Biomechanical analysis of posture and movement coordination during a fatiguing, repetitive upper limb task

Jason Robert Fuller

Department of Kinesiology and Physical Education
Faculty of Education
McGill University, Montréal

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Abstract

Repeating an arm movement has been shown to result in complex reorganization in the activity across the arm and the trunk musculature leading to changes in whole body coordination. Yet, the relationship between fatigue, arm movement and postural control is poorly understood. As such, the primary aim of this thesis was to investigate the effects of upper limb repetitive motion-fatigue on the control of posture and movement. Three-dimensional whole-body kinematics were recorded as subjects performed a repetitive pointing task between two shoulder height targets. The repetitive reaching task was performed until fatigue was introduced to the upper limb region as indicated by ratings of perceived exertion during the task and later verified using quantitative measures (maximal force output, electromyography signal changes). In addition, we applied stance perturbations in the form of surface translations every minute during the protocol.

Kinematic adaptations were observed to occur in the presence of fatigue; these included both global postural measures as well as joint angle and position measures of the arm, shoulder and trunk. These adaptations developed soon after the start of the task. Adaptations also occurred in the temporal domain with significant changes occurring at both the inter- and intra-reach level. These adaptations occurred in multiple directions with predominant adaptations occurring in directions orthogonal to the main movement direction. Despite these changes, the coordination between the postural (CoM) and focal task components (finger trajectory) was unaffected by fatigue, even during the surface translations. However, surface translations induced changes in kinematic characteristics of the arm and trunk, predominantly in the anterior-posterior direction, while changes in the mediolateral kinematic characteristics of the shoulder occurred with fatigue.

The findings presented in this thesis support the conclusion that repetitive motion induced arm fatigue leads to both movement and postural adaptations and that the central nervous system (CNS) takes advantage of redundant degrees of freedom by making these adaptations in multiple directions spatially and across various temporal domains. The responses to shoulder fatigue and to postural perturbations occur predominantly in directions orthogonal to each other, and thus minimally interact with each other, suggesting that strategies are consistent with the principle of minimal interaction of motor control.

Abrégé

Il a été démontré que les mouvements répétitifs du bras résultent en une réorganisation complexe de l'activité des muscles du bras et du tronc, amenant des changements de coordination corporelle. Cependant, la relation entre la fatigue et le contrôle des mouvements du bras et de la posture est mal comprise. L'objectif principal de cette thèse était d'investiguer les effets de la fatigue induite par les mouvements répétitifs du membre supérieur sur le contrôle de la posture et du mouvement. La cinématique corporelle tridimensionnelle a été enregistrée alors que les sujets effectuaient une tâche répétitive de pointage entre deux cibles placées à la hauteur de l'épaule. La tâche répétitive de pointage a été effectuée jusqu'à ce que la fatigue soit induite au membre supérieur, telle qu'indiquée par les scores de perception de l'effort durant la tâche et ensuite vérifiée à l'aide de mesures quantitative (force maximale produite, changements dans les signaux électromyographiques). De plus, nous avons appliqué des perturbations à la posture debout sous forme de translation de la surface de sustention chaque minute durant le protocole.

Des adaptations cinématiques ont été observées en présence de la fatigue; celles-ci ont inclu des changements de posture globale ainsi que des différences angulaires et positionnelles au bras, à l'épaule et au tronc. Ces changements se sont développés rapidement après le début de la tâche. Les adaptations se sont également produites dans le domaine temporel avec des différences significatives entre les mouvements ainsi que durant chaque mouvement. Ces adaptations ont été apportées dans plusieurs directions, avec les changements prédominants apportés dans les directions orthogonales à la direction principale du mouvement. Malgré ces changements, la coordination entre les composantes posturales (CoM) et focale (trajectoire du doigt) n'a pas été affectée par la fatigue, même durant les translations de la surface. Cependant, celles-ci ont induit des changements dans les caractéristiques cinématiques du bras et du tronc, surtout dans la direction antéropostérieure, alors que les changements dus à la fatigue se sont produits surtout dans la direction médiolatérale.

Les résultats présentés dans cette thèse supportent la conclusion que la fatigue induite par les mouvements répétitifs du bras amènent des adaptations de la posture et du mouvement et que le SNC utilise avantageusement la redondance de ses degrés de liberté en effectuant ces adaptations dans plusieurs directions et à travers plusieurs domaines temporels. Les réponses à la fatigue et aux perturbations posturales sont effectuées dans des directions principalement orthogonales l'une de l'autre et donc interagissent minimalement ensemble, suggérant que les stratégies sont cohérentes avec le principe d'interaction minimale du contrôle moteur.

Table of Contents

List of figures

List of tables

List of abbreviations

Abd	abduction
Add	adduction
AP	anteroposterior (anterior-posterior) direction
APA	anticipatory postural adjustment
APR	anticipatory postural response
BoS	base of support
BP	backward perturbation
CNS	central nervous system
CoG	centre of gravity
CoM	centre of mass
CoP	centre of pressure
CRIR	Centre de recherche interdisciplinaire en réadaptation
DoF	degrees-of-freedom
EMG	electromyography
END	distal target touch
EP	endpoint (fingertip)
EPH	equilibrium point hypothesis, lambda model
Ext	extension
Flx	flexion
FP	forward perturbation
FR	frame of reference
FT	fatigue-terminal
Fx	mediolateral ground reaction force
Fy	anteroposterior ground reaction force
Fz	vertical ground reaction force
LFF	low-frequency fatigue
ML	medioateral direction
MMG	mechanomyography
MNF	mean power frequency
MVC	maximum voluntary contraction (synonymously used with MVIE)
MVIE	maximum voluntary isometric exertion
NF	no-fatigue
NIRS	near infrared spectroscopy
OFF	platform movement offset
ON	platform movement onset
RMS	root-mean squared amplitude
RoM	range of motion
RPE	rating of perceived exertion
RRT	repetitive reaching task
SD	standard deviation
SI	super-inferior (vertical) direction
TPR	triggered postural response

Statement of Originality

All material presented in this thesis contains original work completed by the author and has not been published elsewhere except where specific references are indicated. The manuscripts presented in chapters 3, 4 and 5 represent original material and contribute to our advancement of knowledge in the fields or posture and movement control. To the knowledge of this author, the studies presented within are the first to investigate the relationship between posture and movement control during the presence of repetitive motion induced upper limb fatigue.

All data presented in this thesis were collected at the Feil & Oberfield CRIR (Centre de Recherche Interdisciplinaire en Réadaptation) Research Centre of the Jewish Rehabilitation Hospital, which is affiliated to McGill University. The protocols used in this study have been approved by the Research Ethics Board of CRIR, which is recognized by McGill University.

Contribution of Authors

All manuscripts contained in this thesis were primarily prepared by Jason Fuller, including the design of the studies, subject recruitment, data analysis and preparation of the manuscripts for publication. This entire work was done with the direct guidance and supervision of Dr. Julie Côté. All studies were critically reviewed by Dr. Joyce Fung, who also provided helpful suggestions in regard to study design and data analysis. For the manuscript contained in chapter 3, Dr. Karen Lomond assisted with computer programming for some of the data analyses performed.

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Chapter 1: Introduction

1.1 Rationale

Repetitive movements are an integral part of daily activity. Repetitive motions involving the upper limb are a major facet of many workplace tasks (e.g. manufacturing, assembly line tasks, construction, packaging and handling) as well as many sporting and leisure activities (Putz-Anderson et al. 1997; Zakaria et al. 2002). The prolonged performance of repetitive movement involving the upper limb is widely believed to be linked to medical conditions such as rotator cuff tendonitis (shoulder), lateral epicondylitis (elbow) and carpal tunnel syndrome (forearm-wrist) (Sommerich et al. 1993), which result from chronic overuse affecting muscles, nerves and/or joints and typically leading to inflammation and pain (Murphy et al. 2006). Repetitive motion disorders (RMDs), also referred to as repetitive strain injury (RSI) or cumulative trauma disorders (CTD), are umbrella terms used to describe medical conditions resulting from repeated movements (Melhorn 1998; Tjepkema 2003; Murphy et al. 2006). In the last decades, the prevalence of RMDs has been recognized as a major health concern among many industrialized including Australia, Japan, the United States and Canada (Melhorn 1998). As reported in a 2001 census, 10.1% of Canadians aged 20 years or older reported that a RMD had limited their activity during the previous year, a proportion that had risen significantly from 1997 (8.0%) and 1999 (9.4%) (Statistics Canada 2001; Tjepkema 2003). While 75% of all RMDs involve the upper limb (Statistics Canada 2001) most research on RMDs has focused on investigated disorders of the lower back (Marras et al. 1998) and hence little in known about upper limb RMDs.

1.2 Problem statement

One predominant underlying issue that is currently limiting the understanding of RMD development is a limited knowledge of how upper limb movements are controlled during repetitive conditions. Complicating the investigation of repetitive upper limb tasks is the inherent relationship between repetition and the development of fatigue – a phenomenon known to pose an "internal perturbation" to many aspects of the sensory, central and motor control systems. In the literature, the development of fatigue has been linked to both altered movement coordination local to the site of fatigue *and* to altered global postural characteristics. However, to date, the effect of upper limb fatigue has only been investigated on movement and postural components individually and thus, the combined relationship between fatigue, upper limb movement and postural control remains unknown.

1.3 Scientific background

Repetitive activities that require sustained arm postures at or above shoulder height are known to combine numerous risk factors associated with the development of neck/shoulder RMD (e.g. sustained static contraction of shoulder/neck musculature, repetition, impaired blood circulation, prolonged awkward posture) (Hagberg 1981; Sjogaard et al. 1986; Sommerich et al. 1993) and are known also to induce fatigue (Nussbaum 2001; Nussbaum 2003). During sustained maximal voluntary contraction (MVC), fatigue is defined as a decline in force output (Enoka and Stuart 1992). While upper limb contractions required during the performance of common repetitive tasks rarely near maximal capacity, submaximal muscular contractions may also induce fatigue-related changes. Studies have shown that efforts of as little as 5 to 10% MVC can result in lingering fatigue effects and discomfort after prolonged periods of activity (Blangsted et al. 2005). As such, during low-force tasks, fatigue has been referred to as an ongoing process which may not necessarily result in a decline in target submaximal force but rather is manifested as an increase in perceived effort

(Jones and Hunter 1983) and a reduction in the maximal force generating capacity (Vøllestad 1997).

In addition to reduced muscle capacity, fatigue in the upper limb has been linked to altered static (Schieppati et al. 2003; Stapley et al. 2006) and dynamic postural control (Nussbaum 2003) as well as reduced joint proprioception (Gandevia 1998). Furthermore, fatigue in the upper limb and other areas such as the hand, legs and trunk has been suggested to lead to a multi-muscle reorganization and a change in multijoint coordination (Bonnard et al. 1994; Sparto et al. 1997; Forestier and Nougier 1998; Danion et al. 2000a; Danion et al. 2001b; Singh et al. 2010a). However, few studies have tried to quantify the effects of fatigue on indices of multijoint coordination during repetitive arm tasks. In studies by Côté et al. (Côté et al. 2002; Côté et al. 2005) examining the performance of repetitive hammering and sawing tasks until fatigue, multijoint and multi-muscle adaptations emerged in the trunk, not just the area in the upper limb local to fatigue suggesting that postural adaptations also had occurred although this was not quantitatively verified.

1.4 General aim

As such, the general aim of this work was to examine the effect of upper limb fatigue on both postural and movement characteristics during the performance of a repetitive upper limb task. To this end, several studies were performed to investigate more specific aspects of the fatigue, movement and posture relationship. A description of the objectives, hypotheses and appropriate rationale for these individual studies follows.

1.5 Objectives and Hypotheses

1.5.1 Chapter 3: Posture-movement changes following repetitive motion-induced shoulder muscle fatigue

In a previous study by Côté et al. (2008) which examined muscle activities during repetitive hammering induced fatigue, it was observed that motion adaptations were accompanied by increased electromyography (EMG) activity in the upper limb musculature (trapezius) as well as in muscles distant to the area of fatigue (external oblique). These findings suggested: 1) that changes in inter-muscular coordination occur with fatigue, and 2) since the external oblique is both a trunk flexor and trunk rotator, motion adaptations during fatigue may have occurred multi-directionally (i.e. occurred beyond the main movement direction). As such, previous studies may have been limited by a two-dimensional analysis within the plane containing the predominant motion when examining fatigue adaptations. It is possible that when performing complex movements involving many joints, additional degrees-of-freedom of movements are involved to take advantage of the overall motor redundancy of the system to prolong task performance (Bernstein 1967). The possibility that this could translate into complex posture and movement changes in all multiple directions of motion had never been explored. **Therefore, the objective of chapter 3 was to characterize three-dimensional (3D) postural and movement adaptations occurring in the presence of fatigue induced by performing a repetitive reaching task with the upper limb. We hypothesized that fatigue induced by repetitive movements gives rise to global postural and movement reorganization that occur in more than one plane.**

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1.5.2 Chapter 4: Time-dependent adaptations to posture and movement characteristics during the development of repetitive reaching induced fatigue

Few studies have attempted to examine the effect of fatigue on temporal characteristics of posture and movement. Multiple studies have suggested that fatigue leads to within movement alterations at both the inter-segmental and inter-muscular levels and could also involve changes in the temporal characteristics associated with the task (Bonnard et al. 1994; Forestier and Nougier 1998; Côté et al. 2005a). Another aspect of repetitive movements that emphasizes a temporal component is movement variability. Several studies have suggested that increased motor variability may have a positive effect on mitigating fatigue development (Farina et al. 2008; Madeleine and Farina 2008; Cignetti et al. 2009). Despite these advances, relatively little is known about how muscle fatigue may affect time-dependent characteristics of both posture and movement control when performing an upper limb task. Knowledge in this area is important to further our understanding of posture-movement coordination occurring with fatigue. Moreover, changes in the temporal coordination of multijoint movements may represent another way in which the system can manage its redundancy in adapting to fatigue; however, very little work has focused on describing the changes in temporal coordination occurring with fatigue. **As such, chapter 4 focuses on the effect of fatigue on three temporal aspects of posture and movement control during a repetitive upper arm task: (1) the onset of adaptations over the duration of the task,**

(2) variability between movement repetitions, and (3) within-movement inter-segmental coordination changes. We hypothesized that: (1) changes in spatial parameters across the body would begin to occur soon after the repetitive task started (2) between repetition variability of upper limb and postural measures would increase with fatigue, and (3) there would be significant changes in the temporal organization of individual joint movements during fatigue.

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1.5.3 Chapter 5: Posture-movement response to stance perturbations and upper limb fatigue during a repetitive pointing task

Chapter 5 more closely examines the motor control and coordination of posture and movement components together and the interaction of posture-movement control with fatigue. It has often been explained in the literature that when reaching to a target the central nervous system (CNS) must concomitantly satisfy two independent subtasks: 1) successfully reaching the hand to an object or target and 2) successfully maintaining postural stability. Prior to the current work, it had been repeatedly shown that when reaching to an anterior target centre of mass displacement is not minimized in the same manner as it is during a postural task alone, but rather contributes to the displacement of the hand/endpoint (Stapley et al. 1998; Pozzo et al. 2002; Patron et al. 2005). As such, increases in postural sway occurring with fatigue may not necessarily represent a loss of control nor be a negative consequence but rather may represent a voluntary mechanism employed by the CNS aimed at compensating for upper limb fatigue by actively contributing to the movement of the arm. One way to further challenge this proposed posture-movement relationship would be to examine the coordination between CoM and EP following a sudden postural perturbation applied to the subject during the performance of the repetitive reaching task. Such a paradigm would permit testing of whether or not CoM and EP remain moving in phase when faced with suddenly altered postural conditions.

While chapters 3 and 4 examine how fatigue can lead to both spatial and temporal adaptations to posture and movement components **the objective of chapter 5 was to examine the relationship between postural and focal tasks following a postural perturbation as well as to further assess the task-specificity of the fatigue adaptations to our repetitive reaching task during the perturbed postural condition**. To achieve this, we administered sudden standing surface translations intermittently throughout the reaching task to examine if the movement task characteristics remained coupled to the postural task characteristics following the perturbation as fatigue developed. **We hypothesized that sudden perturbations would dissociate the relationship between postural and movement trajectories such that the focal task would be preserved despite the increased postural demands. We also hypothesized that biomechanical patterns would emerge in a manner consistent with the principle of minimal interaction of the referent configuration hypothesis of motor control such that the system would be able to satisfy both postural and focal characteristics associated with the task, not only in the presence of fatigue but also in the presence of the postural threat.**

This manuscript has been prepared for the Journal of Neurophysiology. Fuller JR, Fung J, and Côté JN. Posture-movement response to stance perturbations and upper limb fatigue during a repetitive pointing task.

Chapter 2: Literature review

2.1 Control of motor actions: theoretical frameworks

Modeling how the central nervous system (CNS) controls motor actions, such as arm movement, has been a prominent area of focus in the movement sciences literature. Two main theories of motor control have evolved in attempt to explain how motor actions emerge: internal models and the lambda model of the equilibrium point hypothesis (EPH). A number of additional theories and concepts complementary to these two have also been developed but these are typically premised on core notions from either the internal model theory or the equilibrium point hypothesis. A brief discussion of the most prominent theories of motor control and coordination follows.

2.1.1 Internal Models

2.1.1.1 General concept

The general concept of internal models is that the motor control system explicitly programs the forces patterns which will lead to joint movements that allow the preferred endpoint coordinates to be reached (Kawato 1999). These force commands are computed by the motor control system through hypothetical neural mechanisms called internal models. To program motor commands, all models of motor control, internal models included, explain that the central nervous system integrates task-related information such as: perceptions of the external environment (e.g. external forces, obstacles, amplitude between body and goal) perceptions of the internal environment (e.g. joint positions, muscle/tendon tensions, muscle length/contraction velocities) and task specific instructions (e.g. what is the goal of the movement, how accurate does the movement need to be, how fast does the movement have to be) (Bernstein 1967; Kawato 1999; Ostry and Feldman 2003; Latash 2008a). Using this information combined with repeated task experiences, the motor control system formulates an internal model that specifies forces from which body coordinates emerge that satisfy task constraints. For example it may be desired for the tip of a finger (endpoint) to be placed on a button or that one's foot collide with a soccer ball. Existing internal models transform information about these tasks into commands dictating the necessary muscle force patterns that will result in joint configurations which will satisfy the task. For newly encountered tasks for which no internal model exists, the control system at first applies the best fitting existing model (or combination of models) and then continuously modifies the internal model until the desired task is achieved in subsequent repetitions of the task.

There are hypothesized to be two forms of internal models in the CNS that would be able to perform such transformation computations: feedback models and feedforward models. Feedback models transform sensory information into motor commands by performing a series of inverse computations to find a motor scheme that satisfies the desired endpoint coordinates when implemented (Kawato 1999). In other words, feedback models begin with the perception of desired endpoint coordinates which are then used to calculate required joint angles from which the required joints torques are calculated to produce those joint angles from which muscle forces, α-motoneuron activations and central commands can all be calculated in subsequent order using an inverse dynamics computational approach (Kawato 1999). Although this means solving a series of equations with a growing number of unknowns, internal model theory states that the motor control system has the computational power to do so. One limitation to the feedback model approach is that by the time the computations are completed and results are sent back to the periphery, muscle and limb changes may have occurred such that the inversely computed command is providing slightly outdated information. To deal with this problem, the motor control system complements the indirect model with a feedforward model which computes motor commands based on prediction algorithms (Kawato 1999). Feedforward models transform sensory information into force patterns that will lead to the desired endpoint coordinates in a predicative manner taking into account the possible muscle and limb changes which may occur during the time taken by the motor command to reach the muscle (Kawato 1999).

2.1.1.2 Evidence of internal models

Evidence of internal models has predominantly been developed from experiments studying the control and learning of reaching movements within external force fields (Shadmehr and Mussa-Ivaldi 1994; Shadmehr and Brashers-Krug 1997; Hinder and Milner 2003; Milner and Franklin 2005). In these types of experiments subjects often grasp and move an arm manipulandum from one target to another. Experimenters are able to control torques produced at the joints of the manipulandum allowing for external force fields to be created in which the handle (effector) of the manipulandum can be moved by the subject. Generally these experiments require subjects to perform movements from one target to another in a condition with no external force field and then after a period of adaptation, a novel external force field is introduced unexpectedly. The unexpected presence of the external force field typical results in error of the movement in trying to reach the target (Shadmehr and Mussa-Ivaldi 1994). Internal model theorists suggests that this error occurs because the motor control system is delivering motor commands to muscles based on the internal model constructed around the previous environmental conditions (Shadmehr and Mussa-Ivaldi 1994). After the performance of successive trials in the new environment, subjects are able to learn a new internal model. Based on this new internal model, motor commands can be computed in feedforward manners which are specific to the force field conditions thus leading to the production of successful movements in the novel conditions (Shadmehr and Mussa-Ivaldi 1994; Milner and Franklin 2005). If the external force field is then unexpectedly removed, movements will again be unsuccessful (since the current internal model has been built for the external force condition) until adaptive changes can be made. Shadmehr and Brashers-Krug (1997) have shown that adaptive changes to more than one novel condition can be retained in memory provided that sufficient time (~5 hrs) separates the training sessions. Internal models stored in memory may allow for a more expedited adaptation to new external conditions (Shadmehr and Brashers-Krug 1997).

2.1.2 Equilibrium-point hypothesis

2.1.2.1 General theory

One alternative theory of motor control to that of internal models is the equilibrium-point hypothesis (EPH). In particular, the lambda model (λ-model) will be considered. For single joint movement, according to this hypothesis, the motor control system shifts physiological variables associated with the muscle activation threshold lengths of muscles. In the λ-model, such thresholds are determined by the λ* which is a length value of the muscle at which the tonic stretch reflex will be activated (Feldman and Levin 1995). This length parameter, λ*, is dependent on a number of components as defined by the relationship:

$$\lambda^* = \lambda + \mu V + f(t) + \rho$$

where λ is the central contribution to λ* and μ reflects its velocity-sensitivity (Feldman and Latash 2005). The other variables are determined by passive mechanisms (Feldman and Latash 2005). *V* is the time derivative of muscle length, ρ is the effect of inter-muscular interactions and *f(t)* is the history-dependent change in threshold (Feldman and Latash 2005). Neurophysiologically, these parameters are believed to alter the state of the average resting membrane potential of the motoneuronal pool thus making it more or less likely to be depolarized by action potentials generated by stretch activated afferent signals from the muscle spindles (Latash 2008b). In other words, increases in the resting membrane potential will make the motoneuronal pool more sensitive to smaller changes in length. Conversely, decreasing the average resting membrane potential will require greater changes in muscle length (i.e. a larger magnitude of stretch reflex) to depolarize the same motoneuron pool.

Changes to any of the parameters will alter the resting membrane potential defining a new length dependent activation threshold, λ*. If this new λ* represents a muscle length shorter than the actual muscle length (x), muscle force patterns will arise naturally without the need to be previously computed. Also it follows that at the point when λ* equals the actual muscle length (a point referred to as the as the equilibrium point), minimal EMG will be observed. In other words, EMG patterns are not controlled but emerge in proportion to the difference between λ* and x. As such, according to the EPH, the only parameters which the motor control system has to define are the λs (centrally controlled parameters) to produce the desired λ*s for each muscle. Such relationships may be defined based on prior experiences (Latash 2008b).

Error between the effector and goal within external space may develop if inadequate λs are chosen for the desired movement; as such, sensory information on this error may be used to update λs until the desired goal is eventually reached (Gribble and Ostry 2000). It is worth noting that this concept of selecting and storing λs is different than the view of internal models. Internal models build representations of the internal and external physical environments and use this information to compute motor commands associated with goals in the external environment. In contrast, in the EPH λ-model, commands for λs are associated with particular λ*s dictating muscle lengths.

It should also be mentioned that the equilibrium point can be located at any muscle length for which the arising muscle forces (corresponding to the difference between a given muscle length (x) and the current muscle length (λ*)) are equal to the current external load placed on the muscle (Feldman and Latash 2005). Therefore, a difference between λ* and x does not necessarily represent an error signal. In fact the difference between λ* and x is indicative of the force which will be produced by the muscle. When no external load is present, and the muscle is static, the equilibrium point is the point where λ* is equal to x.

2.1.2.2 Reciprocal (R) and co-activation (C) commands

Two other centrally controlled variables are important when considering the coordination of control of λs necessary for agonist and antagonist muscle coordination: R and C commands (Flanagan et al. 1993). In order for a joint to move from one position to another, it must decrease λ* of the desired agonist muscle (i.e. decrease the length at which it will be activated) and increase this same variable of the antagonist. To accomplish this, the R command governs central λ commands to each of these muscles simultaneously, thus shifting the equilibrium point of the joint. In contrast, the C command influences joint stiffness by specifying the angular range for which both the flexor and extensor muscles of a joint are tonically active (Flanagan et al. 1993). Essentially, the C command alters the λs of both the flexors and extensors by the same magnitude so that their respective λ*s also decrease by the same amount. The concurrent λ* decrease of the flexors and extensors does not change the EP, rather it increases the level of co-contractive force among the muscle pairs (Feldman and Levin 1995). Controlling co-activation is important for the motor system as it increases the stiffness at the joint allowing it to resist passive movement when exposed to perturbations. While the C command cannot produce movement on its own, it can be used in conjunction with the R command to stabilize joint movement (Feldman and Levin 1995).

For whole-body control, the EPH proposes that the CNS delivers a global, task-related command to control body configuration. When the actual body configuration (i.e. all actual body angles) is not equal to the configuration specified by the global command, force patterns emerge. This premise is based on the observation that when an external load is unexpectedly removed from the body, a new configuration will be adopted (Feldman et al. 2007). According to the EPH, the actual body configuration observed in the presence of an external load is referred to as the Q configuration and the configuration adopted when no load is present is referred to as the R configuration. In the EPH model, the CNS delivers a central command which sets threshold values of motor neurons thus determining the range of external input at which action potentials will be generated (Feldman et al. 2007). In other words, this empirically based theory suggests that the nervous system does not control muscle activity or limb position directly, but instead specifies the threshold at which muscles become active i.e., the position, R, at which the activity of muscles would become silent. As such, any Q configuration then that does not equal the R configuration will result in emergent muscle activities. From the global R-configuration command, which may be the combined output of a few or many neuronal pools, the individual EMG patterns would emerge due to the interactions of local factors, such as peripheral and inter-muscular reflexes, muscle properties and the presence of external forces. In turn, the selection of processes would be guided by what is referred to as the principle of minimal interaction (Gelfand and Tsetlin 1971; Feldman et al. 2007) defined by Feldman et al. as “neuromuscular elements acting individually or collectively to diminish the imposed activity and interactions by minimizing the gap between the actual and threshold positions”.

2.1.2.3 Evidence of in support of the equilibrium-point hypothesis λ-model

As with internal models, many experiments have been done over the years experimentally showing how the EPH and λ-models explains many facets of motor control. More specifically, predictions of the EPH have been shown to hold true in the areas of: learning and adaptation of arm movements in different force fields (Gribble and Ostry 2000; Foisy and Feldman 2006), simulation of trajectory and velocity profiles (Flanagan et al. 1993) and the control of upright stance (Zatsiorsky and Duarte 1999). But perhaps the most cited evidence in support of the EPH λ-model is its ability to explain how muscles are able to relax at different joint positions (Feldman and Levin 1995). According to the EPH, this phenomenon is possible because of the motor control system’s ability to reset the postural state by adjust muscle activation thresholds (Feldman and Levin 1995). By changing muscle activation thresholds, forces arise via the tonic stretch reflex producing movement of the joint until a new equilibrium point is reached. Once the new equilibrium point is reached, this associated posture becomes the new stabilized posture. In the case where no load is present, λ^* is equal to x (actual muscle length) and no force is produced. In cases where a load is present, once the new EP is reached, force is reduced at a level which stabilizes the load at the new EP. In either case, one would predict from the EPH that the EMG activity level, which is generally proportional to force (Henneman et al. 1965), would rise during movement and then return to a level consistent with what it was before the movement onset. Work by

Osrty and Feldman has indeed shown this to be the case during a rapid elbow flexion movement (Ostry and Feldman 2003). Passive oscillations given to the arm before and after the movement highlighted the similarity of the posture stabilizing mechanisms at the two different joint positions (i.e. force is produced to resist changes in EP) (Ostry and Feldman 2003). Similar findings have been published by Foisy and Feldman (2006) when subjects moved a manipulandum from one position to another with no load. Advocates of the EPH claim that the internal model theory is incapable of explaining this phenomenon of how muscles are relaxed at different postures and cite these findings as evidence for the rejection of internal models (Ostry and Feldman 2003).

2.1.3 The problem of motor redundancy

To this point, two motor control theories have been stressed: internal models and the equilibrium-point hypothesis. While each of these theories offers alternative views on which variables are used to control muscles, as different as they are, they both ultimately face the same dilemma: the problem of motor redundancy (i.e. what to control and at what time to control it). The human body is comprised of many joints, many of which have the ability to move in multiple dimensions thus giving the body a high number of degrees-of-freedom (DoF). The high number of DoF the body possess allows the body to realize many equivalent solutions for a task in the three-dimensional external world that we live in (Bernstein 1967). This presents a problem to the motor control system: how can we define a particular set of joint configurations to achieve the desired effector position from such a large supply of possibilities? The problem becomes even more complex when considering that many joints are crossed by more than two muscles, increasing the dimensionality that the motor control system has to account for. Other levels of the body also increase the redundancy of the system (multijoint muscles, motor unit pools, synapses). One approach to deal with the redundant motor system that is becoming widely accepted is to assume that the movement patterns are associated with many tasks that are arranged into synergies. Certain tasks (e.g. walking, reaching) may perhaps then be controlled simply by activating the necessary synergy and scaling it in magnitude and space. Such a feature would greatly relieve the computational strain on the motor control system trying to deal with such a large amount of redundancy.

2.1.4 Synergies

2.1.4.1 General concept

The existence of movement synergies appears to be quite widely accepted even among those who are proponents of differing hypotheses of motor control (Scholz et al. 2000; Adamovich et al. 2001; d'Avella et al. 2006; van der Linden et al. 2007). This may be in large part due to the generally vague definition that is associated with the term. The general idea underlying synergies is that coordinated movement behaviours are controlled through the involvement of co-varying elements. All of the elements involved form a synergy which can be altered in both amplitude and time to produce the same coordinated behaviour at different speeds and magnitudes. Different researchers have different views on what form the elements of a synergy may be (e.g. muscles, motor units, joints etc.) but generally synergies are viewed as integral to the performance of coordinated movements and provide a framework within which the central nervous system can deal with the large amount of motor redundancy. In other words, a synergy may be viewed as a consolidation of multiple DoFs into a task-specific control unit that is simpler to manage for the control system.

2.1.4.2 Uncontrolled manifold hypothesis

One common way to study the degree of co-variation among element outputs (e.g. joint kinematics, muscle forces) within synergies is to use the approach of principle component analysis (PCA). The main advantage of this technique is that it can describe large portions of variance with a few vectors called principle components (PCs). PCA has often been applied to large sets of data, such as patterns of muscle activation during whole-body perturbations, to identify a few PCs which may reflect relationships among many variables (Ting and Macpherson 2005). Another approach to analyzing synergies is the uncontrolled manifold (UCM) hypothesis (Latash et al. 2007). The main principle of the UCM hypothesis is that it views the motor system not as redundant but abundant system (Latash et al. 2007). It suggests that the motor control system acting on a set of elemental variables only tries to limit the variability of those elements which produce "bad variability" or variability that will not lead to an equivalent solution for the chosen task (Latash et al. 2007). Elements whose variability does not affect the desired outcome are said to be producing "good variability" and the motor control system allows these elements to produce a relatively large amount of variability (Latash et al. 2007). The elements of this subspace producing "good variability" are said to be in the uncontrolled manifold (UCM) (Latash et al. 2007). In this way when the motor control system delegates to a synergy, it does not have to control what all of the elements within the synergy need to do, it just needs to govern feedback loops that ensure successful task performance by limiting contribution of those elements producing bad variability. Within this framework, a group of elements that are controlled in such a way to keep the variability of a performance variable down thus ensuring accurate motor performance is called a synergy (Latash et al. 2007). As an example, in a study where subjects were required to quickly lift and shoot a laser gun at a target (< 250 ms to task completion), the orientation of the gun's barrel with respect to a vector joining the gun and the target was the variable most controlled by the subject (Scholz et al. 2000). Changes in joint configurations that lead to changes in this variable were the most reduced (i.e. outside the UCM) compared to changes in joint configurations that did not affect this variable (i.e. within the UCM) (Scholz et al. 2000). In a second part to this study, an elastic band restricted the movement of the elbow joint but subjects were still able to perform a successful shot on the first attempt. The authors suggested that the observed accurate shooting in this condition was made possible by a multijoint synergy stabilizing the barrel's orientation with respect to the target by altering the motion of the other joints (Scholz et al. 2000). Similarly, in a study examining standing postural response to surface perturbations, it was found that following a perturbation, postural stability was achieved through selective, motor equivalent joint configurations that led to stabilization of the centre of mass (CoM) (Scholz et al. 2007). Joint configurations that moved the (CoM) further away from its pre-perturbation average were presumably minimized (Scholz et al. 2007). Such strategies highlight one of the key characteristics of synergies: they have ability to use the abundance of the motor system to quickly adapt to unplanned circumstances (whether they are due to external perturbations or unplanned internal variability) and maintain successful task performance.

