

The Pennsylvania State University
The Graduate School
College of Health and Human Development

MULTI-MUSCLE COORDINATION
IN POSTURAL TASKS

A Dissertation in

Kinesiology

by

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Submitted in Partial Fulfillment
of the Requirements
for the Degree of

Doctor of Philosophy

August 2008

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Abstract

In order to stand upright, humans are required to overcome a series of challenges posed by the mechanical design of our body. The vertical orientation of the head-leg-trunk segments, high center of mass, large number of joints, and narrow base of support contribute to making the body mechanically unstable. We study multi-muscle synergies involved in the control of vertical posture. For most of the studies to be presented, we define synergies as task-specific organizations of elemental variables, which stabilize particular performance variables, in a sense of reducing their variability across repetitive trials. We use a computational method of identifying and analyzing muscle synergies, based on the uncontrolled manifold (UCM) hypothesis. UCM analysis is performed in the space of hypothetical elemental variables (M-modes) during repetitive or cyclic whole body tasks. As such, the analysis involves two steps. First, M-modes have to be identified over sets of trials at similar tasks with different parameters. Second, variance in the magnitude of the M-modes has to be analyzed with respect to particular performance variables over repetitive attempts at the same task. More specifically, we studied the multi-muscle coordination during the performance of cyclic whole-body voluntary movements (sway) in the anterior-posterior (AP) direction and production of the moment of force around the vertical axis of the body (MZ). Three studies were performed assuming the existence of at least two levels of control with synergies possible at each level. At the higher level, values or time profiles of specific mechanical variables (COP or MZ trajectory) are stabilized by covariation of magnitudes of M-modes. The hierarchically lower level is the level where M-modes are formed. This lower level ensures proportional involvement of muscles within a group; in other words, it defines the direction of an eigenvector in muscle activation space corresponding to a M-mode. The main findings of the studies are: (1) The UCM method allows to quantify multi-muscle synergies; (2) Postural muscles are united into a small set of M-modes similar across subjects and task parameters for simple sway tasks; (3) The number of significant M-modes and their composition change when the tasks are performed in more challenging condition; (4) Synergies stabilizing performance variables can be built on different sets of M-modes.

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CHAPTER 1

INTRODUCTION

The central issue of this Thesis is the control of upright human posture.

In order to stand upright, humans are required to overcome a series of challenges posed by the mechanical design of our body. For example, stabilization and support of the trunk, upper limbs and the head over the lower limbs is required. Some factors such as the vertical orientation of the head-leg-trunk segments, high center of mass, large number of joints, and narrow base of support contribute to making the body mechanically unstable. Hence, in order to maintain body's mechanical equilibrium while standing up, the postural system must ensure an accurate control of muscles that are activated to support the body against the force of gravity and possible mechanical perturbations applied to the body.

At any level of description of the system for human movement production there are more independent variables describing the state of the system (degrees of freedom, DOF) than the number of independent parameters describing a motor task. This makes the human neuromotor system redundant and, as a result, the controller (central nervous system, CNS) faces the apparent problem of choosing one solution from an infinite set. This problem is often referred to as the motor redundancy problem. It was first formulated by Bernstein (Bernstein 1967) based on his observations of the execution of multi-joint tasks. This problem will be referred to several times in this Thesis.

In studies of quiet standing posture, the human body has often been modeled as an inverted pendulum (Fitzpatrick et al 1992a; Day et al. 1993; Winter et al. 1993; Winter et al. 1998; Morasso and Schieppati 1999). Although such a system with only a single joint is difficult to equilibrate even when no external forces (other than gravity) act on it, in reality, the problem is much more complex. There are not only several joints to be controlled along the vertical axis but also several muscles crossing each of these joints. The stability of such complex systems is also affected by mechanical perturbations such as those experienced when being pushed while standing (external perturbation) or during performing a voluntary movement (internal perturbation). In order to overcome the effects of these perturbations and

stabilize body posture, postural muscles need to be finely controlled and coordinated such that the center of mass (COM) projects within the small base of support.

The main purpose of this Thesis is to study multi-muscle coordination involved in stabilization of the body and head posture.

1.1 Main issues addressed in this Thesis

Any movement performed by a standing person requires simultaneous control of posture. For example, quick motion of the arms results in forces and moments of force at the shoulder joint that could disturb postural equilibrium (Bouisset and Zattara 1983; Bouisset and Zattara 1987; Ramos and Stark 1990). Thus, control of posture and execution of movement are very closely linked and fine coordination between the two is required to effectively perform daily tasks.

Since execution of voluntary movements is so closely linked with the control of posture, it has been suggested that every movement comprises two distinct components. The first component is related to the execution of the desired movement while the second component is related to maintenance of posture (Hess 1943; Belen'kiy et al. 1967, Bernstein 1967). The coordination between the two components has been described using the notion of **postural synergies** (Bernstein 1967). Bernstein considered synergies to be built-in combinations of motor commands to a number of muscles leading to a desired common goal such as keeping the COM projection over the base of support. In his view, the presence of synergies simplifies the control of vertical posture by at least partially solving the problem of motor redundancy.

Bernstein (Bernstein 1967) suggested that the human control of movements is organized hierarchically in at least 4 different levels (A, B, C, and D). Level A was considered to be the level of muscle tone. Level B was considered to be the level of muscular-articular links. Level C was considered to be the level of space and level D was considered to be the level of actions. According to Bernstein, level B is the level of synergies where interactions within the redundant sets of elements involved in the movement are organized. Bernstein emphasized that synergies were probably the way of solving the motor

redundancy problem since they reduced the total number of variables to be manipulated by the CNS.

Relatively recently, the notion of synergies has been defined operationally following traditions set by Gelfand and Tsetlin (Gelfand and Tsetlin 1966), and a computational approach to the identification and analysis of synergies has been suggested, namely, the **uncontrolled manifold (UCM) hypothesis** (Scholz and Schoner 1999; Latash et al 2002b). The UCM hypothesis assumes that the controller (the central nervous system, CNS) acts in the state space of elemental variables and selects in this space a manifold corresponding to a value of a performance variable, which needs to be stabilized. Further, the controller organizes co-variation among the elemental variables that stabilizes (in a sense of decreasing variability across repetitive trials) an important performance variable (for example, endpoint trajectory of a multi-joint limb or the total force produced by the digits of the hand). If several attempts at a motor task are analyzed, variance in the space orthogonal to such a manifold is expected to be reduced as compared to the variance within the manifold.

The UCM approach has been applied to investigate the coordination among the muscle activation patterns prior to and during the execution of a motor task (Krishnamoorthy et al. 2003b, 2004; Wang et al. 2005). Mostly, these studies addressed hypothetical muscle synergies involved in the control of vertical posture, and the results have suggested that the controller unites the muscles into functional groups (**muscle modes or M-modes**) and then co-varies the magnitudes of the M-modes to stabilize such mechanical variables as coordinate of the body's center of pressure (COP, the point of application of the resultant vertical force acting on the body from the support). These investigations pioneered the use of the UCM framework to identify and quantify multi-muscle synergies stabilizing a time profile of a mechanical variable.

In this Thesis, we also define synergies as task-specific organizations of elemental variables, which stabilize particular performance variables, in a sense of reducing their variability across repetitive trials. For most of the studies presented in this dissertation, we use a computational method of identifying and analyzing muscle synergies, based on the UCM hypothesis (Scholz and Schoner 1999; Latash et al 2002b). UCM analysis is performed in the space of hypothetical elemental variables (M-modes) during repetitive or cyclic whole-body tasks. As such, the analysis involves two steps. First, M-modes have to be identified

over sets of trials at similar tasks with different parameters. Second, variance in the magnitude of the M-modes has to be analyzed with respect to particular performance variables over repetitive attempts at the same task. More specifically, we studied the multi-muscle coordination during the performance of cyclic whole-body voluntary movements (sway) in the anterior-posterior (AP) direction and production of the moment of force around the vertical axis of the body (M_Z). Three studies were performed assuming the existence of at least two levels of control with synergies possible at each level. At the higher level values or time profiles of specific mechanical variables (COP trajectory or M_Z time profile) are stabilized by covariation of magnitudes of M-modes. The hierarchically lower level is the level where M-modes are formed. This lower level ensures proportional involvement of muscles within a group; in other words, it defines the direction of an eigenvector in muscle activation space corresponding to a M-mode.

The following main issues are addressed:

Issue 1- viability of the UCM hypothesis as a method of identifying and quantifying multi-muscle synergies in whole-body motor tasks,

Issue 2- composition of elemental variables (M-Modes) under different motor tasks (voluntary sway and cyclic M_Z generation) and experimental conditions during whole-body actions, such as different frequencies of motion, motion with closed eyes, under application of high-frequency, low-amplitude muscle vibration to the Achilles tendons, and while standing on one foot.

Issue 3- ability of the central nervous system to co-vary magnitudes of M-modes to ensure reproducibility of a performance variable across repetitive trials under different experimental conditions of whole-body movement execution,.

The following hypotheses are tested:

Hypothesis 1: M-mode composition can change when whole-body voluntary sway tasks are executed under varying conditions such as at different frequencies of motion, during motion with closed eyes, under application of high-frequency, low-amplitude muscle vibration to the Achilles tendons, and while standing on one foot.

Hypothesis 2: A decrease on the index of multi-M-mode synergies stabilizing the mechanical variables (performance variables) trajectory is expected during the execution of a whole-body voluntary sway task under more challenging conditions such as different frequencies of motion, motion with closed eyes, under application of high-frequency, low-amplitude muscle vibration to the Achilles tendons, and while standing on one foot.

Hypothesis 3: More complex tasks, for example production of a cyclic time profile of the moment of force about the vertical body axis, may be associated with sets of M-modes whose composition varies across both subjects and movement frequencies. The CNS will be able to create multi-M-mode synergies stabilizing the performance variable (the moment of force time profile) based on such dissimilar sets of M-modes

A secondary issue to be addressed in this Thesis is **anticipatory postural adjustments (APAs)** during head stabilization. When a person makes a fast voluntary movement, changes in the background activity of the leg and trunk muscles are observed up to 150 ms prior to the onset of the movement (Belen'kiy et al 1967; Cordo and Nashner 1982; Aruin and Latsah 1995b; Aruin and Latsah 1995b; Aruin and Latash 1996; Shiratori and Latash 2000). These early changes have been called APAs and they have been hypothesized to represent feed-forward postural preparations that counteract a forthcoming postural perturbation associated with the intended movement. APAs have been studied under several experimental conditions such as prior to the execution of a voluntary arm, trunk, and leg movements during vertical stance (Belen'kiy et al 1967; Cordo and Nashner 1982; Breniere and Do 1986; Mouchino et al. 1991, Danna-dos-Santos et al. 2007b); forearm loading and unloading (Hugon et al. 1982; Dufosse et al. 1985, Johanson and Magnusson

1989; Laquantini and Maioli 1989; Paulignan et al. 1989; Aruin and Latash 1995a; Bennis et al. 1996); and quick loading and unloading of the upper extremities during sitting and standing (Lavender et al. 1993; Aruin and Latash 1995b; Aruin and Latash 1996; Shiratori and Latash 2000).

Most studies of APAs in standing persons have naturally focused on trunk stabilization (reviewed in Massion, 1992). It has been suggested, however, that during daily activities such as walking and running, and also during acrobatic movement such as salto, the head posture with respect to the trunk is well stabilized to ensure a reliable reference frame (Berthoz and Pozzo, 1994 and Pozzo et al., 2001). The importance of head stability during whole-body actions performed by standing persons has received support in another recent study (Freitas et al., 2006). However, very few studies addressed the role of APAs in head stabilization, and their results are controversial (Gurfinkel et al. 1988; Van der Fits et al. 1998).

In this Thesis, one experiment is dedicated to the investigation of the role of the postural muscles of the legs and trunk on stabilization of the head with respect to the trunk prior to self-induced mechanical perturbation applied directly to the head, to the trunk, or to the head and trunk simultaneously. We focused on a possibility of existence of both reciprocal and co-contraction patterns of neck muscle activation during APAs depending on the predictability of the mechanical effects of the perturbation on head posture. These were manipulated by changing the site of application of the perturbation (directly to the head, to the trunk, or to the head and trunk simultaneously).

The following specific hypothesis is tested:

Hypothesis 4: APA patterns in the neck flexor–extensor muscles can change from a time-shifted (reciprocal) pattern to a synchronized (co-activation) pattern when the source of the perturbation changes from a mechanical perturbation applied directly to the head to a mechanical perturbation applied to the trunk or to the head and to the trunk simultaneously.

1.2 Organization of Thesis

This Thesis is organized in seven chapters organized as the following:

Chapter 1 is an introduction to the Thesis.

Chapter 2 reviews the literature related to the topic of the Thesis.

Chapter 3 is based on the published article Danna-Dos-Santos A, Slomka K, Zatsiorsky VM, Latash ML (2007) Muscle modes and synergies during voluntary body sway. *Exp Brain Res.* 2007 Jun 179(4):533-50 where the coordination of muscle activity during voluntary body sway performed by human subjects at different frequencies was studied. Subjects stood on the force platform and performed cyclic shifts of the center of pressure (COP) while being paced by the metronome. A major question was: does the makeup of muscle synergies and their ability to assure reproducible sway trajectory vary with the speed of the sway? Principal component analysis was used to identify three muscle groups (M-modes) within the space of integrated indices of muscle activity. M-mode vectors were similar across both subjects and sway frequencies. There were also similar relations between changes in the magnitudes of all three M-modes and COP shifts (the Jacobians) across the sway frequencies. Variance in the M-mode space across sway cycles was partitioned into two components, one that did not affect the average value of COP shift ("good variance") and the other that did. An index (DeltaV) was computed reflecting the relative amount of the "good variance"; this index has been interpreted as reflecting a multi-M-mode synergy stabilizing the COP trajectory. The average value of DeltaV was similar across all sway frequencies; DeltaV showed a within-a-cycle modulation at low but not at high sway frequencies. The modulation was mostly due to variations in the "good variance". We conclude that muscle modes and their mapping on COP shifts are robust across a wide range of rates of COP shifts. Multi-M-mode synergies stabilize COP shifts (assure its reproducibility) within a wide range of its speeds, but only during cyclic COP changes. Taken together with earlier studies that showed weak or absent multi-M-mode synergies during fast discrete COP shifts, the results suggest a basic difference between the neural control assuring stability of steady-state

processes (postural or oscillatory) and transient processes (such as discrete actions). Current results provide the most comprehensive support for the notion of multi-M-mode synergies stabilizing time profiles of important performance variables in motor tasks involving large muscle groups.

Chapter 4 is based on the article in press Danna-Dos-Santos A, Degani AM, Latash ML. Flexible Muscle Modes and Synergies in Challenging Whole-Body Tasks where the idea of hierarchical control of a motor system was used to study multi-muscle synergies during a whole-body sway task performed by a standing person. Within this view, at the lower level of the hierarchy, muscles are united into groups (M-modes). At the higher level, gains at the M-modes are co-varied by the controller in a task specific way to ensure low variability in important physical variables. In particular, the following hypotheses were tested; a) the composition of M-modes could adjust and b) an index of M-mode co-variation would become weaker in more challenging conditions. Subjects were required to perform a whole-body sway at 0.5 Hz paced by a metronome. They performed the task with eyes open and closed, while standing on both feet or on one foot only, with and without vibration applied to the Achilles tendons. Integrated indices of muscle activation were subjected to principal component analysis to identify M-modes. An increase in the task complexity led to an increase in the number of principal components that contained significantly loaded indices of muscle activation from 3 to 5. Hence, in more challenging tasks, the controller manipulated a larger number of variables. Multiple regression analysis was used to define the Jacobian of the system mapping small changes in M-mode gains onto shifts of the center of pressure (COP) in the anterior-posterior direction. Further, the variance in the M-mode space across sway cycles was partitioned into two components, one that did not affect an average across cycles COP coordinate and the other that did (good and bad variance, respectively). Under all conditions, the subjects showed substantially more good variance than bad variance interpreted as a multi-M-mode synergy stabilizing the COP trajectory. An index of the strength of the synergy was comparable across all conditions, and there was no modulation of this index over the sway cycle. Hence, the first hypothesis was confirmed, while the second one was falsified. Interpretation of the observations is given as suggesting that adjustments at the lower level of the hierarchy – in the M-mode composition – allowed the subjects to

maintain a comparable level of stabilization of the COP trajectory. The findings support the (at least) two-level hierarchical control scheme of whole-body movements.

Chapter 5 is based on the study. Postural Control during Upper Body Locomotor-Like Movements: Similar Synergies Based on Dissimilar Muscle Modes where we explored the organization of leg and trunk muscles into groups (M-modes) and co-variation of M-mode involvement (M-mode synergies) during whole-body tasks associated with large variations of the moment of force about the vertical body axis. We explored the following hypotheses: (1) Can muscle activation patterns during such tasks be described with a few M-modes consistent across tasks and subjects? (2) Do these modes form the basis for synergies stabilizing the moment time pattern? (3) Will this organization differ between an explicit body rotation task and a task associated with alternating arm movements? Healthy subjects stood on the force platform and performed two motor tasks while paced by the metronome at 0.7, 1.0, and 1.4 Hz: Cyclic rotation of the upper body about the vertical body axis (body rotation task), and alternating rhythmic arm movements imitating those during running or quick walking (arm movement task). Principal component analysis (PCA) with factor extraction was used to identify muscle groups (M-modes) within the 13-dimensional space of integrated indices of muscle activity. The M-mode directions differed both across subjects and across movement frequencies. Variance in the M-mode space across sway cycles was partitioned into two components, one that did not affect the average value of moment shifts ("good variance") and the other that did ("bad variance"). An index was computed reflecting the relative amount of the "good variance" such that its positive values have been interpreted as a multi-M-mode synergy stabilizing the moment time profile. The index was positive for both tasks and for all three frequencies. It was lower for 1 Hz movements as compared to the other two frequencies. We interpret the results within a two-level hierarchical control scheme as evidence for multi-M-mode synergies stabilizing time profiles of the moment of force about the vertical body axis. The results show that variable sets of M-modes (at the lower level of the hierarchy) can be used to stabilize important mechanical variables by co-variation of their magnitudes at the upper level of the hierarchy. The lower indices of synergy for movements at 1Hz (close to the preferred movement frequency) corroborate the idea that patterns of M-mode co-variation are defined by central neural processes. The findings have

failed to find significant differences between the organization of muscle synergies during body rotation and locomotion-like arm movements.

Chapter 6 is based on the published article Danna-Dos-Santos A, Degani AM, Latash ML. (2007) Anticipatory control of head posture. *Clin Neurophysiol.* Aug 118(8):1802-14 where a hypothesis on two patterns of anticipatory postural adjustments (APAs) in neck muscles was tested. More specifically, this study focused on the rationale that reciprocal and co-activation muscle patterns may be used in a task-specific way. This study also explored possible relation of APAs in leg and trunk muscles to head stabilization. Load perturbations (loading and unloading) were applied to the head, trunk, and head and trunk simultaneously using similar hand actions by standing persons. Electromyographic signals (EMGs) from 10 muscles were recorded. Shifts of the center of pressure and EMG indices were computed over typical time intervals for APA. Time-shifted (reciprocal) activation of neck flexor and extensor muscles during APAs was seen when perturbations were applied directly to the head. Simultaneous activation dominated when the perturbations were applied to the trunk. Minimal APAs were seen in the leg/trunk muscles during head perturbation tests. APAs during trunk perturbation were not different from those during trunk and head perturbation. The results confirm the existence of two different patterns of APAs in neck muscles. A time-shifted (reciprocal) pattern is more likely to be used in anticipation of a perturbation acting directly on the head. A simultaneous activation (co-activation) pattern is used when direction of head perturbation cannot be predicted with certainty. Leg/trunk APAs are unlikely to help stabilize head posture. These results are important for better understanding of feed-forward mechanisms of the control of head posture with possible implications for neurological patients who suffer from impaired feed-forward postural control.

Chapter 7 is a summary of the main conclusions driven by the results obtained on Chapters 3 to Chapter 6.

CHAPTER 2

BACKGROUND AND LITERATURE REVIEW

This chapter contains a review of the literature on the control of human posture. First, specific terminology will be introduced followed by an outline of literature regarding human postural control. A description of the mechanical challenges faced by the controller will be given and the importance of sensory information for the process of postural control will be summarized. The main domains of research in posture control will also be described as well as the notion of synergies with respect to postural control. Particular emphasis will be placed on the literature pertaining to identification and quantification of synergies using computational methods associated with the uncontrolled manifold hypothesis.

2.1 Some definitions

Along the life span, one becomes very familiar with the ability to use the body to execute a great variety of daily motor tasks. Among many others actions, the ability to keep the body in certain postures in space is crucial to allow humans to execute a variety of motor tasks. For example, using a screwdriver demands a certain position of the whole body in order to properly approach and use such a tool. This ability to keep the body in a certain configuration is commonly referred as a '*postural task*' and, for adults, this ability is a simple routine generated smoothly and without a great deal of thought. One only starts realizing how difficult and complicated it is to keep the body in such postures when considering motor effects in the presence of a neurological diseases (such as parkinsonism, stroke, and peripheral neuropathies), trauma, or aging.

The physiological processes involved in controlling the performance of postural tasks involve many anatomical structures that form an intricate and complex system. To name a few, these involve the spinal cord, the brain stem, the cerebellum, the cortex of the large hemispheres, proprioceptive neurons, eyes, skin receptors, the vestibular system, and many

others. The collection of such structures involved in this process will be referred in this Thesis as '*posture control system*'.

Along this Thesis, terms such as *body posture*, *postural perturbation*, *postural sway*, *center of pressure*, *center of mass*, and *quiet stance* will appear several times. In order to avoid possible confusions, definitions given by Zatsiorsky (2002) will be used. The term *body posture* will be considered as the configuration of the body in space such that this configuration may or may not change over time. The term *postural perturbation* will be considered as any external force (generated by the environment, applied to any part of the body) or internal force (mechanical force generated by contraction of muscles or movement of one segment that propagates to adjacent segments) that can induce changes in the current body configuration. *Postural sway* will be used to denote small variations in body position when subjects are asked to maintain a certain posture (e.g. upright stance). *Center of pressure* (COP) is the point of application of the ground reaction force to the body. *Quiet stance* will be considered as the maintenance of the upright posture in absence of any other motor task.

2.2 Posture control and a brief outline of its development

Systematic investigation of mechanisms involved in human posture control began with experimentation on four-legged animals (Sherrington, 1906). In the beginning of the 20th century, Sherrington (1906) used cat specimens to study reflexes mediated by the spinal cord and midbrain. He used a preparation in which the midbrain and spinal cord was isolated from higher areas within the CNS (e.g. cortical areas); this technique is now known as '*decerebration*'. His observations included an increase in the level of muscle activity of extensor muscles in all four legs and other anti-gravity muscles when the decerebration was performed between the superior and inferior colliculi. This pattern of muscle increased activity was termed '*rigidity*', which was sometimes able to keep the animal standing unsupported. Sherrington (1906) also observed an opposite result in situations where the decerebration was accompanied by disruption of the afferent information carried by the sensory nerves (process called '*deafferentation*'). Once the deafferentation was applied, instead of rigidity, a complete absence of muscle activity was observed, suggesting that afferent signals are crucial to posture control. Sherrington's interpretations led him to

propose the first theory about posture control, suggesting that the rigidity of extensor muscles represents the foundation of posture control.

Work by other scientists reinforced this basic idea proposed by Sherrington. For example, Rudolf Magnus (1924) transected the brain of the cat at higher levels and uncovered series of hierarchically organized reflexes, varying from simple to more complex motor outputs depending on the site where decerebration was performed. The closer the decerebration was to the higher brain centers, the more complex were the resultant motor actions. These results led Magnus to conclude that posture control could be achieved by a summation of these reflexes.

Nowadays, strong evidence suggests that reflexes do not fully account for all postural control (Belen'kiy et al 1967; Cordo and Nashner 1982; Aruin and Latash 1996; Shiratori and Latash 2000). In particular, research has shown that postural adjustments can occur prior to the application of mechanical stimulus in cases of voluntary movements (Bouisset and Zattara 1987; Massion 1992). However, reflexes and reflex-like reactions may still be integral in the maintenance of postural equilibrium.

Studies regarding posture control were also performed by Nicolai Bernstein (Bernstein 1967) who suggested that such complex systems might be controlled partly by the formation of '*postural synergies*'. His view included the notion that postural synergies were a combination of control signals to postural muscles, whose purpose it is to ensure the body equilibrium in anticipation to a voluntary movement or in response to an external perturbation (Bernstein 1967; Alexandrov et al. 1998). Using multi-muscle synergies for the purpose of control decreases the number of variables that the CNS needs to manipulate. Currently, some researchers have dedicated their effort to propose a strict definition of the term synergy as well as propose reliable methods to quantify and test Bernstein's suggested principles (Gelfand and Latash 1998; Scholz et al 2000; Latash et al 2005; Latash et al 2007; Latash 2008).

In summary, postural control has been studied under different perspectives and different approaches in order to target the issue of how an unstable mechanical system, such as the skeletal system, can be stabilized in space. Biomechanical approaches were used to investigate the mechanical complexity of the human body. Behavioral and neurophysiological studies have been performed in order to understand the integration of

sensory information with motor responses. Each area has given valuable and complementary information to this immense puzzle.

2.3 The mechanical challenge

The human body obeys the laws of physics. In physics, a rigid body is in mechanical equilibrium when the sum of all forces on all particles of the body is zero, and also the sum of all torques on all particles of the body is zero. However, the human body is not a rigid body but it consists of multiple linked segments (kinematic chain) connected to each other by muscles, tendons, ligaments, skin and other soft tissues.

A kinematic chain is said to be in mechanical equilibrium when all the links of the chain are in equilibrium (Zatsiorsky, 2002). However, this mechanical equilibrium can also be characterized accordingly to its stability. If a mechanical system returns to equilibrium after being subjected to small disturbances, the same is referred to be in a stable equilibrium. In another hand if the system depart from an equilibrium state after the application of a mechanical disturbance, the same system is referred to be in a unstable equilibrium.

The natural arrangement of the human body segments along its longitudinal axis during vertical stance makes much more difficult to keep the whole body in a stable equilibrium since the joints connecting individual segments can have several axes of rotation and their interactions are far from simple (Zatsiorsky 2002). Any movement performed on the lower limbs will generate mechanical repercussions on the neighboring segments and joints. Thus, if the body posture must be kept in a situation of stable equilibrium while one of the segment moves, the forces and torques created by the movement must be synchronously counteracted.

To make the matter more complex, most of the muscles responsible for generating this counteraction cross several joints, which enhance movement interaction among segments (Jacobs and Macpherson 1996; Bolhouis et al. 1998). Thus, the action of a given muscle can stabilize one joint and destabilize another.

2.4 The importance of afferent information

Collecting information regarding the relation of the body and its surrounding environment is crucial to postural control since it provides a reliable time-to-time neural representation of body configuration. Such representation is most likely achieved by combining, within the CNS, a great variety of sensory inputs coming from different parts of the body (Kandel et al. 2000). This representation may be used mainly to produce a coherent representation of the body in space such as its state (e.g. moving), its orientation on the gravitational field, and its relative position regarding to elements of environment (e.g. a close obstacle). This representation is also used to promote corrections of body position by means of muscle contractions when necessary. Important sensory inputs (afferent inputs) come from three different sources: (a) the vestibular system, (b) the visual system, and (c) a great number of sensory receptors embedded in the muscles, tendons, joint capsules and skin commonly referred to as proprioceptive receptors. Tactile receptors embedded in the skin are also source of sensory inputs

The roles of visual, vestibular, and proprioceptive information regarding to human postural control have been extensively studied (Roll et al. 1980; Dijkstra et al. 1994a; Fitzpatrick and McCloskey 1994; Kuo et al. 1998). The role of cutaneous information from the sole of the foot and from the fingers have been studied in healthy and special populations (Jeka and Lackner 1994; Jeka 1997; Kavounoudias et al. 1998; Rabin et al. 1999, Danna-dos-Santos 2000). The effects of different types of afferent information are commonly reflected in changes of postural sway characteristics during the simple task of quiet stance. Such characteristics include the total sway area, ranges, lengths, velocity or standard deviation of COP trajectories (Murray et al. 1975; Diener et al. 1984).

Visual information is viewed as the most important sources of information for postural control. Under conditions of altered information from other sensory sources, subjects are able to almost completely compensate for the loss of that information by using vision. Several studies have shown that indices of postural sway increase when the eyes are closed (Allum and Pfaltz 1985; Fitzpatrick et al. 1992a; Simoneau et al 1992; Schumann et al. 1995). Further, manipulations of the visual environment have been shown to have profound impact on the maintenance of one's posture. A typical method used in this type of experimentation is the paradigm of the 'moving room'. Under this paradigm, the visual

environment of a subject is manipulated by either actually moving the room or altering the display in front of the subjects mimicking motion of the visual environment (Lee et al. 1980; Schöner 1991; Dijkstra et al. 1994a; Dijkstra et al. 1994b). When the visual environment accelerates towards the subject, the subject perceives this as a forward sway of their body and reacts by an actual backward sway of the body.

Studies of the role of vestibular information for human postural control commonly use galvanic stimulation applied at the vestibular apparatus behind the ear. Such stimulation changes the firing rate of peripheral vestibular afferent information. Depending on the position of the subject's head and the polarity of the current, subjects show body lean in a particular direction (Hlavacka et al. 1995; Hlavacka et al. 1996; Coats and Stoltz 1969). When a subject faces forward and a positive current is applied to the right vestibular organ, a sway to the right is observed. When a similar current is applied but the subject's head is initially positioned in rotation to the right, a movement of the whole body in the posterior direction (backwards) is observed (Hlavacka and Njiokikjien 1985). An increase in the amplitude of the vestibular stimulation leads to an approximately linear increase of the body sway (Coats and Stoltz 1969). Sinusoidal stimulation results in body sway towards the positive stimulus and away from the negative one, which leads to a sinusoidal sway pattern at low frequencies (Petersen et al. 1995).

Another source of afferent information used to control the body posture comes from the muscle spindles located among the striated fibers of skeletal muscles. Muscle-tendon vibration has been used as a powerful stimulus for the muscle spindles (Ia afferents). There is a linear correspondence between the muscle spindle discharge and the stimulus at frequencies below 100 Hz (Lackner and Levine 1979). Muscle vibration generates a tonic contraction of the muscle often called '*the tonic vibration reflex*'. The contraction starts a few seconds after the beginning of the vibration, increases gradually, and then stays at a relatively constant level until few seconds after the stimulus is turned off.

Muscle-tendon vibration is also known to result in kinesthetic illusions (Lackner and Levine 1979; Calvin-Figuiera et al. 1999). The CNS interprets the increased activity in the muscle spindle endings as a sign that the muscle is lengthening, and in the absence of another sensory information (optical or haptic), this generates an illusory perception of a new joint position corresponding to the increased muscle length (Eklund and Hagbarth 1966; Eklund

1969). When the tendon of a postural muscle is vibrated, such as the Achilles tendon, the illusory increase in length is interpreted as a change in the orientation of the body and is compensated by an actual change in body position in the opposite direction. This correction can result in body sway or protective stepping, known as '*vibration induced fall*' or VIF. This effect is especially strong when the eyes are closed (Nakagawa et al. 1993). Under circumstances where the base of support is reduced, the effects of muscle vibration on postural sway are reduced (Ivanenko et al 1999). Depending on the postural, cognitive, and multi-sensory context, the same muscle may show different responses to muscle-tendon vibration (Lackner and Levine 1979; Feldman and Latash 1982; Latash 1995). For instance, switching from segmental to whole-body postural reactions may take place if a wrist muscle is vibrated when involved in a postural task, such as touching a support surface (Roll et al. 1980).

The third main source of sensory information comes from the skin receptors. It has been shown that a light touch by a finger tip at mechanically non-supportive force levels ($< 1\text{N}$) greatly attenuates postural sway during quiet stance (Holden et al. 1994; Jeka and Lackner 1994). More specifically, the index finger, with its higher receptor density, is believed to play an important role in detecting minute changes in force level and direction which contributes to the decrease in sway (Holden et al. 1994; Jeka and Lackner 1994). The effect of touch is observed even in blind individuals and those with vestibular loss. In both cases, the touch information is more effective in reducing sway as compared to using vestibular information (Jeka et al. 1996; Lackner et al. 1999). When the supporting surface under the finger oscillates, there is coherent sway of the head and body (Jeka et al 1997; Jeka et al. 1998). This relation is in phase at frequencies below 0.4 Hz while phase lag is seen at higher frequencies (Jeka et al. 1998).

Rabin et al (1999) investigated the directional specificity of touch contact. They revealed that finger touch was more effective in reducing sway in the direction of greatest sway, that is, when finger contact is provided in front of the body a reduction in sway in the AP direction is verified. However, when contact is provided besides the body a reduction in the ML direction is observed. This result suggests that fingertip contact provides information both about the amplitude and direction of sway. Further, Riley et al (1999) investigated whether or not the cutaneous information from the fingertip plays the primary role in

reducing sway or if it is the implicit task of keeping the finger at a fixed position that plays a larger role. In the study, subjects either touched a hanging curtain as a mere result of extending the forearm or they were instructed to minimize the force and movement at the point of contact. Only under the latter instruction did the subjects show decreased postural sway. This finding emphasized the importance of active touch rather than having a fixed reference point for the reduction in postural sway. Contrary to these conclusions, Rogers and his colleagues (Rogers et al. 2001) have shown that ‘passive’ tactile cues at the shoulder and at the lower leg can reduce postural sway. The touch was ‘passive’ in a sense that the subjects were not required to minimize applied forces or remain in contact with the touched surface.

The interaction between vision and touch was investigated by Jeka et al (Jeka et al. 2000). In this study, both the visual field and touch surface were manipulated. The researchers accounted for the sensory integration of visual and cutaneous information as a linear additive model. In 2000, Lackner et al (2000) examined the relation between cutaneous and muscle spindle information. They instructed subjects to stand in the Romberg position (feet touching each other in parallel arrangement) while their peroneus longus and brevis tendons were vibrated. The subjects either stood unsupported or with a light finger touch. It was found that finger touch to a stable surface was sufficient to suppress the destabilizing effects of vibration.

2.5 Control of quiet stance

During quiet stance, the body shows small variations in its position. It oscillates in both the anterior-posterior (AP) and medial-lateral (ML) directions. This oscillation is quantified by different methods including the use of force platforms. By using a force platform, one can record the time-to-time position of the COP. COP movements are commonly used to assess body oscillation during quiet stance. Normally in quiet stance, the COP migrates approximately 0.4 cm in AP direction and 0.18 cm in ML direction while COM displacements are somewhat smaller (Winter et al. 1996; Winter et al. 1998). The differences in migration of COP and COM in the AP direction have been associated with the generation of torques at the ankle joints, while displacements in the ML direction have been

associated with activity of hip muscles (Winter et al. 1996). Several models have been suggested to explain and describe COP migration in quiet stance. Three of them will be addressed in the following paragraphs.

Upright human posture has been frequently modeled as an inverted pendulum (Fitzpatrick et al 1992b; Winter et al. 1993; Winter et al. 1998; Morasso and Schieppati 1999). Modeling the human body as an inverted pendulum is based on assumptions that (a) joint motion occurs only in the ankle joints, (b) the body sway is very small, and (c) the feet do not move (Zatsiorky and King 1998). Since the stability of the system requires that the COM falls within the base of support, it is believed that the COM coordinate is the controlled variable of the unstable body system. Winter et al (1998) suggested that whole body COM is regulated through continuous movement of the COP and stabilized around a fixed reference point. They showed that the COP-COM error signal is proportional to the horizontal acceleration of the COP in the AP and ML directions. Their model assumes that muscles act as springs to cause the COP to move in phase with the COM as the body sways about a desired equilibrium position. The model predicts instant corrective responses due to the stiffness of the postural muscles placed around the joints and thereby reduces the necessity of the CNS to intervene along the process of posture control.

There has been strong criticism regarding to this idea of stiffness controlling of body balance in quiet stance. Morasso and colleagues (Morasso and Schieppati 1999; Morasso and Sanguinetti 2002) state that muscle stiffness alone is not enough to keep the body upright. According to this group of scientists, sensory information from the pressure receptors in the soles of the feet and muscle receptors is likely to contribute to the control of the posture in quiet stance. In addition, it has been argued that the assumption of a fixed reference point for stabilization of posture may not be correct since several studies have pointed at a moving reference point (Gurfinkel et al 1995; Accornero et al. 1997; Zatsiorsky and Duarte 1999). Criticism also came from the assumption that only motion at the ankle is of importance (Day et al. 1993; Kuo and Zajac 1993; Accornero et al. 1997; Aramaki et al 2001).

Another theory of quiet stance is that proposed by Collins and De Luca (1993). They view control of vertical posture as a stochastic process and analyzed COP trajectories as one- and two-dimensional random walks. They were able to find consistent, subject-specific stabilogram patterns showing two control systems operating during quiet stance. They

concluded that during short term intervals ($< 1s$), an open-loop control mechanism is called to act and in the long-term there is a close-loop mechanism (diffusion constants for short-term were larger than in the long-term and there was a positive correlation of COP position in the short-term and negative correlation in the long-term). Their interpretation is that the CNS allows for a certain amount of 'sloppiness' in the control of balance and it is only when the information from the sensory systems indicates that the COP has moved beyond a certain threshold value that feedback mechanisms are used to bring the COP back into a 'safety zone'.

Another model for the control of posture has been formulated by Zatsiorky and Duarte (1999, 2000). They introduced a method of decomposing COP trajectories into two components; termed rambling and trembling. The decomposition first identifies instant equilibrium points (IEP). An IEP is the position of the COP, when the resultant horizontal force is zero. At these moments the projection of the COM onto the base of support coincides with the COP position. The individual IEPs, connected through a spline fitting function, form the rambling trajectory, while the difference between rambling and COP trajectories is called the trembling trajectory. The authors suggest that the rambling trajectory describes the motion of a moving reference point with respect to which the body's equilibrium is instantly maintained, while the trembling trajectory describes body oscillation around the reference point trajectory.

2.6 Lines of defense against postural perturbations that can result in fall

Despite the challenges faced by the CNS in terms of body posture control, we are able to maintain our upright posture in the field of gravity and at the same time handle objects, walk and carry heavy loads without falling over. There are several lines of defense against the forces that threaten the body stability. These lines of defense are, in the order of latency:

- 1- anticipatory postural adjustments;
- 2- passive elasticity of the soft tissues surrounding joints such as muscles, tendons, ligaments, and capsules which oppose the perturbing forces;
- 3- stretch reflexes at the latency of 30-50 ms;

- 4- preprogrammed reactions at the latency of 50-100 ms;
- 5- voluntary actions.

In the following paragraphs, some of these lines of defense and their pertaining literature are reviewed.

2.6.1 Anticipatory postural adjustments (APAs)

While the first two lines of defense previously described are very effective while a person is in quiet stance, they are not sufficient to counteract larger postural perturbations such as those created by voluntary movements. Voluntary movements, especially those with large amplitudes and executed quickly by large body segments, can disturb postural equilibrium. There are two main reasons for this occurrence. First, the forces and torques that are intended to produce the movement are transmitted to other body parts through linked segments. Second, rapid changes in the position of a limb or the body results in changes in mass distribution resulting in a change in the COM position (Bouisset and Zattara 1987; Massion 1992).

The disturbing effects of voluntary movements are anticipated by the CNS, which produces changes in the background activity of postural muscles (anticipatory postural adjustments, APAs) in a feed-forward manner. In this way, there is at least a partial compensation for the upcoming perturbation as a result of shifting the center of gravity in the opposite direction regarding to the perturbation (Bouisset and Zattara 1983; Bouisset and Zattara 1987). Simulation studies have shown that forces and moments generated by a voluntary movement can be large enough to shift the COM outside the base of support and cause the body to fall (Friedly et al. 1984; Ramos and Stark 1990). Ramos and Stark (1990) showed that in rapid arm raising movements, there is a large destabilizing upward angular momentum of the arms, which could cause a backward fall, if not counteracted by anticipatory muscle activity.

APAs were first observed by Belen'kiy and colleagues (Belen'kiy et al. 1967) who reported that during arm raising in a standing position, the leg muscles involved in postural control are activated 50-100 ms prior to the prime mover activation. Since then, APAs have

been described for several movements, such as movements of the arm, leg, trunk, and head while standing (Belen'kiy et al 1967; Cordo and Nashner 1982; Breniere and Do 1986; Mouchino et al. 1991, Danna-dos-Santos et al. 2007b); forearm loading and unloading (Hugon et al. 1982; Dufosse et al. 1985, Johanson and Magnusson 1989; Laquantini and Maioli 1989; Paulignan et al. 1989; Aruin and Latash 1995a; Bennis et al. 1996); and quick loading and unloading of the upper extremities during sitting and standing (Lavender et al. 1993; Aruin and Latsah 1995b; Aruin and Latash 1996; Shiratori and Latash 2000).

APAs are commonly quantified by using EMG signals, body segment kinematics and displacements of the COP. Previously, it was believed that APAs were only generated when expected movements are performed by large body parts and not when the movement is produced by a smaller effector, such as finger, or when a predictable perturbation is introduced by an external source. For instance, it was reported that when a subject held a load in a hand and the experimenter triggered a load release, even if the perturbation was predictable, no APAs were observed (Hugon et al. 1982; Dufosse et al. 1985; Paulignan et al. 1989; Scholz and Latash 1998). More recent studies have shown that APAs can be generated not only by small movements such as that of a finger but also in the absence of movements. In their study, Aruin and Latash (1995b) used different effectors to trigger the same unloading perturbation. In another condition, the experimenter caused the same perturbation. They confirmed that only self-initiated perturbations were accompanied by APAs, but even a very small finger movement was enough to trigger APAs. Later, Shiratori and Latash (2001) reported that when a standing subject is required to catch a load without any movement, visual information about the falling object was sufficient to trigger APAs.

In general, the generation of APAs is affected by the following factors: a) expected direction and magnitude of the perturbation; b) characteristics of voluntary movements associated with the perturbation; c) the current postural task where situations of extreme stability/instability tend to decrease APAs magnitude and, in extreme cases, they are abolished (Aruin et al. 1998); d) time constraints such reaction time is able to delay APAs and turn them suboptimal (Slijper 2001).

2.6.2 Passive elasticity of the soft tissues surrounding joints

‘Muscle stiffness’ is a common term used to describe the mechanical property of the muscle-tendon unit to generate an opposing force when it is deformed. This term has received elaborated criticism (Latash and Zatsiorky 1993) and, in order to follow a more accurate terminology, here the term “apparent elasticity” will be used to describe this relation.

The apparent elasticity of the muscle-tendon unit has been assumed to play an important role for the control of the posture sway during quiet stance since these tissues generate opposing forces to help restore the body equilibrium (Fitzpatrick et al. 1992b; Magnusson et al. 1994; Winter et al. 1998; Morasso and Schieppati 1999). Studies have suggested that the apparent elasticity around the ankle joints is enough to maintain quiet standing (Fitzpatrick et al. 1992b and Winter et al. 1998). Fitzpatrick et al (1992b) found a linear relation between ankle torque and the ankle angular displacement under very small perturbations of the posture. The perturbations were applied with similar magnitudes of those representing the body sway. The ability of the ankle passive elasticity to maintain upright stance was assessed when the subjects balanced a load equivalent to their mass when neither vestibular nor visual information were used. They found that in standing subjects, the ankle passive elasticity was sufficient to maintain the upright posture. Winter et al (1998) described similar results. They assumed that the apparent elasticity of the muscle-tendon unit acts as a spring and is the cause of the COP moving in phase with the COM. They used the inverted pendulum model to calculate the apparent stiffness of the mechanical system and showed that the restoring forces act at very small delays. Since the delay was below the threshold of any vestibular or proprioceptive response, they concluded that balance during quiet standing can be controlled merely by setting the appropriate “stiffness”.

The results presented by Fitzpatrick (1992b) and Winter (1998) have been criticized by those who believe that the apparent elasticity of the muscle-tendon unit is not enough to keep the body stable in quiet standing. Morasso and Schieppati (1999), using their own method of computing “stiffness”, showed that the restoring forces provided by the passive elasticity of the muscle-tendon unit are too low to maintain vertical posture. They also suggested the existence of contributions from sensory information to the control of quiet stance. However, it is important to note that the two groups defined stiffness differently and

this fact might have lead to the difference of opinion in the role of muscle stiffness in posture control (Latash and Zatsiorsky 1993).

2.6.3 Preprogrammed reactions to external perturbations

External perturbations to upright posture are usually counteracted by both passive and actively generated responses. While passive resistance of the surrounding joint tissue and stretch reflexes are commonly considered enough to maintain postural balance under small displacements of the COM as in quiet stance, in case where perturbations become larger, preprogrammed reactions are used. These preprogrammed reactions consist of a combination (spatial and temporal) of muscle activation specific for a given perturbation and acting at a time delay of approximately 50-100 ms after the perturbation has been applied. Preprogrammed reactions are considered different as compared to spinal reflexes since they depend on the instruction given to the subject and their magnitude is independent of the magnitude of the applied perturbation. In the past, it was hypothesized that preprogrammed reactions represented a transcortical reflex involving neurons located in the cortex. However, these reactions were observed in decerebrated and spinalized animals which contradicts the transcortical theory.

These reactions have been studied in humans with the use of specially designed force platforms (Nashner 1976). These platforms can either translate in AP or ML directions, or rotate clockwise and counterclockwise directions around the horizontal axis crossing the center of the platform. In response to sudden platform perturbations, stereotypical postural responses in the leg and trunk muscles are observed. In the case of a person subjected to a backward support surface translation, the body sways forward. At a latency of about 80 ms, an increase in the background activity of dorsal muscles is observed (soleus, biceps, femoris, erector spinae). Muscles are recruited in a distal-to-proximal recruitment order, pulling the body backwards. With a forward translation, the ventral muscles are activated in a distal-to-proximal order resulting in pulling the body forward. These activation patterns and consequent changes in kinematics are commonly called as '*the ankle strategy*' since most of the observed movement in response to the perturbation occurs at the ankle joint. This strategy

is commonly seen in young, healthy subjects during small and slow horizontal displacements of the supporting surface on firm and long surfaces (Horak and Nashner 1986).

When subjects are subjected to perturbations larger in magnitude, for example in situations where either the base of support is very small or its displacement is performed faster, the recruitment order of preprogrammed reactions in postural muscles changes to proximal-to-distal. Also, in order to minimize the excursion of the COM housed in the lower trunk, subjects tend to flex or extend the hip. Thus, the denomination '*hip strategy*' is commonly used to describe this type of reaction. Changes in the ankle and or hip strategies have been found to occur with age. For example, in young subjects, an ankle strategy is observed in response to a surface translation while in elderly subjects the same perturbation might generate a hip strategy or even a step strategy (Woollacott and Shumway-Cook 1990). Ankle and hip strategies can be viewed as postural synergies; among the infinite number of possible relations between the joints and muscles, the maintenance of upright balance relies on a small number of more or less fixed relationships among joint rotations.

