4(8)	3(6)	4(8)	3(14)	2(4)	2(5)	1(2)
Subject 13*	1(2)	3(7)	3(6)	5(11)	3(8)	1(3)	1(3)	3(12)
mean	**2(5)**	**2(6)**	**2(4)**	**3(8)**	**3(8)**	**2(5)**	**3(6)**	**3(6)**

Number of fixed groupings (number of muscles accounted by these groupings)
*no LLE signal

Table 5.2 – Fixed muscle groups in sitting

	X	XnY	nY	nXnY	nX	nXY	Y	XY
Subject 1	1(6)	2(9)	2(7)	2(5)	1(2)	2(7)	2(5)	2(10)
Subject 2	5(16)	3(8)	2(4)	3(6)	4(9)	3(8)	1(2)	4(15)
Subject 3	4(11)	2(7)	3(12)	4(11)	0(0)	1(2)	3(8)	2(8)
Subject 4	2(5)	4(11)	4(10)	3(7)	2(4)	2(6)	1(2)	3(6)
Subject 5	3(9)	2(5)	2(4)	3(7)	3(9)	0(0)	2(4)	3(10)
Subject 6	2(8)	1(2)	5(10)	4(9)	0(0)	1(2)	1(5)	3(7)
Subject 7	4(9)	3(6)	0(0)	2(4)	3(9)	3(7)	3(8)	2(4)
Subject 8	4(15)	2(7)	3(6)	3(7)	3(10)	2(5)	2(8)	4(11)
Subject 9*	4(13)	4(9)	2(5)	0(0)	2(4)	0(0)	2(4)	3(7)
Subject 10	1(3)	2(5)	3(6)	1(3)	1(2)	1(2)	2(7)	4(12)
Subject 11	4(13)	3(8)	2(7)	2(5)	3(7)	4(8)	0(0)	1(3)
Subject 12	3(8)	4(8)	2(4)	2(5)	2(4)	3(9)	2(5)	3(8)
Subject 13*	3(9)	3(12)	1(4)	2(6)	1(2)	2(5)	1(4)	2(9)
mean	**3(10)**	**3(7)**	**2(6)**	**2(6)**	**2(6)**	**2(5)**	**2(5)**	**3(8)**

Number of fixed groupings (number of muscles accounted by these groupings)
*no LLE signal

In addition to the variability across subjects, the fixed groupings identified for each individual subject displayed very little symmetry. In general, when fixed groupings were compared for the anterior diagonals (XY and XnY), the lateral directions (Y and nY) and the posterior diagonals (nXY and nXnY), the groupings involving right sided muscles in one direction of perturbation were not mirrored by groupings of the paired left sided muscles for the opposing perturbation direction. Even for those cases in which a degree of symmetry was noted for these comparisons, the identified groupings were never exactly mirrored copies of one another.

The muscle groupings for a representative subject, for the diagonal support surface translation directions, are shown for Figure 5.2, for the standing condition, and Figure 5.3, for sitting. Several fixed muscle groupings were identified for this subject. The symmetry of these fixed groupings, however, was largely limited to the anterior diagonals in the sitting condition, and even then these groupings were not fully mirrored for the right and left sided muscles. A tendency can be noted, however, in both postures, for the muscles of the trunk to be grouped along anatomical lines, although this is once again more evident in the sitting condition (illustrated in the colour-coding of this figure). This same tendency towards anatomical groupings was noted for all subjects, and for both test postures, although it was not robust across trials, and was only minimally symmetrical. An increase in the consistency of muscle groupings in the sitting condition was also present across the subject population, although not always to the degree illustrated in these two figures (see also Tables 5.1 & 5.2).

Repeated Muscle Groupings

The somewhat more relaxed criteria used to identify repeated muscle groupings (requiring pairings in only 3 of 4 trials) found at least one repeated grouping for all possible subject × direction combinations, in both test postures. These repeated groupings, however, accounted for all of the muscles studied in only 22% of the possible subject × direction combinations in standing, with a mean of 1 to 4 muscles unaccounted for in each of the 8 perturbation directions. In sitting, the repeated groupings accounted for all of the muscles studied in 25% of the possible subject × direction combinations, with a mean of 1 to 5 muscles unaccounted for in each of the 8 perturbation directions.

Across the subject population, a small number of common repeated groupings was identified, occurring in 4 of the 8 directions of perturbation for both test postures. In standing, the bilateral RA were the muscles most commonly grouped together, with this pairing occurring in the anterior (X) (10 of 11 subjects), anterior-leftward (XY) (10 of 13 subjects), and posterior (nX) (11 of 13 subjects) directions. Two other repeated groupings were also identified in the posterior (nX) direction, each consisting of 3 muscles (LTE9, RLE and RMF; RTE9, LLE and LMF), with each within-group muscle pairing meeting the minimum *a priori* criteria for repeated groupings. The last muscle grouping which repeated across the subject population occurred in the posterior-leftward (nXY) direction, with LTE9 and LMF pairing together for 10 of 13 subjects. Similar to the finding for the fixed muscle groupings, however, no subject displayed any robust symmetry in their repeated muscle groupings in standing (Figure 5.2), with this asymmetry also evident in the population groupings.