2.1.4.3 Summary of synergies and uncontrolled manifold hypothesis

As was discussed in the previous section, the uncontrolled manifold hypothesis provides a framework in which to analyze synergies. The uncontrolled manifold hypothesis uncovers the elements of a particular synergy which are important for task performance (within the UCM) and those which a free to vary more having no impact on the ability to perform the task. Analysis of the variance associated with these two groups of elements reveals the proportion of good variability to bad variability; the greater this ratio, the stronger the synergy is. Synergies provide researchers a construct in which to describe coordinated movements with respect to a given task. Neurophysiologically, synergies may be a way for the motor control system to increase its efficiency by delegating the performance of a task to a group of elements with specified feedback loops and which are capable of adapting movement to minimize performance error. By way of synergies, the motor control system then just has to determine when to activate a synergy and how to scale it in amplitude. Although synergies allow for a way to describe how coordinated movement occurs, how such synergies might be controlled by the motor control system is another issue on its own and will be discussed further in the following section.

2.1.5 Control of synergies

Several studies have been done with the goal of investigating how synergies adapt to different task conditions in an attempt to gain insight into how they are controlled by the motor control system. Ma and Feldman (1995) investigated reaching movements to targets in the ipsilateral work space during conditions of no trunk movement, forward trunk movement and backward trunk movement. They found that regardless of trunk involvement the same endpoint trajectory was produced. In conditions with trunk motion, movement of the trunk preceded and outlasted endpoint movement. These results were interpreted as evidence for the existence of independent arm and trunk synergies that are reconciled by a compensatory synergy. Adamovich et al. (2001) investigated this arm-trunk compensatory synergy further by unexpectedly arresting the trunk while performing a similar reaching movement. The endpoint trajectory remained invariant while there was substantial coordination changes of inter-joint movement patterns corroborating the role a compensatory arm-trunk synergy. Since these changes occurred after only a short-latency it has been postulated that vestibular and proprioceptive afferents may drive the gain of compensatory synergy. Adamovich et al. (2001) also performed an experiment where the target moved with voluntary trunk movement to produce a task reference frame which was relevant to the body. Again, no differences were observed in the endpoint trajectories from trials where the target was maintained in the external reference frame suggesting that the suppression of the compensatory synergy was dependent on the frame of reference (FR) shift. The idea that centrally adjusting FRs may result in a change of the synergy gain has been suggested in a theoretical framework by Ghafouri et al. (2002). It is conceivable that adjustment of FRs may be the neurophysiological analog to the adjustment of the EPH's λ*s, albeit at the level of synergy/global joint coordination control as opposed to muscle control in the case of λ*, but much more investigation is needed to strengthen this association. Interestingly however, post-stroke hemiparetic patients have difficulty in utilizing the arm-trunk compensatory synergy during uninterrupted voluntary reaching movements to the hemiparetic (ipsilateral) side work space (Reisman and Scholz 2006). This finding may suggest the presence of a neural deficiency among these patients to alter central commands which might adjust the gain of the arm-trunk compensatory synergy. Conversely, inability to implement the compensatory synergy may have been due to the hindrance other physical attributes such as poor flexibility in the trunk and arm (Reisman and Scholz 2006).

In summary of the control of synergies, current literature suggest that synergies may be adapted to external perturbations very quickly at low-latencies (< 50 ms) suggesting that vestibular and/or proprioceptive afferents may have a role in adjusting synergy gains in a reflexive manner

(Adamovich et al. 2001). A theoretical framework has been proposed suggesting that frames of reference may be neurophysiological structures which may be altered to adjust the relative contribution of compensatory synergies (Ghafouri et al. 2002). This theoretical framework appears to be compatible with theoretical framework of the equilibrium-point hypothesis and is worth exploring in more detail in future studies.

2.1.6 Optimal feedback control

An alternative theory to solve the problem motor redundancy is based on the principles of optimization. Whereas synergies deal with the problem of motor redundancy by allowing variability in among DoFs that will not affect the task while facilitating many possible solutions to he task, optimization approaches try to find the best possible solution to the task among the redundant possibilities (Todorov and Jordan 2002). One of the most widely accepted theories to make use of optimal control is the optimal feedback theory (Todorov and Jordan 2002). The general concept of this model is that the motor control system approximates the best possible control solution given the state of the current feedback (Todorov and Jordan 2002; Scott 2004). In this manner the motor system resolves the problem of redundancy moment by moment in time (Todorov and Jordan 2002). When error is introduced either due to natural motor variability or due to external environmental physical properties, the motor system adapts by finding a new optimal solution which considers the new physical state (Todorov and Jordan 2002). The general concept of optimal feedback control theory is consistent with the uncontrolled manifold hypothesis in that it allows flexible behaviours to lead to a desired goal. In fact it is conceivable, that the UCM hypothesis could make use of such optimization processes to determine the formation of the UCM. A possible limitation to optimal feedback control which may need to be addressed in the future is its high dependency on feedback loops which may deliver inaccurate information with sometimes long latencies. This may complicate the computational processes in determining the next optimal solution. However, this is just speculation and for the time being, optimal feedback control offers an interesting alternative to the control of synergies.

2.1.6.1 Summary of motor control theories

Four prominent theories explaining various aspects of motor control have been outlined in the proceeding sections: internal models, equilibrium-point hypothesis, synergy control and optimal feedback control. While the former two deal more directly with the nature of the actual motor commands by discussing how the motor control system defines variables that lead to muscle contraction; the latter two deal more with coordination of joints, limbs and muscles and how the motor control system defines a particular movement amongst an abundance of possibilities. While each of these four theories offer an explanation of how the motor control system transforms of task information into motor commands to produce movement they all fall short of reconciling control and coordination. Eventually the aspects of control and coordination must be united into a single scheme. Some more recent theoretical frameworks presented by Ghafouri et al. (2002) and Latash et al. (2007) attempt to unite the concepts from synergy control and the equilibrium-point hypothesis. Such research directions hold promising futures for the progression of human movement science.

2.2 Postural control

Controlling posture orientation and postural equilibrium are necessary in almost all tasks we encounter during everyday activities. From previous literature, it is generally agreed that postural control refers to the control of the body segments in the environment for the purposes of maintaining equilibrium and desired orientation in space (Horak and Macpherson 1996; Woollacott and Shumway-Cook 2002). Since two thirds of the human body mass is located two thirds of our body height above the ground, in addition to all the intrinsic and extrinsic processes perturbing this mass (e.g. breathing, being bumped, carrying a load), humans are inherently unstable during a standing posture and require a control system to maintain postural stability (Winter 1995). The postural control system can generally be described as primarily consisting of three general components. First, the motor/mechanical components such as motor neurons, muscles, ligaments and tendons are required to create forces and torques that act on body segments to alter the relative orientation of the segments to each other and in space, thus creating motor action (Winter et al. 1996; Henry et al. 1998a; Winter et al. 1998). Second, sensory components obtain important information on the external space (e.g. body's position in global space, surrounding surfaces and obstacles) as well as information on the body's internal state (e.g. position of individual segments relative to each other, presence of fatigued and damaged areas) (Fitzpatrick and McCloskey 1994). Lastly, the central component (or central nervous system) integrates sensory and motor components together with centrally set factors such as intent (McIlroy et al. 2004), attention (Maki and McIlroy 1996), fear (Adkin et al. 2006) and prior experience (Sveistrup and Woollacott 1997). These three components are integrated together via a series of feedback and feedforward neural pathways and are coordinated to control body mechanics in a manner that maintains a stable posture (Fitzpatrick and McCloskey 1994). The contribution that each of these three components make in maintaining postural control will be discussed in greater detail in the following sections, followed by discussion of experimental observations of postural control under various conditions (e.g. quiet stance, perturbed stance, when performing a voluntary movement, during the presence of fatigue).

2.2.1 Biomechanics of quiet stance postural control

First, to give further background to the concepts of postural control and stability, the classic biomechanical model of quiet stance posture will be discussed. During quiet stance, a stable posture has mechanically been attributed to maintaining the vertical projection of the centre of mass (CoM) within the base of support (BoS) (Winter 1995). To maintain a completely static posture, all forces acting on the body must sum to zero as follows from the Newtonian law: acceleration equals force divided by mass. Of course, the gravitational force is constantly acting on the CoM, vertically accelerating it downward, so an equal but opposite force must be created to maintain the CoM in a static position. The vertical counteracting force is the net of the vertical ground reaction forces which are exerted on the bottom of the foot. The point location of the application of the net ground reaction forces is referred to as the centre of pressure (CoP) (Winter 1995). In other words, the location of the CoP is a weighted average of all the pressures under the foot in contact with the ground and can be directly controlled by altering activity in the musculature of the lower legs (Winter 1990). When the location of the CoP and the location of the vertical projection of the gravity force vector acting on the CoM (centre of gravity (CoG)) are the same, the CoM will not accelerate and thus remain static (Winter et al. 1998).

In reality, the CoG is constantly shifting, even during quiet stance due to continuous internal perturbations as a result of small segment reorientations brought about by muscle contractions associated with respiration (Jeong 1991) and other internal processes (cardiovascular activity, digestion, etc.). Using a simplified segmental model of the body, Winter et al. (1998) showed that when the location and magnitude of these force vectors are not equal, the CoM will begin to accelerate angularly, predominantly about the ankle (sagittal plane) and hip joints (coronal plane). In the sagittal plane, when the CoG is situated further away from the ankle joint (fulcrum of the inverted pendulum model) than the CoP, the CoM will accelerate towards the ground. To decelerate the CoM, the CoP must be relocated in the opposite direction to a greater distance away from the fulcrum to create a greater counteracting moment about the ankle in which the CoM is accelerating; this will decelerate the CoM and keep it from accelerating to the ground. As such, it should be no surprise that the movement CoG and CoP have been observed to have an in phase relationship in which the CoP constantly tracks the CoG during quiet stance (Winter et al. 1998; Corriveau et al. 2000). By continuously accelerating and decelerating the CoM, control of the CoP helps to maintain the CoM within the base of support during quiet stance. If the CoM moves beyond the BoS, the CoP will not be able to move beyond the CoG position and the CoM accelerate fall to the ground unles the BoS is adequately adjusted (i.e. feet are moved so that the BoS once again contains the CoG).

Although Winter and colleagues (1998) have proposed a simple model of balance control whereby the central nervous system (CNS) adjusts the stiffness of the lower limb musculature, thus altering CoP position such that the CoG is contained in within the BoS, this model assumes a simplified 2-segment model of the human body and may not apply to more complex models and tasks. Indeed, studies examining postural responses during surface perturbations have shown that musculature across the body, notably in the hip (Henry et al. 1998b), trunk (Ting and Macpherson 2005; Torres-Oviedo and Ting 2007) and arms (McIlroy and Maki 1995; Pijnappels et al. 2010) has been shown to play an important role in the maintenance of posture as shall be discussed later in this review. Nevertheless, the mechanical model proposed by Winter and colleagues (1998) highlights the ability of the CNS to coordinate postural control through optimizing internal and external forces to achieve desired whole-body acceleration and thus maintain equilibrium.

2.2.2 Sensory factors in postural control

Regardless of the precise mechanics in which posture is controlled, it is well known that the CNS requires sensory information about the internal and external environments which in turn influence the motor actions required to maintain posture in a manner which respects environmental constraints. For example, when standing on solid ground the sensory systems will combine to provide the CNS with information of the stability of the environment and an appropriate motor plan can then be created to maintain posture. In contrast, when standing on a swaying boat, for example, the sensory systems must provide information about the dynamically shifting environment so that the motor actions can be adapted in such a way to maintain postural equilibrium during the dynamically changing surface conditions.

The major sensory systems that play roles in postural control are the visual, vestibular and somatosensory systems. Each of these sensory systems provides unique information about the external and internal environments which the CNS then combines in order to create appropriate motor tasks with respect to existing environmental constraints (Fitzpatrick and McCloskey 1994). With respect to postural control, vision provides the CNS with information about the surrounding external environment relative to the body (egocentric frame of reference) and also provides sense of motion via the perception of optic flow (Gibson 1958). The vestibular system provides information in regard to head acceleration while somatosensory information provides cues about segment positions and movement as well as contact with external objects (Fitzpatrick and McCloskey 1994). In healthy individuals, the somatosensory system has the greatest acuity for detecting sway followed by the visual system and then the vestibular system (Fitzpatrick and McCloskey 1994). As such, when somatosensory input is diminished and only vestibular and vision inputs are accessible, the threshold for detecting postural sway is significantly increased (i.e. perception of postural sway is reduced) (Fitzpatrick and McCloskey 1994). The importance of somatosensory feedback for postural control has been shown in a number of studies in which postural sway increased when somatosensory information was experimentally altered in healthy young(Horak et al. 1990; Kavounoudias et al. 1999; Thompson et al. 2010) or diminished in pathological populations due to disease(Bloem et al. 2002; Nardone and Schieppati 2004). For healthy persons standing still on a stable surface the relative weighting of information contributed from the three somatosensory systems to maintain posture has been estimated to be 70% for somatosensory, 20% for vestibular and 10% for visual (Peterka 2002). However, as will bee seen in the coming section, the central nervous system can reweight the contribution of each of these senses during altered internal (disease) and environmental conditions.

2.2.3 Central factors of postural control

The reweighting of sensory information is predominantly the responsibility of the central nervous system particularly since the CNS is the structural area where afferents from somatosensory, visual and vestibular systems converge. The ability of subjects to reweight sensory information is important when faced with disease that diminishes one of the senses or when changing environmental conditions either limit or alter incoming sensory information (e.g. walking into a dark room, standing aboard a swaying ship). As such, impairment of the ability to reweight sensory information may contribute to decreased postural stability as is believed to be the case in some pathologies such as Alzheimer's disease (Horak 2006).

Other central factors such as cognitive processing and psychological states are also known to play an important role in modulating postural control (Woollacott and Shumway-Cook 2002) with more difficult postural tasks requiring more cognitive processing (Teasdale and Simoneau 2001). For instance, reaction times during standing postural tasks are longer than in sitting tasks implying an increase in cognitive resources allocated to postural control during the mechanically more challenging standing (Lajoie et al. 1993). Other factors associated with cognitive processing such as experience, intent, expectation and fear have also been shown to modulate postural response providing further evidence that the influence cognitive factors have on postural control (Burleigh et al. 1994; Horak 1996; Shupert and Horak 1999; Adkin et al. 2000; Adkin et al. 2002; Carpenter et al. 2004). For example, healthy young subjects who anticipate perturbations that are larger than the ones that are actually administered tend to over-respond (Horak et al. 1989).

The development of fatigue is another factor which is believed to alter central integration processes (Allen and Proske 2006) and therefore may play a role in influencing postural control. Vuillerme and colleagues (2002b) showed reaction time to decrease in healthy young subjects while performing a quiet standing postural task during fatigue suggesting that fatigue increases attention (central) demand during postural tasks. Fatigue has also been known to decrease central motor drive to the muscles (Gandevia 2001); if postural muscles were to receive decreased motor drive, the capacity of the postural control system could be mechanically compromised meaning, for example, fatigued subjects may have difficulty performing postural tasks which require increased muscle activity of the postural muscles (e.g. responding to external perturbations).

2.2.4 Motor factors of postural control

The third major system associated with postural control is the motor system, which is responsible for carrying out the necessary motor actions needed to control posture. Movement strategies associated with postural control have been separated into two general categories: feedback based strategies typically observed to return the body to equilibrium following unexpected perturbations (e.g. sudden standing surface translations) and feedforward strategies which for instance, coordinate postural control during expected perturbations (e.g. voluntary movement).

2.2.4.1 Feedback mechanisms of postural control

One way to simultaneously test the combined contribution of many facets of the postural control system is by applying a standing surface perturbation thus challenging stability. Surface translations have been used to examine the postural control responses for many years beginning with the work of Lewis Nashner and colleagues (1976). The use of this paradigm allows for a sudden, yet controlled, change of the physical environment which the postural control system must then adapt to. The resulting movement strategy following the perturbations is often referred to as either the automatic postural response (APR) or triggered postural response (TPR). The typical effect that the standing surface translations has on body mechanics is that the CoM and other body segments are perturbed in the opposite direction of the surface acceleration (Henry et al. 1998a). Following the onset of the perturbation, the somatosensory, vestibular and visual sensory systems will detect the sudden change in equilibrium and trigger an automatic postural response to stabilize the CoM within the base of support. The resulting motor response to a surface translations is stereotypical and well documented beginning with activation in the lower leg musculature at a latency of approximately 100 ms (Nashner 1977; Burleigh et al. 1994; Shupert and Horak 1999) then followed by activation of the hip, trunk (Horak and Nashner 1986) and arms musculature (McIlroy and Maki 1995).

While these postural reactions were originally believed to be controlled through reflex responses acting directly from the sensory afferents onto motor units through feedback loops (Weisz 1938; Roberts 1973) more contemporary models explain that these responses may be selected from centrally preprogrammed postural modes, or synergies (Nashner and McCollum 1985; Torres-Oviedo and Ting 2007). According to this model, the CNS chooses the most appropriate preprogrammed muscle synergy or combination of synergies based on biomechanical/environmental constraints, available sensory information, intent and prior experience (Horak et al. 1989; Torres-Oviedo and Ting 2010) in order to produce a stabilizing motor response.

Typical movement responses to maintain balance following a surface perturbation have been broadly categorized as parts of an ankle strategy, a hip strategy or a stepping strategy (Horak and Nashner 1986). Small perturbations to equilibrium evoke the ankle strategy, during which the body moves about the ankle as an inverted pendulum (Horak and Nashner 1986) similar to the model described by Winter and colleagues (1998) whereby the lower leg muscles are the predominant muscle group involved in the response. The hip strategy is employed during larger perturbations during which the CoM is required to move more rapidly or when constraints to the standing surface (i.e. standing surface smaller than the feet) limit the use of the ankle strategy (Horak and Nashner 1986; Diener et al. 1988; Horak 2006). The hip strategy is also shown to be highly involved during mediolateral direction translations as the ankles have reduced range of motion in this direction. Finally, a stepping strategy is used during very fast and large magnitude perturbations for which the ankle and hip strategies are inadequate. During these large perturbations, the CoM moves either outside the base of support or quickly accelerates towards the limits of BoS. By initiating a step to expand the BoS such that it once again contains the CoM, equilibrium can be preserved (Horak and Nashner 1986; Horak et al. 1989).

The selection of the strategy can vary not only according to the magnitude, velocity and direction characteristics of the perturbation (Diener et al. 1988) but also with characteristics such as initial posture, environmental constraints, available sensory information, attention, practice and instructions given to the subject (Horak et al. 1984; Horak and Nashner 1986; Moore et al. 1988; Horak et al. 1989; Horak et al. 1990; Horak and Moore 1993; Maki and Whitelaw 1993; Henry et al. 1998b; Wu 1998; Henry et al. 2001; Adkin et al. 2008; Caudron et al. 2008). For example, during a series of trials experiencing the same perturbation, subjects showed significantly reduced muscle activation and joint range of motion in response to perturbations in later trials than they did in the first few trials (Horak et al. 1989). To mitigate the effect of experience as a confounder, it is common to have subjects perform a series of practice perturbations prior to experimental testing so that the studied responses are more stable and consistent. While at least one study has shown that subjects continue to adapt their response even after as many as 100 trials (Horak et al. 1989), others have shown that the most significant adaptations occur within the first 4-5 trials (Wu 1998). As such most research paradigms have subjects perform 5-10 practice perturbations before beginning experimentation (Wilson et al. 2006; Davidson et al. 2009).

The kinematic characteristics examined can also impact the type of postural response that is ultimately documented. For instance models typically assume the trunk to be one rigid segment, however, Preuss and Fung (2008) described a spatiotemporal intra-segment trunk coordination sequence in response to perturbations when maintaining postural control (Preuss and Fung 2008). Similarly, arm movement has been shown to have a role in creating stabilizing moments to restore balance following perturbations yet the arms are seldom included in kinematic models of postural control (McIlroy and Maki 1995; Bloem et al. 2002; Grin et al. 2007).

In summary, while there are numerous factors that influence the nature of the strategy employed by the CNS in response to a surface perturbation, the general automatic response appears stereotypical: first beginning in the lower limbs and then travelling upwards through the trunk and upper limbs. As constraints and environmental conditions change, the CNS likely recruits different (or additional) synergies that modify the motor strategy such that equilibrium can be maintained through a wide variety of encountered scenarios.

2.2.4.2 Feedforward mechanisms of postural control

In addition to external perturbations to equilibrium, internal perturbations such as reconfiguration of body segments resulting from breathing or voluntary arm movements can pose perturbations to equilibrium as well. Whereas postural control following external perturbations relies heavily on sensory feedback, postural control during internal perturbations can be controlled more in a feedforward manner since the onset, magnitude, direction and other perturbation parameters can be predicted.

The most commonly studied type of internal perturbation to postural control has been voluntary arm movement. Since CoM is a weighted sum of all the body segments, moving the arm will change the relative orientation of body segments to each other and ultimately a change in CoM position unless compensatory movements are made in other segments to maintain a steady CoM position. For example, when performing a standing, reaching task with the upper limb the central nervous system must satisfy two independent subtasks: a focal task (e.g. reorient arm segments to reach towards an object) and a postural task (i.e. successfully keep the body upright and balanced). Typically, behavioural studies examining the interaction between posture and arm movement utilize measures of endpoint (EP) and whole-body CoM position as indicators of the focal and postural tasks, respectively (Kaminski et al. 1995; Pozzo et al. 1998; Stapley et al. 1999; Stapley et al. 2000; Pozzo et al. 2002; Patron et al. 2005). Originally, changes to posture during voluntary movements with the arm were believed to be strictly a consequence of the movement itself, however, recent work has shown that CoM movement may be a strategy employed by the CNS to contribute to the performance of the upper limb movement (Massion 1992). More specifically, research has shown that when performing a pointing or reaching task with the upper limb to an anterior target, CoM movement is not minimized but moves in phase with EP trajectory (Stapley et al. 2000; Pozzo et al. 2002; Patron et al. 2005). Interestingly, similar observations have been made during zero gravity environments (Patron et al. 2005) and during environments where the base of support (BoS) is reduced (Fautrelle et al. 2010) suggesting this relationship is preserved by the CNS despite varying environmental conditions. Also, this relationship is conserved even when the arm is removed from the CoM model indicating that CoM displacement towards the target during reaching is not simply a function of arm displacement but rather that other more proximal segments are also actively controlled towards the target so as to aid EP displacement (Pozzo et al. 2002). Moreover, whole-body reaching simulations have shown that reaching to anterior target can in fact be performed without CoM displacement (i.e. forward displacement of the arm mass offset by posterior displacement of the hip) (Stapley et al. 2000) further suggesting that the CNS chooses not to minimize CoM movement during a reaching task. Finally, preparatory adjustments to CoM movement actually precede the onset of endpoint movement (Stapley et al. 1998; Leonard et al. 2009; Leonard et al. 2011). Taken together, these results suggest that CoM movement during voluntary reaching is a feedforward control strategy of the CNS and not a simply an emergent one due following arm movement alone.

2.2.5 Posture-movement control: single-process or dual-process?

While it is apparent that postural aspects of a reaching task are actively controlled during such tasks as opposed to being a more simple, emergent phenomenon due to arm movement, a question that remains under much investigation is whether posture- and movement-associated motor actions are controlled as a single, global process or as dual, parallel processes (Massion 1992; Robert et al. 2007). Aruin and Latash (1995) have argued that a single command controls both posture and movement following results that anticipatory postural adjustments differed depending on the type of kinematic strategy subjects used to drop a held weight. Similarly, Stapley et al. (2000) observed postural segments to be involved in whole-body reaching in such a way that they participated in the act of the focal task and implied that this finding may be indicative of a common central command controlling both posture and movement.

Alternatively, the absence of endpoint alterations during postural compensations has been argued as evidence for a dual-process control (Robert et al. 2007). Similarly, Trivedi et al. (2010) have shown that when stance is perturbed while performing a pointing task, the initial postural response is unmodified as compared to perturbed quiet stance thus suggesting that the postural response in unaffected by movement of the arm. The same study goes on to describe that the prolonged voluntary postural response is then integrated with the movement strategies. Taken together, these findings suggest that the CNS has the ability to control posture and movement separately when faced with a postural threat and can later reintegrate movement and postural control commands together to carry out the desired reaching movement. Moreover, experiments from the field of neurophysiology (Schepens and Drew 2004; Schepens et al. 2008) have produced findings consistent with the hypothesis that movement and postural commands are tightly integrated within the CNS yet may arise from independent groups of neurons within the brain. In their studies, Schepens and Drew (2004; 2008) show that different groups of neurons are active in the brain of cats during postural tasks, compared to reaching tasks. While it is uncertain if data measured from quadruped stance in a cat model is applicable to humans, many have taken this data to be representative of separate, parallel processes for posture and movement control. Another possibility is that the commands for posture and movement arise from different pools of neurons but are centrally integrated together and descend as a common global command.

In summary, at the present time it remains unclear if the control of posture and movement is a single or dual-process. Further neurophysiological data combined with continuing development of motor control models should help to clarify the mechanisms underlying the behavioural observations of posture and movement control.

2.3 Fatigue

2.3.1 Introduction to muscular fatigue

Everyday tasks often involve repetitive movements. For instance, those working on assembly lines in manufacturing plants often are required to perform the same task repeatedly. Even in leisure activities, one might frequently repeat the same movement, such as when playing a musical instrument or a sport. One of the possible and frequent consequences of repeating a movement is the development of neuromuscular fatigue. Despite its prevalence, neuromuscular fatigue, from here forward simply referred to as “fatigue”, is a poorly understood phenomenon. The physical symptoms that one might experience with fatigue include muscles soreness, stiffness, pain and elevated perceived exertion (Jones and Hunter 1983a; Dugan and Frontera 2000; Hampson et al. 2001; Taylor and Gandevia 2008).

The rate of development of fatigue is dependent on the level of muscle activation intensity, type of task and duration (Taylor and Gandevia 2008). Also, how one might develop fatigue is very much contingent on the task at hand. For instance, when performing an intense, maximal activity (e.g. lifting heavy furniture), fatigue occurs quite rapidly. However, performing low-intensity, long duration activities (e.g. computer work) can also cause fatigue over time (Blangsted et al. 2005).

Fatigue is classically defined as a gradual phenomenon that begins to develop soon after activity onset leading to a reduction in the maximum force and/or power the involved muscles can produce (Enoka and Stuart 1992). Maximal force production is achieved when all motor units are active and there is optimal excitation-contraction coupling within individual muscle fibers. As such, any exercise-induced factor that leads to an inability to activate all motor units and/or leads to a reduction in the efficiency of excitation-contraction coupling is a potential cause of fatigue. However, it is important to note that the presence of fatigue does not always imply a reduction in task performance. Indeed, fatigue has been shown to develop during submaximal exercise (as manifested by a decrease in intermittent measures of MVC force) despite no change in the desired submaximal force output (Bigland-Ritchie et al. 1986b). As such, during low-force tasks, fatigue is an ongoing process which may not necessarily result in a decline in target submaximal force but is typically manifested as an increase in perceived effort (Jones and Hunter 1983) and a reduction in the maximal force generating capacity (Vøllestad 1997).

2.3.2 Mechanisms of fatigue

2.3.2.1 Peripheral mechanisms of fatigue

2.3.2.1.1 Primary metabolic substrates associated with fatigue

Regardless of task intensity, the potential causes of fatigue are as numerous as the mechanisms leading to excitation-contraction coupling (Davis and Walsh 2010). Within the literature fatigue mechanisms are generally divided into two groups: peripheral factors and central factors (Dugan and Frontera 2000; Gandevia 2001; Taylor and Gandevia 2008; Ament and Verkerke 2009; Place et al. 2010). Peripheral factors refer to factors of fatigue occurring within the muscle itself (i.e. below the neuromuscular junction) and typically are related to the accumulation of metabolic substrates which ultimately alters the excitation-coupling mechanism taking place in muscle fibers (Place et al. 2010). The substrates most prominently associated with peripheral fatigue development include hydrogen (H^+), inorganic phosphate (Pi), potassium (K^+) and magnesium (Mg^+), although the exact mechanism by which each of these may lead to development of fatigue is not fully understood. The accumulation of Pi and Mg^+ are related to the inhibition of Ca^{++} release due to interactions of these ions within in the sarcoplasm

(Lamb and Stephenson 1991). Also inhibiting Ca^{++} is the efflux of K^+ which reduces action potential propagation (Juel 1986; Juel 1988). The release of Ca^{++} into the sarcoplasm is necessary to bind to troponin which in turn frees myosin heads to bind to actin, thereby initiating sarcomere contraction (Åstrand et al. 2003). In addition to the inhibition of Ca^{++}, the cross-bridge cycling between actin and myosin may also be directly affected by H^+ and Pi (Cooke et al. 1988; Millar and Homsher 1992; Potma et al. 1994; Potma et al. 1995). The precise mechanisms by which these metabolites interact and lead to decreased force production has yet to be elucidated, however, it is well demonstrated that metabolic by-products are associated with the development of fatigue during exercise (Place et al. 2010).

2.3.2.1.2 Build-up of metabolic substrates and importance of blood flow

The accumulation of metabolic substrates is related to the intensity of exercise. Indeed, higher force contractions recruit larger motor units whivh are associated with Type II muscle fibres (Henneman et al. 1965). These Type II muscle fibres create more metabolic substrates due to the method in which they break down ATP (Åstrand et al. 2003). Also, during higher intensity exercises, the intramuscular pressure increases, thus occluding blood flow (Sjogaard et al. 1988; Jensen et al. 1993). When blood flow is occluded, metabolite accumulation within the muscle increases as the metabolites cannot be efficiently removed from the muscle (Åstrand et al. 2003). Proper blood flow to the muscle is also essential for the delivery of oxygen which is utilized for the breakdown of ATP by slow-oxidative fibres (Åstrand et al. 2003). For these two reasons, sufficient blood flow to the muscle is an important factor in preventing fatigue (Sjogaard et al. 1988). In most muscles, blood flow begins to become restricted at 10 to 20% maximum voluntary contraction (Sjogaard et al. 1986). Complete occlusion occurs at over 50% MVC although these numbers may vary depending on the muscle geometry (e.g. long, short, pennate) and other structural parameters (Sjogaard et al. 1988). Blood flow during dynamic contractions is believed to be improved due to lengthening and contracting of the muscle augmenting venous return (Masuda et al. 1999). As such, the type of contraction (static or dynamic) may also have a considerable effect on fatigue development particularly in relation to peripheral factors such as metabolite build-up.

2.3.2.1.3 Fatigue during dynamic, low-force

During dynamic, low-force contractions, it is predominantly oxidative muscle fibres that are activated in accordance with the size recruitment principle (i.e smaller motor diameter motor neurons, connected to Type I oxidative fibres, depolarize first; as exercise intensity increases, larger motor neurons depolarize which activate Type IIa/b fibres) (Henneman et al. 1965). Furthermore, the lower force of the contraction results in a lower intramuscular pressure existing within the muscle (i.e. blood flow is less occluded) (Sjogaard et al. 1986). Together, these attributes of low-force contractions mean that there is less likelihood that the mechanism of low-force fatigue is related to the build-up of metabolites. In contrast, during sustained submaximal activity, glycogen stores become depleted, halting the production of ATP in oxidative fibres (Coyle et al. 1986); the lack of ATP the eventually leads to a reduction in cross-bridge cycling. Also unique to submaximal contractions, structural changes to the fibres themselves, such as disruptions to mitochondria and moth-eaten fibres which can inhibit proper sarcomere contraction, may occur over time (Hagg 2000; Tiidus 2010). These fatigue mechanisms common to low-force contractions may lead to different motor adaptations and sensations as compared to maximal contractions. For example, low-force contractions are typically not associated with decreased performance but have been shown to lead to long, lingering effects on small motor units post submaximal isometric exercise (Blangsted et al. 2005).

2.3.2.2 Central mechanisms of fatigue

Central factors are all other potential mechanisms of fatigue development within the body occurring proximal to the CNS from the neuromuscular junction. Most of the attention in the study of central fatigue has been focused on the central nervous system itself where several mechanisms have been identified that may lead to reduced motor drive to the muscles (Gandevia 2001). First, the excitability of motor cortex neurons can be altered during sustained motor activities (Taylor et al. 1996) although the mechanism by which this may occur is unclear. Secondly, action potentials traveling down motor neurons may become slowed resulting in a loss of muscle fibre activation (Juel 1988). Thirdly, changes in the activity of reflex afferents from the muscle spindles and Golgi tendon organs may alter the motor drive coming from higher centers (Garland and Kaufman 1995). Finally, stimulation of the chemoreceptors and nociceptive afferents by metabolic by-products of fatigue are hypothesized to be involved in a feedback loop which decreases motor cortex output and motor neuron firing rate (Garland and Kaufman 1995). While the precise physiological mechanisms of how these central factors contribute to fatigue is still relatively unknown the presence of some sort of central fatigue is well established. Indeed, when transcranial magnetic stimulation is applied to the motor cortex or electrical stimulation is applied to motor nerves during maximum voluntary contraction motor output increases suggesting a reduced central drive to the muscles occurring with fatigue (Bigland-Ritchie et al. 1986b; Taylor and Gandevia 2001; Taylor et al. 2006). Analysis using functional magnetic resonance imaging and other techniques to model neural networks may help to uncover more precisely the regions within the motor cortex and CNS in general that are the greatest contributors to the development of central fatigue.

2.3.3 Fatigue factors associated to altered motor performance

Not only do physiological changes brought on by fatigue cause discomfort to the individual, but fatigue-related sensations and their associated physiological effects can also impact on task performance. Essentially, fatigue can act as an "internal perturbation" to the individual which can eventually lead to either a decline in task performance or an adaptation of the neuromuscular control strategy. In other words, as the capacity of the working muscle diminishes, altered control strategies emerge in order to facilitate the continuity of the fatiguing task. The following section discusses three major alterations resulting from fatigue that affect movement execution.