The main point of describing these defenses against postural perturbations is to provide an idea about the control necessary to compensate the effects inflicted by postural perturbations. The tuning of the temporal and spatial distribution of motor activity among muscles with such precision found in APAs and preprogrammed reactions exemplifies the matter. However, one must not forget that this tuning must also be part of another relation, a relation between a posture directed motor task and the actual generation of movements.

2.7 Supra-spinal control of human posture

The human brain has fascinated many researchers for a long time and this interest has resulted in the development of several techniques of investigation about how the brain and its structures are involved in the generation of movements and processes of postural control. Results from behavioral studies, clinical observations and brain imaging techniques are the most common methods of investigation which have provided valuable evidence suggesting the involvement of the cerebral cortex and other brain structures to processes related to the control of human posture.

Behavioral studies and clinical observations have provided strong evidence of supra-spinal contributions to the postural control by relating changes in body behavior to specific

injured areas and areas usually targeted by pathologies. An extensive literature have been produced with the purpose of study the abnormalities on posture control of humans survivors of stroke, patients with Parkinson's and Alzheimer disease, and traumatic brain injury (Diener et al 1984; Bazalgette et al 1986; Viallet et al 1987; Bouisset and Zattara 1990; Horak and Diener 1994; Nakamura and Meguro 1997; Slobounov et al 2006b; Slobounov et al 2008). The result of these studies are suggestive that not only a few but a great number of structures in the central nervous system are fundamentally involved on the processes of posture control; to name a few, the cerebellum, basal ganglia, thalamus, and many cortical areas are commonly described in an extensive number of studies Diener et al 1984; Bazalgette et al 1986; Viallet et al 1987; Bouisset and Zattara 1990; Horak and Diener 1994; Ouchi 1996; Karnath 2000a,b; Slobounov 2006a).

According to Latash (2008b) disorders of balance are the most common clinical consequences of cerebellar injuries. These disorders may appear alone when the vermis or the fastigial nucleus of the cerebellum is affected or, in combination with disorders of limb movements. Patients with cerebellar disorders typically show increased postural sway (Diener et al 1984; Horak and Diener 1994) and in many patients, this increased sway is seen in anterior-posterior direction. These patients also tend to react to unexpected perturbations of their base of support with exaggerated postural responses (Horak and Diener 1994). Both groups of muscles acting at the ankle joint show an increase in their response as compared to responses seen in a person without a cerebellar disorder.

Neurophysiological abnormalities of the basal ganglia such as those associated with Parkinson's disease also affect normal postural behavior (Bazalgette et al 1986; Viallet et al 1987; Bouisset and Zattara 1990). Patients with Parkinson's disease commonly demonstrate profoundly different postural adjustments. More specifically, APAs seen in a postural muscles before the execution of a voluntary movements have a smaller amplitude as compared to healthy subjects (Bazalgette et al 1986). These patients more frequently demonstrate anticipatory co-contraction of antagonist muscles (Viallet et al 1987; Bouisset and Zattara 1990). While anticipatory co-contraction apparently stiffens a joint and stabilizes it against perturbations, it is less efficient than the more common pattern of alternating activity in postural muscle groups. In addition, patients with Parkinson's disease also show an impairment of the ability to voluntarily modulate their pre-programmed reactions

associated with postural perturbations. All these observations taken together indicate, first, a fundamental role of the basal ganglia in the processes of controlling posture; and second, an impaired ability of patients with Parkinson's to program and initiate movements, and to voluntarily modulate the course of their actions after a postural perturbation has been applied.

Studies on the role of supra-spinal structures on the regulation and control of posture also involve the postural behavior of survivors of stroke (Brunnstrom 1970; Davies 1985; Bohannon 1986; Pedersen et al 1996; Karnath 2000a,b). Although the consequences of such events extensively vary among patients due to the different brain areas affected, a common general clinical finding of paresis (decrease of muscle strength and impairment on the ability to move and control joints in certain segments) on the side of the body contra-lateral to the side of the brain lesion is described. The term, hemiparesis, is commonly used to describe impairments on the control of the trunk, upper and lower limbs contra-lateral to the side of the brain lesion. A large number of patients suffering of hemiparesis have a relatively good trunk balance soon after the stroke, some patients may lose lateral balance and fall toward the paralyzed side even when sitting (Brunnstrom 1970; Davies 1985; Bohannon 1986; Pedersen et al 1996; Karnath 2000a,b) and others actually exhibit a even more peculiar behavior of using the non-affected arm or leg to actively push the body away from the non-paretic side. Davies (1985) was the first to describe this peculiar behavior in hemiparetic patients and termed it as contraversive pushing. Only relatively recently the origin of the contraversive pushing was uncovered and its cause has been attributed to an altered perception of the body orientation in relation to gravity (Karnath et al 2000a,b). Karnath et al (2000b) results suggest that contraversive pushing patients commonly have lesions located on the ventral posterior and lateral posterior nuclei of the posterior thalamus. Their result also point at a brain structure fundamentally involved in the control of the upright body posture, the thalamus.

Another growing body of experimental studies demonstrating the role of supra-spinal structures involved in postural control comes from a series of behavioral studies involving patients suffering from post-traumatic consequences of mild brain injury, or MTBI. Although the results of these studies do not point at any specific supra-spinal structure, they suggest that even in mild cases where no anatomical tissue lesions are verified within the brain matter, the blunt trauma affects the intricate network of mechanisms controlling the upright

posture. Several previous studies have identified a negative effect of MTBI on postural stability not only shortly after the injury but also as long-term effects of the trauma (Ingersoll and Armstrong 1992; Wober et al 1993; Slobounov et al 2006b; Slobounov et al 2008). More specifically, an increase in postural sway is observed with a larger increase in the anterior-posterior (AP) direction (Ingersoll and Armstrong 1992; Wober et al 1993). In addition to traditional measurements of the body's center of pressure displacement (COP), other measurements such as virtual time to contact (VTC) have revealed similar results illustrating the ability to detect longer lasting effects of the brain trauma than COP based measures (Slobounov et al 2006b; Slobounov et al 2008). Patients who suffered MTBI also exhibit postural dysfunction when performing more challenging postural tasks (Slobounov et al 2006b) such as responses to visual field motion.

Another important observation from behavioral studies on the role of supra-spinal structure involved in mechanisms of postural control is the existence of the anticipatory postural adjustments (APAs) prior to postural perturbations. As described earlier (see the APA section) these anticipatory adjustments are used by the controller to overcome (at least partially) the mechanical effects of external and internal mechanical perturbations to the stability of the body (Belen'kiy et al 1967; Cordo and Nashner 1982; Aruin and Latash 1996; Shiratori and Latash 2000; Shiratori and Latash 2001). APAs commonly occur prior to the application of postural perturbation and therefore are suggestive of the existence of feed-forward mechanisms of control. Although the existence of APAs does not point directly to the involvement of any specific cortical involvement, it is the modulation of APAs based upon on the subject's prior knowledge (cognitive function) on the mechanical effects of such perturbation that suggests participation of cortical structures in human posture control. For example, Shiratori and Latash (2001) have shown correlations between the kinetic energy carried by an object released by an experimenter and APA magnitudes in the trunk, leg and arm muscles during the task of catching a load while standing. Their results have demonstrated that subjects are able to recognize and anticipate the effect of a predictable perturbation and modulate their anticipatory muscle activity with respect to the time of impact and the mechanical effect caused by the load. It is likely that cognitive centers of the brain, such as the frontal lobe, are involved in this task as well as cortical areas responsible

for processing multisensory information such as temporal-parietal cortex, supplementary motor area, and prefrontal cortex (de Waele et al, 2001; Quant et al, 2004; Adkin et al, 2006).

Along with behavioral studies and clinical observations, several lines of research using brain imaging techniques have helped researchers to understand the intricate task of producing movements and controlling the human posture. Deecke et al (1969) studied the electroencephalogram (EEG) in humans and observed that structures within the frontal lobe were activated much earlier than the primary motor area (about 1.5 s prior to the first EMG modulation changes). This finding had driven the authors to suggest that the primary motor area serves as a muscle activator area but not as a planner of complex motor behaviors. The activity reported by Deecke et al (1969) represented a negative cortical potential recorded over the frontal lobe and the center of the scalp. Nowadays, this evoked potential is commonly referred to as the Bereitschaftspotential. Although EEG technique has been used with success in studies involving voluntary movement, only a few studies have been performed related to postural control (Dietz et al, 1985; Ackermann et al, 1986; Dimitrov et al, 1996; Saitou et al, 1996; Slobounov et al, 2000; Quant et al, 2004a,b; Slobounov et al 2005; Adkin et al, 2006) . These studies have suggested, in particular, that postural adjustments and compensatory postural movements involve supra-spinal, including cortical structures. Saitou et al (1996) described the existence of MRCP (motor-related cortical potentials) in tasks involving ballistic movements of the body (tip-toe rising) similar to those seen prior to the execution of voluntary movements of the limbs. Slobounov et al (2005) confirmed these results and expanded the knowledge by describing an increase in the gamma-range activity about 200 ms prior to the reversal point during body sway in the anterior direction. These results taken together support the notion that postural adjustments are not just automatic muscle responses to perturbation mediated by the brain stem and spinal cord but cortically controlled intentional movements. Also, the burst of gamma activity close to the perceived safety boundaries of stability indicates the existence of a neural detector for postural instability triggering the initiation of compensatory postural movement to prevent a fall. In addition, Slobounov et al (2000) found a decrease in the EEG power in concussed individuals during a task requiring the recognition of unstable postures and thus inferred that people who have suffered mild traumatic brain injury (MTBI) have an impaired ability to recognize the limits of their functional boundaries of stability. These finding may result from

damage to the brain that causes reduced local excitation as well as reduced synchronization of the active generators of the higher frequency bands as measured by EEG (Thompson, 2005).

The use of brain image techniques as a method of recognizing increased activity on specific structures of the brain matter also includes the use of event-related functional Magnetic Resonance Imaging (fMRI). Although the use of fMRI is still very limited in its practical application to studies of posture control (in order to collect data, subjects must be kept as immobile as possible what makes its application to posture studies very restricted) Slobounov et al (2006a) cleverly set experimentation using FMRI to relate brain activation sites to postural tasks. They evaluated the ability of health subjects to recognize unstable positions of a projected image of a virtual body while they could submit the subject to fMRI. They explored the possible existence of a neural detector for postural instability and found that successful recognition of unstable postures induces activation of distinct areas of the brain including bilateral parietal cortex, anterior cingulate cortex and bilateral cerebellum In addition, significant activation is observed in the basal ganglia (caudate nucleus and putamen) but only during perception of animated postures. Their findings point to the existence of modality-specific distributed activation of brain areas responsible for detection of postural stability.

Ouchi (1999) used another brain imaging technique, positron emission tomography (PET) to investigated the role of different brain structures involved in the control of different postures: supine with eyes open; standing with feet together (eyes open or closed); unipedal standing on one foot; and standing with two feet in tandem. Their results have shown that, as compared with the supine posture, standing under all configurations studied revealed activation of cerebellar structures and visual cortex. Specifically, these results suggest that the cerebellar efferent system plays an important role in maintenance of standing posture and that the visual association cortex may sub-serve regulating postural equilibrium while standing.

2.8 The relation between posture control and movement generation

Since forces and moments generated by a voluntary movement can destroy the postural equilibrium (Ramos and Stark 1990), it has been suggested that any movement performed has two distinct components (Bernstein 1967). The first component is directed to the execution of the desired motor act. The second component is directed to the regulation of the posture. Two different views exist about how these components are coordinated.

The first view suggests that postural synergies form a separated group of motor programs. This postural motor program can be combined with another plan controlling the desired motor act (Massion et al. 1999). This view was termed ‘dual control scheme’ or DCS by Slijper (2001). The second view suggests that such distinction between the organization of the movement and the organization of the posture does not exist and they are part of a same motor plan. This later view was termed ‘single control scheme’ or SCS by Slijper (2001). Evidence of both views can be found in results of experiments that explored the anticipatory postural adjustments (APA) features under the reaction time paradigm.

Both views have generated predictions about the APAs and their relation to the focal action. The DCS view assumes two independent control processes running in parallel that make it possible to dissociate the onset of a focal movement from the postural adjustments. In another words, the relative timing between the APA and the focal onset can vary when time constraints imposed by reaction time exist. The DCS hypothesis has been supported by results showing the onset independence of the focal and postural acts. Particularly, that the onset of the postural response is delayed in movements made under RT when compared to self-paced conditions (Bouisset and Zattara 1990; Benvenuti et al. 1997).

The SCS view assumes that the generation of APAs and focal movements originate from a single control process and would generate invariant timing between postural and focal components. Evidence for the SCS hypothesis has been found in experiments showing a dependency of APAs on features of the focal action that triggered the perturbation (Aruin and Latash 1995; Touissant et al. 1997a,b). In a study performed by Aruin and Latash (1995), APAs scaled with the magnitude of the focal action while the perturbation was constant and predictable. In the studies performed by Touissant et al. (1997a,b), changes in APAs were dependent on the technique used to lift the load. Taken together, these results corroborate the

SCS hypothesis since there is a dependency of the focal movement and the postural generation processes.

In a series of studies conducted by Slijper (2001), both hypotheses were tested in regard to self-paced (SP), simple reaction time movements (SR), and choice reaction time (CRT) instructions. In one of these studies, a standard mechanical perturbation was used consisting of a load release task that eliminated any confounding mechanical factor. The APAs of trunk and lower limb muscles were recorded and compared across the three types of instruction. The main results show that APA onsets under SRT were delayed as compared to SP conditions (similar results were found by Zattara and Bouisset 1988; Benvenuti et al. 1997). In CRT conditions, APAs occurred earlier than in SRT conditions and no differences were found between CRT and SP conditions. These results speak in favor of the DCS hypothesis.

2.9 Synergies

In motor control literature, a large number of studies have been published using the word “synergy”. For example, entering the combination ‘motor synergy’ in Pubmed generates about 250 articles’ titles as result of the search. However, one would be surprised how the concept of the word ‘synergy’ differs among the publications.

In the Cambridge international dictionary of English (1996), synergy is defined as *‘the combined power of a group of things when they are working together which is greater than the total power achieved by each working separately’*. In motor control, it was probably Sir Hughling Jackson (1889) the first to introduce the idea that muscles are controlled in groups and not independently. He did not use the term ‘synergy’ explicitly but instead, the idea is implicated in his so frequently cited quotation *‘...the central nervous system knows nothing about muscles, it knows only movements’*. The great French neurologist Felix Babinski studied motor disorders in persons with cerebellar injuries and used the term “asynergia” to describe certain cases of loss coordination. Sir Charles Sherrington (1906) also used the term synergy as terminology around the beginning of the 20th century. He referred to synergy as sets of muscles (or muscle groups) performing essentially the same action. For instance, all muscles related to flexion of the knee are considered synergistic,

namely biceps femoris, semitendinosus, and semimembranosus. One can argue that this view was established on the beginning of the 20th century when foundations of motor control started to take shape. However, this definition is now the most accepted in clinical practice, is based on the association of the anatomical function of muscles, and does not take into account any other feature necessary to the development of a organized movement such as temporal and scaling relations.

Bernstein (1969) laid down the foundations of human movement coordination studies by describing the problems to be solved by the central nervous system. Bernstein described the possibility of achieving a certain motor purpose by using different limb configurations (the degrees of freedom (DOF) problem) and suggested that human control of movements is organized hierarchically in at least 4 different levels (A, B, C, and D). Level A was considered the level of muscle tone. Level B was considered as the level of muscular and articular links. Level C was considered as level of space and level D was considered as level of actions. According to Bernstein (1969), the level B is the level of synergies where the elements performing the movement interact with each other. Bernstein emphasized that the occurrence of synergies is probably the way of solving the degrees of freedom problem since it reduces the total number of variables to be dealt with by the CNS. In summary, Bernstein was able to formalize the main problems facing researchers studying the control of movements, while emphasizing that the problem of studying movements is one of understanding the control of a redundant system. He ruled out any straight-forward and unambiguous relation between the nervous impulses and the movements themselves.

In line with Bernstein's ideas, Gelfand and Tsetlin (1966) defined functional synergies as *a fixed and reproducible interaction of the joints or groups of joints, organized and controlled by the CNS for effective solution of a specific problem*. These task-specific or intention-specific structural units have certain properties:

- 1- The internal structure of the unit is more complex than its interaction with the environment.

- 2- Part of a structure cannot itself be considered a structural unit for the same tasks.

3- Parts of a structural unit that do not work with respect to a task is eliminated or it adapts itself within the main task.

In addition, these authors also proposed the *principle of minimal interaction* which they described at two levels: 1) at the level of interaction among elements (local) where the functional outcome of each element on its own state is minimally dependent on the output of other elements; and 2) at the level of interaction between individual elements and the higher level of the hierarchy (global) where the effect of changes in the output of each element on the common, functionally defined outcome of the unit is minimized by changes in the output of other elements (Gelfand and Latash 1998).

It is clear that the definition of motor synergy purposed by Gelfand and Tsetlin (1966) is far more complete than others presented earlier. Their definition has not only a more detailed description but its practical application has allowed others to develop tools to recognize a synergy and explore its features.

The term postural synergy was introduced by Bernstein considering it as a combination of control signals to a number of muscles whose purpose is to assure the stability of a limb or the whole body in anticipation of a predictable postural perturbation or in response to an actual perturbation (Latash, 1998). Traditionally, postural synergies have been viewed as a separate group of motor programs that can be mixed with the programs of the desired movement. An alternative view is that there is only one program involving both aspects of the movement, postural control and limb motion. According to the latter view, any movement involves many more joints than those apparently used to produce the movement. Thus, changes in activity of postural muscles become not an addition to a motor program but an inherent part of it.

Postural synergies have traditionally been studied in the context of postural reactions to external perturbations and postural adjustments related to voluntary movements. Studies have examined both kinematics and muscle activity (EMGs) as the variables of interest. Alexandrov and his collaborators (1998) studied the axial synergies during upper trunk bending and found that forward and backward movements were performed simultaneously with opposite movement of the lower body segments. This strategy kept the body center of mass within the boundaries of the base of support. A principal component of analysis on the

joint displacement with respect to time was performed and a very strong correlation among joint action was found. The correlation was strong enough such that the first PC accounted for approximately 99% of the total variance. These results showed that the ratio among the movements performed by the joints did not vary much, thus ensuring the position of the COM within the base of support.

Another example of studies involving motor synergies and using the kinematics as variables of interest comes from a group of collaborators led by Scholz and Schöner (1999). This group developed a different approach to explore the synergistic features of the motor system; the uncontrolled manifold hypothesis (UCM hypothesis) (Scholz and Schöner, 1999). The UCM hypothesis implies that the controller acts in the space of elemental variables (for example, joint angles or digit forces) and creates synergies that stabilize (in a sense of decreasing variability across repetitive trials) an important performance variable (for example, endpoint trajectory or the total force produced by the hand). As such, the hypothesis emphasizes a feature of motor synergies that can be called stability/flexibility: Synergies ensure stability of a performance variable while allowing variability of elemental variables that allows to perform other tasks and/or to deal with perturbations to actions.

According to this hypothesis, when a controller wants to stabilize a particular performance by using the activity of multiple elements, it selects a subspace within the space of the elements' action corresponding to a desirable value of the performance variable. This subspace is the uncontrolled manifold. These authors studied tasks as sit-to-stand where the joint configuration observed at each point in normalized time was analyzed with respect to the variability found across the trials. The variability was decomposed into components that did and did not affect the variables considered as describing the performance to be controlled, in particular COM displacement. The first variability component is parallel to the uncontrolled manifold (UCM) while the second one is orthogonal to the UCM (ORT). The results showed that the position of the COM in the sagittal plane was very well stabilized by co-variations of the joint rotations. Scholz and Schöner also analyzed other performances variables such as head position, which was found to be stabilized to a lesser degree. Other experiments using different tasks have been reported by this group such as kinematics of the arm during quick draw pistol (Scholz et al. 2002), freesbie launching, and recently the method was used in a study of quiet stance.

EMGs of postural muscles have also been used in the study of postural synergies. For instance, in an experiment performed by Cordo and Nashner (1982) postural muscle activity was recorded during a pushing (or pulling) of one's body by a stiff handle that was held or subjects were instructed to pull or push rapidly on the handle. The results showed postural reactions in response to both perturbations and also postural activity prior to the movement initiation (APAs). They found certain temporal and spatial patterns in the activation of the postural muscles (postural synergies). For example, proximal muscles were activated first followed by distal muscles. However, the idea of fixed synergies is not well accepted since other factors such as magnitude and direction of perturbation can change the temporal and the spatial distribution of the muscle activation (Horak and Nashner 1986). Also, analysis of latency or magnitude of EMGs modulation have been used to define synergies. Various statistical techniques have been applied to recognize synergies and they include cross-correlations (Danna-dos-Santos et al. 2007b), ratios between related pairs of muscles (Nashner 1977), correlation and regression (Bouisset et al. 1977), and principal component analysis (Alexandrov et al 1998).

More recently the UCM method was also applied in studies involving EMGs as the elemental variables of interest (Krishmanoorhty et al. 2003; Wang et al. 2006; Danna-dos-Santos et al. 2007a).

2.10 The uncontrolled manifold hypothesis

As stated earlier, one of the central problems investigated in motor control literature is the degrees-of-freedom problem described by Bernstein in 1967. This problem has also been called the motor redundancy problem and has arisen from observations made by Bernstein on the work of blacksmiths during the beginning of the 20th century. Bernstein observed that during the execution of the laborious task of hammering all the joints showed higher variability of angular movements than the tip of the hammer used to hit the chisel. Bernstein's insight, based on the idea that the trajectory of the tip of the hammer was being kept more stable than the parts generating the movement, was that the CNS has no sensory elements linking physically the hammer to the brain. Thus, Bernstein concluded that, in some way, the joints were capable of putting the hammer in certain positions by using a variety of

configurations. This pattern reflects a commonly seen feature in human movements: motor variability.

Most theories of human movement control attempted to solve the redundancy problem by selecting an optimal solution based on some criteria (e.g. Cole and Abbs 1986; Viviani and Flash 1995). These theories try to eliminate DOFs in order to find a singular solution that optimizes the chosen criteria. Although these theories explain some human motor behavior, their biological meaning is still obscure. It was Gelfand and Latash (1998) who expanded the ideas published by Gelfand and Tsetlin (1966) and proposed the '*principle of abundance*'. According to this principle, there is no elimination of DOFs but instead, all DOFs participate in the motor task. In this way, the numerous elements are able to accomplish the motor goal and also ensure a certain amount of flexibility in case of sudden perturbation or execution of a secondary concomitant task.

In experimental situations, stability of a performance variable can be assessed by quantifying the variability of the variable across time samples or its reproducibility across different trials (Schöner, 1990). This analysis of variability is the core of the UCM hypothesis. This approach has made possible to address important questions in the motor control scenario such as:

- 1- when is a synergy present?
- 2- how to quantify the strength of a synergy.
- 3- how to test the development of a new synergy.

This approach has been used to study a number of kinematic, kinetic and muscle activation variables. Scholz and Schöner (1999) studied a sit-to-stand task where joint configurations were analyzed with respect to trial to trial variability. By applying the UCM method of computation they found that the position of COM in the sagittal plane was kept more stable than its position at the horizontal plane. The same group also investigated the kinematics of a quick-draw pistol shooting task. They reported that the variable stabilized the most along the execution of the movement was the orientation of the pistol.

The motor control laboratory at Penn State was responsible for expanding the use of the UCM approach to other levels of analysis (Krishnamoorthy et al. 2003b, 2004; Wang et al. 2005). This group has used the UCM approach to investigate the coordination involved among the muscle activation patterns found prior and during the execution of a motor task. The implementation of such method follow required the following steps;

1- Identifying the elemental variables. More specifically they have proposed the use of principal component analysis (PCA) with factor extraction on indices of integrated EMGs across repeated trials. The new set of variables resultant from PCA analysis are referred as muscle modes and considered as the elemental variable.

2-Selection of a performance variable. Displacement of COP, shear forces and moments around the vertical axis are being currently considered among the studies in development.

3-Computation of the Jacobian of the system relating small changes in the important control variable to small changes in the magnitude of the muscle modes. This step is achieved by using multiple linear regression.

4-The UCM is computed and the variance in magnitude of muscle modes is decomposed into two components. The first component, namely V_{ucm} represents the variability that does not exert any changes in the performance variable while the second one, V_{ort} is the component where any variation of muscle-mode magnitude will influence the performance variable.

Mostly these studies have been related to the investigation of muscle synergies involved on the control of vertical posture. Krishnamoorthy et al (2003) performed a series of studies involving load release and voluntary discrete body sways and analyzed the synergies involved in preparation for the self-induced perturbation. The results have pointed in the direction that the controller united the muscles in functional groups to stabilize such variables as the COP coordinate. In summary, the method has been shown to be reliable and a new

group of questions have been raised allowing researchers to go further in the understanding of human movement control.

CHAPTER 3

STUDY #1

Muscle Modes and Synergies during Voluntary Body Sway

3.1 Introduction

The notion of muscle synergies has been used with respect to the control of movements in a variety of species ranging from chick embryos to spinal frogs, cats, and humans (Bradley and Bekoff 1990; Holdefer and Miller 2002; Johnson and Bekoff 1996; Lemay and Grill 2004; Saltiel et al. 2001). Using muscle synergies has been viewed as a solution to the notorious problem of motor redundancy (Bernstein 1967; Turvey 1990) by decreasing the number of degrees-of-freedom at the control level. Correlation techniques and matrix factorization methods have been used to identify smaller sets of variables that are able to describe the behavior of muscles across a variety of actions or along the time course of an action (d'Avella et al. 2003; Ivanenko et al. 2004, 2006; Maier and Hepp-Reymond 1995; Tresch et al. 2006; Weiss and Flanders 2004).

Recently, a somewhat different approach to motor synergies has been developed based on the principle of motor abundance (Gelfand and Latash 2002) and using the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999; reviewed in Latash et al. 2002). The UCM hypothesis implies that the controller acts in the space of elemental variables (for example, joint angles or digit forces) and creates synergies that stabilize (in a sense of decreasing variability) an important performance variable (for example, endpoint trajectory or the total force produced by the hand). As such, the hypothesis emphasizes a feature of motor synergies that can be called stability/flexibility: Synergies ensure stability of a performance variable while allowing variability of elemental variables that allows to perform other tasks and/or to deal with perturbations to actions.

Muscle activations commonly co-vary; such a co-variation may or may not be related to stabilizing a particular variable (Ivanenko et al. 2004; Ting and Macpherson 2005; Tresch et al. 2006). Since the times of Hughlings Jackson (1889), researchers have assumed that the

brain does not control large muscle groups by sending independent signals to each muscle. Hence, co-variation of muscle activations may reflect not a control strategy specific for a given task but relatively task-independent built-in relations. To deal with this issue the idea of muscle modes (M-modes, Krishnamoorthy et al. 2003a,b) has been introduced as elemental variables manipulated by the controller; a change in the magnitude of each mode is expected to produce parallel changes in activation levels of many muscles. Analysis of variance of muscle modes has revealed multi-muscle-mode synergies stabilizing shifts of the center of pressure (COP, the point of application of the resultant vertical force acting on the body from the support) when a standing person produced an action (Krishnamoorthy et al. 2003b, 2004; Wang et al. 2005).

Two recent studies have shown a drop in an index of multi-M-mode synergies stabilizing COP shifts - this index reflects how well changes in the gains at individual modes co-vary to stabilize a COP shift - when a standing person was initiating a quick action, a quick step or a quick whole-body sway (Wang et al. 2005, 2006). This finding has been interpreted as a purposeful destabilization of the COP coordinate to facilitate its quick change. However, other interpretations of these findings are possible. In particular, the high rate of COP shift could by itself influence the index of synergies, as supported by a recent modeling study (Goodman et al. 2005). It is also possible that the structure of M-modes and/or their effects on COP shifts (the Jacobian of the system) depend on the rate of COP shift.

The main purpose of the current study has been to test how M-modes, their effects of COP shifts (the Jacobian), and multi-M-mode synergies depend on the speed of voluntary COP shift. We used a cyclic voluntary COP change (sway) at different frequencies to produce COP shifts at different rates. Our main hypotheses have been that (1) a change in the sway frequency would lead to changes in the structure of M-modes and/or in the Jacobian, and (2) an increase in the sway frequency would lead to a drop in the index of multi-M-mode synergies. Confirming these hypotheses, particularly the second one, would mean that the earlier conclusions on purposeful destabilization of the COP coordinate during fast actions have to be reconsidered. Refuting the first hypotheses would support the notion of M-modes as preset muscle groups that are used by the controller within a broad range of tasks.

Refuting the second hypothesis would support the idea that the controller can purposefully destabilize a performance variable (COP coordinate) to facilitate its quick change.

3.2 Methods

Subjects

Eight subjects (five males and three females) with the mean age 30.8 years (± 6.5 SD), mean weight 72.5 kg (± 17.2 SD) and mean height 170 cm (± 7.0 SD) participated in the experiment. All the subjects were healthy, without any known neurological or muscular disorder. All subjects were right-handed based on their preferential hand usage during writing and eating. All the subjects gave informed consent based on the procedures approved by the Office for Research Protection of The Pennsylvania State University.

Apparatus

A force platform (AMTI, OR-6) was used to record the moments of force around the frontal and sagittal axes (M_y and M_x , respectively) and the vertical component of the reaction force (F_z). Disposable self-adhesive electrodes (3M Corporation) were used to record the surface muscle activity (EMG) of the following muscles: soleus (SOL), gastrocnemius lateralis (GL), tibialis anterior (TA), biceps femoris (BF), semitendinosus (ST), rectus femoris (RF), vastus lateralis (VL), vastus medialis (VM), lumbar erector spinae (ES), and rectus abdominis (RA). The electrodes were placed on the right side of the subject's body over the muscle bellies. The distance between the two electrodes of each pair was 3 cm.

The signals from the electrodes were amplified ($\times 3000$) and band pass filtered (60-500 Hz). All the signals were sampled at 1000 Hz with a 12-bit resolution. A personal computer (Gateway 450Mhz) was used to control the experiment and to collect the data using the customized Labview-based software (Labview-5 – National Instruments, Austin TX, USA).

Procedures

The experiment started with two control trials that were later used for normalization of the EMG signals (see the next section). In those trials, the subjects were instructed to stand quietly and hold a standard load (5 kg) for ten seconds in front of the body keeping the arms fully extended. The subjects held the load by pressing on two circular panels attached to the ends of a bar. The load was either suspended from the middle of the bar or it was attached through a pulley system such that it produced an upward acting force on the bar (Figure 3.1). Two trials were performed with the load acting downward and upward in a balanced order across subjects. The time interval between the two trials was 30 s.

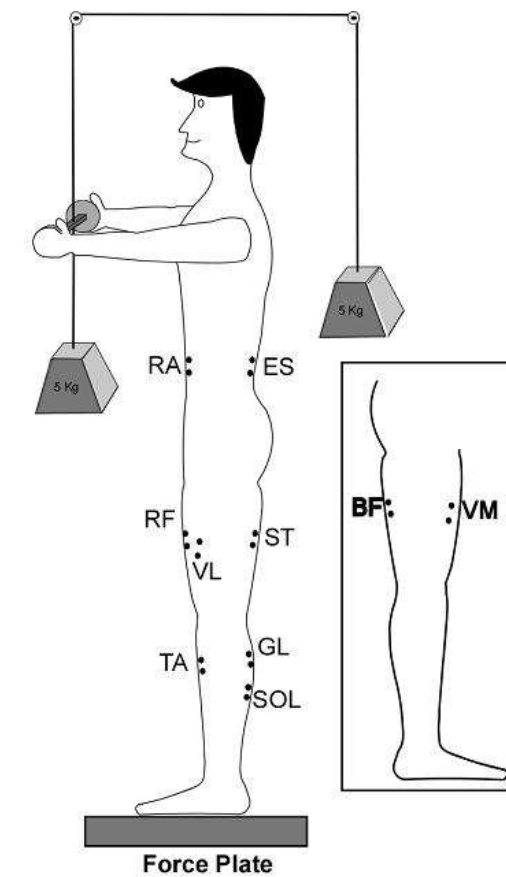


Figure 3.1: A schematic representation of the subject's posture in the control trials. The subject stood on the force plate holding a load (5 Kg) in front of the body or behind the body (using the pulley system) for 10 s. EMG electrode position is shown for soleus (SOL), gastrocnemius lateralis (GL), tibialis anterior (TA), biceps femoris (BF), semitendinosus (ST), rectus femoris (RF), vastus lateralis (VL), vastus medialis (VM), lumbar erector spinae (ES), and rectus abdominis (RA).

The main task involved continuous voluntary sway (VS) in the anterior-posterior (AP) direction at different frequencies. Subjects were instructed to stand on the force plate with their feet in parallel and apart 15 cm. This foot position was marked on the top of the platform and reproduced across all frequencies. The arms were always kept crossed against the chest. The instruction was to produce a continuous sway reaching as far as possible forward and backward while keeping full contact of both heels and toes with the platform during the movement. A metronome paced the subject's movements. The metronome was set at five different frequencies: 0.25 Hz, 0.50 Hz, 1.00 Hz, 1.50 Hz, and 2.00 Hz. Subjects were asked to reach the most backward and most forward positions at each metronome beat; they were free to select their own limits of COP shift. Hence, complete cycles of body sway were performed at 0.125 Hz, 0.25 Hz, 0.50 Hz, 0.75 Hz, and 1.00 Hz, respectively.

A period of familiarization with the task was given to each subject prior to data collection. During the familiarization period, subjects performed the sway under all five frequencies during 2.5 minutes divided into five sections of 30 second each. Continuous visual feedback on the AP location of the center of pressure (COP_{AP}) was provided by the monitor placed 2.0 m in front of the subject at the eye level. The sequence of body sway frequencies was presented in a balanced order. During actual trials, no visual feedback was provided.

Each trial started with the subject standing quietly. Then, the metronome was turned on, and the subject was asked to begin swaying. Data collection started after the subject had completed at least four complete sway cycles and it lasted until fifteen full cycles were recorded. Only one trial was performed at each frequency, and the order of frequencies was randomized across subjects. A resting period of sixty seconds was given between trials when the subjects were allowed to sit and relax. The average duration of the experiment was forty minutes, and none of the subjects complained of fatigue.

Data processing

All signals were processed off-line using LabView-5 and MatLab 6.5 software packages. Signals from the force plate were filtered with a 20 Hz low-pass, second order, zero-lag Butterworth filter and COP_{AP} coordinate was computed using the following approximation:

$$\text{COP}_{\text{AP}} = -M_y/F_z$$

As commonly accepted in studies of COP shifts, we ignored the effects of the shear forces on the moments of forces measured by the platform because of the small lever arm of those forces (the AMTI platforms record the moments with respect to the platform center located 36 mm beneath the surface). Our pilot assessments suggest that the contribution of shear forces to the estimated COP shifts was always well under 10%.

For each sway frequency, twelve complete sway cycles were used for data analysis. The duration of each cycle was time normalized such that the total duration of each cycle was always 100%. The initiation (t_0) and end of each cycle (t_1) was defined by two consecutive extreme anterior positions of COP_{AP} . COP_{AP} displacement ($\Delta\text{COP}_{\text{AP}}$) was computed by subtracting the average COP_{AP} coordinate over a trial from the averaged COP_{AP} coordinate over each 1% window of the cycle.

EMG signals were rectified and filtered with a 50 Hz low-pass, second-order, zero-lag Butterworth filter. Changes in muscle activity associated with COP_{AP} shift were quantified as follows. Rectified EMG signals were integrated over 1% time windows of the cycles (I_{EMG}). In order to compare the I_{EMG} indices across muscles and subjects, we normalized them by the EMG integrals computed for the control trials when the subjects stood and held the 5.0 Kg load. I_{EMG} indices for the dorsal muscles (SOL, GL, BF, ST, ES) were divided by the EMG integrals over a time window of the same duration in the middle of the control trial when the load was held quietly in front of the body. I_{EMG} indices for the ventral muscles (TA, VM, VL, RF, RA) were divided by the EMG integrals obtained in the middle of the control trial when the load was suspended behind the body. This method of normalization is the same used in our earlier studies of muscle mode synergies (Krishnamoorthy et al. 2003a,b; Wang et al. 2005).

Statistics

Defining M-modes with principal component analysis (PCA)

For each subject and each frequency, the *IEMG* data formed a matrix with ten columns corresponding to ten postural muscles and 1200 rows corresponding to 1% time windows of all twelve cycles analyzed. The correlation matrix among the *IEMG* was subjected to PCA (using SPSS software) with *Varimax* rotation. The factor analysis module with principal component extraction was employed.

For each subject, the first three PCs were selected for further analysis based on the following criteria: an inflection point in the scree plots (the following PCs accounted for approximately similar amounts of variance per PC) and having indices of at least one muscle loaded significantly per PC (Krishnamoorthy et al. 2003a; Wang et al. 2005). We are going to address these PCs as muscle modes (M-modes, M_1 , M_2 , and M_3) and hypothesize that magnitudes of (coefficients at) the M-modes are manipulated by the controller to produce COP shifts. In other words, M-modes represent unitary vectors in the muscle activation space that can be recruited by the controller with different magnitudes. PCs number four and higher did not have significantly loaded muscle activation indices and were highly variable across the subjects. Therefore, we do not present data on those PCs although occasionally PC4 could account for a comparable amount of variance to that of PC3.

In order to test the hypothesis that M-modes (PCs) are similar across the different frequencies of sway and subjects, we used a method introduced by Krishnamoorthy and colleagues (2003a). Within this analysis, the M_1 - and M_2 -modes were first sorted by their action on the center of gravity (for details see Results). This method compares a group of vectors in the muscle activation space (for example, the M_1 vectors for a given subject across all the sway frequencies) to a central vector representing another group of vectors (for example, the M_2 vectors for another subject across the same sway frequencies). The central vector is a PC vector for which the sum of squared distances between it and the remaining vectors within the same group is minimal. The method tests an assumption that all vectors of the same number in all subjects and across all frequencies point in similar directions. In this case, cosine of the angle between a central vector and any vector of the same number is

expected to be close to unity, while cosine of the angle between a central vector and any vector of a different number is expected to be close to zero.

The procedure includes the selection of a central vector among the actual PC vectors leading to the identification of three central vectors for each comparison (\mathbf{p}_1 , \mathbf{p}_2 , and \mathbf{p}_3 corresponding to M_1 , M_2 , and M_3). The central vectors were identified for each subject over all frequencies $\{\mathbf{p}_i(s)\}$, and for each frequency over all subjects $\{\mathbf{p}_i(f)\}$. It was hypothesized that (1) for each subject, a PC vector \mathbf{p}_i is collinear to a central vector $\{\mathbf{p}_i(s)\}$ if $i = j$ (where $i, j = 1, 2, 3$) and orthogonal to it if $i \neq j$; and (2) for each task, a PC vector \mathbf{p}_i is collinear to a central vector $\{\mathbf{p}_i(f)\}$ if $i = j$ and orthogonal to it if $i \neq j$.

Absolute values of the cosines between the 10-dimensional PC vectors were used as a measure of closeness of their directions. We used absolute values of the cosines rather than angles themselves for statistical purposes; note that angles 0° and 180° are equivalent for PCs and for absolute cosine values while they are apparently different in angular units. Cosines of angles between each central vector $\mathbf{p}_i(f)$ ($i = 1, 2, 3$) for a selected sway frequency and \mathbf{p}_j for each individual subject performing at each sway frequency and cosines of angles between each $\mathbf{p}_i(s)$ ($i = 1, 2, 3$) for each subject and \mathbf{p}_j for each sway frequency performed by each subject were calculated. These were further transformed into z-scores using Fisher's z-transformation. Further, these values were averaged either across subjects or across frequencies.

A one-way ANOVA with factor *Frequency* (0.125, 0.25, 0.50, 0.75, and 1.00 Hz) was used to analyze possible changes in the amount of variance explained by individual PCs. To test similarities between PCs across the subjects and sway frequencies, a factor *Central Vector* (\mathbf{p}_1 , \mathbf{p}_2 , and \mathbf{p}_3) was used in combination with *Frequency*. Significant effects were further explored with Tukey's pair-wise contrast tests.

Defining the Jacobian (\mathbf{J} matrix)

Linear relations between changes in the magnitudes of M-modes (ΔM) and COP_{AP} shifts (ΔCOP_{AP}) were assumed and the corresponding multiple regression equations were computed over the 12 cycles performed by each subject and at each frequency. The coefficients of the regression equations were arranged in a matrix that is a Jacobian matrix:

$$\Delta\text{COP}_{\text{AP}} = k_1 \cdot \Delta\mathbf{M}_1 + k_2 \cdot \Delta\mathbf{M}_2 + k_3 \cdot \Delta\mathbf{M}_3 ;$$

$$\mathbf{J} = [k_1 k_2 k_3]^T$$

Within this approach, the \mathbf{J} matrices are reduced to (3×1) vector-columns. For each subject, this analysis was run over the twelve individual cycles for each time interval (each 1% of the total cycle). The analysis was run over full cycles (100 intervals per frequency).

A two-way mixed design ANOVA was used with factors *M-mode* (M_1 , M_2 , M_3) and *Frequency* (0.125, 0.25, 0.50, 0.75, and 1.00 Hz) to analyze possible differences in the regression coefficients across the M-modes and frequencies of body sway. A one-way ANOVA was used with factor *Frequency* (0.125, 0.25, 0.50, 0.75, and 1.00 Hz) to analyze possible changes in the total amount of variance explained by the linear regression.

UCM analysis – Index of synergy

The uncontrolled manifold hypothesis assumes that the controller manipulates a set of elemental variables to stabilize a value or a time profile of a performance variable (Scholz and Schöner 1999; reviewed in Latash et al. 2002). In our analysis, M-modes play the role of elemental variables, while COP_{AP} shift represents the performance variable. Hence, we analyze the variance in the M-mode space at each phase of the sway cycle and compare its components that are compatible with a stable, i.e. reproducible from cycle to cycle, value of the COP_{AP} coordinate (estimated as its average value at that phase of the cycle) and those that lead to changes in this coordinate. To do this, for each cycle (n), IEMG indices were computed and transformed into $\Delta\mathbf{M}$ using the results of the PCA in Step-1 of the analysis. The $\Delta\mathbf{M}$ space has dimensionality $n=3$. A hypothesis that a particular magnitude of $\Delta\text{COP}_{\text{AP}}$ is stabilized by co-variation of $\Delta\mathbf{M}$ magnitudes accounts for one degree of freedom ($d=1$). Thus, the system is redundant with respect to the task of stabilizing particular $\Delta\text{COP}_{\text{AP}}$ values. The mean magnitudes of each $\Delta\mathbf{M}$ were computed. Since the model relating $\Delta\mathbf{M}$ to $\Delta\text{COP}_{\text{AP}}$ is linear, the $\Delta\mathbf{M}$ mean values were subtracted from each $\Delta\mathbf{M}$ computed value and the residuals were subjected to further analysis as follows.

The UCM represents combinations of M-modes that are consistent with a stable (reproducible from cycle to cycle) value of $\Delta\text{COP}_{\text{AP}}$. The UCM was calculated as the null space of the corresponding \mathbf{J} matrix (defined at Step-2 of the analysis). The null space of \mathbf{J} is

a set of all vector solutions \underline{x} of a system of equations $\mathbf{J}\underline{x}=\mathbf{0}$. The null space is spanned by basis vectors, \underline{e}_i . The vector of individual mean-free $\Delta\mathbf{M}$ s was resolved into its projection onto the null space:

$$f_{UCM} = \sum_{i=1}^{n-d} (\underline{e}_i^T \cdot (\Delta\mathbf{M})) \underline{e}_i$$

and component orthogonal to the null space:

$$f_{ORT} = (\Delta\mathbf{M}) - f_{UCM}$$

The amount of variance per DOF within the UCM is:

$$V_{UCM} = \sigma_{UCM}^2 = \sum_{i=1}^N f_{UCM}^2 / ((n-d)N_{trials})$$

and orthogonal to the UCM is:

$$V_{ORT} = \sigma_{ORT}^2 = \sum_{i=1}^N f_{ORT}^2 / (dN_{trials})$$

V_{UCM} and V_{ORT} were the main dependent variables used in this analysis. In lay terms, they correspond to “good variability” (V_{UCM} that does not affect ΔCOP_{AP} computed for a certain time interval during the oscillation cycle) and “bad variability” (V_{ORT} that changes ΔCOP_{AP}). A two-way mixed-design ANOVA was used with factors *Frequency* (0.125, 0.25, 0.50, 0.75, and 1.00 Hz) and *Variance* (V_{UCM} and V_{ORT}) to analyze possible differences in the values of these two variables across the sway frequencies. To quantify the relative amount of the total variance that is compatible with stabilization of a particular COP_{AP} shift we used an index (ΔV) reflecting the difference between the variance within the UCM and orthogonal to the UCM. It was computed as:

$$\Delta V = (V_{UCM} - V_{ORT}) / V_{TOT}$$

where all variance indices are computed per degree of freedom; V_{TOT} stands for total variance.

3.3 Results

Although we analyzed the data separately over the two half-cycles of the sway corresponding to the backward and forward COP shift, there were no significant effects of the COP shift direction on any of the important outcome measures. Therefore, for clarity and

brevity, only results representing full cycles will be reported. This section is organized in the following way. First, the basic patterns of COP_{AP} shifts and muscle activity are described. Further, the results of the PCA are presented with analysis of mode similarity across the sway frequencies and subjects. Finally, we describe the results of the uncontrolled manifold analysis applied to the mode data.

Patterns of COP_{AP} and muscle activity

Across all five frequencies of sway, the subjects were able to show qualitatively similar ‘sine-like’ time profiles of COP_{AP} . The average sway frequencies across the eight subjects were 0.12 ± 0.01 Hz, 0.49 ± 0.004 , 0.99 ± 0.02 , 1.45 ± 0.03 , and 1.9 ± 0.17 for the nominal metronome frequencies of 0.125, 0.5, 1.0, 1.5, and 2 Hz. Figure 3.2 shows the COP_{AP} profile averaged across 12 trials during body sway performed by a typical subject at 0.125 Hz and 0.75 Hz (thick line and thin line, respectively). Note the similarity of the shapes and similar peak-to-peak amplitudes in the two panels. Characteristics of COP_{AP} shifts were similar across all other frequencies. Table 3.1 summarizes the averages and standard errors of the peak-to-peak COP_{AP} displacement for each frequency of the sway.