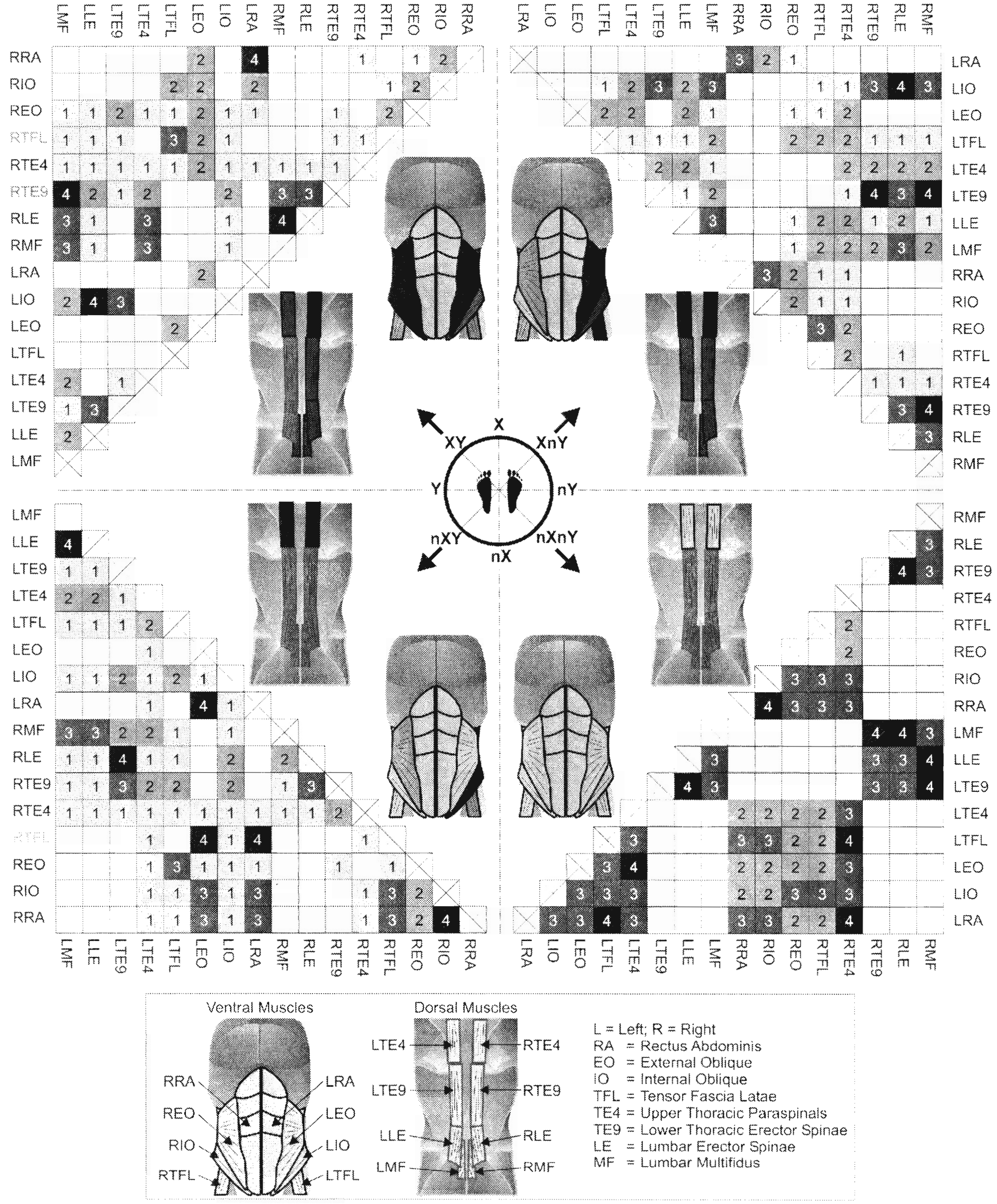
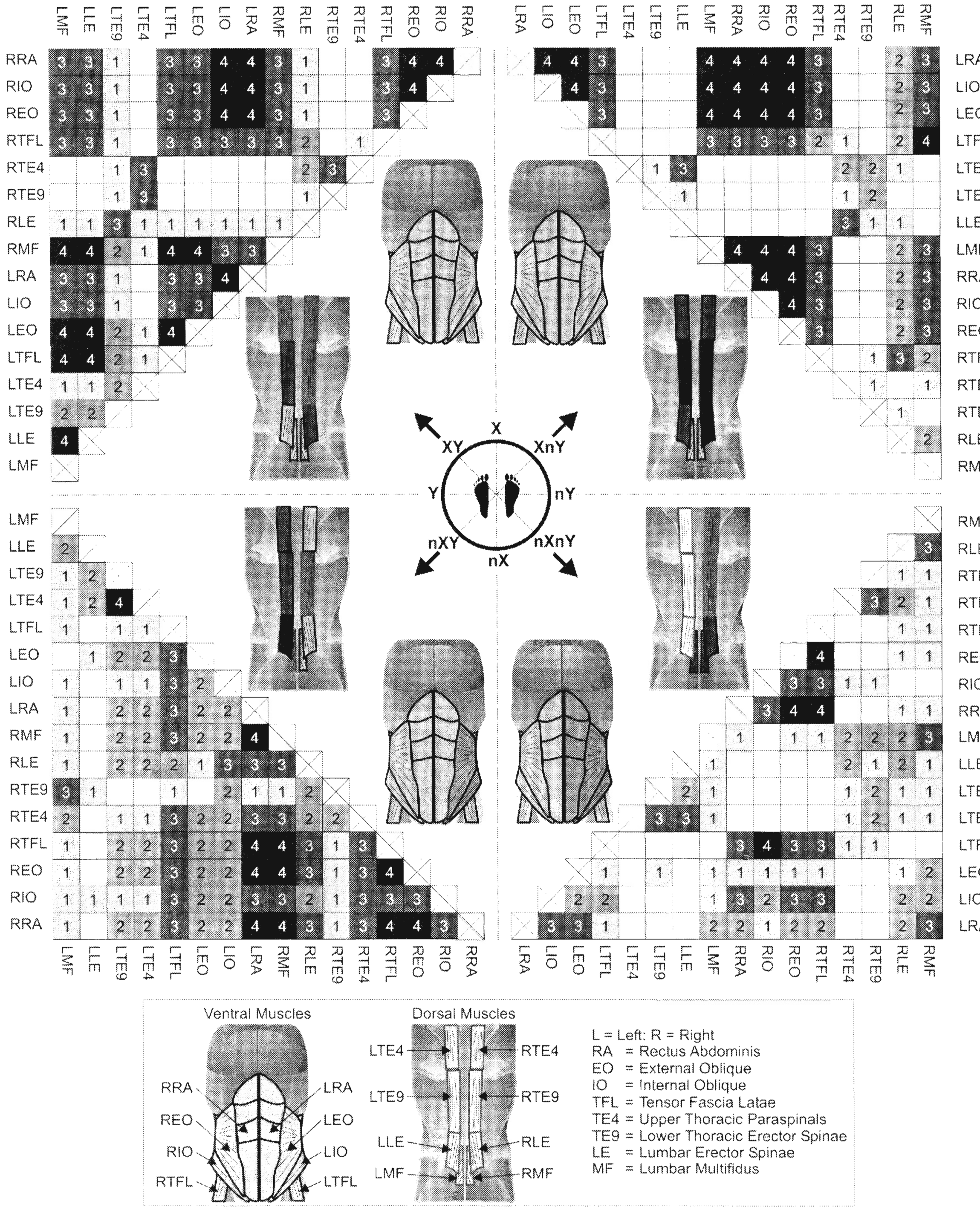