2.3.3.1 Intra-muscular activation changes

During muscle fatigue, muscle contractile efficacy is reduced (Bigland-Ritchie and Woods 1984) leading to reduced functional capacity of a muscle (or group of muscles) to produce force. To maintain performance despite the reduced functional capacity of an involved muscle, the control strategy must be adapted at either the intra- or inter-muscular level to maintain performance. At the intra-muscular level, the recruitment of non-fatigued motor units (Garland et al. 1994; Westgaard and de Luca 1999) and de-recruitment of active motor units (Westgaard and De Luca 2001) may be one strategy in which a muscle may maintain a certain level of submaximal force despite the onset of fatigue in some motor units. For example, Farina et al. (2008) examined subjects who sustained a prolonged contraction of the trapezius. Instead of using the standard bipolar electrode placement, authors used an array of electrodes that measured the activity of trapezius across the entire surface of the muscle. They found that the heterogeneity of spatial activation throughout the muscle increases more so in subjects who sustain the force longer (Farina et al. 2008). Motor unit substitution is believed to be the primary mechanism underlying this finding. As such, intra-muscular activation changes are likely a predominant compensatory mechanism to adapt to fatigue while maintaining task performance.

2.3.3.2 Inter-muscular activation changes

At the inter-muscular level, fatigue has been linked to changes in inter-muscle relationships among agonist muscle groups (Danion et al. 2000; Danion et al. 2001; Kouzaki et al. 2002; Kouzaki and Shinohara 2006; Côté et al. 2008; Singh et al. 2010a; Singh et al. 2010b) and increased co-contraction of agonist-antagonist muscle pairs (Psek and Cafarelli 1993). However, inter-muscle activity changes are not limited to proximally located muscle groups. Côté et al. (2008) observed increased muscle activity in the trunk during a prolonged hammering task that predominantly fatigued muscles of the shoulder, indicating that during complex tasks, fatigue adaptations occur in segments distal to the fatigued muscle. Such adaptations may be a compensation mechanism to prolong task performance by increasing activation of non-fatigued muscles to compensate for those that are fatigued.

2.3.3.3 Altered somatosensory feedback

The metabolic by-products that build up within the muscle are known to alter the output of many types of afferent involved in providing feedback about the current state of the musculoskeletal system. One frequently researched phenomenon has been altered proprioceptive feedback leading to reduced joint position sense during fatigue (Sharpe and Miles 1993). The mechanism leading to reduced joint position sense have been linked to the build-up of metabolic by-products of fatigue such as H^+ which then alter the activation of muscle spindles, Golgi tendon organs, joint receptors and type III and IV afferents (Windhorst and Kokkoroyiannis 1991; Pedersen et al. 1998; Pettorossi et al. 1999; Hill 2001; see Windhorst 2007 for review). The altered information from these sensory neurons is believed to give an inaccurate sense of joint position. An alternative proposed mechanism for reduced joint position sense which has emerged recently is that central factors may alter the processing of afferent signals in the sensorimotor cortex and ultimately lead to reduced position sense (Allen and Proske 2006). Regardless of the mechanism, inaccurate information about the position of joints from sensory neurons may lead to inappropriate motor signals and ultimately, to decreased motor performance or altered motor mechanics.

2.3.4 Non-invasive measures of muscle fatigue

While characterizing movement adaptations during fatiguing activities can be directly quantified through motion capture, the measurement of muscle fatigue involves more indirect methods. There is currently no ideal single method to measure fatigue non-invasively. While many non-invasive measures have been developed to measure fatigue each has a limited scope to offer. A brief description of the most commonly used of these measures and their intended use are discussed the following sections.

2.3.4.1 Maximal voluntary contraction force generation

Force generation during maximum voluntary contraction (MVC) is considered the most direct measure of fatigue as it quantifies the most widely accepted consequence of fatigue (i.e. reduction in muscle force). During the MVC of non-fatigued muscles, it is assumed that the subject is giving their maximum voluntary effort (MVE) during an isometric such that all motor units are maximally active and hence maximal force is produced. Any reduction in force output over time can then be said to be due to fatigue mechanisms. Strong verbal encouragement is typically given to the subject to ensure they are giving their true MVE - a tactic that has been shown to decrease the variability of force output MVCs (Gandevia et al. 1995). Since MVC force output is the integrated result of the entire sequence of physiological force producing mechanisms it is considered the "gold standard" fatigue indicator but other methods must be utilized to provide insight into the actual origin of fatigue (i.e. central or peripheral and further sub-levels of these). Intermittent MVCs have been performed when investigating submaximal, functional tasks to test for the presence of fatigue. Unfortunately, these intermittent MVCs are likely to alter the true fatigue development pattern of the submaximal task making this test for fatigue undesirable during many experimental protocols.

2.3.4.2 Power output

Maximal power output provides similar information to the MVC force output measure in that it is the integrated result of all physiological events leading to muscle contraction during concentric contractions (Vøllestad 1997). Assessment of power is conducted using an isokinetic device and therefore tests for fatigue developing in the moving muscle as opposed to a static muscle as is done during tests of MVC force output (Vøllestad 1997). Therefore, the power output technique may be able to more realistically test the contractions observed in functional tasks as compared to the MVC technique. One limitation of this technique however, is that it is a challenge to design power output tasks to test some muscle groups (e.g. trapezius/shoulder elevators) due to the low range of motion they produce.

2.3.4.3 Tetanic force output

The tetanic force technique involves measuring the force generating capacity of electrically stimulated muscles. This method effectively removes the possible contributions of the central nervous system to the development of fatigue. In other words, muscles are tested for fatigue independent of central motor drive (Bigland-Ritchie et al. 1986b) and hence less susceptible to the variability of factors such as motivation and voluntary effort. The maximum force a muscle can generate under electrical stimulation is called the maximum evocable force (Gandevia et al. 1995; Taylor and Gandevia 2008). Subtracting the MVC force from the maximum evocable force can provide insight into the proportion of fatigue related force loss to central factors (Taylor and Gandevia 2008). A decrease in the tetanic force output could represent fatigue of any of the physiological phenomena below the area of stimulation (Taylor and Gandevia 2008). Difficulties associated with this technique include using it during the performance of functional tasks (electrical stimulation disrupts natural motor control) and also, excessive stimulation may lead to impairment of neuromuscular transmission (Jones 1996).

2.3.4.4 Twitch interpolation force output

Twitch interpolation is a modified version of the tetanic stimulation technique. This method superimposes a twitch contraction over a submaximal contraction or MVC and the force increment generated represents the force reserve (Bigland-Ritchie et al. 1986b). Force generated by the twitch stimulation has been observed to increase with fatigue during attempted MVCs indicating that the motor drive has decreased and therefore, that central fatigue has developed. An advantage of the twitch interpolation technique is that it can be used for concentric and isometric contractions (Gandevia and McKenzie 1988). Disadvantages include the need for very sensitive , small force measurements (Gandevia and McKenzie 1988).

2.3.4.5 Endurance time

Endurance time represents the total time exercise can be performed for until exhaustion. Exhaustion is referred to as the point during exercise that the target force or power output (maximal or submaximal) can no longer be maintained (Vøllestad 1997). Many studies have used a measure of endurance time as a measure of fatigue under the belief that there is association between time to exhaustion and decline in maximal force. It has been shown however, that subjects with equal exhaustion time, will show a large variance in MVC reduction percentage at exhaustion time (Vøllestad et al. 1988) suggesting that endurance time and force generating capacity are separate mechanisms. As such, researchers should refrain from using endurance time as a measure of neuromuscular fatigue as mechanisms separate to the known neuromuscular processes of force generation appear to be involved.

2.3.5 Surface electromyography

2.3.5.1 Bipolar electromyography

Surface electromyography (EMG) measures the electrical activity of superficial muscles (Vøllestad 1997; Jurell 1998) and has been used as a common, indirect measure of fatigue for the past several decades of neuromuscular fatigue research (Bigland-Ritchie et al. 1983a; Basmajian and De Luca 1985; Enoka and Stuart 1992; Jurell 1998). Interpretations of both the amplitude and frequency of this electrical signal have been used to infer fatigue development. The number and the size of the action potentials in the area of the muscle being tested over a period of time determine amplitude of the signal. Changes in the level of activation can be due either to changes in excitation rate of the muscle fibres or changes in the number of active fibres.

EMG amplitude has been observed to fall over the course of an isometric MVC (Bigland-Ritchie et al. 1983a). Since all fibres are assumed to be active during MVCs the observed decrease in amplitude is said to be due to lowering of the firing rate (Bigland-Ritchie et al. 1983a). The simultaneous drop in force has been associated the decreased EMG amplitude during fatigue but the actual mechanism by which changes in EMG amplitude may causes fatigue remains unclear (Vøllestad 1997). Further clouding the EMG amplitude-fatigue relationship is the observation that EMG amplitude progressively rises during repeated or prolonged submaximal contractions (Krogh-Lund 1993). In this scenario, the increased amplitude is believed to be due to an increase in the number and size of active motor units. Motor unit conduction velocity has also been observed to both increase and decrease depending on whether the submaximal contraction is sustained or intermittent (Bigland-Ritchie et al. 1986a; Garland et al. 1994). Furthermore, EMG amplitude has shown opposite changes at different parts of the trapezius muscle during sustained submaximal contractions (Farina et al. 2008). Considering the variability of the EMG amplitude signal, the use of EMG amplitude measured from a single muscle site shows evidence of being an unreliable marker of fatigue, particularly during submaximal contractions and therefore should be accompanied by additional measures of fatigue.

More recent research, however, is beginning to uncover evidence that measuring EMG from multiple sites may be used to indicate the presence of fatigue. For example, some studies have shown that inter-muscle and within-muscle modulation of EMG amplitude during submaximal contractions may contain relevant information on the development of fatigue (van Dieen et al. 1993; Kouzaki and Shinohara 2006; Farina et al. 2008; Larivière et al. 2008). In particular, alternating muscle activation (activation of one muscle in conjunction with simultaneous EMG silence of another agonist muscle) is believed to represent load sharing between agonist muscles during sustained submaximal contractions (Kouzaki et al. 2002; Kouzaki and Shinohara 2006). During a submaximal (≤ 5% MVC) sustained knee extension, an increase in alternate muscle activity between agonist muscles was seen to diminish the reduction of post-test knee extension MVC (Kouzaki and Shinohara 2006). In another study, Larivière et al. (2008) observed the frequency of alternating activity to be less sensitive to fatigue compared to the magnitude of EMG amplitude difference between alternating muscle activations. However, activation intensity during this experiment was much higher (range 21-59% MVC) suggesting that at higher magnitudes there may be less room for alternating activity to occur and more importance placed on the magnitude of the alternating activity as a fatigue attenuation strategy at higher intensities. Another possible contributor to the difference in observations of these two studies could be related to the arising evidence that changes in EMG will vary in different parts of the same muscle over the course of a fatiguing contraction. Such findings have been observed in studies using electrode arrays to provide a higher resolution of within-muscle changes in activity during sustained contractions (Merletti et al. 2003; Farina et al. 2008). This evidence suggests that the EMG activity observed from single site detection may be more location-dependent than originally perceived and therefore not representative of the entire muscle's contribution.

Other EMG parameters that have been popular as fatigue indicators are the EMG median and mean power frequency determined from the power spectrum of the EMG signal (Bigland-Ritchie et al. 1983b; Basmajian and De Luca 1985). Studies have shown spectral shifts towards the lower frequencies during MVCs and prolonged exercise (Bigland-Ritchie et al. 1983b). It has been postulated that this may be caused by a reduction in conduction velocity of muscle fibres, but other research has provided evidence suggesting that changes in conduction velocity cannot entirely account for these spectral shifts (Krogh-Lund and Jorgensen 1992). Investigation of spectral parameters during submaximal contractions have shown little to no change in spectral EMG measures in some work (Moxham et al. 1982) whereas others have observed significant decreases at some muscle sites (van Dieën et al. 2009). Considering all evidence, the relationship between spectral EMG parameters and fatigue remains unclear, particularly for submaximal contractions.

As surface EMG measurement does not restrict or alter natural muscle movement, EMG parameters have been considered as strong candidates for quantitative fatigue indication, particularly when investigating dynamic occupational tasks. Unfortunately, results from field studies have been inconsistent with laboratory observations of sustained submaximal contractions (Hansson et al. 1992). This is not surprising considering the large variance observed among EMG parameters across studies that have looked at similar submaximal contractions during controlled laboratory experiments. There are at least are two possible theories which may help explain the large level of variance observed among EMG parameters. First, because EMG is reflective of fatigue changes only between the levels of the central nervous system and the muscle fibre membrane, changes occurring in the muscle fibre during submaximal contraction may be contributing to the development or attenuation of fatigue independent of the electrical signal being sent to the muscle. Secondly, within muscle heterogenic spatial changes among subjects may explain a large portion of this variability. This second theory has begun to be developed through the use of novel electrode arrays and matrices to measure spatial changes in muscle activity with a higher resolution than what has previously been attempted (Merletti et al. 2003). Some of the emerging evidence associated with this technique along with possible application will be discussed in the following section.

2.3.5.2 Electrode arrays and matrices

The only difference between electrode arrays and matrices is that arrays are EMG detecting electrodes arranged linearly along one axis whereas electrode matrices are arranged two-dimensionally across the plane of the skin surface. By using linear electrode arrays placed along the same direction in which the muscle fibres run, researchers have been able to observe difference in the EMG signal at different locations along the same muscle fibres (Merletti et al. 2003). Specifically, changes in the amplitude of the EMG signal have enabled the location of anatomical structures such as innervation zones and tendons to be identified along with skin locations that show the least variability in EMG detection after shifts in joint amplitude (Farina et al. 2001). Such knowledge may prove to be invaluable when attempting to standardize EMG placement for different subjects and thus help to reduce portions of the spatially dependent heterogeneity common to EMG measurement. Linear electrode arrays also provide a non-invasive method to measure muscle fibre conduction velocity (Farina et al. 2006), a parameter which has often been shown to decrease with fatigue (Merletti et al. 2003). Electrode matrices on the other hand have been used to provide a broader window of observation into muscle activation patterns during sustained contractions (Farina et al. 2008). By measuring EMG from many closely arranged electrode sites on broad muscles such as the trapezius, variances in activation patterns have been observed within areas that in the past have been represented by only one electrode pair which measured activity from a much smaller area (Farina et al. 2008). Furthermore, during sustained submaximal contractions to exhaustion, subjects with a greater shift in the activation centre of gravity had a greater endurance time (Farina et al. 2008). Subjects with the largest changes in centre of gravity also had the least uniform EMG amplitude maps (Farina et al. 2008). The authors of this study suggest that the decrease in entropy of these EMG maps is caused in large part to the recruitment of additional motor units and muscle motor unit substitution (Farina et al. 2006; Farina et al. 2008), a mechanism by which a fatigued motor unit becomes silenced and a separate higher threshold motor unit is activated to compensate (Westgaard and de Luca 1999).

On the whole, electrode matrices show great potential in the measurement of novel EMG parameters associated with fatigue and more investigations using this method are certainly warranted. Of particular interest, combining the electrode matrix measurement with the tetanic force electrical stimulation technique may help elucidate whether the changes in muscle activation entropy maps occur due to modifications of central drive or peripheral changes in membrane potential thresholds.

2.3.6 Mechanomyography

Although electrode matrices show promise in further understanding of changes in the electrical activity of superficial muscles during fatigue, they do not probe further into the fatigue mechanism, i.e. they do not represent any of the fatigue related changes occurring downstream from the muscle fibre membrane in the neuromuscular chain of events that lead to force production (Vøllestad 1997). One technique which may be sensitive to these changes is mechanomyography (MMG). MMG is a measurement of skin displacement typically as acceleration using small, sensitive accelerometers (Shinohara and Sogaard 2006). Sources related to muscle activity that have been proposed to alter skin displacement are pressure pulses (caused by radial thickening of the muscles fibres) and lateral and axial shifts of the muscle (caused asymmetrical contraction forces within the muscle) (Shinohara and Sogaard 2006). Although the precise link between MMG and neuromuscular factors are unknown, motor unit activation and contractile characteristics have an effect on the frequency and amplitude MMG properties (Shinohara and Sogaard 2006). MMG also appears to be sensitive to submaximal contractions showing increases in amplitude without changes in frequency (Shinohara and Sogaard 2006). Possible explanations for this may be due to the fact that both recruitment and reduction in conduction velocity increase the amplitude of MMG (Shinohara and Sogaard 2006). EMG may be less sensitive to such changes since both a decrease conduction velocity and amplitude cancellation due to increase in motor unit recruitment could make amplitude increases in EMG less pronounced. MMG also appears to be more sensitive to the detection of prolonged low-frequency fatigue following sustained submaximal contractions (Blangsted et al. 2005) likely due to the same reasons listed above. Finally, at least one study investigating fatigue using MMG arrays has shown that average rectified entropy value of the MMG map increased with fatigue and that higher entropy is associated with increased endurance (Madeleine and Farina 2008). In summary of MMG, more work is needed to strengthen its claim as a fatigue measurement method but to this point shown to have good sensitivity for detecting changes during fatiguing submaximal contractions, likely due to its ability to be sensitive to contractile properties of motor units. This feature of MMG may make it a more valued measure than EMG when dealing with submaximal contractions although an even stronger methodological approach may be to use both EMG and MMG together as complementary measures. MMG systems are portable and allow flexible unhindered natural movement of muscles making MMG a strong candidate to estimate fatigue in field studies but more controlled, laboratory experiments investigating MMG during dynamic movements are first needed to validate its use as a fatigue index in the field.

2.3.7 Near-infrared spectroscopy

EMG and MMG techniques excel at detecting the electrical activity and mechanical output of motor units, respectively, but they fail to capture more precisely what is occurring at a biochemical level. One technique that is beginning to be more widely used in order to capture biochemical characteristics, non-invasively, is near-infrared spectroscopy (NIRS). NIRS has been used to detect changes in the level of tissue oxygenation of superficial muscles (Hamaoka et al. 2007). However, observations using NIRS to measure fatigue have been mixed. For example, when investigating tissue oxygenation of the back extensors during a prolonged, submaximal contraction, investigators found no change in tissue oxygenation despite having subjects maintain a constant contraction level (van Dieën et al. 2009). In contrast, another study looking at submaximal back extension did observe decreased tissue oxygenation (McGill et al. 2000) but the contractions investigated were only 30 seconds long as compared to 30 minutes in the study by van Dieën et al., and it has been speculated that muscle adaptations during prolonged contractions may serve to attenuate tissue deoxygenation (van Dieën et al. 2009). Still, using NIRS to quantify tissue oxygenation levels may be a promising method that is more sensitive to biochemical factors not observed by any of the previously described measures of fatigue and therefore may provide a complementary measure to EMG and MMG in characterizing fatigue. More investigation of tissue oxygenation using NIRS during dynamic movements is needed to help determine this measure's validity for field use but because it does not hinder natural muscle performance NIRS may be a potential field study indicator of fatigue in the future.

2.3.8 Perceived exertion

The perception of effort is a subjective self-reported measure that involves the integration of many sensory cues (Hampson et al. 2001). It has typically been measured using a 10 or 15 Borg scale (Borg 1970; Borg 1982) in which subjects give their rating of perceived exertion (RPE) according to the descriptions anchored to some values on the scale. It is believed that RPE is a measure, which represents all of the body's sensory information of fatigue, and that the central nervous system uses this to control the efferent command to muscles in order to regulate fatigue development. Some researchers believe that measuring RPE is akin to measuring the integrated sensory signal received by the CNS and that interpretation of the RPE values can be used to determine a level of fatigue or be extrapolated to predict endurance time. Indeed, evidence exists showing RPE to be a strong predictor of endurance time in different environmental conditions during a fixed power output cycling task (Crewe et al. 2008). Jones and Hunter (1983) observed a similar phenomenon where subject's perceived effort increased with endurance time during sustained submaximal arm flexion. Furthermore, perceived effort was dissociated from the perception of force as evidenced by increasing force output of the matching effort contractions with the non-fatigued arm despite constant force output of the fatigued arm (Jones and Hunter 1983). This latter finding supports the theory that RPE during sustained exercise is a multi-dimensional parameter. In summary, RPE appears to be a valid predictor of endurance time allowing information on the development of fatigue to be interpreted. Since RPE is simply a reported score, it is easily transportable and well adapted for field studies. It should be cautioned however that some evidence suggests that its ability to predict endurance time decreases at lower levels of RPE (Hampson et al. 2001) and so RPE may not be a reliable measure at low activation intensities. Also, RPE provides no indication as to the mechanism of the neuromuscular contraction sequence that may be affected by fatigue. For more insight on the fatigue mechanisms, RPE measurement should be paired with additional measures such as EMG, MMG and NIRS.

2.3.9 Summary of non-invasive fatigue measures

Observation of MVC force output reduction has long been the "gold standard" for identifying fatigue and still remains the most direct measure available with the clearest interpretation. However, several difficulties exist with this measure, mainly: MVC force may not be sensitive to neuromuscular changes during submaximal contraction, it does not provide any precise information on the physiological mechanisms underlying the current state of fatigue and it is not easily adapted to the study of dynamic tasks. As a result, further non-invasive measures which are more easily adapted dynamic work have been developed (EMG, MMG, NIRS), showing evidence of being sensitive to fatigue and providing insight into the physiological mechanisms that may be responsible for fatigue. Unfortunately, all measures show some difficulties in being sensitive to fatigue under varied circumstances and they all investigate slightly different physiological mechanisms of fatigue. Until more sophisticated measures of fatigue are developed, the optimal solution to minimize these difficulties for may be to use all or as many as possible of these measures together when investigating fatigue.

2.4 Effects of fatigue on posture and movement

2.4.1 Quiet stance and fatigue

As has been discussed in section 2.2, the postural control system is reliant on many sensory, central and motor factors to maintain equilibrium. It was then discussed in section 2.3 how fatigue may affect many these same postural control system components. Although it is difficult to control the nature of the internal perturbation that fatigue presents, the effects of fatigue on postural control are still of much interest to study because of the strong practical value placed on understanding how fatigue affects movement control. Indeed, many common tasks of daily living are accomplished while facing the presence of fatigue (e.g. manufacturing, construction, sports) and furthermore epidemiological evidence has indicated that fatigue development may play a large role in contributing to falls and injury severity (Hsiao and Simeonov 2001; Kines 2002). As such, a number of studies have taken task to further understand the effects of fatigue on postural control during quiet stance. The presence of muscle fatigue in muscles of the lower limb (Vuillerme et al. 2002a; Vuillerme et al. 2002b; Caron 2003; Corbeil et al. 2003), trunk (Madigan et al. 2006) and neck (Schieppati et al. 2003; Gosselin et al. 2004; Vuillerme et al. 2005; Stapley et al. 2006) has been shown to increase postural sway during quiet stance. Most authors have attributed altered somatosensory information from the fatigued area and/or the reduced force generating capacity of some muscles during fatigue as the likely mechanism for increased postural sway. Interestingly, most findings of increased postural sway during quiet stance are mitigated during conditions in which visual information is permitted, suggesting that the ability of the CNS to compensate for the effects of fatigue during quiet stance is highly dependent on the availability of other sensory information.

2.4.2 Perturbed quiet stance and fatigue

The ability of the postural control system to adapt to a sudden external perturbation also appears altered by fatigue (Lepers et al. 1997; Wilson et al. 2006; Davidson et al. 2009). In the presence of localized fatigue resulting from submaximal concentric contractions of the plantar flexors, Davidson et al. (2009) observed increased measures of postural sway following from perturbations applied to the trunk during quiet stance. In a similar study examining postural perturbations to the trunk following fatiguing of lumbar back extensions, Wilson et al. (2006) found postural reaction strategies change with the development of fatigue and that these adaptations occur across several joints. Interestingly, fatigue did not have effects on peak torque at the low back, the most proximal site to the localized fatigue, thus indicating that under these experimental conditions, the CNS may attempt to stabilize the fatigue area; meanwhile, altering kinematics at other distal joints would allow for the maintenance of task performance. Such a strategy would be consistent with the uncontrolled manifold hypothesis, such that variability from the fatigued area may be perceived to be detrimental to task performance by the CNS (i.e. bad variability) and therefore minimized (Latash et al. 2007). Furthermore, stabilizing the fatigued area is also consistent with the referent configuration hypothesis of the EPH, in that neuromuscular interactions caused by fatigue may divert action away from this area, according to the principle of minimal interaction, and thus, an altered body configuration would emerge (Feldman et al. 2007).

2.4.3 Effects of fatigue on movement

The presence of fatigue is known to lead to many intra- and inter-muscular alterations; in turn, these complex multi-muscle changes may lead to new and/or more variable movement patterns using increased contributions of remote, non-fatigued muscles (Côté et al. 2008). Indeed, movement coordination in the lower and upper limbs has also shown to be significantly altered during the presence of localized fatigue (Bonnard et al. 1994; Forestier and Nougier 1998; Côté et al. 2002; Côté et al. 2005; Côté et al. 2008). In examining repetitive hammering and sawing tasks, Côté et al. (2002; 2005) showed that when segments of the upper limb are fatigued they reduce their movement amplitude while the trunk increases in amplitude yet the main performance measures of the task remain unaffected. Despite this, the task goal may still be achieved so long as the emergent movement pattern, which develops during the presence of fatigue, satisfies the task constraints. Several other papers have reported alterations in joint range of motion and/or average segment positional changes during fatigue while more general task characteristics remained invariant (Bonnard et al. 1994; Sparto et al. 1997; Forestier and Nougier 1998). This common finding suggests that the central nervous system is able to take advantage of the mechanical redundancy of the human motor system by recruiting additional degrees-of-freedom (DoF) to prolong task performance despite the reduced capacity of some fatigued muscles.

In addition to amplitude changes, temporal alterations also occur during fatigue. During a repetitive ball throwing task, Forestier and Nougier (1998) described a more *en bloc* upper limb coordination pattern following repeated ball throwing, whereas Côté et al.(2005) showed more separation between the occurrences of shoulder, elbow and wrist joint peak velocities following repetitive hammering-induced fatigue. Bonnard et al. (1994) showed that with the development of fatigue, some subjects adopted a strategy to activate their gastrocnemius muscle earlier during the landing phase of a repetitive hopping task, possibly to increase stiffness within the muscle. Taken together, these results suggest that fatigue leads to within-movement alterations, which can be both spatial and temporal in nature, occurring at both the inter-segmental and inter-muscular levels. Another aspect of repetitive movements that emphasizes a temporal component is movement variability (Madeleine et al. 2008a; Cignetti et al. 2009). Several studies have suggested that increased motor variability may have a positive effect on mitigating fatigue development (Farina et al. 2008; Madeleine and Farina 2008). More recently, Cignetti et al. (2009) examined cycle-to-cycle variability of gait during cross-country skiing and found arm and leg movements to become more variable between cycles with fatigue, likely representing an altered control strategy to prolong task activity. Despite these advances, relatively little is known about how muscle fatigue may affect time-dependent characteristics of posture and movement control during multijoint tasks.

2.4.4 Effects of fatigue on posture and movement

As discussed in section 2.2, anticipatory postural adjustments are made prior to performing a movement task with the upper limb so as to stabilize equilibrium despite the destabilizing effect of a moving limb. These anticipatory postural adjustments occur in such a way that does not impair the performance of the focal task. During the presence of leg and trunk fatigue, Strang and Berg (2007) have shown that anticipatory postural adjustments (APAs) occur earlier prior to performing an arm-raising task. Since fatigue is believed to impair many aspects of the postural control system earlier onset of APAs during fatigue is believed to be a compensatory strategy of the CNS so that more time is available to ensure that proper postural adjustments are made (Strang and Berg 2007). In contrast, Yiou et al. (2009) and Mezaour et al. (2010) have observed no change in anticipatory postural adjustment onset time during a reaching task after the performance of fatiguing isometric contractions with the lower limb. Differences between these findings have been attributed to the level of fatigue induced. In the studies by Yiou et al. and Mazaour et al., high-level isometric contractions were used and thus it has been suggested that the higher level of fatigue induced may have impaired the postural control system's ability to initiate earlier onset of the anticipatory postural adjustment. In other words, during lower level contractions, the ability to alter posture during fatigue may not be as greatly compromised, thus accounting for the difference between the studies on APA onset time.

Other studies have taken a different approach to examining the effect of fatigue on posture-movement control by fatiguing muscles more involved in the focal movement task itself. This is a different type of perturbation for the posture-movement system in that the movement components are affected by fatigue. These studies typically utilize repetitive motion to induce fatigue and measure postural changes during the task. For example, Schmid et al. (2006) has shown postural measures to decrease in amplitude while endpoint precision remained unchanged during a repetitive pointing task which required subjects to bend over, thus inducing fatigue. Conversely, studies from Sparto et al. (1997) and Nussbaum (2003) have both reported increased postural sway with fatigue, during a repetitive lifting task and a repetitive overhead pointing, respectively. The difference between these studies appears to highlight the fact that differences in task characteristics will lead to differences in the fatigue adaptations observed. Indeed, in the Schmid et al. (2006) study, the movement task was most prominent in the anterior-posterior (AP) direction thus requiring a larger anterior CoM shift to reach to the target. Conversely, the Sparto et al. (1997) and Nussbaum (2003) studies used a task where the prominent direction of the movement was in the coronal plane. As such, one potential reason that could explain why Schmid et al. showed a reduction in AP postural sway may be that subjects already had increased their CoM close the BoS limits and therefore could not adapt to fatigue by increasing postural sway any further. Conversely, in the Sparto et al. (1997) and Nussbaum (2003) studies the tasks under investigation (lifting and pointing overhead) may have required little postural sway relative the Schmid et al. study and therefore subjects participating in these latter studies were better able to adapt to fatigue by increasing postural sway.

2.5 Summary and direction for future investigations

Ultimately, there are many potential reasons for the discrepancy between studies examining the interaction between fatigue and posture-movement control such as: task and environmental constraints, fatigue location, fatigue intensity, sensory modalities manipulated, instructions given to subjects and postural control measures used. Coupled with this is the fact that there have been very few studies on this topic, such that it is difficult to draw conclusions as to the relationship between upper limb fatigue and posture-movement control. Nevertheless, it is clear that fatigue development will lead to spatial alterations to both movement and posture components and that the direction and magnitude of these adaptations appear to be highly task-dependent. In other words the nature of fatigue adaptations appear dependent on the available degrees-of-freedom permitted by the task.

To maximize available degrees-of-freedom, it is likely that adaptations to posture and movement during fatigue also occur in directions other than the direction containing the majority of the movement but this hypothesis remains unverified. Furthermore, the temporal domain also permits to manipulate an extra dimension of motor tasks but it is unclear if temporal adaptations also extend to postural control during repetitive, fatiguing tasks. Finally, it is known that the spatiotemporal relationship between movement and posture is preserved through a variety of environmental conditions when reaching to an anterior target. In this relationship, postural components are not minimized but contribute in aiding the performance of reaching the target. However, as has been discussed in this review, fatigue is known to alter many aspects of posture and movement yet the effect fatigue may have on the posture-movement relationship is unknown. The following work focuses on furthering the understanding of these topics.

Chapter 3: Posture-movement changes following repetitive motion-induced shoulder muscle fatigue

Jason R. Fuller, Karen V. Lomond Joyce Fung, Julie N. Côté

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3.1 Preface

The first manuscript of this thesis was motivated by the perceived gap in the literature investigating both movement and postural adaptations associated with fatigue. Previous literature had identified that fatigue altered postural control during quiet stance and also altered inter-limb coordination; however, no investigation had examined both these components together to identify strategies which may be suggestive as to the nature of the underlying posture-movement control during prolonged repetitive movements. The three-dimensional analysis used in this study was intended, for the first time, to document adaptations which may be occurring in planes other than the main direction of motion in which the repetitive task is performed.

Fuller JR, Lomond KV, Fung J, and Côté JN. Posture-movement changes following repetitive motion-induced shoulder muscle fatigue. *J Electromyogr Kinesiol* 19: 1043-1052, 2009. This manuscript has been reprinted with permission from, Elsevier, publisher of the Journal of Electromyography and Kinesiology. The paper is presented in the same format in which it was published with the exception of formatting to figures and tables to comply with McGill University thesis formatting guidelines.

3.2 Abstract

Repetitive motion-induced fatigue not only alters local motion characteristics but also provokes global reorganization of movement. However, the three-dimensional (3D) characteristics of these reorganization patterns have never been documented in detail. The goal of this study was to assess the effects of repetitive reaching-induced arm fatigue on the whole-body, 3D biomechanical task characteristics. Healthy subjects (N =

14) stood and performed a continuous reaching task (RRT) between two targets placed at shoulder height to fatigue. Whole-body kinematic (Vicon©), kinetic (AMTI© force platforms) and electromyographic (EMG, Noraxon©) characteristics were recorded. Maximal voluntary isometric efforts (MVIE) of the shoulder and elbow were measured pre- and post-RRT. Post-RRT shoulder elevation MVIE was reduced by 4.9 ± 8.3% and trapezius EMG amplitude recorded during the RRT increased by 46.9 ± 49.9% from the first to last minute of the RRT, indicating that arm fatigue was effectively induced. During fatigued reaching, subjects elevated their shoulder (11.7 ± 10.5 mm) and decreased their average shoulder abduction angle by 8.3 ± 4.4°. These changes were accompanied by a lateral shift of the body's centre of mass towards the non-reaching arm. These findings suggest a compensatory strategy to decrease the load on the fatigued shoulder musculature.

3.3 Introduction

Repetitive arm movements constitute a major facet of several workplace tasks (e.g. manufacturing, assembly line work, services) as well as many sporting and leisure activities (Zakaria et al. 2002). Repetitive movement has been known to be associated with the development of repetitive motion disorders (RMDs), a chronic overuse condition affecting muscles, nerves and/or joints leading to inflammation and pain. While 75% of all RMDs involve the upper limb (Statistics Canada 2001), most research on RMDs has focused on disorders of the lower back (Marras et al. 1998) and hence little is known about upper limb RMD etiology. The factors most often associated with neck-shoulder RMD belong to the categories of posture and movement repetition (Madeleine et al. 1999), implying the role of fatigue.