Effects of sway frequency of the peak-to-peak COP_{AP} displacement were tested with a one-way repeated measures ANOVA with the factor *Frequency* (0.125, 0.25, 0.50, 0.75, and 1.00 Hz). No differences across the five frequencies were found ($F_{[4, 35]} = 1.11$, $p > 0.3$). These results confirm that subjects had similar COP_{AP} displacement across the five frequencies. As expected, the peak rate of COP_{AP} scaled with the sway frequency. Averaged across subjects peak rates were 0.10 m/s (± 0.006), 0.21 m/s (± 0.010), 0.37 m/s (± 0.015), 0.49 m/s (± 0.026), and 0.62 m/s (± 0.058) for the 0.125, 0.25, 0.5, 0.75, and 1.0 Hz respectively. A one-way ANOVA showed a significant effects of *Frequency* on the peak rate of COP_{AP} change across the five frequencies ($F_{[4, 35]} = 43.57$, $p < 0.001$). All Tukey's pair-wise comparisons showed significant differences ($p < 0.01$).

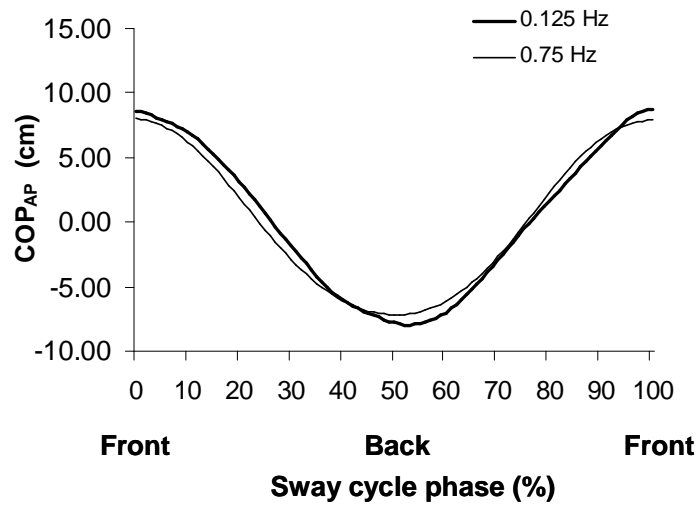


Figure 3.2: Average COP_{AP} displacement across cycles for a representative subject. Thick and thin lines represent COP_{AP} overall pattern for the sway frequency of 0.125 Hz and 0.75 Hz (the lowest frequency and the second highest frequency, respectively). Note the similarity in the time profiles and similar sway amplitudes in these two tasks.

Table 3.1: Peak-to-peak COP displacements across sway frequencies

Frequency (Hz)	0.125 Hz	0.25 Hz	0.50 Hz	0.75 Hz	1.00 Hz
Average COP_{AP} (cm)	16.06 ± 0.62	16.25 ± 0.67	17.80 ± 0.56	15.28 ± 1.17	15.88 ± 1.21

Means and standard errors of peak-to-peak COP_{AP} across subjects for the five different body sway frequencies are shown.

There were regularities in the patterns of activation of the leg and trunk muscles across the sway frequencies. In particular, during the forward-to-backward part of the sway cycle (0 to 50%), there was a decrease in the level of activation of dorsal muscles (SOL, GL, BF, ST, and ES) and an increase in the activity of ventral muscles (TA, VM, VL, RF, and RA). At the instant of the most backward COP displacement (50% of the cycle time), ventral muscle activity was typically high and the dorsal muscle activity was low. Over the backward-to-forward sway (51 to 100%), the ventral muscles activity decreased while the dorsal muscles exhibited an increase in their activity. The overall pattern is illustrated in Figure 3.3 that shows EMG profiles for six of the ten postural muscles in a representative

subject during body sway at 0.125 Hz (thin lines) and 0.75 Hz (thick lines). The subset of six muscles was selected to illustrate typical activation patterns in muscles crossing the three major leg joints. Note that at the higher sway frequency there was an increase in the peak EMG levels and also a shift from the smooth, sine-like changes in the muscle activity (at 0.125 Hz) to more abrupt bursts.

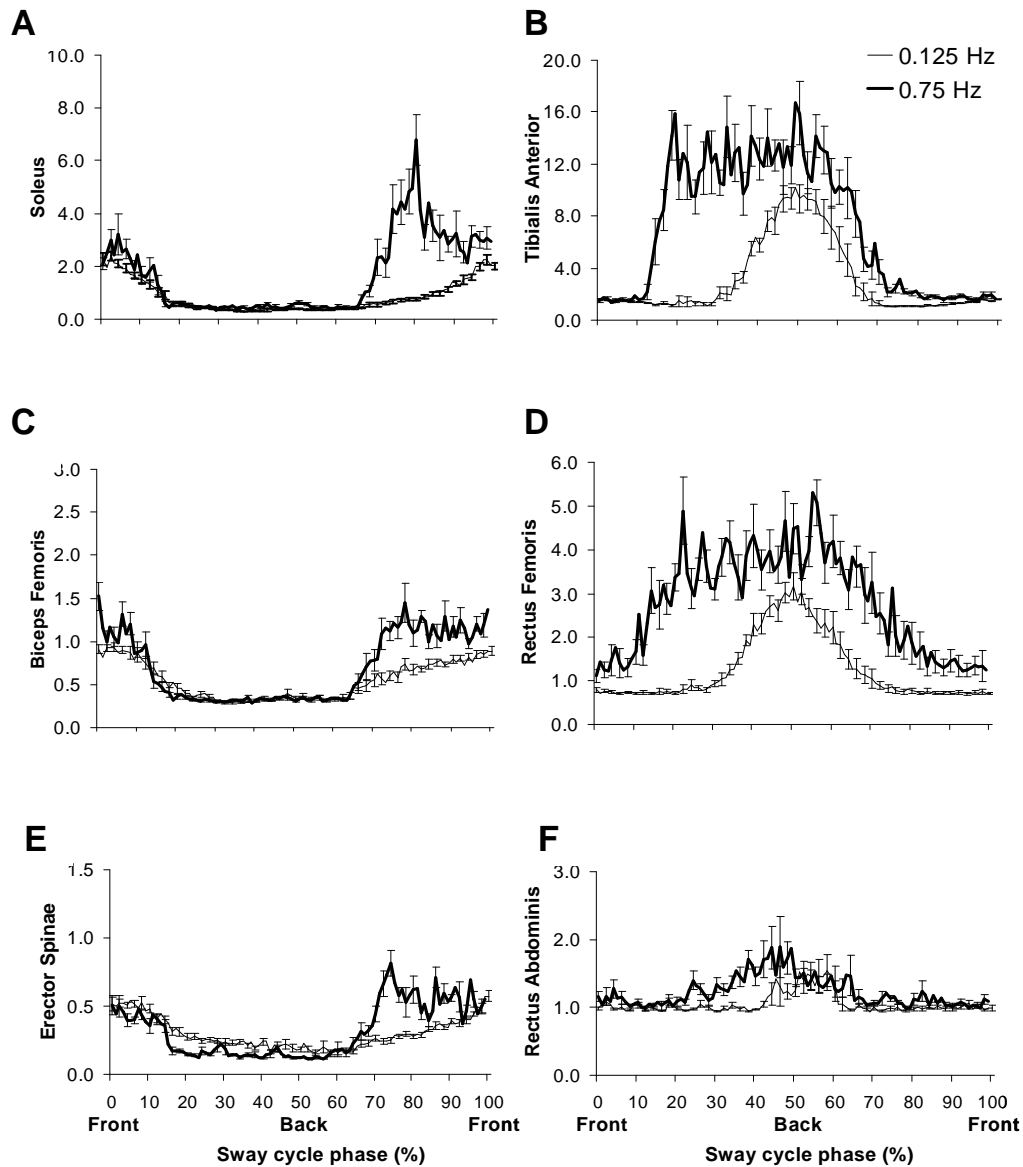


Figure 3.3: Normalized muscle activity averaged across cycles (with standard error bars) for a typical subject. Muscle activity is displayed in arbitrary units and sway cycle is expressed in percentage of its total duration. Phases 0% and 100% indicate the most anterior COP position ('Front') and phase 50% indicates its most posterior position ('Back'). The scales have been selected for better visualization.

Principal component analysis (PCA)

To identify groups of muscles whose activity was modulated in parallel during the sway, we used PCA (as described in the Methods). PCA was run on data over the whole cycle duration. Based on the criteria described in the Methods, three first PCs were chosen in each data set.

The first three principal components (PC1, PC2, and PC3) accounted, on average, for 84.6% ($\pm 1\%$) of the total variance during body sway performed at 0.125 Hz, 77.2% ($\pm 0.3\%$) at 0.25 Hz, 70.9% ($\pm 0.5\%$) at 0.50 Hz, 66.7% (± 0.7) at 0.75 Hz, and 65.4% ($\pm 1\%$) at 1.00 Hz. Figure 3.4 (Panel A) illustrates the dependence of the total amount of variance explained by the first three PCs on sway frequency. A significant decrease in the z-scores of the amount of variance explained by the first three PCs ($F_{[4, 115]}=82.64$, $p<0.001$) was confirmed by a one-way ANOVA with factor *Frequency* (0.125, 0.25, 0.50, 0.75, and 1.00 Hz). Tukey's pair-wise contrasts showed significant differences between all frequency pairs ($p<0.05$) with the exception of 0.75 Hz and 1.00 Hz pair. Although the variance explained by the first three PCs decreased as a function of sway frequency, across the whole range of frequencies the total amount of explained variance was similar or higher than values reported in earlier studies using PCA for muscle mode identification (Krishnamoorthy et al. 2003b; Wang et al. 2005).

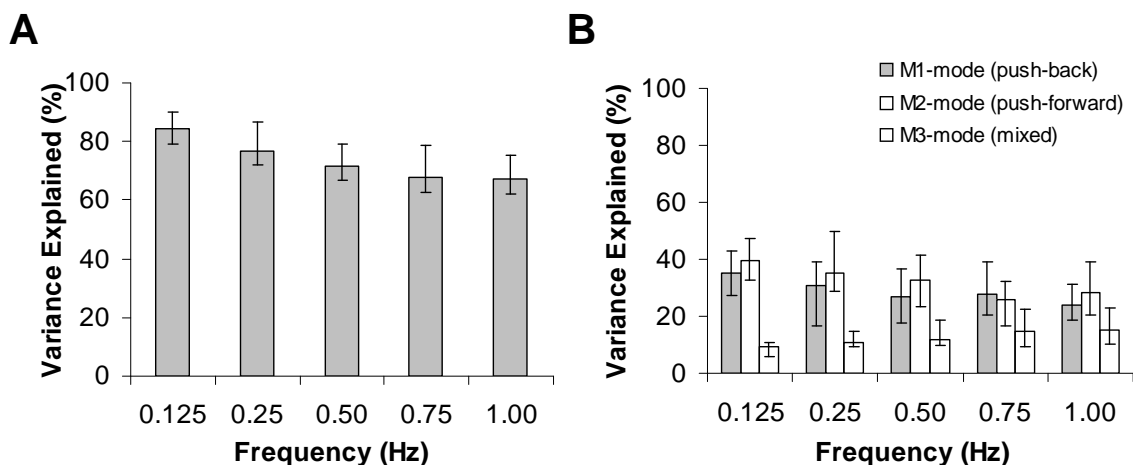


Figure 3.4: Panel A: Averages across subjects, maximum and minimum ranges of the amount of variance explained by the three first principal components. Note the drop in the amount of variance with sway frequency. Panel B: Averages across subjects, maximum and minimum ranges of variance explained by each mode (Mode 1= push-back; Mode 2= push-forward; and Mode 3= mixed).

Loadings at individual muscle activation indices for the first two PCs were similar across both subjects and frequencies. In particular, one of the first two PCs showed high loading values for the IEMG indices of the dorsal muscles, while the other PC showed high loading values for the IEMG indices of the ventral muscles (Table 3.2). Table 3.2 shows individual loadings for all muscles under all five sway frequency conditions, averages for each muscle loading were calculated across subjects. The third PC typically showed only a couple of muscles significantly loaded, and these muscles varied across the subjects. Because this pattern was similar to that described by Krishnamoorthy and colleagues (2003a,b), we decide to use the same names for the PCs, namely the “*push-back*” M-mode (or M_1), the “*push-forward*” M-mode (M_2), and the “*mixed*” M-mode (M_3).

Variations in muscle activation during the sway cycle were accompanied by cyclic changes in the magnitudes of the M-modes. In general, during the forward-to-backward part of the cycle (0 to 50%) there was an increase in the magnitude of M_1 - and M_3 - modes and a decrease in the magnitude of M_2 -mode. During the backward-to-forward part of the cycle (51 to 100%) this pattern changed to a decrease in M_1 - and M_3 - modes and an increase in M_2 -mode magnitude. This pattern is illustrated in Figure 3.5 that shows M-mode profiles averaged across subjects during body sway at 0.125 Hz (Panel A) and 0.75 Hz (Panel B).

The average amount of variance accounted for by each of the three M-modes is illustrated in Figure 3.4 (Panel B) across the sway frequencies. Since, in different subjects the “*push-back*” or the “*push-forward*” modes could account for larger amounts of variance, the averaging was performed over the modes of the same name rather than over the modes that accounted for most variance. Note that the first two modes accounted, on average, for 60% to 80% of the total variance.

A two-way mixed-design ANOVA with the factors *Frequency* (0.125, 0.25, 0.50, 0.75, and 1.00 Hz), and *M-mode* (M_1 , M_2 , and M_3) was used on the z-scores. There were significant main effects of *Frequency* ($F_{[4, 315]} = 21.45$, $p < 0.001$) and *M-mode* ($F_{[2, 315]} = 417.76$, $p < 0.001$). There was also a significant *Frequency* \times *M-mode* interaction ($F_{[8, 315]} = 14.29$, $p < 0.001$). Tukey’s pair-wise comparisons confirmed significant differences between 0.125 Hz and all other frequencies ($p < 0.01$) with the exception of 0.25 Hz. The same method confirmed that the data for the three modes were significantly different from each other ($p < 0.05$).

Table 3.2: Loading coefficients for the PCA for all muscles under all sway frequencies

Muscle	0.125 Hz			0.25 Hz			0.50 Hz			0.75 Hz			1.00 Hz		
	PC ₁	PC ₂	PC ₃	PC ₁	PC ₂	PC ₃	PC ₁	PC ₂	PC ₃	PC ₁	PC ₂	PC ₃	PC ₁	PC ₂	PC ₃
	M1-mode	M2-mode	M3-mode	M1-mode	M2-mode	M3-mode	M1-mode	M2-mode	M3-mode	M1-mode	M2-mode	M3-mode	M1-mode	M2-mode	M3-mode
SOL	0.86 ± 0.07	-0.26 ± 0.16	0.08 ± 0.17	0.84 ± 0.06	-0.27 ± 0.10	0.02 ± 0.03	0.70 ± 0.24	-0.30 ± 0.13	0.15 ± 0.31	0.76 ± 0.23	-0.21 ± 0.11	0.16 ± 0.3	0.70 ± 0.30	-0.17 ± 0.09	0.28 ± 0.39
GL	0.88 ± 0.04	-0.13 ± 0.13	0.08 ± 0.15	0.84 ± 0.05	-0.22 ± 0.14	0.04 ± 0.04	0.72 ± 0.25	-0.23 ± 0.17	0.17 ± 0.32	0.77 ± 0.22	-0.19 ± 0.11	0.18 ± 0.32	0.68 ± 0.32	-0.16 ± 0.10	0.30 ± 0.40
BF	0.80 ± 0.14	-0.17 ± 0.13	0.12 ± 0.29	0.79 ± 0.05	-0.12 ± 0.25	-0.03 ± 0.11	0.77 ± 0.10	-0.19 ± 0.13	0.03 ± 0.23	0.62 ± 0.25	-0.14 ± 0.19	0.17 ± 0.48	0.57 ± 0.30	-0.19 ± 0.19	0.38 ± 0.35
ST	0.54 ± 0.46	0.13 ± 0.51	0.16 ± 0.32	0.42 ± 0.45	0.27 ± 0.55	-0.01 ± 0.09	0.51 ± 0.41	0.25 ± 0.42	0.05 ± 0.31	0.38 ± 0.33	0.20 ± 0.47	0.22 ± 0.44	0.40 ± 0.40	0.14 ± 0.36	0.37 ± 0.43
ES	0.75 ± 0.10	-0.35 ± 0.12	0.09 ± 0.14	0.70 ± 0.11	-0.32 ± 0.14	0.04 ± 0.08	0.58 ± 0.12	-0.39 ± 0.16	0.07 ± 0.16	0.59 ± 0.06	-0.23 ± 0.14	0.04 ± 0.32	0.52 ± 0.23	-0.24 ± 0.19	0.29 ± 0.30
TA	-0.08 ± 0.28	0.84 ± 0.05	0.14 ± 0.17	-0.19 ± 0.17	0.77 ± 0.09	0.16 ± 0.22	-0.21 ± 0.24	0.69 ± 0.13	0.03 ± 0.24	-0.31 ± 0.15	0.54 ± 0.12	0.12 ± 0.33	-0.19 ± 0.24	0.60 ± 0.17	-0.13 ± 0.14
VL	-0.19 ± 0.10	0.90 ± 0.03	0.01 ± 0.06	-0.27 ± 0.07	0.84 ± 0.02	0.05 ± 0.05	-0.20 ± 0.14	0.80 ± 0.06	0.01 ± 0.07	-0.20 ± 0.11	0.76 ± 0.06	0.00 ± 0.14	-0.19 ± 0.18	0.72 ± 0.07	-0.03 ± 0.19
VM	-0.18 ± 0.11	0.91 ± 0.03	0.07 ± 0.10	-0.27 ± 0.12	0.83 ± 0.10	0.10 ± 0.08	-0.23 ± 0.07	0.84 ± 0.05	0.00 ± 0.09	-0.23 ± 0.11	0.76 ± 0.15	0.07 ± 0.25	-0.22 ± 0.06	0.78 ± 0.09	-0.07 ± 0.12
RF	-0.23 ± 0.10	0.91 ± 0.04	0.07 ± 0.09	-0.31 ± 0.10	0.82 ± 0.08	0.10 ± 0.10	-0.24 ± 0.09	0.84 ± 0.04	0.02 ± 0.12	-0.24 ± 0.11	0.77 ± 0.11	0.07 ± 0.26	-0.24 ± 0.10	0.78 ± 0.05	-0.08 ± 0.12
RA	0.13 ± 0.21	0.27 ± 0.28	0.71 ± 0.50	0.05 ± 0.05	0.12 ± 0.08	0.97 ± 0.03	0.08 ± 0.10	0.14 ± 0.20	0.61 ± 0.61	-0.03 ± 0.11	0.23 ± 0.25	0.52 ± 0.52	-0.04 ± 0.12	0.46 ± 0.25	0.12 ± 0.56

Averaged across subjects data are shown with standard deviations. SOL – soleus, GL – lateral gastrocnemius, BF – biceps femoris, ST – semitendinosus, ES – erector spinae, TA – tibialis anterior, VL – vastus lateralis, VM – vastus medialis, RF – rectus femoris, RA – rectus abdominis.

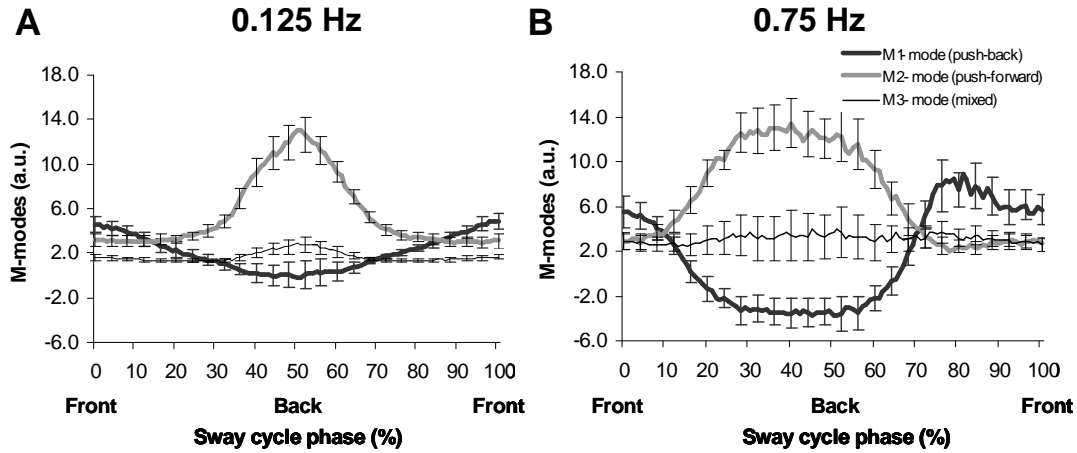


Figure 3.5: **Modulation of the three mode magnitudes within the sway cycle for a low frequency (0.125 Hz, panel A) and for a high frequency (0.75 Hz, panel B) sway. Averages across subjects are shown with standard error bars. M1-mode magnitude is shown by dark thick lines while M2- and M3-mode magnitudes are represented by dark thin lines and dashed lines, respectively. Mode magnitudes are displayed in arbitrary units and sway cycle is expressed in percentage of its total duration. Phases 0% and 100% indicate the most anterior COP position and phase 50% indicates its most posterior position.**

Verification of M-mode similarity across frequencies and subjects

As described in Methods, we used absolute values of the cosines between M-modes in the muscle activation space as a measure of similarity. Cosines between central vectors, \mathbf{p}_i , and each individual M-mode vector were computed and compared across the five frequencies of body sway and across subjects. For this purpose, the absolute cosine values were transformed into z-scores. Figure 3.6 shows the mean z-scores of cosines for analysis across the sway frequencies. Note the significantly higher z-scores between a central vector and individual vectors of the same M-mode. The contrast is particularly obvious for the first two M-modes (M_1 and M_2).

A two-way mixed-design ANOVA with factors *M-mode* (M_1 , M_2 , and M_3) and *Central Vector* (\mathbf{p}_1 , \mathbf{p}_2 and \mathbf{p}_3) was used on the z-scores (Figure 3.6). There were significant main effects of *M-mode* ($F_{[2, 108]}=12.11$, $p<0.001$) and of *Central Vector* ($F_{[2, 108]}=6.47$, $p<0.01$). There was also a significant *M-mode* \times *Central Vector* interaction ($F_{[4, 108]}=86.97$, $p<0.001$). Tukey's pair-wise comparisons confirmed significantly higher z-scores for cosines of the angles between the M_1 -and M_2 -modes for the different frequencies and the central vectors of the same number ($p<0.001$). Hence, the individual M-mode vectors M_1 and M_2

clustered around their central vectors (cosine values close to unity), i.e. the M-modes observed at different sway frequencies were approximately similar. Adding a factor *Subject* to this analysis did not change the results since this factor showed no significant effects.

A similar pattern was found for analysis across subjects. Figure 3.7 is organized similarly to Figure 3.6 but it presents data for all sway frequencies separately. In this case, a three-way ANOVA with factors *Frequency* (0.125, 0.25, 0.50, 0.75, and 1.00), *M-mode* (M1-, M2-, and M3- modes) and *Central Vector* (**p1**, **p2** and **p3**) was preformed. The results were similar to those described in the previous paragraph. In particular, there was a significant *M-mode* \times *Central Vector* interaction ($F_{(4,270)} = 9.01$ $p < 0.001$) confirming the significantly higher z-scores for cosines of the angles between the M₁- and M₂-modes for the different subjects and the central vectors of the same number ($p < 0.001$). Hence, the individual M-mode vectors M₁ and M₂ clustered around their central vectors, i.e. the M-modes found in different subjects were approximately similar.

The third mode (M₃) was much more variable across both subjects and frequencies. As a result, the cosine values between individual M₃ vectors and the M₃ central vector were not dramatically different than between vectors the M₃ central vector and vectors M₁ and M₂.

Taken together, these findings confirm similarity of M-mode composition in the muscle space across both subjects and sway frequencies, at least for the first two M-modes. It corroborates the idea similar sets of muscle modes are used to control large groups of muscles involved in whole-body sway at different frequencies.

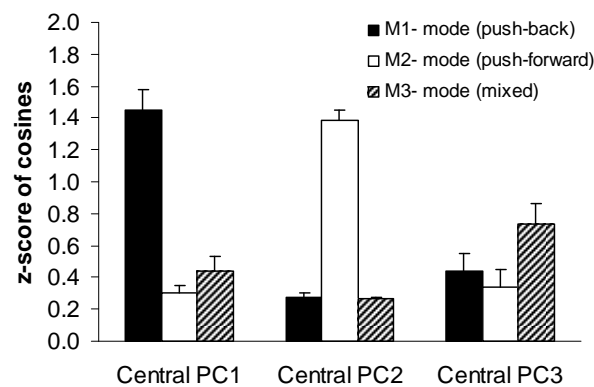


Figure 3.6: Averages and standard errors of z-scores of the absolute values of cosines between a central vector, p_i , and each mode vector; the data were averaged across body sway frequencies (with standard error bars). Note that z-scores are higher between a central vector and mode vectors corresponding to the same mode group.

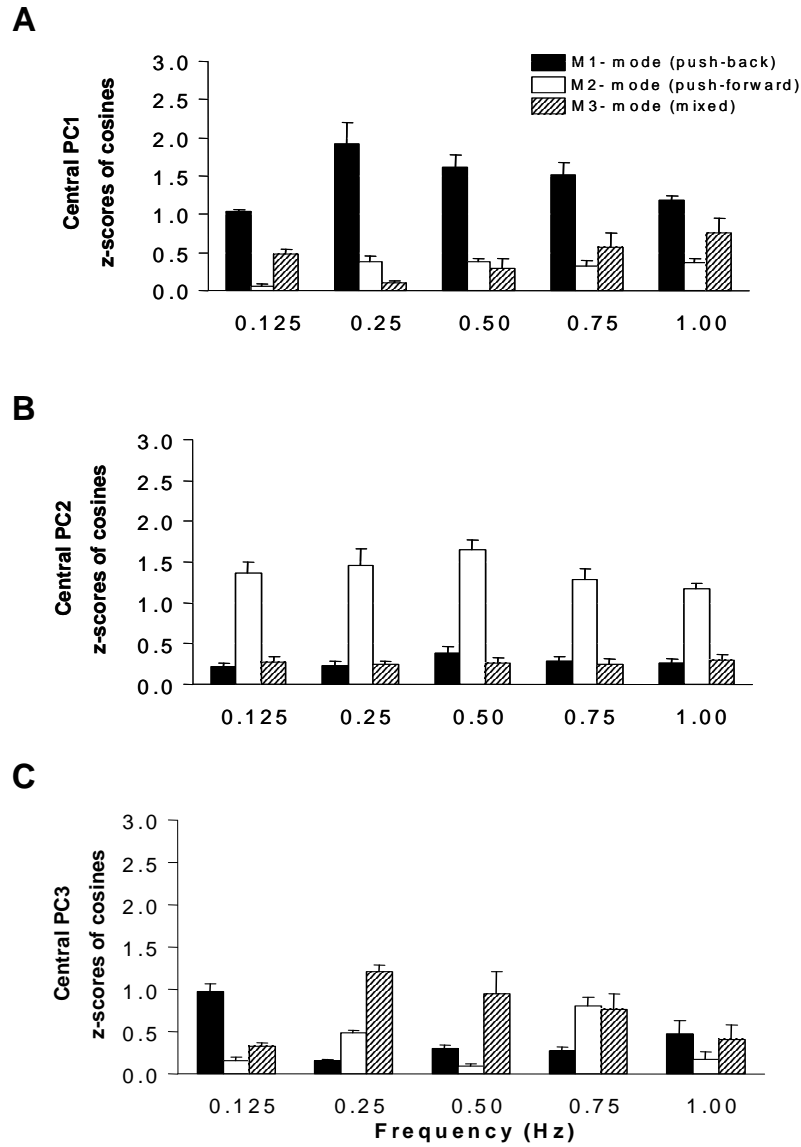


Figure 3.7: Panels A through C show Z-scores of the absolute values of cosines between a central vector, p_i , and each mode vector, PCs, averaged across subjects under different sway frequencies (with standard errors). Note that z-scores are highest between a central vector and mode vectors corresponding to the same mode group.

Identifying the Jacobians: Results of multiple regression analyses

This analysis investigated whether similar linear relations between gains at the M-modes and COP shifts can describe the data at different sway frequencies. The linear relations between changes in the magnitudes of M-modes (ΔM s) and the associated COP_{AP} shifts (ΔCOP_{AP}) were computed using multiple regression analysis. For each regression

analysis, the data were pooled over the time intervals within a cycle and across the 12 cycles. The coefficients of the multiple regression analysis are presented in Table 3.3 for each subjects and each sway frequency. The data in Table 3.3 show that in most cases M_1 -, M_2 -, and M_3 -modes were significant predictors of $\Delta\text{COP}_{\text{AP}}$ magnitude. Table 3.3 also shows information on how often each M-mode was a significant predictor ($p < 0.05$) of $\Delta\text{COP}_{\text{AP}}$. Note that M_1 -mode was the best predictor in a sense that its partial correlation with $\Delta\text{COP}_{\text{AP}}$ magnitude was significant in more cases than for the other two M-modes, followed by M_2 -mode, while M_3 -mode happened to be the worst predictor among the three.

The mean values and standard errors across subjects for each regression coefficient are displayed in Figure 3.8 (panel A). A two-way mixed design ANOVA was used with factors *M-mode* (M_1 , M_2 , and M_3) and *Frequency* (0.125, 0.25, 0.50, 0.75, and 1.00 Hz). There was a significant main effect of *M-mode* ($F_{[2, 30]} = 1.13$, $p < 0.05$) but no effect of *Frequency* ($F_{[2, 30]} = 5.74$, $p > 0.10$). Tukey's post-hoc contrasts confirmed that the regression coefficients for M_1 - and M_3 -modes were different from the regression coefficient for the M_2 -mode ($p < 0.05$).

Panel B of Figure 3.8 shows the amount of variance in $\Delta\text{COP}_{\text{AP}}$ explained by the regression model, i.e. its coefficient of determination. The plot shows a drop in the amount of variance explained with an increase in the sway frequency. This effect was confirmed by a one-way ANOVA with factor *Frequency* (0.125, 0.25, 0.50, 0.75, and 1.00 Hz) that showed significant main effect on z-scores of the variance ($F_{[4, 105]} = 101.64$, $p < 0.001$). Tukey's pairwise comparisons showed that z-scores were different across all body sway frequencies ($p < 0.05$). Note that despite the low absolute value, the regression coefficient at the M_2 -mode was significantly different from zero ($p < 0.05$).

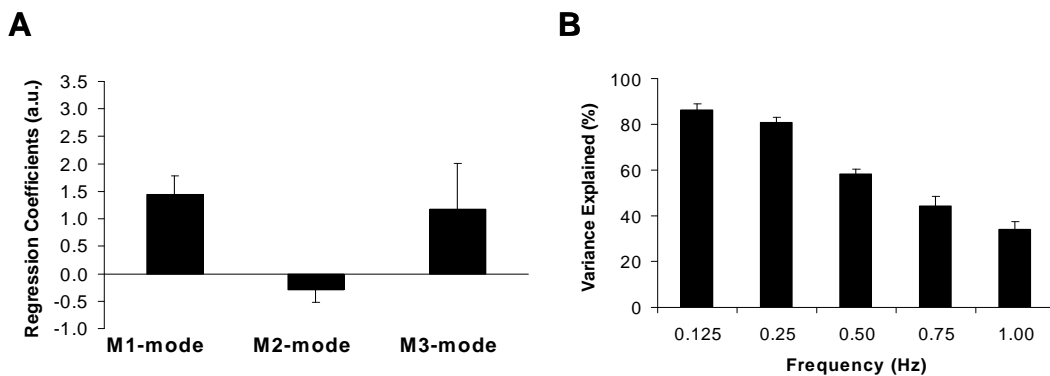


Figure 3.8: **A: Linear regression coefficients between each M-mode and COP shifts with standard error bars. B: Variance explained by linear regression of $\Delta\text{COP}_{\text{AP}}$ against the three M-mode magnitudes. Note the drop in the amount of variance explained with sway frequency.**

Table 3.3: Linear regression coefficients between M-modes and COP shifts

Freq Subject	0.125 Hz			0.25 Hz			0.50 Hz			0.75 Hz			1.00 Hz		
	M1- mode	M2- mode	M3- mode	M1- mode	M2- mode	M3- mode	M1- mode	M2- mode	M3- mode	M1- mode	M2- mode	M3- mode	M1- mode	M2- mode	M3- mode
1	2.90 **	-0.10	0.60 *	3.13 **	-0.03	0.27 **	2.44 **	0.32 **	0.71	0.37 **	-0.50 **	0.02	0.52 **	-0.37 **	-0.46
2	1.55 **	-0.45 **	4.51 *	2.17 **	0.16 *	6.66 **	1.30 **	0.35 **	0.75	1.34 **	0.23 *	4.15 **	1.48 **	-0.07	0.28 **
3	1.33 **	-0.87 **	1.66 **	4.71 **	0.20	-3.73 *	1.90 **	-0.59 **	0.21	-0.52 **	-0.24 **	1.86 **	1.12 **	-0.03	-0.07
4	0.34 **	0.00	10.05 **	0.98 **	-0.44 **	4.01 **	0.49 **	-0.24 **	4.13 **	-0.48 **	-0.41 **	1.76 **	-0.39 **	-0.12 *	1.42 **
5	2.81 **	-0.71 **	-0.29	1.34 **	-0.55 **	0.86	1.13 **	-0.15	-0.18	0.67 **	0.03	-0.60	1.39 **	0.78 **	-7.37 **
6	3.18 **	-1.23 **	12.01 **	3.76 **	0.92 **	-2.70	1.54 **	-0.49 **	0.25 *	3.45 **	0.28 **	-0.61 **	1.93 **	0.18 **	-0.27 **
7	1.70 **	-2.39 **	2.15 **	2.40 **	-0.54 *	-1.52	1.57 **	-0.61 **	0.51	0.70 **	0.20	-0.65 **	0.48 **	-0.36 **	1.32 **
8	2.14 **	-0.51 **	3.94 **	0.72 **	-0.21 *	0.91 **	0.17 **	-0.34 **	0.69	0.32 **	0.17 **	-0.34 **	-0.02	-0.05	0.37 **

Results of multiple regression analysis are shown for each subject under the five different sway frequencies (Freq).

* $p < 0.05$ ** $p < 0.001$.

UCM analysis

Data from twelve continuous sway cycles under five different frequencies were used to perform analysis of the structure of variability across each sway cycle in the space of M-modes. The method partitioned the total variance in the M-mode space across cycles into two components. The first component (V_{UCM}) was within an uncontrolled manifold (UCM) computed as the null-space of the corresponding \mathbf{J} matrix defined at an earlier step of analysis. The other component (V_{ORT}) was within a sub-space orthogonal to the UCM. Further, we used an index (ΔV) reflecting the difference between V_{UCM} and V_{ORT} , both normalized by the degrees-of-freedom in each sub-space. We interpret positive values of ΔV as reflecting a multi-M-mode synergy stabilizing the average COP shift.

In general, subjects demonstrated an increase in both V_{UCM} and V_{ORT} when the sway frequency increased. These results are displayed in Figure 3.9(Panel A), which shows the V_{UCM} and V_{ORT} per degree-of-freedom averaged across subjects. Note that V_{UCM} (black bars) was always larger than V_{ORT} while both increased with the sway frequency.

To analyze the effects of sway frequency on the two variance components, a two-way ANOVA with repeated measures, with the factors *Frequency* (0.125 Hz, 0.25 Hz, 0.50 Hz, 0.75 Hz, and 1.00 Hz) and *Variance-Component* (V_{UCM} and V_{ORT}) was performed. There were significant main effects of both *Frequency* ($F_{[4, 70]} = 4.38$, $p < 0.01$) and *Variance-Component* ($F_{[1, 70]} = 25.82$, $p < 0.001$) without a significant interaction ($p > 0.1$). Tukey's pair-wise comparisons showed significant differences between both 0.125 Hz and 0.25 Hz as compared to 1.00 Hz ($p < 0.01$ and $p < 0.05$, respectively). All other pair-wise comparisons did not reach significance.

To test whether the two variance components changed similarly with changes in the sway frequency and phase, an index (ΔV) reflecting their normalized difference was used. Time changes of this index for three sway frequencies are shown in panel B of Figure 3.9. Note that at low sway frequencies, ΔV was modulated within the sway cycle (black solid lines), while for the highest frequency, it was nearly constant. The dependence of the average magnitude of ΔV on sway frequency is shown in panel C. ΔV was always significantly larger than zero for all frequencies, which means that most variance within the M-mode space was within the UCM. We interpret this as a sign of a multi-M-mode synergy stabilizing COP shifts. There were no differences in ΔV across the five sway frequencies: The one-way

repeated measures ANOVA with factor *Frequency* (0.125 Hz, 0.25 Hz, 0.50 Hz, 0.75 Hz and 1.00 Hz) showed no effect of *Frequency* on ΔV ($F_{[4,39]} = 0.65$, $p > 0.5$).

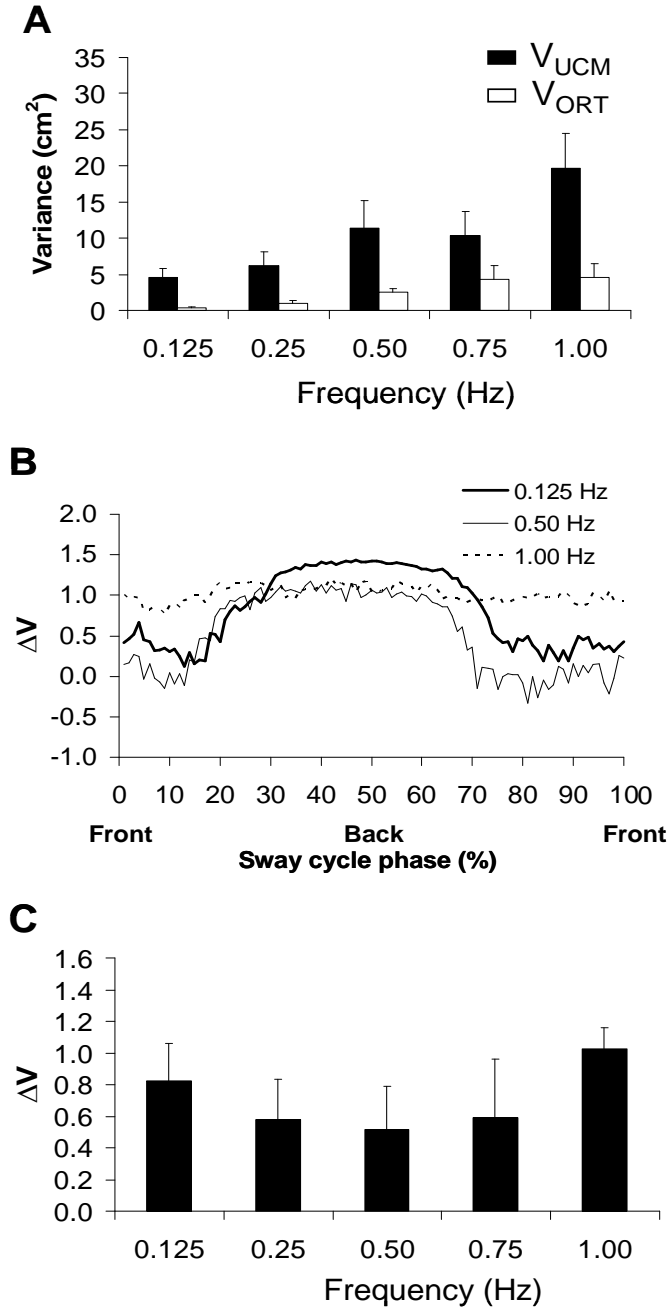


Figure 3.9: **A:** Averaged across subjects V_{UCM} and V_{ORT} components of the total variance for each sway frequency (with standard error bars). Dark bars represent V_{UCM} while light bars represent V_{ORT} . Note larger V_{UCM} and an increase in both variance components with frequency. **B:** Time profiles of ΔV averaged across subjects over the full sway cycle under three different sway frequencies, 0.125 Hz (the dark thick line), 0.50 Hz (the dark thin line), and 1.0 Hz (the dashed line). **C:** Means and standard errors for ΔV across subjects. Note that the values are positive and show inconsistent changes with frequency.

To further analyze possible modulation of M-mode variance and its components within the sway cycle, V_{UCM} and V_{ORT} were averaged within each 10% windows of the full cycle. The results are shown in Figure 3.10 where different panels displays results obtained under different sway frequencies. V_{UCM} data are shown with dark bars while V_{ORT} is shown with light bars.

It is clear from Fig. 11 that there was modulation of the two variance components within the cycle, particularly pronounced for V_{UCM} and for the low sway frequencies. For the higher frequencies, this effect is less pronounced, while V_{UCM} showed a general increase in magnitude. For instance, for the very first window of analysis, V_{UCM} was 1.84 cm^2 at 0.125 Hz, 2.45 cm^2 at 0.25 Hz, 4.55 cm^2 at 0.50 Hz, 6.45 cm^2 at 0.75 Hz, and 11.48 cm^2 at 1.00 Hz. V_{ORT} showed much less pronounced modulation within the cycle across all sway frequencies.

A three-way ANOVA with repeated measures, with factors *Frequency* (0.125 Hz, 0.25 Hz, 0.50 Hz, 0.75 Hz, 1.00 Hz), *Variance-Component* (V_{UCM} , V_{ORT}), and *Cycle phase* (1-10, 11-20 ... 91-100) was performed. There were significant main effects of all three factors, *Frequency* ($F_{[4, 700]} = 25.24$, $p < 0.001$), *Variance-Component* ($F_{[1, 700]} = 140.48$, $p < 0.001$), and *Cycle Phase* ($F_{[9, 700]} = 4.99$, $p < 0.001$). Two interactions were also statistically significant, *Frequency* \times *Variance-Component* ($F_{[4, 700]} = 8.42$, $p < 0.001$), and *Variance-Component* \times *Cycle Phase* ($F_{[4, 700]} = 25.24$, $p < 0.001$) reflecting the stronger modulation of V_{UCM} as compared to V_{ORT} with both sway frequency and cycle phase.

Two two-way ANOVAs were performed as a follow-up to test the effects of frequency and cycle phase on V_{UCM} and V_{ORT} separately. Both *Frequency* and *Cycle phase* had significant effects on V_{UCM} ($F_{[1, 350]} = 17.14.48$, $p < 0.001$; $F_{[1, 350]} = 4.43.48$, $p < 0.001$) while only *Frequency* showed a significant effect on V_{ORT} ($F_{[1, 350]} = 14.33$, $p < 0.001$). No interactions were significant.

Tukey's pair-wise comparisons showed that V_{UCM} during sway at 0.125 Hz was different from V_{UCM} during sways at 0.50, 0.75, and 1.00 Hz ($p < 0.05$). Significant differences were also seen between 1.00 Hz vs. 0.25, 0.50, and 0.75 Hz ($p < 0.001$). V_{ORT} showed significant differences between 0.125 Hz vs. 0.75 and 1.00 Hz ($p < 0.001$) as well as between 0.25 Hz vs. 0.75 and 1.00 Hz ($p < 0.001$). For comparisons among the cycle phases, V_{UCM} showed differences between the first 10% vs. phases 21-30%, 31-40%, 41-50%, and

51-60% ($p < 0.05$). Significant differences were also reached between 91-100% vs. 31-40% and 51-60% ($p < 0.05$).

Overall, this analysis confirms the existence of multi-mode synergies stabilizing COP shifts across the studied range of sway frequencies. Although the two components of variance, V_{UCM} and V_{ORT} , showed pronounced modulation across frequencies and phases of the sway cycle, the index of synergy (ΔV) stayed at comparably high levels across all the sway frequencies.

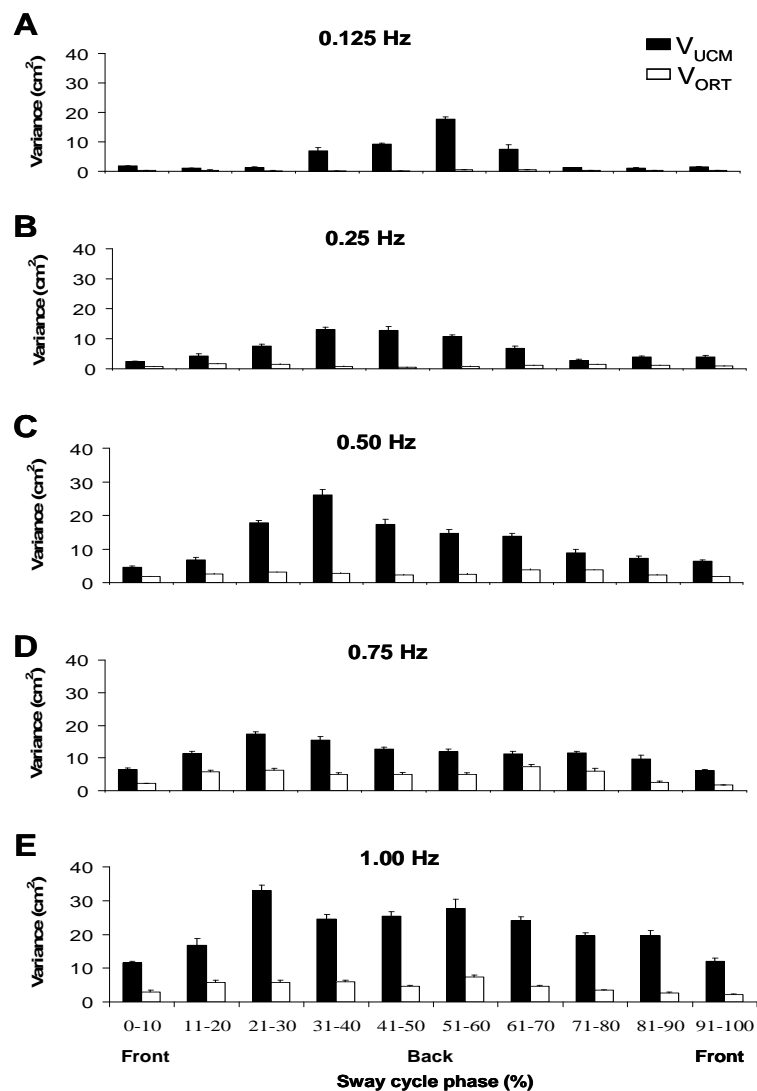


Figure 3. 10: V_{UCM} and V_{ORT} averaged within 10% windows of the sway cycle (with standard errors). Panels A through E show results obtained under the five different frequencies of sway. Dark bars show V_{UCM} while light bars show V_{ORT} , both in cm^2 . Note the larger V_{UCM} values and stronger V_{UCM} modulation within the sway cycle, which tends to become smaller at the higher frequencies.