Figure 5.2 – Muscle groupings in standing for a representative subject
Grids representing the frequency with which pairs of muscles were found to cluster together, in PC space, for the four trials in standing, for each of the diagonal support surface translation directions, for a representative subject (same subject as Figure 5.1). Muscle diagrams have been shaded, based on repeated groupings (≥3/4 trials) to reflect the tendency towards grouping along anatomical lines.



L = Left; R = Right
RA = Rectus Abdominis
EO = External Oblique
IO = Internal Oblique
TFL = Tensor Fascia Latae
TE4 = Upper Thoracic Paraspinals
TE9 = Lower Thoracic Erector Spinae
LE = Lumbar Erector Spinae
MF = Lumbar Multifidus

Figure 5.3 – Muscle groupings in sitting for a representative subject
Grids representing the frequency with which pairs of muscles were found to cluster together, in PC space, for the four trials in sitting, for each of the diagonal support surface translation directions, for a representative subject (same subject as Figures 5.1 & 5.2). Muscle diagrams have been shaded, based on repeated groupings (≥3/4 trials) to reflect the tendency towards grouping along anatomical lines..

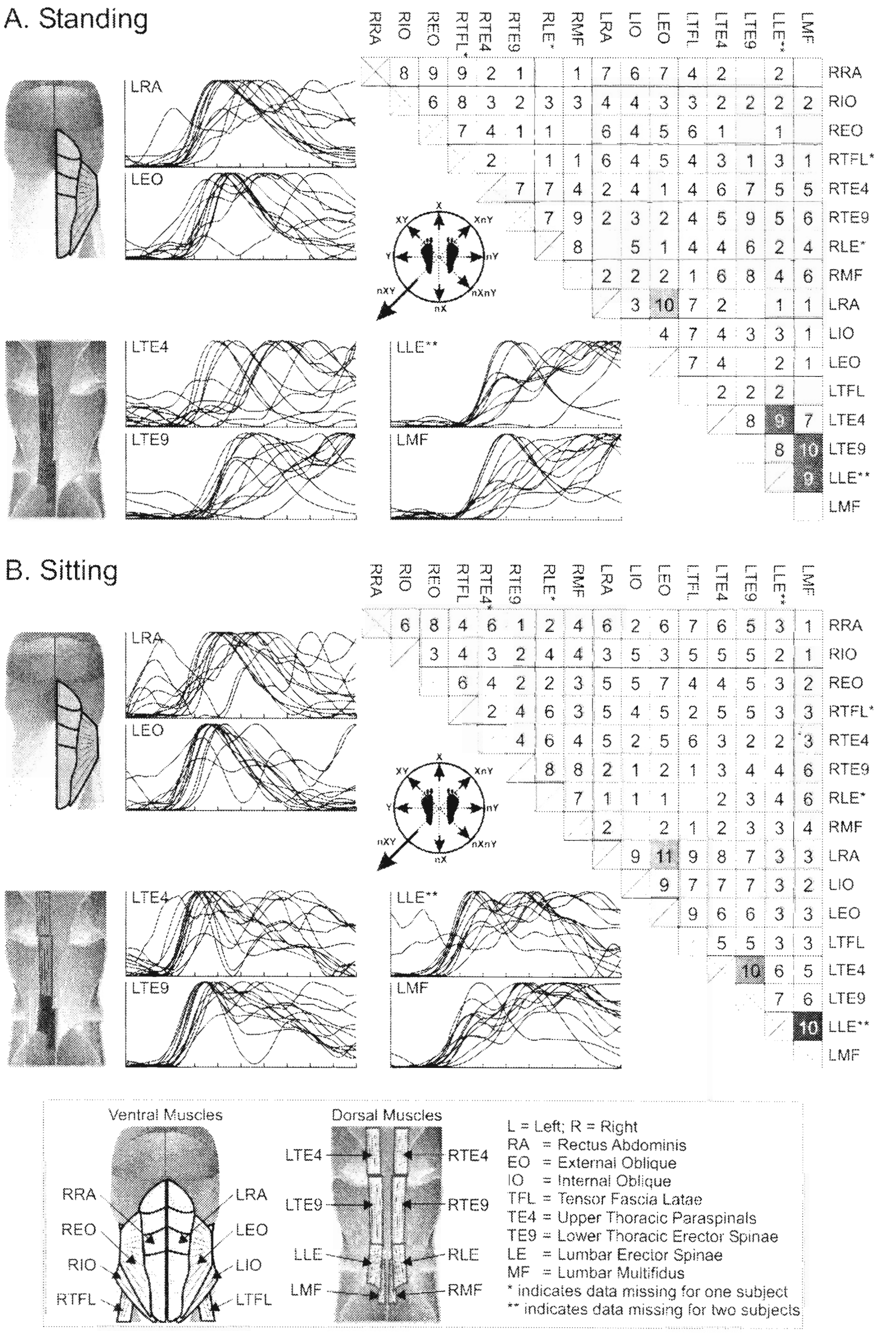
In sitting, the bilateral RA were once again the muscles most commonly grouped together, with this pairing occurring in both the anterior (X) (12 of 13 subjects) and anterior-left (XY) (11 of 13 subjects) directions. In the anterior (X) direction, a second muscle grouping, consisting of the bilateral MF (11 of 13 subjects) was also found. In the anterior-left (XY) direction, 3 other muscles (LIO, LEO and LTFL) were found to group with the bilateral RA, although not every pairing in this repeated grouping met the *a priori* criteria of 10 of 13 subjects. In the leftward (Y) direction, a single muscle grouping (LIO with LTFL) was found, with this pairing displaying common activation patterns for 10 of 13 subjects. Finally, two