Repetitive muscle use generally leads to a reduced functional capacity of that muscle, a phenomenon commonly referred to as fatigue. During sustained maximal contraction, fatigue is observed as a decline in force output (Bigland-Ritchie et al. 1983b). In low-force tasks, fatigue is an ongoing process which may not necessarily result in a decline in target submaximal force but is typically manifested as an increase in perceived effort (Jones and Hunter 1983) and a reduction in the maximal force generating capacity (Vøllestad 1997). The effects of fatigue on a muscle's peripheral characteristics such as reductions in maximal voluntary muscle force, velocity of muscle contraction and relaxation, and power output are well documented (Bigland-Ritchie et al. 1983b; Enoka and Stuart 1992; Vøllestad 1997; Blangsted et al. 2005). The effects of fatigue on a muscle's output have also been assessed using characteristics of its electromyogram (EMG), which show compression of the power spectrum towards lower frequencies (Bigland-Ritchie et al. 1983b; Christensen 1986; Milner-Brown et al. 1986; Hagg et al. 1987; Sommerich et al. 1993; Madeleine et al. 2002) due to reduced motoneuronal excitation (Gandevia 2001). Other studies have shown increases in measures of the EMG amplitude (e.g. root-mean-square (RMS) value) concomitant to decreases in the frequency characteristics with fatigue development during submaximal contractions (Bigland-Ritchie et al. 1986a; Hammarskjold and Harms-Ringdahl 1992; Madeleine et al. 2002). More attention has been paid recently to the mechanisms of low force muscle fatigue, indicating selective fatigue of low-threshold motor units during sustained wrist extensions (Blangsted et al. 2005) and other changes in physiological parameters (interleukin-6, muscle lactate, K^+, local tissue oxygenation, total haemoglobin) at the neuromuscular junction (Rosendal et al. 2004; Rosendal et al. 2005; Crenshaw et al. 2006) of the trapezius muscle during low-load repetitive arm tasks. In addition, gender differences in various aspects of the fatigue response mechanisms (e.g. endurance time, strategies of muscle adaptation) have been documented recently (Ge et al. 2005; Yoon et al. 2007; Falla et al. 2008).

Recent studies have examined the effects of muscle fatigue on other aspects of the neuromuscular pathway. Some have shown evidence of reorganization of the patterns of activity within individual muscles e.g. trapezius muscle (Holtermann and Roeleveld 2006; Farina et al. 2008; Holtermann et al. 2008; Madeleine and Farina 2008). At the inter-muscle level, fatigue has been associated with increased co-contraction of agonist-antagonist muscle pairs (Psek and Cafarelli 1993), modifications of inter-muscle coordination among agonist muscle groups (Danion et al. 2000; Danion et al. 2001) and reduced trans-joint inhibition of synergistic muscles (Aymard et al. 1995). It is also believed that these changes may be accompanied by other more complex, higher-level adaptations as fatigue develops, which is supported by findings of cortical cell firing changes in parallel with peripheral EMG signal alterations in monkeys (Belhaj-Saif et al. 1996). Only a few studies have attempted to measure how fatigue may affect coordination across multiple segments and joints throughout the body (Bonnard et al. 1994; Forestier and Nougier 1998). As subjects performed a prolonged hopping task to fatigue of the ankle plantar flexors, increased knee flexion and quadriceps activation, as well as earlier activation of the gastrocnemius, were observed, indicating involvement across multiple joints and muscles of the legs (Bonnard et al. 1994). In comparing the performance of throwing a ball at targets under fatiguing and non-fatiguing conditions, a decrease in temporal delay between peak elbow and wrist velocity was observed with fatigue (Forestier and Nougier 1998), suggesting an altered multi-segmental strategy associated with repetitive motion-induced fatigue.

Other studies have investigated the effects of postural and cervical muscle fatigue on postural stability during quiet standing (Vuillerme et al. 2002a; Corbeil et al. 2003; Schieppati et al. 2003; Gosselin et al. 2004), as well as on some aspects of coordination (Vuillerme et al. 2002a). They have shown that postural muscle fatigue modulates postural sway, supporting the hypothesis that localized muscle fatigue affects global sensorimotor integration mechanisms. However, these studies have all investigated postural sway during quiet stance after inducing muscle fatigue at specific muscle sites, and very few studies have investigated the effects of fatigue induced by performing repetitive movements.

The relationship between posture and repetitive movement, and the influence of fatigue on posture-movement coordination, are not well understood. Increased centre of pressure (CoP) displacement area and peak velocity were observed when performing a repetitive overhead arm task to fatigue (Nussbaum 2003). In a study on repetitive load lifting, decreased motion at the knees and hips, as well as increased trunk motion leading to an increase in the body's centre of mass (CoM) excursion, were observed with fatigue (Sparto et al. 1997). Similarly, Côté et al. (2002; 2005) have shown that smaller motion amplitude at the elbow resulting from repetitive motion-induced arm fatigue was compensated by increased trunk motion during both hammering and sawing. In another study which examined muscle activity during hammering to fatigue, it was observed that motion adaptations were accompanied by an increased EMG activity in upper limb musculature (trapezius) as well as in muscles distant to the area of fatigue (external oblique) (Côté et al. 2008). These findings provide not only evidence that changes in inter-muscular coordination occur with fatigue, but also suggest that motion adaptations may occur across several planes since the external oblique is both a trunk flexor and trunk rotator. These studies may be limited by a two-dimensional analysis within the direction containing the predominant motion. It is possible that when performing complex movements involving many joints, additional degrees of freedom of movements are involved to take advantage of the overall motor redundancy of the system (Bernstein 1967) to prolong task performance. The possibility that this could translate into complex posture and movement changes in all possible directions of motion at the main joint acted upon by the agonist as well as at other joints as fatigue develops has never been explored. The aim of the current work was to characterize three-dimensional postural and movement adaptations occurring in the presence of fatigue induced by performing a repetitive reaching task with the upper limb. We hypothesized that fatigue induced by repetitive movements gives rise to global postural and movement reorganization that occur in more than one plane.

3.4 Methodology

3.4.1 Participants

A convenience sample of 14 healthy young adults (8 men, 6 women, mean age = 25.1 ± 5.9 years) was recruited from the University student population. Subjects were excluded if they displayed any of the following: history of mechanical upper limb/shoulder and or back pain or injury; history of any neurological, vestibular or other conditions affecting balance. All subjects provided written, informed consent prior to participation. All subjects were right-handed. Ethical approval for this study was received from the ethics committee of the Montreal Centre de recherche interdisciplinaire en réadaptation (CRIR).

3.4.2 2.2 Experimental protocol

The protocol consisted of performing a repetitive reaching task (RRT) with the dominant arm to fatigue. Prior to performing the RRT, subjects performed four series of maximal voluntary isometric efforts (MVIE) for dominant shoulder elevation and flexion, and elbow flexion and extension using a dynamometric system (BTE Simulator II^{TM} (Sim-II), BTE Technologies$^{©}$, Baltimore, MD, USA, serial number: 1113ST) to measure maximum force output. The Sim-II consists of a software-based controller interface, a position adjustable exercise head that includes an electromagnetically activated resistance control, and a set of interchangeable attachments against which subjects exert force. For this protocol, we used custom-made attachments in the isometric mode where attachments were locked in desired positions as forces applied on the attachments were recorded. After MVIEs, subjects were asked to stand naturally with their feet placed on two adjacent force platforms and their arms resting by their sides. The initial foot position was marked on the support surface in order to ensure that the same foot position was replicated throughout the reaching protocol. Then, the two cylindrical touch-sensitive targets (length: 6cm, radius: 0.5cm, response time: 130ms, Quantum Research Group Ltd.) used to guide the RRT were adjusted to be placed at shoulder height, in front of the subject's midline, at 100% (distal target) and 30% (proximal target) of arm length. To ensure that the subject maintained arm motion in the horizontal plane at shoulder height while performing the reaching task, an elliptically shaped mesh barrier (major axis: 24.5cm, minor axis: 20.5cm) was placed under the elbow joint's functional range of motion, providing a spatial reference to the elbow throughout the task. The mesh barrier was carefully placed far enough away from the body so that it did not restrict natural trunk movement. The RRT consisted of continuous reaching movements with the dominant arm from one target to the other, using the index finger to lightly touch each target while keeping the elbow above and not touching the mesh barrier. The subject performed this task from a standing position, with the non-dominant arm resting naturally on the side of the body. A metronome was used to help subjects maintain a rhythm of one movement per second (1 Hz), and subjects received auditory feedback when touching each target such that they had to match the touch sounds with the metronome sounds. Subjects performed the repetitive task until fatigue while biomechanical data, heart rate and self-perceived task difficulty (Borg CR-10 scale, (Borg 1982)) were collected during the last thirty seconds of each minute. The RRT was performed until either the 1 Hz movement frequency could no longer be maintained, or subjects reached a perceived level of exertion of 8 for the shoulder region on the Borg CR-10 scale (Hammarskjold and Harms-Ringdahl 1992; Côté et al. 2002). Subjects were not aware of these stoppage criteria before beginning the protocol. The first and last 30-s blocks of experimental data collected prior to the termination of the protocol constituted No-Fatigue (NF) and Fatigue-Terminal (FT) data, respectively, for each subject. Following termination of the RRT, subjects immediately sat down to perform Fatigue-Terminal MVIE trials.

3.4.3 2.3 Data Acquisition

3.4.3.1 2.3.1 MVIE and heart rate

Force outputs during MVIEs were measured using the BTE Simulator II™ dynamometric system. In all MVIE trials, the subject sat in a chair and their upper torso was fixed to the back rest using Velcro™ straps, with their contralateral arm resting comfortably on their side, and pushed against the concave side of a custom block attached to the dynamometer. For shoulder elevation trials, resistance was placed over their acromio-clavicular joint, the arm hanging parallel to the torso in the anatomical position. Subjects elevated their dominant shoulder against the resistance. Simultaneously, they elevated their contralateral arm against a Velcro strap placed over the shoulder to minimize trunk roll towards the contralateral side. For shoulder flexion trials, the elbow was fully extended and the shoulder was flexed 45 degrees while resistance was applied to the distal two thirds of the upper arm. During each MVIE, subjects were instructed to flex the shoulder, pushing their upper arm upward into the resistance. For elbow flexion trials, the shoulder was placed into anatomical position, the upper arm was stabilized to the chair using a Velcro strap, and the elbow was flexed 90º while the resistance was placed on top of the middle third of their forearm, which was supine. During the MVIE, subjects were instructed to flex the elbow, pushing their forearm upwards into the resistance. The arm position for elbow extension trials was identical to that of elbow flexion except that the resistance was placed below the forearm. During the elbow extension MVIE, subjects were instructed to extend the elbow, pushing their forearm downwards into the resistance. For each trial, at the signal of the tester, subjects pushed for approximately five seconds in a ramp-up-and-hold effort. They were provided online feedback and were verbally encouraged to surpass their previous force level. For each MVIE position, two trials were recorded both before and after the RRT.

Heart rate was recorded continuously using a Polar s610 Heart Rate Monitor (Polar Electro, Kempele, Finland). Data collected during the RRT was sampled every five seconds over the latter 30 seconds of each minute the RRT was performed. 30-s heart rate data points were then averaged to give a mean heart rate for each minute that the RRT was performed.

3.4.3.2 EMG

Surface EMG was acquired using a TeleMyo sEMG measurement system (Noraxon USA Inc.) with an operating bandwidth of 10–350 Hz, an effective common mode rejection ratio of 130 dB DC, greater than 100 dB at 60 Hz, a minimum of 85 dB throughout the operating bandwidth, and a fixed overall per-channel gain of 2000. EMGs were digitally converted using a 16 bit A/D board over a ±10 V range, sampled at 1080 Hz, and stored for further analysis. All recordings were acquired using pre-gelled, disposable silver/silver chloride electrodes (Ambu©, Denmark), with a 10-mm diameter circular conductive area, in a bipolar configuration. Electrodes were positioned with a centre-to-centre distance of 3 cm, parallel to the muscle fibers, and following careful preparation of the skin overlaying the muscle sites of interest (cleaned, shaved and lightly abraded). Prior to analysis, all EMG signals were filtered using a dual-pass, fourth-order Butterworth filter, with a band-pass of 20-500 Hz. EMG data was acquired from the descending trapezius, anterior deltoid, biceps brachii and long head of triceps brachii of the reaching arm. The electrode pairs were placed over these following locations: descending trapezius – approximately 25 mm medial to the midpoint between the C7 vertebra and angle of acromion; anterior deltoid – 2 cm below the lateral third of the clavicle; biceps brachii – midway on the anterior part of the upper arm, over the muscle belly; long head of triceps brachii - 2 cm medial to the vertical midline of the posterior arm and midway between the acromion and the olecranon process (Basmajian and Blumenstein 1980). The descending trapezius and anterior deltoid muscles were chosen based on prior evidence that they show signs of fatigue during at or above shoulder height tasks (Christensen 1986; Gerdle et al. 1988; Nussbaum et al. 2001; Ebaugh et al. 2005) whereas the biceps and triceps muscles were selected because of their roles as agonists at both the shoulder and elbow joints.

3.4.3.3 Kinematics

Three-dimensional whole body posture and movement characteristics were recorded (sampling frequency = 120 Hz) using a high-resolution six-camera Vicon MX3 motion capture system (Vicon Peak, Oxford Metrics ltd., Oxford, UK) with a series of passive, reflective markers. These were fixed using double-sided adhesive tape on the anatomical landmarks according to the requirements of our linked-segment model. The model used reflective markers placed over palpable bony landmarks, dividing the body into 15 segments: head (head to C7; 5 markers), bilateral upper arms (shoulder to elbow; 3 markers per upper arm), bilateral forearms (elbow to wrist; 4 markers per arm), bilateral hands (distal to wrist; 3 markers per hand), trunk (C7-T10; 5 markers), pelvis (5 markers), bilateral thighs (hip to knee; 3 markers per thigh), bilateral legs (knee to ankle; 3 markers) and bilateral feet (3 markers per foot).

The kinematic variables of interest corresponded to the following parameters: the body's CoM, right and left shoulder, and elbow, wrist and endpoint (defined as the tip of the index finger) on the reaching side. The coordinates of these parameters were computed in the three directions, anterior-posterior (AP), mediolateral (ML), superior-inferior (SI), in global space. Elbow flexion/extension angle, shoulder flexion/extension angle and shoulder abduction/adduction angle were also measured by quantifying the relative orientations of the corresponding reconstructed segments in global space using Euler xyz rotations. These kinematic variables were determined using a representation of the above model created in Bodybuilder software (Vicon Motion Systems Ltd., Oxford, UK) and then low-pass filtered at 7 Hz using a dual-pass, 4th order digital Butterworth filter. Digital filtering was performed in Matlab (MathWorks, Massachusetts, USA).

3.4.3.4 2.3.4 Kinetics

Three-dimensional ground reaction forces and moments applied on the support surface under each foot were obtained from two triaxial strain gauge force plates (AMTI© OR6-7, AMTI Inc, Watertown, USA) at a sampling frequency of 1080 Hz. Raw forces and moments were low-pass filtered at 10 Hz, using a dual-pass, 4th order digital Butterworth filter. Ground reaction force data was used to locate the net CoP under the feet, in both AP and ML directions, according to the method described by (Winter 1995). The focus of this measure was to quantify CoP movement under the feet during the RRT and not to investigate postural sway as it has been often used in the literature (Vuillerme and Nougier 2003; Lafond et al. 2004; Vuillerme et al. 2005).

3.4.4 Data Analysis

3.4.4.1 Gender, heart rate and MVIE

To address possible gender differences in endurance time and in the main outcome measures of fatigue, we performed t-tests on the time to RRT termination and on the percent change of each fatigue measure between NF and FT conditions, comparing both gender sub-groups. The highest force output for each of the four MVIE test positions and for each experimental condition (NF and FT) was kept for statistical analyses. Mean heart rate from the first minute (NF) and last minute (FT) of the RRT were also compared. Statistical comparisons were assessed for each of the MVIEs and for heart rate by computing one-way analyses of variance with fatigue as a within-subject factor ($p < 0.05$). All statistical analyses were computed using Statistica v7 software (Statsoft, Tulsa. OK, USA).

3.4.4.2 Kinematics and kinetics

The beginning and end of each reach was determined as the onset of activation of each of the two targets. Data from forward (proximal to distal target) and backward (distal to proximal target) phases of the RRT were separated and identified as forward and backward reaches. Further analyses for this paper were done only on the first five forward reaches from the first minute of the RRT (NF data) and the first five forward reaches of the last minute the RRT (FT data). For each forward reach, the average position and range of motion (RoM) (maximum – minimum position) of the kinematic and kinetic parameters of interest were calculated. For each calculated parameter, the within-subject average of the five NF reaches and five FT reaches were computed. Each kinematic and kinetic parameter was analyzed using a 2-way ANOVA with repeated measures where conditions of Fatigue (NF, FT) and parameter Direction (ML, AP, SI) were treated as independent factors. Where a significant Fatigue by Direction interaction or Fatigue main effect existed, Tukey's post hoc comparisons were made to determine significant pair-wise differences ($p < 0.05$).

3.4.4.3 EMG

Root-mean-squared (RMS) amplitude for the descending trapezius, anterior deltoid, biceps and triceps muscles was calculated over the entire duration of each of the five forward reaches representing NF and FT conditions for each subject. The muscle RMS values for the five reaches of each fatigue condition were then averaged for each subject. The differences between NF and FT RMS data were statistically compared using a one-way analysis of variance with repeated measures, with fatigue as a within-subject factor ($p < 0.05$).

3.5 Results

3.5.1 Evidence of fatigue

Subjects performed the repetitive reaching task (RRT) for an average time of 7.9 ± 4.0 minutes. For 13 out of 14 subjects, the reason for stoppage of the RRT was reporting a Borg rating of 8 or above for the shoulder/upper arm region. Only one subject self-terminated the RRT stating that he could perform it no longer; his last reported Borg CR-10 rating being 6. Preliminary analysis did not reveal this subject's data to be an outlier among the group and therefore, the data from this subject were not excluded from further analysis. Moreover, the average time to RRT termination for the female sub-group was 9.33 ± 5.32 min while it was 6.88 ± 2.70 min for the male sub-group. T-test analysis showed that there was no significant difference between both sub-groups (p = 0.33). T-test analyses comparing percent change of other fatigue measures (heart rate, MVIE force outputs and EMG RMS values) from NF to FT conditions between gender sub-groups also revealed no significant differences.

Heart rate, shoulder elevation MVIE, trapezius RMS and biceps RMS all showed a main effect of Fatigue. Average heart rate across all subjects was significantly higher during FT ($p<0.01$, Table 3-1). Significant indicators of local fatigue reached during the RRT at the shoulder/upper limb included average increases in descending trapezius ($p<0.005$, Table 3-1) and biceps RMS ($p<0.05$). These findings were corroborated by a decrease in shoulder elevation MVIE as measured immediately after the RRT ($p<0.05$), although elbow flexion MVIE remained unchanged (Table 3-1). Force output during shoulder flexion and elbow extension MVIEs also remained unchanged following the RRT, as did anterior deltoid and triceps RMS (Table 3-1).

Moreover, the effects of fatigue on these parameters showed no significant gender effect.

Table 3-1 No-fatigue (NF) and Fatigue-terminal (FT) values and percent change (SD) in global and local measures of fatigue. ns = not significant.

Parameter	No-Fatigue	Fatigue-Terminal	% change	Fatigue main effect p <
Heart Rate (beast/min)	73.8 (14.2)	82.3 (12.7)	12.9 (12.4)	0.01
Shoulder elevation MVIE force (N)	412.1 (67.5)	392.1 (73.1)	-4.9 (8.3)	0.05
Shoulder flexion MVIE force (N)	199.4 (75.2)	185.2 (86.8)	-6.9 (21.4)	ns
Elbow flexion MVIE force (N)	311.3 (120.6)	307.4 (90.1)	4.53 (29.7)	ns
Elbow extension MVIE force (N)	230.6 (62.0)	241.0 (84.1)	3.4 (18.5)	ns
Descending trapezius RMS (mV)	0.181 (0.081)	0.264 (0.129)	46.5 (49.9)	0.005
Anterior deltoid RMS (mV)	0.163 (0.086)	0.206 (0.127)	29.0 (42.3)	ns
Biceps RMS (mV)	0.097 (0.058)	0.134 (0.090)	40.6 (49.3)	0.05
Triceps RMS (mV)	0.116 (0.336)	0.133 (0.367)	28.0 (34.5)	ns

3.5.2 Kinematics of the reaching arm's shoulder

Figure 3-1 shows the 3D joint displacements for filtered, representative subject data over a 10-s interval. Statistical analysis revealed that all shoulder joint parameters except shoulder joint RoM showed significant main (Fatigue) and interaction (Fatigue x Direction) effects. Post-hoc analyses showed that the average shoulder joint position was located more superior in the SI direction ($p<0.05$), more towards the non-reaching side in the ML direction ($p<0.0005$) and more posterior in the AP direction ($p<0.05$) during FT (Table 3-2). The RoM of the shoulder joint increased in the AP direction ($p<0.0005$, Table 3-3). The average shoulder angle became more adducted during FT ($p<0.0005$, Table 3-2). Additionally, shoulder RoM showed a significant increase during FT (Table 3-3).

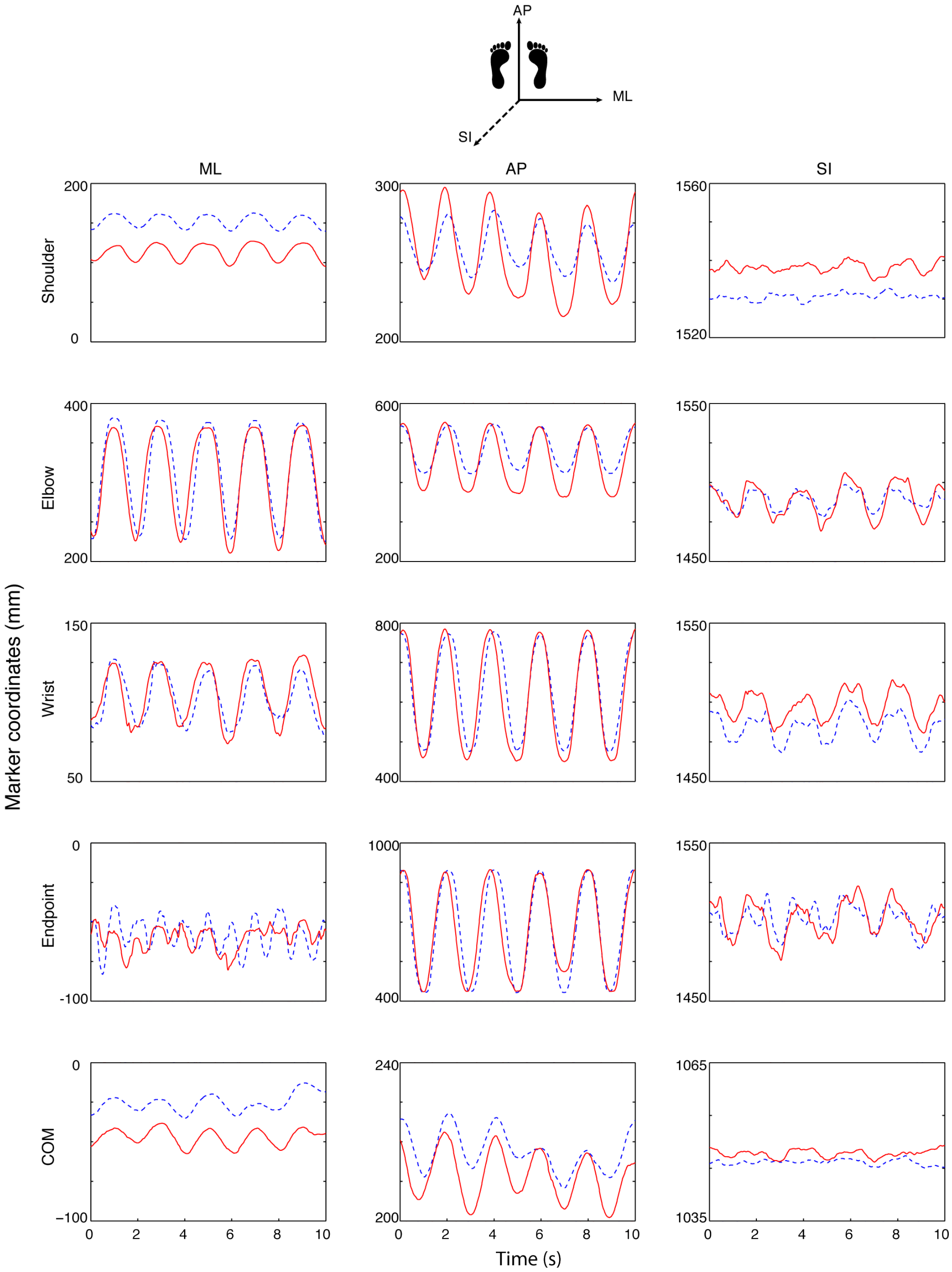

Figure 3-1. Ten-second samples of the 3D components of kinematic parameters from representative subject data (CoM: S13; others parameters: S3). No-fatigue: dashed blue line; Fatigue: red solid line.

3.5.3 Reaching arm and endpoint kinematics

Analysis of average elbow flexion/extension angle and RoM did not show a Fatigue main effect (Table 3-3). However, average elbow joint position and RoM, as well as average wrist joint position and RoM showed significant main (Fatigue) and (Fatigue × Direction) interaction effects. Post-hoc analysis revealed that the average elbow position was located significantly more posterior during FT ($p<0.0005$) while ML and SI average elbow positions were unaltered (Table 3-2). The elbow joint linear RoM also increased in the AP direction ($p<0.0005$, Table 3-2). In similar fashion to the average shoulder and elbow joint positions, average wrist joint position was located more posterior during FT ($p<0.0005$, Table 3-2) while ML and SI average elbow positions were unaltered (Table 3-2). The wrist joint linear RoM also increased in the AP direction ($p<0.0005$, Table 3-3). Finally, there were no significant interactions or main effects for either endpoint average position or endpoint RoM (Tables 3-2 and 3-3).

3.5.4 Kinematics of the non-reaching arm's shoulder

The average contralateral shoulder joint position showed significant main (Fatigue) and (Fatigue × Direction) interaction effects. Post-hoc analysis revealed that it was located more towards the non-reaching side ($p<0.005$) in the ML direction during FT while the AP and SI average shoulder positions were unaltered (Table 3-2). Additionally, the shoulder joint RoM showed an overall increase during FT (Fatigue main effect, Table 3-3), but no Fatigue x Direction interaction.

Table 3-2 Statistical analysis of average positions between No-fatigue (NF) and Fatigue-terminal (FT) repetitive reaching characteristics (forward phase). The FT – NF mean differences (SD) are reported. Abd/Add = Abduction/Adduction; Flx/Ext = Flexion/Extension; ns = not significant. Positive values indicate a more anterior, rightward, or superior position for AP, ML and SI parameters, respectively.

Parameter	Direction	Change in average position	Fatigue p <	Fatigue x Direction p <	Pos-hoc p <
Shoulder joint angle (°)	Abd/Add	-8.3 (4.4)	0.0005	0.0005	0.0005
	Flx/Ext	-3.0 (5.1)			0.05
Shoulder joint (mm)	AP	-11.9 (13.6)	0.005	0.00001	0.05
	ML	-23.5 (15.2)			0.0005
	SI	11.7 (10.5)			0.05
Elbow joint angle (°)	Flx/Ext	2.0 (4.1)	ns	--	--
Elbow joint (mm)	AP	-29.7 (19.3)	0.00001	0.001	0.0005
	ML	-9.6 (11.1)			ns
	SI	-8.8 (10.2)			ns
Wrist joint (mm)	AP	-19.0 (19.7)	0.005	0.005	0.0005
	ML	-2.4 (7.2)			ns
	SI	-2.5 (10.8)			ns
Endpoint (mm)	AP	-7.6 (19.2)	ns	ns	--
	ML	0.1 (5.4)			
	SI	-1.1 (8.5)			
Shoulder joint (mm)	AP	-5.6 (18.4)	0.05	0.05	ns
(Non-reaching arm)	ML	-14.6 (14.1)			0.005
	SI	1.0 (8.2)			ns
CoM (mm)	AP	-4.1 (10.0)	0.01	0.0005	ns
	ML	-11.6 (9.7)			0.0005
	SI	1.2 (2.8)			ns
CoP (mm)	AP	-2.0 (11.2)	0.05	0.05	ns
	ML	-11.1 (9.9)			0.005

Table 3-3 Statistical analysis of ranges of motion (RoM) between No-fatigue and Fatigue-terminal repetitive reaching characteristics (forward phase). Groups means (SD) are reported. Abd/ Add = Abduction/Adduction; Flx/Ext = Flexion/Extension; ns = not significant.

Parameter	Direction	No-Fatigue range	Fatigue-Terminal range	Fatigue p <	Fatigue x Direction p <	Post-hoc p <
Shoulder joint angle (°)	Abd/Add	6.7 (7.1)	9.1 (6.6)	0.05	ns	--
	Flx/Ext	21.3 (7.5)	22.2 (7.8)			--
Shoulder joint (mm)	AP	57.2 (29.8)	78.6 (32.2)	0.00001	0.00001	0.0005
	ML	27.4 (9.8)	30.1 (7.8)			ns
	SI	7.8 (8.1)	11.3 (7.6)			ns
Elbow joint angle (°)	Flx/Ext	92.1 (9.9)	91.4 (12.2)	ns	--	--
Elbow joint (mm)	AP	159.8 (44.1)	208.2 (49.2)	0.00001	0.00001	0.0005
	ML	156.9 (28.4)	167.6 (40.0)			ns
	SI	22.2 (14.1)	32.5 (11.0)			ns
Wrist joint (mm)	AP	318.3 (35.9)	342.0 (39.9)	0.0005	0.005	0.0005
	ML	52.0 (20.1)	62.8 (26.6)			ns
	SI	22.3 (6.6)	24.4 (8.1)			ns
Endpoint (mm)	AP	463.3 (51.2)	463.3 (52.7)	ns	ns	--
	ML	30.2 (15.2)	31.4 (16.9)			--
	SI	25.5 (7.4)	30.8 (11.5)			--
Shoulder joint (mm)	AP	21.0 (9.1)	29.7 (13.5)	0.001	ns	--
(Non-reaching arm)	ML	7.0 (2.6)	14.3 (6.9)			--
	SI	3.6 (1.6)	6.6 (2.5)			--
CoM (mm)	AP	14.6 (7.0)	20.1 (8.6)	0.01	0.05	0.005
	ML	20.0 (6.7)	28.1 (10.6)			ns
	SI	8.3 (3.3)	13.6 (5.3)			ns
CoP (mm)	AP	31.9 (14.6)	44.2 (16.7)	0.01	0.05	0.005
	ML	15.5 (7.4)	18.7 (7.2)			ns

3.5.5 Whole-body postural measures

CoM and CoP average positions and ROMs all showed significant main (Fatigue) and (Fatigue × Direction) interaction effects. Post-hoc analysis revealed that average CoM and CoP positions were both shifted more laterally toward the non-reaching side during FT ($p<0.0005$ and $p<0.005$ for CoM and CoP respectively, Table 3-2). AP direction RoM increased in both parameters ($p<0.005$ and $p<0.005$, CoM and CoP respectively, Table 3-3). Figure 3-2 shows filtered CoM data in the transverse plane over a 10-s interval for a representative subject (S1). This figure illustrates an increased CoM RoM in the AP direction and a shifted CoM average position toward the ML direction during FT.

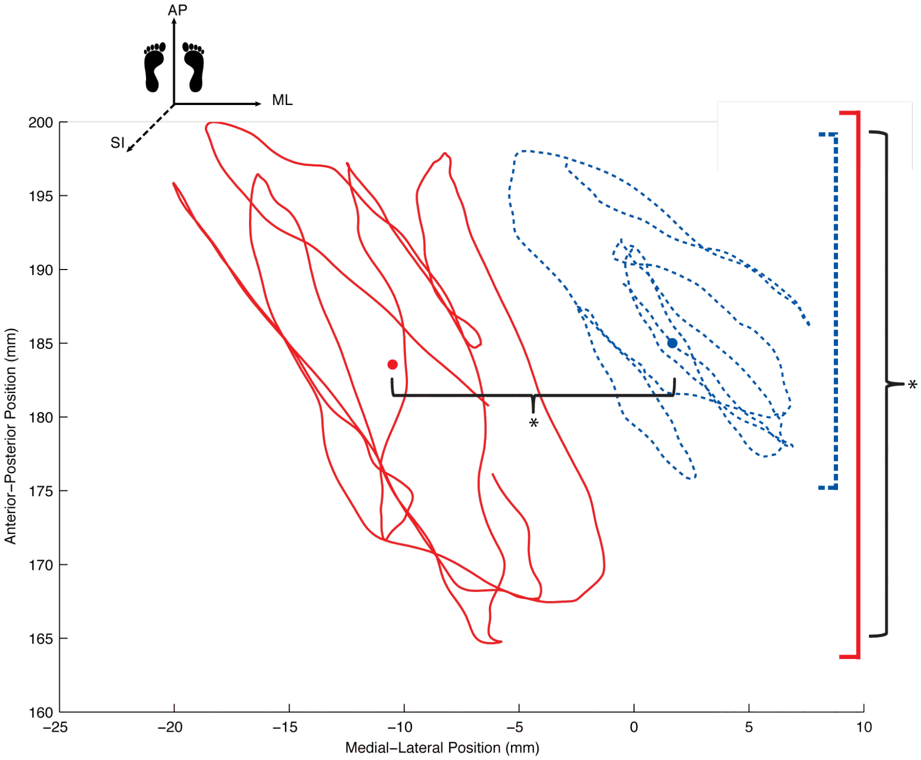

Figure 3-2Ten-second sample of transverse plane CoM for a representative subject (S1). No-fatigue: dashed blue line; Fatigue-terminal: red solid line. Average CoM position is located further towards the non-reaching arm (left) during the Fatigue condition, while CoM amplitude increases in the anterior-posterior direction.