3.4 Discussion

The main outcome of the study is the rejection of both hypotheses formulated in the Introduction. An increase in the sway frequency led to major changes in the peak rate of COP trajectory accompanied by substantial changes in the EMG patterns. Nevertheless, there were no significant changes in the composition of the muscle modes (M-modes) and in the mapping between small changes in the M-mode magnitudes and COP shifts (the Jacobian). The total variance of M-modes increased significantly with an increase in the sway frequency. However, this increase was not associated with significant changes in the index ΔV of the multi-M-mode synergy stabilizing the COP trajectory. These results provide the most comprehensive support for the notion of multi-M-mode synergies in whole-body tasks. They also support the idea that the central nervous system can modulate the level of participation of such synergies in a task-specific way. The results also have implications for such important issues of motor control as the control of discrete and rhythmic movements and the use of motor abundance.

Modes and synergies

We would like to emphasize the main differences between our approach to muscle synergies and approaches that have been used in most other studies. When a person performs an action involving many muscles, muscle activation patterns show variations both along the time course of the action and across its repetitions. Analysis within the space of muscle activations reveals co-variations that allow to describe the data more economically, with a smaller set of variables. Each variable from this smaller set maps onto many muscles and leads to parallel changes in their activation. A variety of computational methods have been used to discover such smaller sets of variables (d'Avella et al. 2003; Ivanenko et al. 2004, 2006; Maier and Hepp-Reymond 1995; Weiss and Flanders 2004); a recent study compared several methods and showed that they all lead to more or less similar results (Tresch et al. 2006). Variables from such smaller sets have been called synergies. These have been reported for a variety of human actions involving, among others, hand action (Maier and Hepp-Reymond 1995; Weiss and Flanders 2004), balance (Allum et al. 1995), locomotion (Ivanenko et al. 2004, 2006), and sit-up (Cordo et al. 2006). They have also been described

for patients with spinal cord injury (Minassian et al. 2004). The main role of synergies has been assumed to help solve the problem of motor redundancy, although they have also been discussed in relation to optimizing biomechanical factors (Stokes and Gardner-Morse 2001).

We accept the proposition that the central nervous system reduces the number of variables it manipulates for tasks involving large groups of muscles. However, we would like to view the variables defined with the help of PCA or other matrix factorization techniques not as synergies but as elemental variables (M-modes) corresponding to a smaller number of degrees-of-freedom but still leaving room for flexibility to perform typical motor actions. If one considers COP shifts in the anterior-posterior direction, manipulating magnitudes of three M-modes may be viewed as a means to simplify control as compared to manipulating activations of a dozen or so muscles. However, this does not by itself define a single solution for the problem of motor redundancy. The residual abundance (Gelfand and Latash 2002) of three M-modes allows forming synergies that stabilize a coordinate or a trajectory of the COP.

In a recent study (Torres-Oviedo et al. 2006), a qualitatively similar approach has been taken in the analysis of combinations of muscle modes stabilizing the center of mass during postural perturbations. The modes in that study were defined using non-negative matrix factorization methods. That study, however, did not use a formal model between changes in M-mode magnitudes and center of mass displacements that would be equivalent to the Jacobian used in our study.

Concepts of stability and flexibility are central to our understanding of synergies. The main function of synergies is to ensure stability properties, i.e. small in-trial or between-trials variability of an important performance variable (low V_{ORT}) while allowing relatively high variability of elemental variables (high V_{UCM}). Potentially, this leaves room for performing other concurrent tasks with the same set of elemental variables (M-modes) or dealing with unexpected perturbations (cf. Yang et al. 2006). This understanding originates from the principle of abundance (Gelfand and Latash 2002), which views the apparently redundant design of the motor apparatus not as the source of computational problems but as a powerful, flexible apparatus.

Note that the differences between the two approaches to synergies are not only linguistic. Our understanding emphasizes that synergies are functional in a sense that they

reflect control strategies that provide stability of important performance variables, while the alternative approach views any stable relations among elemental variables as a synergy. To use an intuitive illustration: The four legs of a table are a synergy according to the more traditional approach (their forces scale together with the weight of objects placed on the top of the table) but not according to our approach (the scaling reflects a single M-mode that reflects the structural design of the table, not a control strategy).

M-modes and COP displacements

Hypothetically, different sets of M-modes can be created within the same space of muscle activations. Depending on planned action, the same leg and trunk muscles can be united into sets of modes that are optimal to ensure stabilization of relevant performance variables. The three modes identified in the current study are used for COP stabilization across subjects and velocities of COP shift. However, a different set of modes may be assembled by the central nervous system for a different action, for example kicking a football. Indeed, an earlier study with subjects balancing on a narrow support and using light touch has revealed sets of M-modes that were qualitatively different from those observed during more natural standing (Krishnamoorthy et al. 2004). However, in other studies, M-modes observed in different subjects performing different actions while standing were shown to be similar (Krishnamoorthy et al. 2003a; Wang et al. 2005). All the mentioned studies compared a few discrete actions associated with COP shifts at similar rates.

In the present study, we used a much broader range of rates of COP shifts. Comparison of the absolute values of cosines between pairs of M-mode vectors in the space of muscle activations confirmed similarity of M-modes both across subjects and across sway frequencies. The mappings between M-mode magnitudes and COP shifts (the Jacobian) were also similar across the sway frequencies. This result is non-trivial, because sways at different frequencies within this range involve different joint coordination patterns: An increase in the sway frequency has been shown to lead to a decrease in the ankle joint motion amplitude and an increase in the hip joint motion amplitude (Alexandrov et al. 1998; Duarte and Freitas 2005; confirmed in our experiments by a pilot analysis of kinematics in selected subjects). We conclude, therefore, that the method of defining M-modes is robust across the used range of rates of COP shifts. This conclusion is in line with the general idea that a smaller number

of variables (M-modes in our study or “synergies” in earlier studies) can be used to construct behaviors with different characteristics (Loeb et al. 2000; Saltiel et al. 2001; d'Avella and Bizzi 2005; Ting and Macpherson 2005). We view the contrast between the different motor patterns and similar sets of M-modes stabilizing COP shifts as corroborating this general idea.

Despite the general similarity of M-modes across the sway frequencies, there was a significant decline in the amount of variance in the original data accounted for by the three M-modes at higher frequencies. At slow sway frequencies, the first three M-modes accounted for about 80-85% of the total variance (this compares favorably with earlier studies, which reported only 60% to 70% of the total variance accounted for by similar sets of three M-modes, Krishnamoorthy et al. 2003a,b; Wang et al. 2005). The amount of variance dropped to under 70% for the fastest sway frequencies. There was also a decline in the amount of variance in the COP shifts accounted for by the linear regression model based on the three M-modes. Note that these relatively modest amounts of variance explained by the three M-modes can be due to two factors, the inherently noisy nature of the raw signals (EMG) and the participation of the same muscles in actions different from the explicit task (see later).

There may be several explanations for these findings. First, swaying at higher frequencies may be viewed as a more challenging task, and an increase in task complexity has been shown to be associated with violations in proportional scaling of muscle activations (Cordo et al. 2006). It is also possible that COP shifts at a higher frequency are associated with an increase in the role of other task components such as, for example, keeping the trunk vertical or stabilizing the location of the center of mass (cf. Freitas et al. 2006). An increase in the role of those “other task components” might bring about two consequences. First, a larger number of M-modes based on the same set of muscles could play important roles. Second, there may be a drop in the total amount of variance in the muscle activation space related to performance of the explicit task, that is shifting the COP.

Discrete and continuous whole-body actions

Our study showed, on average, similar indices of multi-M-mode synergies across all the sway frequencies. As such, its results are strikingly different from those of two earlier studies with the initiation of a quick step and of a quick voluntary sway (Wang et al. 2005,

2006). In those studies, COP shifts at rates comparable to those at the highest sway frequencies in our experiment were associated with a dramatic drop in a similar index of multi-M-mode synergies (ΔV). Why did the two groups of studies from the same laboratory that used similar methods of data recording and analysis produce such contrasting results?

A major difference is that the former studies used discrete tasks performed on the background of steady-state standing while the current study used continuous cyclic COP shifts. Several recent papers have suggested qualitative differences between the neural control of discrete and cyclic actions (Wei et al. 2003; Schaal et al. 2004). We would like to build on this view and suggest that stability of a performance variable across repetitive trials may not necessarily be directly related to its speed but can be modified by the controller independently of the speed.

Within the equilibrium-point hypothesis of motor control (Feldman 1966, 1986), a discrete action may be viewed as resulting from a shift in the equilibrium state of a system or, in the dynamic systems parlance, a shift of its point attractor. A cyclic action may be viewed as a consequence of another steady-state of a system, a limit-cycle attractor. Within this framework, posture and cyclic actions are similar in a sense of both resulting from a steady-state at a control level. A discrete action is qualitatively different representing consequences of a change in a steady-state.

Recent studies of multi-finger synergies (Shim et al. 2005; Olafsdottir et al. 2005) and multi-M-mode synergies (Wang et al. 2005, 2006) have suggested that a synergy stabilizing a steady-state value of a performance variable (total force or COP coordinate, respectively) may be weakened or destroyed in anticipation or in the process of a quick shift of the performance variable. This makes sense: Otherwise, the synergy would counteract the required change in the variable. Does this mean that the central nervous system cannot stabilize a trajectory of a performance variable during its quick change (as would also be supported by recent modeling work, Goodman et al. 2005)?

Our current results suggest that this is not so. If a performance variable (COP coordinate) changes as a result of a steady-state oscillation, it can be stabilized by a synergy among elemental variables (M-modes), even if the speed of the process is high. This result underscores a basic difference between stability of steady-state processes (postural or oscillatory) and transient processes.

Modulation in the use of muscle abundance

Despite the fact that the average magnitude of the index of multi-M-mode synergy (ΔV) was similar across the sway frequencies, its modulation within the sway cycle showed substantial variations. The modulation was pronounced at slower sway frequencies and it all but disappeared at the highest frequency. Note that the modulation primarily involved changes in the V_{UCM} component of the variance (“good variance”) while the amount of V_{ORT} (“bad variance”) stayed relatively unchanged. In particular, at low sway frequencies, the controller allowed relatively more M-mode variability when the COP coordinate was close to its most backward location (50% in Fig. 10) as compared to its most forward location (0% and 100% in Fig. 10). These observations confirm that the CNS can modify the amount of “good variance” (flexibility) in a task-specific way (cf. Yang et al. 2006).

We can offer only a tentative interpretation of the observed pattern of modulation of the two components of M-mode variance. At low sway frequencies, the body’s center of mass was expected to move together with the COP (with a lag) such that the subjects could use vision to grade their sway amplitude, particularly during forward sway. They were expected to rely more on proprioception during backward sway. This might lead to more stereotypical muscle activation (M-mode) patterns while approaching the most forward COP coordinate as compared to those during approaching the most backward coordinate. At the highest sway frequency, the COP displacements occurred so quickly that they did not lead to visible body displacements. As a result, the within-a-cycle modulation of V_{UCM} disappeared.

Concluding comments

The method of identifying muscle modes and multi-M-mode synergies has proven to be robust across a variety of multi-muscle whole-body tasks. Still many important aspects of multi-M-mode synergies remain to be explored. Among those are the following:

How does muscle mode composition depend on sensory signals? A few studies have led to inconsistent results on the effects of sensory signals on multi-muscle groups (Allum et al. 1995; Cheung et al. 2005).

What are the neurophysiological mechanisms that assure stability of M-modes and M-mode synergies? A recent study on human subjects by Ivanenko and colleagues (Ivanenko et al. 2006) has suggested an important role of the spinal cord in the organization of multi-

muscle modes (addressed as synergies in the cited study). This view has been supported by earlier animal studies (Mussa-Ivaldi et al. 1994; d'Avella et al. 2003; Lemay and Grill 2004). On the other hand, supraspinal structures, such as the cerebellum and the motor cortex, have also been implied in discussions of muscle groups (Houk and Gibson 1987; Lemon et al. 1998; Schieber 2001; Holdefer and Miller 2002; Kargo and Nitz 2003; Thach and Bastian 2003).

What is the role of feedback and feed-forward mechanisms in multi-muscle synergies? Several recent models have suggested that both mechanisms can lead to structuring motor variability as predicted by the UCM hypothesis (Todorov and Jordan 2002; Latash et al. 2005; Goodman and Latash 2006). We are still at the very early stages of studies of multi-muscle synergies, but the current results are encouraging showing that we possess tools for quantitative assessment of such synergies.

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CHAPTER 4

STUDY #2

Flexible Muscle Modes and Synergies in Challenging Whole-Body Tasks

4.1 Introduction

Over the past few years, the notion of multi-muscle synergies has been explored using a variety of computational methods. All these approaches have assumed that a neural controller manipulates a few control variables that later translate into changes in activation levels of numerous muscles (cf. Hughlings Jackson 1889). In particular, matrix factorization techniques have been used to identify muscle groups, within which levels of muscle activation scale in parallel (d'Avella et al. 2003, 2005; Krishnamoorthy et al. 2003a,b, 2004; Ivanenko et al. 2004, 2005; Ting and Macpherson 2005; Tresch et al. 2006). Such groups have been addressed as muscle synergies or muscle modes (M-modes). In some of the studies, another step was taken. Namely, co-variation of hypothetical control variables (gains at which M-modes are recruited) have been studied in relation to specific performance variables such as coordinate of the center of pressure (COP, the point of application of the resultant force acting on the body from the support), which is assumed to be important for postural tasks (Krishnamoorthy et al. 2003b; Wang et al. 2005, 2006; Danna-Dos-Santos et al. 2007).

The latter approach is based on the idea of a hierarchical control of complex, multi-muscle actions that dates back to the seminal work by Gelfand and Tsetlin (1966). A recent development of these ideas (reviewed in Latash et al. 2002, 2007; Ting 2007) suggests that neural control is based on a hierarchy of synergies defined as neural organizations responsible for organizing a redundant set of elemental variables such that it stabilizes an important global variable. According to this view, there may be a hierarchically lower synergy that stabilizes composition of muscle groups and ensures proportional involvement of muscles within a group; in other words, it stabilizes the direction of a vector in muscle

activation space corresponding to a M-mode. Then, there is a hierarchically higher synergy that coordinates involvement of the M-modes to stabilize an important mechanical variable, for example COP coordinate.

Several experiments with postural tasks have revealed a small number of M-modes that showed similar compositions across both tasks and subjects (Krishnamoorthy et al. 2003a; Wang et al. 2005, 2006; Danna-Dos-Santos et al. 2007). One study, however, reported that when subjects were asked to perform the simple tasks of quick arm movements and voluntary body sway while standing on a board with a narrow support area, the composition of the M-modes changed (Krishnamoorthy et al. 2004). These observations have been confirmed in a recent study where the subjects were asked to stand on a narrow base of support and release a load held in front of the body (Asaka et al. 2007). Changes in the M-mode composition were rather dramatic: While commonly observed M-modes involved muscles crossing different postural joints on the dorsal or ventral side of the body, the “atypical modes” involved joint-specific parallel changes in activation levels of agonist-antagonist muscle pairs. Hence, they have been addressed as co-contraction M-modes.

In this study, we hypothesized that the composition of M-modes could indeed change under challenging conditions. To induce more subtle changes in the M-mode composition, we explored a range of complicating factors that made the task more challenging but did not lead to losing balance (unlike the cited studies where the subjects stood on boards with the very narrow support area, Krishnamoorthy et al. 2004 and Asaka et al. 2007). Namely, we explored the effects of closing the eyes, applying high-frequency, low-amplitude muscle vibration to the Achilles tendons, and standing on one foot on the M-mode composition during voluntary postural sway in the anterior-posterior direction. These manipulations are known to make postural tasks more challenging (Allum and Pfaltz 1985, Goodwin et al. 1972; Lackner and Levine 1979; Roll et al. 1989).

To explore possible changes at the upper level of the hypothetical hierarchy, we used the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999; Latash et al. 2002). This framework allows to quantify the co-variation among elemental variables (M-modes) that helps stabilize a performance variable (COP coordinate). More specifically, the analysis produces a quantitative index that shows how much variance in the space of M-modes is compatible with a certain value of the COP coordinate. We

hypothesized that adjustments in the composition of M-modes under more challenging conditions would make it harder for the controller to organize such a co-variation leading to a drop in the index of multi-M-mode synergies.

4.2 Methods

Subjects

Ten subjects (four males and six females) with the mean age 30.1 years (± 6.4 SD), mean weight 74.4 kg (± 14.2 SD) and mean height 1.73 m (± 0.051 SD) participated in the experiment. All the subjects were healthy, without any known neurological or muscular disorder. All the subjects were right-handed based on their preferential hand usage during writing and eating. All the subjects gave informed consent based on the procedures approved by the Office for Research Protection of The Pennsylvania State University.

Apparatus

A force platform (AMTI, OR-6) was used to record the moment of force around the frontal and sagittal axes (M_Y and M_X , respectively), the vertical component of the reaction force (F_Z), and the horizontal component of the reaction force in the anterior-posterior direction (F_X). Disposable self-adhesive electrodes (3M Corporation) were used to record the surface electrical activity (electromyogram, EMG) of the following muscles: soleus (SOL), gastrocnemius medialis (GM), gastrocnemius lateralis (GL), tibialis anterior (TA), biceps femoris (BF), semitendinosus (ST), rectus femoris (RF), vastus lateralis (VL), vastus medialis (VM), lumbar erector spinae (ES), and rectus abdominis (RA) (see Figure 4.1). The electrodes were placed on the right side of the subject's body over the muscle bellies. The distance between the two electrodes of each pair was 3 cm.

The signals from the electrodes were amplified ($\times 3000$) and band pass filtered (60-500 Hz). All the signals were sampled at 1000 Hz with a 12-bit resolution. A desktop computer (Gateway 450Mhz) was used to control the experiment and to collect the data using the customized LabView-based software (LabView-5 – National Instruments, Austin TX, USA).

A set of two muscle vibrators (VB100- Dynatronic) was used. The vibrators were placed over the right and left Achilles tendons and secured with elastic bands. The vibration at 100 Hz was used in some of the conditions (see later).

Procedures

The experiment started with three control trials that were later used for normalization of the EMG signals (next section). In the first trial, subjects were instructed to stand on the force plate quietly for ten seconds keeping the body vertical, with the arms crossed on the chest and looking at a stationary target placed 1.0 m in front of the subject at the eye level. The feet were kept parallel and apart 15 cm. This foot position was marked on the top of the force plate and reproduced across all the trials (except those when unipedal stance was required).

In the second and third control trials, the subjects were instructed to stand quietly and hold a standard load (5 kg) for ten seconds in front of the body while keeping the arms fully extended. The subjects held the load by pressing on two circular panels attached to the ends of the bar. In order to create a downward force requiring the subject to activate the dorsal muscles, the load was suspended in front of the subject from the middle of the bar. In the other control trial, an upward force was produced requiring the subjects to activate the frontal muscles; the force was produced by the load attached to the bar but suspended behind the subject through the pulley system (Figure 4.1). The time intervals between all three trials were 30 s. The subjects were instructed to stand in similar postures across the three control trials. To check similarity of the postures across the control trials, COP average location was computed immediately after each trial. A trial with holding a load was only accepted when both COP_{AP} and COP_{ML} average coordinates were close to the coordinates during the quiet standing trial: Namely, the difference between the conditions in the COP average coordinate had to be within 20% of the maximal COP migration range during the quiet standing trial. If this criterion was not met, the subject was asked to repeat the load holding trial.

The main task involved continuous voluntary sway in the anterior-posterior direction (AP) at a frequency of 0.5 Hz under five different experimental conditions: bipedal stance with eyes opened (BO); bipedal stance with eyes closed (BC); bipedal stance with eyes closed and vibration applied bilaterally to the Achilles tendons (BV); unipedal stance with

eyes opened (no vibration) (UO); unipedal vibration with eyes opened and vibration applied unilaterally to the Achilles tendon of the supporting leg (UV).

In conditions with bipedal stance (BO, BC, and BV), subjects were instructed to stand on the force plate in the same position as during the control trials, keeping their feet parallel and apart 15 cm, and arms crossed against the chest (Figure 4.2A). In conditions with unipedal stance (UO and UV), subjects were instructed to stand with the right foot over the center of the force plate while the left foot was lifted by flexing the knee (Figure 4.2B). The left knee was kept in contact with the right knee while the left foot was above the ground in a self-selected, comfortable position.

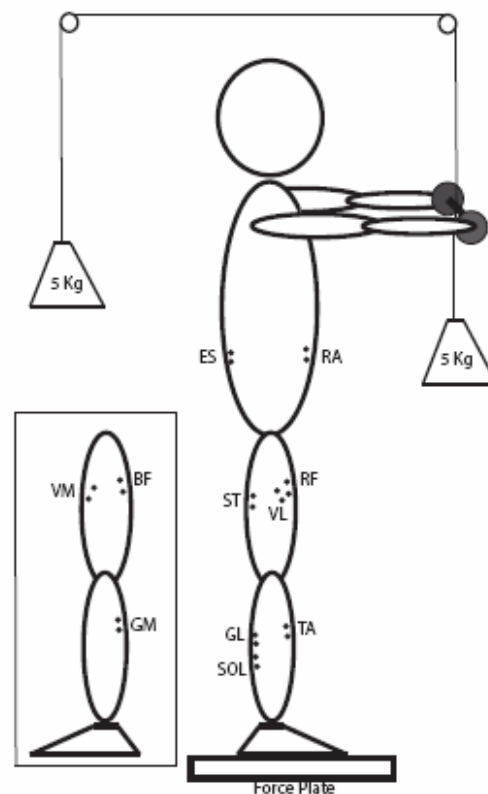


Figure 4.1: A schematic representation of the subject's posture in the control trials. The subject stood on the force plate holding a load (5 Kg) in front of the body or behind the body (using the pulley system) for 10 s. EMG electrode position is shown for soleus (SOL), gastrocnemius medialis (GM), gastrocnemius lateralis (GL), tibialis anterior (TA), biceps femoris (BF), semitendinosus (ST), rectus femoris (RF), vastus lateralis (VL), vastus medialis (VM), lumbar erector spinae (ES), and rectus abdominis (RA). The two drawings represents a lateral and a medial view of the electrodes placement.

The instruction under all the conditions was to produce a continuous sway of the body in the AP direction in such a way that the displacement of the body's COP was approximately 40% of the subject's foot length. An auditory metronome paced the subject's movements, and visual feedback on the AP location of the center of pressure (COP_{AP}) was provided by the monitor placed 1.0 m in front of the subject at the eye level. Subjects were asked to sway the body using mainly ankle rotation ("ankle strategy", Horak and Nashner 1986; Alexandrov et al. 2001) and reach the most forward and backward point of the required distance at each metronome beat (Figure 4.2A and 2B); the metronome frequency was set at 1 Hz. Visual feedback was used only during the initial phase to promote similar peak-to-peak COP_{AP} displacement across the experimental conditions. The visual feedback was unavailable over the period of data recording.

A period of familiarization with the task was given to each subject prior to data collection. During the familiarization period, subjects performed the body sway for 3 minutes under each condition (except BV and UV) divided into 3 episodes of 60 s each. Since during the actual trials visual feedback was used only at the beginning of the trial, the subjects practiced to keep swaying while maintaining their pattern of COP displacement unchanged once the visual feedback was turned off. Vibration was not used during the familiarization period to avoid possible adaptation of its effects along the actual experiment. The sequence of conditions during the familiarization period was presented in a balanced order.

Each trial started with the subject standing upright quietly. Then, the metronome was turned on, and the subject was asked to begin swaying. Under the BO and UO conditions, data collection started after ten seconds of swaying and it lasted for 30 s. Under the other three conditions (BC, BV and, UV), data collection started 40 s after the initiation of sway. This was done to reach steady-state and avoid transient effects during either the eyes closed or vibration condition (Polonyova and Hlavacka 2001).

Only one trial was performed for each condition. From this single trial, twelve continuous sway cycles were taken for further analyzes (details in *Data processing*). The order of conditions was balanced across subjects (it was different for different subjects). Resting periods of two minutes were given between trials. A chair was placed behind the subject close to the force plate such that the subject could sit and take a rest without moving

the feet. The average duration of the experiment was forty-five minutes, and none of the subjects complained of fatigue.

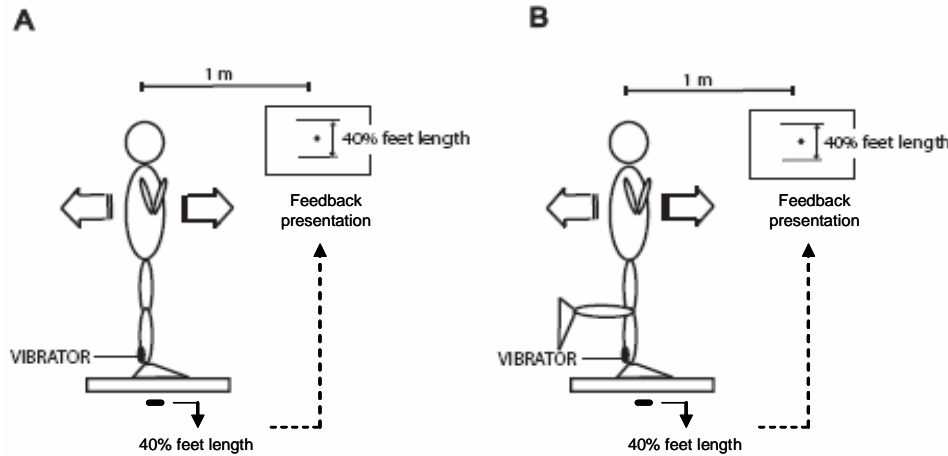


Figure 4.2: Schematic representation of the experimental set-up. Subjects were instructed to sway rhythmically while standing on both feet or on one foot (Panels A and B, respectively). Variations of these conditions included application of vibration to the Achilles tendon and closing the eyes. The nominal COP amplitude was 40% of the foot length, and the frequency was 0.5 Hz.

Data processing

All signals were processed off-line using LabView-5 and MatLab 6.5 software packages. Signals from the force platform were filtered with a 20 Hz low-pass, second order, zero-lag Butterworth filter, and COP_{AP} coordinate was computed using the following approximation:

$$COP_{AP} = (-M_Y + (F_X * h)) / F_Z,$$

where h is the distance between the force platform origin of coordinates and its top surface ($h = 36$ mm according to the manufacturer's specifications)

For each experimental condition, twelve complete sway cycles recorded within a single trial were used for data analysis. The initiation (t_0) and end of each cycle (t_1) were defined by two consecutive extreme anterior positions of COP_{AP} . The duration of each cycle was time normalized such that the total duration of each cycle was always 100%. COP_{AP} coordinates within each 1% window were averaged resulting in a sequence of 100 points,

each representing 1% of the sway cycle. COP_{AP} displacement was computed by subtracting the average COP_{AP} coordinate computed over the whole trial from the averaged COP_{AP} coordinate computed over each 1% window of the cycle.

EMG signals were first rectified and filtered with a 50 Hz low-pass, second-order, zero-lag Butterworth filter. Changes in muscle activation associated with COP_{AP} shift were quantified as follows. Rectified EMG signals were integrated over 1% time windows of each cycle ($IEMG$) as described in the previous paragraph. This procedure resulted in a sequence of 100 points for each muscles and each sway cycle.

In order to compare the $IEMG$ indices across muscles and subjects, we normalized them by the EMG integrals computed for the control trials when the subjects stood and held the 5.0 Kg load. Within each of the two control trials, the rectified EMG signals were integrated over a time interval corresponding to the duration of 1% of the sway cycle as defined earlier. This time interval was selected in the middle of the control trials when all the muscles showed steady activation levels. $IEMG$ indices for the dorsal muscles (SOL, GL, GM, BF, ST, ES) were divided by the EMG integrals computed for the control trial when the load was held quietly in front of the body. $IEMG$ indices for the ventral muscles (TA, VM, VL, RF, RA) were divided by the EMG integrals computed for the control trial when the load was suspended behind the subject's body. This method of normalization was used in earlier studies of muscle modes and synergies (Krishnamoorthy et al. 2003a,b; Wang et al. 2005; Danna-dos-Santos et al. 2007).

Statistics

Defining M-modes with principal component analysis (PCA)

For each subject and each experimental condition, the $IEMG$ data formed a matrix with eleven columns corresponding to the eleven postural muscles and 1200 rows corresponding to 1% time windows of all twelve cycles analyzed. The correlation matrix among the $IEMG$ was subjected to PCA (using SPSS software) with *Varimax* rotation. The factor analysis module with principal component extraction was employed. For each subject, the first five PCs were selected since PCs number six and higher did not have significantly loaded muscle activation indices in any of the conditions. Besides, analysis of the scree plots

also showed that PCs number six and higher accounted for about the same amounts of the total variance across all the conditions.

We are going to address the first five PCs as muscle modes (M-modes, M_1 , M_2 , M_3 , M_4 , and M_5) and hypothesize that magnitudes of (gains at) the M-modes are manipulated by the controller to produce COP shifts. In other words, M-modes represent unitary vectors in the muscle activation space that can be recruited by the controller with different magnitudes.

The loadings at individual muscle activation indices were studied across the first five M-modes. In order to investigate qualitatively the structure of each M-mode, we analyzed how the loadings of IEMG indices of activation of the recorded postural muscles were organized within each M-mode and how they were distributed among the M-modes. We considered a muscle as part of a M-mode when its loading had an absolute value equal or larger than 0.50. We will refer to such cases as *significant loadings* (Krishnamoorthy et al. 2003a,b; Wang et al. 2005; Danna-dos-Santos et al. 2007).

Changes in the M-mode composition across conditions were studied using the number of occurrences of significant loadings in each M-mode. These were further studied with non-parametric methods. A Friedman's test with the factors *M-mode* (M_1 , M_2 , M_3 , M_4 , and M_5) and *Condition* (BO, BC, BV, UO, and UV) was ran, and Mann-Whitney tests were used as post-hocs to explore significant effects. One-sample Wilcoxon's tests were used as post-hocs in cases where no significant loadings were observed within a PC across all ten subjects; this happened in the BO and BC conditions.

Defining the Jacobian (*J* matrix) with multiple regression

Linear relations between changes in the magnitudes of M-modes (ΔM) and COP_{AP} shifts (ΔCOP_{AP}) were assumed and the corresponding multiple regression equations were computed over the 12 cycles performed by each subject and at each experimental condition. The coefficients in the regression equations were arranged in a Jacobian matrix (**J**):

$$\Delta COP_{AP} = k_1 * \Delta M_1 + k_2 * \Delta M_2 + k_3 * \Delta M_3 + k_4 * \Delta M_4 + k_5 * \Delta M_5;$$

$$\mathbf{J} = [k_1 \ k_2 \ k_3 \ k_4 \ k_5]^T$$

Within this approach, the \mathbf{J} matrices are reduced to (5×1) vector-columns. For each subject, this analysis was run over the twelve individual cycles for each time interval (each 1% of the total cycle). The analysis was run over full cycles (100 intervals per experimental condition).

UCM analysis: Computing the synergy index

The uncontrolled manifold (UCM) hypothesis assumes that the controller manipulates a set of elemental variables to stabilize a value or a time profile of a performance variable (Scholz and Schöner 1999; reviewed in Latash et al. 2002, 2007). In our analysis, gains at M-modes play the role of elemental variables, while COP_{AP} shift represents the performance variable. Hence, we analyze the variance in the M-mode space at each phase of the sway cycle and compare its two components. One component of the M-mode variance is compatible with a stable, i.e. reproducible from cycle to cycle, value of the COP_{AP} coordinate (estimated as its average value at that phase of the cycle). The other variance component led to changes in the COP_{AP} coordinate. To compute the two variance components, the following analysis was performed.

For each cycle (n), IEMG indices were computed and transformed into $\Delta\mathbf{M}$ using the results of the PCA in Step-1 of the analysis. Further, two types of analysis were run. The first analysis used only the first three M-modes that satisfied the acceptance criteria under each of the five conditions. Under the three most challenging conditions (BV, UO, and UV), M_4 and M_5 were accepted as well. Hence, under those conditions the analysis was repeated for the complete set of five M-modes.

Hence, the $\Delta\mathbf{M}$ space had the dimensionality of either $n=3$ or $n=5$. A hypothesis that a particular magnitude of $\Delta\text{COP}_{\text{AP}}$ is stabilized by co-variation of $\Delta\mathbf{M}$ magnitudes accounts for one degree of freedom ($d=1$). Thus, the system is redundant with respect to the task of stabilizing particular $\Delta\text{COP}_{\text{AP}}$ values. The mean magnitudes of each $\Delta\mathbf{M}$ were computed for each subject and each task separately across samples over a trial. Since the model relating $\Delta\mathbf{M}$ to $\Delta\text{COP}_{\text{AP}}$ is linear, the $\Delta\mathbf{M}$ mean values were subtracted from each $\Delta\mathbf{M}$ computed value and the residuals were subjected to further analysis as follows.

The UCM represents combinations of M-mode magnitudes that are consistent with a stable (reproducible from cycle to cycle) value of $\Delta\text{COP}_{\text{AP}}$. The UCM was calculated as the

null-space of the corresponding \mathbf{J} matrix (defined at Step-2 of the analysis). The null-space of \mathbf{J} is a set of all vector solutions \underline{x} of a system of equations $\mathbf{J}\underline{x}=\mathbf{0}$. This space is spanned by basis vectors, $\underline{\epsilon}_i$. The vector of individual mean-free $\Delta\mathbf{M}$ s was resolved into its projection onto the null-space:

$$f_{UCM} = \sum_{i=1}^{n-d} (\underline{\epsilon}_i^T \cdot (\Delta\mathbf{M})) \underline{\epsilon}_i.$$

and component orthogonal to the null-space:

$$f_{ORT} = (\Delta\mathbf{M}) - f_{UCM}$$

The amount of variance per DOF within the UCM is:

$$V_{UCM} = \sigma_{UCM}^2 = \sum_{i=1}^N f_{UCM}^2 / ((n-d)N_{trials})$$

and orthogonal to the UCM is:

$$V_{ORT} = \sigma_{ORT}^2 = \sum_{i=1}^N f_{ORT}^2 / (dN_{trials})$$

V_{UCM} and V_{ORT} were the main dependent variables used in this analysis. In lay terms, they correspond to “good variability” (V_{UCM} that does not affect ΔCOP_{AP} computed for a certain time interval during the oscillation cycle) and “bad variability” (V_{ORT} that changes ΔCOP_{AP}). Two-way mixed design ANOVA with the factors *Condition* (BO, BC, BV, UO, and UV) and *Variance-Component* (V_{UCM} and V_{ORT}) was performed to analyze the effects of experimental conditions on the two variance components.

To quantify the relative amount of the total variance that is compatible with stabilization of a particular COP_{AP} shift we used an index (ΔV) reflecting the difference between the variance within the UCM and orthogonal to the UCM. ΔV was computed as:

$$\Delta V = (V_{UCM} - V_{ORT}) / V_{TOT}$$

where all variance indices are computed per degree of freedom; V_{TOT} stands for total variance. A one-way ANOVA with the factor *Condition* (BO, BC, BV, UO and UV) was used to test the effect of condition on ΔV when only the first three M-modes were considered. A two-way mixed design ANOVA with factors *Condition* (BV, UO and UV) and

Dimensionality ($n=3$; $n=5$) was used to test the effect of condition and the use of either three or five M-mode sets during the data processing on ΔV .

4.3 Results

This section is organized in the following way. First, the basic patterns of COP_{AP} shifts and muscle activity are described. Further, the results of the PCA are presented, and M-modes are identified and analyzed. Finally, we describe the results of the UCM analysis applied to the M-mode data.

Patterns of COP_{AP} and muscle activity

Across all five conditions of body sway, the subjects were able to show qualitatively similar, sine-like time profiles of COP_{AP} . The average COP_{AP} displacements across the ten subjects are shown in Figure 4.3A (dark bars); they were $38.47 \pm 1.30\%$, $46.99 \pm 2.39\%$, $44.43 \pm 2.17\%$, $41.10 \pm 1.60\%$, and $39.70 \pm 1.78\%$ of foot length for the BO, BC, BV, UO, and UV conditions, respectively. To remind, the nominal target amplitude was 40% of the foot length. Figure 4.4 shows the COP_{AP} profile averaged across 12 cycles during body sway performed by a typical subject under all five experimental conditions. Note the similarity of the shapes across all five conditions. Figure 4.3A (dark bars) also presents the average mean velocity of COP_{AP} shift and its average frequency of oscillation across the ten subjects. The average mean velocity of COP_{AP} was 9.90 ± 0.45 cm/s, 12.07 ± 0.64 cm/s, 11.45 ± 0.58 cm/s, 10.96 ± 0.37 cm/s, and 10.62 ± 0.44 cm/s for the BO, BC, BV, UO, and UV conditions respectively. The average frequency of COP_{AP} was 0.50 ± 0.00 Hz, 0.50 ± 0.00 Hz, 0.49 ± 0.07 Hz, 0.50 ± 0.00 Hz, and 0.49 ± 0.00 Hz for the BO, BC, BV, UO, and UV conditions respectively (Figure 4.3B).

Effects of the five different experimental conditions on peak-to-peak COP_{AP} displacement, mean velocity, and oscillation frequency were tested with three one-way repeated measures ANOVAs with the factor *Condition* (BO, BC, BV, UO, and UV). ANOVA confirmed significant effect of *Condition* on peak-to-peak COP_{AP} displacement ($F_{[4, 36]} = 5.63$, $p < 0.01$) and on the mean velocity of COP_{AP} ($F_{[4, 36]} = 5.45$, $p < 0.01$). The pair-wise comparisons showed significant differences only between the BO and BC conditions ($p < 0.05$). There were no significant effects of *Condition* on frequency of oscillation ($F_{[4, 36]} =$

1.06, $p > 0.05$). Altogether, these results indicate that the subjects were able to keep the pace and COP_{AP} trajectories similar across the conditions.

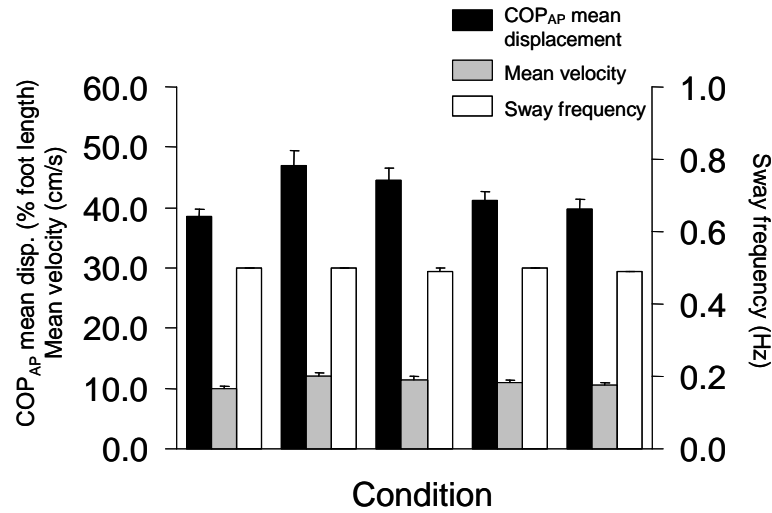


Figure 4.3: Means and standard errors of peak-to-peak COP_{AP} in % of foot length (Panel A, dark bars), mean velocity (Panel A, light bars), and frequency of body oscillation (Panel B) across subjects for the five different experimental conditions are shown. BO - bipedal stance with eyes open, BC - bipedal stance with eyes closed, BV - bipedal stance with eyes closed and vibration applied bilaterally to the Achilles tendons, UO - unipedal stance with eyes open (no vibration), UV - unipedal vibration with eyes open and vibration applied unilaterally to the Achilles tendon.

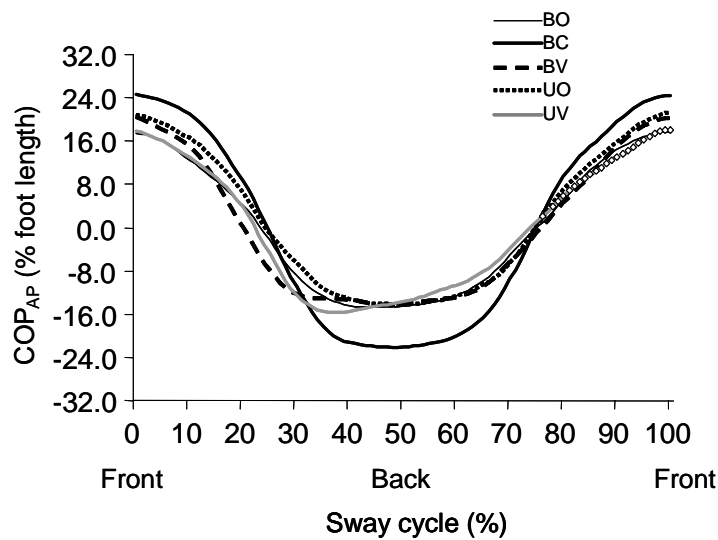


Figure 4.4: Average COP_{AP} displacement across 12 cycles for a representative subject (subject 2). Different lines represent COP_{AP} patterns under the five experimental conditions. Note the similarity in the time profiles and similar sway amplitudes in the five tasks.

There were regularities in the patterns of activation of the leg and trunk muscles across all five experimental conditions of sway. In particular, during the forward-to-backward part of the sway cycle (0 to 50%), there was a decrease in the level of activation of dorsal muscles (SOL, GL, GM, BF, ST, and ES) and an increase in the activity of ventral muscles (TA, VM, VL, RF, and RA). At the instant of the most backward COP location (50% of the cycle time), ventral muscle activity was typically high and the dorsal muscle activity was low. Over the backward-to-forward sway (51 to 100%), the ventral muscles activity decreased while the dorsal muscles exhibited an increase in their activity. This overall pattern is illustrated in Figure 4.5 that shows EMG profiles for ten postural muscles in a representative subject during body sway under BO (thick lines) and UV(dashed lines). Note that some muscles (SOL, GM, GL, ST, TA, RF, and VM) showed an increase in the peak EMG levels and also a shift from the smooth, sine-like changes in the muscle activity (at BO) to more abrupt bursts under the UV condition. However, other muscles (BF, ES, and VL) did not show any visible increase in the level of activity under more challenging conditions such as UV. *Principal component analysis (PCA)*

To identify groups of muscles whose activity was modulated in parallel during the sway, we used PCA (as described in the Methods). PCA was run on data combined over the whole cycle duration and over the 12 sway cycles, i.e. on the 1200x11 IEMG matrix. Based on the criteria described in the Methods, the first five PCs were chosen in each data set. The five first PCs were selected since under the BV, UO, and UV conditions, each of the first five PCs could contain significantly loaded muscle activation indexes. Across all conditions, PC6 through PC11 showed no significant loadings. Under the BO and BC conditions, virtually all significant loading were in the first three PCs with a few (for the total of six cases across all subjects) in PC4 and none in PC5.

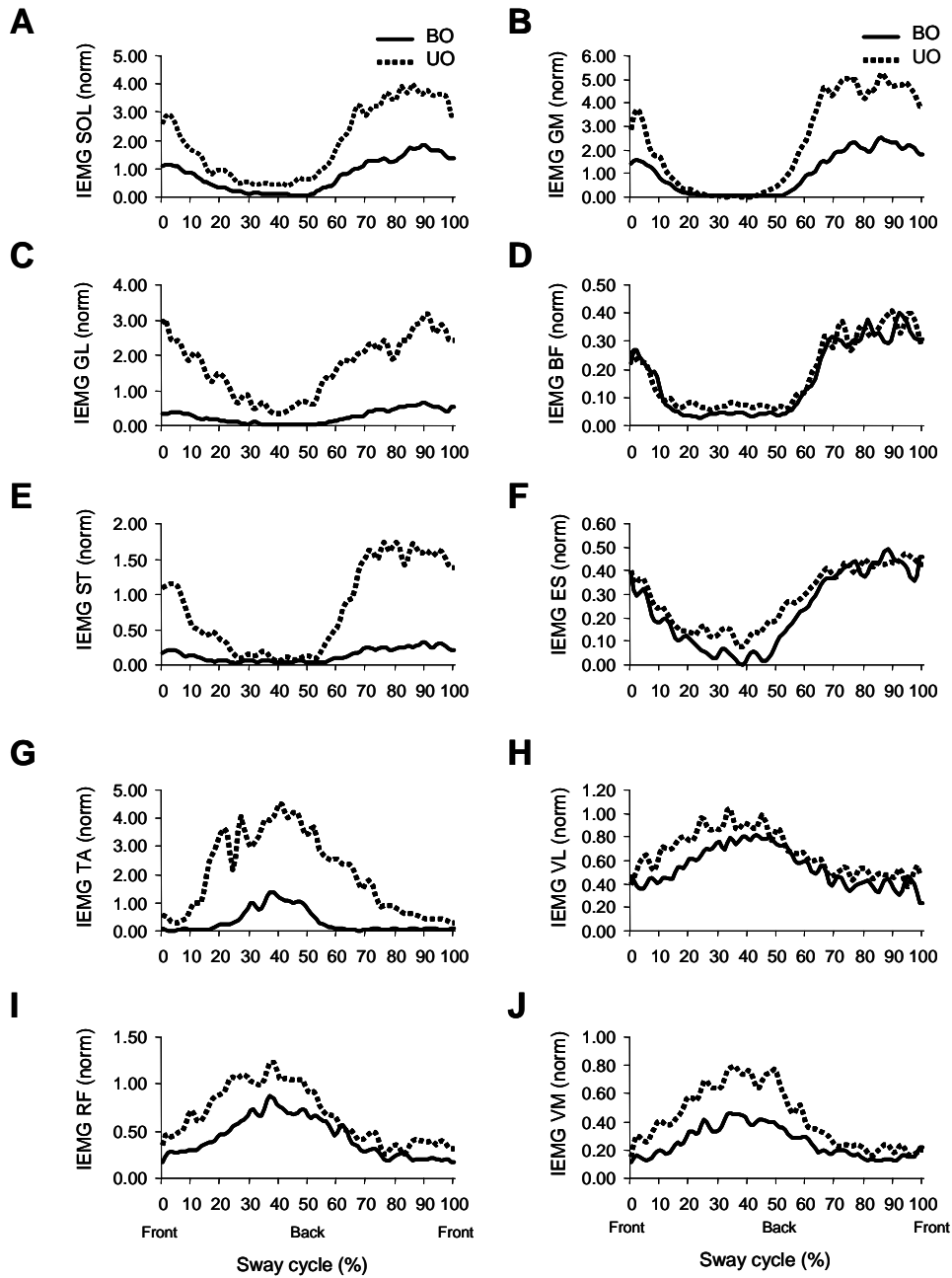


Figure 4.5: Integrated over each 1% of the cycle and normalized muscle activation indices (IEMG) averaged across 12 cycles for a typical subject under the BO (bipedal stance, open eyes) and UO (unipedal stance, open eyes) conditions (solid and dashed lines, respectively). Panels A-F show IEMG of dorsal muscles (SOL, GM, GL, BF, ST, ES) and panels G-J show IEMG of ventral muscles (TA, VL, RF, VM, RA). IEMG is in arbitrary units, and sway cycle is percent of its total duration. Phases 0% and 100% indicate the most anterior COP position ('Front') and phase 50% indicates its most posterior position ('Back'). The scales have been selected for better visualization.