muscle groupings were found in the rightward (nY) direction. The first consisted of the right sided abdominals with RTFL, although not every pairing within this grouping occurred for 10 of 13 subjects. The second was LTE9 with LLE, which displayed common activation patterns for 9 of 11 subjects in this direction. As for the fixed groupings, more repeated groupings were identified in the sitting condition, and these tended to be more symmetrical than in the standing condition (Figures 5.2 and 5.3). This was not, however, the case for all subjects, and this symmetry was only minimally evident in those repeated groupings identified for the subject population (see above for the Y and nY directions).

Averaged Muscle Groupings

At least one averaged muscle grouping was found across the subject population for each perturbation direction, in both test postures. These averaged muscle groupings, however, failed to account for the majority of the muscles tested. Figure 5.4 illustrates the frequency with which specific muscle pairings were identified across the study population, for posterior-leftward perturbations in standing (Figure 5.4A) and sitting

(Figure 5.4B), along with the ensemble averaged EMG traces, from all 13 subjects, for those muscles which met the *a priori* criteria for an averaged muscle grouping.

Figure 5.4 – Averaged muscle groupings for the posterior-leftward translation direction



A. Standing

	RRA	RIO	REO	RTFL*	RTE4	RTE9	RLE*	RMF	LRA	LIO	LEO	LTFL	LTE4	LTE9	LLE**	LMF
RRA		8	9	9	2	1		1	7	6	7	4	2		2	
RIO			6	8	3	2	3	3	4	4	3	3	2	2	2	2
REO				7	4	1	1		6	4	5	6	1		1	
RTFL*					2		1	1	6	4	5	4	3	1	3	1
RTE4						7	7	4	2	4	1	4	6	7	5	5
RTE9							7	9	2	3	2	4	5	9	5	6
RLE*								8		5	1	4	4	6	2	4
RMF									2	2	2	1	6	8	4	6
LRA										3	10	7	2		1	1
LIO											4	7	4	3	3	1
LEO												7	4		2	1
LTFL													2	2	2	
LTE4														8	9	7
LTE9															8	10
LLE**																9
LMF																