3.6 Discussion

3.6.1 Evidence of fatigue

The average time to fatigue and standard deviation (average time of 7.9 ± 4.0 minutes) was similar to that observed in a study examining a sustained 90° bilateral shoulder abduction to failure (6.4 ± 2.7 minutes) (Farina et al. 2008). Although subjects in the present study showed a large variability in the time to fatigue (± 4.0 minutes), all but one of the subjects ended the task at the same level of perceived exertion and pre-post MVIE force output showed strong signs of muscular fatigue among ensembled group data. Taken together with the robustness of the biomechanical parameters observed, the variability in the time to fatigue is believed to have had little effect on the results presented in this paper, although it is possible that subjects who performed the RRT longer used different compensation strategies than those who performed the RRT for a shorter period.

Contrary to recent studies (Hunter et al. 2004; Yoon et al. 2007), our results did not show differences between men and women in our main fatigue outcome measures, even though these studies also focused on upper limb efforts of comparatively low intensities (Hunter et al.: 50% elbow flexor MVC; Yoon et al.: 20% elbow flexor MVC). This could be due to our small and uneven sample size of male and female subgroups (N = 8 males, N = 6 females) and also because our study targeted fatigue of the descending trapezius muscle rather than the elbow flexors. With both genders collapsed together, our results show that isometric arm efforts, EMG, kinematic, heart rate and perceived exertion characteristics were affected by the RRT, providing evidence that the RRT protocol was indeed successful at inducing fatigue. The most predominant indicators of muscle fatigue were observed in the area of the shoulder elevators as evidenced by decreased force output during the shoulder elevation MVIE and increased trapezius RMS during the FT condition. These results are consistent with other studies showing that the shoulder elevators are the most sensitive to fatigue when performing tasks with the upper limb at or above shoulder level (Hagberg 1981; Sommerich et al. 1993; van der Windt et al. 2000; Nussbaum 2001; Andersen et al. 2003). Other recently documented effects of fatigue on the trapezius muscle include increased spatial heterogeneity of the electromyographic patterns across different areas of the trapezius in sustained as well as in ramp contractions (Farina et al. 2008; Holtermann et al. 2008). In our study, little evidence of fatigue (e.g. decreases in MVIE force output, changes in EMG RMS) were observed at other sites of the arm (shoulder flexors/anterior deltoid, elbow flexors/biceps, elbow extensors/triceps), however, changes may have been present in other areas of the shoulder, shoulder girdle and arm musculature that were not explicitly tested by the MVIE and RMS measures. Biceps RMS did show an increase in the presence of fatigue, although the absence of a decrease in the elbow flexion MVIE force output suggests that the RRT had a more complex and equivocal effect on fatigue in this region. These results could also be indicative of reorganization of motor unit activation patterns within the biceps with fatigue, similar to those changes known to occur in the trapezius muscle (Westgaard and de Luca 1999; Farina et al. 2008).

3.6.2 Arm motion adaptations to fatigue

Analysis of the reaching arm kinematics shows that adaptations to fatigue occur across multiple segments of the limb, as well as in multiple directions. The kinematic parameters most affected by fatigue were predominantly shoulder characteristics of the mediolateral direction. Although no changes were observed in shoulder abduction/adduction range of motion, all subjects showed an average abduction angle decrease despite the presence of the mesh barrier beneath the elbow trajectory. This would contribute to reducing the adduction moment produced by the mass of the upper arm about the shoulder joint, effectively reducing the load on the descending trapezius muscle. Kinematic parameters which appear to be related to this strategy include: average shoulder joint position moving more superior and more towards the non-dominant side as well as lateral shifts of the CoM, CoP and non-dominant arm shoulder average positions towards the non-dominant side. It follows that these kinematic changes may be part of the strategy to reduce shoulder abduction throughout the reaching task despite the constraint of the elbow height. Consistent with these observations, CoM and CoP ML data suggest that subjects leaned toward their non-reaching side when fatigued. Coupled with the finding of a higher average reaching shoulder position with fatigue, this could reflect a strategy of elevating the reaching shoulder joint and thus increasing the vertical margin between the shoulder and the mesh barrier. This way, subjects could afford to adopt a less abducted shoulder average position throughout the reaching movements. Taken together, these findings indicate global compensation strategies which appear to be dependent on the main task characteristics (e.g. constraints of movement timing, feet placement, elbow height, endpoint trajectory amplitude).

Changes in kinematic parameters were also observed in the AP direction during fatigue. An increase in average shoulder flexion angle was accompanied by increases in AP linear ranges of motion in the shoulder, elbow and wrist. Interestingly, average shoulder, elbow and wrist joint positions all moved more posterior with fatigue, suggesting that the RoM increases seen in these joints are due to a more posterior maximum position of these joints (i.e. when subjects reached to the near target). CoM as well as CoP AP RoM also increased with fatigue, due in large part to an increase in maximum posterior position. On the whole, AP direction alterations to kinematic parameters suggest that the main adjustments within the AP direction occur when the subject reaches back for the proximal target. The increase in posterior amplitude of arm and postural parameters may correspond to a whole-body position where torques on the shoulder are minimized, suggesting that when fatigued, subjects favor this arm configuration where less torque is created at the shoulder, in accordance to our interpretation of findings in the ML direction.

Previous studies that have examined arm movement and postural stability measures have concluded that trunk movement is not minimized but appears to make a voluntary assistive contribution to the arm movement task, suggesting that arm movement and posture may be controlled by some common central pathway (Stapley et al. 1999; Pozzo et al. 2002). Other studies have suggested that these posture-movement relationships may be modulated in the presence of fatigue (Sparto et al. 1997; Côté et al. 2002; Côté et al. 2008). Similarly, our results show that postural amplitude measures (CoM and CoP) are not minimized when performing reaching movements during fatigue but rather increase. Further, the changes observed in CoM and CoP measures mirror those seen in the upper limb kinematic parameters (amplitude changes in the AP direction and average positional changes in the ML direction) suggesting a global task objective shared by the postural and the focal task components. The observation that endpoint measures across all directions remain unaltered despite the many kinematic changes occurring across the arm and body provides further support of the hypothesis of a global control strategy, of which parts can be modulated but as a whole, remains unaffected by fatigue during the RRT. Such an integrated, hierarchical control strategy could be responsible for adapting both postural and arm movement characteristics, strategically modulating the involvement of body degrees-of-freedom to prolong task performance in challenging conditions.

3.6.3 Possible consequences of movement adaptation

Adaptations of the movement and postural components in response to repetitive motion-induced fatigue appear to be predominantly organized towards reducing the load on the fatigued shoulder region. In particular, changes in whole-body patterns appear to be part of a global motor strategy to adapt to localized muscle fatigue in the upper limb, thus assisting the performance of the motor system in the fatigued situation. Indeed, small increases in trunk movement towards endpoint motion may make significant contributions to endpoint travel due to the mechanical advantage of this strategy. These adaptations, however, may introduce detrimental effects. The changes to ML and AP CoM observed in this study may move the CoM closer to the edges of the base of support which could compromise postural stability particularly in the presence of an external perturbation (Horak et al. 2005). As such, fatigue could be a factor in the occurrence of slips and falls among fatigued persons. Future studies could examine the effect of such externally administered perturbations on postural control while performing repetitive reaching movements in the presence of fatigue. Another consequence of the observed postural adaptations is that the ML CoM shift toward the non-dominant arm may result in an increased asymmetry of vertical ground reaction forces on the body, suggesting that persons who often perform repetitive, fatiguing tasks similar to our RRT may also be at an increased risk to injuries related to chronic exposure of asymmetrical loading.

3.6.4 Conclusions

In our study, repetitive reaching at shoulder height resulted in upper limb fatigue as evidenced through force, EMG and kinematic measures taken from this region. Global kinematic adaptations to fatigue were observed in all three directions, supporting the importance of conducting a three-dimensional kinematic analysis. The major arm movement and postural adaptations to fatigue were observed in the ML direction and not the AP direction where most of the task amplitude was contained. It is likely that the majority of changes occurring in the ML direction were due to the characteristics of the task itself (e.g. elbow height requirement) highlighting the ability of the motor system to adapt in a task-specific way when facing fatigue. Both arm movement and global postural adaptations appear to be aimed at reducing the load on the shoulder elevator region where the most profound effects of fatigue were observed. More work needs to be done to understand the progression of these adaptations over the course of task performance as well as to understand the temporal coordination between upper limb and postural components during the performance of fatiguing upper limb tasks.

3.6.5 Acknowledgements

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Chapter 4: Time-dependent adaptations to posture and movement characteristics during the development of repetitive reaching induced fatigue

Jason R. Fuller, Joyce Fung and Julie N. Côté

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4.1 Preface

While chapter 3 concluded that fatigue adaptations appear to be task-specific and occur to both postural and movement components three-dimensionally, the question still remained as to whether these adaptations occur only in the later stages of fatigue (i.e. the final minute of the task), as a last resort, or if adaptations begin to occur soon after the onset of the repetitive movement task. Answering this question was one of the three main goals of chapter 4. The two other objectives of chapter 4 were also of temporal nature. More specifically, this chapter investigated inter-reach (or reach-to-reach) variability of kinematic parameters during fatigue as well as intra-reach coordination adaptations. All together, the objective of this chapter was to provide insight into the fatigue adaptations that occur in the temporal domain – an often overlooked area within fatigue research.

Fuller JR, Fung J, and Côté JN. Time-dependent adaptations to posture and movement characteristics during the development of repetitive reaching induced fatigue. *Exp Brain Res* 211: 133-143, 2011. This manuscript has been reprinted with permission from, Elsevier, publisher of Experimental Brain Research. The paper is presented in the same format in which it was published with the exception of formatting to figures and tables to comply with McGill University thesis formatting guidelines.

4.2 Abstract

Repetitive movements are common to many daily activities but often lead to the development of fatigue. We have previously shown that fatigue leads to changes in tridimensional spatial characteristics of the whole body. However, temporal aspects of these posture and movement adaptations have yet to be investigated. Healthy subjects (N = 14) performed a continuous reaching task by pointing between two targets placed at shoulder height, at 100% and 30% arm's length, anterior to the subject's midline until fatigue (assessed using the Borg CR-10 scale). Whole body kinematics and upper trapezius EMG were recorded and analyzed at one-minute intervals to document the progression of fatigue on outcome variables. For all upper limb and postural variables analyzed, changes began to occur approximately midway to fatigue and were followed by an increase in trapezius activity from baseline. Reach-to-reach variability of joint average positions and range of motion (RoM) increased in multiple directions for shoulder and elbow parameters. Reach-to-reach variability of the centre-of-mass RoM also increased in several directions. Changes were also observed in within-movement inter-segmental timing. The peak velocities of elbow and endpoint occurred closer together in time during fatigue while the shoulder peak velocity occurrence showed a greater reach-to-reach variability. Our results suggest that the effects of fatigue on repetitive movement kinematics can be observed across three temporal dimensions of the task: 1) within individual movements; 2) from one movement to the next; and 3) as fatigue develops. Each observed change is discussed as a potential contributor to task-specific control strategies to prolong task performance.

4.3 Introduction

Repetitive movements involving the upper limbs are a part of many everyday occupational and recreational activities (Zakaria et al. 2002). They often lead to fatigue development and ultimately to altered movement patterns when performed over extended periods of time. Enoka and Stuart (1992) define fatigue as impairment in performance that leads to both the inability to maintain a certain level of force and an increased perception of task difficulty. During fatiguing activities, the functional capacity of muscles becomes reduced (Vøllestad 1997). In addition, studies have shown evidence of reorganization of the patterns of activity within individual muscles e.g. trapezius muscle (Holtermann et al. 2005; Farina et al. 2008; Holtermann et al. 2008; Madeleine and Farina 2008). At the inter-muscle level, fatigue has been associated with increased co-contraction of agonist–antagonist muscle pairs (Psek and Cafarelli 1993), decreased inhibition between synergist muscles (Aymard et al. 1995) and changes in inter-muscular coordination between agonist groups (Danion et al. 2000; Danion et al. 2001). It is also believed that these changes may be accompanied by other more complex, higher-level adaptations as fatigue develops, which is supported by findings of cortical cell firing changes in parallel with peripheral EMG signal alterations in monkeys (Belhaj-Saif et al. 1996). In turn, these more complex multi-muscle changes may lead to new and/or more variable movement patterns using increased contributions of remote, non-fatigued muscles (Côté et al. 2008). Despite this, the task goal may still be achieved so long as the emergent movement pattern which develops in the presence of fatigue satisfies the task constraints. For example, when examining movement reorganization during a sawing task to fatigue, Côté et al. (Côté et al. 2002) observed decreased movement amplitude at the elbow joint and an increased movement about the wrist, shoulder and trunk while saw trajectory measures of movement direction and duration did not change. Several other papers have reported alterations in joint range of motion and/or average segment positional changes during fatigue while more general task characteristics remained invariant (Bonnard et al. 1994; Sparto et al. 1997; Forestier and Nougier 1998; Côté et al. 2005; Fuller et al. 2009). This common finding suggests that the central nervous system is able to take advantage of the mechanical redundancy of the human motor system by recruiting additional degrees-of-freedom (DoF) to prolong task performance despite the reduced capacity of some fatigued muscles. In turn, the mechanisms underlying fatigue adaptations may be similar to those underlying other kinds of motor adaptations, with evidence from the neuroscientific literature pointing to the important role played by the cerebellum in organizing these adaptations (Prsa et al. 2010).

While the effects of fatigue on the spatial organization of movement are becoming more known, the outcomes on temporal characteristics of movement have been reported in only a few studies. During a repetitive ball throwing task, Forestier and Nougier (1998) described a more *en bloc* upper limb coordination pattern following repeated ball throwing, whereas Côté et al. (2005) showed more separation between the occurrences of shoulder, elbow and wrist joint peak velocities following repetitive hammering-induced fatigue. Bonnard et al. (1994) showed that with the development of fatigue, some subjects adopted a strategy to activate their gastrocnemius muscle earlier during the landing phase of a repetitive hopping task to increase stiffness within the muscle. Taken together, these results suggest that fatigue leads to within movement alterations at both the inter-segmental and inter-muscular levels. Another aspect of repetitive movements that emphasizes a temporal component is movement variability (Madeleine et al. 2008a; Cignetti et al. 2009). Several studies have suggested that increased motor variability may have a positive effect on mitigating fatigue development (Farina et al. 2008; Madeleine and Farina 2008). More recently, Cignetti et al. (2009) examined cycle-to-cycle variability of gait during cross-country skiing and found arm and leg movements to become more variable from cycle to cycle with fatigue likely representing an altered control strategy to prolong task activity. Despite these advances, relatively little is known about how muscle fatigue may affect time-dependent characteristics of posture and movement control during multijoint tasks.

In our previous study, we investigated a repetitive reaching task at shoulder height, a task similar to many observed in work settings, and found that immediately before stopping the task due to fatigue, healthy subjects displayed increased upper limb activity, higher shoulder position and a less abducted shoulder throughout arm movements, concomitantly to laterally shifting the whole-body centre of mass towards the non-reaching arm (Fuller et al. 2009). We interpreted these changes to be indicative of global compensations for muscular fatigue imparted on the shoulder by the task. However, the temporal aspects of these changes have not been previously described. This additional information could help understand the inter-relationships between the changes in posture-movement coordination occurring with fatigue. Moreover, changes in the temporal coordination of multijoint movements may represent another way in which the system can manage its redundancy in adapting to fatigue, however very little work has focused on describing the changes in temporal coordination occurring with fatigue. The present study focuses on the effect of fatigue on three temporal aspects of posture-movement control during a repetitive upper arm task: 1) the onset of spatial parameter change during the development of fatigue, 2) reach-to-reach variability during non-fatigued and fatigued states and 3) within-reach changes in inter-segment coordination during non-fatigued and fatigued states. We hypothesized that: 1) changes in spatial parameters across the body would begin to occur throughout the task, before the final minute (fatigue terminal) was reached and that these changes would be preceded by changes in electromyographical characteristics of the moving upper limb; 2) reach-to-reach variability of upper limb and postural measures would increase with fatigue; and 3) there would be significant changes in the temporal organization of individual joint movements.

4.4 Methods

4.4.1 Participants

A convenience sample of 14 healthy young adults (8 men, 6 women, mean age = 25.1 ± 5.9 years) was recruited from the university student population. Subjects were excluded if they displayed any of the following: history of mechanical upper limb/shoulder and or back pain or injury; history of any neurological, vestibular or other conditions affecting balance. All subjects provided written, informed consent prior to participation. All subjects were right-handed. Ethical approval for this study was received from the ethics committee of the Montreal Centre de recherche interdisciplinaire en réadaptation (CRIR).

4.4.2 Experimental protocol

The experimental setup is described in detail in Fuller et al. (2009). Briefly, the protocol consisted of performing a repetitive reaching task (RRT) with the dominant arm to fatigue. Prior to performing the RRT, subjects completed maximal voluntary contractions (MVC) for dominant shoulder elevation using a dynamometric system (BTE Simulator II^{TM} (Sim-II), BTE Technologies$^{©}$, Baltimore, MD, USA, serial number: 1113ST) to measure maximum force output. After MVCs, subjects were asked to stand naturally with their feet placed on two adjacent force platforms and their arms resting by their sides. Two cylindrical touch-sensitive targets (length: 6cm, radius: 0.5cm, response time: 130ms, Quantum Research Group Ltd.) used to guide the RRT were adjusted to be placed at shoulder height, in front of the subject's midline, at 100% (distal target) and 30% (proximal target) of arm length. To ensure that the subject maintained arm motion in the horizontal plane at shoulder height while performing the reaching task, an elliptically shaped mesh barrier was placed under the elbow joint's functional range of motion. The RRT consisted of continuous reaching movements from one target to the other, using the index finger to lightly touch each target while keeping the elbow above the mesh barrier. A metronome was used to help subjects maintain a rhythm of one movement per second (1 Hz). Subjects performed the repetitive task until fatigue while biomechanical data and self-perceived task difficulty (Borg CR-10 scale, (Borg 1982)) were collected during the last thirty seconds of each minute. As such, the first thirty reaches at the beginning of the RRT were not analyzed to ensure only continuous reaching movements were analyzed and also to allow subjects time to stabilize their motor pattern. To assess task difficulty, we showed an 8.5 x 11-in print-out of the Borg CR-10 scale to subjects and asked them to tell us which number corresponded to their current perception of task difficulty while continuing the task. The RRT was performed until either the 1 Hz movement frequency could no longer be maintained, or subjects reached a perceived level of exertion of 8 for the shoulder region on the Borg CR-10 scale (Hammarskjold and Harms-Ringdahl 1992; Côté et al. 2002). Subjects were not aware of these stoppage criteria before beginning the protocol. Following termination of the RRT, subjects immediately performed Fatigue-Terminal shoulder elevation MVC trials.

4.4.3 Data Acquisition

4.4.3.1 MVC

For shoulder elevation force trials, resistance was placed over their acromio-clavicular joint, the arm hanging parallel to the torso in the anatomical position. The task was to have subjects push upward with their dominant shoulder joint against the resistance, in a linear direction upwards, similar to a shoulder shrug. Simultaneously, they elevated their contralateral arm against a velcro strap placed over the shoulder to minimize trunk roll towards the contralateral side. For each trial, at the signal of the tester, subjects pushed as much as possible for approximately five seconds in a ramp-up-and-hold effort. They were provided online feedback and were verbally encouraged to surpass their previous force level. Two trials were recorded both before and after the RRT.

4.4.3.2 EMG

Surface EMG was acquired using a TeleMyo sEMG measurement system (Noraxon USA Inc.) with an operating bandwidth of 10–350 Hz, an effective common mode rejection ratio of 130 dB DC, greater than 100 dB at 60 Hz, a minimum of 85 dB throughout the operating bandwidth, and a fixed overall per-channel gain of 2000. EMG data were acquired from the descending trapezius. The electrode pair was placed approximately 25 mm medial to the midpoint between the C7 vertebra and angle of acromion (Basmajian and Blumenstein 1980). The descending trapezius was chosen based on prior evidence that it shows signs of fatigue during at or above shoulder height tasks (Christensen 1986; Gerdle et al. 1988; Nussbaum et al. 2001; Ebaugh et al. 2005). Recordings were acquired using pre-gelled, disposable silver/silver chloride electrodes (Ambu©, Denmark), with a 10-mm diameter circular conductive area, in a bipolar configuration. Electrodes were positioned with a centre-to-centre distance of 3 cm, parallel to the muscle fibers, and following careful preparation of the skin overlaying the muscle sites of interest (cleaned, shaved and lightly abraded). At acquisition, all EMG signals were filtered using a dual-pass, fourth-order Butterworth filter, with a band-pass of 20-500 Hz. EMGs were then digitally converted using a 16 bit A/D board over a ±10 V range, sampled at 1080 Hz, and stored for further analysis.

4.4.3.3 Kinematics

Three-dimensional whole body posture and movement characteristics were recorded (sampling frequency = 120 Hz) using a high-resolution six-camera Vicon MX3 motion capture system (Vicon Peak, Oxford Metrics ltd., Oxford, UK). A modified version of the Vicon Plug-in-Gait model along with standard anthropometric measures and data (de Leva 1996) was applied to the kinematic data using Vicon Bodybuilder to estimate the CoM of each segment defined by reflective markers placed on the body. Whole-body CoM was estimated as a weighted sum of the individual segment COMs. The model used reflective markers placed over palpable bony landmarks, dividing the body into 15 segments: head (head to C7; 5 markers), bilateral upper arms (shoulder to elbow; 3 markers per upper arm), bilateral forearms (elbow to wrist; 4 markers per arm), bilateral hands (distal to wrist; 3 markers per hand), trunk (C7-T10; 5 markers), pelvis (5 markers), bilateral thighs (hip to knee; 3 markers per thigh), bilateral legs (knee to ankle; 3 markers) and bilateral feet (3 markers per foot). The kinematic variables of interest corresponded to the following parameters: the body's CoM, right and left shoulder, and elbow, wrist and endpoint (defined as the tip of the index finger) on the reaching side. These were identified as the main parameters indicative of whole-body changes as a result of fatigue for our experimental task, as evidenced in Fuller et al. (2009). The coordinates of these parameters were computed in the three directions, anterior-posterior (AP), mediolateral (ML), superior-inferior (SI) in global space. Elbow flexion/extension angle, shoulder horizontal abduction/adduction angle and shoulder abduction/adduction angle were also measured by quantifying the relative orientations of the corresponding reconstructed segments in global space using Euler xyz rotations. These kinematic variables were then low-pass filtered at 7 Hz using a dual-pass,

4^{th} order digital Butterworth filter. Digital filtering was performed in Matlab (MathWorks, Massachusetts, USA).

4.4.3.4 *Kinetics*

Three-dimensional ground reaction forces and moments applied on the support surface under each foot were obtained from two triaxial strain gauge force plates (AMTI© OR6-7, AMTI Inc, Watertown, USA) at a sampling frequency of 1080 Hz. Raw forces and moments were low-pass filtered at 10 Hz, using a dual-pass, 4^{th} order digital Butterworth filter. Ground reaction force data were used to locate the net CoP under the feet, in the AP direction according to the method described by (Winter 1995):

$$COP_{AP_{net}} = COP_{AP_{left}} \frac{F_{Z_{left}}}{(F_{Z_{left}} + F_{Z_{right}})} + COP_{AP_{right}} \frac{F_{Z_{right}}}{(F_{Z_{left}} + F_{Z_{right}})}$$

where F_z is the vertical ground reaction force. CoP in the ML direction was calculated using the same formula substituting CoP ML from the left and right force plates for the AP terms.

4.4.4 Data Analysis

4.4.4.1 *Kinematics and kinetics*

The beginning and end of each reach was determined as the onset of activation of each of the two targets. Data from forward (proximal to distal target) and backward (distal to proximal target) phases of the RRT were separated and identified as forward and backward reaches. To reduce data and to simplify data analysis, further analyses for this paper were done only on the first five forward reaches from each consecutive minute the RRT was performed by each subject. For each forward reach, the average position, range of motion (RoM) (maximum – minimum position) and occurrence of peak velocity (taken from the time derivative of displacement) of the kinematic and kinetic parameters of interest were calculated. Peak velocity was chosen as the maximum velocity value within individual reach cycles. For each calculated parameter, the within-subject average and within-subject standard deviation (reach-to-reach variability) of the five reaches from each minute were computed. The first and last minutes of the RRT were used to represent No-Fatigue (NF) and Fatigue-Terminal (FT) data, respectively.

The time at which each spatial parameter began to deviate from baseline was determined as the minute in which the parameter continuously deviated ± 2 SD from the value measured during the first minute of reaching. The minute at which the deviation occurred was recorded and then expressed as a percentage of the total time the RRT was performed for each individual subject. The parameters chosen for this analysis were selected based on previous results that showed these parameters to change from the first minute to the last minute during our experimental task (Fuller et al. 2009). Only parameters which showed a deviation from baseline in a strong majority of subjects (≥ 75%) are reported in this paper to ensure the observations were representative of the group.

Within-reach changes in inter-segment coordination were examined using the peak linear velocity occurrence (Côté et al. 2005) of endpoint, elbow, shoulder and CoM. The occurrence of peak velocity of each kinematic parameter for each forward reach was determined in the AP direction only as this is the direction in which the majority of the movement occurred. The occurrence of peak velocity was expressed as a percentage of total reach duration.

Kinematic parameters were compared using within-subject repeated measures MANOVA with a condition of Fatigue (NF, FT). In the result of a statistically significant main effect of Fatigue ($p<0.05$), this test was followed by a Bonferroni post hoc test.

4.4.4.2 *MVC and EMG*

The highest of the two force outputs for the shoulder elevation MVC test for each experimental condition (NF and FT) was kept for statistical analyses. Root-mean-squared (RMS) amplitude for the electromyographic data of the descending trapezius was calculated over the entire duration of each of the five forward reaches representing each minute the RRT was performed for each subject. The EMG RMS values for the five reaches of each minute were then averaged for each subject. Statistical comparisons were assessed for each of the MVCs, and trapezius EMG RMS by computing one-way analyses of variance with fatigue as a within-subject factor ($p < 0.05$). The occurrence of deviation of trapezius EMG RMS from baseline was computed in the same manner as for the deviation occurrence of kinematic parameters. Finally, to assess the strength of the relationships between muscular and whole-body changes, Pearson correlation coefficients were computed between the change from baseline in trapezius EMG RMS and changes from baseline in reach-to-reach variability, average position and RoM of kinematic parameters at minutes 2, 3 and at each subject's last minute of performing the repetitive reach task.

4.5 Results

4.5.1 Fatigue measures

Subjects performed the repetitive reaching task for an average time of 7.9 ± 4.0 minutes. Shoulder elevation MVC (significant decrease, $p<0.05$) and trapezius EMG RMS (significant increase, p<0.005) both showed a main effect of Fatigue. Further fatigue measures are reported in Fuller et al. (2009).

4.5.2 Development of posture and movement changes during fatigue

Trapezius muscle fatigue, as determined by the mean time of trapezius EMG RMS increase from baseline, was observed to occur at 65.5 ± 27.2% of task duration, from the beginning of the fatigue protocol (Table 4-1, see Figure 4-1 for representative data). The first parameter to exceed ± 2 SD its baseline value in more than 75% of subjects was the mean AP coordinate of the elbow marker (42.9 ± 29.5%). This was followed by deviations in the ML CoP (leftward), ML CoM (leftward), ML shoulder (leftward), SI shoulder (vertical increase) and the shoulder abduction angle (decreased abduction), respectively, all of which exceeded ± 2 SDs their baseline value between 44 and 53% of the overall RRT duration (Table 4-1).

Table 4-1Time of deviation from baseline for each parameter relative to overall RRT duration

Parameter	N	Time (%)	SD
AP Elbow	13	42.82	29.52
ML CoP	12	44.35	36.4
ML CoM	11	46.4	37.1
ML Shoulder	13	50.56	29.67
SI Shoulder	14	51.03	27.89
Shoulder Abduction	13	52.56	25.11
trapezius RMS	11	65.5	27.27

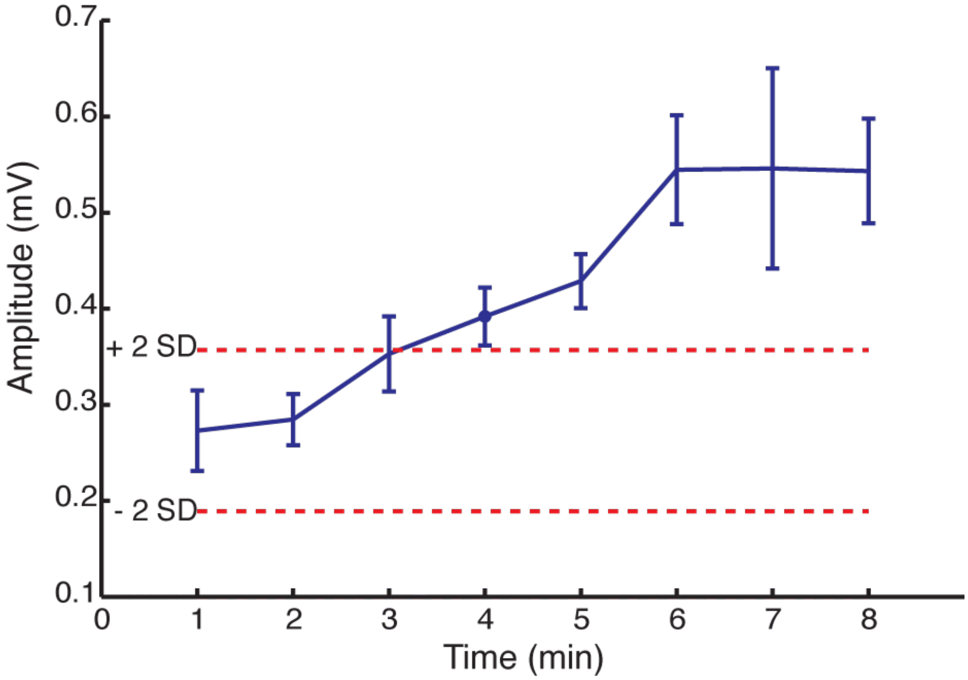

Figure 4-1Average trapezius root-mean-squared amplitude (solid blue line) and 1 SD error bars at each minute of the reaching task (representative subject). Red-dashed lines represent ±2 SDs of the mean trapezius EMG RMS during the initial minute. Blue filled dot represents the minute the average trapezius root-mean-squared amplitude exceeded ±2 SDs of the first minute value

Percent change in trapezius EMG RMS was significantly correlated with percent change in vertical shoulder position from minute 1 to minute 2 ($r = 0.77$, $p<0.05$), from minute 2 to minute 3 ($r = 0.66$, $p<0.05$) and from minute 1 to the last minute of the RRT ($r = 0.79$, $p<0.05$), indicating that subjects who showed the largest increase in trapezius EMG RMS also showed the greatest increases in shoulder height. In addition, trapezius EMG RMS change was significantly correlated to percent change in shoulder adduction/abduction angle but only from the first minute to the last minute ($r = 0.70$, $p<0.05$). No other change in any spatial parameter examined showed a significant correlation with change in trapezius EMG RMS.

4.5.3 Within-reach inter-segmental timing

Representative data from one subject depicting typical linear velocity profiles in the AP direction for parameters of interest can be seen in Figure 4-2. The chronological sequence of peak velocity occurrences for the observed parameters in the AP direction during NF was as follows: endpoint, elbow, CoM, shoulder. During FT this sequence was preserved, but the time spacing between parameters changed. MANOVA revealed a significant Fatigue effect ($p=0.045$). Post-hoc comparisons revealed that during NF, the peak velocities for endpoint and elbow occurred at significantly different times ($p<0.0001$, Figure 4-3) but not during FT ($p=0.217$). There was also a significant effect for the reach-to-reach variability of shoulder peak velocity occurrence, with variability increasing during FT ($p=0.046$, Figure 4-4).