The first five principal components (which we refer to as muscle modes, M_1 , M_2 , M_3 , M_4 , and M_5) accounted, on average, for 98.41% ($\pm 0.18\%$) of the total variance during body sway performed under the BO condition, 98.64% ($\pm 0.13\%$) under the BC condition, 97.82% ($\pm 0.24\%$) under the BV condition, 96.07% (± 0.68) under the UO condition, and 95.39% ($\pm 0.84\%$) under the UV condition. Figure 4.6A illustrates the total amount of variance explained by the first five M-modes averaged across subjects under each experimental condition. Note that there is a drop in the variance explained from BO and BC through UV. This drop was significant according to a one-way ANOVA with the factor *Conditions* (BO, BC, BV, UO, and UV) on the z-scores of the amount of variance explained by the first five M-modes ($F_{[4, 45]}=12.08$, $p<0.001$).

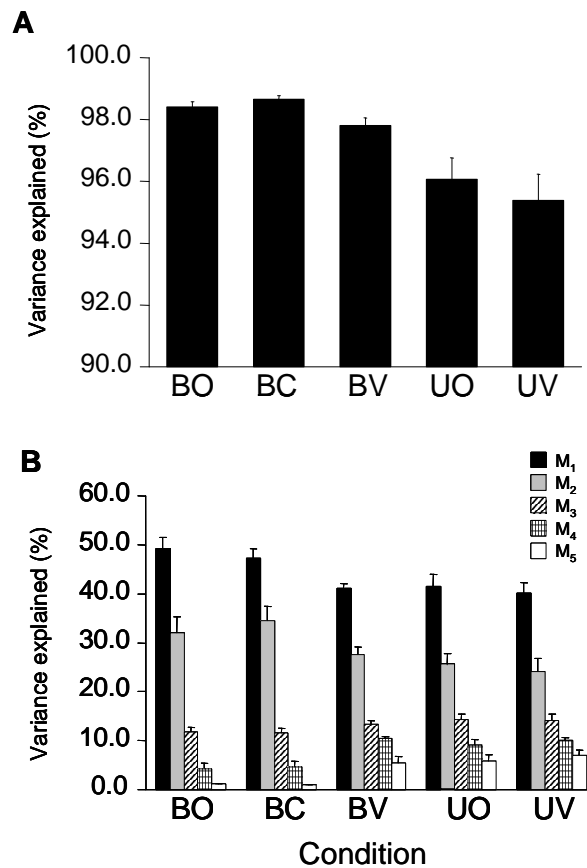


Figure 4.6: **Panel A:** Averaged across subjects amounts of variance explained by the five first principal components (M-Modes). Note the drop in the amount of variance from BC through UV conditions. **Panel B:** Averaged across subjects amounts of variance explained by each M-mode (M_1 through M_5). Note that there is a drop in the variance explained by the first two M-modes and an increase of the variance explained by the last three M-modes across the five conditions.

Tukey's pair-wise contrasts showed significant differences between the following comparisons: BC vs. UO and UV ($p < 0.001$); BO vs. UO and UV ($p < 0.01$); and BV vs. UV ($p < 0.05$). However, we would like to emphasize that the total amount of explained variance was high across all conditions reaching values always over 90%.

The amount of variance accounted for by each M-mode varied across the experimental conditions. Specifically, the first two M-modes (M_1 and M_2) showed a drop in the amount of variance from the relatively easy conditions (BO and BC) to the more challenging conditions (BV, UO, and UV), while the remaining three M-modes showed an opposite trend (Figure 4.6B). This finding is illustrated in Figure 4.6B where the average amount of variance explained by each M-mode across the ten subjects is shown. Note that both black and gray bars (M_1 and M_2 , respectively) show a drop in their values from BO through UV while the striped, checkered and white bars representing M_3 , M_4 , and M_5 show an increase in their values. The average amount of variance explained by M_1 and M_2 combined ($\Sigma Var(M_1, M_2)$) was $81.37 \pm 1.77\%$, $81.64 \pm 2.08\%$, $68.61 \pm 1.72\%$, $66.94 \pm 3.47\%$, and $64.27 \pm 2.66\%$ for the BO, BC, BV, UO, and UV conditions, respectively. For the same conditions, the average amount of variance explained by the remaining 3 M-modes ($\Sigma Var(M_3, M_4, M_5)$) was $17.11 \pm 1.68\%$, $17.00 \pm 1.98\%$, $29.20 \pm 1.64\%$, $29.13 \pm 2.89\%$, and $31.12 \pm 2.04\%$. This trend was confirmed by a two-way mixed-design ANOVA with factors *Condition* (BO, BC, BV, UO, and UV), and *Variance* ($\Sigma Var(M_1, M_2)$; $\Sigma Var(M_3, M_4, M_5)$). There was a significant *Condition* \times *Variance* interaction ($F_{[4, 90]} = 19.74$, $p < 0.001$) in addition to significant main effects of *Condition* ($F_{[4, 90]} = 3.73$, $p < 0.01$) and *Variance* ($F_{[1, 90]} = 697.41$, $p < 0.001$). The effect of *Variance* confirmed that $\Sigma Var(M_1, M_2)$ was higher than $\Sigma Var(M_3, M_4, M_5)$ across all conditions. The effects of *Condition*, reflected a significant difference between BC and UV (Tukey's pair-wise comparisons, $p < 0.05$). *Condition* \times *Variance* interaction reflected a significant difference between changes in $\Sigma Var(M_1, M_2)$ and $\Sigma Var(M_3, M_4, M_5)$ between each of the two easier conditions (BO and BC) and each of the three more challenging conditions (BV, UO and UV) confirmed by Tukey's pair-wise comparisons ($p < 0.05$).

The composition of individual M-modes was similar across subjects and between the BO and BC conditions; however, under the BV, UO, and UV conditions this composition showed modifications. In general, under the BO and BC conditions, subjects showed

significant loadings of the muscle activation indices mainly concentrated in the first two M-modes. The third M-mode rarely had more than one significantly loaded muscle index. Commonly, significant loadings of the indices for the dorsal muscles (SOL, GM, GL, BF, ST, and ES) were united in one of the first two M-modes, while the indices for the ventral muscles (TA, VL, VM, and RF) were united in the other of the two first M-modes. Sometimes, indices for most muscles, dorsal and ventral, were found in the same M-mode (M_1), but in such cases the loading coefficients for the dorsal and ventral muscles always had opposite signs.

Substantial modifications of the M-mode composition were found under the BV, UO, and UV conditions. In particular, we observed a tendency of the significant loadings to emerge in the third, fourth, and fifth M-mode (M_3 , M_4 , and M_5).

Table 4.1 shows individual loadings for all muscles under the BO and UV conditions for a typical subject. Note that under the BO condition, two distinct subgroups of significant loadings can be seen in the first M-mode (significant loading values are shown with bold numbers). The first subgroup contains indices for all six dorsal muscles with positive loading factors while the second subgroup contains indices for four ventral muscles with negative loading values. M_2 shows one significant loading for a dorsal muscle (SOL) and four significant loadings of the opposite sign for the ventral muscles (TA, VL, RF, and VM). Under the UV condition, significant loadings were seen in M_3 (for BF and ST), M_4 (for RA), and M_5 (ES).

The data summarizing the total number of significant loadings observed in each M-mode for all ten subjects are shown in Figure 4.7. Note that, as compared to the BO and BC conditions, there is a decrease in the total number of significant loadings within M_1 and M_2 under the BV, UO, and UV conditions (black and gray bars, respectively) and a parallel increase in the number of significant loadings in M_4 and M_5 (white and checkered bars). This finding was confirmed by a series of non-parametric statistic tests. First, a Friedman's test performed with factors *M-mode* (M_1 , M_2 , M_3 , M_4 , and M_5) and *Condition* (BO, BC, BV, UO, and UV) showed overall significance ($\chi^2_{[4]} = 18.68$, $p < 0.01$). Kruskal-Wallis tests ran as post-hocs confirmed a significant effect of *M-mode* but not of *Condition*. Mann-Whitney tests showed significant differences for the following comparisons: M_1 vs. all other M-modes

($p < 0.01$ for all comparisons), M_2 vs. all other M-modes ($p < 0.01$ for all comparisons), M_3 vs. M_4 and M_5 ($p < 0.05$), and M_4 vs. M_5 ($p < 0.05$).

To analyze possible interactions between the factors *M-mode* (M_1 , M_2 , M_3 , M_4 , and M_5) and *Condition* (BO, BC, BV, UO, and UV) on the number of significant loadings observed, another series of Mann-Whitney tests were ran. For M_1 , M_2 , M_4 , and M_5 the tests showed that the BO and BC conditions were significantly different from the BV, UO, and UV conditions ($p < 0.05$ for all comparisons). For M_3 , the BC condition was significantly different from the BV, UO, and UV conditions ($p < 0.05$ for all comparisons). So, taken together these results suggest that under more challenging conditions, more significantly loaded muscle indices appeared in M_4 and M_5 .

Table 4. 1: Loading coefficients for the PCAs

BO						BV					
	PC1	PC2	PC3	PC4	PC5		PC1	PC2	PC3	PC4	PC5
SOL	0.85	-0.50	0.07	-0.06	-0.01	SOL	0.54	-0.77	-0.28	0.17	-0.01
GM	0.87	-0.46	0.13	0.00	-0.03	GM	0.60	-0.67	-0.37	0.17	-0.04
GL	0.90	-0.38	0.03	-0.13	-0.05	GL	0.39	-0.82	-0.34	0.20	0.01
BF	0.86	-0.42	0.18	0.12	0.09	BF	0.61	-0.49	-0.54	0.23	-0.14
ST	0.85	-0.45	0.18	0.00	0.04	ST	0.73	-0.51	-0.35	0.20	-0.20
ES	0.95	0.10	0.15	0.02	0.26	ES	0.06	-0.28	-0.95	0.01	0.01
TA	-0.61	0.71	-0.05	0.31	0.02	TA	-0.92	0.32	0.00	-0.06	0.13
VL	-0.58	0.77	-0.03	-0.17	0.08	VL	-0.91	0.31	0.14	-0.15	-0.13
RF	-0.60	0.79	-0.06	0.01	0.00	RF	-0.91	0.33	0.14	-0.18	-0.01
VM	-0.56	0.81	-0.03	0.03	0.00	VM	-0.92	0.27	0.13	-0.22	0.01
RA	0.05	-0.18	0.95	-0.02	-0.26	RA	-0.20	0.18	0.05	-0.96	0.01
UO						UV					
	PC1	PC2	PC3	PC4	PC5		PC1	PC2	PC3	PC4	PC5
SOL	-0.61	0.49	0.34	-0.50	0.06	SOL	0.85	-0.48	0.09	0.12	0.13
GM	-0.67	0.38	0.22	-0.57	0.08	GM	0.80	-0.54	0.13	0.10	0.10
GL	-0.57	0.53	0.36	-0.47	0.02	GL	0.85	-0.45	0.09	0.13	0.20
BF	-0.40	0.71	0.11	-0.53	0.06	BF	0.76	-0.27	0.51	0.17	0.13
ST	-0.18	0.98	-0.03	-0.09	-0.05	ST	0.22	0.04	0.95	0.08	-0.17
ES	0.32	0.02	-0.93	0.11	0.03	ES	-0.39	0.38	0.37	0.09	-0.74
TA	0.60	-0.34	-0.48	0.38	-0.11	TA	-0.71	0.52	-0.20	-0.06	-0.26
VL	0.94	-0.23	-0.14	0.10	-0.13	VL	-0.37	0.91	0.00	-0.04	-0.14
RF	0.91	-0.17	-0.29	0.21	-0.07	RF	-0.42	0.88	0.01	-0.07	-0.19
VM	0.88	-0.22	-0.29	0.25	-0.09	VM	-0.44	0.87	0.03	-0.09	-0.13
RA	0.13	0.02	0.01	0.04	-0.99	RA	0.15	-0.08	0.09	0.98	-0.04

Data for a typical subject under the BO (bipedal stance with eyes open), BV (bipedal stance with eyes open and vibration applied bilaterally to the Achilles tendon), UO (unipedal stance with eyes open), and UV (unipedal stance with eyes open and vibration applied unilaterally to the Achilles tendon) conditions are shown. Loadings over 0.5 are shown in bold (significant loadings). SOL – soleus, GM – medial gastrocnemius, GL – lateral gastrocnemius, BF – biceps femoris, ST – semitendinosus, ES – erector spinae, TA – tibialis anterior, VL – vastus lateralis, VM – vastus medialis, RF – rectus femoris, RA – rectus abdominis.

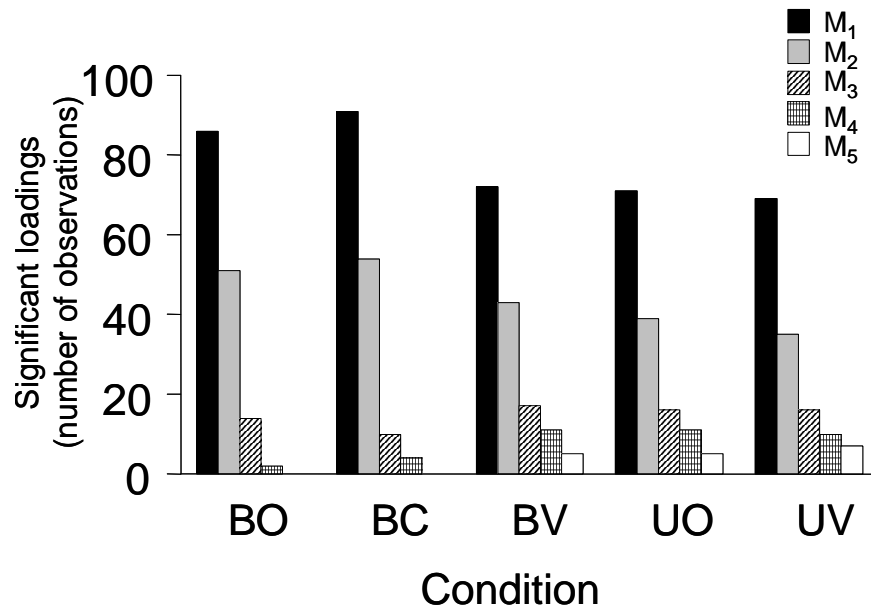


Figure 4.7: The total number of significant loadings of the indices of muscle activation for each M-mode for all ten subjects under each experimental condition. Note a decrease in the number of significant loadings in the M₁- and M₂- modes from BC through UV conditions and a parallel increase in the number of significant loadings for the M₃- M₄-, and M₅-modes.

UCM analysis

Data from twelve continuous sway cycles for each of the five experimental conditions were used to perform analysis of the structure of variability in the space of M-modes. The method partitions the total variance in the M-mode space across cycles into two components. The first component (V_{UCM}) is within an uncontrolled manifold (UCM) approximated as the null-space of the corresponding \mathbf{J} matrix describing the linear relations between changes in the magnitude of M-modes (ΔM) and COP_{AP} shifts (ΔCOP_{AP}) (see Methods). The other component (V_{ORT}) is within a sub-space orthogonal to the UCM. Further, we computed an index (ΔV) reflecting the normalized difference between V_{UCM} and V_{ORT} . We interpret positive values of ΔV as reflecting a multi-M-mode synergy stabilizing the average COP shift.

Using the same data sets we performed two separated analyzes that differed in the number of accepted M-modes. First, we analyzed the variability in the 3-dimensional space of the first 3 M-modes across all five conditions. In the second analysis, we considered the 5-

dimensional space of the first five M-modes (dimensionality $n=5$). For this second analysis, only the data for the three most challenging experimental conditions were considered (BV, UO, and UV). We did not perform this analysis for the BO and BC conditions, because modes M_4 and M_5 accounted for little variance and had no significantly loaded muscle indices in those conditions.

The \mathbf{J} matrix was computed using multiple linear regression of changes in the magnitudes of M-modes (ΔM) against COP_{AP} shifts (ΔCOP_{AP}) over the 12 cycles performed by each subject, for each experimental condition separately. The coefficients in the regression equations were arranged in a vector matrix (\mathbf{J} matrix) and its null-space was used to approximate the uncontrolled manifold. In cases where we accepted only the first three M-modes for further analysis, the \mathbf{J} matrix was a 3×1 vector-column. In cases where the five first M-modes were accepted, the \mathbf{J} matrix was a 5×1 vector column.

Figure 4.8 shows the average across the ten subjects amount of variance in ΔCOP_{AP} explained by the regression model (with standard errors). The average amount of variance explained based on the first 3 M-modes was $50.55 \pm 2.93\%$, $49.82 \pm 2.60\%$, $47.25 \pm 3.49\%$, $43.57 \pm 3.03\%$, and $40.03 \pm 4.08\%$ for the BO, BC, BV, UO, and UV conditions, respectively. For the same conditions, the average amount of variance explained based on the first 5 M-modes was $53.26 \pm 3.01\%$, $54.59 \pm 2.61\%$, $49.75 \pm 3.04\%$, $45.43 \pm 3.03\%$, and $41.92 \pm 3.85\%$. Note that there was a decrease in the amount of variance explained by the linear model from less challenging conditions through the more challenge ones (BO through UV). A two-way mixed design ANOVA with factors *Condition* (BO, BC, BV, UO and UV) and *Dimensionality* ($n=3$; $n=5$) was run on the z-scores of the variance accounted for by the linear model. There was only a significant effect of *Condition* ($F_{[4,90]}=4.16$, $p<0.01$). Tukey's tests confirmed a significant difference between BO and UV, and between BC and UV.

In the three-M-mode analysis, there was an increase of V_{UCM} from BO through BV conditions; the averaged across subjects V_{UCM} values were similar for the UO and UV conditions but higher than those computed for the BO, BC, and BV conditions. These results are displayed in Figure 4.9A, which shows the V_{UCM} and V_{ORT} indices per degree-of-freedom averaged across all ten subjects. Note that V_{UCM} (black bars) was consistently larger than V_{ORT} .

To analyze the effects of the experimental conditions on the two variance components for the three-M-mode analysis, a two-way mixed-design ANOVA with the factors *Condition* (BO, BC, BV, UO, and UV) and *Variance-Component* (V_{UCM} and V_{ORT}) was performed. There were significant main effects of both *Condition* ($F_{[4, 90]} = 6.44$, $p < 0.001$) and *Variance-Component* ($F_{[1, 90]} = 15.20$, $p < 0.001$) without a significant interaction ($p > 0.1$). The effect of *Variance-Component* confirmed that $V_{UCM} > V_{ORT}$. Tukey's pair-wise comparisons showed significant differences between the following pairs: BO and UO ($p < 0.001$), BO and UV ($p < 0.01$), BC and UO ($p < 0.01$), BC and UV ($p < 0.01$), BV and UO ($p < 0.01$), BV and UV ($p < 0.01$). All other pair-wise comparisons did not reach significance.

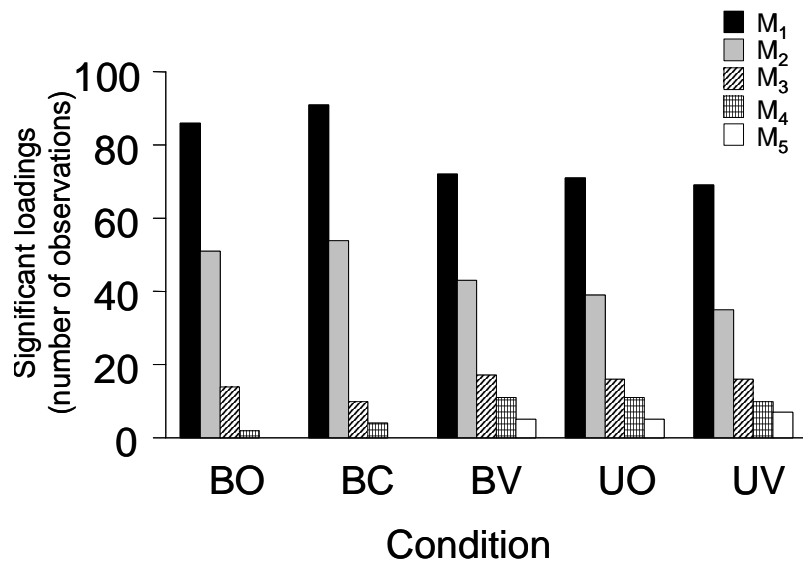


Figure 4.8: Variance explained by linear regression of ΔCOP_{AP} against changes in the three M-mode (black bars) and in the five M-mode magnitudes (white bars). Note the drop in the amount of variance explained from BO through UV

The five-M-mode analysis also showed lower V_{UCM} values in the BV condition as compared to the UO and UV conditions that were not different from each other (Figure 4.9B). This analysis confirmed significantly higher V_{UCM} values as compared to V_{ORT} . Two-way mixed-design ANOVA with the factors *Condition* (BV, UO, and UV) and *Variance-Component* (V_{UCM} and V_{ORT}) showed significant main effects of both *Condition* ($F_{[2, 54]} = 3.48$, $p < 0.05$) and *Variance-Component* ($F_{[1, 54]} = 15.86$, $p < 0.001$) without a significant interaction ($p > 0.1$). The effect of *Variance-Component* confirmed that $V_{UCM} > V_{ORT}$. Tukey's

pair-wise comparisons showed significant differences between BV and UO conditions ($p < 0.05$). All other pair-wise comparisons did not reach significance.

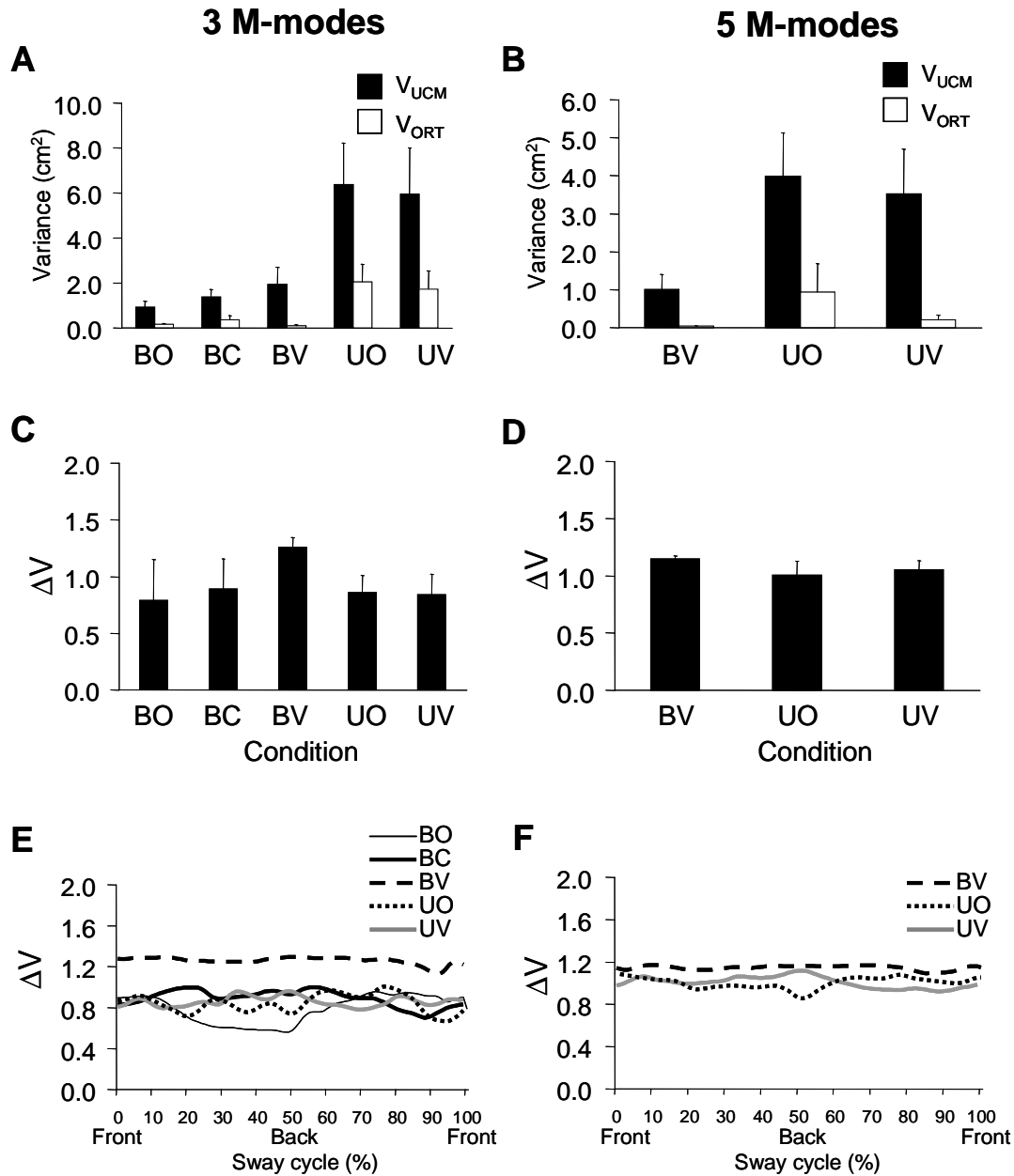


Figure 4.9: Panels A and B: Averaged across subjects V_{UCM} and V_{ORT} components of the total variance for each condition (with standard error bars) when 3 or 5 M-modes were considered. Dark bars represents V_{UCM} while light bars represent V_{ORT} . Panels C and D: Means and standard errors for ΔV across subjects when 3 or 5 M-modes were considered. Note that the values are positive and show inconsistent changes with the task. Panels E and F: Time profiles of ΔV averaged across subjects over the full sway cycle under all five experimental conditions of body sway when 3 or 5 M-modes were considered.

To test whether the two variance components changed similarly across the experimental condition, an index (ΔV) reflecting their normalized difference was used. The dependence of the average magnitude of ΔV on the experimental conditions is illustrated in Figure 4.s 9C and 9D. The ΔV index was always significantly larger than zero for all conditions and for both three-M-mode and five-M-mode analyses, which means that most variance within the M-mode space was within the UCM.

A one-way ANOVA with the factor *Condition* (BO, BC, BV, UO and UV) was used to test the effect of condition on ΔV when only the first three M-modes were considered. This ANOVA showed no effect of *Condition* ($F_{[4,45]} = 0.68$, $p > 0.5$). A two-way mixed design ANOVA with factors *Condition* (BV, UO and UV) and *Dimensionality* ($n=3$; $n=5$) was used to test the effect of condition and the type of analysis (three or five M-modes) on ΔV . This two-way ANOVA shows significant main effect for *Condition* ($F_{[2,54]} = 3.30$, $p < 0.05$) but no effect of *Dimensionality* ($F_{[1,54]} = 0.70$, $p > 0.5$) and no interaction ($p > 0.1$). Tukey's pair-wise comparisons showed significant differences between the BV condition as compared to the UO and UV conditions ($p < 0.05$). All other pair-wise comparisons did not reach significance.

Time changes of the ΔV index for all five conditions are shown in panels E and F of Figure 4.9. No clear pattern of ΔV modulation within the sway cycle was found.

4.4 Discussion

The results of the study provide support for the first hypothesis that the composition of M-modes could adjust under challenging conditions. However, the results speak against the second hypothesis that the index of M-mode co-variation would become weaker in more challenging conditions. In particular, in accordance with the first hypothesis, more challenging postural tasks were associated with an increase in the number of principal components (M-modes) that contained significantly loaded indices of muscle activation. However, the performance of more challenging tasks was not associated with a decrease in the index of the multi-M-mode synergy stabilizing COP shifts. The introduced index of the synergy was comparable across all conditions, and there was no modulation of this index over the sway cycle. Further in the Discussion, we analyze the findings with respect to the hierarchical organization of muscle groups in tasks that require keeping vertical posture.

Muscle modes in the hierarchy of postural control

At virtually any level of description, human bodies have too many elements to be controlled independently by the central nervous system. Bernstein was arguably the first to make the redundancy of the neuromuscular system a central issue of motor control (Bernstein 1967). He suggested that the controller united elements into groups (synergies) and used a fewer number of control variables partly solving the problem of motor redundancy.

A recent development of these ideas combined with the principle of abundance (Gelfand and Latash 1998) has allowed to introduce a definition of synergies that made possible their quantitative analysis (reviewed in Latash et al. 2002, 2007). At any level of a control hierarchy, synergies have been defined as neural organizations of elements that ensure low variability (high stability) of a particular overall output variable of that level. For example, in multi-digit studies, two levels of control have been identified. At the upper level, the task is distributed between the actions of the thumb and the virtual finger (VF, an imagined finger with the mechanical action equal to combined action of the four fingers, Arbib et al. 1985; Mackenzie and Iberall 1994). At the lower level, the action of VF is distributed among the actual fingers of the hand. Synergies stabilizing the overall mechanical action of the hand at the thumb-VF level and those stabilizing the VF action at the individual finger level have been described (reviewed in Zatsiorsky and Latash 2004).

The two-level hierarchical scheme of postural control mentioned in the Introduction may be viewed as similar to that of the hierarchical control of the hand. One may view M-modes as “virtual muscles” manipulated at the higher level of the control hierarchy, while mapping of M-modes on actual muscle activation is analogous to mapping of the VF action on individual finger actions. The only difference is that there are always two digits considered at the higher level of the hierarchy in hand studies, the thumb and VF, while the number of “virtual muscles” can vary at least between three and five as shown in our current study.

Recently, the idea that the neural controller unites muscles into groups to reduce the number of control variables (Hugblings Jackson 1889) has led to the emergence of a variety of methods identifying such muscle groups during whole-body tasks such as postural preparation and responses to perturbations, stepping, and swaying (Krishnamoorthy et al. 2003a,b; Ivanenko et al. 2004, 2005; Ting and Macpherson 2005; Torres-Oviedo et al. 2006;

Torres-Oviedo and Ting 2007). Many of these studies used matrix factorization techniques to identify eigenvectors in the space of muscle activations including the principal component analysis with factor extraction (for comparison of different methods see Tresch et al. 2006). Such eigenvectors have been termed synergies or muscle modes (M-modes).

The latter term was introduced to imply that such muscle groups play the role of elemental variables to construct synergies for the purpose of ensuring low variability (high stability) of important performance variables (Krishnamoorthy et al. 2003a,b). However, as mentioned in the Introduction, addressing a variable as a performance variable stabilized by a synergy or as an elemental variable depends on the level of analysis. For example, muscle activation level may be viewed as a performance variable stabilized by co-varied activity of motor units or as an elemental variable forming a multi-muscle synergy. Hence, in this study we accepted, as an axiom, that the control of whole-body movements is based on an at least two-level hierarchy. At the lower level, M-modes are formed by synergies in the space of individual muscle activations while at the higher level M-modes play the role of elemental variable and form synergies stabilizing physical variables important for the interaction with the environment.

This hypothesis implies, in particular, that M-mode composition may change under certain changes in external conditions of task execution. A few studies have indeed described atypical co-contraction M-modes when subjects performed whole-body tasks while standing on a board with a reduced support area (Krishnamoorthy et al. 2004b; Asaka et al. 2007).

In the current study, we used relatively minor complicating factors for the postural tasks. For example, closing eyes is known to increase postural sway (Allum and Pfaltz 1985; Fitzpatrick et al. 1992; Schumann et al. 1995) but it is not associated with losing balance in most persons. Standing on one foot is a more challenging task, (Tropp and Odenrick 1988; Goldie et al. 1992; Harrison et al. 1994), but most people can do it easily. Vibration applied to the Achilles tendons is known to produce major destabilizing effects on vertical posture during quiet standing (Lackner and Levine 1979; Nakagawa et al 1993; Calvin-Figuere et al. 1999), likely because of the unusually high level of activity of primary muscle spindles (Lackner and Levine 1979). It is also known to lead to reorganization of postural adjustments to self-triggered perturbations (Kasai et al. 2002; Slijper and Latash 2004) and to produce significant changes in locomotor patterns (Ivanenko et al 2000). Note, however, that even in

the most challenging condition of our study – swaying while standing on one foot with vibration of the Achilles tendon – the subjects were able to perform the task successfully without losing balance. This is in contrast to the frequent losses of balance reported in the mentioned studies by Krishnamoorthy, Asaka and their colleagues who used more challenging tasks performed while standing on a narrow support surface (Krishnamoorthy et al. 2004; Asaka et al. 2007).

While the two least challenging conditions (swaying with the eyes open and closed) were associated with three M-modes (similar to earlier studies, Krishnamoorthy et al. 2003a,b, Wang et al. 2005, Danna-Dos-Santos et al. 2007), the three more challenging ones were associated with the emergence of the fourth and fifth M-modes that showed significant loadings of muscles that used to be significantly loaded in one of the first three M-modes under the BO and BC conditions. Was this a split of one M-mode into two or a more complex reorganization? We cannot answer this question, partly because of the relatively arbitrary identification of significantly loaded muscle activations as those with the loading factors over 0.5. However, overall, the increase in the number of M-modes may be interpreted as an increase in the number of control variables manipulated by the controller at the higher level of the hierarchy as the tasks became more complex.

There was substantial variability across the subjects in the composition of the fourth and fifth M-modes; more frequently these M-modes contained significantly loaded indexes of activation for dorsal proximal muscles such as BF, ST, and ES (see Table 4. 1). These observations fit the hypothesis on different roles of the distal and proximal muscles in anticipatory postural adjustments during challenging postural tasks (Shiratori and Latash 2000). They are also compatible with the reports on muscle groupings seen during balance recovery following an external perturbation that resemble the hip-strategy of postural stabilization (Torres-Oviedo et al. 2006; Torres-Oviedo and Ting 2007).

The observed adjustments in the composition and number of M-modes corroborate the idea that M-modes represent not hard-wired muscle groupings but flexible combinations of muscle activations. On the other hand, several earlier studies have shown similarity of the M-mode composition across subjects and tasks when whole-body tasks were performed in natural standing conditions without any complicating factors (Krishnamoorthy et al. 2003b; Danna-Dos-Santos 2007). This combination of low variability and flexibility of the M-mode

composition is a trademark of a synergy (Latash et al. 2007) supporting the hypothesis that M-modes represent synergies at the lower level of the assumed control hierarchy.

What is the purpose of multi-muscle synergies?

Within our approach, synergies are viewed as neural organizations of elemental variables with the purpose to stabilize a performance variable (reviewed in Latash et al. 2007). This definition implies that the main purpose of a synergy is to decrease variability of the corresponding performance variable. Recent studies, however, have emphasized another important feature of synergies, namely that they allow the central nervous system to perform secondary tasks, using the same set of elemental variables, without sacrificing accuracy of performing the primary task (Gorniak et al. 2008; Zhang et al. 2008). For example, a multi-joint synergy involved in carrying a cup of coffee allows to use the same arm to open the door without spilling the contents of the cup.

In postural studies, several performance variables could be stabilized by co-varied involvement of the same set of M-modes. In particular, COP trajectories in the anterior-posterior and in the medio-lateral direction could be stabilized simultaneously in preparation to stepping (Wang et al. 2005), while COP trajectory in the anterior-posterior direction and the shear force in the same direction could be stabilized simultaneously during an unusual task of producing a large shear force pulse (Robert et al. 2008). *A priori*, we hypothesized that an increase in the number of M-modes could make the task more challenging for the controller and would have adverse effects on its ability to form COP-stabilizing synergies. This prediction, however, has been falsified in the experiments (see Figure 4.8). With the benefit of a hindsight, this outcome makes sense. It fits the general view on motor redundancy as not a complicating factor for the controller but as a luxury that allows to ensure stable behaviors with respect to various performance variables and in various conditions (Latash et al. 2007; Zhang et al. 2008). Hence, adding elements at any level of a hierarchy is not expected to make control more complex, rather to make it more powerful.

In our study, the larger sets of M-modes could have allowed the same muscles to be used to stabilize not only the explicitly required variable (COP coordinate in the anterior-posterior direction) but also other variables. For example, during swaying while standing on one leg, COP coordinate in the medio-lateral direction had to be kept within a relatively

narrow range corresponding to the decreased support area. When tendon vibration was applied, the distorted sensory information from the calf muscles (Lackner and Levine 1979) could force the central nervous system to attend to other sources of sensory information (for example, from proximal leg muscles, as suggested by studied of patients with diabetes, Van Deursen and Simoneau 1999) and stabilize corresponding mechanical variables. Having a larger set of M-modes allowed the controller to attend to those secondary components of the task without a detrimental effect on the index of stabilization (ΔV , see Figure 4.9) of the performance variable related to the explicit, primary task component (COP coordinate in a sagittal plane).

Potential role of sensory and biomechanical factors

We manipulated both sensory signals and mechanical conditions for the main task of body sway. In particular, closing the eyes may be viewed as a purely sensory manipulation. Vibrating the Achilles tendons has a strong sensory effect, particularly on the primary endings of the muscle spindles (Brown et al. 1967) but it can also lead to the tonic vibration reflex (Eklund and Hagbarth 1966), which may affect the mechanics of the movement. On the other hand, performing the task while standing on one foot may be viewed as mechanically more challenging because of the smaller size of the support area in the medio-lateral direction. In unipedal conditions, however, there are also changes in the sensory information coming from both legs, the unloaded one and the twice-loaded one.

Earlier studies have reported modifications in the composition of muscle modes in response to changes in both biomechanical (Krishnamoorthy et al. 2004) and sensory factors (Cheung et al. 2005; M-modes have been addressed as synergies in that study). In our study both, primarily sensory (vibration) and primarily mechanical (unipedal stance), factors had comparable effects on the M-mode composition.

There have also been reports of task-specific changes in the muscle groupings, for example during forward and backward pedalling (Raasch and Zajac 1999; Ting et al. 1999). In this study, we did not modify the explicit task. However, earlier studies used a variety of tasks such as quick arm motion, load release, stepping, and voluntary sway at a variety of frequencies, and, as long as the tasks were performed during natural bipedal stance, no differences were seen in the M-mode composition (Krishnamoorthy et al. 2003a; Wang et al.

2005, 2006; Danna-dos-Santos et al. 2007). There was a common feature across the tasks, that is they were all associated with reproducible COP shifts. In a recent study, different compositions of M-modes were seen when the subjects performed an unusual task that required the production of a large pulse of the shear force in a sagittal plane (Thomas et al. 2008). As such, this finding is similar to the reports in the cited studies of pedalling. Taken together, it is possible to conclude that substantial changes in the task and/or in the external conditions (both sensory and mechanical) may produce changes in the composition of M-modes.

Comments on methodological issues

Principal components analysis with factor extraction has been used in several studies of multi-muscle systems participating in postural tasks (Krishnamoorthy et al. 2003a,b; Ting and Macpherson 2005; Wang et al. 2005, 2006; Torres-Oviedo et al. 2006; Danna-dos-Santos et al. 2007; Torres-Oviedo and Ting 2007). Other matrix factorization tools have also been used, in particular non-negative matrix factorization techniques (Saltiel et al. 2001). A recent paper compared the results of several of those methods and found that several of the methods led to comparable results including the PCA with factor extraction (Tresch et al. 2006). All these tools use linear methods of data analysis and, as such, they may lead to unreliable or misleading results when applied to sets of variables that show strong non-linear relations to each other.

The strongest argument in favor of applying linear methods of analysis is the large amount of variance that the method can account for. In that sense, the large amounts of total variance accounted for by the sets of M-modes (Figure 4.6) may be viewed as supporting applicability of the used method of M-mode identification. On the other hand, the amount of variance explained showed a tendency to decrease under more challenging conditions, which may be interpreted as a tendency towards more non-linear relations among muscle activation indices. Note, however, that even the lowest amount of variance explained was over 95%.

4.5 References

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CHAPTER 5

STUDY #3

Postural Control during Upper Body Locomotor-Like Movements: Similar Synergies Based on Dissimilar Muscle Modes

5.1 Introduction

Recently, the control of large muscle groups has been addressed using the classical notion of multi-muscle synergies (Bernstein 1967). In all these studies, an assumption has been made that the central nervous system (CNS) manipulates a few variables to produce task-specific changes in many muscles (Krishnamoorthy et al. 2003a,b, 2004; Ivanenko et al. 2004, 2005; Ting and Macpherson 2005; Wang et al. 2005, 2006; Danna-Dos-Santos et al. 2007). Different matrix factorization techniques (d’Avella et al. 2003; Ivanenko et al. 2004, 2005; Tresch et al. 2006) have been used to identify such stable muscle groups addressed in some studies as “muscle synergies” (Ivanenko et al. 2004, 2005; Ting and Macpherson 2005) and in other studies as “muscle modes” (or M-modes, Krishnamoorthy et al. 2003a,b, 2004; Wang et al. 2005, 2006; Danna-Dos-Santos et al. 2007). The latter term reflects a view that the CNS creates synergies in a low-dimensional space of elemental variables (magnitudes of M-modes) to stabilize an important mechanical variable (Scholz and Schoner 1999; reviewed in Latash et al. 2002, 2007; Latash 2008).

Several recent studies have confirmed that repetitive trials at a number of whole-body tasks (such as standing, swaying, and stepping) show co-variation of magnitudes of the M-modes compatible with a stable trajectory of such variables as coordinate of the center of pressure (COP, the point of application of the resultant force acting on the body from the support surface) and shear force magnitude (Krishnamoorthy et al. 2003; Danna-Dos-Santos et al. 2007; Robert et al. 2008). In this study, we focus on a different mechanical variable, namely the moment of force about the longitudinal axis of the body; for brevity, we will address it as M_z . Control of this variable may be important for a number of everyday actions

associated with asymmetrical limb actions, for example locomotion or fast one-arm movements. Only a few studies have addressed issues of muscle coordination during large M_Z changes (e.g., Aruin et al. 2001).

Recently, an observation has been made that some patients with spinal cord injury who cannot move their legs voluntarily, demonstrate alternating leg swings when they are asked to perform vigorous alternating arm movements while suspended using a parachute strap as well as while lying on the back with the legs suspended (Shapkova EYu 1997, 2004). These leg movements were associated with cyclic muscle activation changes. Such patterns were not observed when the patients rotated the upper body with the arms crossed on the chest, although they could emerge after several weeks of training. These findings were interpreted as reflecting activation of a hypothetical locomotion pattern generator at the lumbar spinal level via propriospinal pathways or cyclically modulated reflexes from proprioceptors induced by the mechanical coupling of the body segments.

In this study, we explore multi-M-mode synergies involved in asymmetrical upper body actions. In particular, we have been interested in possible differences between the organization of muscle activation patterns during alternating bilateral arm movements (as during running or quick walking) and during upper-body rotation that does not involve arm movements. We focused on the following three hypotheses: (1) Muscle activation patterns during such tasks can be described with a few M-modes, consistent across persons; (2) These modes form the basis for synergies stabilizing M_Z time pattern; and (3) This organization will differ between an explicit body rotation task and a task associated with alternating arm movements.

5.2 Methods

Subjects

Ten healthy subjects, 5 females and 5 males, mean weight 66.1 kg (6.7 SD), mean age 28.9 (7.2 SD) and mean height 174.2 cm (4.4 SD) participated in the experiment. All the subjects were healthy, without any known neurological or muscular disorder. All the subjects were right-handed based on their preferential hand usage during writing and eating. All the subjects gave informed consent based on the procedures approved by the Office for Research Protection of The Pennsylvania State University.

Apparatus

A force platform (AMTI, OR-6) was used to record the moment of force around the vertical axis (M_z). Disposable self-adhesive electrodes (3M Corporation) were used to record the surface electrical activity (electromyogram, EMG) of the following muscles from the right side of the body: gastrocnemius lateralis (GL), tibialis anterior (TA), biceps femoris (BF), semi-tendinosus (ST), vastus medialis (VM), rectus femoris (RF), tensor fasciae latae (TFL), gluteus maximus (GT), obliques abdominal (OA), rectus abdominis (RA), serratus (SER), lumbar erector spinae (ERL), and thoracic erector spinae (ERT). The electrodes were placed within the central part of the muscles bellies, with inter-electrode distance of 3 cm. A reference electrode was attached to the lateral aspect of the fibula on its distal portion.

The signals from the electrodes were amplified ($\times 3000$) and band pass filtered (60-500 Hz). All the signals were sampled at 1000 Hz with a 12-bit resolution. A desktop computer (Gateway 450Mhz) was used to control the experiment and to collect the data using the customized LabView-based software (LabView-5 – National Instruments, Austin TX, USA).

Procedures

The experiment started with one control trial that was later used for normalization of the EMG signals (next section). In this trial, subjects were instructed to stand on the force plate quietly for ten seconds keeping the body vertical, with the arms crossed on the chest and looking at a stationary target placed 1.8 m in front of the subject at the eye level. Feet

were kept parallel and apart 15 cm. This foot position was marked on the top of the force plate and reproduced across all the trials.

Two main tasks were performed, namely (a) continuous whole body rotation around its longitudinal axis (Body rotation), and (b) alternating movements of the upper arms (Arm movement). Both tasks (body rotation and arm movement) were performed at frequencies of 0.7 Hz, 1 Hz, and 1.4 Hz. An extra weight of 1 lb (mass of 0.45 kg) was added to the palm of every hand using fitness gloves (Cory Everson Fitness) to increase the mechanical effects of the arm movements. In order to perform the body rotation task subjects were asked to stand on the force platform keeping the same posture with arms crossed on the chest. Then, they were asked to start moving their body in a cyclic fashion about the vertical longitudinal axis under the pace of the metronome. To prevent asymmetry and define the amplitude of body rotation a small laser pointer attached to the chest of the subjects was used. Two vertical lines marked on the wall (3.6 meters apart) in front of the subject showed nominal targets for the body rotation. The targets were spaced The subjects were instructed to perform a symmetrical, cyclic body rotation such that the pointer beam oscillated between the two targets. Subjects continuously rotated their body first moving the right shoulder forward and left shoulder backward such that the projected laser beam moved from the right vertical line to the left vertical line, then they rotate their body in opposite fashion moving their left shoulder forward and the right shoulder backward. We will refer to the first and last 50% of the cyclic movement as *right shoulder forward* and *left shoulder forward* phases, respectively.

During the second task (arm movement task) subjects stood on the force platform with the elbows flexed by about 100 degrees and performed alternating rhythmic arm movements. The subjects were instructed to imitate sprint running or sportive walking; the movements were performed primarily in the shoulder joints (60-100 degrees), some of the subjects also flexed and extended elbow joints (by about 10-20 degrees); there were no visible wrist or hand movements. The subjects were suggested a virtual target: Moving each hand between the face and hip levels. Prior to data collection, subjects performed 2 familiarization trials under each movement frequency (0.7, 1.0 and 1.4 Hz) for each task.