B. Sitting

	RRA	RIO	REO	RTFL	RTE4*	RTE9	RLE*	RMF	LRA	LIO	LEO	LTFL	LTE4	LTE9	LLE**	LMF
RRA		6	8	4	6	1	2	4	6	2	6	7	6	5	3	1
RIO			3	4	3	2	4	4	3	5	3	5	5	5	2	1
REO				6	4	2	2	3	5	5	7	4	4	5	3	2
RTFL*					2	4	6	3	5	4	5	2	5	5	3	3
RTE4						4	6	4	5	2	5	6	3	2	2	3
RTE9							8	8	2	1	2	1	3	4	4	6
RLE*								7	1	1	1		2	3	4	6
RMF									2		2	1	2	3	3	4
LRA										9	11	9	8	7	3	3
LIO											9	7	7	7	3	2
LEO												9	6	6	3	3
LTFL													5	5	3	3
LTE4														10	6	5
LTE9															7	6
LLE**																10
LMF																

L = Left; R = Right
RA = Rectus Abdominis
EO = External Oblique
IO = Internal Oblique
TFL = Tensor Fascia Latae
TE4 = Upper Thoracic Paraspinals
TE9 = Lower Thoracic Erector Spinae
LE = Lumbar Erector Spinae
MF = Lumbar Multifidus
* indicates data missing for one subject
** indicates data missing for two subjects

Grids representing the frequency with which pairs of ensemble averaged muscle traces were found to cluster together across the subject population, for the posterior-leftward translation direction, in standing (A) and sitting (B). The illustrated muscles have been shaded to represent the averaged muscle groupings identified for this direction of perturbation. The ensemble averaged EMG traces, for all 13 subjects, are illustrated for those muscles included in these averaged muscle groupings.

Despite the presence of at least one averaged muscle grouping under all perturbation conditions, these groupings were not strongly symmetrical in the standing posture. The strongest symmetry was evident in the posterior diagonal directions, with the ipsilateral TE9, LE and MF often grouped together. Certain of these pairings, however, did not strictly meet the *a priori* criteria of ≥10 of 13 subjects (Figure 5.4A). A trend was evident, however, for the musculature to group along anatomical lines.

In sitting, somewhat more symmetry was evident in the averaged muscle groupings. For translations along the anterior diagonals, the anterior musculature tended to group, as did the contralateral muscles of the lower back and the MF bilaterally. A similar trend was also evident in the other perturbation directions, but with co-activation appearing more frequently in the left-sided musculature than the right. Once again, however, many of these groupings did not strictly meet the *a priori* criteria for averaged muscle groupings (Figure 5.4B).

5.6 Discussion

The purpose of this paper was to test the hypothesis that the explicit activation of fixed, time-varying muscle synergies by the CNS is responsible for the high degree of neuromuscular coupling observed in the trunk following support surface translation. This theory of motor control suggests that fixed motor programs exist within the CNS (muscle synergies), which explicitly activate the musculature as functional groups. Each synergy may be independently shifted in time, and scaled in amplitude, such that the variability of muscle activation that exists during natural behaviour can be achieved through the simultaneous and independent activation of a relatively limited number of synergies (d'Avella et al., 2003). Animal studies have also suggested that these synergies are not only fixed for a given individual, but represent universal motor programs that are robust both within and between individual subjects (d'Avella et al., 2003; Ting and Macpherson, 2005; Torres-Oviedo et al., 2006). The use of surface EMG with human subjects, however, greatly complicates the comparison of even relative EMG amplitudes between subjects, due to the multitude of factors that affect the amplitude of the acquired signals (Clancy et al., 2002; De Luca, 1997), even when normalized to some subject-specific reference level (Lehman and McGill, 1999; Yang and Winter, 1984). As such, we chose to focus on the time-varying properties of the EMG signals, rather than their amplitudes.

We have previously established that a high degree of neuromuscular coupling occurs in the trunk, following horizontal support surface translations (chapter 4 of this thesis). With the effects of amplitude removed from the acquired EMG signals through normalization, and with the stochastic aspects of these signals minimized using PCA, we stipulated that three criteria would need to be met in order to support the hypothesis that the observed neuromuscular coupling is due to the activation of fixed, universal muscles synergies, as defined above. First, the EMG activity of those muscles involved in the postural response must be characterized by groups of muscles with similar time-varying patterns of EMG activity. Second, a degree of consistency must be evident in any muscle groupings identified for a given perturbation condition (direction and posture). Third, similar muscle groupings must be identifiable across subjects, with symmetrical groupings occurring for perturbations with opposite lateral components.