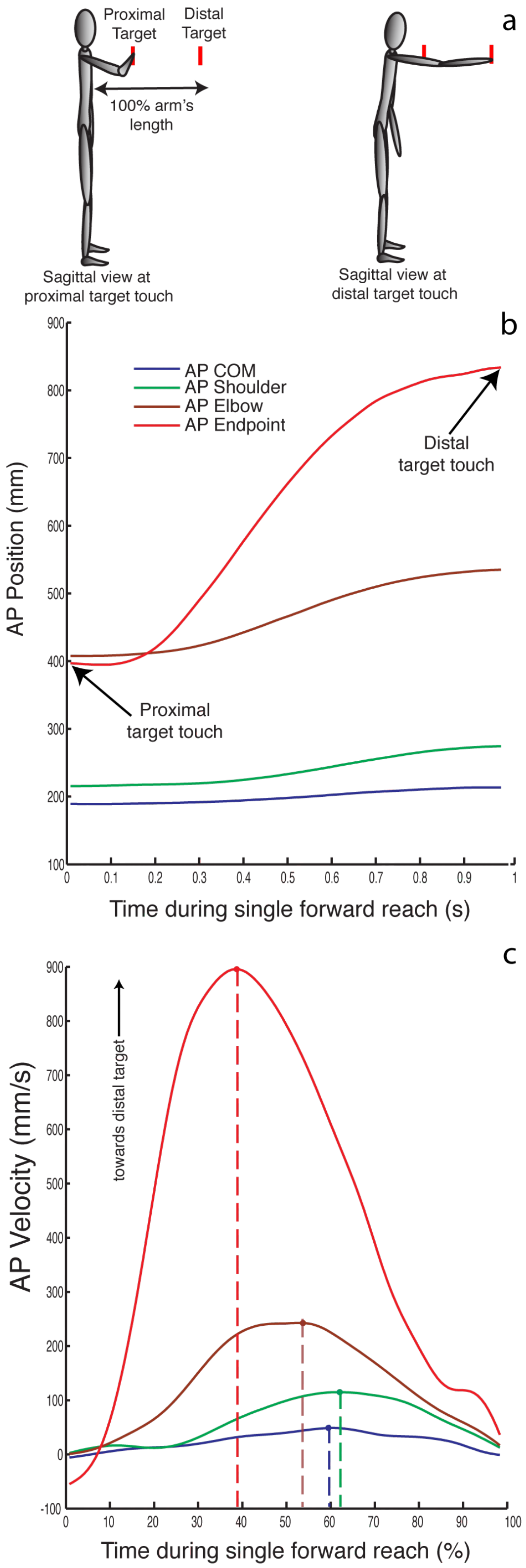

Figure 4-2 Experimental schematic a, displacement b and velocity c c profiles in the AP direction for CoM, shoulder, elbow and endpoint as the subject reaches from the proximal to distal target (representative subject). Solid dots represent the occurrence of peak velocity

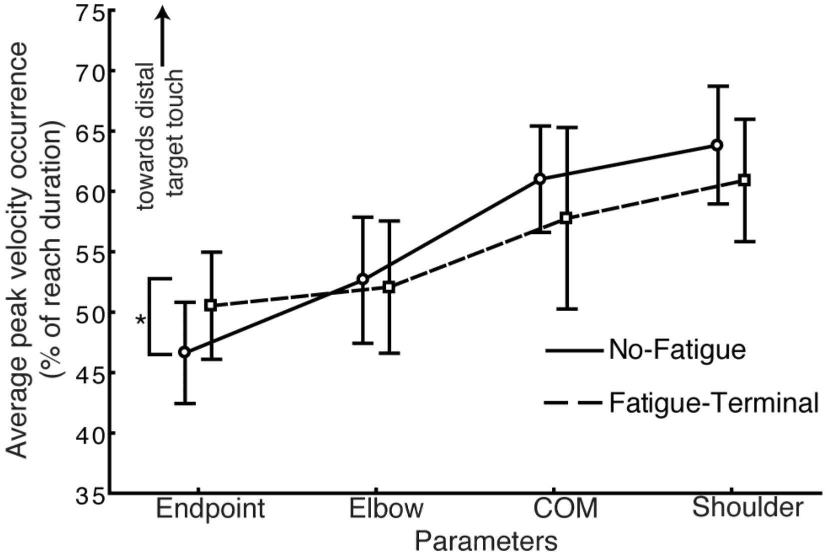

Figure 4-3 Group averages and 1 SD error bars of occurrences of peak velocity of endpoint, elbow, CoM, and shoulder, in the AP direction (solid line: No-Fatigue, dashed line: Fatigue-Terminal)

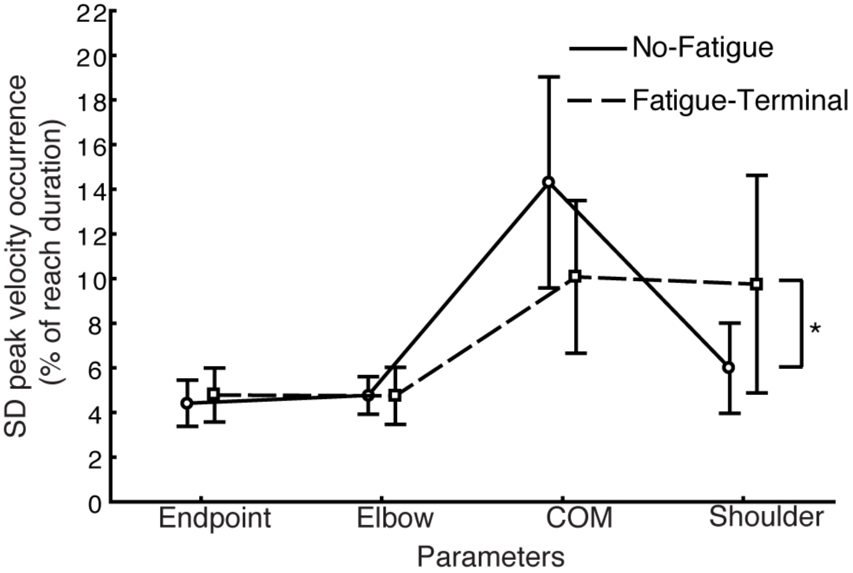

Figure 4-4 Group averages and 1 SD error bars of reach-to-reach variability of peak velocity of endpoint, elbow, CoM, and shoulder, in the AP direction (solid line: No-Fatigue, dashed line: Fatigue-Terminal)

4.5.4 Effects of fatigue on reach-to-reach variability

Reach-to-reach variability of average shoulder joint horizontal abduction/adduction angle increased as did the reach-to-reach variability of the shoulder position (Table 4-2) in both AP and SI directions of motion. Similarly, average elbow joint position reach-to-reach variability also increased in the AP direction (Table 4-2). The reach-to-reach variability in average CoM increased in the SI direction only. The reach-to-reach variability of CoP position was not affected by fatigue. Finally, reach-to-reach variability of endpoint position increased only in the ML direction. Changes in reach-to-reach variability were also observed for ranges of motion (Table 4-3). There were fatigue effects on variability of shoulder, elbow and CoM ranges of motion. Range of motion variability increased with fatigue at the shoulder in the AP, ML and SI directions and at the elbow in the AP direction (Table 4-3). Variability also increased for CoM in the ML and SI directions. There were no effects of fatigue on reach-to-reach variability in any other directions for endpoint range of motion. It is worth noting that none of the parameters tested showed a decrease in reach-to-reach variability (Tables 4-2 and 4-3).

Table 4-2 Summary of results detailing the difference in reach- to-reach variability of the average position of kinematic parameters from No-Fatigue to Fatigue-Terminal conditions

Parameter	Direction		No-Fatigue		Fatigue-Terminal	
		p	Mean	SD	Mean	SD
Shoulder angle (°)	Abd/Add	ns	1.2	0.8	2.3	2.2
	Horizontal Abd	0.031	1.3	0.7	2.1	1.5
Shoulder joint (mm)	AP	0.009	4.7	2.0	9.4	6.5
	ML	ns	2.6	0.9	5.9	7.3
	SI	0.01	1.4	0.7	3.4	2.7
Elbow angle (°)	Flx/Ext	ns	2.7	0.8	2.5	1.3
Elbow joint (mm)	AP	0.019	6.4	2.4	13.6	9.7
	ML	ns	4.3	1.8	5.4	3.7
	SI	ns	4.3	2.3	4.3	1.9
Endpoint (mm)	AP	ns	11.2	4.0	12.2	6.9
	ML	0.007	3.4	1.2	5.1	1.6
	SI	ns	3.6	1.7	4.9	1.6
CoM (mm)	AP	ns	3.1	2.0	3.6	1.4
	ML	ns	1.8	0.6	4.0	5.1
	SI	0.017	0.5	0.3	1.2	1.0
CoP (mm)	AP	ns	3.8	2.3	10.3	6.7
	ML	ns	1.8	0.7	6.4	2.9

Table 4-3 Summary of results detailing the difference in reach- to-reach variability of the range of motion of kinematic parameters from No-Fatigue to Fatigue-Terminal conditions

Parameter	Direction		No-Fatigue		Fatigue-Terminal	
		p	Mean	SD	Mean	SD
Shoulder angle (°)	Abd/Add	ns	2.2	2.1	3.5	3.8
	Horizontal Abd	ns	2.9	1.2	3.8	2.2
Shoulder joint (mm)	AP	0.049	7.1	2.8	11.9	7.4
	ML	0.022	3.9	1.2	7.4	5.3
	SI	0.003	1.5	0.8	3.6	2.5
Elbow angle (°)	Flx/Ext	ns	2.8	1.7	3.9	2.6
Elbow joint (mm)	AP	0.018	8.2	4.7	17.2	12.1
	ML	ns	6.7	2.9	9.1	6.3
	SI	ns	6.3	4.2	10.3	6.7
Endpoint (mm)	AP	ns	3.6	1.8	6.6	7.3
	ML	ns	5.3	2.1	5.9	2.3
	SI	ns	6.7	3.3	8.8	3.3
CoM (mm)	AP	ns	4.1	2.0	5.4	3.7
	ML	0.014	1.8	0.7	3.7	2.6
	SI	0.03	0.6	0.5	1.1	0.7
CoP (mm)	AP	ns	7.1	3.3	9.1	5.4
	ML	ns	3.1	1.5	8.9	12.2

4.6 Discussion

The aim of the study was to quantitatively describe the temporal characteristics of adaptations to the development of shoulder fatigue produced by repetitive reaching. The following section highlights the main findings in relation to within-movement, movement-to-movement, and minute-to-minute changes occurring with fatigue.

4.6.1 Development of spatial changes during repeated movements

The first parameter to deviate more than 2 SD of its NF value in the majority of subjects was the AP elbow position at 42.9% of the overall RRT duration. This was followed by ML CoM position, ML CoP position, ML shoulder position, SI shoulder position and mean shoulder abduction/adduction angle (Table 4-1). Interestingly, all observed parameters began to deviate from their baseline before FT. Surprisingly, using the same criteria of 2 SDs to indicate a significant change from baseline, we found that signs of trapezius muscle fatigue, quantified using EMG RMS, occurred later, only at 65.5% of RRT duration, whereas we had hypothesized that changes in shoulder muscle fatigue indices would lead to (i.e. precede) whole-body changes. This might indicate that the 2 SD criteria is not as sensitive to distinguish change for EMG RMS variables. Moreover, while these results may refute our working hypothesis, they may also indicate that more subtle and earlier changes at the main agonist muscle site trigger whole-body changes in a feedforward manner, before clear signs of muscle fatigue can be detected. While no known studies to date have examined the occurrence of kinematic changes in relation to upper limb fatigue development, a few studies on running to exhaustion have reported significant changes in lower limb joint angle amplitudes and ground impulses at the midway point to exhaustion (Gazeau et al. 1997). In studies examining trapezius muscle activity during isometric contractions to exhaustion, indicators of fatigue such as reorganization of motor unit activation patterns were observed to begin as early as 25% of the way to exhaustion (Farina et al. 2008; Madeleine and Farina 2008). While such intra-muscular changes may also explain our findings, follow-up studies are needed to determine the sequence of changes from the intra- to the inter-muscular level.

To gain further insight into the relationships between change in kinematic parameters and fatigue and also into a possible dose-response between muscle fatigue and kinematic changes, we computed correlations between changes in trapezius EMG RMS with kinematic changes. We did so following the hypothesis that the largest changes in muscle characteristics would be related to the largest changes in kinematic characteristics. These analyses show that vertical shoulder position was signifcantly correlated with percent change in trapezius EMG RMS at all minute increments into the RRT, suggesting that subjects who had higher changes in trapezius EMG RMS also had greater changes in shoulder height. Given that the nature of the trapezius muscle is to raise the shoulder joint, this finding is not surprising. Interestingly however, the change in average shoulder adduction/abduction angle had a significant correlation to change in trapezius EMG RMS only from the first minute to the last minute, indicating that individuals who showed the greatest change in trapezius EMG RMS had smaller average abduction angles and hence lower torque about the shoulder joint. No other spatial parameters examined showed a significant correlation with trapezius EMG RMS. Taken together, our results suggest that the greater the increase in trapezius muscle fatigue, as measured through an increase in EMG RMS, the greater the change in shoulder kinematics.

4.6.2 Reach-to-reach variability changes with fatigue

Several kinematic parameters at the shoulder and elbow displayed an increase in reach-to-reach variability within particular directions during FT (Table 4-2 and 4-3). Despite these changes in the upper limb, the reach-to-reach variability in CoM average position and range of motion remained unchanged in the predominant direction of movement (AP). However, CoM did show reach-to-reach variability increases in the ML and SI directions (Tables 4-2 and 4-3). These results suggest that subjects may search for ways to optimize the contributions of ML and SI directions movements as they continue the task towards fatigue while maintaining steady control in the predominant direction of the task. Indeed, small, multi-directional changes in postural parameters may be additive in contributing to the adjustment of the postural system, and as such, an efficient strategy to compensate for arm fatigue towards the completion of the RRT. Despite these changes, the task goal of reaching from one target to the other was preserved and reach-to-reach variability remained invariant across most endpoint measures. This suggests that CoM movement variability was controlled in a hierarchical manner to ensure successful accomplishment of the main task objective (i.e. endpoint motion). This conclusion is similar to that which has been reached by Singh et al. (2010c) who observed that variance in total force output due to index finger fatigue was mitigated by increased variance in force production of the three non-fatigued fingers. This type of movement variability which does not affect successful completion of the end goal (in this case, reaching between the two targets) is commonly described as variability within a controlled manifold (Latash et al. 2002). Conversely, variability which leads to segmental configurations which do not satisfy the end goal is deemed variability outside the controlled manifold. Little has been documented on the development of increased variability during upper limb fatigue. Gates and Dingwell (2008) showed no significant changes in endpoint speed and distance variability with fatigue during an upper limb block pushing task but joint kinematic characteristics were not measured. Cignetti et al. (2009) observed an increase in cycle-to-cycle movement variability of the legs and arm in association to the development of whole-body fatigue during cross-country skiing.

In a study which looked at kinematic variability during experimentally induced pain, Madeleine et al. (Madeleine et al. 2008a) showed that variability of arm range of motion and arm and trunk movement area increased. It has been further theorized that increasing motor variability may be a mechanism for preventing chronic injury since a cross-sectional study observed pain-free butchers had greater motor variability than butchers with pain (Madeleine et al. 2008b). In the future, prospective studies are needed to examine the development of injury in association to measures of motor variability to test this hypothesis. Caution needs to be taken when drawing parallels between data from pain and fatigue interventions. Although perceived discomfort is certainly one aspect of fatigue (Gandevia 2001) cross-sectional studies which have compared healthy-fatigued subjects and non-fatigued injured subjects have shown difference in movement trajectory and joint angle acceleration between groups (Côté et al. 2005b). The key in understanding the effects of fatigue and of pain on movement variability may lie in the type of pain studied. Indeed, similarities between the effects of fatigue and of acute pain on movement variability may reflect that they are both consequences of acute stimuli, illustrated by a rapid search for a solution, whereas individuals with chronic pain may have already learned a pain-minimizing strategy on which they focus most of their patterns.

During repetitive tasks where the task goal is preserved, increased reach-to-reach variability of kinematic parameters may be representative of subjects exploring new movement strategies to adapt to localized fatigue and prolong task duration. Variability increases in areas proximal to the site of fatigue may be a consequence of fatigue-related deficits such as those affecting the proprioceptive system (Björklund et al. 2000). At the whole-body level, increased variability may be representative of subjects exploring new movement strategies to prolong task duration while accounting for localized fatigue inhibition of some degrees-of-freedom. Our results support this theory as changes in variability were observed in areas both local to the site of fatigue (shoulder) as well as distally (CoM RoM) yet the emergent movement patterns preserved the task goal.

4.6.3 Within-reach inter-segmental timing changes with fatigue

Analysis of the mean occurrence of peak linear velocity data showed a clear pattern of inter-segmental coordination across subjects. Peak velocities were first reached at the endpoint followed by elbow, CoM, shoulder. This sequence was maintained during both NF and FT conditions, however during FT, endpoint and elbow peak velocity occurred more closely together indicating a temporal adjustment in inter-segmental coordination suggestive of more rigid coordination of the distal joints of the limb (Figure 4-3). This finding is similar to that of Forestier and Nougier (1998) who observed that during a forceful ball throwing task, linear peak velocities of arm joints occurred closer together with fatigue resulting in a more rigid link system. Conversely, Côté et al. (2005b) observed no fatigue related changes in the temporal sequence of upper limb motion during repetitive hammering although angular, not linear, peak velocity occurrence was used as the dependent measure which may account for differences. One limitation in comparing our data to previous work is that the task used in the present paper inherently required that peak velocity peaked around the midway point of a reach duration in order to prepare for the backward reach phase, in contrast to the studies by Côté et al. and Forestier and Nougier, who studied more forceful tasks where maximal endpoint velocity could occur later (i.e. at the time of force application). Furthermore, in our study movement timing was constrained (using the metronome) whereas Forestier and Nougier did not constrain timing but constrained posture below the shoulder. In the study by Côté et al., there were no postural or timing constraints. Thus, while some aspects of whole-body adaptations to fatigue such as increased variability may be general findings, as we have shown previously (Fuller et al. 2009), other aspects may also largely depend on the nature of the task performed.

Very few studies have been used to examine the effects of fatigue on temporal characteristics of inter-segmental coordination. Studies which have examined inter-segmental coordination during gait observed more rigid or "*en bloc*" inter-segmental control as a characteristic of younger children (Assaiante et al. 2000) implying that more rigid coordination between segments is a property of less developed control systems. As fatigue develops, thus inhibiting preferred movement of the system, perhaps it is the simplest solution for the CNS to adopt a more *en bloc* control strategy as systems of increased rigidity and reduced degrees-of-freedom may be computational simpler for the CNS to control. Finally, reach-to-reach inter-segmental timing of the shoulder joint becomes more variable (Figure 4-4) during fatigue, which may indicate that localized fatigue is inhibiting control in that area.

4.7 Conclusions

Although fatigue did not adversely affect the success of the reaching task, our results demonstrate that localized upper limb muscle fatigue developing from repetitive reaching alters both movement and posture control over three temporal domains: the complete task, reach-to-reach, and within-reach. This study is the first to show that task specific changes in spatial parameters begin to develop well before exhaustion would be reached. We also confirm that reach-to-reach variability increases across several postural and upper limb spatial parameters indicating movement patterns during fatigue fluctuate more as compared to the non-fatigued state. This may be a possible strategy to limit exposure in fatigued areas and to adopt a new movement strategy despite reduced capacity of some muscles as has been suggested previously in similar research investigating the effects of pain. At the within-reach level, increased coupling between distal arm segments combined with increased variability of shoulder joint timing suggest increased rigidity of distal segments may be a strategy to reduce error associated with the more proximal shoulder joint. Whether these temporal changes have an adverse or inconsequential effect on postural stability remains unknown and may be explored in future work examining the relationship between upper limb fatigue and the coupling between focal and postural task control.

4.8 Acknowledgements

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Chapter 5: Posture-movement response to stance perturbations and upper limb fatigue during a repetitive pointing task

Jason R. Fuller, Joyce Fung and Julie N. Côté

Prepared for the Journal of Neurophysiology

5.1 Preface

Chapter 5 more closely examines the motor control aspects of the coordination of posture and movement components together. It has often been explained in the literature that when reaching to a target the CNS must concomitantly satisfy two independent subtasks: 1) successfully reaching the hand to an object or target and 2) successfully maintain postural stability. Prior to the current work, it had repeatedly been shown that when reaching to an anterior target, centre of mass displacement is not minimized in the same manner it is during a postural task alone but rather contributes to this displacement of the hand/endpoint (Pozzo et al. 2002). While in chapters 3 and 4 we show that fatigue can lead to both spatial and temporal adaptations to posture and movement components it remained unknown if fatigue would alter the combined spatiotemporal coordination of the postural and reaching subtasks; as such, this became the focus of chapter 5. To further elucidate the interaction between postural and movement components, a perturbation platform was used to administer a standing surface perturbation to the participant providing and additional challenge to posture-movement control system.

This manuscript is in the final formatting stages of preparation to be submitted to the Journal of Neurophysiology.

5.2 Abstract

We examined the effects of surface translations and fatigue, induced by a repetitive reaching task, on posture-movement coordination. We hypothesized that postural perturbations would dissociate postural and movement trajectories and that fatigue adaptations would minimally interact with this response. Subjects stood on a motion base platform and repetitively reached between two shoulder-height targets fixed to the platform until fatigue. Every minute, subjects experienced a posterior and an anterior perturbation (5 cm) while reaching to the distal target. When fatigued, regardless of the perturbation condition, subjects increased leftward trunk flexion (1.6±0.44°) and shoulder adduction (7.3±1.5°), likely to reduce shoulder load. During the anterior perturbations, centre of mass (CoM) and endpoint (EP) trajectories were decoupled (r =-0.512); also, at the time of distal target touch, CoM position was significantly more posterior (27.5±10.3mm) and there were increases in elbow extension (7.4±1.1°), shoulder flexion (3.4±1.1°) and trunk rotation (3.1±0.5°) and flexion (2.0±0.5°). During posterior perturbations, the CoM-EP relationship remained strong (r =0.92±0.13) and at the time of distal target touch CoM position was significantly more anterior (27.2±7.5mm) and elbow flexion was increased (9.9±1.5°). CoM position remained well within the base of support (BoS) during both perturbations (anterior: 8.2±10.4 BoS%; posterior: 44.3±12.2 BoS%). We conclude that the posture-movement relationship is dissociated only during the anterior perturbations. During both perturbations, kinematic adaptations predominantly occurred in the direction of the reach while fatigue adaptations occurred in direction orthogonal to the reach. We interpret the findings within the framework of the referent-configuration hypothesis: fatigue and postural compensations may occur according to the principle of minimal interaction so as to preserve the global task characteristics of endpoint motion.

5.3 Introduction

In order to perform a task using the upper limb while standing, the central nervous system (CNS) must satisfy the constraints and demands of two independent tasks: a focal task (e.g. reaching towards an object with the upper limb) and a postural task (i.e. keeping the body upright and balanced). Typically, studies examining the interaction between the two tasks utilize measures of the fingertip movement known as endpoint (EP) and the whole-body centre of mass (CoM) position as performance indicators of these focal and postural tasks, respectively. Research from this domain has shown that when performing a pointing or reaching task with the upper limb, CoM movement is not minimized but rather moves in phase with EP trajectory (Pozzo et al. 1998; Stapley et al. 1999; Pozzo et al. 2002; Patron et al. 2005). Similar observations have been made during tasks accomplished in zero-G environments (Patron et al. 2005) and during environments where the size of the base of support (BoS) is reduced (Fautrelle et al. 2010). Interestingly, the strategy of CoM moving with endpoint during reaching is conserved even when the arm is removed from the CoM model, indicating that CoM displacement towards the target is not simply a function of arm displacement but rather that the CoM is actively controlled towards the target so as to aid EP displacement (Pozzo et al. 2002). Furthermore, biomechanical simulations have shown that that these reaching movements are mechanically possible to make without CoM displacement (Stapley et al. 2000), further strengthening the hypothesis that moving the CoM toward the target during reaching is a strategy chosen by the CNS.

Recent studies have obtained findings consistent with the hypothesis that movement and postural commands are tightly integrated in the CNS, although the commands may arise from independent areas of the motor cortex (Brown et al. 2003; Schepens and Drew 2004; Kurtzer et al. 2005; Schepens et al. 2008). Furthermore, Trivedi et al. (2010) have shown that when stance is perturbed, the initial reflexive postural response is unaffected by reaching. In contrast, the same study shows that the long-latency postural response (>100 ms following perturbation onset) is modified to assist movement. Taken together, these findings suggest that the commands for posture and movement may emerge separately within the CNS but then integrate into a global command that coordinates the multi-muscle, multijoint response needed to satisfy both the focal and postural tasks.

One model of motor control that attempts to explain the coordinated multi-muscle control of posture and movement is the referent configuration hypothesis (RC-hypothesis). A large body of work has been presented in support of this hypothesis with the core premise being based on the observation that when an external load is unexpectedly removed from the body, a new configuration will be adopted (Feldman and Levin 1995; Feldman et al. 2007; Feldman 2009). The RC-hypothesis proposes that the CNS delivers a global, task-related command to control whole-body position in space, The actual body configuration displayed in the presence of the external load is called the Q configuration and the configuration adopted when the load is released is referred to as the R configuration. In this case, to get from Q to R, the CNS delivers a central command which sets threshold values of motor neurons across multiple muscles, thus determining the range of external input at which action potentials will be generated. In other words, this empirically based theory suggests that the nervous system does not control muscle activity or limb position directly, but instead specifies the threshold of muscle activities i.e., the position, R, at which the activity of respective muscles would become silent. As such, any Q configuration then that does not equal the R configuration will result in emergent muscle activities. From the global R-configuration command, the individual EMG patterns would emerge due to the action of local factors, such as peripheral and inter-muscular reflexes, muscle properties and the presence of external forces, guided by processes that follow a common principle of minimal interaction (Gelfand and Tsetlin 1971; Feldman et al. 2007). Applied to whole-body reaching, this model proposes that under varying external (e.g. postural perturbations) and internal conditions (e.g. fatigue), multi-muscle responses will emerge which satisfy both the postural and focal tasks. One way to examine this theory would be to examine the spatiotemporal relationship between postural and focal task kinematics as well as the emerging joint kinematics under conditions of postural instability (induced by sudden surface perturbations). Another perturbation which can be used to test this theory could be presented internally through the presence of fatigue.

One of the consequences of repeating a movement is fatigue. Muscle fatigue is typically defined as a gradual phenomenon that leads to both the inability to maintain a certain level of force and to an increased perception of task difficulty (Enoka and Stuart 1992). Muscle fatigue is known to reduce muscle contractile efficacy (Bigland-Ritchie and Woods 1984) leading to reduced muscular output. In low-force tasks, fatigue is an ongoing process which may not necessarily result in a decline in target submaximal force but is typically manifested as an increase in perceived effort (Jones and Hunter 1983) and a reduction in the maximal force generating capacity (Vøllestad 1997). Apart from reducing the functional capacity of the muscle, fatigue is also associated with reduced joint position sense (Sharpe and Miles 1993) which may be due to altered sensory output of muscle spindles and Golgi tendon organs (Windhorst and Kokkoroyiannis 1991; Pedersen et al. 1998; Pettorossi et al. 1999; see Windhorst 2007 for review) or altered central integration of sensory information due to an increasing sense of effort (Allen and Proske 2006). The importance of afferent feedback mechanisms for postural control has been shown in a number of studies on healthy young (Horak et al. 1990; Kavounoudias et al. 1999; Thompson et al. 2010) and pathological populations (Bloem et al. 2002; Nardone and Schieppati 2004) in which afferent information has experimentally altered or diminished due to disease. Knowing this, it is not surprising that the presence of muscle fatigue in the lower limb (Vuillerme et al. 2002a; Vuillerme et al. 2002b; Caron 2003; Corbeil et al. 2003), trunk (Madigan et al. 2006) and neck (Schieppati et al. 2003; Gosselin et al. 2004; Vuillerme et al. 2005; Stapley et al. 2006) has been shown to increase postural sway during quiet stance. Movement coordination in the lower and upper limbs has also been shown to be significantly altered during the presence of localized fatigue (Bonnard et al. 1994; Forestier and Nougier 1998; Côté et al. 2002; Côté et al. 2005; Côté et al. 2008) yet the interaction between fatigue, movement and posture remains largely unexplored and the few studies which have investigated interactions between these three factors have shown mixed results. Yiou et al. (2009) and Mezaour et al. (2010) have observed that anticipatory postural adjustments (APAs) during a reaching task are not altered after the performance of fatiguing isometric contractions to the lower limb. In contrast, Strang and Berg (2007) have shown earlier onset of APAs during an arm raising task in the presence of leg and trunk fatigue. Schmid et al. (2006) have shown postural sway measures to decrease in amplitude while endpoint precision remained unchanged during a repetitive bend-to-reach task which induced fatigue in the hip flexors. In contrast, Sparto et al. (1997) and Nussbaum (2003) have both reported increased postural sway during a repetitive lifting task and a repetitive pointing task, respectively. Taken together, the mixed results of these studies examining the interaction of fatigue, posture and movement can probably be attributed to differences in the magnitude of fatigue induced and in the level of constraint associated with both the postural and focal task components, making it difficult to draw conclusions as to the general role of fatigue during posture and movement. Indeed, the dynamic relationship of these factors ensures that more experimental data will be needed before the interaction of fatigue, posture and movement is clearly understood.

Research from our group has shown that fatigue alters both postural and movement kinematics of the upper limb during a repetitive pointing task and we have argued that these adaptations may be task-specific (Côté et al. 2002b; Côté et al. 2005b; Côté et al. 2008; Fuller et al. 2009). More specifically, we have previously shown that in the presence of upper limb fatigue, kinematic and EMG characteristics were indicative of altered upper limb function occurring in parallel with increased contribution of whole-body CoM in the direction of the arm movement (Fuller et al. 2009). This suggested that the CNS used a strategy of combining focal and postural commands to compensate for fatigue and prolong task performance. However, this was accomplished in conditions of quiet stance with little postural demands. One way to further investigate the relationship between posture-movement control and fatigue would be to increase the postural demand and examine if postural and movement characteristics are similarly affected under varying fatigue conditions.

The objective of the paper was to further assess the task-specificity characteristics of the fatigue adaptations to our repetitive reaching task, by adding a postural constraint to the task. To achieve this, we administered sudden standing surface translations intermittently throughout the reaching task to examine if the movement task remained coupled to the postural task following the postural perturbation as fatigue developed. We hypothesized that sudden perturbations would dissociate the relationship between postural and movement trajectories such that the focal task would be preserved despite the increased postural demands. To achieve this, we hypothesized that biomechanical patterns would emerge in a manner consistent with the principle of minimal interaction such that the system would be able to satisfy both postural and focal characteristics associated with the task, not only in the presence of fatigue but also in the presence of the postural perturbation.

5.4 Materials and Methods

5.4.1 Subjects

Thirteen healthy young volunteers (8 males; 5 females) were taken from a convenience sample of university students (mean age 25.5 +/- 6.1 years). Subjects were excluded if they displayed or reported any of the following when asked: history of mechanical upper limb/shoulder and or back pain or injury; history of any neurological, vestibular or other conditions affecting balance. All subjects provided written, informed consent prior to participation. All subjects were right-handed and thus performed the repetitive reaching task with their right arm. Ethical approval for this study was received from the ethics committee of the Montreal Centre de recherche interdisciplinaire en réadaptation (CRIR).

5.4.2 Protocol

5.4.2.1 Non-fatiguing shoulder elevation maximum voluntary contractions

To assess the effects of the repetitive reaching task on shoulder force, subjects completed maximal voluntary contractions (MVCs) for dominant shoulder elevation using a dynamometric system (BTE Simulator II^{TM} (Sim-II), BTE Technologies$^{©}$, Baltimore, MD, USA) to measure maximum force output. Resistance was placed over their acromio-clavicular joint, the arm hanging parallel to the torso in the anatomical position. The task was for subjects to push upward with their dominant shoulder joint against the resistance, in a linear direction upwards, similar to a shoulder shrug. For each trial, at the signal of the tester, subjects pushed as much as possible for approximately five seconds in a ramp-up-and-hold effort. They were provided online feedback and were verbally encouraged to surpass their previous force level. Two trials were recorded both before and after the repetitive reach task described below.

5.4.2.2 *Platform movement and practice perturbations*

After MVCs and prior to the repetitive reach task (RRT), subjects experienced sudden translations of the support surface in both tested directions (anterior and posterior) to familiarize themselves with the platform movement and to make sure they could maintain their balance in response to the perturbations. The six-degree-of-freedom moveable platform had a circular surface of 1.6 m in diameter and was servo-controlled by six electrohydraulic actuators (platform details further described in: Fung and Johnstone 1998; Fung et al. 2003). A ramp-and-hold perturbation was applied, such that the platform was translated a total distance of 5 cm during 300 ms, corresponding to a constant peak velocity of 0.17 m/s and a peak acceleration/deceleration of 2.5 m/s^2. These perturbation parameters were chosen based on pilot work showing that subjects could react to the perturbations while still performing a reaching task without invoking a stepping response (hence allowing subjects to maintain the same position in local platform coordinates throughout the task). Initially, subjects were asked to stand naturally on the platform with their hands by their sides and with their feet naturally placed apart. Each subject then experienced 5-10 perturbations in each direction, spaced by 10-20 seconds, until a stepping response was no longer invoked and they reported feeling comfortable standing on the platform. To acclimatize subjects to the perturbations while performing the RRT, subjects then practiced the RRT (described below) and 5-10 perturbations in each direction were delivered while performing the reaching task until the subjects felt comfortable with the task.

5.4.2.3 Repetitive reaching task

After acclimatization to the task, subjects rested for at least 10 minutes to allow any potential fatigue effects arising from the practice sessions to subside, prior to performing the RRT. The protocol consisted of performing repetitive reaching with the dominant arm to fatigue. Two cylindrical, touch-sensitive targets (length: 6cm, radius: 0.5cm, response time: 130ms, Quantum Research Group Ltd.) were used to guide the RRT and placed at shoulder height, in front of the subject's midline, at 100% (distal target) and 30% (proximal target) of arm length (Figure 5-1). When touched, the targets sent an electrical signal to the data collection computer such that we were able to record at all times when the subject was touching the target. To ensure preservation of the focal task in global space independently from the perturbation, the targets were fixed to the platform using a custom-made, adjustable metal pole (Figure 5-1) such that the targets were translated along with the platform. In this manner, when the subject was translated in global space, they were not translated toward or away from the targets. To ensure that the subject maintained arm motion at shoulder height in the horizontal plane while performing the reaching task, an elliptically shaped barrier was placed under the elbow joint's functional range of motion (Figure 5-1). The RRT consisted of continuous reaching movements from one target to the other, using the index finger to lightly touch each target while keeping the elbow above the mesh barrier. A metronome was used to help subjects maintain a rhythm of one reach per second (1 Hz), and because the targets also produced an auditory beep when touched, the subjects were instructed to match the auditory signals of the metronome to those of the target. Subjects were instructed to reach between the two targets to the beat of the metronome while standing and to avoid moving their feet. Tape was used to mark the outline of the subjects' feet on the floor to assist detection of any change in foot placement. Subjects performed the repetitive task until fatigue while biomechanical data and self-perceived task difficulty (Borg CR-10 scale, (Borg 1982)) were collected during the last thirty seconds of each minute (Figure 5-2). As such, the first thirty reaches at the beginning of the RRT were not analyzed to ensure only continuous reaching movements were analyzed and also to allow subjects time to stabilize their motor pattern. During the final 15-18 seconds (randomly determined) of each one-minute cycle of the RRT, an anterior (forward) surface translation was delivered (Figure 5-2), followed by a posterior (backward) translation of the platform 6 to 8 seconds later (randomly determined). The signal from the proximal touch target was used to act as a switch to activate platform movement, with platform translations in both anterior and posterior directions activated 400 ms after the randomly selected proximal target touch. This time sequence was chosen based on pilot work so that perturbations occurred while the reaching hand was in between the targets as opposed to touching one of them. Subjects were instructed to maintain the reaching task to the best of their ability during the perturbations and not to use either of the targets or the barrier as support.