Each trial of the main series started with the subject standing upright quietly; the subject began performing the task paced by the metronome. Data collection started after 10 s

of continuous movement and lasted for 30 s. One trial was performed for each of the six experimental conditions: two tasks (body rotation and arm movement) executed at three different frequencies (0.7, 1.0, and 1.4 Hz). The order of conditions was balanced across subjects. Rest periods of about 1 min were given between trials. The average duration of the experiment was thirty minutes; fatigue was not an issue.

Data processing

All signals were processed off-line using LabView-5 and MatLab 6.5 software packages. Signals from the force platform were filtered with a 20 Hz low-pass, second order, zero-lag Butterworth filter. For each experimental condition, twelve complete movement cycles were used for data analysis. The initiation (t_0) and end of each cycle (t_1) were defined by two consecutive peaks of M_z values. The duration of each cycle was time normalized such that the total duration of each cycle was always 100%. M_z values within each 1% window were averaged resulting in a sequence of 100 points representing the movement cycle.

EMG signals were first rectified and filtered with a 50 Hz low-pass, second-order, zero-lag Butterworth filter. Changes in muscle activation associated with M_z changes were quantified as follows. Rectified EMG signals were integrated over 1% time windows of the cycles ($IEMG$).

In order to compare the $IEMG$ indices across muscles and subjects, we corrected them by subtracting $IEMG$ indices obtained during the quiet standing control trial and normalized them by the highest $IEMG$ indices observed for each particular muscle and each particular subject across all the trials. Hence, the $IEMG$ indices varied between 0 and 1.

Statistics

Defining M-modes with principal component analysis (PCA)

For each subject and each experimental condition, the $IEMG$ data formed a matrix with thirteen columns corresponding to the 13 postural muscles and 1200 rows corresponding to 1% time windows of all twelve cycles analyzed. The correlation matrix among the $IEMG$ indices was subjected to PCA (using SPSS software) with *Varimax* rotation. The factor extraction was employed resulting in three factors for each subject. Factors (PCs) number

four and higher did not have significantly loaded muscle activation indices under any of the conditions. Besides, analysis of the scree plots also showed that PCs number four and higher accounted for about the same amounts of the total variance across all the conditions.

We are going to address the first three PCs as muscle modes (M-modes, M_1 , M_2 , M_3) and hypothesize that magnitudes of (gains at) the M-modes are manipulated by the controller to produce changes in M_z . In other words, M-modes represent unitary vectors in the muscle activation space that can be recruited by the controller with different magnitudes.

The loadings at individual muscle activation indices were studied across the first three M-modes. In order to investigate qualitatively the structure of each M-mode, we analyzed how the loadings of IEMG indices of activation of the recorded postural muscles were organized within each M-mode and how they were distributed among the M-modes. We considered a muscle as part of a M-mode when its loading had an absolute value equal or larger than ± 0.50 . We will refer to such cases as *significant loadings* (Krishnamoorthy et al. 2003a,b; Wang et al. 2005; Danna-dos-Santos et al. 2007).

In order to test the similarity of M-modes (PCs) are across the different frequencies of sway and subjects, we used a method similar to the one introduced by Krishnamoorthy and colleagues (2003a). Within this analysis, the M_1 - and M_2 -modes were first sorted accordingly to the amount of variability explained by each of them. This method compares a group of vectors in the muscle activation space (for example, the M_1 vectors for a given subject across all the sway frequencies) to a central vector representing another group of vectors (for example, the M_2 vectors for another subject across the same sway frequencies). The central vector is a PC vector for which the sum of squared distances between it and the remaining vectors within the same group is minimal. The method tests an assumption that all vectors of the same number in all subjects and across all frequencies point in similar directions. In this case, cosine of the angle between a central vector and any vector of the same number is expected to be close to unity, while cosine of the angle between a central vector and any vector of a different number is expected to be close to zero.

The procedure includes the selection of a central vector among the actual PC vectors leading to the identification of three central vectors for each comparison (p_1 , p_2 , and p_3 corresponding to M_1 , M_2 , and M_3). The central vectors were identified for each subject over all frequencies $\{p_i(s)\}$, and for each frequency over all subjects $\{p_i(f)\}$. It was hypothesized

that (1) for each subject, a PC vector \mathbf{p}_i is collinear to a central vector $\{\mathbf{p}_i(s)\}$ if $i = j$ (where $i, j = 1, 2, 3$) and orthogonal to it if $i \neq j$; and (2) for each task, a PC vector \mathbf{p}_i is collinear to a central vector $\{\mathbf{p}_i(f)\}$ if $i = j$ and orthogonal to it if $i \neq j$.

Absolute values of the cosines between the 13-dimensional PC vectors were used as a measure of closeness of their directions. We used absolute values of the cosines rather than angles themselves for statistical purposes; note that angles 0° and 180° are equivalent for PCs and for absolute cosine values while they are apparently different in angular units. Cosines of angles between each central vector $\mathbf{p}_i(f)$ ($i = 1, 2, 3$) for a selected sway frequency and \mathbf{p}_j for each individual subject performing at each sway frequency and cosines of angles between each $\mathbf{p}_i(s)$ ($i = 1, 2, 3$) for each subject and \mathbf{p}_j for each sway frequency performed by each subject were calculated. These were further transformed into z-scores using Fisher's z-transformation. Further, these values were averaged either across subjects or across frequencies.

Defining the Jacobian (\mathbf{J} matrix) with multiple regression

Linear relations between changes in the magnitudes of M-modes (ΔM) and M_z shifts (ΔM_z) were assumed to be linear and the corresponding multiple regression equations were computed over the 12 cycles performed by each subject and at each experimental condition. The coefficients in the regression equations were arranged in a Jacobian matrix (\mathbf{J}):

$$\Delta M_z = k_1 * \Delta M_1 + k_2 * \Delta M_2 + k_3 * \Delta M_3;$$

$$\mathbf{J} = [k_1 \ k_2 \ k_3]^T$$

Within this approach, the \mathbf{J} matrices are reduced to (3×1) vector-columns. For each subject, this analysis was run over the twelve individual cycles for each time interval (each 1% of the total cycle). The analysis was run over full cycles (100 intervals per experimental condition). A two-way mixed-design ANOVA with factors *Task* (body rotation, and arm movement), and *Frequency* (0.7Hz, 1Hz, and 1.4 Hz) was performed to analyze possible effects of the movement task and movement frequency on the amount of variance explained by the linear model relating changes in the magnitudes of M-modes (ΔM) and M_z shifts (ΔM_z).

UCM analysis: Computing the synergy index

The uncontrolled manifold (UCM) hypothesis assumes that the controller manipulates a set of elemental variables to stabilize a value or a time profile of a performance variable (Scholz and Schöner 1999; reviewed in Latash et al. 2002, 2007). In our analysis, gains at M-modes play the role of elemental variables, while M_z shift represents the performance variable. Hence, we analyze the variance in the M-mode space at each phase of the movement cycle and compare its two components. One component of the M-mode variance is compatible with a stable, i.e. reproducible from cycle to cycle, value of the M_z (estimated as its average value at that phase of the cycle). The other variance component led to changes in the M_z values. To compute the two variance components, the following analysis was performed.

For each cycle (n), IEMG indices were computed and transformed into $\Delta \mathbf{M}$ using the results of the PCA in Step-1 of the analysis. Hence, the $\Delta \mathbf{M}$ space had the dimensionality of $n=3$. A hypothesis that a particular magnitude of ΔM_z is stabilized by co-variation of $\Delta \mathbf{M}$ magnitudes accounts for one degree of freedom ($d=1$). Thus, the system is redundant with respect to the task of stabilizing particular ΔM_z values. The mean magnitudes of each $\Delta \mathbf{M}$ were computed for each subject and each task separately across samples over a trial. Since the model relating $\Delta \mathbf{M}$ to ΔM_z is linear, the $\Delta \mathbf{M}$ mean values were subtracted from each $\Delta \mathbf{M}$ computed value and the residuals were subjected to further analysis as follows.

The UCM represents combinations of M-mode magnitudes that are consistent with a stable (reproducible from cycle to cycle) value of ΔM_z . The UCM was calculated as the null-space of the corresponding \mathbf{J} matrix (defined at Step-2 of the analysis). The null-space of \mathbf{J} is a set of all vector solutions \underline{x} of a system of equations $\mathbf{J}\underline{x}=\mathbf{0}$. This space is spanned by basis vectors, $\underline{\epsilon}_i$. The vector of individual mean-free $\Delta \mathbf{M}$ s was resolved into its projection onto the null-space:

$$f_{UCM} = \sum_{i=1}^{n-d} (\underline{\epsilon}_i^T \cdot (\Delta \mathbf{M})) \underline{\epsilon}_i$$

and component orthogonal to the null-space:

$$f_{ORT} = (\Delta \mathbf{M}) - f_{UCM}$$

The amount of variance per DOF within the UCM is:

$$V_{UCM} = \sigma_{UCM}^2 = \sum_{i=1}^N f_{UCM}^2 / ((n-d)N_{trials})$$

and orthogonal to the UCM is:

$$V_{ORT} = \sigma_{ORT}^2 = \sum_{i=1}^N f_{ORT}^2 / (dN_{trials})$$

V_{UCM} and V_{ORT} were the main dependent variables used in this analysis. In lay terms, they correspond to “good variability” (V_{UCM} that does not affect ΔM_z computed for a certain time interval during the oscillation cycle) and “bad variability” (V_{ORT} that changes ΔM_z). Three-way mixed design ANOVA with the factors *Task* (body rotation, and arm movement) *Frequency* (0.7Hz, 1Hz, and 1.4 Hz), *Variance-Component* (V_{UCM} and V_{ORT}) was performed to analyze the effects of experimental conditions on the two variance components.

To quantify the relative amount of the total variance that is compatible with stabilization of a particular M_z shift we used an index (ΔV) reflecting the difference between the variance within the UCM and orthogonal to the UCM. ΔV was computed as:

$$\Delta V = (V_{UCM} - V_{ORT}) / V_{TOT}$$

where all variance indices are computed per degree of freedom; V_{TOT} stands for total variance. A two-way mixed-design ANOVA with the factors *Task* (body rotation, and arm movement) and *Frequency* (0.7Hz, 1Hz, and 1.4 Hz) was used to test the effect of condition on ΔV index values

5.3 Results

Although we analyzed the data separately over the two half-cycles of the body movement corresponding to the shifts of M_z (right shoulder forward and left shoulder forward) there were no significant effects of the M_z shift direction on any of the important outcome measures. Therefore, for clarity and brevity, only results representing full cycles will be reported. This section is organized in the following way. First, the basic patterns of M_z changes and muscle activity are described. Further, the results of the PCA are presented, and M-modes are identified and analyzed. Finally, we describe the results of the UCM analysis applied to the M-mode data.

Patterns of moment of force about the vertical axis (M_z) and muscle activity

Across all conditions, the subjects were able to execute the task under the pace of the metronome. The averages \pm standard errors of the actual frequency of M_z changes for the body rotation task were 0.67 ± 0.01 , 1.05 ± 0.01 , and 1.30 ± 0.05 Hz, and for the arm movement task they were 0.70 ± 0.01 , 1.07 ± 0.05 , and 1.30 ± 0.02 Hz. A two-way mixed design ANOVA with factors *Task* (arm movement vs. body rotation) \times *Frequency* (0.7, 1.0, and 1.4 Hz) showed significant effect for both factors *Task* ($F_{[1,54]} = 30.68$, $p < 0.001$) and *Frequency* ($F_{[2,54]} = 29.11$, $p < 0.001$) was found, Tukey's pair-wise comparisons showed significant differences among the three nominal frequencies ($p < 0.05$). There was no significant interaction ($p > 0.1$).

All subjects produced qualitatively similar, sine-like time profiles of M_z . Figure 5.1 shows M_z profiles averaged across 12 cycles for a typical subject under all six experimental conditions. Note the similarity of the shapes across all conditions. Averaged across subjects peak-to-peak M_z values for both tasks and all three frequencies are shown in Figure 5.2. Note that subjects produced larger peak-to-peak changes in M_z during the body rotation task and at higher frequencies. For the body rotation task the average values of peak-to-peak M_z were 26.44 ± 2.65 Nm, 46.29 ± 6.07 Nm, and 61.74 ± 6.64 Nm (0.7, 1.0, and 1.4 Hz, respectively). For the arm movement task, they were $16.69 \pm 1.62\%$, $29.33 \pm 3.32\%$, and $34.41 \pm 3.81\%$ (0.7, 1.0, and 1.4 Hz, respectively). A two-way ANOVA with factors *Task* and *Frequency* showed significant effects of both *Task* ($F_{[1,54]} = 25.16$ $p < 0.001$) and

Frequency ($F_{[2,54]} = 18.47$, $p < 0.01$) without an interaction. The pair-wise comparisons showed significant differences between all three frequencies ($p < 0.05$).

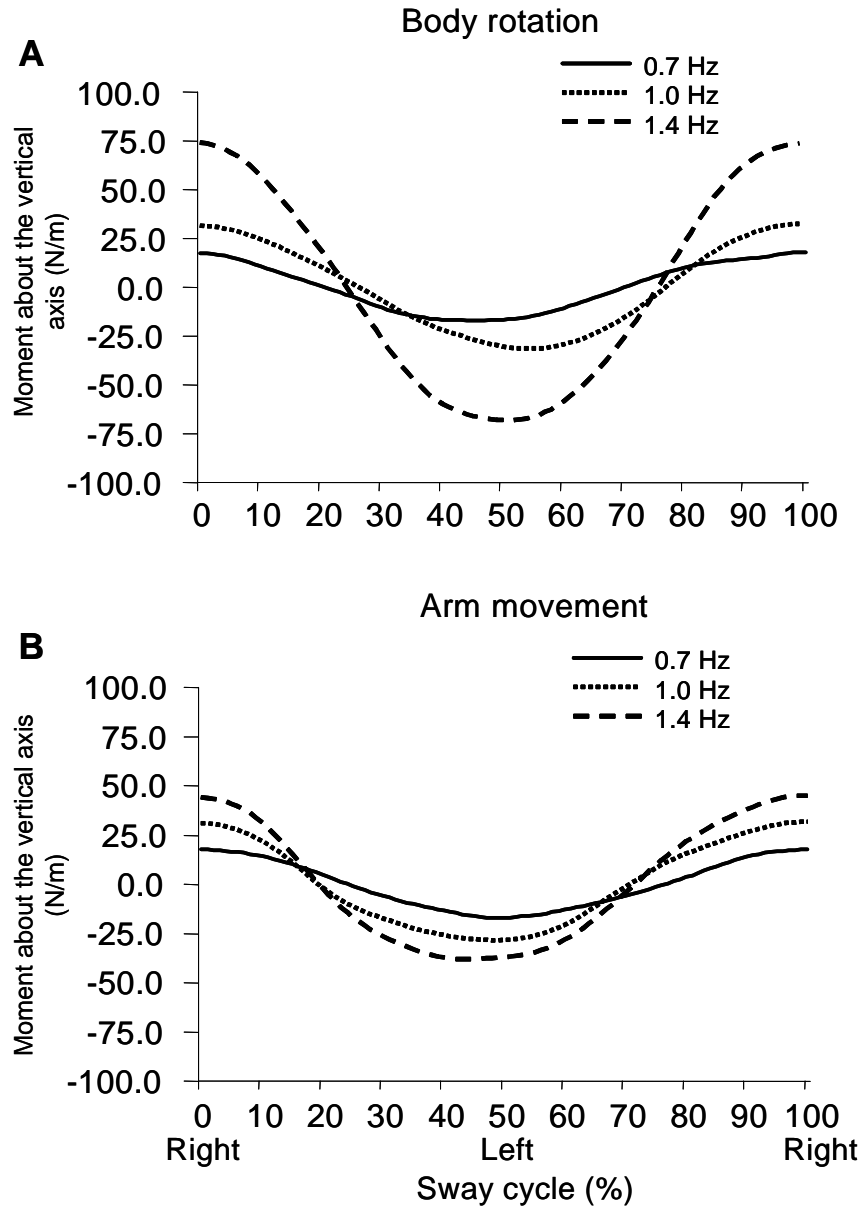


Figure 5.1: Average variation of moment of force (M_z) across 12 cycles for a representative subject for the body rotation task (Panel A) and arm movement task (Panel B). Different lines represent M_z patterns under different frequencies of movement performance. Note the similarity in the time profiles in both Panels. Phases 0% and 100% indicate the highest value of M_z when body is rotated from right to the left ('Right shoulder forward') and phase 50% indicates highest value of M_z when body is rotated from the left to the right ('Left shoulder forward').

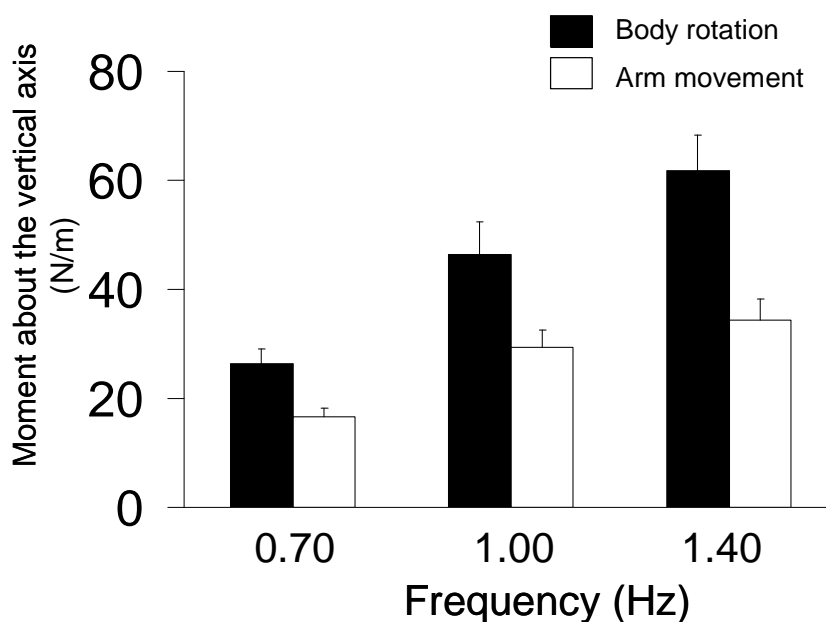


Figure 5.2: Means and standard errors across subjects of peak-to-peak M_z under the execution of the body rotation task (dark bars), and arm movement task (light bars) at different frequencies of body movement (0.7, 1.0, and 1.4 Hz).

During the execution of both tasks, all muscles showed larger levels of activation at higher movement frequencies. There were both significant variations and common features in the muscle patterns across the subjects. In particular, for the body rotation task, during the right shoulder forward part of the movement cycle (0 to 50%), there was a decrease in the level of activation of BF, ST, GT, OA, and SER and an increase in the activity of RF, VM, ESL, and ERT muscles. TA, and GL showed a decrease in activation level immediately followed by its increase during the first half of the movement cycle. Over the second half of the movement cycle (51 to 100%, left shoulder forward), the activation of RF, VM, ESL, and EST decreased while TA, GL, BF, ST, TFL GT, OA, and SER exhibited an increase in their activity. RA did not show reproducible changes in its activity over the movement cycle. This typical activation pattern for the body rotation task is illustrated in Figure 5.3. Figure 5.3 shows averaged EMG profiles across all the subjects for the 13 postural muscles recorded during the execution of the body rotation task at a frequency of 1.4 Hz.

The arm movement task also showed regularities in the patterns of activation of the leg and trunk muscles across the three frequencies. In particular, leg muscles commonly showed an increase in their activation over one of the two halves of the movement cycle followed by a periods of very low activation. GL, RF, VM and TFL showed larger activity levels over the first half of the movement cycle (0 to 50%, right shoulder forward), while TA, BF, ST, and GT were more active over the second half (51 to 100%, left shoulder forward). The trunk muscles OA, SER and EST showed changes in their level of activation in both halves of the movement cycle while RA and SER did not show reproducible modulation patterns.

The muscle activation patterns during the arm movement task are illustrated in Figure 5.4 that shows averaged EMG profiles across subjects for all 13 postural muscles recorded during the execution of the movement at 1.4 Hz.

Body rotation 1.4 Hz

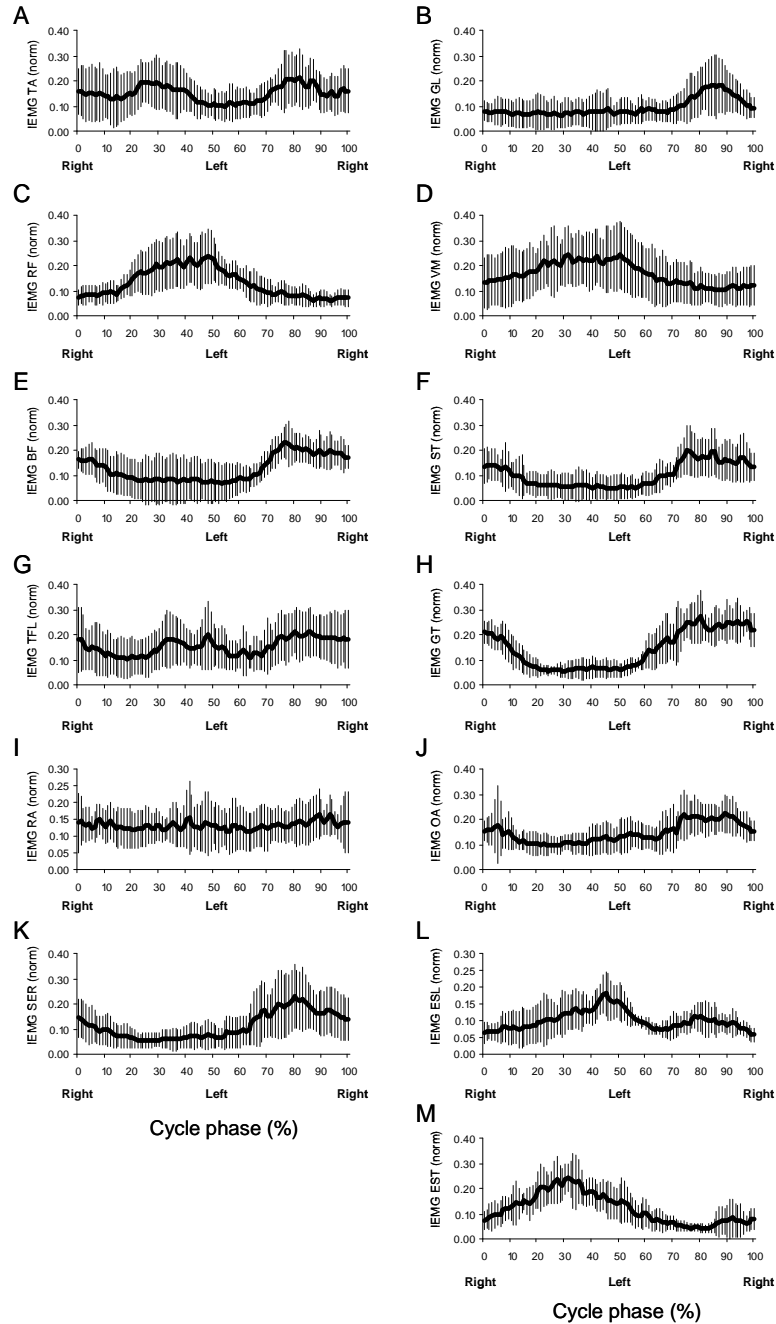


Figure 5.3: Integrated over each 1% of the cycle and normalized muscle activation indices (IEMG) averaged across subjects under the body rotation task performed at 1.4 Hz. Panels A-M show IEMG of all 13 postural muscles recorded (TA, GL, RF, VM, BF, ST, TFL, GT, RA, OA, SER, ESL, and EST). Phases 0% and 100% indicate the highest value of M_z when body is rotated from right to the left ('Right shoulder forward') and phase 50% indicates highest value of M_z when body is rotated from the left to the right ('Left shoulder forward'). The scales have been selected for better visualization.

Arm movement 1.4 Hz

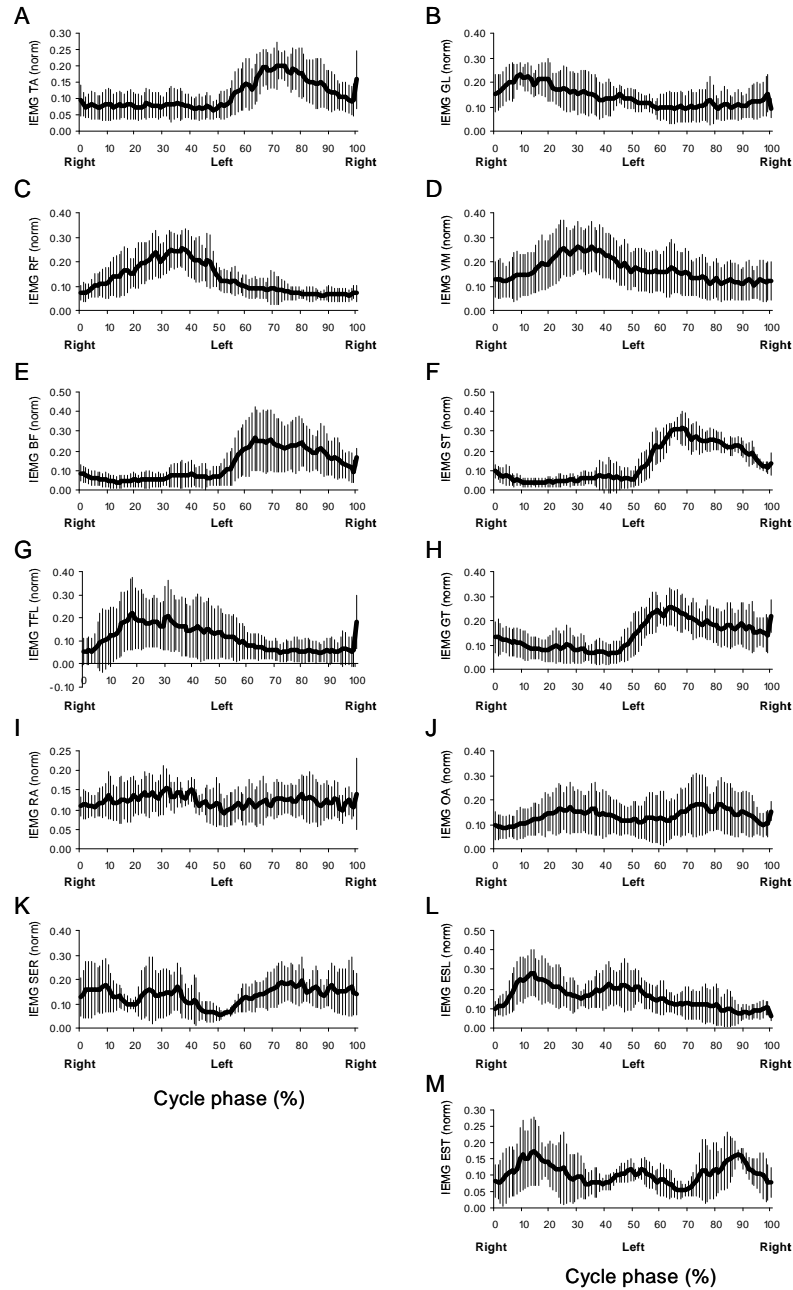


Figure 5.4: Integrated over each 1% of the cycle and normalized muscle activation indices (IEMG) averaged across subjects under the arm movement task performed at 1.4 Hz. Panels A-M show IEMG of all 13 postural muscles recorded (TA, GL, RF, VM, BF, ST, TFL, GT, RA, OA, SER, ESL, and EST). Phases 0% and 100% indicate the highest value of M_z when body is rotated from right to the left ('Right shoulder forward') and phase 50% indicates highest value of M_z when body is rotated from the left to the right ('Left shoulder forward'). The scales have been selected for better visualization.

Principal component analysis (PCA)

To identify groups of muscles whose activity was modulated in parallel during the cyclic M_Z changes, we used PCA (as described in the Methods). PCA was run on data combined over movement cycle duration and over 12 cycles, i.e. on the 1200×13 IEMG matrix. Based on the criteria described in the Methods section, the first three PCs were chosen for each data set. For the body rotation task the first three principal components (which we refer to as muscle modes, M_1 , M_2 , and M_3) accounted, on average, for 67.94 ± 1.66 , 68.71 ± 2.01 , and $71.04 \pm 1.71\%$ of the total EMG variance for movements performed at 0.7, 1.0, and 1.4 Hz, respectively. For the arm movement task, the first three PCs accounted, on average, for 66.17 ± 2.76 , 68.45 ± 2.34 and $70.97 \pm 2.19\%$ of the total variance for movements performed at 0.7, 1.0, and 1.4 Hz, respectively.

Figure 5.5A illustrates the total amount of variance explained by the first three M-modes averaged across subjects and under each experimental condition. Note that there is a slight increase in the variance explained for both tasks at the highest frequency (1.4 Hz). This increase was not significant, however, according to a two-way ANOVA with factors *Task* and *Frequency*. This analysis showed no significant effects.

The amount of variance accounted for by each M-mode varied across the experimental conditions. Specifically, for the body rotation task the first M-mode (M_1) showed an increase in the amount of variance from the lowest (0.7 Hz) to the highest (1.4 Hz) frequency, while the variance accounted for by the third M-mode (M_3) showed an opposite trend. This finding is illustrated in Figure 5.5B where the average amount of variance explained by each M-mode across the ten subjects is shown. Note that the black bars (M_1) show an increase from 0.7 Hz to 1.4 Hz. while the striped bars (M_3) show a drop in their values. This trend was confirmed by a two-way mixed-design ANOVA with factors *M-mode* (M_1 , M_2 , and M_3), and *Frequency* which showed a significant *M-mode* \times *Frequency* interaction ($F_{[4, 81]} = 7.79$, $p < 0.001$). In addition, a significant main effect of *M-mode* ($F_{[2, 81]} = 114.54$, $p < 0.001$) was also found. Tukey's pair-wise comparisons showed significant differences on the amount of variance explained by all three M-modes ($p < 0.05$ all comparisons). No significant effect of *Frequency* was found ($F_{[2, 81]} = 0.52$, $p > 0.5$).

For the arm movement task, the two-way mixed-design ANOVA with factors *M-mode* (M_1, M_2 , and M_3), and *Frequency* (0.7Hz, 1Hz, and 1.4 Hz) run on the amount of

variance explained by each of the first three PCs showed a significant effect only for *M-mode* factor ($F_{[2, 81]} = 79.01$, $p < 0.001$). Tukey's pair-wise comparisons showed significant differences on the amount of variance explained by all three M-modes ($p < 0.05$ all comparisons). No effect of *Frequency* ($F_{[2, 81]} = 1.36$, $p > 0.1$) nor *M-mode* \times *Frequency* interaction ($F_{[4, 81]} = 0.69$, $p > 0.5$) were found significant.

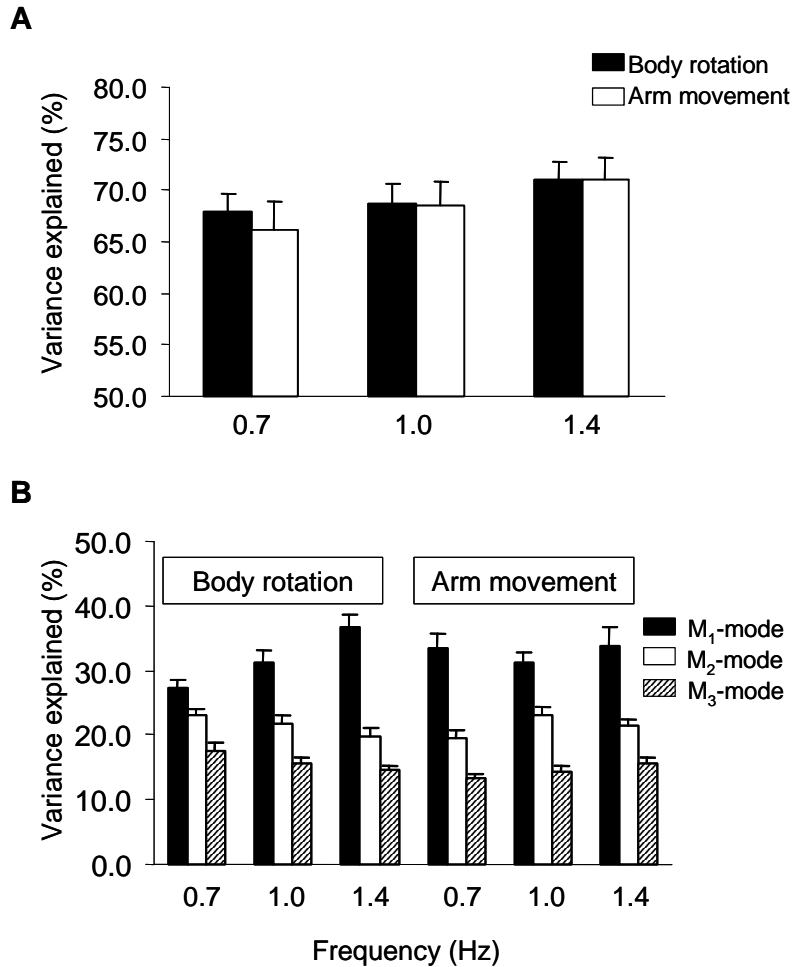


Figure 5.5: Averaged and standard error across subjects amounts of variance explained by the three first principal components (M-Modes) for the body rotation task (first three set of bars) and for the arm movement task (last three set of bars). Different bars represent the amount of variance explained by each M-mode: M₁-mode (dark bars), M₂-mode (white bars), and M₃-mode (stripped bars). Note the increase in the variance explained by M₁-mode and decrease of the variance of M₂- and M₃- modes for the body rotation task from the lower to the higher frequencies of movement. Note that this trend is not present at the execution of the arm movement task.

The composition of individual M-modes varied substantially among the subjects. Table 1 shows a set of loadings obtained for a typical subject under the execution of both tasks at the three frequencies. Significant loadings are shown in bold. No reproducible pattern of distribution of the significant loadings could be found.

Table 5.1: Loading coefficients for the PCA for a typical subject under body rotation and arm movement tasks performed the frequencies of 0.7, 1.0 and 1.4 Hz. M_1 = M_1 -mode (PC1), M_2 = M_2 -mode (PC2), and M_3 = M_3 -mode (PC3).

BODY ROTATION TASK									
	0.7Hz			1.0Hz			1.4Hz		
	M_1	M_2	M_3	M_1	M_2	M_3	M_1	M_2	M_3
TA	0.82	-0.11	-0.02	0.47	-0.72	0.22	-0.01	-0.10	0.76
GL	0.73	-0.11	0.18	0.84	0.12	0.03	0.26	0.24	0.70
RF	-0.25	0.89	0.03	-0.24	-0.89	-0.23	-0.79	0.41	-0.18
VM	0.01	0.88	-0.08	-0.17	-0.83	0.10	-0.50	0.60	-0.19
BF	0.82	-0.01	-0.14	0.79	0.30	0.11	0.77	-0.10	0.28
ST	0.76	-0.57	-0.04	0.71	0.43	0.48	0.87	-0.08	0.35
TFL	0.66	-0.53	0.04	0.73	0.11	0.39	-0.02	0.77	0.02
GT	0.28	-0.77	-0.23	0.14	-0.05	0.75	0.60	0.13	0.02
RA	0.15	0.27	0.77	-0.44	-0.17	0.60	0.01	0.12	-0.69
OA	0.53	-0.27	0.27	0.40	0.17	0.66	0.79	0.18	-0.02
SER	0.61	-0.65	-0.07	0.58	0.39	0.64	0.92	0.11	-0.13
ESL	0.09	-0.32	0.65	0.59	-0.17	0.03	0.15	0.69	-0.02
EST	-0.39	0.48	0.65	-0.15	-0.63	-0.51	-0.74	0.41	0.11
ARM MOVEMENT TASK									
	0.7Hz			1.0Hz			1.4Hz		
	M_1	M_2	M_3	M_1	M_2	M_3	M_1	M_2	M_3
TA	-0.81	-0.13	0.17	-0.83	-0.34	-0.13	0.60	0.63	-0.37
GL	0.13	0.29	-0.51	0.18	0.25	-0.72	-0.20	0.00	0.79
RF	-0.07	-0.05	-0.72	0.42	0.27	0.81	-0.69	-0.52	-0.31
VM	-0.71	0.01	-0.48	0.23	0.15	0.89	-0.56	-0.36	-0.51
BF	-0.91	-0.20	0.17	-0.82	-0.48	0.07	0.60	0.69	-0.29
ST	-0.86	-0.26	0.18	-0.79	-0.45	-0.01	0.65	0.59	-0.28
TFL	-0.25	-0.03	0.64	-0.59	0.06	-0.11	-0.12	0.14	-0.72
GT	-0.69	0.01	0.05	-0.81	-0.11	-0.10	0.36	0.66	-0.23
RA	0.31	0.86	-0.19	0.12	0.93	0.08	-0.92	-0.04	-0.02
OA	-0.28	0.73	-0.18	-0.62	0.46	0.05	-0.15	0.86	-0.01
SER	-0.74	0.28	0.03	-0.67	-0.17	-0.17	0.31	0.80	0.26
ESL	-0.09	0.91	0.06	0.09	0.89	0.00	-0.87	-0.03	0.11
EST	0.35	0.89	0.03	0.42	0.81	0.04	-0.79	-0.37	-0.10

Data for a typical subject under body rotation and arm movement tasks performed the frequencies of 0.7, 1.0 and 1.4 Hz are shown. Loadings over 0.5 are shown in bold (significant loadings). TA-tibialis anterior, GL-lateral gastrocnemius, RF-rectus femoris, VM-vastus medialis, BF-biceps femoris, ST-semitendinosus, TFL- tensor fascia lata, GT-gluteus maximus, RA- rectus abdominis, OA-obliquus abdominis, SER-serratus, ESL- erectus spinae lumbar, EST- erectus spinae thorax.

The data summarizing the total number of significant loadings observed in each M-mode for all ten subjects are shown in Figure 5.6. Note that for the body rotation task the first M-mode (M_1) showed an increase in the total number of significant loadings from the lowest (0.7 Hz) to the highest (1.4 Hz) frequency, while the third M-mode (M_3) showed an opposite trend. For the arm movement task this trend was not observed. Non-parametric tests ran for each of the tasks showed similar results across the two tasks. Friedman's test performed with factors *M-mode* and *Frequency* showed overall significance for both tasks ($\chi^2_{[2]} = 6.00$, $p < 0.05$). Kruskal-Wallis tests ran as post-hocs confirmed a significant effect of *M-mode* but not of *Frequency* for both tasks. Mann-Whitney tests showed significant differences for the following comparisons in both tasks: M_1 vs. all other M-modes ($p < 0.001$ for all body task comparisons; $p < 0.05$ for all arm movement tasks), M_2 vs. M_3 ($p < 0.001$ for all body task comparisons; $p < 0.05$ for all arm movement tasks). Mann-Whitney tests showed a significant difference for M_1 between 0.7 Hz and 1.4 Hz ($p < 0.01$) for the body rotation task.

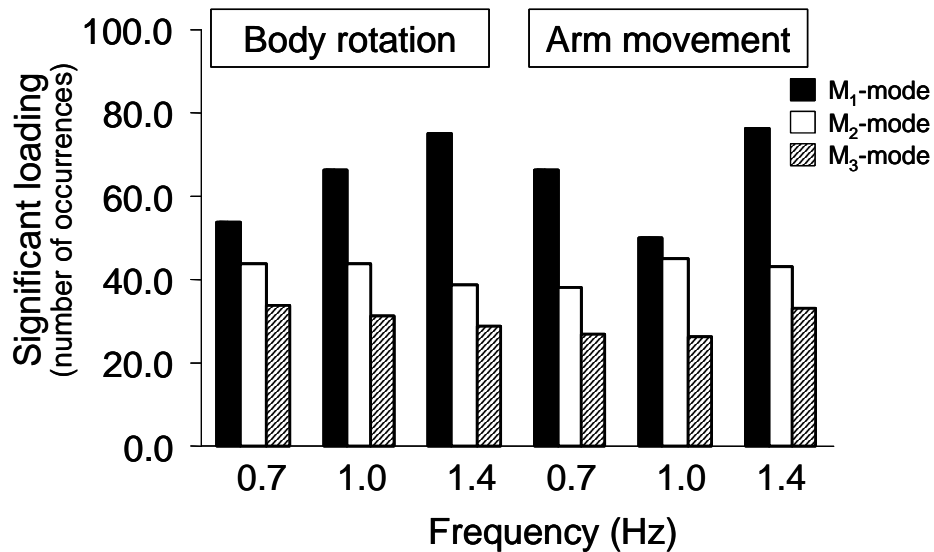


Figure 5.6: The total number of significant loadings of the indices of muscle activation for each M-mode for all eight subjects under the execution of the body rotation task (dark bars), and arm movement task (light bars) at different frequencies of body movement (0.7, 1.0, and 1.4 Hz). Note the increase in the number of significant loadings observed at M_1 -mode and decrease of the number observed at M_2 - and M_3 - modes for the body rotation task from the lower to the higher frequencies of movement. Note that this trend is not present at the execution of the arm movement task.

As described in Methods, we used absolute values of the cosines between M-modes in the muscle activation space as a measure of similarity. Computations were performed separately for the body rotation and arm movement tasks. For each task, cosines between central vectors, \mathbf{p}_i , and each individual M-mode vector were computed and compared across the three frequencies and across subjects. For this purpose, the absolute cosine values were transformed into z-scores. Figure 5.7 shows the mean z-scores of cosines for analysis across the sway frequencies for the body sway task (Figure 5.7A) and arm movement task (Figure 5.7B). Note that there is no significantly higher z-scores between a central vector and individual vectors of the same M-mode for both tasks.

Two-way mixed-design ANOVAs with factors *M-mode* (M1, M2, and M3) and *Central Vector* (\mathbf{p}_1 , \mathbf{p}_2 and \mathbf{p}_3) was used separately on the z-scores of the body rotation (Figure 5.7A) and arm movement tasks (Figure 5.7B). Both ANOVAs revealed no significant main effects of *M-mode* ($F_{[2, 261]}=1.15$, $p>0.1$ and $F_{[2, 261]}=1.66$, $p>0.1$ for body rotation and arm movement tasks, respectively) and of *Central Vector* ($F_{[2, 261]}=1.26$, $p>0.1$ and $F_{[2, 261]}=0.26$, $p>0.5$ for body rotation and arm movement tasks, respectively). No significant of *M-mode* \times *Central Vector* interaction was found for both tasks ($p>0.1$ in both tasks). Hence, the individual M-mode vectors \mathbf{M}_1 and \mathbf{M}_2 did not clustered around their central vectors (cosine values not close to unity), i.e. the M-modes observed at different sway frequencies weren't approximately similar.

A similar pattern was found for analysis across subjects. Figure 5.8 is organized similarly to Figure 5.7 but it presents data for all frequencies separately. Body rotation task results are presented in panels A, C and E while results regarding to the arm movement task are presented on panels B, D and F. In this case, two three-way ANOVAs with factors *Frequency* (0.7, 1.0, and 1.4 Hz), *M-mode* (M1-, M2-, and M3- modes) and *Central Vector* (\mathbf{p}_1 , \mathbf{p}_2 and \mathbf{p}_3) was preformed. The results were similar to those described in the previous paragraph. In particular, for both tasks there was not significant effects of *M-mode* ($F_{[2, 243]}=1.12$, $p>0.1$ and $F_{[2, 243]}=0.36$, $p>0.1$ for body rotation and arm movement tasks, respectively), *Central Vector* ($F_{[2, 243]}=1.11$, $p>0.1$ and $F_{[2, 243]}=1.6426$, $p>0.1$ for body rotation and arm movement tasks, respectively) and *Frequency* ($F_{[2, 243]}=0.51$, $p>0.1$ and $F_{[2, 243]}=2.25$, $p>0.1$ for body rotation and arm movement tasks, respectively). No interactions were found significant. These results confirmed no significantly higher z-scores for cosines

of the angles between the M_1 - and M_2 -modes for the different subjects and the central vectors of the same number. Hence, the individual M-mode vectors M_1 and M_2 did not clustered around their central vectors, i.e. the M-modes found in different subjects were not approximately similar.

Taken together, these findings confirm no similarity of M-mode composition in the muscle space across both subjects and frequencies for both tasks.

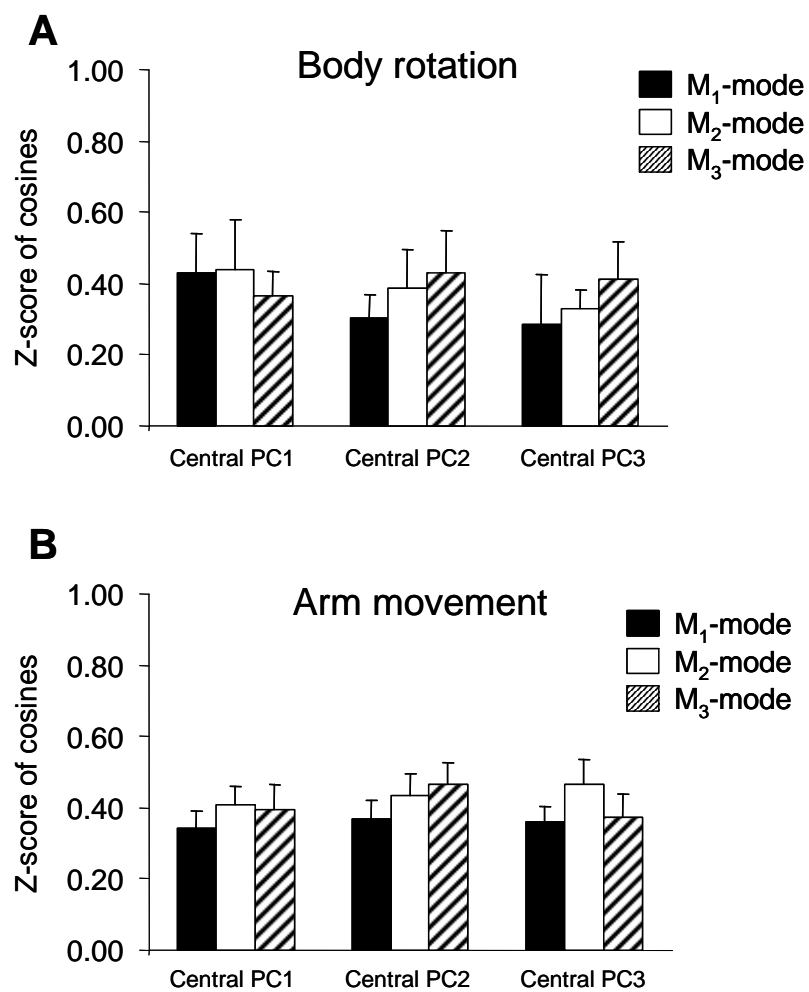


Figure 5.7: Body rotation (Figure 5.7A) and arm movement tasks (Figure 5.7B) averages and standard errors of z-scores of the absolute values of cosines between a central vector, p_i , and each mode vector; the data were averaged across body movement frequencies (with standard error bars).