The data presented in this study appear to satisfy only the first of these criteria. For all data sets, groups of muscles with similar time-varying properties were identified by a combination of PCA and cluster analysis (Figure 5.1), confirming that synergic muscle activity is evident in the neuromuscular response in the trunk following support surface translation. Those muscle groupings which were identified as being fixed for the individual subjects (i.e. which occurred for all trials in any given perturbation condition), however, on average accounted for less than half of the muscles studied (Tables 5.1 & 5.2, Figures 5.1 & 5.2). As such, a degree of trial-by-trial variance was evident in the relative spatio-temporal activation profiles of most of the muscles tested. While the coordinated EMG activity in the trunk may therefore be described as synergic, these synergies do not appear to be fixed with respect to the perturbation condition, even within subjects. Finally, no muscle pairing met the population criteria for a fixed muscle grouping, and the degree of symmetry that was observed in the identified muscle groupings was limited, particularly in the standing posture (Figure 5.2). As such, the synergic activity that was observed in the trunk musculature was neither common across subjects, nor symmetrical within or between subjects. These data, therefore, do not support the hypothesis that the coordinated activity of the trunk musculature was achieved though the use of fixed, universal motor programs.

As the grouping criteria were relaxed, first with repeated groupings and then averaged groupings, a limited degree of consistency did emerge across subjects. Specifically, an underlying trend appears to be present in these data towards trunk muscle activation being grouped along anatomical lines (Figures 5.2, 5.3 and 5.4). Given the study paradigm, and the lack of evidence for fixed muscle synergies in these data, this most likely reflects a biomechanical link between the activation profiles of these muscles and the actual perturbation experienced by the trunk as a result of the support surface movement. As similar findings have been previously noted for the direction-specific amplitude of activation in these same muscles (Chapter 3), as well as for the muscles of the lower limbs under a similar perturbation protocol (Henry et al., 1998a), it may be suggested that the neuromuscular aspect of the postural response to perturbation is related to the spatial aspects of movement (Feldman et al., 1998b; Lestienne et al., 2000; St-Onge and Feldman, 2004), or to the control of some biomechanical property such as impedance (Darainy et al., 2007; Hogan, 1985), rather than to fixed muscle synergies acting within the CNS. This theoretical approach to motor control stipulates that specific parameters may be controlled by the CNS in order to determine the point at which the system will reach an equilibrium state within its environment (Feldman et al., 1998b; St-Onge and Feldman, 2004; Tresilian, 1999). Muscle activity is then the implicit result of some deviation in the actual state of the system from that equilibrium point, such as a postural perturbation. One means by which this control might be achieved would be through the use of specific length-dimensional parameters by the CNS. EMG activity in a muscle, for example, could be initiated when the difference between the actual length of a muscle meets or exceeds a specified, and modifiable, threshold length, causing the postsynaptic potential to exceed the threshold potential of the motorneuron (Adamovich et al., 1997; St-Onge and Feldman, 2004). Such a relationship between EMG activation and muscle length would serve to explain how individual muscles (Nichols, 2002), and by extension multi-articular systems (Hogan, 1985) like the trunk, typically behave in a "spring-like" manner (i.e. there exists a relationship between displacement and force output (Hogan, 1985)). This would also serve to explain the asymmetry in the muscle groupings evident in Figures 5.2 and 5.3, as physical asymmetries, which are relatively common in the trunk musculature (Rankin et al., 2006; Stokes et al., 2005), would likely result in differences in the bilateral biomechanical properties of the paired muscles, which in turn could serve to alter the spatio-temporal responses in these muscles when faced with similar (symmetrical) perturbations.

For all grouping criteria, and in particular for the averaged muscle groupings, the results of this study in the sitting posture tended towards slightly larger muscle groups, accounting for slightly more muscles, than in standing. This difference between postural conditions most likely stems from the fact that the actual perturbation experienced by the trunk in sitting was less complex than in standing (Chapter 3). Specifically, the perturbation in sitting was directly tied to the motion of the support surface, resulting in a mono-phasic postural response in the trunk. In standing, however, the dynamic response in the lower limbs delayed the onset of trunk motion in the direction of support surface motion, while often introducing an early pelvic rotation, particularly in the sagittal plane. The result was a bi-phasic postural response from the trunk. If the EMG response is tied to the spatial aspects of the movement, the increased kinematic complexity of the trunk response in standing would introduce more potential for variability in the EMG response. This would then cause more variability in the identified muscle groupings, as was observed in these data.

Many previous studies have analyzed EMG signals with the express purpose of identifying muscle synergies. Ting and Macpherson (2005), and more recently Torres-Oviedo et al. (2006), have described a limited number of muscle synergies to explain the postural response in the cat hindlimb across multiple directions of support surface translation. The synergies identified by these authors, however, were based on averaged EMG amplitudes, and do not, therefore account for potential differences in the time-varying activation of the muscles making up each individual synergy. Other authors have, however, tackled the time-varying aspects of the EMG signals, and reached the same conclusions: that the observed EMG patterns could be reconstructed as a combination of a limited number of muscle synergies. Ivanenko et al. (2004) assessed EMG patterns during the human gait cycle, concluding that 5 factors accounted for a large fraction of the EMG variance across an extensive muscle set. These factors, however, tended to explain a much smaller fraction of the waveform variance for the individual subjects than for data averaged across subjects. Similarly, d'Avella et al. (2003) extracted sets of synergies that, when appropriately shifted in time and amplitude, were capable of explaining a large portion of the variance of the EMG activity observed for a variety of movements in the frog hindlimb. Specifically, three synergies described the EMG activation during defensive kicks in different directions, while movements such as jumping, swimming and walking were best described by four synergies. The potential drawback in these findings, however, is that the similarities in the synergies across the different movement patterns were somewhat limited. Given the diversity of movements that may be performed by biological systems, and the limited overlap between the synergies extracted for the movements observed by these authors, it would seem that the number of fixed synergies required to perform even the simplest of daily routines would quickly outstrip the number of muscles involved in those movements. As such, it would appear that while synergic activation of muscles may be desirable for the coordination of movement, the use of fixed synergies may be impractical.