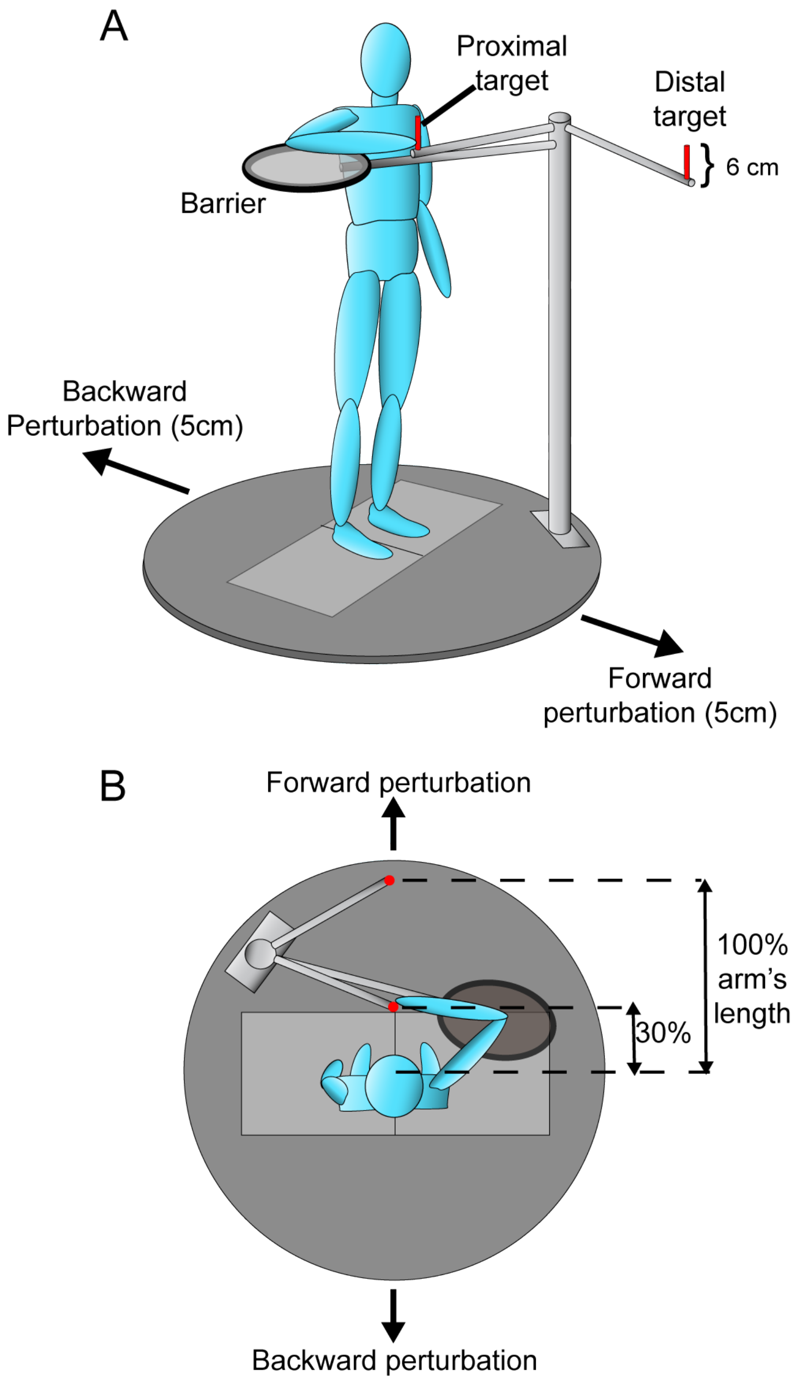

Figure 5-1 Experimental setup of the repetitive reaching task depicted from the front-right (A) and top (B) views. Subject pointed back and forth with their dominant arm at a rate of 1 Hz (guided by a metronome) between two targets, placed at shoulder height and affixed to the platform. Subjects were required to keep their arm above and not touching a mesh barrier. The platform delivered anterior and posterior translations during the forward reaching phase of the task, although catch perturbations during the backward reach were also administered. The targets could not be used for support.

5.4.2.4 Catch perturbations to minimize predictability

To minimize the effect of subject's ability to predict the occurrence of platform perturbations, "catch" perturbations were delivered during the first 30 seconds of each one-minute RRT block while data was not being collected (Figure 5-2). These were of the same magnitude as those administered during the final 15 seconds (recording period). Determination of which direction of perturbation would be presented first during the catch perturbation phase was randomized between three conditions: 1) initial anterior translation followed by posterior; 2) posterior translation followed by anterior; and 3) no perturbation. Time between the first and the second of the catch perturbations was determined in the same manner as for the perturbations which occurred during the data collection phase. To further minimize the ability of subjects to predict the occurrence of perturbations, catch perturbations were sometimes triggered by the distal target touch such that the subject experienced the perturbation as they were reaching from the distal target to the proximal target.

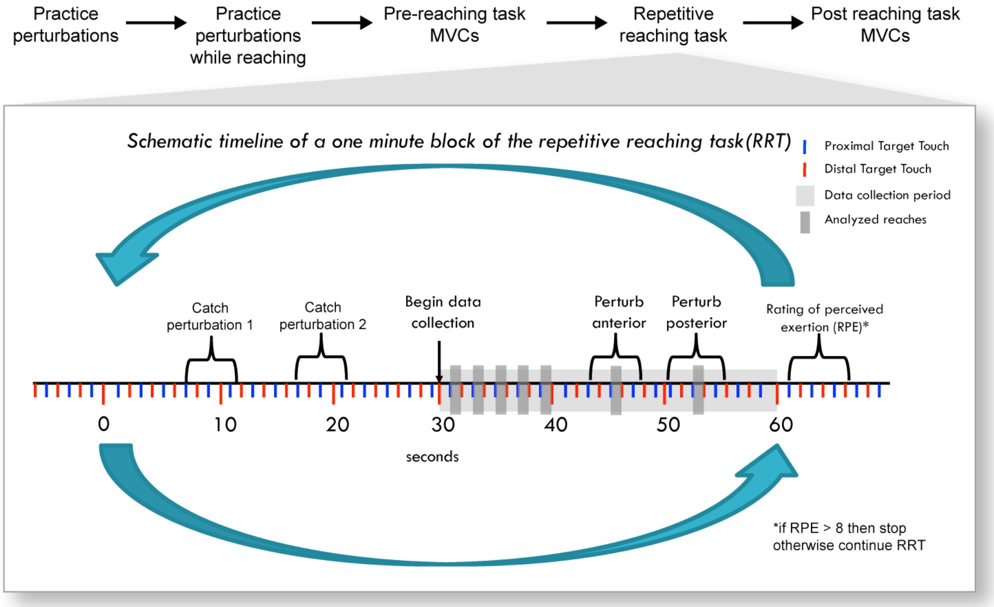

Figure 5-2 **Schematic of the steps in the experimental protocol and a sample one-minute cycle during the repetitive reaching task. Subjects performed continuous cycles until they reported a rating of perceived exertion of 8 out of 10 for the upper limb/shoulder region according to the Borg CR-10 scale (Borg, 1982). Subjects were unaware of this stoppage criteria. When experimental perturbations were administered, the onset was 400 ms after the proximal target touch.**

5.4.2.5 Stoppage criteria and fatigued MVCs

To assess perceived exertion, we showed a print-out of the Borg CR-10 scale (8.5 x 11-inch schematic) to subjects and asked them to tell us which number corresponded to their current perception of task difficulty for the shoulder/upper limb region while continuing the task. The RRT was performed until either the 1 Hz movement frequency could no longer be maintained, or subjects reached a perceived level of exertion of 8/10 for the shoulder region on the Borg CR-10 scale (Hasson et al. 1989; Hammarskjold and Harms-Ringdahl 1992; Côté et al. 2002; Côté et al. 2005; Fuller et al.

2009). Subjects were not aware of these stoppage criteria. Following termination of the RRT, subjects immediately performed shoulder elevation MVC trials.

5.4.3 Data Acquisition

5.4.3.1 Electromyography

Surface electromyography (EMG) was acquired using a TeleMyo EMG measurement system (Noraxon USA Inc.) with an operating bandwidth of 10–350 Hz, an effective common mode rejection ratio of 130 dB DC, greater than 100 dB at 60 Hz, a minimum of 85 dB throughout the operating bandwidth, and a fixed overall per-channel gain of 2000. EMG data were acquired from the descending trapezius. The descending trapezius was chosen based on prior evidence that it shows signs of fatigue during at or above shoulder height task (Christensen 1986; Gerdle et al. 1988a; Nussbaum 2001). Recordings were acquired using pre-gelled, disposable silver/silver chloride electrodes (Ambu©, Denmark), with a 10-mm diameter circular conductive area, in a bipolar configuration. The electrode pair was placed approximately 25 mm medial to the midpoint between the C7 vertebra and angle of acromion (Basmajian and Blumenstein 1980). Electrodes were positioned with a centre-to-centre distance of 3 cm, parallel to the muscle fibers, and following careful preparation of the skin overlaying the muscle sites of interest (cleaned, shaved and lightly abraded). At acquisition, all EMG signals were filtered using a dual-pass, fourth-order Butterworth filter, with a band-pass of 20-500 Hz. EMGs were then digitally converted using a 16 bit A/D board over a ±10 V range, sampled at 1080 Hz, and stored for further analysis.

5.4.3.2 *Kinematics*

Three-dimensional whole body posture and movement characteristics were recorded (sampling frequency = 120 Hz) using a high-resolution six-camera Vicon MX3 motion capture system (Vicon Peak, Oxford Metrics ltd., Oxford, UK). A modified version of the Vicon Plug-in-Gait model along with standard anthropometric measures and data (Winter 1990; de Leva 1996) was applied to analyze the kinematic data using Vicon Bodybuilder to estimate the CoM of each segment defined by reflective markers placed on the body. The model used reflective markers placed over palpable bony landmarks, dividing the body into 15 segments: head (head to C7; 5 markers), bilateral upper arms (shoulder to elbow; 3 markers per upper arm), bilateral forearms (elbow to wrist; 4 markers per arm), bilateral hands (distal to wrist; 3 markers per hand), trunk (C7-T10; 5 markers), pelvis (5 markers), bilateral thighs (hip to knee; 3 markers per thigh), bilateral legs (knee to ankle; 3 markers) and bilateral feet (3 markers per foot). Whole-body CoM was estimated as a weighted sum of the individual segment CoMs. The kinematic variables of interest were the CoM in the mediolateral (ML) and anterior-posterior (AP) directions and the AP endpoint (EP, the marker on the dominant hand index finger tip). Elbow flexion/extension angle, shoulder horizontal abduction/adduction angle, shoulder abduction/adduction angle, trunk flexion/extension angle, trunk rotation angle and trunk side flexion angle were also measured by quantifying the relative orientations of the corresponding reconstructed segments in global space using Euler xyz rotations (Fuller et al. 2009). These kinematic variables were then low-pass filtered at 7 Hz using a dual-pass, 4th order digital Butterworth filter. Digital filtering was performed in Matlab (MathWorks, Massachusetts, USA).

5.4.4 Data Analysis

5.4.4.1 Experimental conditions

There were two main independent factors in this study: FATIGUE and PERTURBATION. FATIGUE contained two levels: No-Fatigue (NF) and Fatigue-Terminal (FT). NF consisted of data collected in the first minute of the RRT as well as pre-RRT MVCs whereas FT consisted of data collected in the final minute before the RRT was terminated as well as post-RRT MVCs. There were three levels of PERTURBATION: No-Perturbation (NP), Anterior- or Forward-Perturbation (FP) and Posterior- or Backward-Perturbation (BP). A third factor, TIME, corresponded to different points in time within a single reach and was utilized in some analyses to explore whether CoM was corrected by the end of the reach in which the perturbation occurred. Up to three levels of TIME were explored where appropriate: time of perturbation movement onset (ON), time of perturbation movement offset (OFF) and time of distal target touch or the end of the reach (END).

5.4.4.2 Kinematics

The beginning and end of each reach was determined as the onset of activation of each of the two targets. Data from forward movement (proximal to distal target) and backward movement (distal to proximal target) phases of the RRT were separated. To reduce data and to simplify data analysis, further analyses for this paper were done only on the forward reaches of recorded blocks of data (Figure 5-2). In each block, the first five forward reaches were analyzed to represent non-perturbed reaches, as was each block's forward reach that included FP and BP conditions. Reaches were then time normalized to 100% of reach time. Unless otherwise specified, all kinematic analysis was focused on the AP direction as this was the main direction of movement.

5.4.4.3 *CoM-EP relationship*

To assess the relation between the CoM and EP displacements in the AP direction, the time series of these two parameters were correlated with each other from the onset of perturbation until distal target touch with the outcome measure being the Pearson product-moment correlation coefficient. A correlation coefficient between the CoM and EP was computed for each subject and each condition. To test whether the relationship between CoM and EP changed across conditions, a FATIGUE x PERTURBATION repeated measures ANOVA was used to examine within-subject differences of the dependent variable (correlation coefficient between CoM and EP). The independent factor of FATIGUE contained two levels (NF and FT) while PERTURBATION factor contained three levels (NP, FP and BP). Alpha for the ANOVA was set to 0.05. If significant, post hoc paired t-test comparisons, corrected for multiple comparisons using the Bonferroni method, were used to examine differences between conditions.

5.4.4.4 *Explanatory variables*

If the previously described ANOVA comparing the effects of PERTURBATION and FATIGUE on the CoM-EP relationship showed a significant interaction or main effect, further explanatory variables were tested to characterize the effects of the conditions on the individual CoM and EP trajectories. The first set of explanatory variables aimed to generally describe the effects of each perturbation on the spatiotemporal aspect of the individual CoM and and EP trajectories. To accomplish this, the NP CoM trajectory was correlated to the FP CoM trajectory from the time of perturbation onset to distal target touch using Pearson product-moment correlations for each fatigue condition. The NP and BP CoM trajectories were also correlated to each other in the same manner. The same analysis was then repeated for the EP parameter. The outcome measure of these correlations was the correlation coefficient which provided a measure of how far the perturbed trajectories of the CoM and EP deviated from the predicted (non-perturbed trajectory).

The second set of explanatory variables focused on the effect of the perturbation on the CoM and EP position. To do so, the effect that the different experimental conditions (FATIGUE, PERTURBATION) had on CoM position at different times (perturbation offset and distal target touch) was analyzed. A FATIGUE x PERTURBATION x TIME repeated measures ANOVA was used to examine within-subject differences on displacement of CoM during the different conditions. Alpha for the tests was set to 0.05. When significant, post hoc paired t-test comparisons corrected for multiple comparisons using the Bonferroni method were used to examine differences between conditions. Displacement of the CoM from baseline position (non-perturbed/non-fatigued) is presented. Positive values of the calculated CoM displacement between conditions indicated that the CoM position was more anterior as compared to the non-perturbed/non-fatigued value. The vertical significance bars in Figure 5-3 illustrate examples of the comparisons made. Endpoint displacements during the different conditions were analyzed in the same manner as the CoM using another ANOVA; however, for the EP displacement analysis, TIME was omitted as an independent factor since endpoint position at the time of distal target touch had extremely small variation due to the experimental design (i.e. the endpoint always ended at the same place: the distal target). As such, the ANOVA for EP examined displacement only at time of perturbation offset (OFF) for conditions of FATIGUE and PERTURBATION.

Finally, to examine the emergent joint kinematic compensations to the PERTURBATION and FATIGUE conditions, within-subject differences in joint angle positions (dependent variables) were analyzed using a FATIGUE x PERTURBATION x TIME repeated measures MANOVA. Dependent variables included were selected based on previous work (Fuller et al. 2009) and included: elbow flexion/extension angle, shoulder horizontal abduction/adduction angle and shoulder abduction/adduction angle, trunk flexion/extension angle, axial trunk rotation angle and trunk side flexion angle. Alpha for multivariate test was set to 0.05. When the MANOVA was significant, appropriate univariate and post hoc paired t-test comparisons corrected for multiple comparisons using the Bonferroni method were used to examine differences between conditions.

5.4.4.5 *Centre of mass position within the base of support*

The effect of fatigue and the perturbations on postural control was measured by analyzing the CoM position in the transverse plane within the estimated base of support (BoS) in a manner similar to the model described by Maki (1997). BoS was estimated to be a rectangle with a width spanning from the right to left ankle marker and a height spanning from the average of the two heel markers to the average of the two toe markers. CoM position within the BoS was normalized for each subject in both the ML and AP direction. To accomplish this, the ML position of the left ankle marker was set as 100% BoS_{left}, the ML position of the right ankle marker as 100% BoS_{right} and the position directly in between the two ankle markers as 0% BoS in the ML direction (see Figure 5-5 for clarification). For the AP direction, the average AP position of the right and left heel markers was set as 100% $BoS_{posterior}$, the average AP position of the right and left toe markers was set as 100% $BoS_{anterior}$ and the average AP position of the right and left ankle markers was set as 0% BoS for the AP direction. In this manner, anytime the CoM was at a position greater than 100% BoS in either the ML or AP direction it would be determined to be outside of the BoS. Similarly, a CoM position at 0% BoS for both the ML and AP directions is known to be in the middle of a line connecting the right and left ankle markers and well within the BoS. Within-subject differences on the normalized AP and ML CoM positions (dependent variables) were analyzed using a FATIGUE x PERTURBATION x TIME repeated measures MANOVA. Alpha for multivariate test was set to 0.05. When the MANOVA was significant, appropriate univariate and post hoc paired t-test comparisons corrected for multiple comparisons using the Bonferroni method were used to examine differences between conditions.

5.4.4.6 MVC and EMG

To document the effects of fatigue on the shoulder, the highest of the two force outputs for the shoulder elevation MVC test for each FATIGUE condition (NF and FT) was kept for statistical analyses. Root-mean-squared (RMS) amplitude for the electromyographic data of the descending trapezius was calculated over the entire duration of each of the five forward reaches representing each minute the RRT was performed for each subject. The EMG RMS values for the five reaches of analyzed in each minute were then averaged for each subject. Statistical comparisons were assessed for each of the MVCs, and trapezius EMG RMS with paired t-tests, with a p-value < 0.05 accepted as significant.

5.5 Results

5.5.1 Performance of the repetitive reaching task and evidence of fatigue

Subjects performed the RRT for an average time of 8.2 ± 4.1 minutes. Significant indicators of fatigue were a decrease in shoulder elevation MVC by 4.9 ± 8.0% ($p<0.05$) and an increase in trapezius RMS by 46.5 ± 49.0% ($p<0.005$) during FT. As intended, subjects had no trouble touching either of the targets throughout the experiment. This was confirmed through the recorded touch target signals which showed that subjects never missed an intended target touch during any of the experimental conditions.

5.5.2 CoM-EP relationship

Results from the ANOVA showed that the correlation coefficient between CoM and EP was significantly affected by PERTURBATION ($F(2,24)=321.86$, $p<0.001$) but not by FATIGUE nor FATIGUE x PERTURBATION interaction. Post hoc analysis revealed that during both the No-Perturbation and Backward-Perturbation conditions, the CoM and EP showed a strong, positive correlation to each other (across-subject means were NP: $r = 0.98 \pm 0.02$ and BP: $r = 0.92 \pm 0.13$, respectively, see Figure 5-3). In contrast, during FP, the CoM and EP showed a moderate negative correlation to each other (mean $r = -0.51 \pm 0.33$) which was significantly different from strong positive correlation for the NP condition (mean $r = 0.98 \pm 0.02$, $p<0.001$).

5.5.3 Explanatory variables

Since the CoM-EP relationship was significantly affected by the task, we explored the individual trajectories (CoM and EP, respectively) to examine if both CoM and EP deviated during the perturbation or if change in just one of these trajectories was responsible for alteration of the CoM-EP relationship.

5.5.3.1 CoM

During the forward perturbation, the time series of the CoM trajectory was negatively correlated to NP CoM position (across-subject mean was $r = -0.45 \pm 0.37$, see Figures 5-3E and 5-3G: correlation was between black and coloured lines). During the backward perturbation, CoM position was positively correlated to non-perturbed CoM position (mean $r = 0.84 \pm 0.21$, Figures 5-3F and 5-3H; correlation between black and coloured lines). The ANOVA examining CoM displacement showed a PERTURBATION x TIME interaction (F(2,24) = 807.322, p=0.002). Post hoc analysis revealed that at the time of the perturbation offset (OFF), FP CoM AP position was 39.6 ± 3.2mm more posterior to the NP CoM position (p<0.001, Figure 5-3 E, 5-3H). The BP CoM position was 29.9 ± 9.8 mm more anterior to the NP CoM position (p<0.001, Figure 5-3F, 5-3G). CoM position at the time of distal target touch (END) did not return to the NP value in either the forward (27.5 ± 10.3 mm more posterior to NP, p<0.001, Figure 5-3E, 5-3H) or backward perturbation conditions (27.2 ± 7.5 mm more anterior to the NP, p<0.001, Figure 5-3F, 5-3G). However, during the forward perturbation condition, CoM position at the time of distal target touch was significantly more anterior in comparison to the CoM position at the time of perturbation offset for the same condition, indicating that a significant correction of CoM position towards the non-perturbed value had occurred during forward perturbation (p<0.001, Figure 5-3E, 5-3H). In contrast, during the backward perturbation, there was no difference between CoM position at time OFF and END meaning the CoM position at time END was not corrected towards the NP value (Figure 5-3F, 3G) but remained at the same position following the perturbation.

5.5.3.2 *Endpoint*

During both the forward and backward perturbations, endpoint trajectory was strongly correlated to that of the no-perturbation condition (across-subject means of the correlation coefficients were FP: $r = 0.98 \pm 0.01$ and BP: $r = 0.99 \pm 0.01$, Figures 5-3 A-D, black vs. coloured lines). The ANOVA analyzing EP displacement showed that endpoint position during both the FP and BP conditions did not significantly differ from the NP condition at the time of perturbation offset (across-subject mean displacements from the

NP condition were FP: 26.5 ± 36.8 mm more posterior (not significant) and BP: 13.5 ± 34.5 mm more anterior (not significant), see Figure 5-3 A-D).

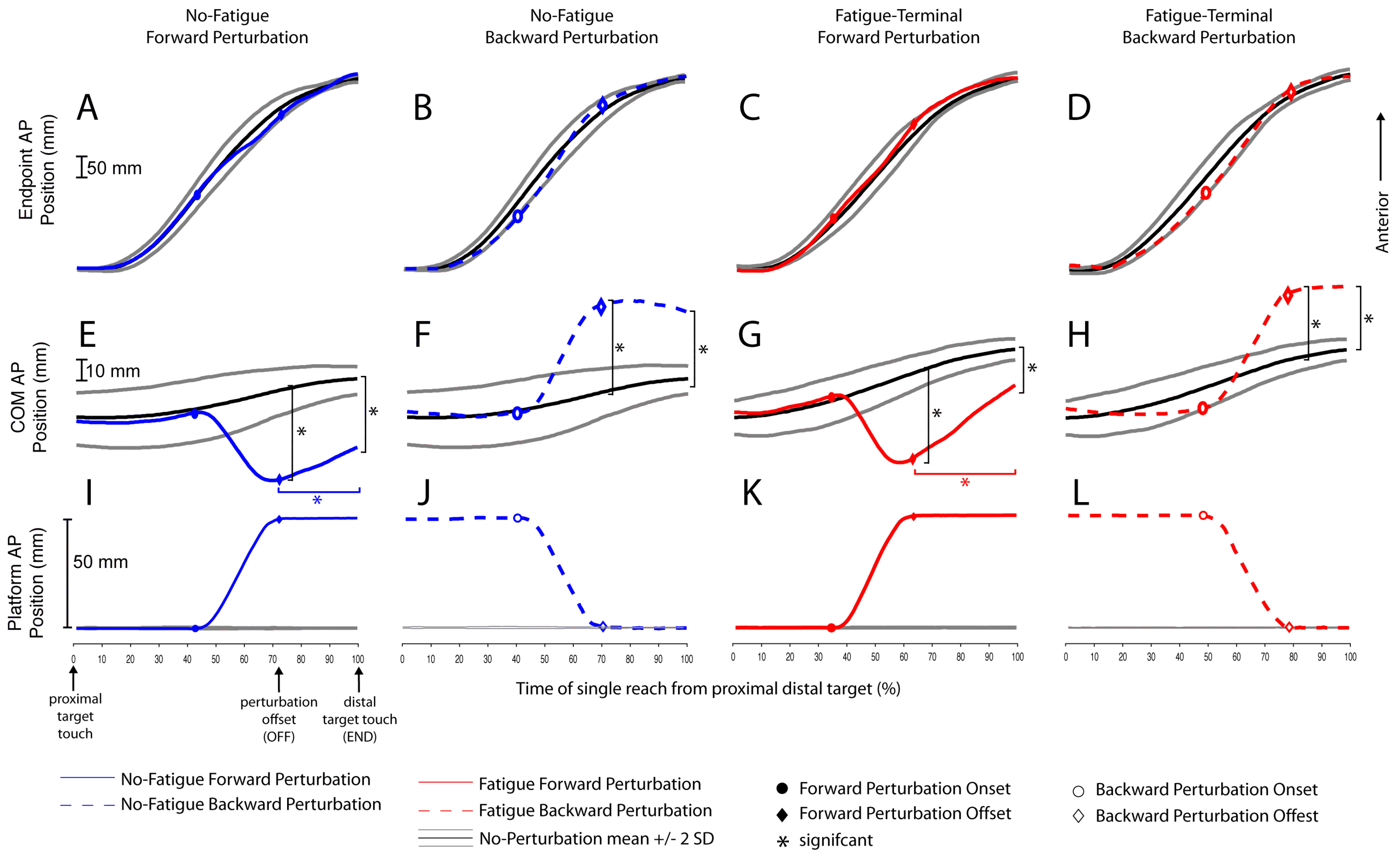
No-Fatigue
Forward Perturbation
No-Fatigue
Backward Perturbation
Fatigue-Terminal
Forward Perturbation
Fatigue-Terminal
Backward Perturbation
A
B
C
D
Endpoint AP
Position (mm)
50 mm
Anterior
E
F
G
H
COM AP
Position (mm)
10 mm
*
I
J
K
L
Platform AP
Position (mm)
50 mm
0
10
20
30
40
50
60
70
80
90
100
proximal
target
touch
perturbation
offset
(OFF)
distal
target touch
(END)
Time of single reach from proximal distal target (%)
No-Fatigue Forward Perturbation
No-Fatigue Backward Perturbation
Fatigue Forward Perturbation
Fatigue Backward Perturbation
No-Perturbation mean +/- 2 SD
Forward Perturbation Onset
Forward Perturbation Offset
signifcant
Backward Perturbation Onset
Backward Perturbation Offest

Figure 5-3 **Endpoint (A-D), centre of mass (CoM) (E-H) and platform anteroposterior trajectories for a representative subject for each experimental condition. All EP and CoM positions are relative to the local platform coordinate system. EP and CoM showed a strong, positive correlation to each other in non-perturbed, non-fatigued trials (correlation of black lines in panes A, D with black lines in panes E, H, respectively) but showed a moderate, negative correlation during the forward perturbation trials (correlation of black lines in panes A, C with black lines in panes E, G, respectively). During the perturbation trials, CoM was displaced posterior during the anterior perturbation direction and anterior during the posterior perturbation; despite this EP was unaffected from the non-perturbed trials. Fatigue had no effect on either CoM, EP or the CoM-EP relationship.**

5.5.3.3 Joint kinematics

As indicated by the MANOVA, joint kinematics were altered under the various experimental conditions showing a PERTURBATION x TIME interaction (Roy's Largest Root = 5.037, F(6,46) = 38.618, p=0.012) as well as a FATIGUE main effect (Roy's Largest Root = 4.697, F(6,7) = 5.480, p=0.021). Univariate analysis showed the PERTURBATION x TIME interaction to be significant for elbow flexion/extension (F(4,48) = 22.860, p<0.001), shoulder horizontal adduction/abduction (F(1.9, 23.5) = 8.853, p=0.001), trunk flexion/extension (F(4,48) = 33.747, p<0.001) and trunk rotation (F(4,48) = 27.792, p<0.001). Post hoc comparisons showed that the adaptations to the forward perturbation spanned across several joints. More specifically, the elbow was more extended during FP as compared to NP at both time OFF (p=0.02) and END (p<0.001; Figure 5-4A). The shoulder was more horizontally adducted during FP as compared to NP at both time OFF (p<0.001) and END (p<0.001; Figure 5-4B). The trunk was more flexed during FP as compared to NP at both time OFF (p<0.001) and END (p<0.001; Figure 5-4C). Finally, the trunk rotated more in the counter-clockwise direction (i.e. right shoulder forward, left shoulder backward) during FP as compared to NP at both time OFF (p=0.02) and END (p<0.001; Figure 5-4D). All joint angle displacements were of greater magnitude at the time of distal target touch as compared to the time of perturbation offset, except for trunk flexion, which showed no time difference (Figure 5-4).

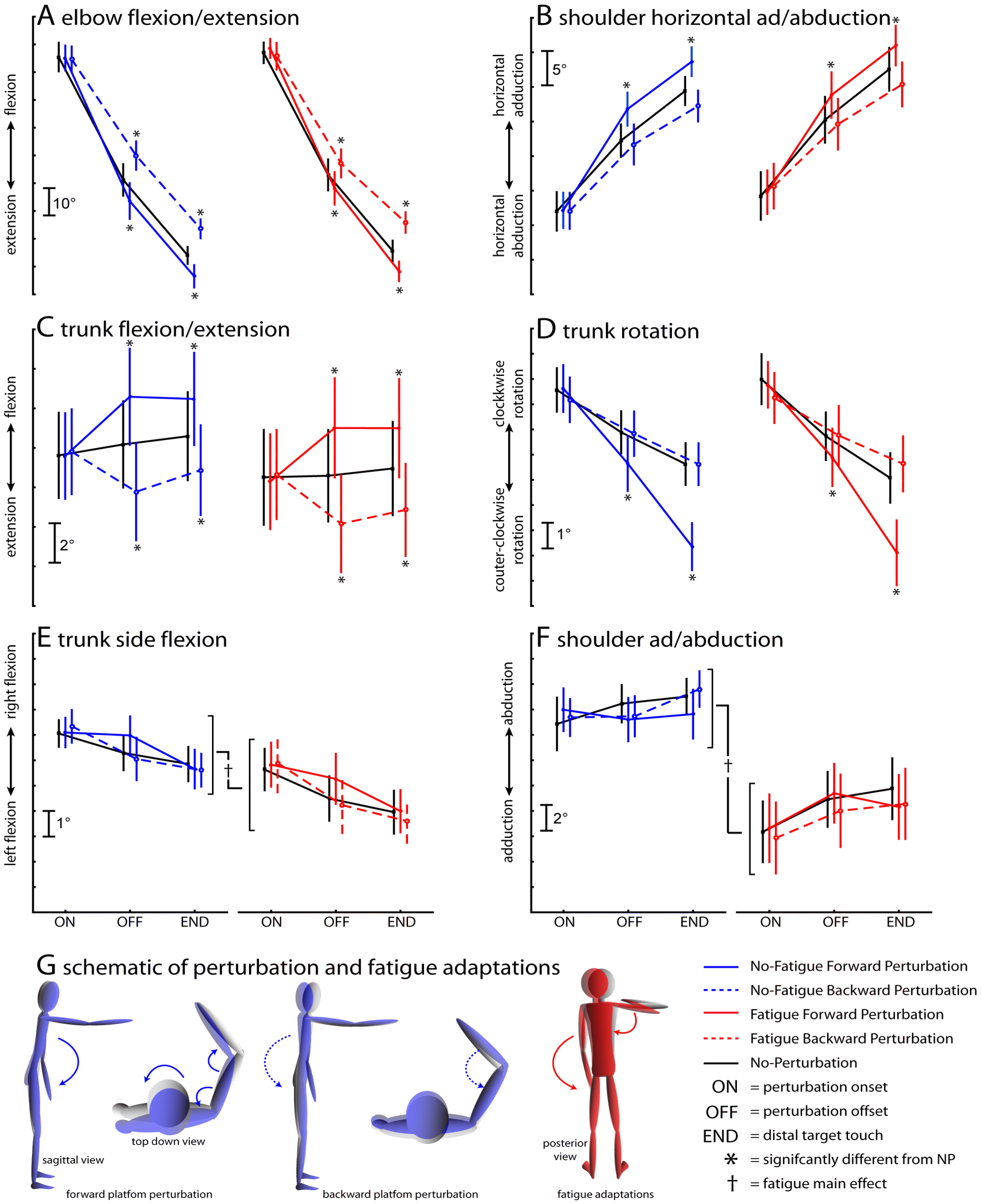

Figure 5-4 Joint kinematics, group means ± 1 SD. Pane G shows a schematic representation summarizing the significant joint kinematic adaptations to the different experimental conditions. The grey stickman denotes no-perturbation/no-fatigue condition, blue stickman denotes perturbation conditions and the red stickman denotes the fatigue condition.