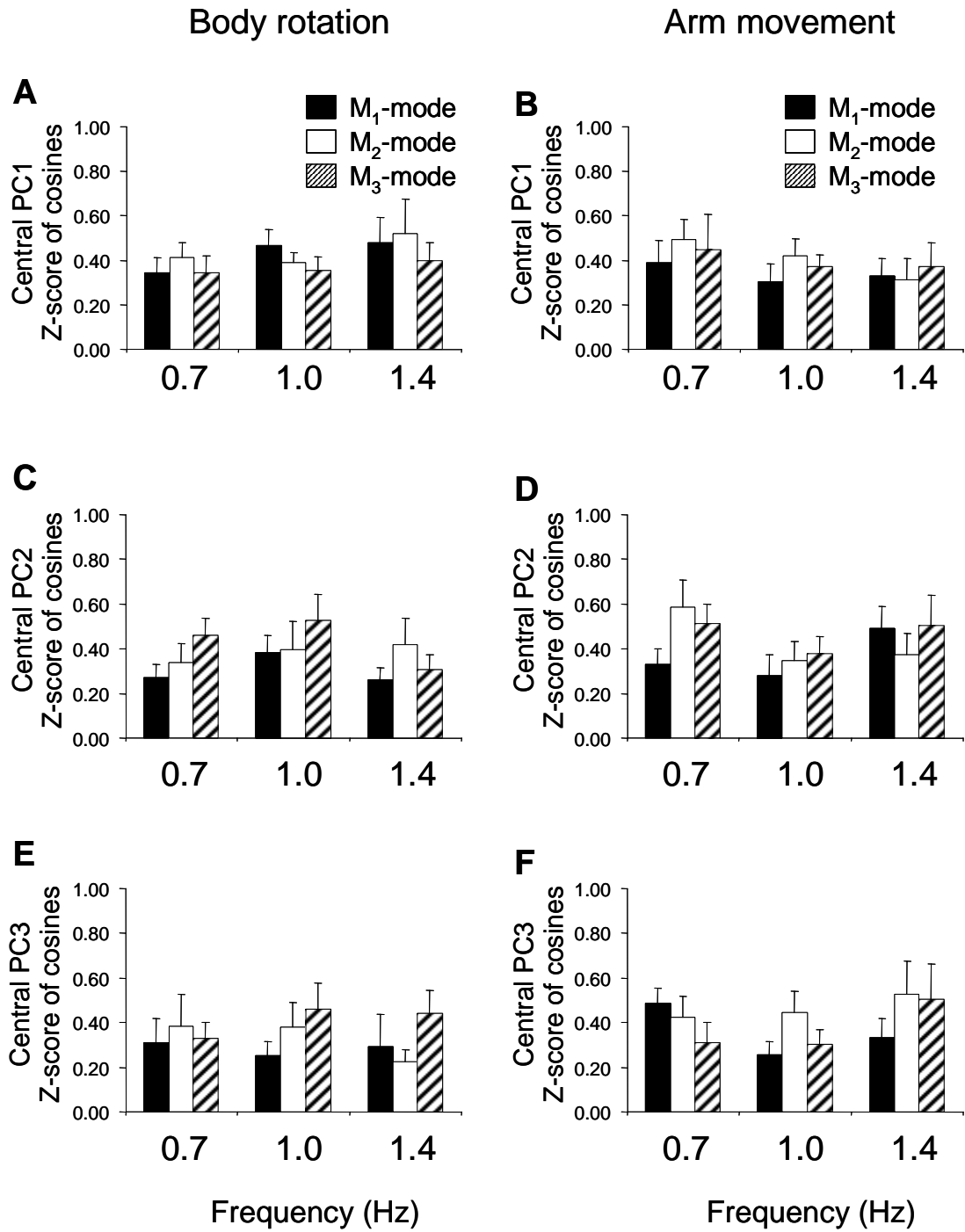


Figure 5.8: Body rotation (Figures 5.8A, 5.8C, and 5.8E) and arm movement tasks (Figures 5.8B, 5.8D, and 5.8F) Z-scores of the absolute values of cosines between a central vector, p_i , and each mode vector, PCs, averaged across subjects under different frequencies (with standard errors).

UCM analysis

Data from twelve continuous sway cycles for each of the five experimental conditions were used to perform analysis of the structure of variability in the space of M-modes. The method partitions the total variance in the M-mode space across cycles into two components. The first component (V_{UCM}) is within an uncontrolled manifold (UCM) approximated as the null-space of the corresponding \mathbf{J} matrix describing the linear relations between changes in the magnitude of M-modes (ΔM) and M_z shifts (ΔM_z) (see Methods). The other component (V_{ORT}) is within a sub-space orthogonal to the UCM. Further, we computed an index (ΔV) reflecting the normalized difference between V_{UCM} and V_{ORT} . We interpret positive values of ΔV as reflecting a multi-M-mode synergy stabilizing the average M_z shift.

The \mathbf{J} matrix was computed using multiple linear regression of changes in the magnitudes of M-modes (ΔM) against M_z shifts (ΔM_z) over the 12 cycles performed by each subject, for each experimental condition separately. The coefficients in the regression equations were arranged in a 3x1 vector-column (\mathbf{J} matrix) and its null-space was used to approximate the uncontrolled manifold.

Figure 5.9 shows the average amount of variance in ΔM_z explained by the regression model across the ten subjects (with standard errors). For the body rotation task the average amount of variance explained was $69.49 \pm 6.30\%$, $87.61 \pm 3.92\%$, and $81.60 \pm 5.69\%$ (0.7, 1.0, and 1.4 Hz, respectively). For the arm movement task, these values were $59.89 \pm 8.04\%$, $70.86 \pm 5.29\%$, and $62.00 \pm 5.00\%$ (0.7, 1.0, and 1.4 Hz, respectively). Note that the amount of variance is higher for the body rotation task under all three frequencies when compared to the averages for the arm movement task. A two-way mixed-design ANOVA with factors *Task* and *Frequency* run on the amount of variance explained by the linear model confirmed a significant effect of *Task* ($F_{[1, 54]} = 16.60$, $p < 0.001$) but not of *Frequency* ($F_{[2, 54]} = 1.69$, $p > 0.1$). No significant interaction was found ($F_{[2, 54]} = 1.23$, $p > 0.1$).

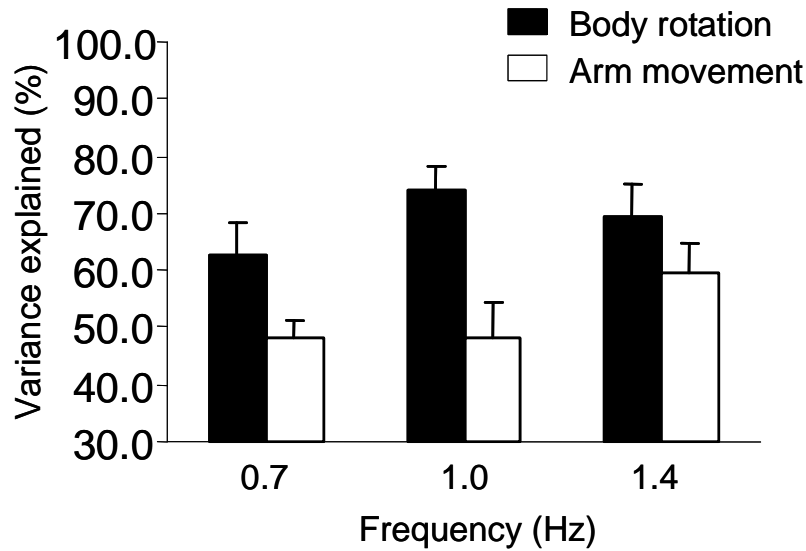


Figure 5.9: Variance explained by linear regression of ΔM_z against changes in the three M-mode (black bars). Note the larger amount of variance explained for the body rotation task when compared to the variance explained for the linear model regarding to the arm movement task. Note also the increase in the amount of variance explained from 0.7 Hz through 1.4Hz.

Regarding to the variance components, we found that, in average, subjects V_{UCM} values were similar for the two tasks. These results are displayed in Figure 5.10A, which shows the V_{UCM} and indices per degree-of-freedom averaged across all ten subjects. Note that V_{UCM} values for the body rotation task (black bars) are close to those values for the arm movement task (white bars). Similarly, V_{ORT} values were also similar for the two tasks (Figure 5.10B). However, in average, V_{UCM} showed consistently larger values than V_{ORT} for both tasks and all three frequencies studied. These findings were confirmed by the three-way mixed-design ANOVA run with factors *Task*, *Frequency*, and *Variance-Component* (V_{UCM} and V_{ORT}) run on the values of variance of the components. This ANOVA confirmed a significant effect of *Variance-Component* ($F_{[1, 108]} = 21.41$, $p < 0.001$) without any other effects ($p > 0.1$).

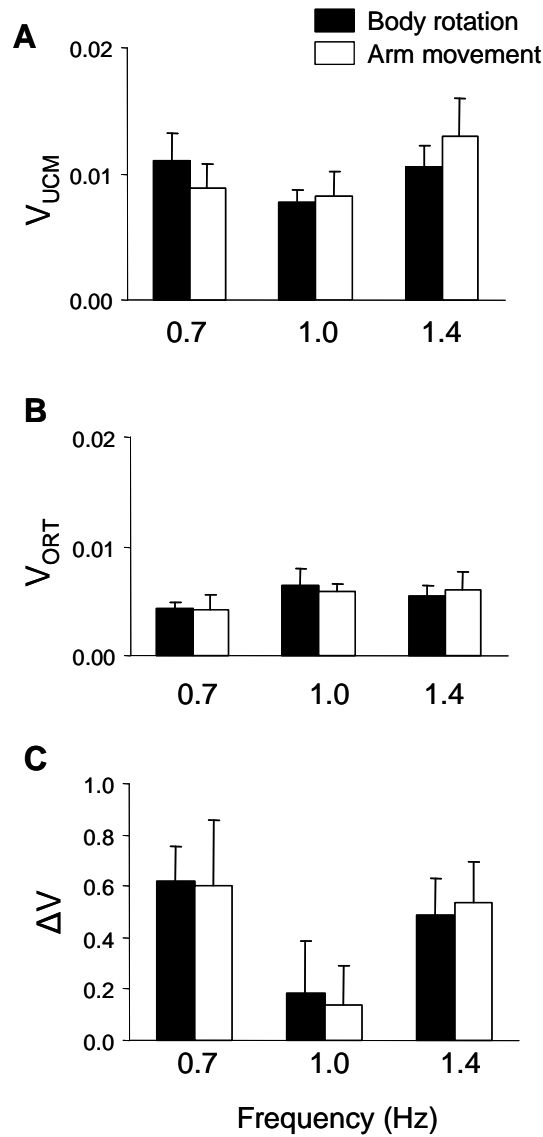


Figure 5.10: **Panels A and B:** Averaged across subjects V_{UCM} and V_{ORT} components of the total variance for each condition (with standard error bars). Dark bars represents V_{UCM} while light bars represent V_{ORT} . **Panel C:** Means and standard errors for ΔV across subjects. Note that the values are positive.

To test whether the two variance components changed similarly across the conditions, an index (ΔV) reflecting their normalized difference was used (Figures 5.10C). On average, ΔV was larger than zero for both tasks and all three frequencies studied. We also found that ΔV was smaller for both tasks for the frequency of 1 Hz. Note that in Figure 5.10C, both

black and white bars show lower ΔV values when both tasks were performed at 1 Hz. These findings were confirmed by a two-way mixed-design ANOVA with factors *Task* and *Frequency* on ΔV values. There was a significant effect of *Frequency* ($F_{[2, 54]} = 3.43$, $p < 0.5$), but not of *Task* ($F_{[1, 54]} = 0.00$, $p > 0.5$) without an interaction.

Time changes of ΔV for both tasks and all three frequencies are shown in Figure 5.11. In general, no clear pattern of ΔV modulation within the movement cycle was found for both tasks at the lowest and highest movement frequencies (0.7 and 1.4 Hz). This finding is illustrated in Figure 5.11A and 11B where averages across subjects of ΔV index time profiles are presented. Note that in both panels the dark and gray thick lines representing ΔV time profiles for body movements executed at 0.7 and 1.4 Hz do not show large modulations. In contrast, ΔV showed a drop when both tasks were performed at 1 Hz (thin line). For the body rotation task (Figure 5.11A) this drop occurred during the second half of the movement cycle while for the arm rotation task (Figure 5.11B) this drop was during the first 50% of the movement cycle.

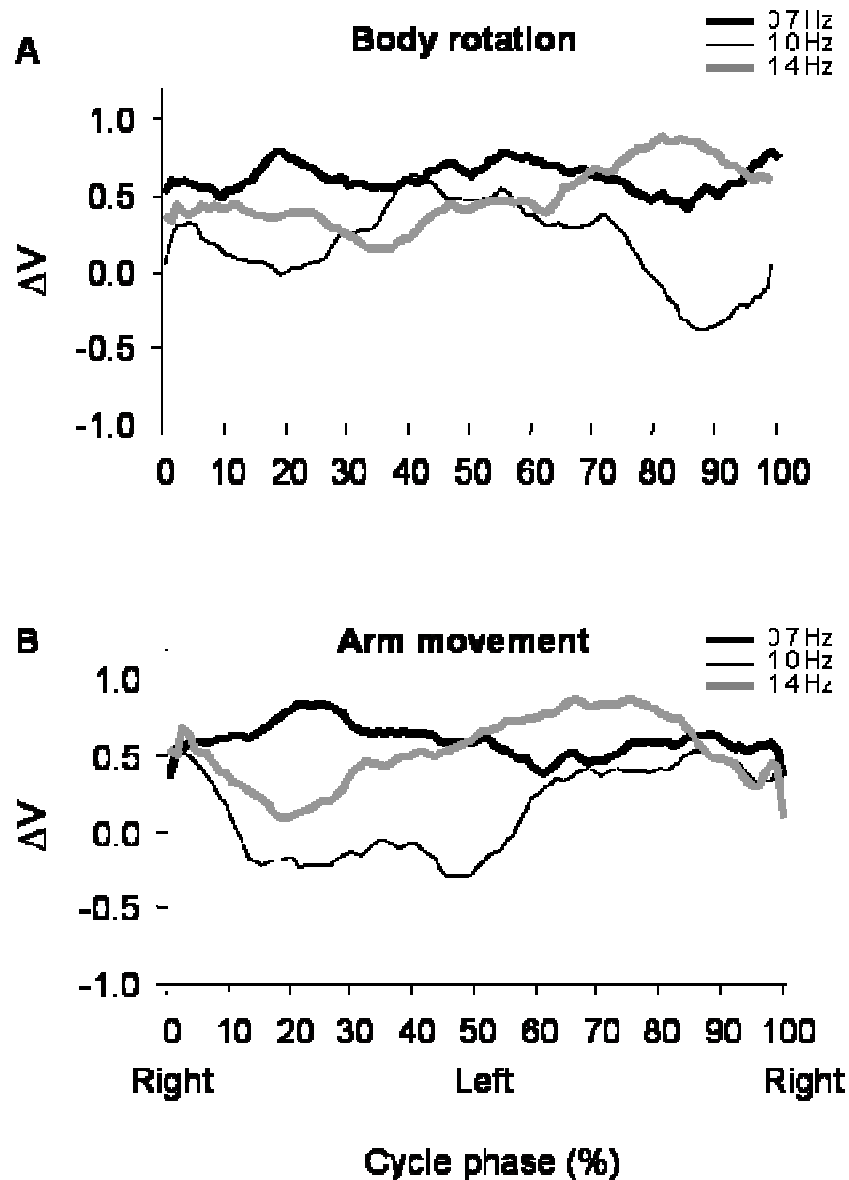


Figure 5.11: Panels A and B Time profiles of ΔV averaged across subjects over the full movement of body rotation task (Panel A) and arm movement task (Panel B). Thick dark, light dark, and thick gray lines represent the three movement frequencies executed by the subjects. Note that only at 1Hz there is consistent modulation of ΔV index values. Phases 0% and 100% indicate the highest value of M_z when body is rotated from right to the left ('Right shoulder forward') and phase 50% indicates highest value of M_z when body is rotated from the left to the right ('Left shoulder forward').

5.4 Discussion

The results of this study have provided an unexpected set of answers to the hypotheses formulated in the Introduction. With respect to the first hypothesis, muscle activation patterns during both tasks could indeed be described with a set of a few (three) M-modes; however, these sets were not consistent across the participants. Moreover, the composition of individual M-modes was not consistent within each participant across the different frequencies of movement. The second hypothesis has been confirmed: The sets of three M-modes formed the basis for synergies stabilizing M_Z time pattern across both tasks and all three frequencies. We found no evidence to support the third hypothesis: Both the organization of M-modes and the M-mode co-variation indices did not differ significantly between the two tasks. In the rest of this section, we discuss the findings and their implications for the two-level hierarchical control of whole-body, multi-muscle actions.

Different Sets of M-modes as the Basis for M-mode Synergies

Recently, studies of whole-body actions have been dominated by an idea that the central nervous system (CNS) manipulates a handful of variables that correspond to very stable and reproducible patterns of recruitment of individual muscles both across subjects and tasks (Krishnamoorthy et al. 2003a; Torres-Oviedo et al. 2006; Danna-Dos-Santos et al. 2007). In particular, these studies have reported similar directions of the eigenvectors in the muscle activation space, as defined by the PCA, across subjects and tasks (Krishnamoorthy et al. 2003a; Danna-Dos-Santos et al. 2007). Recent studies of locomotion and responses to postural perturbations have also resulted in a handful (five to six) of “muscle synergies” that were similar across the participants and conditions (Ivanenko et al. 2004; Torres-Oviedo et al. 2006; Torres-Oviedo and Ting 2007).

The results of this study illustrate limitations of such a simplified approach to the control of large muscle groups. We used a method of analysis of similarity of the directions within the groups of eigenvectors (M-modes) identical to the one used earlier (Krishnamoorthy et al. 2003a). However, the results were dramatically different: We did not find clustering of the eigenvectors corresponding to the same M-modes in different subjects or across different tasks. In fact, the composition of the M-modes was vastly different across both subjects, tasks, and movement frequencies such that no common features of the M-

modes could be identified that would be comparable to the “push-back”, “push-forward”, and “co-contraction” M-modes reported in earlier studies (Krishnamoorthy et al. 2003b, 2004; Danna-Dos-Santos et al. 2007).

Despite the different composition of the M-modes, all the subjects showed co-variation of the gains at which the M-modes were recruited across movement cycles that helped stabilize the M_Z trajectory. These results exemplify an important feature of motor synergies, namely their flexibility (Latash et al. 2007), that is, an ability to organize co-variation of elemental variables at a higher hierarchical level of control in a task-specific way while manipulating sets of different elemental variables (M-modes).

We can only speculate why the M-mode composition results of this study are qualitatively different from results of earlier studies that used similar data processing techniques for different tasks. It may be that the M-mode composition was significantly affected by the exact orientation of the vertical axis of the body. To make the task natural, we did not insist that the subject stood in a very rigid manner. This might lead to slight deviations of the vertical body axis both across subjects and across trials resulting in different patterns of muscle recruitment. Most muscles analyzed in our study generated joint torques in a sagittal plane such that a disbalance between the action of the muscles on the left and right sides of the body was the likely cause of M_Z changes. The unavoidable migration of the center of pressure (postural sway) about different locations (Zatsiorsky and Duarte 1999; Duarte and Zatsiorsky 1999) might also contribute to changes in muscle activation patterns across subjects and conditions.

Synergies as Reflection of Neural Control

Motor patterns during cyclic tasks reflect an interaction between neural control signals and mechanical properties of the moving effector, in particular its natural frequency (reviewed in Kugler and Turvey 1987). In particular, experiments with the reconstruction of hypothetical control signals within the equilibrium-point hypothesis (EP-hypothesis, Feldman 1986) framework during elbow cyclic movements have shown that the peak-to-peak excursions of the equilibrium trajectory were minimal at an intermediate frequency corresponding to the estimated natural frequency of the lower arm (Latash 1992). In other words, the CNS has to interfere minimally with an ongoing motion if its frequency fits the

natural frequency of the moving effector. One of the results of our current experiments seems to corroborate this general idea: During both tasks, the index of M-mode co-variation was the smallest at the intermediate frequency (1 Hz) as compared to both the lower (0.7 Hz) and the higher (1.4 Hz) frequencies.

Synergies have been defined as neural organizations of elemental variables with the purpose to stabilize a value or a time profile of a performance variable (reviewed in Latash et al. 2002, 2007). This definition implies, in particular, that the index of synergy (ΔV) is not expected to be highly positive if motion happens due to mechanical properties of the effector, without much intervention from the controller, i.e., at the effector's natural frequency. As a pilot post-hoc, we asked a few subjects of this study to perform both tasks (arm movement and body rotation) at a comfortable, self-selected frequency. They all performed these movements at frequencies within the 1-1.2 Hz range. Note that several studies have shown that self-selected frequencies are typically close to the natural frequencies for the effectors (Hatsopoulos and Warren 1996; Goodman et al. 2000; Yu et al. 2003). Hence, we offer the following interpretation for the significantly lower ΔV indices for the two tasks:

When the movement is performed at its natural frequency, changes in muscle activation, within both the explicitly involved effectors and the apparently postural muscles, reflect movement mechanics and the action of reflex loops. Neural commands to the muscles and joints (for example, $\lambda(t)$ functions within the EP-hypothesis) start exerting significant effects on muscle activation patterns when the required movement has to deviate substantially from the natural (preferred) frequency. Only in the latter case, strong co-variation in the space of elemental variables is expected stabilizing the salient mechanical variables. In other words, synergies, as quantified with the introduced index ΔV , reflect both quality and quantity of control. The latter reflects to what extent external mechanical patterns are defined by control signals as compared to peripheral factors such as mechanics and reflex loops, while the former reflects how well appropriate control variables co-vary.

Relations of the Results to Locomotion

In one aspect, the study has failed to provide a definitive answer to one of the main questions that motivated the design of the study. The two tasks were selected to reveal

possible differences in the organization of muscle activation patterns in the lower body during locomotor-like alternating arm movements and during another type of movement (body rotation) that produced a similar pattern of M_z changes. The expectations of differences in the organization of muscle modes and/or multi-M-mode synergies were based on clinical observations in patients with spinal cord injury who showed entrainment of leg movements by alternating arm movements, but not by upper body rotation at a similar frequency, unless given several weeks of practice (Shapkova 1997).

We have failed to detect significant differences between the two tasks. This might be partly due to the broadly varying M-mode composition both across the subjects and across the movement frequencies. It is also possible that the used method of EMG analysis is too crude to detect differences in muscle activation patterns that are produced by a spinal central pattern generator and those produced by other pathways when the patterns of the lower-body mechanics are qualitatively similar.

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CHAPTER 6

STUDY #4

Anticipatory control of head posture

6.1 Introduction

When a standing person performs a fast arm movement, the vertical posture is perturbed. A major feed-forward mechanism of postural stabilization in such conditions is the anticipatory postural adjustments (APAs) that represent changes in the activity of postural muscles prior to the initiation of voluntary motor actions (Belen'kii et al., 1967, Marsden et al., 1978, Cordo and Nashner, 1982 and Bouisset and Zattara, 1987). In particular, APAs have been described in the leg and trunk muscles prior to a fast arm action or load manipulation (Lee, 1980, Horak et al., 1984, Bouisset and Zattara, 1987, Aruin and Latash, 1996, Shiratori and Latash, 2000, Slijper et al., 2002 and Shiratori and Aruin, 2004). Many of the mentioned studies quantified APAs as changes in the muscle activation levels within a time window selected to avoid action of stretch reflexes and other feedback mechanisms.

The purpose of APAs has been commonly considered as producing appropriate shifts of the point of application of the resultant force acting on the body from the supporting surface (center of pressure, COP, Bouisset and Zattara, 1987 and Massion, 1992). These shifts are produced by coordinated changes in the muscle activity (Krishnamoorthy et al., 2003). COP shifts are viewed as a major mechanism to produce shifts of the center of mass (COM) that is commonly viewed as a major controlled variable in postural tasks (Winter et al., 1996). During APAs, however, the purpose of COP shifts is to avoid COM motion that otherwise could be induced by the perturbation.

Most studies of APAs in standing persons have naturally focused on trunk stabilization (reviewed in Massion, 1992). It has been suggested, however, that during daily activities such as walking and running, and also during acrobatic movement such as salto, the head posture with respect to the trunk is well stabilized to ensure a reliable reference frame (Berthoz and Pozzo, 1994 and Pozzo et al., 2001). The importance of head stability during whole-body actions performed by standing persons has received support in another recent

study (Freitas et al., 2006). However, only a couple of studies addressed the role of APAs in head stabilization, and their results are controversial.

Gurfinkel et al. (1988) described increased activation of neck extensors and a drop in the activity of neck flexors about 60 ms prior to the activation of the prime mover (deltoid muscles). This pattern was time locked with APAs in leg muscles, and the authors suggested that the combined APAs in the neck, trunk, and leg muscles formed a complex posture-stabilizing pattern. Van der Fits et al. (1998) used a similar task in a variety of subject postures, standing, sitting, and supine. These authors described a co-contraction pattern of neck flexors and extensors across all conditions.

The discrepancy in the results of the two mentioned studies led us to the following hypothesis. We suggest that APA patterns in neck muscles may be defined by two factors, local (a predictable perturbation acting on the head) and global (a perturbation acting on the center of mass of the body and affecting the head indirectly, due to the mechanical coupling between the trunk and the head). If the direction of a perturbation acting on the head is well predictable, a reciprocal APA pattern in neck muscles can be used to counteract the mechanical effects of the perturbation on the head posture. In contrast, if a self-triggered perturbation acts on the trunk, APAs in leg and trunk muscles stabilize the trunk posture, but the combined action of those APAs and the original perturbation may perturb the head posture due to the mechanical coupling. Since the direction and magnitude of such a perturbation acting on the head may not be well predictable, an increase in the apparent neck stiffness (co-contraction) may be used as an APA to increase resistance to perturbation in any direction.

To test the main hypothesis on two APA patterns, we performed experiments where similar initial positions of the body and similar actions by the subject were associated with perturbations acting predominantly on the head, predominantly on the trunk, and on the trunk and the head together. Our first specific hypothesis (Hypothesis #1) was that APA patterns in the neck flexor–extensor muscles would change from a time-shifted (reciprocal) pattern to a synchronized (co-activation) pattern when the source of the perturbation changes from that applied directly to the head to resulting from joint coupling. We also explored a possibility that APAs in trunk and leg muscles contributed to head stabilization. If so, a combined perturbation to the trunk and to the head could be expected to lead to significantly larger

APAs in those muscles than a perturbation applied to the trunk alone (Hypothesis #2). Large APAs in the leg/trunk muscles could also be expected when a perturbation is applied directly to the head (Hypothesis #3).

6.2 Methods

Subjects

Seven subjects (four males and three females) with the mean age 30.1 years (± 2.9 , SD), mean mass 77.7 kg (± 20.3 , SD), and mean height 170.4 cm (± 7.9 , SD) participated in the study. All the subjects were healthy, without any known neurological or muscular disorders. All subjects were right-handed based on their preferential hand usage during writing and eating. The subjects gave informed consent based on the procedures approved by the Office for Research Protection of The Pennsylvania State University.

Apparatus

A force platform (AMTI, OR-6) was used to record the moment of force around the frontal and sagittal axes (M_y and M_x , respectively) and the vertical component of the ground reaction force (F_z). These signals were used to compute the displacement of the body center of pressure (COP).

Disposable self-adhesive electrodes (3M Corporation) were used to record the surface electromyogram (EMG) of the following muscles: gastrocnemius lateralis (GL), tibialis anterior (TA), biceps femoris (BF), rectus femoris (RF), lumbar erector spinae (ES), rectus abdominis (RA), and sternocleidomastoid as the neck flexor (NF). We also recorded the surface EMG activity at the dorsal part of the neck. Since the dorsal part of the neck has multiple layers of muscles, the recorded signals reflected the activity not only of the most superficial muscle (superior fibers of trapezius) but also of deeper muscles (semispinalis, splenius cervicis, and splenius capitis). We will refer to this signal as reflecting neck extensor (NE) activity.

All muscles recorded were chosen based on their potential role in postural stabilization of the head and the trunk and their accessibility to surface EMG recording. The electrode pairs were placed over the muscle bellies; the distance between the two electrodes of each pair was 3 cm. Lower limb and trunk electrodes were placed only unilaterally on the

right side of the subject's body due to the limitation in the number of channels. Neck electrodes were placed bilaterally over the right (R) and the left (L) muscles (NFL, NFR, NEL, and NER). The electrode pairs recording the NE activity were placed parallel to the spine with the upper electrodes positioned about 2 cm below the occipital protuberance. Electrodes recording NF activity were placed along the sternocleidomastoid midway between its sternum and mastoid insertions.

The EMG signals were amplified ($\times 3000$) and band-pass filtered (60–500 Hz). All the EMG signals were sampled at 1000 Hz with a 12-bit resolution. A personal computer (Gateway 450 MHz) was used to control the experiment and to collect the data with a customized Labview-based software (Labview-5 – National Instruments, Austin, TX, USA).

A ProReflex motion analysis system (Qualysis Track Manager vs 1.7.187 – Qualysis Medical) was used to capture the coordinates of a passive marker placed on the lateral aspect of the index finger metacarpophalangeal joint on the right hand. Three more markers were placed laterally on the customized helmet (described later) and their coordinates were used to detect angular displacement of the head in a sagittal plane (these data were collected only in four subjects). This motion analysis system was synchronized with the computer collecting the force plate and EMG data; it recorded 3D coordinates of the marker at 200 Hz. An accelerometer was placed on the dorsal side of the right hand; its signal was used to detect the moment of hand movement initiation during off-line data processing.

A customized hockey helmet was used to apply perturbations to the subject's head. This helmet was firmly fitted onto the subjects' head; the chin support piece was used to improve helmet stability. Two levers (50 cm long) were attached to the front and back portions of the helmet about 2 cm above the eye level line; they were used to attach loads during the experiment (see Section 2.3). The distance between the center of the helmet's top and the point where the load was attached to the lever was 0.6 m. A pole (1.77 m height) was positioned 0.7 m in front of the subject for series of trials involving trunk perturbation (Figure 6.1). A horizontal lever was attached to the pole, and a load (0.5 kg) suspended on a flexible fishing line was aligned with the inferior portion of the sternum (see Section 2.3).

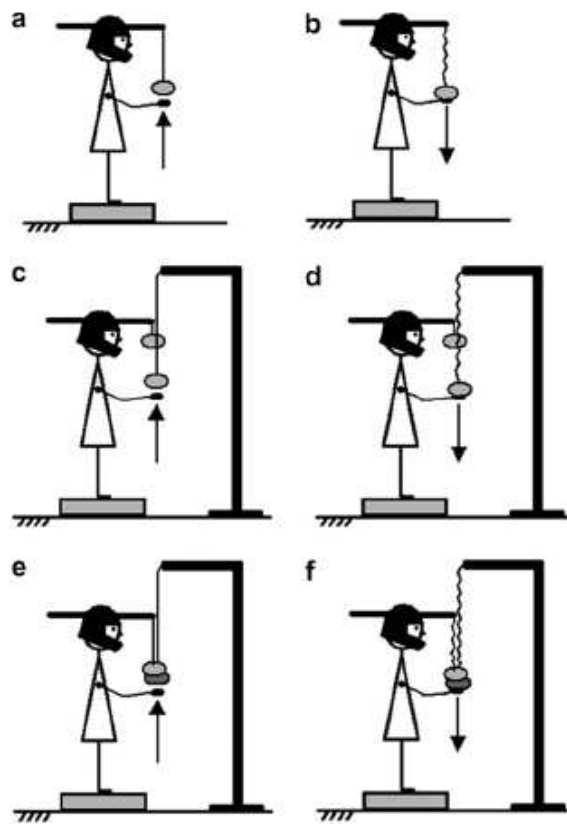


Figure 6.1. An illustration of the six main experimental series: Head perturbations (HP, panels a and b), trunk perturbation (TP, panels c and d), and head and trunk perturbation together (HTP, panels e and f). Arm upward and downward movements were used to produce perturbations in different directions.

Procedures

The experiment started with three control tests used for normalization of the postural sway data (COP displacement) and the EMG signals as described in the following section (Data processing). The first control test involved a single trial with quiet standing. This test was used to obtain measures of natural postural sway that were later used to normalize COP migration during APAs for across-subjects comparisons. The subjects were instructed to stand quietly on the force plate for 10 s while looking at the target placed 2.3 m in front of them at the eye level.

The other two tests were used to get quantitative indices of activity of postural muscles associated with a standard task of quiet standing with an additional load that

generated torque in a sagittal plane acting to rotate the head and the trunk either forward or backwards. These data were used to normalize integral EMG indices during APAs for across-subjects comparisons. In these tests the subjects were instructed to stand quietly and to hold a 5 kg load for 10 s with the arms fully extended while another load (1 kg) was attached to one of the helmet's levers. The subjects were asked to keep both the head and the trunk vertical; this was controlled by the experimenter. In one of the tests both loads created moments of force that tended to rotate the head and the trunk forward. In the other test the same loads held through a pulley system created moments of force that tended to rotate the head and the trunk backwards.

The main portion of the experiment involved three tasks (Figure 6.1). The tasks required the subjects to produce hand actions that triggered three types of perturbations in the sagittal plane. The three perturbations were; (a) head perturbation (HP) created by a fast, low-amplitude arm movement with the arm moving the load acting on the head; (b) trunk perturbation (TP) created by a fast, relatively large-amplitude movement of the arms that moved the load acting on the trunk; and (c) both head and trunk perturbation (HTP) by a fast, relatively large-amplitude movement of the arms that moved both loads acting on the head and on the trunk. For each task, two different conditions were used involving arm movement in opposite directions (upward and downward) and resulting in different perturbations to the posture. As a result, there were six different series of trials: three tasks (type of perturbation) and two actions (direction of arm movement).

In all series, the subjects were instructed to stand on the force plate with their feet parallel to each other, spaced by 18 cm, with the body weight evenly distributed between the feet and look straight at the same target that was used in the control tests. The foot position was marked on the top of the platform and reproduced across all trials. The arms were extended forward but not outstretched completely, with the elbows flexed and wrists extended, such that the hands were at the level of the load(s) (see Figure 6.1). Before the upward arm movement series, the two hands formed a "cup" placed just under the load without touching it (Figure 6.1a, c, and e). Prior to the series with downward arm movements, the load rested on the hands such that the line connecting the load to the helmet and/or the pole was slightly loose (Figure 6.1b, d, and f). In all series, the instructed arm movement was a very fast bilateral shoulder flexion (upwards) or extension (downward).

In order to generate perturbation acting mainly on the head (HP), a standard load (0.5 kg) was attached to the helmet's front lever and suspended at about the level of the inferior sternum extremity with a flexible fishing line. In one series, the subjects were instructed to move the load quickly upwards over the nominal distance of 10 cm in a self-paced manner 1–2 s after an auditory signal, a “beep” (Figure 6.1a). This action unloaded the helmet leading to a head extension perturbation. In another series, the subjects were instructed to hold the load in the hands such that the fishing line was slightly loose and then perform a quick hand motion downwards over the nominal distance of 10 cm in a self-paced manner 1–2 s after a “beep” (Figure 6.1b). This action resulted in loading the helmet and generating a head flexion perturbation.

To generate perturbation acting mainly on the trunk (TP), the same 0.5 kg load was attached to the helmet's front lever. Another 0.5 kg load was attached to the pole standing on the floor in front of the subject. The subjects were instructed to perform similar series of trials as in the HP series: to move the load attached to the pole quickly upward (Figure 6.1c) and downward (Figure 6.1d) in different series. In order to increase the magnitude of the perturbation acting on the trunk, the instruction for these two series was to perform a very fast hand movement over the nominal distance of 25 cm. We used this relatively small load (leading to relatively small trunk perturbations) to avoid fatigue and to have comparable magnitudes of the perturbation in cases when it was applied to the head and when it was applied to the trunk. Therefore, we were limited by perturbations that were safe and not uncomfortable when applied to the head.

The last task (HTP) was a combination of the two already described in order to generate a perturbation acting on both the head and trunk at the same time. Both 0.5 kg loads were used. The first was attached to the helmet's front lever and the second load was attached to the pole. Both loads were kept close to each other and suspended at the level of the sternum. The instructions were to perform a very fast movement over the nominal distance of 25 cm (same as in the TP task) upward (Figure 6.1e) and downward (Figure 6.1f) lifting and releasing the two loads together in two different series.

A familiarization period was given to each subject prior to data collection. During the familiarization period, subjects were asked to perform at least five trials for each of the tasks and actions. The experimenter paid particular attention to the initial vertical posture of both

head and trunk and to reproducible arm movement over trials within each series. Seven trials were performed for each series, and the order of the series was balanced across subjects. Resting periods of 30 s were given between trials, and at least 1 min between series. The average duration of the experiment was 45 min, and after the procedures all the subjects were asked about feeling fatigue. None of the subjects complained about any type of discomfort or fatigue.

Data processing

All signals were processed off-line using LabView-5 and MatLab 6.5 software packages. Signals from the accelerometer were not filtered to allow better detection of movement initiation. For all trials and conditions, all data from force plate, EMG, and 3D motion capture system were aligned according to the first visible change in the signal from the accelerometer attached to the right hand. This moment of the hand movement initiation will be referred to as ‘time zero’ ($t_0 = 0$).

Signals from the force plate were filtered with a 20 Hz low-pass, second-order, zero-lag Butterworth filter. Center of pressure coordinates in the anterior–posterior (AP) and medial–lateral (ML) directions (COP_{AP} and COP_{ML} , respectively) were computed using an approximation:

$$COP_{AP} = -M_y / F_z \quad (1A)$$

$$COP_{ML} = M_x / F_z. \quad (1B)$$

As commonly accepted in studies of COP shifts, the effects of the shear forces on the moments of force measured by the platform were ignored because of the small lever arm of those forces (the AMTI platforms record the moments with respect to the platform center located 36 mm beneath the surface). The assessments suggest that the contribution of shear forces to the estimated COP shifts was always well under 10%.

Changes in the COP displacement happen in two directions, anterior–posterior and medio-lateral, even when the perturbation is mostly limited to a sagittal plane. The COP shifts are typically rather small during the APAs (e.g., Aruin and Latash, 1995). Therefore, to

quantify them we have used a general measure of COP migration during the time window typical of APAs – the area of the ellipse that included most of the COP migration data. To quantify COP migration prior to the perturbation, the COP time series were processed as follows. Ellipses were fitted to the COP data collected over two time intervals: from –500 ms to –350 ms (baseline COP migration) and from –100 ms to +50 ms with respect to t_0 (COP migration during APAs). Each ellipse contained 85.3 % of the COP data points (cf. Oliveira et al., 1996). The area of each ellipse was computed. The first time interval captured the COP baseline migration (COP_{BL}) and the second interval captured possible anticipatory changes in the COP trajectory associated with the action (COP_{APA}). COP_{APA} was then corrected by COP_{BL} . For across-subjects comparison, the difference ($COP_{APA}-COP_{BL}$) was normalized by the area of a third ellipse computed for the data collected over the same period of 150 ms in the middle of the control trial when the subject stood quietly without any load, $COP_{CONTROL}$. An index, I_{COP} , was computed as follows:

$$I_{COP}=(COP_{APA}-COP_{BL})/(COP_{CONTROL}). \quad (2)$$

All EMG signals were rectified and filtered with a 50 Hz low-pass, second-order, zero-lag Butterworth filter. The accelerometer signal was used to align the rectified EMG by t_0 . After the alignment, all seven trials within each series were averaged and APAs were quantified as follows. EMG signals for each muscle were integrated over two time intervals: from –500 ms to –350 ms and from –100 ms to +50 ms with respect to t_0 . The first time interval captured the muscle background activity ($\int EMG_{BG}$) and the second interval captured possible anticipatory changes in the activity ($\int EMG_{APA}$) associated with the action. The interval of EMG integration associated with APAs was selected to include most of the changes in muscle activity that occur in a feed-forward manner while avoiding possible effects of stretch reflexes. $\int EMG_{APA}$ was then corrected by $\int EMG_{BG}$.

In order to compare the EMG indices ($\int EMG$) across muscles and subjects, we normalized them by the EMG signals integrated over the same period of 150 ms in the middle of the control trial ($\int EMG_{CONTROL}$) when the subjects held the two loads while standing quietly. $\int EMG$ indices for the dorsal muscles (GL, BF, ES, and NE) were divided by EMG integrals obtained when the loads were held in front of the body. $\int EMG$ indices for the

ventral muscles (TA, RF, RA, and NF) were divided by the EMG integrals obtained when the loads were suspended behind the body:

$$\int \text{EMG} = \int_{-150}^0 \text{EMG}_{\text{APA}} - \int_{-500}^{-350} \text{EMG}_{\text{BG}} \quad (3A)$$

$$I_{\text{EMG}} = \frac{\int \text{EMG}}{\int \text{EMG}_{\text{CONTROL}}} \quad (3B)$$

Statistics

Standard methods of descriptive statistics and parametric statistical methods were used (SPSS-13). Four sets of analysis were performed:

(1) The COP index (I_{COP}) was analyzed with a two-way mixed design ANOVA with factors *Perturbation* (HP, TP, and HTP) and *Direction* (Up and Down).

(2) EMG indices (I_{EMG}) of the leg and trunk muscles (GL, TA, BF, RF, ES, and RA) were analyzed using a two-way MANOVA with factors *Perturbation* and *Direction*.

(3) EMG indices (I_{EMG}) of the neck muscles (NF_L, NF_R, NE_L, and NE_R) were analyzed using a three-way MANOVA with factors *Perturbation*, *Direction*, and *Side* (Right and Left).

(4) To investigate the relative timing of changes in the activity of neck muscles, a cross-correlation function between the neck flexor and extensor muscles over a time period from -200 ms to $+200$ ms with respect to t_0 was computed. This analysis was done separately for the right and left muscle pairs. Prior to this analysis, the EMG signals were filtered at 20 Hz with a low-pass, second-order, zero-lag Butterworth filter to obtain EMG envelopes. For each trial, the peak magnitude of the correlation coefficient (R-peak) and the time lag (Δt) of R-peak were computed. In order to normalize the R data these data were log-transformed into z -scores by Fisher's transformation:

$$z\text{-score}_{(\text{R-peak})} = 0.5 * (\log(1 + \text{R-peak}) / (1 - \text{R-peak})) \quad (4)$$

Further, the average z -score and Δt data for each condition were calculated across the trials. Two one-way ANOVAs (*Perturbation* as the factor) were performed on the z -score and Δt variables.

In all sets of analysis, Tukey's honestly significant difference (HSD) tests and pairwise contrasts were used as post-hocs for significant effects. The significance level for all analyses was kept at 0.05.

6.3. Results

All subjects were able to accomplish successfully all tasks. Figure 6.2 shows a data set from a TP trial performed by a typical subject (subject #1). Time zero was defined as the earliest signal from the accelerometer (panel a). For better interpretation of this Figure 6., EMGs of pairs of muscles are displayed together (panels d–h). In the Figure 6., the rectified EMG signals of TA, RF, RA, NF_R, and NF_L muscles are inverted (turned into negative values) to avoid superimposed lines. Note that anticipatory changes in muscle activity (APAs) started before time zero in BF, ES, NE_R, NE_L, NF_R, and NF_L. Note the simultaneous changes in the activity of NE and NF. Note also a relatively small head displacement associated with the arm movement (panel b).

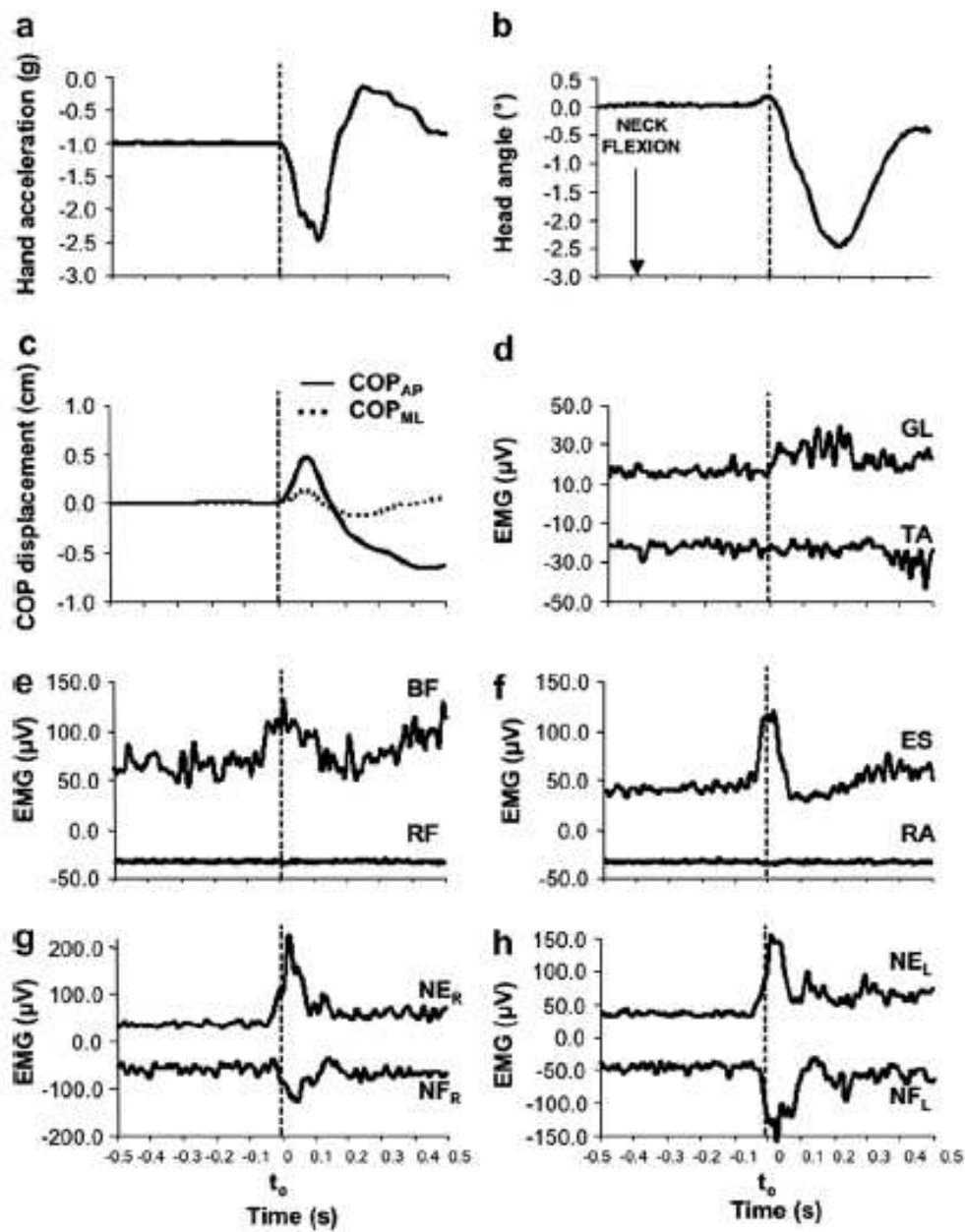


Figure 6.2. A typical data set from a representative subject (subject #1) during downward arm movement in a TP trial. Hand acceleration (panel a), Head angular displacement (panel b), displacement of COP in both directions (panel c), and EMGs of all 10 muscles recorded (Panels d through h) are displayed. Time zero (t_0) corresponds to the initiation of hand action. Note: TA, RF, RA, NF_R , and NF_L EMG time profiles were inverted (turned into negative values) to avoid superposition of lines; for these muscles negative values of larger magnitude indicate increased muscle activation.