The results of the current study suggest that the EMG activation in the trunk, following support surface translation, does not result exclusively from the activation of fixed motor programs. These data, however, cannot rule out the possibility that explicit muscle synergies may be encoded at some level(s) within the CNS, but that the exact structure of these commands is altered prior to the output signals being recorded by surface electromyography. This type of downstream modulation, for example, may result from the action of afferent signals processed in parallel with the initial synergic command from the CNS.

As with all studies, these data, and the techniques used to analyze these data, are subject to several limitations. The use of surface EMG with human subjects, for example, has several innate limitations (De Luca, 1997), which were not present for the surgically implanted electrodes in the animal studies described above (d'Avella et al., 2003; Ting and Macpherson, 2005; Torres-Oviedo et al., 2006). Many of these difficulties, however, relate to the amplitude and frequency content of the acquired signals, both of which were largely accounted for by the filtering and normalization methods used in this study. Furthermore, it has been suggested that PCA may not be the best method to identify muscle synergies in EMG data (Tresch et al., 2006). The goal of this study, however, was not to identify muscle synergies, but rather to determine if evidence of their presence might be found in the existence of groups of muscles with common time-varying patterns of activation. For this, the combination of PCA with cluster analysis appears to perform quite well (Figure 5.1). These statistical methods, however, are not without their own limitations. There exists no single agreed upon method to determine the number of PCs to retain from PCA, regardless of the type of data being analyzed (Jolliffe, 1986). As such, the dimensionality of the PC space used in the cluster analysis may not have accurately reflected the true underlying dimensionality of the EMG data. Furthermore, the maximum number of clusters to be found in the second step of the analysis was determined by the number of EMG channels acquired, and as such may have been inadequate for the intended purpose, as the current study did not include all of the muscles of the trunk in these analyses.

5.7 Conclusion

The data presented in this study do not support the use of fixed, time-varying muscle synergies in the control of upright trunk equilibrium following support surface translations. While temporal relationships were found in the activation profiles of specific muscle groups, in all EMG data sets, these groupings did not display the consistency, or symmetry, that would be expected if their activation was driven by fixed, universal motor programs.

6. Summary and Conclusion

The principal objective of this work was to characterize the neuromuscular, kinematic and kinetic response of the multi-segmental trunk to unexpected, multi-directional support surface translations. As expected, non-negligible inter-segmental movement was observed in the trunk, in both the standing and sitting postures, following perturbation. Trunk motion tended to progress in a caudo-rostral direction, with the actual magnitude of the observed trunk motion tending to be greater at the more caudal levels. This movement was accompanied by a significant and specific increase in the activation of the trunk musculature. These biomechanical and neuromuscular descriptors of the trunk postural response were found to be significantly affected by both the direction of the support surface translation and the initial subject posture, with an interaction effect between these variables.

An initial qualitative examination of these data suggested that the postural response in the trunk was largely explained by the interaction between the biomechanical properties of the trunk and the actual perturbation experienced. Furthermore, a degree of interdependence was noted in the movements occurring at the different trunk levels, suggesting a degree of inter-segmental coordination.

Statistical pattern analysis revealed that the variability in the neuromuscular and biomechanical descriptors of trunk motion could be largely explained by as few as two independent variables. These results, for the EMG data, suggest that a high degree of neuromuscular coupling was present in the trunk following support surface translation. Furthermore, the dimensionality of this neuromuscular coupling was similar in the standing and sitting conditions, and across the different perturbation directions, as were the basis vectors underlying that dimensionality. Two independent components were also sufficient to explain the majority of the variability in the biomechanical variables of the trunk. Only the results from the kinematic data, however, fit closely enough with those of the EMG data to suggest that the control of these variables may be an explicit goal of this neuromuscular coupling. Specifically, this suggests that the neuromuscular coupling observed in the trunk serves to reduce the actual kinematic degrees of freedom of the trunk.

Despite the high degree of apparent neuromuscular coupling in the trunk, further statistical analysis found the relationship between that actual time-varying EMG patterns to be inconsistent with the theory of fixed muscle synergies. Specifically, the observed synergic activity in the musculature (i.e. groups of muscles with similar time-varying patterns of activation) was variable, both within and between subjects, when support surface perturbations were repeated in the same directions, and under the same initial postural condition (standing vs. sitting). The observed differences in the time-varying muscle activation profiles, however, may be readily explained as the implicit result of a preset impedance of the trunk about the upright posture, rather than the expression of preset muscle activation patterns.