The adaptation to the backward perturbation involved primarily greater elbow flexion and greater trunk extension. Post hoc analysis showed the elbow to be more flexed following BP as compared to NP at both time OFF ($p=0.01$) and END ($p<0.001$; Figure 5-4A). The elbow continued to become more flexed from time OFF to END (Figure 5-4A). The trunk was more extended following BP as compared to NP at both time OFF ($p<0.001$) and END ($p<0.001$; Figure 5-4C).

While the presence of fatigue had no observable effect on the kinematic response to either of the perturbations (i.e. no FATIGUE x PERTURBATION effect), it did affect joint kinematics generally (main FATIGUE effect). In the presence of fatigue, the trunk was flexed more towards the non-reaching side ($F(1,12) = 13.233$, $p=0.003$, Figure 5-4E, 5-4G). Also, the shoulder on the reaching side became more adducted with fatigue ($F(1,12) = 22.879$, $p<0.001$, Figure 5-4F, 5-4G).

5.5.3.4 *Centre of mass position within the base of support*

CoM was always located anterior to the ankle joint centers and had a tendency to be located leftward of the mid-point between the ankle joint centers in the ML direction during all conditions (Figure 5-5). MANOVA revealed a PERTURBATION x TIME interaction (Roy's Largest Root = 0.638, $F(2,24)=7.650$, $p=0.003$) on CoM position within the BoS. Post hoc analysis showed that during the backward perturbation, the AP mean position of the CoM at time of distal target touch was located at 44.3 ± 12.2% $BoS_{anterior}$ which was 13.3 ± 3.8% closer to the edge of the BoS than during the non-perturbed condition at the same time ($p<0.001$, see Figure 5-5B). CoM AP position during the backward perturbation at the time of distal target touch was not significantly greater than the position during the same condition at time of perturbation offset (END: 44.3 ± 12.2% vs. OFF: 42.4 ± 10.5%).

During the forward perturbation, CoM AP position at time OFF was located at 8.2 ± 10.4% $\text{BoS}_{\text{anterior}}$ which was 19.5 ± 2.3% more posterior compared to NP (p<0.0001, see Figure 5-5A) and 9.1% ± 4.5% more posterior to CoM position at time END during FP (p<0.001, Figure 5-5B). At no point in time did the CoM approach the limits of the BoS (100% BoS), in fact, CoM position never increased beyond 50% of the BoS length in any direction.

The MANOVA also showed a FATIGUE main effect (Roy's Largest Root – 1.531, F(2,11)=8.422, p=0.006). Further univariate analysis showed that that the main effect of FATIGUE was for the CoM ML position only (F(1,11) = 1375.082, p=0.001) and that fatigue had no effect on the AP position. Post hoc tests showed that during FT, the CoM ML position was located significantly more leftward (towards the non-reaching limb) as compared to no-fatigue (11.0 ± 10.6% BoS_{left} vs. 5.1 ± 10.3% BoS_{left}, for FT vs. NF, respectively, F=16.939, p=0.001, Figures 5A and 5B). There were no effects of PERTURBATION or TIME on CoM ML position.

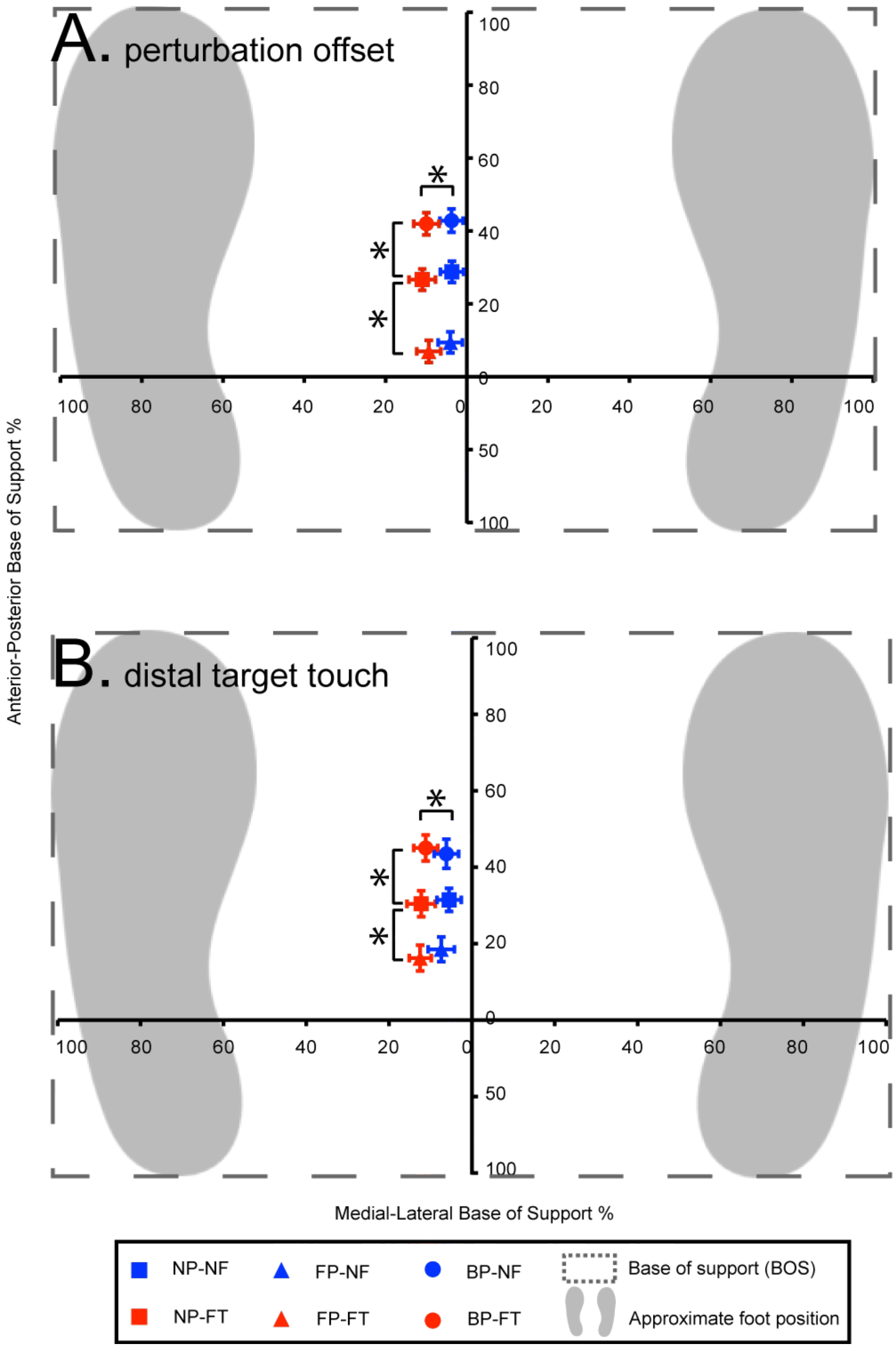

Figure 5-5 Centre of mass position (average and standard error) within the estimated base of support during all experimental conditions at the time of perturbation offset (A) and distal target touch (B). CoM position was always displaced leftward (all subjects reached with the right arm) when fatigued. As similarly shown in Figure 5-3, during the forward perturbation at the time of perturbation offset, the CoM was displaced posterior and during the backward perturbation the CoM was displaced anterior. At the time of distal target touch, the CoM remains significantly displaced from no-perturbation position. In all conditions and directions, the CoM remained far from the limits of the base of support.

5.6 Discussion

The goal of this study was to examine the effects of fatigue and postural perturbation on the control and coordination between posture and focal task movements as well as overall postural control. We show for the first time that a forward perturbation decouples the typically close relationship between the CoM and EP during reaching. During the forward perturbation, the CoM was displaced in the opposite direction of the reaching movement yet the EP trajectory remained unaffected from the unperturbed condition (Figures 5-3A and 5-3E). We found no FATIGUE main effects or FATIGUE x PERTURBATION interactions on the relationship between CoM and EP during non-perturbed reaching. Upper limb fatigue did not affect any of the perturbation responses (Figure 5-3, red lines).

5.6.1 Unique aspects of the methodology

At this point, it is important to specifically highlight several unique elements that distinguish the current work from other similar studies. First, the targets which subjects were reaching to were fixed to the platform and were therefore also perturbed the same distance in global space as the subject. This is an important distinction as this feature allows for the preservation of the distance between the targets and the subject during the postural perturbation, thus preserving the reaching characteristics of the task despite the presence of the perturbations. In this manner, the task in this experiment is somewhat similar to what one would experience when reaching for a handle on a bus when the bus suddenly accelerates (i.e. the standing surface and the handle accelerate equally). Most other postural perturbation studies involved reaching to targets placed off the perturbation platform and therefore the subject was translated either toward or away from the intended target in global space. A second unique feature of our paradigm was to induce fatigue in the upper limb using a repetitive reaching task, instead of using an isometric contraction. Repetitive, motion-induced fatigue has important ecological relevance as the task is similar to those encountered in many everyday manufacturing, construction, sporting and music performance activities. Finally, our study is the first to combine experimental conditions of fatigue and postural perturbations during a task that integrates characteristics of postural stability with the maintenance and performance of a repetitive upper limb task. Aside from the fundamental implications of our work, it also has applied implications that are relevant to occupations that regularly require such behaviour (e.g. manual activities on a train, plane, boat etc).

5.6.2 Non-fatigued repetitive reaching during postural perturbations

When reaching from the proximal to the distal target during the no-perturbation conditions, CoM position moved in the anterior direction toward the distal target (Figure 5-3E, black line). The CoM and EP were highly correlated together (r = 0.97, Figure 5-3A and 5-3E, black lines). This finding corroborates observations of previous studies investigating non-perturbed, non-fatigued reaching which have also showed that CoM movement is not minimized in the sagittal plane during reaching (Pozzo et al. 2002). During the backward perturbation, the CoM-EP relationship was not significantly affected by the perturbation (r = 0.92, Figure 5-3B and 5-3F, blue dashed lines). During the backward perturbation, the CoM is perturbed toward the focal task, which is the direction where the base of support has the greatest area (in front of the ankle joint centers). After the perturbation, the centre of mass is significantly displaced forward, however, despite this shift, the overall relationship between the CoM and endpoint over time is preserved (Figure 5-3). The anterior displacement of the CoM during the backward perturbation may serve an assisting role in EP transport as evidenced by the CoM not returning to its predicted non-perturbed position. Taken together, these findings suggest that a forward postural sway is induced by a backward translation of the support surface, which orients a person towards the targets.

In contrast, an increased postural challenge was induced by a forward translation of the support surface when the body is oriented away from the targets. Indeed, we found that the CoM trajectory is controlled in a much different manner following the forward perturbation as compared to the non-perturbed and backward-perturbation conditions. Specifically, during the forward perturbation the CoM is propelled in the posterior direction (Figure 5-3E), yet EP trajectory remains unaffected resulting in a negative correlation between the CoM and EP. In further contrast to the backward perturbation, following the forward perturbation, CoM is corrected towards the non-perturbed position (Figure 5-3E, 5-3G) suggesting that once the CoM is stabilized post-perturbation, postural control commands are reintegrated with the motor plan for EP movement (Figures 5-3E, 5-3G). However, similarly to the backward perturbation, the final CoM position still remained significantly altered to the non-perturbed value indicating the CNS does not require full correction of the perturbed CoM position to successfully complete the focal task. Taken together, these results show that during the forward perturbation, the CoM and EP are decoupled as the CNS controls for the postural challenge while maintaining EP trajectory. Following decoupling of the CoM and EP, successful performance of the focal task is not dependent on the CoM returning to the non-perturbed position. However, following the perturbation offset the CoM does start to return towards the non-perturbed value by the time of distal target touch (although it is still significantly different) indicating that after stabilizing the CoM following the postural perturbation, later postural adjustments are made to assist endpoint towards the reaching target.

Previous experimental work has observed CoM moving in phase with EP under a wide variety of task constraints when reaching (Stapley et al. 1999; Pozzo et al. 2002; Patron et al. 2005). Furthermore, others have theorized that the pairing of CoM-EP is not mechanically necessary (Stapley et al. 2000). Taken together these results suggest the CNS chooses to actively control the CoM towards the focal task target. Here we provide evidence that decoupling of the posture and movement characteristics have the potential to be decoupled during a forward reaching task if the CNS chooses to do so. Indeed, during the forward perturbation condition, a significant decoupling effect on the CoM-EP relationship is observed (Figure 5-3). It is important to note that the decoupling between CoM-EP had no effect on the successful performance of the focal task as indicated by the endpoint trajectory during the forward perturbation which showed no change in comparison to the non-perturbed EP trajectory (Figure 5-3A). To our knowledge, these observations are the first to show that the CNS does not always control the CoM position in phase with the endpoint when performing an anterior reaching task.

We observed no change in endpoint trajectory during the perturbation (see Figures 3A-D) despite significant changes in CoM trajectory (Figures 5-3 E-H) suggesting that, at least for perturbations similar to the one used in the current work, the CNS can easily coordinate both the focal and postural tasks despite the increased demands for stability to the postural system. The same may not hold true for larger scale perturbations since larger perturbations amplify postural responses (Diener et al. 1988; Park et al. 2004). An amplified response during a larger perturbation may evoke arm movements to assist in balance recovery, as previously shown in balance recovery during quiet stance (McIlroy and Maki 1995; Allum et al. 2002; McIlroy et al. 2004) and gait (Marigold et al. 2003; Misiaszek 2003; Roos et al. 2008; Pijnappels et al. 2010). Presumably, a large perturbation causing associated arm movements may cause a disruption in the reaching task and alter the CoM-EP relationship observed.

5.6.3 Fatigued repetitive reaching during postural perturbations

Subjects performed prolonged repetitive reaching which fatigued the upper limb. All participants were deemed to be fatigued as evidenced by the RPE, EMG and MVC data, which are well-accepted measures of fatigue (Vøllestad 1997; Fuller et al. 2009; Lomond and Côté 2010; Lomond and Côté 2011). During fatigue, no effects were observed on the spatiotemporal CoM-EP relationship or EP position in any of the perturbation conditions (NP, FP, BP) despite previous findings of fatigue related changes to individually analyzed components of posture and movement(Fuller et al. 2009; Fuller et al. 2011; Lomond and Côté 2011).Taken together, these results suggest that the overall control of the CoM-EP relationship is robust, despite the presence of fatigue-related changes in individual movement components. This observation may have important ecological implications, as it would seem that subjects are able to maintain upper limb task performance during suddenly changing environmental conditions even when exhibiting fatigue-related changes.

5.6.4 Control of CoM within the base of support during perturbations

As stated above, both forward and backward perturbations had a significant effect on moving the CoM position in the AP direction at the time of perturbation offset, however, the CoM remained far from the limits of base of support during all perturbation conditions. Furthermore, the perturbation-related changes in CoM position were not affected by fatigue. However, as in our previous work, we observed a leftward shift of the CoM towards the non-reaching side with the development of fatigue (Fuller et al.

2009). The change in ML CoM position within BoS that we observed was small (6% increase towards BoS limit) and the net CoM position remained far from the edge of BoS (Figure 5-5). These results suggest that during postural perturbations, postural stability is not *further* compromised by fatigue in a repetitive upper limb task. Interestingly, several other studies have reported increased postural sway during fatigue when performing a repetitive task (Sparto et al. 1997; Nussbaum 2003; Fuller et al. 2009) as have others examining fatigue during perturbations (Davidson et al. 2009) . Combining our previous finding showing increased postural sway during the same task (Fuller et al. 2009) with the current finding that CoM remains far from the BoS during fatigue and perturbation conditions indicates measures of postural sway may not be an ideal measure of postural stability during similar conditions (Figure 5-5). In other words, significant differences in postural sway measures may not represent a functional compromise to stability. We have shown in the current work that despite fatigue-related changes to posture and movement characteristics, postural stability can be well maintained.

5.6.5 Joint kinematics

As demonstrated in our study, postural adaptations occur during conditions of fatigue and of surface perturbations; yet, achievement of focal task is minimally affected by these altered conditions implying the role of these joint kinematic adaptations in actively preserving the focal task. In other words, (and keeping in mind that the target moved with the platform thus preserving the focal task) following the perturbation, if the CoM is in a different position at the time of distal target touch, altered body kinematics must emerge to satisfy the focal task. Indeed, we observed joint kinematic changes to occur across the trunk and upper limb in all experimental conditions (Figure 5-4). It is also likely that joint kinematic changes occurred at joints which were not examined in the present study. In particular, the ankle, knee and hip joints have previously been shown to be the sites of major compensations to surface perturbations to quiet stance (Nashner 1976; Henry et al. 1998a). Nevertheless, the current work provides insight into how the CNS organizes the mechanics of the upper limb and trunk following a sudden challenge to whole body stability during a standing reaching task.

In particular, following the forward perturbation (i.e. CoM accelerated backwards, Figure 5-3E), compensations at the elbow (increased extension), shoulder (increased horizontal adduction) and trunk (increased flexion and counter-clockwise rotation) combine together to create a strategy consistent with maintaining performance of the focal task (see Figure 5-4G). Examination of these joint kinematic changes at the time of perturbation offset show that much adaptation has occurred even before the platform stops moving (Figure 5-4) and before posterior displacement of the CoM has been stopped (see Figure 5-3E and Figure 5-4). Following stabilization of the CoM around the time of perturbation offset (Figure 5-3E), CoM begins to move back towards the focal target, yet joint kinematic changes continue to occur. Taken together, these results indicate that following a forward surface perturbation the CNS stabilizes the CoM while concurrently making adjustments in the upper limb to maintain the focal task. Once the CoM has been stabilized, postural components are reintegrated back into the strategy to produce the focal movement task, as indicated by forward displacement of the CoM from the time of perturbation offset to distal target touch (Figure 5-3E). Similarly, observations were made by Trivedi et al. (2010) who analyzed electromyographic data of postural muscles during perturbed reaching. These authors noted that the initial postural response is unchanged from that of quiet stance, yet the latent postural response is altered in a manner that suggests the reintegration of postural components into the movement strategy to reach the target. The kinematic findings in the current work support this hypothesis.

In contrast to the kinematic characteristics of the forward perturbation response, those of the backward perturbation response seem relatively simple. The joint compensations to the CoM being thrust forward occur predominantly in the trunk (more extended; see Figure 5-4C) and the elbow (more flexed; see Figure 5-4A). In contrast to the forward perturbation condition, following perturbation offset during the backward perturbation condition, the CoM does not move back towards the non-perturbed value. In this manner, our findings suggest that the control of posture during a backward-perturbed reaching task is similar to control during backward-perturbed quiet stance. Trivedi et al. (2010) came to a similar conclusion when they found that activity in postural muscles did not differ during backward perturbed reaching as compared to backward perturbed quiet stance. Since the base of support is large in the anterior direction and the CoM is perturbed while reaching towards the distal target, the backward perturbation appears to pose a smaller threat to the control of the posture-movement task and this is evident in both the relative simplicity of the adaptations to both postural and movement characteristics following the backward perturbation as compared to the forward perturbation condition.

Altered joint kinematics were also evident during the presence of fatigue in the upper limb/shoulder region. In particular, all subjects leaned toward the non-reaching side (leftward) by flexing the trunk in this direction (Figure 5-4E), an adaptation that contributed to increased leftward shift of the CoM (Figure 5-5). Fatigue compensations were also seen at the shoulder joint, with subjects adducting the shoulder more during fatigue (Figure 5-4F). Together, these adaptations had the net effect of subjects leaning leftward, raising the shoulder joint and thus allowing subject to adduct the shoulder despite the presence of the barrier below the elbow joint (see Figure 5-4G for schematic of net fatigue effect). Presumably, this strategy allowed subjects to reduce strain on the fatiguing musculature of the shoulder, as we had previously shown and discussed (Fuller et al. 2009).

Interestingly, the effects of fatigue had no effect on either the postural or movement compensations occurring during the surface perturbations (Figures 4 and 5). Thus, the kinematic adaptations that emerged during fatigue had minimal effects on the posture-movement task and also minimally affected the ability to respond to the postural perturbations. Indeed, fatigue adaptations during the current task occurred in the mediolateral direction whereas perturbation adaptations occurred predominantly in the anterior-posterior direction (Figure 5-4G), suggesting a strategy of dissociating effective shoulder fatigue response strategies from postural stabilization strategies, which may be linked to the principle of minimal interaction of the RC-hypothesis. Indeed, according to the RC-hypothesis, during altered task conditions (e.g. perturbations, fatigue) new joint kinematics patterns emerge which ensure successful completion of the task. One way the CNS may coordinate these emergent joint kinematic changes despite many redundant options is by specifying a global referent configuration to restore equilibrium following a perturbation to the system (Feldman et al. 2007). In other words, muscle activities are coordinated through interactions between the various neuromuscular elements and environmental constraints (some of which are altered due to the presence of fatigue and surface perturbations) such that a unique action emerges (Feldman et al. 2007). In this manner, the CNS may be able to take advantage of the redundancy of the system to mitigate the effects of perturbations such as fatigue and surface translations so that the main goal of the task (reaching between two targets) is preserved. Moreover, our data support that the ensemble of changes occurring at the level of individual degrees of freedom is selected in accordance with the principle of minimal interaction. Indeed, kinematic changes associated with fatigue were different than the ones associated with the postural response. An explanation of this could be that the system detected the presence of shoulder fatigue and found postural response strategies that allowed for minimal interaction with the less reliable fatigued structures. Nevertheless, the system was able to preserve the main task objective despite both fatigue and perturbation, offering more support of the presence of an overarching global factor, such as the referent configuration, in guiding solutions to the performance of such a complex task.

5.7 Acknowledgments

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Chapter 6: Summary & Conclusions

The goal of this work was to investigate the role of fatigue in the control of posture and movement during repetitive work performed with the upper limb. Despite the prevalence of repetitive tasks during everyday activities, research to date has predominantly focused on one of two areas: 1) the effect of fatigue, developed during isometric contractions, on static postural control, or 2) the effect of repetitive motion induced fatigue on segment coordination local to the area of fatigue. This collection of work is the first to provide insight into how fatigue affects the relationship between inter-segmental coordination and postural control.

Previous work from our laboratory showed that during the performance of repetitive hammering and sawing tasks to fatigue, multijoint and multi-muscle adaptations emerge across the body to maintain task performance (Côté et al. 2002b; Côté et al. 2005b). However, altered movement strategies spanning across multiple body segments, not just the area in the upper limb local to fatigue, suggested postural adaptations also occurred in conjunction with movement adaptations. The present work sought to understand the nature of both posture and movement adaptations during the presence of upper limb fatigue and how they may be coordinated both spatially and temporally.

6.1 Chapter 3

In chapter 3, it is first shown that repetitive reaching at shoulder height resulted in upper limb fatigue as evidenced through changes in force output, EMG and kinematic measures taken from the shoulder region. It is then shown, for the first time in the literature, that global kinematic adaptations to upper limb fatigue occur in all directions, not only in the primary direction of the arm task, supporting the importance of conducting a three-dimensional kinematic analysis when studying fatiguing, multijoint tasks. In fact, the major changes to arm movement and postural adaptations to fatigue were observed in the *mediolateral* direction and not the anterior-posterior direction where most of the task amplitude was contained. It is likely that the majority of the changes occurring in the mediolateral direction were consequent to some inherent characteristics of the task itself (e.g. elbow height requirement), highlighting the ability of the motor system to adapt in a task-specific way when dealing with fatigue. Indeed, both global postural and arm movement adaptations (leaning leftward; raising the right shoulder; adducting the arm more towards the body) appear to be strategies aimed at reducing the load on the shoulder elevator region, where the most profound effects of muscular fatigue were observed. However, such an adaptation strategy may come at the consequence of increasing asymmetrical loading on the body since the centre of mass is moved more leftward during fatigued reaching. Ergonomists should take this finding into consideration when analyzing and designing unilateral repetitive upper limb tasks as increased asymmetry of ground reaction forces on the body may in turn lead to increased risk exposure to back and lower limb injuries.

6.2 Chapter 4

While chapter 3 concludes that fatigue adaptations appear to be task specific and occur to both postural and movement components three-dimensionally, the question still remained as to whether these adaptations occur only in the later stages of fatigue as a last resort (i.e. the final minute of the task as exhaustion is neared), or if fatigue adaptations begin to occur soon after the onset of the repetitive movement task. Answering this question was one of the three main goals of chapter 4. The two other objectives of chapter 4 were also of temporal nature. More specifically, this chapter investigated inter-reach (or reach-to-reach) variability of kinematic parameters as well as intra-reach coordination adaptations associated the presence of fatigue. All together, the objective of this chapter was to provide insight into the fatigue adaptations that occur in the temporal domain – an often overlooked area within fatigue research.

The results of chapter 4 show that although fatigue did not adversely affect the success of the reaching task (i.e. subjects were still able to reach back and forth between the two targets even when fatigued), localized upper limb fatigue does alter both movement and posture control over the three temporal domains investigated (the complete task, reach-to-reach, and within-reach). This study is the first to show that task specific changes in spatial parameters begin to develop well before exhaustion is reached. We also confirm that reach-to-reach variability increases across several postural and upper limb spatial parameters indicating movement patterns during fatigue fluctuate more as compared to the non-fatigued state. This may be a possible strategy to reduce exposure in fatigued areas and to adopt a new movement strategy or pattern, despite reduced capacity of some muscles which is in accordance with what others have previously suggested in similar research investigating the effects of pain (Madeleine et al. 2008a). Moreover, we are the first to show that variability occurs across multiple planes of motion available for the task. At the within-reach level, increased coupling between distal arm segments combined with increased variability of shoulder joint timing suggest that increased rigidity of distal segments may be a simplified *en bloc* movement strategy to reduce error associated with fatigue of the more proximal shoulder joint. Taken together, these results also reveal that analysis of spatial adaptations alone may not be sufficient for analyzing the effect of fatigue on the control of posture and movement. Indeed, the temporal domain offers additional degrees-of-freedom that the CNS may take advantage of when adapting to the internal perturbation induced onto the system by fatigue.

6.3 Chapter 5

Chapter 5 more closely examines the motor control aspects of the coordination of posture and movement components together. It has often been explained in the literature that when reaching to a target the CNS must concomitantly satisfy two independent subtasks: 1) successfully reaching the hand to an object or target and 2) successfully maintaining postural stability. Prior to the current work, it had previously been shown that when reaching to an anterior target, centre of mass displacement is not minimized in the same manner it is during a postural task alone but instead contributes to the displacement of the hand/endpoint (Pozzo et al. 2002). While in chapters 3 and 4 we show that fatigue can lead to both spatial and temporal adaptations to posture and movement components, it remained unknown if fatigue would alter the combined spatiotemporal coordination of the postural and reaching subtasks; as such, this became the focus of chapter 5. Additionally, to further challenge the control of posture and movement, a perturbation platform was used to administer standing surface perturbations to the participant during the performance of the repetitive reaching task. The setup used in this study is novel, in that it also perturbed the targets (which were attached the moving platform) thus preserving the nature of the reaching subtask. In essence, the perturbation experienced was similar to what would be experienced while standing on an idle bus and reaching for a support rail when the bus suddenly accelerated forward. This unique setup allowed any changes in posture-movement control to be attributed solely to the surface perturbation as opposed to studies in which the targets were placed off of the platform thus altering the nature of the reaching task (Trivedi et al. 2010). Chapter 5 is also the first to study how fatigue affects this control, a situation faced regularly by people who work while standing on unstable surfaces (e.g. planes, trains, boats etc.).

The results of the study in chapter 5 show that during non-perturbed, non-fatigued repetitive reaching, the whole-body centre of mass moved in phase with the fingertip endpoint towards the target in the sagittal plane, confirming what has been similarly shown in pervious studies (Pozzo et al. 2002). When an anterior surface translation inducing backward sway, the centre of mass-endpoint relationship becomes decoupled despite continued successful maintenance of both the postural and focal tasks individually. The postural response, in terms of the centre of mass movement to the perturbation is similar to that which has been observed in previous studies, but this study provides evidence that surface perturbations had no effect on the fingertip endpoint trajectory. As such it can be concluded that during small perturbations, the central nervous system can easily control both postural and focal tasks even when upright stability is challenged. During all perturbation conditions, the CoM remains well within the base of support, suggesting that postural stability was not compromised by the perturbation magnitude used in this study. Moreover, upper limb fatigue induced through repetitive reaching had no effect on the coordination of the focal and postural tasks, or on the maintenance of upright stability. The study presented in chapter 5 also presents the first findings on the joint kinematic adaptations that emerge following a surface perturbation while performing a repetitive reaching task. These results suggest that the CNS tasks advantage of the redundancy of the system by adapting to the presence of fatigue and the perturbation of posture in a manner in which adaptations to one minimally affects the other. This conclusion is drawn from the data depicting that joint kinematic changes specific to fatigue occur in the mediolateral direction (i.e. orthogonal to the perturbation and major direction of movement) while adaptations to the perturbation occur predominately to alter endpoint movement in the sagittal plane. Finally, in chapter 5, we draw parallels between our finding of fatigue adaptations developing orthogonal to perturbations adaptations and the predictions of the referent configuration hypothesis of motor control, which is one of the few motor control models that addresses how we can manage the many degrees-of-freedom of the human body in performing complex, multi-muscle movements. The RC-hypothesis proposes that the CNS delivers a global, task-related command to control whole-body position in space. From the global R-configuration command, the individual EMG patterns emerge due to the action of local factors, such as peripheral and inter-muscular reflexes, muscle properties and the presence of external forces, guided by processes that follow a common principle of minimal interaction (Gelfand and Tsetlin 1971; Feldman et al. 2007). Our data support that the ensemble of changes occurring at the level of individual degrees of freedom is selected in accordance with the principle of minimal interaction. Indeed, kinematic changes associated with fatigue were different than the ones associated with the postural response. As such, the system was able to preserve the main task objective despite both the development of fatigue and the occurrence of surface perturbation, offering more support of the presence of an overarching global factor, such as the referent configuration, in guiding solutions to the performance of such a complex task.

6.4 Significance of the work with respect to fundamental research

At the fundamental level, we show that 1) fatigue adaptations to posture and movement components are task-specific and multi-directional, with major adaptations occurring in directions orthogonal to the primary movement direction (chapter 3); 2) the central nervous system also takes advantage of the additional degrees-of-freedom provided by the temporal domain to adapt to fatigue (chapter 4); and 3) even following an anterior-posterior perturbation, the coordination between posture and movement components in the major movement direction (anterior-posterior) are minimally affected by the presence of upper limb fatigue. Instead, fatigue adaptations are predominantly contained in the mediolateral direction and minimally affect the response to the perturbation. In light of this last conclusion, it would be interesting to examine the same experimental task while also introducing perturbations to the mediolateral direction to determine if stability in this direction would be compromised due to fatigue adaptations or if fatigue adaptations would evolve differently knowing postural stability could suddenly be challenged in multiple directions. It would also be interesting to repeat the first two experiments without the presence of the perturbations in the protocol as we acknowledge that the inclusion of the perturbations during studies one and two may have affected the postural control of the subjects. Although studies one and two analyzed only non-perturbed reaches, the subjects' knowledge that a perturbation would be coming at some point may have altered subjects' postural control during the non-perturbed reaches.

6.5 Significance of the work with respect to applied fields

Although more attention was given to the fundamental aspects of this collective work in the dissemination of results, the combined results of this work also provide practical significance that should not be overlooked. First, knowledge that fatigue adaptations to posture and movement occur in multiple directions and in both the spatial and temporal domains should be taken into account when designing future studies examining fatigue and movement. Indeed, most studies to date that have examined fatigue and movement focus only on mean spatial adaptations in the main direction of movement only and may be missing important adaptations occurring in off-planes and in different time domains. Similarly, ergonomists and other professionals that frequently analyze repetitive movement tasks should give more consideration to often ignored three-dimensional and temporal parameters. Secondly, as aforementioned, it is shown that the performance of a unilateral, shoulder height repetitive reaching task when standing can lead to fatigue adaptations which may increase the asymmetrical loading of forces on the lower limbs and trunk. As such, it is important for ergonomists studying similar tasks to not just focus on the risk factors involving the upper limb but also consider subtle adaptations that may occur distal to the site of fatigue and that may increase injury exposure to these areas. Finally, results from chapter 5 present new insights into how the body adapts to dynamic working conditions involving unstable standing surfaces, repetitive movement and fatigue; working conditions which are often encountered by individuals working on unstable surfaces such as boats, planes and trains and for which less fundamental and epidemiological studies exist. Ergonomists and other professionals who analyze tasks commonly associated with these workplaces and that are often associated with complaints of accidents and injuries should take note of the findings presented in the current work; in particular, small, intermittent surface perturbations administered while performing repetitive tasks with the upper limb may not pose a serious threat to the one's stability or task performance. In other words, during work conditions similar to those described in the current study, workers may be able to easily adapt to small surface perturbations and still complete the tasks at hand. However, while these conditions hold consequences that are subtle and may easily be overlooked they are nevertheless systematic and thus could hold serious consequences over prolonged periods in more realistic and dynamic environments. For instance, our findings that kinematic characteristics of the shoulder in directions orthogonal to the endpoint motion, which are only affected by fatigue and not by the perturbations, could imply that the system does not allow the fatigued shoulder to contribute to stabilizing posture when faced with a perturbation. If that were the case, the consequence would be that the body would benefit from fewer degrees of freedom to deal with a postural perturbation when the upper limb is fatigued. In the long run, this may translate into a reduced opportunity to share load between muscles while working in such complex conditions, which we know is associated with the development of musculoskeletal injuries. Future analysis of varied perturbation and fatigue conditions will allow for further recommendations to be made with regard to repetitive work being performed during dynamically changing standing surface environments.

Chapter 7: References

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