Upper limb movements and COP displacements

Off-line analysis of the vertical displacement of the passive marker placed on the subject's hand showed a sigmoid trajectory (Figure 6.3). Figure 6.3 shows the vertical hand displacement during upward (panel a) and downward (panel b) arm movements averaged across subjects for each task separately. The amplitude of the movement was much smaller in the head perturbation series (HP) as compared to the trunk perturbation (TP) and head and trunk perturbation (HTP) tasks. The amplitude of the vertical hand displacement was 10.0 cm (± 0.8 SE), 23.0 cm (± 1.8 SE), and 22.5 cm (± 1.5 SE) during upward arm movements under the HP, TP and HTP tasks, respectively. During downward movements, the average displacements were 7.0 cm (± 0.9 SE), 41.0 cm (± 2.0 SE), and 39.8 cm (± 1.9 SE) for the HP, TP and HTP tasks, respectively. Movement time was close to 250–300 ms across all series.

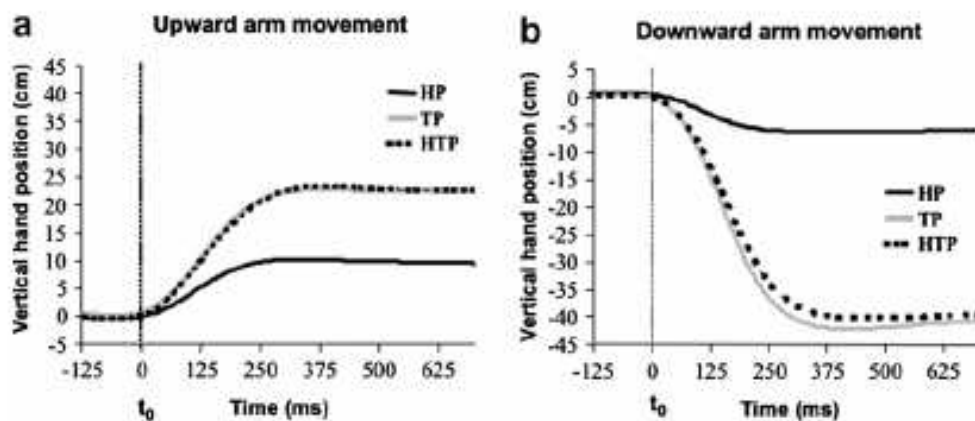


Figure 6.3. Vertical hand displacement during upward and downward arm movements (panels a and b, respectively). Each panel shows the average time profiles across subjects for head perturbation (HP), trunk perturbation (TP), and head and trunk perturbation (HTP) tasks. The vertical dashed lines indicate the moment of movement initiation (t_0). Standard error bars are not presented to make the Figure 6.readable.

The hand motion was accompanied by relatively small COP displacements. Peak-to-peak COP displacements in both anterior–posterior (AP) and medio-lateral (ML) directions were typically under 1 cm. Figure 6.4a illustrates averaged across subjects COP_{AP} time profiles during downward arm movements for the three tasks, HP, TP, and HTP. In TP and HTP tasks, COP_{AP} showed larger displacement for the period starting about 100 ms before t_0 and ending about 300 ms after t_0 , as compared to the HP task.

Figure 6.4a also illustrates larger COP displacements forward in the TP and HTP tasks at about 400 ms after the movement initiation. COP migration was quantified with an index I_{COP} computed for the time window from -100 ms to $+50$ ms with respect to t_0 (see Section 2). Figure 6.4b shows larger I_{COP} in the TP and HTP tasks as compared to HP. This finding was confirmed by a two-way ANOVA (*Perturbation* \times *Direction*) that showed a significant effect of *Perturbation* ($F_{2,36} = 3.35$, $p < 0.05$). Tukey's HSD tests confirmed significant differences between HP and TP and also between HP and HTP ($p < 0.05$). There were no significant effects of *Direction* and no significant interaction.

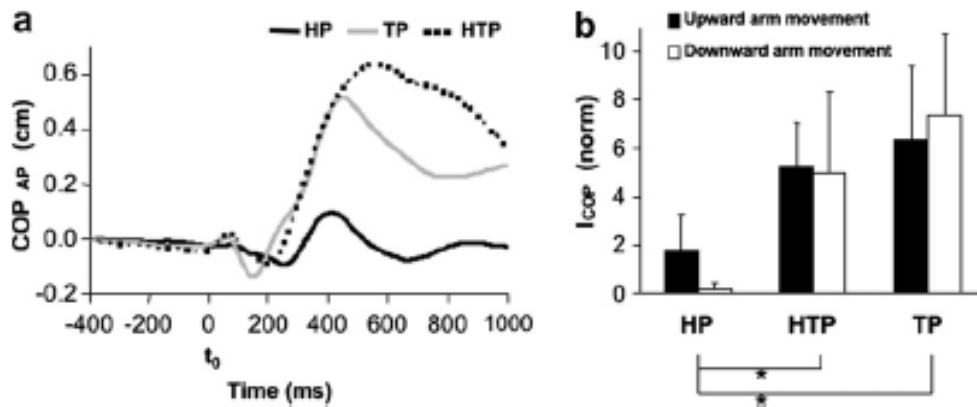


Figure 6.4. **Panel a** shows the anterior–posterior center of pressure displacement (COP_{AP}) for downward arm movement condition under head, trunk, and head and trunk perturbations (HP, HTP, and TP, respectively). Average time profiles across subjects are shown and standard error bars are not presented to make the Figure 6.readable. Positive values indicate anterior COP displacement. **Panel b** shows the index of COP shift (I_{COP}) over the period from -100 ms to $+50$ ms with respect to t_0 during upward and downward arm movements and the HP, HTP, and TP tasks. Averages across subjects with standard error bars are shown; * means $p < 0.05$. Lines connecting the mean bars indicate significant differences.

Muscle activation during APAs: neck muscles

The patterns of changes in the neck muscle activity differed across the HP, TP, and HTP tasks. Figure 6.5 illustrates typical EMG time profiles for the right neck flexor and extensor muscles in a representative subject (subject #1) performing downward arm movements in the HP, TP, and HTP tasks. The subject showed APAs only in the extensor muscle for the HP task and in both flexor and extensor muscles in the TP and HTP tasks. Note that the flexor and extensor both showed an increase in the activity during APAs in the

TP and HTP tasks. The left neck muscles presented similar pattern to those seen in the right neck muscles.

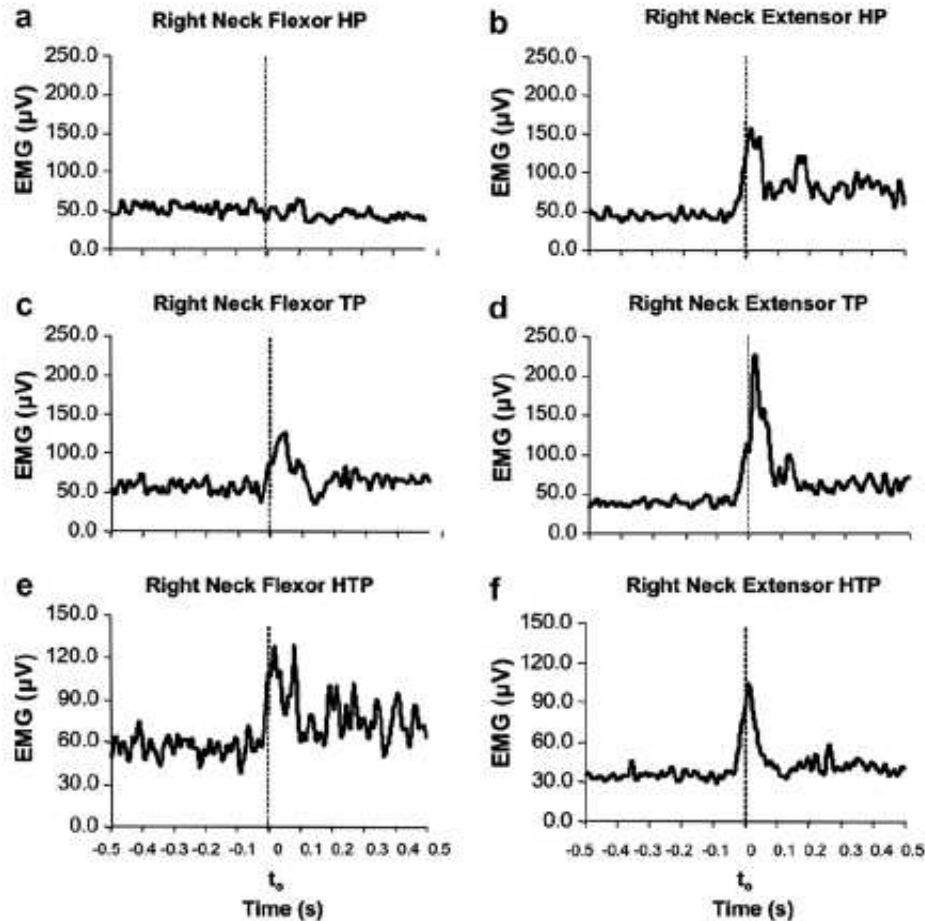


Figure 6.5. EMG of the right neck muscles (averages across trials by a representative subject, subject #1) during downward upper limb movements. The neck flexor (panels a, c, and e) and neck extensor (panels b, d, and f) activity under the head perturbation (HP), trunk perturbation (TP), and head and trunk perturbation (HTP) tasks, respectively. Note the APAs only in the extensor muscle for the HP task and in both flexor and extensor muscles in the TP and HTP tasks. The vertical dashed lines indicate the moment of the movement initiation (t_0).

Figure 6.6 shows the index of integrated muscle activity, I_{EMG} (see Section 2), for the neck muscles across all tasks and conditions (averages across subjects with standard error bars). I_{EMG} for both flexors and extensors was higher in the TP and HTP tasks as compared to the HP task. In general, I_{EMG} for the neck extensor muscles were, on average, 2.5 times larger for the TP tasks and 2.6 times larger for the HTP tasks as compared to HP task. A similar

trend was seen for the flexor muscles, where I_{EMG} in TP and HTP tasks was 2.9 and 1.9 times larger than in HP task, respectively.

Three-way MANOVA (*Perturbation*, *Direction*, and *Side* as factors) on I_{EMG} showed no effect of *Direction* and *Side* and no significant interactions. However, a significant effect of *Perturbation* was confirmed ($F_{4,142} = 3.06$, Wilks' Lambda $p < 0.05$). Two three-way mixed design ANOVAs were conducted on I_{EMG} of the neck flexor and extensor muscles separately. The results confirmed a significant main effect of *Perturbation* for both muscles ($F_{2,72} > 2.98$, $p < 0.05$) without significant effects of *Direction* or *Side*, and no significant interactions. Tukey's HSD tests confirmed larger I_{EMG} for both neck extensor and flexor muscles under the TP and HTP tasks as compared to the HP task ($p < 0.05$).

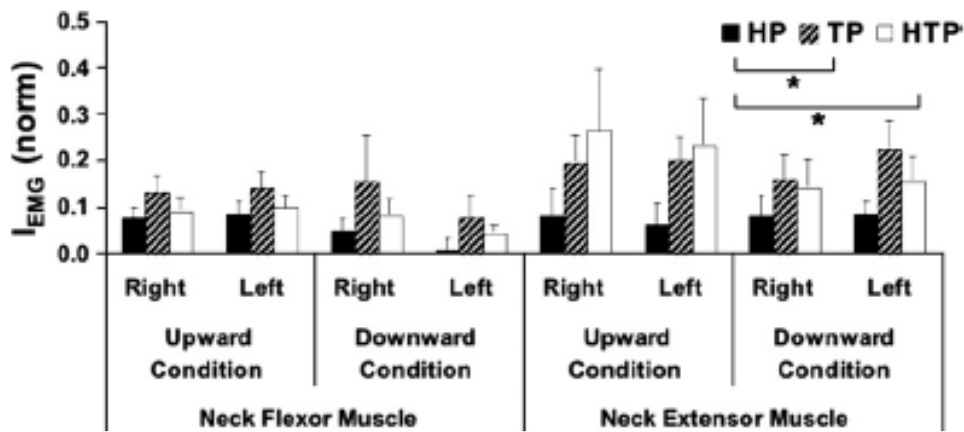


Figure 6.6. Integrated EMG index (I_{EMG}) of the left and right neck flexor and extensor muscles (NF_L , NF_R , NE_L , and NE_R , respectively) during upward and downward arm movements, and under head, trunk, and head and trunk perturbations (HP, TP, and HTP, respectively). Average time profiles across subjects and standard error bars are shown; * means $p < 0.05$. Lines connecting different experimental conditions on the legend indicate significant differences across conditions.

Relative timing of neck muscle activation during APAs

To explore the relative timing of the changes in the neck flexor and extensor muscle activity, cross-correlation analyses were run separately for the EMGs in the left and right side muscle pairs. Figure 6.7a shows z-scores of the average peak correlation coefficients (R-peak) computed from the cross-correlation between neck flexor and extensor muscles. This Figure 6. shows combined data from the right and left side muscles because there were no significant

differences between the two sides (described below). TP and HTP tasks showed higher R-peak values between the neck flexor and extensor muscle activation patterns for both right and left sides and for both upward and downward arm movements, as compared to the HP task.

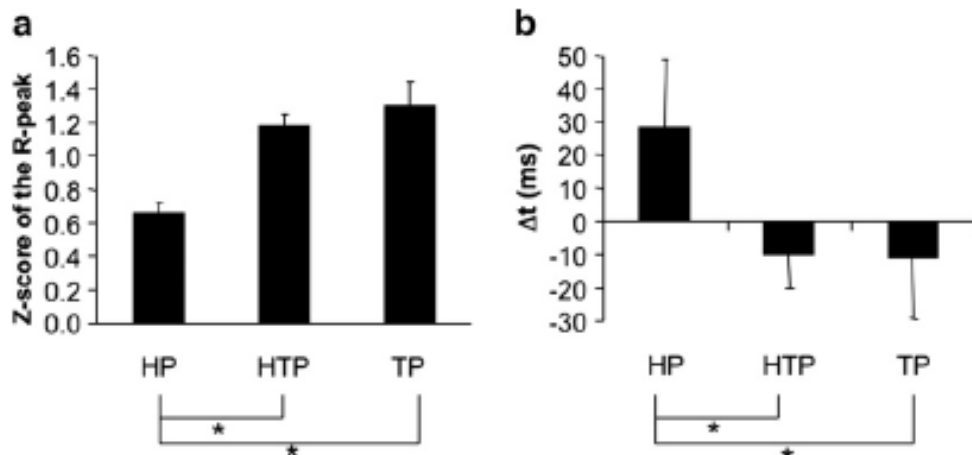


Figure 6.7. Results of the cross-correlation analysis between neck flexor and extensor EMGs. Panel a shows averaged across subjects z -scores with standard error bars of the peak correlation coefficient (R-peak). Panel B shows the average time lag (Δt) at R-peak under the head, trunk, and head and trunk perturbations (HP, TP, and HTP, respectively). Positive values in panel b indicate an earlier EMG burst in the neck extensor as compared to the neck flexor. * means $p < 0.05$. Lines connecting the mean bars indicate the differences found.

The average across subjects time lag (Δt) at the moment of R-peak is shown in Figure 6.7b. The positive time lag for the HP task indicates an earlier burst of the neck extensor activity as compared to the neck flexor burst. The average time lag for TP and HTP was negative indicating an earlier burst of neck flexor activity about 10 ms before the neck extensor burst. On average, there was a difference of about 40 ms in Δt between HP and the other two tasks (TP and HTP). Despite its relatively small magnitude, this difference was statistically significant. The relatively low average value of Δt in the HP task was partly due to the fact that some subjects showed clear time-shifted (reciprocal) patterns of activation in the neck flexors and extensors while others showed nearly simultaneous (co-activation) patterns. The small number of subjects in each subgroup did not allow us to test these differences statistically; hence, this remains a qualitative observation.

One-way ANOVAs confirmed the significant effect of *Perturbation* on both z -scores ($F_{2,81} = 17.89, p < 0.01$) and Δt ($F_{2,81} = 3.54, p < 0.05$). Tukey's HSD tests confirmed higher

z-scores of the R-peak and smaller Δt for the TP and HTP tasks as compared to HP task ($p < 0.05$).

Muscle activation during APAs: leg and trunk muscles

The actions used in our experiments produced relatively mild perturbations for the trunk. As a result, a few muscles such as gastrocnemius lateralis, tibialis anterior, and rectus femoris did not show reproducible APAs that would differ across the tasks and conditions. However, APAs in biceps femoris (BF), erector spinae (ES), and rectus abdominis (RA) were reproducible and showed task dependence.

Figure 6.8 illustrates typical EMG patterns in BF, ES, and RA for a representative subject (subject #4). The upper four panels show the EMGs of BF and ES during upward (panels a and c) and downward (panels b and d) arm movements in the HP task. Prior to head unloading, there was a reduction in the BF and ES activity, while prior to head loading these muscles showed an increase in the activity. Similar pattern of changes in the activity of these muscles was also observed in the TP and HTP tasks (not illustrated).

Panels e and f (Figure 6.8) shows the RA activity during upward arm movements under the HP (panel e) and TP and HTP (panel f) tasks. No visible APAs were seen in the HP task, while there was an increase in the RA activity in the TP and HTP tasks. Similarly, during downward arm movements, APAs in RA were absent in the HP task and present in the TP and HTP tasks (not illustrated, see Figure 6.9).

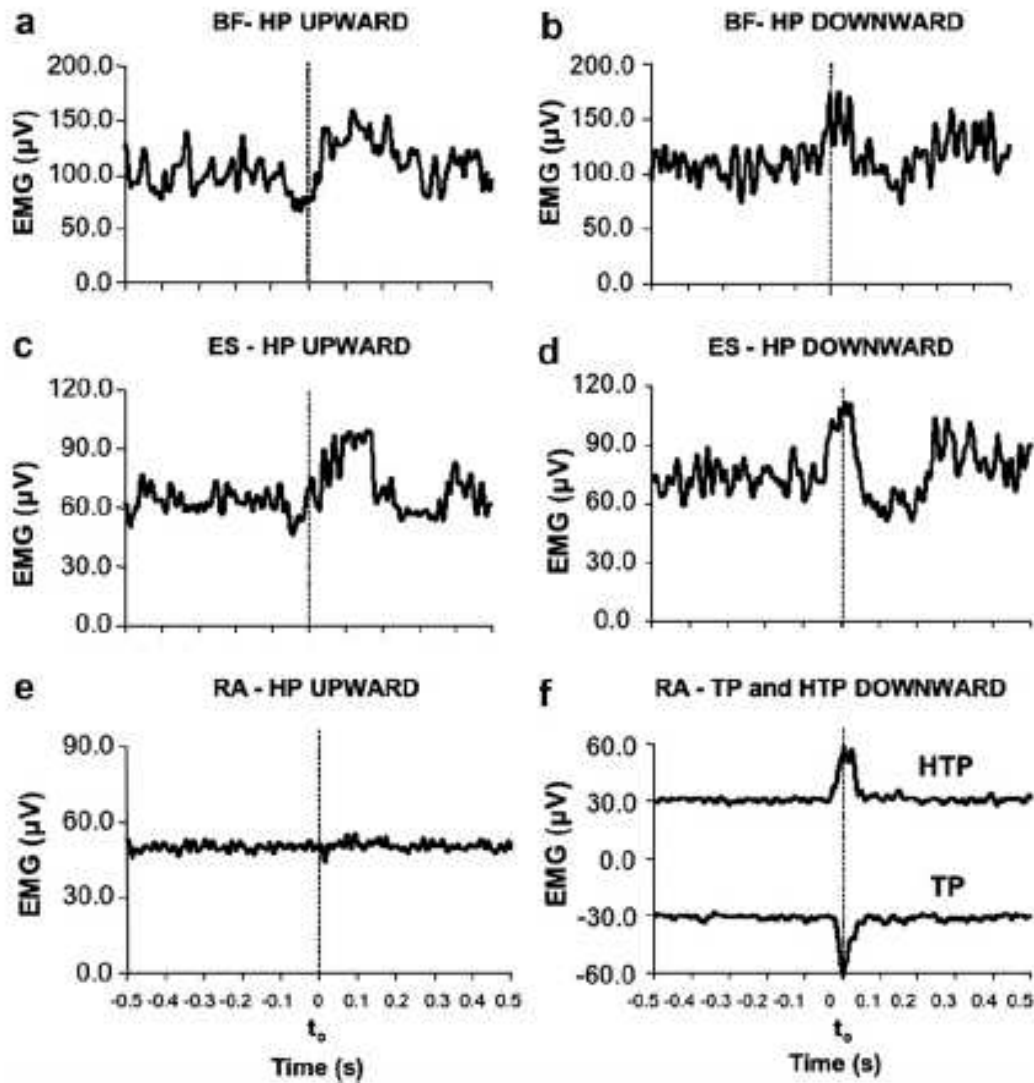


Figure 6.8. Panels a–d: Averaged across seven trials EMGs of biceps femoris (BF) and erector spinae (ES) muscles are shown for a representative subject (subject #4) who performed the HP task. Data for upward arm movements are shown in panels a and c, and data for downward arm movements are shown in panels b and d. Note the opposite changes in muscle activity during APAs for different arm movement directions. Panels e and f: rectus abdominis (RA) EMG during upward arm movements in the HP task (panel e) and TP and HTP tasks (panel f). The vertical dashed line indicates the moment of the movement initiation (t_0). Note: RA time profile for the TP condition (panel F) was inverted (turned into negative values) to avoid superposition of lines; negative values of larger magnitude indicate increased muscle activation.

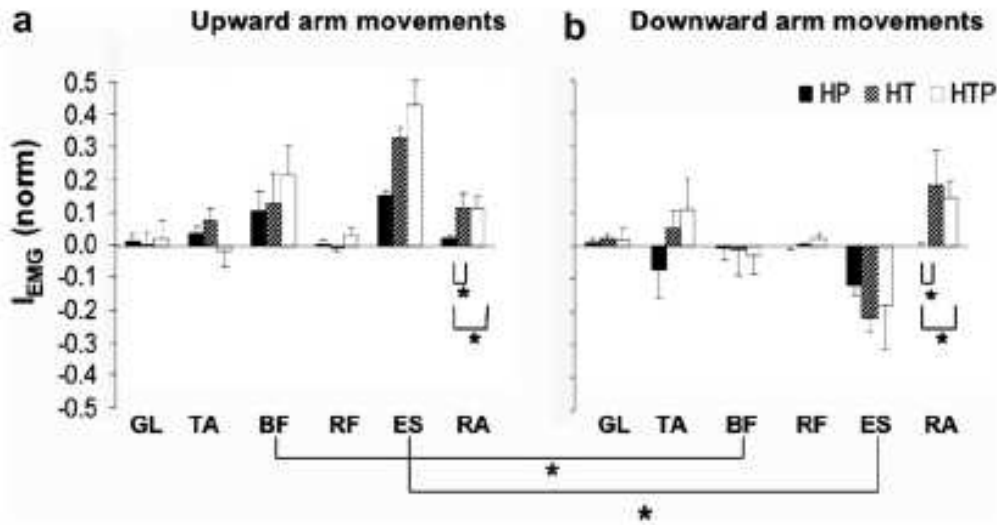


Figure 6.9: Integrated EMG index (I_{EMG}) of gastrocnemius lateralis (GL), tibialis anterior (TA), biceps femoris (BF), rectus femoris (RF), lumbar erector spinae (ES), and rectus abdominis (RA) during upward and downward upper limb movements (panels a and b, respectively) for the three tasks, head perturbations, trunk perturbation, and head-and-trunk perturbation (HP, TP, and HTP, respectively). Average data across subjects with standard error bars are shown; * means $p < 0.05$. Lines connecting the mean bars and * signs indicate significant differences

APAs in the leg and trunk muscles were quantified using an index of integrated EMG activity (I_{EMG}) over the period from -100 ms to $+50$ ms with respect to t_0 (see Section 2). Figure 6.9 shows I_{EMG} (averages across subjects with standard error bars) for all the leg and trunk muscles during upward (panel a) and downward (panel b) arm movements in the HP, TP, and HTP tasks. Note the effect of hand movement direction on I_{EMG} for BF and ES, and the effect of task on I_{EMG} for RA.

A two-way MANOVA ($Direction \times Perturbation$) was used to test these differences. It showed a significant effect of *Direction* ($F_{6,31} = 2.83$, Wilks' Lambda $p < 0.05$) on I_{EMG} , while the effect of *Perturbation* was just under the level of significance ($F_{12,62} = 1.75$, Wilks' Lambda $p = 0.077$). We explored both effects using ANOVAs. Six ANOVAs (*Direction* as the factor) were used as post-hocs on I_{EMG} for each muscle. There was no difference between upward and downward arm movements for TA, GL, RF, and RA. There were significant differences for both BF and ES ($F_{2,36} = 7.70$, $p < 0.01$; and $F_{2,36} = 13.65$, $p < 0.01$, respectively). As illustrated in Figure 6.9, there were larger (positive) I_{EMG} for BF and ES muscles during upward arm movements as compared to the downward movements. Tukey's HSD tests confirmed this result ($p < 0.05$). One-way ANOVA (*Perturbation* as the factor)

revealed differences in I_{EMG} for RA ($F = 3.76$, $p < 0.05$). Tukey's HSD test confirmed larger I_{EMG} for RA in the TP and HTP tasks as compared to the HP task ($p < 0.05$).

6.4 Discussion

The main hypothesis tested in the study suggests the existence of two patterns of APA in neck muscles, reciprocal and co-activation, used in a task-specific way. The main findings of the experiments related to this hypothesis can be summarized as follows. When perturbations were applied directly to the head, APAs in the neck muscles showed a reciprocal pattern that is an increase in the activity of one muscle of a flexor–extensor pair without an increase in the activity of its antagonist (Figure 6.5, Figure 6.6 and Figure 6.7, similar to results described by Gurfinkel et al., 1988). When perturbations were applied to the trunk, APAs represented predominantly unidirectional changes (co-contraction) of the activity in both neck flexor and neck extensor muscles (Figure 6.2, Figure 6.5, Figure 6.6 and Figure 6.7, similar to the report by Van der Fits et al., 1998). Taken together, these observations support our first specific hypothesis formulated in Section 1.

Note that any muscle activation pattern during fast actions has elements of both co-activation and reciprocal muscle activation. Even the famous tri-phasic EMG pattern during single-joint fast movements may be viewed as a combination of time-shifted (reciprocal) bursts of activation in the agonist and antagonist muscles superimposed on their co-activation (e.g., Gottlieb et al., 1989). In our study, we found a shift from nearly perfectly simultaneous bursts of muscle activity in the neck flexor–extensor pair, which we address as “co-activation”, to a pattern characterized by a significantly larger time delay between the two EMG bursts, which we address as “reciprocal”.

The remaining two specific hypotheses were falsified. In particular, the results showed similar APAs when perturbations were applied to the trunk and to the trunk and the head simultaneously, but APAs were much weaker or even absent when perturbations were applied to the head (Figure 6.6 and Figure 6.9).

APAs in neck muscles: two patterns for two purposes?

Two APA patterns were observed in our experiments. One represented time-shifted (reciprocal) activation of the neck flexors and extensors while the other consisted in nearly

simultaneous unidirectional changes in the activity of both muscle groups (co-activation). The first pattern was more frequently observed when perturbations were applied directly to the head (HP series) while the second pattern dominated in trials with perturbations involving the trunk (TP and HTP). Another potentially important observation is the high magnitude of APAs in the neck muscles in the series with perturbation applied to the trunk (TP condition), at least as high as in the HP condition. Taken together, these observations allow to offer the following interpretation.

A predictable perturbation applied to the head may be expected to be associated with APAs organized optimally to minimize the effects of the perturbation on the head posture. A reciprocal pattern of changes in muscle activation leads to a time-varying net torque either in flexion or in extension to counteract the expected direction of the perturbation. Reciprocal APA patterns have been indeed reported in many studies of vertical posture (Cordo and Nashner, 1982, Horak et al., 1984, Bouisset and Zattara, 1987, Aruin and Latash, 1995 and Aruin and Latash, 1996).

However, all APAs are based on prediction and are expected to lead to under-compensation in some trials and over-compensation in others (reviewed in Massion, 1992). Hence, the net result of a combined action of an APA and an external perturbation on the trunk may be hard to predict. For example, the COM can in one trial deviate forward and in the next trial, under seemingly identical conditions – backward. This may be the reason for much more reproducible EMG indices during APAs as compared to mechanical indices such as COP shifts (Massion, 1992, Aruin and Latash, 1995, Aruin and Latash, 1996 and Shiratori and Latash, 2000). Because of the mechanical coupling across the body segments, perturbations applied to the trunk and leg/trunk APAs are both sources of head perturbation. The direction of this net perturbation may be poorly predictable. Co-contraction of neck flexors and extensors may be viewed as a method of increasing the apparent neck stiffness to a perturbation irrespective of its direction – a method of alleviating effects of perturbations whose direction is poorly predictable. This interpretation remains speculative since we did not manipulate predictability of perturbations and have no independent measure of how the subjects perceived predictability of the direction of the perturbations.

As suggested in Section 1, APAs may be defined by two groups of factors, local and global. The former represent effects of perturbations acting directly on a particular segment.

The latter reflect perturbations that are secondary to a perturbation acting on the COM of the whole body. Earlier publications (reviewed in Massion, 1992) and the current results suggest that a default APA pattern to deal with local perturbations represents time-shifted (reciprocal) changes in activation of agonist–antagonist muscle pairs. Perturbations from the second group may be associated with reciprocal or co-contraction patterns depending on predictability of direction of their net effects.

Co-contraction patterns of changes in muscle activation during APAs have been described in a number of studies. In particular, they are more common in persons whose postural control system may be challenged such as elderly (Woollacott et al., 1988) and persons with Down syndrome (Aruin and Almeida, 1997). They can also be seen in young control subjects in challenging conditions such as standing on roller-skates (Shiratori and Latash, 2000) or on a surface with decreased support area (Aruin et al., 1998 and Slijper and Latash, 2000). In all these studies, co-contraction patterns have been interpreted as reflecting a trade-off between efficacy and safety, which is ensured by increased joint apparent stiffness that counteracts any perturbation, very much in line with the interpretation offered in this study.

Do APAs in the leg and trunk muscle help stabilize the head?

APAs in trunk and leg muscles produce joint torques that act on the head because of the mechanical coupling among the body segments. These effects can help stabilize head posture or produce additional perturbations for the head. Based on previous studies that have documented head stabilization during a variety of actions (Berthoz and Pozzo, 1994 and Pozzo et al., 2001), we hypothesized that leg/trunk APAs might contribute to head stabilization. This is an attractive hypothesis because of two reasons. First, the functional importance of head stability during standing is obvious. The sensitivity of posture to visual and vestibular information (Lestienne et al., 1977, Horstmann and Dietz, 1988, Buchanan and Horak, 1999 and Maurer et al., 2006) makes it imperative for the central nervous system to ensure stability of sensory signals of those modalities during standing. Second, APAs are typically associated with rather small net changes in such variables as COP location and shear forces (e.g., Massion, 1992 and Aruin and Latash, 1995). For example, COP shifts during APAs are typically of the order of 1 mm. Mechanical effects of such small shifts on

vertical posture seem unlikely, particularly if one considers the much higher amplitude of typical spontaneous COP shifts during quiet standing (e.g., Winter et al., 1996).

However, in our experiments, perturbations applied only to the trunk led to APAs that were not different from perturbations applied to the trunk and the head. In other words, when the same action led to larger head perturbation (in addition to the trunk perturbation), the controller did not use larger APAs. Moreover, a perturbation applied to the head only induced minimal APAs in the leg and trunk muscles. Taken together, these results fail to support the hypothesis on the importance of APAs in leg/trunk muscle for head stability.

If APAs in the leg/trunk muscles are not generated by the central nervous system to ensure head stability, they represent an additional source of head perturbation. The idea that APAs may be viewed by the central nervous system as perturbing factors is not novel; it was invoked to interpret APA changes during standing on surfaces with a decreased support area (Aruin et al., 1998).

Our results suggest that the main purpose of APAs in postural muscles is to ensure stability of a body segment, which is directly under the control of these muscles. In particular, APAs in leg/trunk muscles try to alleviate mechanical effects of expected perturbations on vertical posture, while APAs in neck muscles try to ensure head stability under perturbations coming from the trunk as well as from the environment. This is the most straightforward interpretation on our results as well as of many earlier studies (reviewed in Massion, 1992).

One of the limitations of the current study is the use of relatively unusual tasks and perturbations. As in most studies with relatively artificial (but easy to standardize) tests, we have assumed that the behaviors observed in our experiments reflected adjustments of previously learned APAs based on the variety of everyday actions associated with perturbations to the trunk and to the head. We have also assumed that APAs developed over the lifetime can be scaled and adjusted to new tasks based on a couple of practice trials. Unfortunately, using artificial laboratory tests remains an unavoidable component of movement studies that allows to separate and explore specific factors that affect movement patterns (although see Cordo et al., 2006). Within this study, we did not explore learning effects over the short series of trials and hope to address this issue in future.

6.5 References

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CHAPTER 7

CONCLUSIONS

The notion of muscle synergy has been used for many years (Hughlings Jackson 1889, Gelfand and Tsetlin 1966; Bernstein 1967; Horak and Nashner 1986; Sabatini 2002). However, this term has not been unambiguously defined and has frequently been used with different meanings in the literature. The main aim of this dissertation was to study multi-muscle synergies involved in body posture control using an operational definition offered recently (reviewed in Latash et al. 2002, 2008). More specifically, we studied a) the viability of the uncontrolled manifold hypothesis as a method to identify and quantify such synergies among muscles involved in whole-body continuous movements, b) the composition of elemental variables (M-Modes) under different experimental conditions of whole-body movement execution, and c) the ability of these M-modes to co-vary and ensure reproducibility of a performance variable across repetitive trials.

We defined synergies as task-specific groups of variables, which stabilize a particular performance variance, in a sense of reducing its variability across repetitive trials. For most of the studies presented on this dissertation, we used a computational method of identifying and analyzing muscle synergies, based on the framework of the uncontrolled manifold hypothesis (UCM hypothesis, Scholz and Schoner 1999; Latash et al 2002b). UCM analysis was performed in the space of elemental variables, M-modes, computed as linear combinations of changes in the activation of postural muscles during a variety of of continuous whole-body movements performed by standing persons.

In chapter 3, we used the UCM approach to study the effects of a range of whole-body movement frequencies on the composition of the M-modes. We also studied the structure of the total variance within the space of the M-modes across repetitive cycles of body sway in anterior-posterior direction with respect to changes in a specific performance variable (anterior-posterior coordinates of body's center of pressure, COP_{AP}). This study tested a hypothesis on the effects on the rate of change of COP_{AP} on the index of synergies: Note that earlier studies suggested that an increase in the rate of a performance variable leads

to a drop in the synergy index with the purpose not to stabilize the variable that changes quickly. We showed that this is not necessarily true for steady-state processes such as cyclic swaying, even if those are performed at high frequencies.

In chapter 4, the same approach was used. However, we focused on the effects of challenging postural tasks on the composition of M-modes and on the components of total variance in the M-mode space. These challenging situations included swaying the whole body in the anterior-posterior direction with closed eyes, or with vibration of the Achilles tendons, or while standing on a reduced base of support (one leg support). The main purpose of this study was to test a hypothesis that M-mode composition can change without a detrimental effect on multi-M-mode synergies. The hypothesis was confirmed.

In chapter 5, whole-body continuous rotation around the vertical axis was studied. We again focused on the composition of M-modes and their ability to co-vary such that variance of the moment of force around the vertical axis (M_z) across repetitive trials is reduced. All the earlier studies addressed changes in the center of pressure as the performance variable. The purpose of this study was to generalize the findings for another important variable, M_z , and to test a hypothesis that a M_z time profile can be stabilized by multi-M-mode synergies. The study showed a variety of M-modes forming the basis for M_z stabilization across subjects and across conditions. It has supported the earlier hypothesis that a hypothesis that M-mode composition can change without a detrimental effect on multi-M-mode synergies.

In chapter 6, the UCM approach was not used. Instead, we studied the effects of comparable magnitudes of self-inflicted perturbations applied to different body segments (head, trunk, and head/trunk combined) on the neck muscle patterns of activation prior to the perturbations. The study showed that patterns of muscle activation may change in a qualitative way, from reciprocal to co-contraction, when the mechanical effects of perturbation on the head become less predictable.

Based on the results of all the studies, the following conclusions have been made.

7.1 The UCM approach and multi-muscle synergies.

The UCM approach has proven itself to be a useful method for the identification and quantification of multi-muscle synergies during whole-body continuous movements. **We have shown that, by using the UCM method, it is possible to link muscle activation**

patterns to changes of mechanical variables describing the interaction of the body with the environment (COP_{AP} , Mz).

The first step in using this approach is to identify elemental variables. The second step is to relate small changes in these variables to shifts in a potentially important performance variable that is hypothesized to be stabilized by the controller. Finally, the UCM analysis is performed across multiple cycles (repetitions) of a task in the space of the elemental variables.

In previous studies using the UCM approach, where kinematic and kinetic variables were analyzed (Scholz and Schoner 1999; Scholz et al. 2000, Latash et al 2001; Latash et al. 2002a), the first two steps were relatively straightforward. However, in analysis of muscle synergies, these two steps present a challenge. First, muscles are not independently controlled but are united into groups (Huglhings Jackson 1889), so elemental variables (M-modes) have to be defined experimentally. Second, the relationship between changes in the magnitudes of M-modes (measured in microVolts*seconds or similar units) and shifts of the performance variables (measured in mechanical units such as newtons, meters, and newtonmeters) must be computed. These two problems have been overcome by the work of Krishnamoorthy (Krishnamoorthy et al 2003a,b) who introduced the principal component analysis (PCA) as a method of identifying the elemental variables and multiple regression analysis to relate changes in M-modes to shifts in the performance variables. However, a large number of trials was needed to perform such analyses. **We developed this method for continuous movements. This improvement has allowed to avoid using numerous trials, saved time spent on the data collection, decreased the risk of subject fatigue, and allowed to compare many more conditions within a single experiment.**

7.2 The two level hierarchy for postural control.

One of the main assumptions of our studies is the existence of a hierarchical scheme of postural control with at least two levels. At the higher level, M-modes play the role of elemental variable and form synergies stabilizing mechanical variables important for the interaction with the environment. At the lower level, M-modes are formed within the space of individual muscle activations. One may view M-modes as “virtual muscles” manipulated at the higher level of the control hierarchy.

Recently, the idea that the central nervous system unites muscles into groups to reduce the number of control variables (Huglings Jackson 1889) has led to the emergence of a variety of methods identifying such muscle groups during whole-body tasks such as postural preparation and responses to perturbations, stepping, and swaying (Krishnamoorthy et al. 2003a,b; Ivanenko et al. 2004, 2005; Ting and Macpherson 2005; Torres-Oviedo et al. 2006; Torres-Oviedo and Ting 2007). All these studies used matrix factorization techniques to identify eigenvectors in the space of muscle activations including PCA with factor extraction (for comparison of different methods see Tresch et al. 2006). However, usually the studies of multi-muscle synergies stopped at this point. **The studies presented in this Thesis took a step further and related the activity of these groups (which we called M-modes) to the time profiles of mechanical variables such as COP coordinate and M_z .**

The currently dominant view regarding the composition of muscle groups identified with matrix factorization techniques is that they are very stable across both subjects and tasks (Ivanenko et al. 2004, 2005; Ting and Macpherson 2005; Torres-Oviedo et al. 2006; Torres-Oviedo and Ting 2007). **In contrast, we have found changes in the composition of M-modes (Chapters 4 and 5) with task complexity and when the task required a rotational whole-body action.** This finding corroborates the idea that M-modes represent not hard-wired muscle groupings but flexible combinations of muscle activations. In other words, the controller may manipulate a few strings (M-modes) at the higher level of the hierarchy, while the projections of each of those strings to inputs to individual muscles at the lower level may differ. In addition, we have found that **changes in the composition of the M-modes did not lead to changes in the synergy index. Taken together, these findings support the idea of a two-level scheme of postural control.**

7.3 Effects of movement frequency on M-modes composition and synergies.

M-mode composition has been shown to be consistently similar across subjects and movement frequencies when the body sway was performed in the anterior-posterior direction during bipedal standing in the absence of complicating factors but not for whole-body rotational movements. In Chapter 3, we studied the effects of a range of whole-body sway frequencies on the composition of M-modes and their ability to ensure

low variability of COP_{AP} trajectory across trials by co-variation of the gains of M-mode involvement . We found consistent composition of the first three M-modes that represented the activity of all twelve postural muscles originally recorded. Studies of the direction of the eigenvectors representing M-modes in the original muscle activation space have confirmed the clustering of the M-modes along certain directions. In Chapter 5 we studied the composition of M-modes under different frequencies of whole-body rotations around the vertical axis. In contrast to the findings presented in Chapter 3, the composition of M-modes (the direction of the eigenvectors) varied broadly across both subjects and frequencies of movement.

Despite the variations on the M-mode composition found for rotational whole-body movements, gains at the M-modes co-varied to ensure reproducibility of the performance variable (moment of force about the vertical body axis) across trials at all movement frequencies studied. In both Chapters 3 and 5, an index of synergy was computed (ΔV) such that its positive values reflected co-variation of the M-mode gains compatible with a stable time profile of a performance variable (COP_{AP} trajectory and the moment of force around the vertical axis, M_z) across trials. Hence, varying sets of elemental variables (M-modes) could be used to ensure low variability of potentially important performance variables.

7.4 Effects of challenging postural tasks on M-modes composition and synergies.

An increase in the task complexity forced the controller to manipulate a larger number of elemental variables (M-modes). In Chapter 4, we studied the effects of a range of mechanical and sensory manipulations on the composition of M-modes and their ability to ensure low variability of COP_{AP} trajectory across trials during voluntary whole-body sway. Subjects performed the task with eyes open and closed, while standing on both feet or on one foot only, with and without vibration applied to the Achilles tendons. We found that an increase in the task complexity led to an increase in the number of M-modes that contained significantly loaded indices of muscle activation from 3 to 5. This finding illustrates the ability of the central nervous system to re-arrange projections of its descending signals in a

task-specific way such that a set of postural muscles forms different numbers of M-modes (obviously with different M-mode composition).

Adjustments at the level of the M-mode composition allowed the subjects to maintain a comparable level of stabilization of the COP_{AP} trajectory. Despite the differences in the number of M-modes, the subjects showed substantially more “*good variance*” (variance that does not affect the average COP_{AP} trajectory across cycles) than “*bad variance*” (variance that affects the average COP_{AP} trajectory across cycles) interpreted as a multi-M-mode synergy stabilizing the COP_{AP} trajectory. The findings support the existence of a (at least) two-level hierarchical control scheme for whole-body movements.

7.5 Effects of comparable mechanical perturbations on APA patterns of activation of neck muscles.

APA patterns in the neck flexor–extensor muscles can change from a time-shifted (reciprocal) pattern to a synchronized (co-activation) pattern when the source of the perturbation changes. In Chapter 6, we studied the effect of comparable self-inflicted mechanical perturbations to the head, to the trunk, and to the head and trunk simultaneously and showed that, in the former case, a reciprocal pattern of activation of flexor-extensor neck muscles emerges. However, once this perturbation is applied either directly to the trunk or to the head and trunk simultaneously, the activation of these two muscles groups occurs simultaneously (co-contraction). This finding demonstrates the flexibility of the CNS in feed-forward control of anticipatory postural adjustments based on the predictability of the mechanical effects of an expected perturbation.

7.6 Future plans and directions

The method of performing quantitative analysis of synergies opens a broad horizon of possibilities to study synergies in both healthy persons as well as in the elderly and survivors of diseases and traumas. One of the attractive features of the UCM method is that it permits the use of a single data set to test the existence and to quantify the strength of possible synergies involved in stabilization of different performance variables. However, until this date, most studies addressed one performance variable at a time. Typically, more than one performance variable needs to be stabilized by a set of elemental variables during the

execution of natural movements. We believe that it is possible that performance variables may compete with each other such that stabilization of one of them may lead to destabilization of another. The introduction of such analysis would help to answer questions about what the CNS views as the most important performance variables for a certain motor task.

Another underexplored issue is changes in synergies in tasks that require quick changes in performance variables. Recent studies have pointed at the possibility that the CNS can start turning off a synergy in anticipation of a planned action (Olafsdottir et al 2005, Shim et al 2005). Recent observations have suggested that such an ability is impaired in elderly subjects (Olafsdottir et al 2007). This ability may also be impaired in patients with certain neurological disorders characterized by impaired anticipatory control (for example, in Parkinson's disease).

The UCM method has been used mostly to quantify two components of variability, namely variance along the UCM (or "good variance") and variance orthogonal to it (or "bad variance"). Little attention has been paid to possible structure of variance within the two subspaces. Results from a few studies (Domkin et al 2002; Latash et al 2003; Zhang et al. 2008) have suggested that the controller can modify the structure of variance within the UCM, which does not have a direct effect on performance. Recent studies of stroke survivors by Scholz and his group (e.g. Reisman and Scholz 2003) have suggested that the ability of the controller to use different solutions within the UCM may be impaired in people with motor disorders and lead to a diminished ability of taking advantage of the system's flexibility.

Clinical studies including studies of rehabilitation are another likely direction to be taken and several questions might be posed by the use of the UCM method of analysis. For instance, questions like: (a) Can rehabilitation lead to modifications of pathologically changed synergies? (b) Can a certain rehabilitation approach result in better improvements of synergies? or (c) Is improvement in a synergy always associated with better performance of the associated task?

In summary, the approach used by us in this Thesis is still recently new but has shown to be a powerful tool to be used in the analysis of motor synergies. Many relevant areas of the study of movement control will be positively influenced by the use of the method.

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