The general conclusion of this work, therefore, is that the trunk behaves as a highly coordinated multi-segmental body in response to a postural perturbation. The manner in which this coordination is achieved, however, appears to be related to the interaction between the actual perturbation experienced by the trunk and the biomechanical properties of the trunk, specifically its impedance, rather than to some fixed or pre-programmed postural response, such as direct synergic muscle activation.

This body of work was intended to address three issues in the literature that had been identified as limitations in our understanding of balance and postural control. The first was the treatment of the multi-segmental trunk as a single rigid body. These findings provide conclusive evidence that this assumption is invalid. This does not, however, invalidate the findings of previous studies which have assumed a rigid trunk, as the majority of these have focussed on the role of the lower limbs in balance and postural control. Any data or conclusions derived from a model in which the trunk is treated as a single segment must, however, be viewed in light of this assumption, particularly when global parameters such as centre of mass being described.

The second issue was that little information has been available regarding the role of the trunk musculature in the maintenance of upright posture and balance. The current work has addressed this issue in depth, with three important conclusions summarized above. In brief, the action of the trunk musculature in the regulation of upright posture and balance is highly coordinated, is specific to the actual perturbation experienced by the trunk, but displays a degree of variability that is inconsistent with the theory that these postural responses are driven by fixed motor programs.

The final issue was that it is important to analyse both the neuromuscular and mechanical aspects of movement, if these data are to be fully interpreted. The link between the kinematics of the trunk and the observed neuromuscular response, which was repeatedly identified in these studies, implies that neuromuscular coupling, involving multi-articular muscles, presents a means by which the CNS may solve the issue of kinematic redundancy in a multi-articular system like the trunk.

7. Implications for Clinical Rehabilitation

The results of this research, although drawn from a healthy subject population, have extensive implications for the treatment of many patients for whom trunk control may be impaired. This is particularly true for those patients with neurological conditions affecting the gross motor function of the trunk, such as a spinal cord lesion.

Preliminary research has shown that electrical stimulation of the lumbar erector spinae can provide an added degree of functional trunk support, when reaching, to patients with motor-complete spinal cord injuries in the upper thoracic spine (Kukke and Triolo, 2004). Research into the feasibility of more extensive functional electrical stimulation of the muscles of the trunk, however, is still in its early stages (e.g. Wilkenfeld et al., 2006). The work contained in this thesis may be used to focus the direction of that research. The apparent link between the inter-segmental kinematics of the trunk and the EMG activation, for example, suggests that kinematic feedback may present a potential control variable for the electrical stimulation delivered by a neuroprosthetic device (Anderson and Fuglevand, 2004; Seifert and Fuglevand, 2002). Such a system, for example, could be designed around electrogoniometers incorporated into a flexible corset, along with the electrodes (for a system using surface stimulation), connectors (for a system using surgically implanted electrodes), or radiofrequency transmission coils (for injectable stimulators Loeb et al., 2006)) required for stimulation. Such a system could then be used to control the force-displacement relationship of the trunk about the upright posture (i.e. impedance control).

While a neuroprosthesis to support the upright posture of the trunk has obvious potential benefits for a spinal cord injured population, other patients may also benefit from such a system for therapeutic, as well as orthotic, purposes. There is evidence to suggest, for example, that the trunk musculature may receive more bilateral innervation from the motor cortices than the muscles of the limbs (e.g. Carr et al., 1994). As such, a patient having suffered a vascular insult affecting only one hemisphere might have a greater potential to recover the functional control of the trunk musculature than that of the limbs. The recovery of trunk function after stroke has, in fact, been linked to an increase in ipsilateral motor-evoked potentials following trans-cranial electrical stimulation of the unaffected hemisphere (Fujiwara et al., 2001). As trunk control has been linked to overall functional outcome following stroke (Duarte et al., 2002; Karatas et al., 2004; Verheyden et al., 2006), functional electrical stimulation of the trunk musculature may be a powerful tool for the rehabilitation of these patients, if the same therapeutic effects that are evident in lower limbs following stroke (Preuss et al., 2005b; Yan et al., 2005) and spinal cord injury (Barbeau et al., 2002) can be demonstrated.

It is my intention to follow up on these clinical applications in my post-doctoral work with Dr. Milos Popovic. Specifically, I will be involved in a project to study the feasibility of neuroprosthetic support of the trunk in spinal cord injured patients. Subject data, such as those presented in this thesis, will be used in the development of a control system for a computer-based model of the trunk. This engineering-based approach also provides the potential to expand this work into many other fields of rehabilitation, as a computer model provides the opportunity to study the effects of individual parameters, such as muscle cross-sectional area, on the behaviour of the system. Using parameters initially derived from the computer model, electrical stimulation parameters may be developed for both orthotic and therapeutic purposes. Such a model may even be adapted to individual patient and muscle parameters, derived from MRI or ultrasound data, to better understand the role of muscular impairment in more common disorders such as mechanical low back pain (Panjabi, 2006; Preuss and Fung, 2005). The data presented in this thesis, therefore, represent a step towards the development of more evidence-based rehabilitation techniques for a multitude of neurological and orthopaedic conditions.

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9. Appendices